Compte-rendu de fin de projet ANR Peerless

Pierre Franck

Pierre Franck. Compte-rendu de fin de projet ANR Peerless : Viabilité d'une gestion écologique renforcée de la santé des plantes. 2018. hal-02900132

AGENCE NATIONALE DE LA RECHERCHE ANR	**Compte-rendu de fin de projet**	

Projet ANR-12-AGRO-006

PEERLESS

Agrobiosphère 2012

A IDENTIFICATION

Acronyme du projet	PEERLESS
Titre du projet	Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Coordinateur du projet (société/organisme)	Pierre FRANCK (INRA)
Période du projet (date de début – date de fin)	01/01/2013 – 31/12/2017
Site web du projet, le cas échéant	www.projet-peerless.fr

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B RESUME CONSOLIDE PUBLIC

B.1 RESUME CONSOLIDE PUBLIC EN FRANÇAIS

Viabilité d'une gestion écologique renforcée de la santé des plantes

Les enjeux sont de proposer une gestion viable des populations de ravageurs dans les agroécosystèmes par une approche intégrative combinant différentes échelles spatiales, des cultures pérennes et annuelles et les interactions trophiques entre plusieurs bioagresseurs et leurs ennemis naturels.

Des objectifs finalisés pour une protection plus écologique des cultures…
La régulation des bioagresseurs par les auxiliaires naturellement présents dans les cultures est un des services ecosystèmiques sur lequel s'appuie l'agroécologie afin de diminuer la dépendance de nos systèmes de production agricoles aux pesticides. Bien que les auxiliaires des cultures soient largement mis en avant, les liens entre mode de gestion des cultures, niveau de contrôle des bioagresseurs par les auxiliaires et rendement des cultures restent assez mal compris. Les trois principaux objectifs que s'était fixé le projet PEERLESS sont: 1) identifier les systèmes de culture et les caractéristiques de paysage dans lesquels la

biodiversité fonctionnelle renforce la productivité des cultures; 2) identifier les mécanismes écologiques qui sous-tendent les hétérogénéités spatio-temporelles de densités de populations de bioagresseurs et d'auxiliaires; 3) proposer des déploiements viables de système de culture et d'aménagements d'habitat semi naturel à partir de simulations de scenarii prenant en compte explicitement les paysages agricoles et les dynamiques des bioagreseurs et des auxiliaires en interactions.

… en combinant des recherches en écologie, agronomie, économie et statistiques

Le premier objectif évalue l'impact des pratiques agronomiques et des agencements paysagers sur les pertes de production causées par les ravageurs dans six bassins de productions céréaliers et horticoles. Le second objectif analyse, d'une part, les interactions trophiques entre auxiliaires et bioagresseurs pour déterminer les associations d'espèces les plus pertinentes pour un contrôle biologique des bioagresseurs, et d'autre part, les dynamiques de populations des bioagresseurs et de leurs principaux ennemis naturels en fonction des caractéristiques des paysages. Le troisième objectif propose des stratégies viables de conduites de culture et d'agencements paysagers à l'échelle d'un territoire. Il développe des modèles mécanistes de dynamiques des populations des bioagresseurs et de leurs ennemis pour différents scénarii paysagers d'agencement de cultures et d'espaces semi naturels. Ces scénarii paysagers sont optimisés par rapport à leurs performances agronomiques, écologiques, économiques et environnementales.

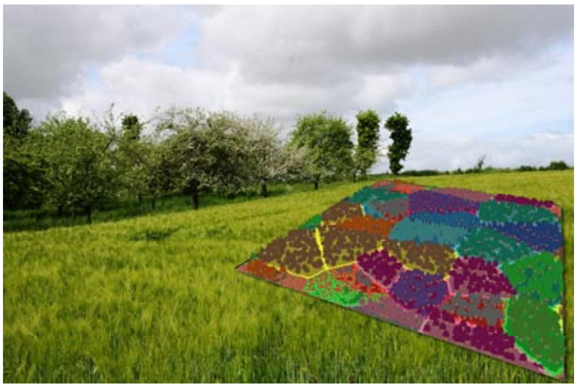
Résultats majeurs

Les populations de ravageurs et d'adventices dans les cultures dépendent principalement des pratiques de gestion des parcelles mais aussi d'interaction entre ces pratiques et le contexte paysager. Une analyse conjointe des dynamiques de populations de bioagresseurs, de leurs principaux ennemis naturels et des interactions biotiques associées est nécessaire pour appréhender les régulations biologiques dans les cultures en fonction du contexte. La conception de paysage agricole plus favorables au contrôle biologique pour une gestion intégrée et viable de la santé des plantes doit s'appuyer sur une modélisation de ces dynamiques et l'intégration des différentes échelles spatio-temporelles auxquels elles s'opèrent.

Productions scientifiques

Les résultats issus de PEERLESS ont été publiés dans une vingtaine d'articles dans des revues à comité de lecture et présenter à l'occasion de conférences et des rencontres techniques avec la profession. Le colloque de restitution « écologisation des systèmes de productions agricoles pour renforcer le contrôle biologique des bioagresseurs » fait une synthèse exhaustive des avancées scientifiques, des développements méthodologiques et des évolutions conceptuelles sur le sujet.

Illustration



PEERLESS ou comment optimiser des paysages agricoles renforçant le contrôle biologique des bioagresseurs par une analyse *in vivo* et *in silico* des processus écologiques. © Thomas Delattre/INRA

Informations factuelles

PEERLESS est un projet de recherche fondamental coordonné par l'INRA. Le projet a commencé en janvier 2013 et a duré 60 mois. Il a bénéficié d'une aide de l'ANR de 807 k€ pour un coût global d'environ 5000 k€

B.2 RESUME CONSOLIDE PUBLIC EN ANGLAIS

Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability

The challenge is to propose viable management of pest populations in agroecosystems through an integrative approach combining different spatial scales, perennial and annual crops and the trophic interactions between several pest species and their natural enemies.

Three applied aims to enhance ecological engineering in crop health…

The control of crop pests by the enhancement of services provided their natural enemies is frequently evocated to reduce dependency of crop production to pesticides. Although, the links between the crop management, the levels of control services provided by the population of natural enemies and the crop productions remain largely unknown. The PEERLESS project has three aims: 1) identifying crop system and landscape characteristic for which the biodiversity functionally enhances crop production, 2) identifying ecological mechanisms linked with spatiotemporal heterogeneity in the density of pest and natural enemies populations, 3) design viable deployments of alternative crop system and semi-natural habitats in spatially explicit landscapes thank to the simulations of the population dynamics of the pests and their natural enemies.

…by combining researches in ecology, economy and statistics

The first pillar evaluates the impact of agronomic practices and landscape arrangements on production losses caused by the crop pests in six different French agricultural zones. The second pillar analyses, on one hand, inter-specific interactions at the parcel and landscape levels to determine the most relevant floral and animal species involved in the biological control of the pests, and on the other hand, the population dynamics of the pests and of their main natural enemies depending on the characteristics of the landscape. The third pillar design strategies of area-wide-management that optimize pest control service, agricultural production and farmer outcomes. It is based on the evaluation of various scenarii of the distribution crop and semi-natural habitat in the landscape in which the population dynamics of the pests and their natural enemies are simulated with mechanistic models. These scenarii are finally optimized base on their agronomic, ecological, environmental and economic performances.

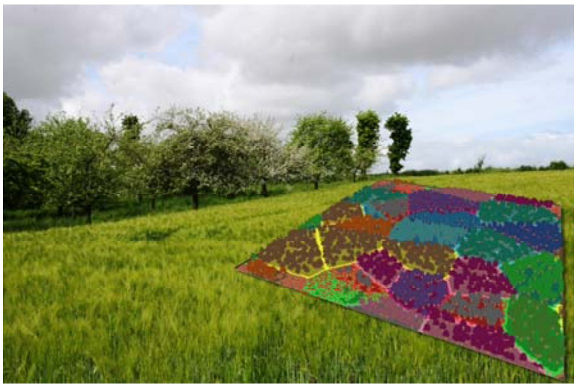
Main results

Pest and weed populations in crop fields primarily depend on plot management practices, but also on the interaction of these practices with the landscape context. A joint analysis of population dynamics of the pests, their main natural enemies and associated biotic interactions is needed to understand the biological regulations in crops according to the context. The design of agricultural landscape that is more favorable to biological control and an integrated and sustainable management of plant health must be based on the modeling of these dynamics and on integrating the different spatio-temporal scales at which they operate.

Scientific productions

The results of the PEERLESS project have been published in about twenty articles in peer-reviewed journals and presented at conferences and technical meetings with the profession. A restitution symposium entitled "écologisation des systèmes de productions agricoles pour renforcer le contrôle biologique des bioagresseurs" makes an exhaustive synthesis of scientific advances, methodological developments and issues on these topics.

Illustration



PEERLESS or how to optimize agricultural landscapes enhancing pest biological control by an in vivo and in silico analysis of ecological processes. © Thomas Delattre/INRA

Factual information

PEERLESS is a fundamental research project coordinated by INRA. The project started in January 2013 and lasted 60 months. It benefited from ANR assistance of € 807,000 for a total cost of around € 5,000,000.

C MEMOIRE SCIENTIFIQUE

Mémoire scientifique confidentiel : Non

C.1 RESUME DU MEMOIRE

L'enjeu de PEERLESS était de proposer une gestion viable des populations de bioagresseurs dans les agroécosystèmes par une approche intégrative combinant différentes échelles spatiales, des cultures pérennes et annuelles et les interactions trophiques entre plusieurs bioagresseurs de ces cultures et leurs ennemis naturels. La régulation des bioagresseurs par les auxiliaires naturellement présents dans les cultures est le service ecosystèmique étudié afin de diminuer la dépendance des systèmes de production agricole aux pesticides.

Pour répondre à un premier objectif visant à caractériser l'impact des pratiques agronomiques et des agencements paysagers sur les pertes de production causées par les ravageurs et les adventices, des suivis écologiques et agronomiques ont été réalisés dans six bassins de productions nationaux et plusieurs sites expérimentaux. Les résultats issus de ces suivis mettent en évidence des effets interactifs entre les pratiques de gestion dans les parcelles agricoles et le contexte paysager sur les populations de bioagresseurs, nécessitant l'appréhension de la santé des plantes à plusieurs échelles spatiales. Pour répondre à un second objectif visant à mieux les comprendre les processus écologiques en jeux, ont été analysées, d'une part, les interactions interspécifiques au niveau de la parcelle pour déterminer les espèces auxiliaires principalement impliquées dans le contrôle biologique des bioagresseurs et d'autre part, les dynamiques de populations des bioagresseurs et des auxiliaires en fonction des caractéristiques de paysages. Les espèces auxiliaires observées dans les parcelles varient sensiblement pour une même culture. Les carabes jouent un rôle central dans le contrôle biologique des adventices et de différents ravageurs, mais ce contrôle varie à la fois en qualité et en intensité en fonction de la complexité du réseau d'interactions. Les proportions et, dans une moindre mesures, les distributions de cultures et d'habitats semi-naturels dans les paysages agricoles impacte la recolonisation des parcelles cultivées par les populations de bioagresseurs et d'auxiliaires. Enfin, pour répondre à un troisième objectif visant à proposer des stratégies viables de conduite de culture et d'agencement paysager à l'échelle d'un territoire, des modèles mécanistes de dynamique des populations des bioagresseurs et de leurs ennemis pour différents scénarios d'agencement de cultures et d'habitat semi naturel dans le paysage ont été développés. Les performances agronomiques, écologiques, environnementales et économiques des scénarios paysagers simulés ont été analysées afin d'aider à la conception de stratégies intégrées de gestion de la santé des plantes et appuyer l'action publique en terme de réduction d'usage des pesticides.

C.2 ENJEUX ET PROBLEMATIQUE, ETAT DE L'ART

L'humanité fait face à des défis sans précédent découlant de l'ampleur de l'activité humaine et de ses impacts en termes de changement global. Prédire la trajectoire du changement global tout en préservant le bien-être de l'humanité nécessite une analyse intégrée de la dynamique des systèmes socio-écologiques.

L'agriculture est l'un des principaux moteurs du changement global et l'une des menaces les plus graves pour la biodiversité. Pour soutenir la rentabilité des productions agricoles, l'agriculture a longtemps favorisé l'augmentation de l'utilisation des fertilisants et pesticides et contribuer à la simplification des agrosystèmes par la réduction et la fragmentation des habitats semi-naturels. L'intensification de l'utilisation des terres a également conduit à des conflits entre la production agricole et d'autres services écosystémiques notamment lié à la perte de biodiversité. La pression exercée sur les ressources limitées en raison de la croissance de la population humaine constitue un défi crucial pour le maintien d'un approvisionnement alimentaire durable avec une perte minimale de biodiversité. Ce défi exige que nous changions de paradigme en passant d'un modèle global d'intensification vers un modèle basé sur le développement durable. Cette révolution peut se faire en maximisant les avantages des services écosystémiques fournis par la biodiversité à l'agriculture, tels que le contrôle des populations de bioagresseurs par les prédateurs et les parasitoïdes grâce à une gestion agroécologique des paysages.

Le cadre législatif des politiques publiques nationales et européennes en faveur de l'agriculture a sensiblement évolué au cours des cinq années du projet. La nouvelle politique agricole commune conditionne depuis 2015 une partie des aides directes que reçoivent les agriculteurs à des mesures agro-environnementales de diversification des cultures, de maintien des prairies permanentes et de préservation de surfaces d'intérêt écologique et vise à promouvoir une gestion durable et viable des territoires. Le plan Ecophyto II lancé en 2016 réaffirme l'engagement de la France à réduire de 50% la consommation nationale de pesticides à l'horizon de 2025.

Ce cadre législatif créé une exigence à développer urgemment des méthodes d'ingénierie du paysage et des solutions de biocontrôle qui puissent nous aider à réduire notre utilisation de pesticides. Comment nos paysages agricoles, contenant à la fois des cultures et des habitats semi-naturels, devraient-ils être structurés et comment les produits phytopharmaceutiques et la lutte biologique devraient-ils être utilisés pour maximiser la fourniture de services écosystémiques ? sont les principaux enjeux auxquels souhaitait répondre le projet PEERLESS.

C.3 APPROCHE SCIENTIFIQUE ET TECHNIQUE

Pour répondre à ces enjeux d'aménagement de paysages agricoles moins dépendant des pesticides et renforcer le service de régulation des bioagresseurs, le projet a été organisé autour de trois objectifs complémentaires :

- identifier les **systèmes de culture** et les **caractéristiques de paysage** dans lesquels la biodiversité fonctionnelle renforce la **productivité des cultures** ;
- caractériser les **mécanismes écologiques** impliqués affectant les **dynamiques de populations** de bioagresseurs et d'auxiliaires et les **interactions trophiques** associées;
- proposer des **déploiements viables** de conduite de culture et d'agencement paysager à l'échelle des territoires à partir de **simulation de scenarios** d'usage des sols.

Deux tâches scientifiques ont été planifiées pour répondre à chacun de ces trois objectifs afin de pouvoir appréhender la régulation des bioagresseurs à différents à niveaux spatio-temporels et évaluer globalement les impacts de la gestion des cultures et du paysage sur les densités de population de bioagresseurs. Chaque tâche a mobilisé les compétences disciplinaires des différents partenaires en écologie, agronomie, économie, statistique et plus collectivement en modélisation.

Tâche 1 : « Caractérisation des effets du paysage, des bordures de champs et des pratiques agronomiques sur la protection des plantes » : à partir d'analyse combinée de données de suivis des pratiques agricoles et de densité de bioagresseurs dans une centaine de parcelles commerciales dans six bassins de production nationaux en grande-culture (blé-colza) ou arboriculture fruitière (pomme).

Tâche 2 : « Evaluation d'ingénierie écologique et de système de culture innovant pour la protection des plantes » portant notamment sur le rôle des infrastructures agroécologiques sur les bioagresseurs et leur contrôle biologique dans les cultures.

Tâche 3 : « Comparaison de la structure des réseaux trophiques dans des systèmes conventionnel et alternatif de protection des plantes » grâce aux développements d'outils d'inférence des liens trophiques et de méthodes d'apprentissage automatique des réseaux d'interactions.

Tâche 4 : « Estimation des dynamiques de populations des bioagresseurs et de leurs ennemis naturels en fonction de l'hétérogénéité des paysages et des pratiques agronomiques » à partir de données géo-spatialisées d'abondances et de diversité génétique et de modèle mécanico-statistique d'inférence de la dispersion

Tâche 5 : « Modélisation du contrôle biologique des bioagresseurs dans des paysages suppressifs » grâce notamment au couplage de modèles proie-prédateur et de paysage pour simuler des dynamiques des populations en interaction en fonction des hétérogénéités d'usage de sol.

Tâche 6 : « Evaluation des performances économiques et agroécologiques de scenarii d'usage de sols et identification de stratégies d'aménagements paysagers favorables au contrôle des bioagresseurs » à partir des modèles de simulation des dynamiques proie-prédateur et à l'aide d'outils d'optimisation multi-objectif.

Enfin, la **tâche 7** était dédiée à la gestion du projet, à la collaboration entre les partenaires, et à l'organisation des séminaires d'échanges annuels et du colloque de restitution.

C.4 RESULTATS OBTENUS

La **tâche 1** a mis en évidence l'importance des effets interactifs entre les pratiques de gestion des bioagresseurs dans les parcelles agricoles et le contexte paysager environnant les parcelles [9,12,17] qui expliquent à la fois, les abondances de ravageurs (L1-1), celles de leurs ennemis naturels, et plus largement le biocontrôle et la production des cultures (L1-2), et justifient l'appréhension de la santé des plantes à plusieurs échelles spatiales (L1-3).

La **tâche 2** a confirmé l'importance des infrastructures agroécologiques (haies, bandes fleuries et enherbement) et de leurs diversités floristiques (L2-1) dans le maintien d'une grande diversité d'arthropodes auxiliaires à proximité des cultures [13], mais aussi leurs faibles efficacités en terme de contrôle biologique des bioagresseurs dans les cultures (L2-2), nécessitant de préciser leurs fonctions (trophiques et non-trophiques) selon le type d'infrastructures [1,20] et d'interfaces [11], la composition floristique des couverts, et la phénologie des espèces d'auxiliaires et bioagresseurs [6].

La **tâche 3** a permis de préciser les liens trophiques entre les bioagresseurs et leurs ennemis prédateurs [2,8] et parasitoïdes [4,5], en utilisant des approches isotopiques et moléculaires (L3-1) et en comparant différentes approches moléculaires d'analyses de contenus stomacaux (L3-2). Des réseaux d'interactions entre espèces dans les cultures (L3-3) ont été établis à partir d'inférences trophiques issues de données de séquençages haut-débits [27] ou de données de cooccurrences écologiques des espèces [3,18]. Ces réseaux d'interactions témoignent de la très grande plasticité des liens trophiques selon les ressources en présences dans les cultures [3,26], suggérant que les préférences alimentaires et les niveaux de prédation d'un prédateur pour un bioagresseur donné dépendent aussi de la complexité des réseaux interactions et en particulier de la présence de leurs propres prédateurs [2].

La **tâche 4** s'est appuyée sur le développement de marqueurs moléculaires (L4-1) et de modèles biostatistiques (L4-4) pour estimer, à partir de données de suivis d'abondances et de structuration génétique, la dynamique des populations de quelques bioagresseurs [7,22,50] et leurs ennemis [12-14,19] en fonction de l'hétérogénéité des paysages (L4-2), et en fonction des pratiques agricoles et des aménagements agroécologiques dans les parcelles (L4-3).

La **tâche 5** s'est attelée à modéliser le contrôle biologique des bioagresseurs (L5-1) en lien avec les usages de sol et les pratiques de phytoprotection dans des paysages agricoles (L5-2) grâce notamment au couplage de modèles génériques proie-prédateur simulant, à l'aide d'équations aux dérivées partielles (EDP), les dynamiques des populations en interaction en fonction des hétérogénéités paysagères [16,22,80].

Enfin, la **tâche 6** a évalué conjointement les performances économiques et agroécologiques de scenarii d'usage de sols [15] et identifié des stratégies d'aménagement paysager favorable au contrôle des bioagresseurs à partir d'un modèle de simulation des dynamiques proie-prédateur (L6-1) en s'appuyant notamment sur une synthèse bibliographique des outils d'estimation de l'efficacité économique de mesures agro-environnementales (L6-2).

C.5 EXPLOITATION DES RESULTATS

Les résultats issus du projet PEERLESS sont à ce jour publiés dans des revues internationales [1-27] à la fois **disciplinaires et généralistes** (dix publications multipartenaires) et ont été présentés à l'occasion d'une trentaine de conférences nationales [51-67] et internationales [29-50] différentes. Le projet a aussi contribué à la formation par la recherche d'une dizaine d'étudiants en master ou élève-ingénieurs et de sept doctorants, dont deux étaient directement soutenues par l'ANR [89,94]. Chacune des six tâches scientifiques a donné lieu à la rédaction de 2 à 4 livrables correspondants à des compilations d'articles (L1-3, L2-1 & L3-3), à des rapports présentant les données recueillies (L1-3, L3-2 & L4-1) ou à des développements méthodologiques (L5-1, L5-2 & L6-1). Deux livrables initialement prévus en lien avec l'analyse des pratiques agricoles dans les cultures ont été abandonnés (L2-3 & L3-4). Les travaux associés à ces deux livrables ont été réalisés dans le cadre des projets GARGAMEL [102] et CASIMIR [104], connexes au projet PEERLESS. Le **colloque de restitution** du projet PEERLESS, organisé conjointement avec le projet SEBIOPAG-Phyto [103], constitue un **livrable supplémentaire** (L7-1). Ce colloque fait la **synthèse des avancées conceptuelles** sur la régulation des bioagresseurs dans les cultures au cours des cinq années du projet et ouvre quelques pistes sur les **leviers** qu'il serait possible de mobiliser pour **renforcer une protection naturelle des plantes** [114].

C.6 DISCUSSION

L'ensemble de ces travaux met en exergue la nécessité de mieux comprendre les **mécanismes écologiques** et le fonctionnement des agroécosystèmes pour pouvoir développer des modèles mécanistes prenant en compte la **variabilité de réponses** des organismes et des espèces en fonction de leurs environnements biotiques et abiotiques.

Le déficit de connaissances écologiques dans les agroécosystèmes est assurément un frein au développement de stratégies viables de protection de la santé des plantes appuyées par les régulations naturelles. Les efforts de recherches pour combler ce déficit nécessitent de poursuivre l'acquisition combinée de **données écologiques, agronomiques** et **économiques** dans un **même référentiel** d'espace et de temps et des **méta-analyses** sur une large gamme d'agro-écosystèmes pour pouvoir appréhender les **interactions** entre les facteurs déterminants le biocontrôle [101,103].

La **modélisation des dynamiques** proie-prédateur requière de modéliser en parallèle l'**hétérogénéité spatio-temporelle** des paysages pour pouvoir rendre compte de ces interactions. La modélisation des **linéaires** dans les paysages agricoles (*e.g.* la présence de haies) et de leurs effets sur la dynamique des **déplacements** des bioagresseurs et des auxiliaires dans des modèles couplés d'EDP à une et deux dimensions [22] est sans doute une perspective intéressante de **développement biostatistique** pour capter la variabilité de réponses des espèces en fonction de leurs environnements et pour mobiliser de nouveaux **leviers de gestion paysagère** de la santé des plantes.

Enfin, l'intégration d'**observations** de terrains à des **modèles réalistes de gestion** des populations de bioagresseurs reste un défi à relever pour aider la décision de traitement des agriculteurs. L'utilisation de la régulation naturelle des biogresseurs par les auxiliaires et la gestion de ce service écosystèmique nécessitent de revisiter une question ancienne en agronomie : celle de **relier** des densités de populations de bio-agresseurs à des dégâts, et des **dégâts** à des **pertes de rendements** et de **profits**.

C.7 CONCLUSIONS

Le projet PEERLESS met en lumière l'importance d'appréhender conjointement l'ensemble des facteurs en interactions et de préciser la nature de ces interactions pour pouvoir mettre en œuvre une gestion durable de la santé des plantes dans les agroécosystèmes. Les **interactions** mis en évidence dans le projet sont **multiples** : entre organismes et entre espèces, entre processus écologiques, entre composition et configuration des paysages, entre échelles spatio-temporelles, entre acteurs d'un territoire et entre choix de développement.

Le pari du projet était d'appréhender ces interactions par une approche **pluri-disciplinaire**. Nous avons collectivement plutôt bien réussi ce pari, grâce à une démarche volontaire d'acquisitions de données écologiques, agronomiques et sociotechniques dans un même cadre d'étude spatio-temporel. Pour autant, le développement de stratégies moins polluantes de gestion de la santé des plantes requière l'intégration de nos recherches dans une démarche **inter-disciplinaire** qui reste à faire. L'optimisation de ces stratégies de gestion et la prédiction de leurs efficacités à l'aide de modèles mathématiques reposent indéniablement sur des **choix de développement** et sur la décision politique.

C.8 REFERENCES

Les numéros L1-1 à L7-1 réfèrent aux numéros de livrables associés à chaque tâche et listés dans la section D.

Les numéros entre crochets réfèrent aux différentes formes de valorisation du projet PEERLESS listés dans les sections E2 et E3 en lien avec chaque livrable.

D LISTE DES LIVRABLES

Date de livraison	N°	Titre	Nature (rapport, logiciel, prototype, données, …)	Partenaires (souligner le responsable)	Commentaires
07/15	1-1	Pest control and landscape database compiling existing data	Données [101]	IGEPP, PSH, Agronomie, AE	
07/16	1-2	Pest control' landscape database compiling new data	Données [105]	IGEPP, PSH, AE	livrable conjoint avec le livrable 1-3
07/16	1-3	Relative contribution of management options at crop and landscape levels to pest control	Articles [9;11;17;28] Rapport [92]	IGEPP, PSH, Agronomie, EP, AE	livrable conjoint avec le livrable 1-2
02/18	2-1	Recommendations to optimize the wildflower strip approach in combination with different alternative cropping systems	Rapports [83;94;96] Articles [1;25]	IGEPP, PSH, Agronomie, AE	
07/16	2-2	Identification of plant species and functional traits that have the potential to improve pest control	Rapports [88;94] Articles [6;20]	IGEPP, Agronomie, AE	
Annulé	2-3	Multicriteria evaluation of ecological engineering effects on weed and pest regulation		IGEPP, PSH, Agronomie, EP, AE	Constitue un livrable du projet CASIMIR
07/16	3-1	Toolsbox for the analysis of foodwebs in agricultural landscapes	Articles, Rapport [4;5]	IGEPP, PSH, AE	
02/18	3-2	Actual food ranges and their variation for several arthropods considered to provide important pest control services	Données [113] Rapports [95]	IGEPP, AE, PSH	
07/16	3-3	Foodweb structure based on pests and weeds, the factors influencing it and its influence on pest control service	Articles [2;3;18;21;27]	IGEPP, AE, PSH	
Annulé	3-4	Ecological engineering effects on weed predation, crop pest insects, their natural enemies and crop damage		IGEPP, AE, Agronomie, PSH	Constitue un livrable du projet GARGAMEL
07/16	4-1	Molecular resources to analyze population genetic structure of several important pests and natural enemies in agricultural landscapes	Données [112] Rapports [89;99]	IGEPP, PSH, Agronomie	
02/18	4-2	Identification of habitats in the agricultural mosaic that affect dynamic and genetic structure in several pest and natural enemy populations	Articles [7;12] Rapports [89;93;99;100]	IGEPP, PSH, Agronomie, BioSP	

Date de livraison	**N°**	**Titre**	**Nature** (rapport, logiciel, prototype, données, …)	**Partenaires** (souligner le responsable)	**Commentaires**
02/18	4-3	Identification of agronomic practices and vegetation that affect pest and natural enemy population dynamics	Articles [10;13;19] Rapports [85;87;89]	IGEPP, PSH, Agronomie, AE	
07/16	4-4	Demographic parameters and landscape features affecting population dynamic in one couple of pest and natural enemy	Articles [22;23]	IGEPP, PSH, Agronomie, AE, BioSP	
07/16	5-1	Population dynamic models to optimize pest control	Programme [111] Rapport [78]	IGEPP, BioSP, PSH, EP, AE, Agronomie	
07/16	5-2	Dynamic landscape patterns for controlling pest mediated plant epidemics	Programmes [101]	IGEPP, PSH, Agronomie, AE	Livrable conjoint avec le livrable 5-3
	5-3	Scientific publications on population dynamic models (in link with tasks 4 and 6)	Articles [16;24]	IGEPP, AE, BioSP, PSH, EP, Agronomie	Livrable conjoint avec le livrable 5-2
02/18	6-1	Eco-efficiency frontier of the landscape agro-ecologic and economic production	Rapport [84]	EP, PSH	
07/15	6-2	Measurement tools to evaluate the distance of an outcome to the Pareto-efficiency frontier	Conférence, Rapport [45]	EP, PSH	
02/18	6-3	Scientific publications in economics and environmental journals	Article, Conférences [15;45;53]	EP, PSH, AE, IGEPP	
12/17	7-1	Ecologisation of agricultural production systems to strengthen biological control of pests	Colloque [114]	IGEPP, PSH, Agronomie, EP, AE, BioSP	Livrable supplémentaire

E IMPACT DU PROJET

E.1 INDICATEURS D'IMPACT

Nombre de publications et de communications (à détailler en E.2)

		Publications multipartenaires	Publications monopartenaires
International	**Revues à comité de lecture**	12	15
	Ouvrages ou chapitres d'ouvrage	0	0
	Communications (conférence)	10	12
France	**Revues à comité de lecture**	0	0
	Ouvrages ou chapitres d'ouvrage	0	1
	Communications (conférence)	7	10
Actions de diffusion	**Articles vulgarisation**	1	2
	Conférences vulgarisation	1	
	Autres	1	1

Autres valorisations scientifiques (à détailler en E.3)

	Nombre, années et commentaires (valorisations avérées ou probables)
Brevets internationaux obtenus	0
Brevet internationaux en cours d'obtention	0
Brevets nationaux obtenus	0
Brevet nationaux en cours d'obtention	0
Licences d'exploitation (obtention / cession)	0
Créations d'entreprises ou essaimage	0
Nouveaux projets collaboratifs	9 projets dont 6 achevés sur la période 2013-2020 [101-109]
Colloques scientifiques	1 colloque de restitution en 2017 [114]
Séminaires internes	5 séminaires annuels internes sur la période 2013-2017 [115]

E.2 LISTE DES PUBLICATIONS ET COMMUNICATIONS

Revues internationales à comité de lecture

1. Albert, L., Franck, P., Gilles, Y., Plantegenest, M., 2017. Impact of agroecological infrastructures on the dynamics of *Dysaphis plantaginea* (Hemiptera: Aphididae) and its natural enemies in apple orchards in Northwestern France. Environmental Entomology 46, 528-537.
2. Charalabidis, A., Dechaume-Moncharmont, F.-X., Petit, S., Bohan, D.A., 2017. Risk of predation makes foragers less choosy about their food. PLoS ONE 12, e0187167.
3. Consortium Quintescence: Bohan, D.A., Landuyt, D., Ma, A., Macfadyen, S., Martinet, V., Massol, F., McInerny, G., Montoya, J.M., Mulder, C., Pascual, U., Pocock, M.J.O., White, P., Blanchemanche, S., Bonkowski, M., Bretagnolle, V., Brönmark, C., Dicks, L.V., Dumbrell, A., Friberg, N., Gessner, M.O., Gill, R.J., Gray, C., Haughton, A., Ibanez, S., Jensen,

J., Jeppesen, E., Jokela, J., Lacroix, G., Lannou, C., Lavorel, S., Le Galliard, J.-F., Lescourret, F., Liu, S., Loeuille, N., Mc Laughlin, O., Muggleton, S., Peñuelas, J., Petanidou, T., Petit, S., Pomati, F., Raffaelli, D., Rasmussen, J., Raybould, A., Reboud, X., Richard, G., Scherber, C., Scheu, S., Sutherland, W.J., Tamaddoni-Nezhad, A., ter Braak, C., Termansen, M., Thompson, M.S.A., Tscharntke, T., Vacher, C., van der Geest, H., Voigt, W., Vonk, J.A., Zhou, X., Woodward, G., 2016. Networking our way to better ecosystem service provision. Trends in Ecology & Evolution 31, 105-115.

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5. Franck, P., Maalouly-Matar, M., Olivares, J., 2017. Molecular tools for the detection and the identification of Hymenoptera parasitoids in Tortricid fruit pests. International Journal of Molecular Sciences 18, 2031.
6. Gardarin, A., Plantegenest, M., Bischoff, A., Valantin-Morison, M., 2018. Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. Journal of Pest Science 91, 943-955.
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8. Kamenova, S., Tougeron, K., Cateine, M., Marie, A., Plantegenest, M., 2015. Behaviour-driven micro-scale niche differentiation in carabid beetles. Entomologia Experimentalis Et Applicata 155, 39-46.
9. Labruyere, S., Bohan, D.A., Biju-Duval, L., Ricci, B., Petit, S., 2016. Local, neighbor and landscape effects on the abundance of weed seed-eating carabids in arable fields: A nationwide analysis. Basic and Applied Ecology 17, 230-239.
10. Labruyere, S., Ricci, B., Lubac, A., Petit, S., 2016. Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes. Agriculture, Ecosystems & Environment 231, 183-192.
11. Labruyere, S., Petit, S., Ricci, B., 2018. Annual variation of oilseed rape habitat quality and role of grassy field margins for seed eating carabids in arable mosaics. Agricultural Forest and Entomology 20, 234–245.
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16. Parisey, N., Bourhis, Y., Roques, L., Soubeyrand, S., Ricci, B., Poggi, S., 2016. Rearranging agricultural landscapes towards habitat quality optimisation: In silico application to pest regulation. Ecological Complexity 28, 1113-1122.
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19. Pollier, A., Dosdat, S., Tricault, Y., Bischoff, A., Plantegenest, M., Jaloux, B., 2016. Using the stable isotope marker C-13 to study extrafloral nectar uptake by parasitoids under controlled conditions and in the field. Entomologia Experimentalis Et Applicata 161, 131-140.
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28. Lavigne, C., Franck, P., Toubon, J.-F., Bouvier, J.-C., Maugin, S., Olivares, J., 2014. Impact de la structure des paysages sur les ravageurs et leurs controle par les auxiliaires. In: Lauri, P.-E. (Ed.), Conception de Systèmes Horticoles innovants: Bases Biologiques, Ecologiques et Socio-Economiques. EcoHort, Montpellier, pp. 181-191.

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35. Franck, P., Maalouly, M., Olivares, J., Toubon, J.-F., Bouvier, J.-C., Lavigne, C., 2014. Spatio-temporal distribution of the parasitoid community affecting a major pest in South-Eastern France orchards. Joint 2014 Annual Meeting British Ecological Society and Société Française d’Ecologie. British Ecological Society Lille, France.
36. Franck, P., Odorizzi, L., Botelho, M., Fernandez, O.A., Lavigne, C., Bischoff, A., 2017. Impact of agro-ecological infrastructures on the control of insect pests in apple orchards. In: Begg, G.S., Smith, B., Holland, J., Gerowitt, B. (Eds.), 7th meeting of the IOBC-WPRS Working Group Landscape management for functional biodiversity. IOBC wprs Bulletin / Bulletin OILB srop, Dundee, Scotland, UK.
37. Juhel, A., Vivet, V., Butier, A., Barbu, C., Valantin-Morison, M., Franck, P., Roger-Estrade, J., 2016. Variation in abundance of pollen beetle, *Meligethes aeneus* and its parasitoid, Tersilochus heterocerus in oilseed rape in relation to proximity to woodlands and grasslands. In: Cook, S.M., Jedryczka, M., Kaczmarek, J., Truman, W., Veromann, E. (Eds.), Working Group Meeting on Prospects and progress for sustainable oilseed crop production. IOBS/WPSR, Tartu, Estonia.
38. Labruyere, S., Bohan, D.A., Biju-Duval, L., Ricci, B., Petit, S., 2015. Importance of habitat, local management and landscape composition on the abundance of weed seed eating carabid species in crop fields. 17th European Weed Research Society Symposium, Montpellier, France.
39. Lavigne, C., Maalouly, M., Monteiro, L.B., Ricci, B., Toubon, J.-F., Bouvier, J.-C., Olivares, J., Maugin, S., Thomas, C., Franck, P., 2017. Landscape scale and local crop protection intensity affect the abundance of the codling moth and its predation and parasitism in apple orchards. In: Begg, G.S., Smith, B., Holland, J., Gerowitt, B. (Eds.), 7th meeting

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41. Lefebvre, M., Franck, P., Toubon, J.-F., Olivares, J., Bouvier, J.-C., Lavigne, C., 2015. The impact of landscape composition on the abundance of a canopy dwelling spider depends on orchard management. INNOHORT 2015, Innovation in Integrated & Organic Horticulture. ISHS, Avignon, France.
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dans les agro-écosystèmes : l'exemple de la gestion des populations de carpocapse en vergers de pommiers. In: Cordonnier, T. (Ed.), Forgeco. GIP Ecofor, Grenoble.

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E.3 LISTE DES ELEMENTS DE VALORISATION

Le projet PEERLESS a contribué à l'initiation de plusieurs projets collaboratifs et de réseau agrégeant une partie de ses partenaires, à la formalisation de bases de données de suivis écologiques et génétiques de bioagresseurs et de leurs ennemis en lien avec la composition des paysages, et au développement de logiciels et de programmes informatiques pour simuler des dynamiques de population et générer des paysages aléatoires. Un colloque de restitution des principales avancées du projet.

Lancement de nouveaux projets

101. COPACABANA (2013-2015) : COmment décrire le PAysage pour Caractériser son effet sur les BioAgresseurs et ennemis Naturels (INRA, Métaprogramme SMaCH) ; rassemble plusieurs bases de données de suivis de bioagresseurs et de leurs ennemis dans les cultures en lien avec la composition des paysages et des programmes informatique pour l'analyse statistique de données spatialisés.
102. GARGAMEL (2014-2016) : Gestion agroécologique des Ravageurs de Grandes cultures à l'Aide de MELanges floraux (INRA, Métaprogramme SMaCH).
103. ESPACE (2017-2019) : Estimer les effetS des variables Paysagères sur les bioAgresseurs et auxiliaires des CulturEs (INRA, Métaprogramme SMaCH).
104. CASIMIR (2014-2017) : CAractérisation SIMplifiée des pressions bIotiques et des Régulations biologiques (Pour et Sur le Plan Ecophyto) ; recense des protocoles de suivi des bioagresseurs et de leurs ennemis naturels.
105. SEBIOPAG-Phyto (2014-2017) : Services Ecosystemiques assurés par la BIOdiversité dans les Paysages Agricoles (FRB, ecophyto) ; co-portage du colloque de restitution.
106. RéPARe (2014-2017) : Régulation Par les Araignée des Ravageurs en verger (FRB, ecophyto).
107. SOLUTION (2014-2017) : StimulatiOn des réguLations natUrelles via la diversificaTION des systèmes de culture à l'échelle du paysage (FRB, ecophyto).
108. NGB (2017-2020) : Next Generation Biomonitoring of change in ecosystem structure and function (ANR, blanc).
109. API-Tree (2017-2020) : Développement de stratégies de contrôle des ravageurs du pommier en s'appuyant sur une approche agro-systémique (Eranet, C-IPM).
110. Réseau Mixte de Recherche Agriculture et Biodiversité (2014-2018).

Programmes informatiques et bases de données

111. MULTILAND: programme Matlab permettant de générer des paysages neutres constitués d'un nombre prédéfini de régions et contrôler la proportion du paysage occupée par chaque région (associé au livrable D5-1).
112. Librairies de marqueurs génétiques (marqueurs microsatellites) de données de génotypage rendant compte de la variabilité génétique dans des populations de ravageurs du colza et du pommier et leurs parasitoides (associées au livrable D4-1 et D4-2) : doi:10.15454/THTFH0.
113. Données de métabarcoding associés à l'analyse des contenus stomacaux des carabes en grande culture (associées au livrable D3-2) : doi:10.15454/DYARY6.

Séminaires et colloque scientifique

114. Diaporamas et résumés des présentations au colloque de restitution « Ecologisation des systèmes de productions agricoles pour renforcer le contrôle biologique des bioagresseurs : apport des projets ANR Peerless et FRB Sebiopag-phyto » (associé au livrable D7-1) : http://www.smach.inra.fr/Toutes-les-actualites/seminaire-ecologisation.
115. Diaporamas des séminaires annuels: Dijon (21-22 mars 2013), Avignon (12-14 février 2014), Anger (3-4 mars 2015), Rennes (24-25 février 2016), Avignon (15-16 février 2017) : doi:10.15454/YLL85D.

E.4 BILAN ET SUIVI DES PERSONNELS RECRUTES EN CDD (HORS STAGIAIRES)

Ce tableau dresse le bilan du projet en termes de recrutement de personnels non permanents sur CDD ou assimilé. Renseigner une ligne par personne embauchée sur le projet quand l'embauche a été financée partiellement ou en totalité par l'aide de l'ANR et quand la contribution au projet a été d'une durée au moins égale à 3 mois, tous contrats confondus, l'aide de l'ANR pouvant ne représenter qu'une partie de la rémunération de la personne sur la durée de sa participation au projet.
Les stagiaires bénéficiant d'une convention de stage avec un établissement d'enseignement ne doivent pas être mentionnés.

Les données recueillies pourront faire l'objet d'une demande de mise à jour par l'ANR jusqu'à 5 ans après la fin du projet.

Identification				Avant le recrutement sur le projet			Recrutement sur le projet				Après le projet				
Nom et prénom	Sexe H/F	Adresse email (1)	Date des dernières nouvelles	Dernier diplôme obtenu au moment du recrutement	Lieu d'études (France, UE, hors UE)	Expérience prof. Antérieure, y compris post-docs (ans)	Partenaire ayant embauché la personne	Poste dans le projet (2)	Durée missions (mois) (3)	Date de fin de mission sur le projet	Devenir professionnel (4)	Type d'employeur (5)	Type d'emploi (6)	Lien au projet ANR (7)	Valorisation expérience (8)
Juhel Amandine	F	juhelamandine1@gmail.com	15/02/18	Master	France	0	Agronomie	doctorant	36	30/11/17	Recherche d'emploie	/	/	/	/
McLaughlin Orla	F	orla.mclaughlin@inra.fr	01/01/17	Doctorat	UE	4	AE	niveau ingénieur	12	31/08/15	Post-doc France	recherche publique	cadre	oui	oui
Pollier Anna	F	anna.pollier@gmail.com	15/01/18	Master	France	2	IGEEP	doctorant + post-doc	36 + 5	31/03/17	CDI	enseignement publique	cadre	non	oui
Kamenova Stephaniya	F	stefaniya.kamenova@gmail.com	15/02/18	Doctorat	France	0	IGEEP	post-doc	12	30/05/15	Post-doc étranger	recherche publique	ingénieur	non	oui
Walker Emily	F	emily.walker@inra.fr	15/02/18	Doctorat	France	5	BioSP	post-doc	12	01/09/13	CDI	recherche publique	ingénieur	oui	oui
Ciss Mamadou	H	mamadouciss@hotmail.com	15/01/18	Doctorat	France	0	PSH	niveau ingénieur	17	31/10/15	CDI	recherche publique	cadre	non	oui
Goussopolos Juliette	F	juliette.gousopoulos@inra.fr	15/02/18	BTS	France	2	PSH	technicien	3 + 5	31/12/16	CDI	recherche publique	technicien	non	oui
Pérez-	F	maperez@ve	15/	Master	UE	0	Economie	niveau	20	31/10/16	Post-doc	recherche	cadre	non	oui

Urdiales Maria		rsailles.inra.fr	06/16				Publique	ingénieur			étranger	publique			
Lubac Antoine	M	Antoine.lubac@inra.fr	01/01/17	Master	France	0	AE	niveau ingénieur	10	12/12/15	CDD	grande entreprise	ingénieur	non	oui
de Iteyssonnière Timothée	M	Timothee.deteyssoniere@inra.fr	01/09/15	Master	France	0	Agronomie	niveau ingénieur	6	02/08/15	sans nouvelle	/	/	/	/
Florian Mézerette	M	florian.mezerette@dijon.inra.fr	01/07/16	Master	France	0	AE	niveau ingénieur	6	30/06/17	étudiant	/	/	non	oui

Aide pour le remplissage

(1) Adresse email : indiquer une adresse email la plus pérenne possible

(2) Poste dans le projet : post-doc, doctorant, ingénieur ou niveau ingénieur, technicien, vacataire, autre (préciser)

(3) Durée missions : indiquer en mois la durée totale des missions (y compris celles non financées par l'ANR) effectuées sur le projet

(4) Devenir professionnel : CDI, CDD, chef d'entreprise, encore sur le projet, post-doc France, post-doc étranger, étudiant, recherche d'emploi, sans nouvelles

(5) Type d'employeur : enseignement et recherche publique, EPIC de recherche, grande entreprise, PME/TPE, création d'entreprise, autre public, autre privé, libéral, autre (préciser)

(6) Type d'emploi : ingénieur, chercheur, enseignant-chercheur, cadre, technicien, autre (préciser)

(7) Lien au projet ANR : préciser si l'employeur est ou non un partenaire du projet

(8) Valorisation expérience : préciser si le poste occupé valorise l'expérience acquise pendant le projet.

Les informations personnelles recueillies feront l'objet d'un traitement de données informatisées pour les seuls besoins de l'étude anonymisée sur le devenir professionnel des personnes recrutées sur les projets ANR. Elles ne feront l'objet d'aucune cession et seront conservées par l'ANR pendant une durée maximale de 5 ans après la fin du projet concerné. Conformément à la loi n° 78-17 du 6 janvier 1978 modifiée, relative à l'Informatique, aux Fichiers et aux Libertés, les personnes concernées disposent d'un droit d'accès, de rectification et de suppression des données personnelles les concernant. Les personnes concernées seront informées directement de ce droit lorsque leurs coordonnées sont renseignées. Elles peuvent exercer ce droit en s'adressant l'ANR (http://www.agence-nationale-recherche.fr/Contact).

Projet ANR-12-AGRO-006

PEERLESS

Compilation de jeux de données sur les bio-agresseurs et leurs contrôles biologiques dans les paysages agricoles

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Compilation de jeux de données sur les bioagresseurs et leurs contrôles biologiques dans les paysages agricoles
Nature du livrable	Donnée
Date de publication	20/07/2015
	Version 2

Rédacteur du livrable	Marie Gosme
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Autres participants	Sylvain Poggi ; Sandrine Petit ; Claire Lavigne ; Muriel Morison ; Pierre Franck
Partenaires impliqués	IGEPP ; AE ; Agronomie ; PSH
Tâche associée	Tâche 1

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

Ce livrable a pour principal objectif de rassembler les jeux de données existants sur les paysages et les pratiques agricoles en lien avec des observations biologiques sur les bioagresseurs, les dégâts qu'ils engendrent et les auxiliaires associés à leurs régulateurs.

B.2 RESUME

Maximum 1 page.

Sept jeux de données existants avant le démarrage du projet ont été rassemblés. Ils portent sur plusieurs bioagresseurs des grandes cultures (mauvaise herbes, puceron, méligèthe) et des vergers (carpocapse) et certains auxiliaires (carabes, araignée, parasitoïdes) impliqués dans le biocontrôle de ces bioagresseurs. Ces observations biologiques correspondent à des mesures d'abondance ou des estimations de la prédation et du parasitisme géolocalisées dans les cultures. Ces observations biologiques sont associées à une description des paysages et des pratiques agricoles au sein et autour des sites d'observation.

C PRESENTATION DES AVANCEES

L'ensemble des sept jeux de données associant la caractérisation de paysages agricoles à des données d'observations biologiques sur des bioagresseurs et/ou sur leurs régulateurs potentiels a été rassemblé sur le site Web du projet COPACABANA : https://www6.inra.fr/projet-copacabana.

Les sept jeux de données sont décrits sur le site web en lien avec les principales publications associées. Le tableau suivant présente succinctement les métadonnées associées aux sept jeux de données.

Jeux de données		Paysages observés						Observations biologiques					
Sites d'observation	Partenaires référents	étendue (km2)	continu/nb de paysages	tailles des rayons ou des dalles d'observation (m)	gamme % culture dans les 1000m alentour	gamme % HSN dans les 1000m alentour	gamme %de culture bio dans les 1000m alentour	durée (mois)	nb dates d'observations	nb de sites d'observation	bioagresseurs	auxiliaires	régulation
Mantois	Agronomie	60	continu	1000	43 à 91%	3 à 44%	0 à 77%	24	12	~100	adventices, pucerons	.	.
Normandie	Agronomie	13000	42	2000	11% à 89%	2 à 81%	.	24	2	~20	méligèthe	.	taux parasitisme
Bourgogne GEDA	AE	3000	66	1000	18% à 96%	18 à 96%	.	12	2	67	.	carabes	prédation graines adventices
Bourgogne Fenay	AE	10	continu		70%	20%	.	60	10	73	adventices	.	.
Basse Vallée de la Durance	PSH	70	continu	500 ou 1000 selon variable	36% à 92%	6% à 54%	0 à 20%	84	7	~50	carpocapse	parasitoides, araignées	taux parasitisme
Sud Ille et Vilaine	IGEPP	3500	20	250 ou 500 selon variables	71 à 96% dans la dalle de 1Km²	0 à 21% dans la dalle de 1Km²	6 à 37% dans la dalle de 1Km²	24	14	40	pucerons	carabes, coccinelles	taux parasitisme
Zone Atelier Armorique	IGEPP	3600	40	500	?	?	?	24	13	80 ou 200	.	carabes	.

Tableau 1: présentations des métadonnées de 7 jeux de données associant une description des occupations du sol et des pratiques dans les paysages agricoles à des observations biologiques géo-référencées dans les cultures.

Malgré l’effort de synthèse pour harmoniser les jeux données sous un même format, la disparité des mesures biologiques et des échelles spatiales d’observation, et le nombre finalement réduit de données rend difficile leur exploitation dans une méta-analyse.

Ces données ont également alimenté une base de données plus globale pour une méta-analyse des effets du paysage sur les services écosystémiques de régulation rendus à l’agriculture conduite dans le cadre du projet Sesync « Decision-Support Tools for Pest Control » : www.pnas.org/cgi/doi/10.1073/pnas.1800042115

Projet ANR-12-AGRO-006

PEERLESS

Transversal analysis of the relative effects of local management and landscape scale factors on pest abundance and crop yields

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Transversal analysis of the relative effects of local management and landscape scale factors on pest abundance and crop yields
Nature du livrable	Article
Date de publication	06/06/2016
	Version 2

Rédacteur du livrable	Sandrine PETIT
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Partenaires impliqués	AE, IGEPP
Tâche associée	Tâche 1 ; sous-tâches 1.3
Livrable associée	Livrable D1-2

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

Pest data has been collected with harmonized protocols in commercial fields over 3 sites, namely Angers, Dijon and Rennes. Our aim was to assess to which extent local field management and landscape scale factors could explain variations in pest abundance. Another objective was to examine to which extent pest abundance impacted crop yield.
In order to do so, data collected in the three sites were compiled and the expected relationships between the different components of the system were summarised in an hypothetical conceptual model. This model was run with PEERLESS data, both in winter cereals and in oilseed rape.

B.2 RESUME

Maximum 1 page en français.

There is currently a will to reduce the use of pesticides in agriculture, giving the fact these products can be harmful for the environment. But currently the pests' populations are mainly reduced with the help of pesticides. A decrease of their use can lead to an increase of crop's damage and to a reduction of the yields. Therefore, others means are needed to limit the pests. The agricultural landscape around the fields could be an answer, by influencing directly the pests' communities or indirectly by increasing the natural enemies' densities. But, first of all, we need to be sure of the relationships linking the agricultural management, the pests and the crop's production. In this purpose, data of weeds' cover, abundance of pests, damage and the crops' management were studied in grain and rapeseed fields, with the landscape described 565m around studied fields. These data were analysed using the PLS-PM approach. The relationship between management and yields was robust and the practices generally reduced the abundance of pests. But the links between pests and yields were not that clear: if weeds reduced the yield, it was not the case for the insect pests and damage. Globally, the landscape had little effects on pests' abundance, but the cereal leaf beetles were affected by the proportion of semi-natural habitats and crops. But several relations can change considering the treatment intensity of the fields for some pests. These results could mean the contribution of the landscape, as described here, could not be enough to sustain the current yields in case of pesticides reduction.

C PRESENTATION DES AVANCEES

L'agriculture repose actuellement en grande partie sur l'utilisation d'intrants, notamment des produits phytosanitaires ou des fertilisants. Cet usage a fortement augmenté durant la seconde moitié du vingtième siècle, avec parallèlement un accroissement des rendements (TILMAN *et al.*, 2002). Néanmoins, certains produits utilisés peuvent présenter des dangers pour la santé humaine ou l'environnement (STOATE *et al.*, 2001) et le développement de résistances aux pesticides chez certains bioagresseurs questionne la durabilité de la lutte chimique. Afin de limiter les risques possibles, une diminution de l'utilisation des produits phytosanitaires est souhaitée (STOATE *et al.*, 2009; CHAUVEL *et al.*, 2012) et certains pays ont mis en en place des programmes de réduction des pesticides, par exemple en France au travers du plan ECOPHYTO 2018 (ANONYME, 2015).

Réduire l'utilisation de produits phytosanitaires peut représenter un risque en termes de contrôle des bioagresseurs des cultures. Ces bioagresseurs sont divers, animaux (*i.e.* les ravageurs : des arthropodes, des mollusques ou encore des vertébrés), des végétaux (plantes adventices des cultures), des virus ou des pathogènes (OERKE, 2006). Mondialement, on estime que ces bioagresseurs provoquent des pertes de rendement de l'ordre de 11 à 59% suivant l'espèce (OERKE, 2006). Les principales pertes de rendement sont dues aux plantes adventices, suivies des ravageurs, des pathogènes et des virus, bien que l'importance de leurs dégâts respectifs puisse varier suivant la culture.

Les recherches actuelles montrent que l'usage de produits phytosanitaires reste aujourd'hui le principal levier de gestion des bioagresseurs. C'est le cas pour l'usage d'herbicides pour gérer les adventices de culture, avec des abondances observées d'adventices souvent plus importantes en agriculture biologique qu'en agriculture conventionnelle (BENGTSSON *et al.*, 2005; WINQVIST *et al.*, 2011). C'est également vrai pour l'utilisation d'insecticides visant le contrôle de populations de ravageurs (NORRIS & KOGAN, 2000). L'abondance des bioagresseurs peut néanmoins être affectée par des pratiques de gestion agricoles autre que la lutte chimique. Le travail du sol ou l'apport en azote minéral peuvent par exemple affecter l'abondance des adventices (ABU-DIEYEH & WATSON, 2007; SANTIN-MONTANYA *et al.*, 2013; PETIT *et al.*, 2016). Le niveau de fertilisation peut aussi modifier les abondances de certains ravageurs, comme les pucerons (AQUEEL & LEATHER, 2011) avec un effet quadratique, c'est à dire une augmentation des abondances jusqu'à un certain niveau de fertilisation et une baisse au-delà de ce seuil (GASH, 2012). En réduisant le contrôle des bioagresseurs, une baisse de l'utilisation de produits phytosanitaires pourrait donc provoquer des pertes de rendement (ZALLER *et al.*, 2008a; STOATE *et al.*, 2009; CHAUVEL *et al.*, 2012). Cette baisse de rendement pourrait toutefois être limitée par d'autres types de gestion agricole notamment de type protection intégrée des cultures, c'est-à-dire en utilisant des combinaisons de leviers agronomiques non chimiques (CHAUVEL *et al.*, 2011; LECHENET *et al.*, 2014). Dans certains cas, on mobilisera également des pratiques favorisant l'abondance d'ennemis naturels de bioagresseurs, de façon à augmenter leur régulation biologique (BOHAN *et al.*, 2011; RUSCH *et al.*, 2013). Ces différents leviers peuvent potentiellement limiter voir gommer les pertes de rendement liées à la réduction de la lutte chimique (LECHENET *et al.*, 2014; ÖSTMAN *et al.*, 2003).

Les recherches récentes ont également souligné qu'à des échelles spatiales dépassant la parcelle cultivée, la composition et la structuration des paysages agricoles peuvent affecter le niveau d'abondance des bioagresseurs. L'organisation du paysage définit en effet la proportion d'habitat

favorable ainsi que les possibilités de dispersion pour une espèce donnée. Cet effet peut être direct, par exemple la complexité des paysages peut affecter l'abondance des adventices (BOHAN & HAUGHTON, 2012; PETIT *et al.*, 2013), ou d'insectes ravageurs (TSCHARNTKE *et al.*, 2012; BOURHIS *et al.*, 2015). La relation peut également être indirecte, les propriétés du paysage affectant cette fois les communautés d'auxiliaires de cultures qui contrôlent les populations de bioagresseurs (BIANCHI *et al.*, 2006; CHAPLIN-KRAMER *et al.*, 2011; VERES *et al.*, 2013). Toutefois aujourd'hui, si l'effet du paysage sur les auxiliaires de culture est globalement bien décrit, celui sur les bioagresseurs n'est pas clair. Les méta-analyses réalisées par CHAPLIN-KRAMER *et al.* (2011) et VERES *et al.* (2013) n'ont pas montré d'influence généralisable du paysage sur les ravageurs, alors que la complexité du paysage influence fortement les ennemis naturels. Ainsi, il est possible que l'augmentation de l'abondance et de la diversité des communautés d'ennemis naturels ne permette pas une diminution systématique des populations de bioagresseurs. Une des raisons peut être que l'effet du paysage sur les ravageurs et les plantes adventices reste relativement peu documenté, notamment en comparaison au nombre d'études ayant porté sur les auxiliaires. Une autre difficulté est que l'effet du paysage sur les bioagresseurs peut également varier en fonction de la gestion menée dans les parcelles cultivées. Ceci a été montré pour la mortalité des pucerons (WINQVIST *et al.*, 2011) qui est stable suivant la proportion en cultures à proximité des parcelles gérées conventionnellement, mais qui diminue dans le cas de parcelles en agriculture biologique. La prédation des graines d'adventices peut également suivre la même tendance, avec une augmentation de la prédation en parcelles conventionnelles suivant la proportion en terres arables, tandis que la prédation diminue dans les parcelles en agriculture biologique (FISCHER *et al.*, 2011). Les bioagresseurs pourraient ainsi être impactés par la complexité du paysage de façon différentielle suivant l'intensité de gestion.
Enfin, nous pouvons faire le constat que peu d'études ont considéré l'effet du paysage sur le rendement. La composition du paysage peut notamment avoir un impact sur les dégâts de cultures, comme dans le cas du colza (RUSCH *et al.*, 2013). Le paysage aurait ainsi un effet indirect, en modifiant les réseaux trophiques entre bioagresseurs et ennemis naturels. Néanmoins, la gestion au sein de la parcelle serait susceptible de limiter l'effet du paysage, qu'il soit positif ou négatif, en réduisant très fortement les abondances en bioagresseurs. En effet, la relation paysage/rendement n'est pas systématiquement retrouvée suivant les études et les bioagresseurs (JONSSON *et al.*, 2015).

Il semble de ce fait nécessaire de réaliser une analyse globale des relations qui peuvent exister entre la gestion agricole, le rendement, les bioagresseurs et le paysage. Les points soulevés précédemment, nous amènent à proposer un schéma conceptuel hypothétique présenté dans la Figure 1.

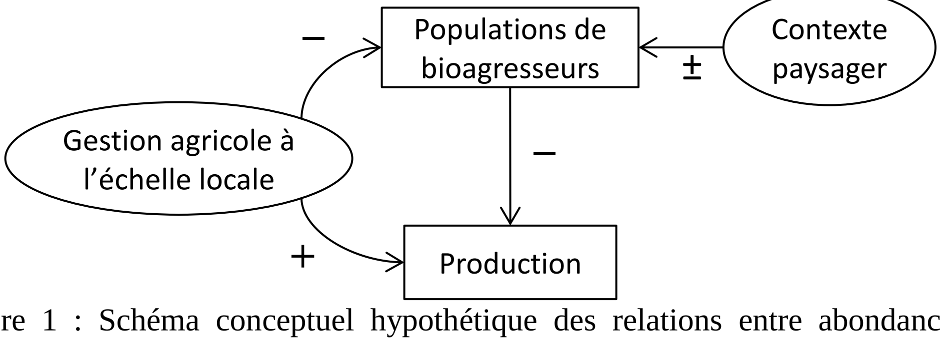

Figure 1 : Schéma conceptuel hypothétique des relations entre abondance de bioagresseurs, paysage, pratiques agricoles et production agricole.

Cette étude considérera donc plusieurs hypothèses : – H1 : l'intensité des pratiques diminue les abondances des bioagresseurs et augmente directement et potentiellement indirectement (*via* une réduction de l'abondance de bioagresseurs) le rendement ; – H2 : les bioagresseurs affectent négativement le rendement ; – H3 : la composition et l'organisation du paysage affectent les populations de bioagresseurs, avec des effets dépendants des espèces ; – H4 : La réponse aux hypothèses H1-H3 pourrait varier en fonction de l'intensité de gestion des parcelles, et notamment du niveau d'utilisation de pesticides.

Pour tester ces hypothèses, des bioagresseurs de cultures de céréales d'hiver et de colza ont été échantillonnés dans trois sites en 2014 et 2015. Les données ont été traitées à l'aide de la méthode des *Partial Least Squares – Path Modeling*. Cette analyse permet de caractériser les relations entre plusieurs variables en leur imposant des liens *a priori* (*cf.* Figure 1).

1. MATERIEL ET METHODES

1.1. ZONES D'ETUDE ET SELECTION DES PARCELLES

Dans le cadre du projet ANR PEERLESS, trois sites ont été échantillonnés en France en 2014 et 2015 (Figure 2) : dans l'est de la Côte-d'Or (coordonnées moyennes des parcelles : 47°23′ N, 5°10′ E, nommée zone d'étude de Dijon), dans la moitié sud de l'Ille-et-Vilaine (47°58′ N, 1°35′ W, zone d'étude de Rennes) et en Maine-et-Loire (47°21′ N, 0°30′ W, zone d'étude d'Angers).

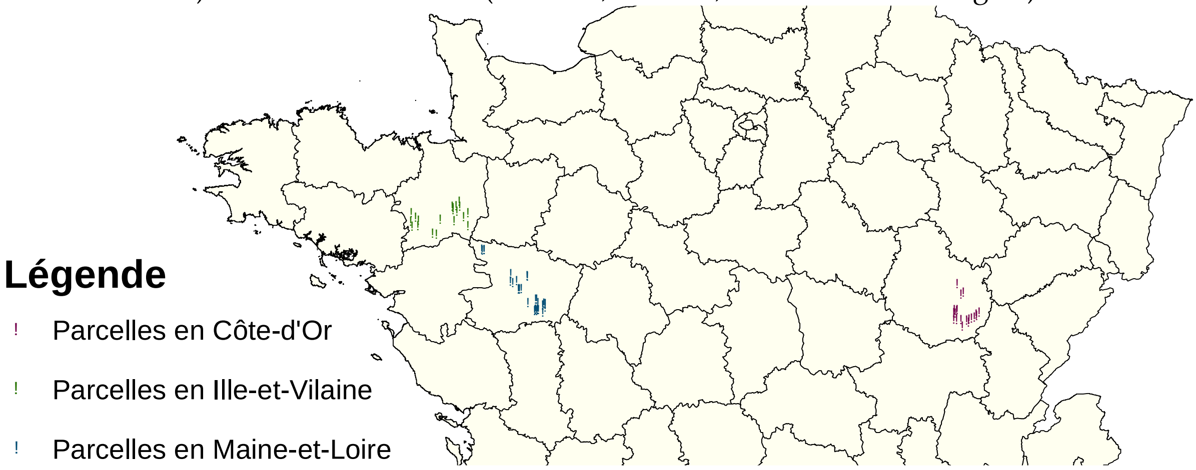

Figure 2 : Localisation des sites et des parcelles étudiées.

Les parcelles des zones d'étude de Dijon et de Rennes ont été sélectionnées suivant un gradient de complexité du paysage. Celui-ci était basé sur un indice de Shannon, sur le pourcentage de cultures annuelles et sur la longueur des interfaces entre cultures et éléments semi-naturels. 10 parcelles en céréales et 10 en colza ont été sélectionnées dans la zone de Dijon et 20 parcelles en céréales l'ont été dans la zone de Rennes en 2014. Ces parcelles ont également été suivies en 2015, mais seules celles étant en culture de céréales ou de colza ont été étudiées. Les parcelles de la zone d'étude d'Angers ont pour leur part été sélectionnées le long d'une diagonale en Maine-et-Loire. Comme aucune donnée de paysage n'était disponible pour ce site, la sélection *via* critères paysagers était impossible à réaliser. Les agriculteurs dans cette zone ont été contactés pour constituer un échantillon de 32 parcelles par année (16 en céréales et 16 en colza). Pour l'année 2015, 2 parcelles en céréales et 3 en colza présentaient des données manquantes et n'ont pas été intégrées à l'analyse. Au total, 114 parcelles ont été échantillonnées suivant la répartition présentée dans le Tableau 1.

Tableau 1 : Répartition et nombre de parcelles par culture en 2014 et 2015.

	Année	Angers	Dijon	Rennes	Total
Céréales	2014	16	10	20	46
	2015	14	11	3	28
Colza	2014	16	10	0	26
	2015	13	1	0	14
	Total	59	32	23	114

1.2. RELEVE DES VARIABLES BIOLOGIQUES

Les échantillonnages ont été menés en 2014 et 2015 et ont concerné plusieurs taxons, différents suivant la culture (Tableau 2). Les relevés ont été effectués à l'intérieur des parcelles, à 50m de la plus proche bordure. Les plantes adventices ont été relevées pour l'ensemble des sites et des années, que ce soit pour les parcelles de céréales et de colza. L'échantillonnage des adventices a consisté en 5 (Angers) ou 10 (Dijon et Rennes) quadrats de 0,25m² répartis sur une ligne parallèle à la bordure de la parcelle.

L'abondance des pucerons (comprenant deux espèces, *Sitobion avenae* (FABRICIUS, 1794) et *Metopolophium dirhodum* (WALKER, 1849)), l'abondance des larves de criocères (principalement *Oulema melanopus* (LINNAEUS, 1758)) et le pourcentage de dégâts par plante ont été relevés en cultures de céréales sur 50 plantes consécutives sur une ligne parallèle à la bordure de la parcelle. En colza, le nombre de graines total et le nombre de graines endommagées par siliques ont été relevés, là aussi sur 50 plantes consécutives parallèlement à la bordure. Néanmoins, contrairement aux relevés des plantes adventices, plusieurs parcelles n'ont pas été échantillonnées pour certaines variables des ravageurs (Tableau 2). Les dates de prélèvement pouvaient de plus varier suivant les sites (Tableau 3).

Tableau 2 : Variables relevées pour chaque site (Angers, Dijon, Rennes).

	Variables échantillonnées	Angers	Dijon	Rennes	Total
Céréales	Adventices	×	×	×	74
	Pucerons	×	×	× (1 ; 2)	69
	Larves de criocères	×	×	× (1 ; 2)	69
	Dégâts des criocères	×	×	× (1 ; 3)	68
Colza	Adventices	×	×	-	40
	Dégâts des siliques	× (1)	× (1)	-	26

(1) : Variables relevées uniquement en 2014 ; (2) : Variable non échantillonnée dans deux parcelles en 2014 ; (3) : Variable non échantillonnée dans trois parcelles en 2014

Afin d'éviter tout problème de pseudo-réplication dans les analyses statistiques, les données des relevés ont été moyennées par parcelle.

Tableau 3 : Date de prélèvement pour chaque type de variable biologique échantillonnée suivant les sites.

		Année	Angers	Dijon	Rennes
Céréales	Adventices	2014	02/06	10/04	Courant mai
		2015	01/06	15/04	08-15/04
	Ravageurs	2014	02/06	05/06	17/06
		2015	01/06	09/06	-
Colza	Adventices	2014	22/04	10/04	-
		2015	21/04	02/04	-
	Ravageurs	2014	16/06	05/06	-

1.3. DESCRIPTION DU PAYSAGE

Les données disponibles dans le projet décrivent l'occupation du sol dans un 565m de rayon (soit un cercle d'une superficie de 1km²) autour de la bordure de parcelles près de laquelle les mesures biologiques ont été effectuées. Les taxons étudiés peuvent répondre de façon différenciée au paysage et suivant l'échelle considérée. Celle utilisée ici représente un compromis pour l'ensemble des bioagresseurs, les adventices étant principalement influencées par le paysage à une échelle locale (GABA *et al.*, 2010), mais pouvant être plus importante (GABRIEL *et al.*, 2005). Les pucerons sont eux davantage influencés par le paysage à grande échelle (O'ROURKE *et al.*, 2011), mais des effets plus locaux peuvent être observés (AL HASSAN *et al.*, 2012).

Quatre classes d'utilisation du sol ont été considérées dans cette étude : la proportion en éléments semi-naturels (comprenant les zones boisées, les prairies et les friches), la proportion en cultures, celle en céréales d'hiver et celle en cultures d'oléagineux (comprenant le colza et les cultures de moutarde). Ceci a nécessité d'homogénéiser les différences de nomenclature entre sites. Le plus bas niveau de correspondance a ainsi été utilisé pour les cultures et éléments semi-naturels présents dans les différents sites. Les différentes cultures de céréales d'hiver des zones de Dijon et de Rennes ont par exemple été regroupées en une seule catégorie, similaire à la précision de la zone d'Angers. La plupart des cultures a cependant pu être distinguée de façon individuelle, comme le maïs ou le colza. Le recouvrement des différents milieux a été calculé à l'aide du logiciel ArcGIS (ESRI, 2015).

Le choix des métriques paysagères utilisées dans chaque modèle a été dicté par la bibliographie et/ou certaines hypothèses écologiques. Nous avons ainsi retenu :

- La diversité du paysage. Elle peut influencer l'abondance des adventices (BOHAN & HAUGHTON, 2012) et impacte souvent positivement l'abondance d'ennemis naturels (CHAPLIN-KRAMER *et al.*, 2011). Ici, nous avons calculé deux indices de Shannon ($H' = -\sum p_i \times \log(p_i)$). Le premier a été calculé en intégrant les proportions des différentes cultures annuelles, hors maraichage, c'est à dire céréales d'hiver, cultures de printemps, oléagineux et cultures d'été (défini comme étant Shannon 1). Le second indice a été calculé en intégrant les cultures pérennes et les éléments semi-naturels (Shannon 2).
- La proportion en éléments semi-naturels et celle en cultures. Ces variables sont souvent utilisées pour décrire la complexité des paysages (*e.g.* THIES *et al.*, 2005) et présentent des effets sur les bioagresseurs, que ce soit par une augmentation de la richesse spécifiques des adventices ou de l'abondance des ravageurs (GABRIEL *et al.*, 2005; MARTIN *et al.*, 2013; PETIT *et al.*, 2013).
- La proportion en culture hôte. Elle peut impacter les communautés de bioagresseurs en leur fournissant un habitat favorable pour leurs besoins en ressources ou en zones de ponte. Néanmoins, une forte présence de cultures hôtes dans le paysage peut conduire à des phénomènes de dilution (O'ROURKE *et al.*, 2011).

1.4. DONNEES DE PRATIQUES AGRICOLES

Les données disponibles pour cette étude proviennent d'enquêtes réalisées chez les agriculteurs dans chaque site. Dans cette analyse, nous avons considéré la pression phytosanitaire et quelques autres pratiques susceptibles d'impacter l'abondance de bioagresseurs.

La pression phytosanitaire a été quantifiée comme suit.

Le nom et la dose des produits phytosanitaires utilisés, *i.e.* pesticides, ont été relevés, permettant d'obtenir l'indice de fréquence de traitement (IFT), calculé selon :

$$\mathrm{IFT} = \frac{\text{Dose de produit utilisé} \times \text{Surface traitée}}{\text{Dose de référence du produit} \times \text{Surface totale}}$$

Les IFT des produits ont été discriminés suivant la catégorie des cibles, *i.e.* entre fongicides, herbicides, insecticides et IFT total pour ceux utilisés dans cette étude. Les pesticides étant utilisés pour limiter les abondances de bioagresseurs, leur prise en compte était nécessaire. D'autre part, malgré le fait que certains bioagresseurs n'étaient pas spécifiquement visés par les traitements, des pesticides agissant sur une cible donnée peuvent impacter d'autres taxons, comme les herbicides sur les insectes ou les fongicides sur les plantes (NORRIS & KOGAN, 2000; GEIGER *et al.*, 2010). Comme quatre parcelles en céréales sur les 74 avaient été traitées avec des insecticides, seul l'IFT total a été considéré afin de déterminer l'impact de la gestion sur les populations et les dégâts des ravageurs. D'autre part, l'IFT fongicides a été pris en compte dans les analyses du couvert des plantes adventices.

La quantité d'azote minéral épandue sur la parcelle a également été considérée. Certaines études ont en effet détecté des effets négatifs sur les abondances des adventices (PETIT *et al.*, 2016) et la fertilisation minérale est connue pour son impact sur leur richesse spécifique (PETIT *et al.*, 2013). L'effet sur les ravageurs est néanmoins moins évident, mais certaines études mettent en avant un effet positif indirect *via* l'augmentation de la teneur en azote des plantes, notamment sur les populations de pucerons (AQUEEL & LEATHER, 2011; JONSSON *et al.*, 2015).

Certaines parcelles étaient conduites en agriculture biologique, représentant 16 parcelles sur les 74 en céréales et 6 parcelles sur les 40 en colza. Comme les impératifs de gestion ne permettent pas l'utilisation de produits phytosanitaires de synthèse ni de fertilisation minérale, deux variables ont été prises en compte afin de garantir une variabilité au sein de cette catégorie de parcelles.

Le travail du sol est connu pour impacter les communautés d'adventices, notamment le labour (SANTIN-MONTANYA *et al.*, 2013), et est un des moyens de gestion en agriculture biologique. Toutefois, le nombre de travaux du sol n'était pas corrélé avec les autres types de gestion. Le nombre de passages mécaniques et de désherbages manuels sur la parcelle a donc été utilisé. Il prend en compte le nombre de travaux du sol, de traitements phytosanitaires, de fertilisations ainsi que le semis et la moisson.

Même si les parcelles en agriculture biologique ne peuvent pas utiliser de fertilisation minérale, celle organique est autorisée. Néanmoins, le calcul de cette fertilisation s'avère complexe et peut ne pas être fiable en utilisant des valeurs de référence ou sans considérer la cinétique de minéralisation de l'azote organique (BOUTHIER *et al.*, 20XX). De ce fait et afin de prendre en compte cette action de gestion, le nombre de fertilisations minérales et organiques a également été considéré, faisant également partie du nombre de passages.

L'ensemble de ces variables doit permettre de situer les parcelles étudiées sur un gradient d'intensité de gestion.

1.5. ANALYSES STATISTIQUES

1.5.1. PARTIAL LEAST SQUARE PATH MODELING

Les relations entre paysage, bioagresseurs, pratiques agricoles et rendement ont été analysées à l'aide de la méthodes de *Partial Least Square Path Modeling* (PLS-PM) (TENENHAUS *et al.*, 2005; SANCHEZ, 2013). Cette méthode statistique permet de modéliser les relations entre variables latentes (VL), estimées à partir de variables observées, ou manifestes (VM). Cette analyse est de type « composantes » et présente divers intérêts. En effet, elle ne nécessite pas de prérequis vis-à-vis de la distribution des variables et ne requiert théoriquement pas un grand nombre d'observations (ESPOSITO VINZI, CHIN, *et al.*, 2010).

Deux types de modèles coexistent en PLS-PM. Le modèle de mesure (ou *outer model*) décrit le poids (l'importance) de chaque variable manifeste dans la construction de sa variable latente associée (Figure 3). Les poids sont calculés de façon itérative en considérant le type de relation entre VM et VL (appelé *mode*) et celui du modèle interne (appelé schéma). Différents *modes* existent, mais deux ont été utilisés dans cette étude : le *mode A* (ou réflectif) et le *mode PLScore*. Sous le *mode A*, le poids des VM à leur VL associée est obtenu à l'aide de régressions linéaires simples. Dans ce *mode*, la VL doit décrire les VM la constituant et il est nécessaire que ces dernières soient fortement corrélées entre elles. Pour cela, les *loadings* entre VM et VL associée doivent être élevées, avec une valeur limite retenue ici de 0,7, comme préconisé par SANCHEZ (2013). Le *mode PLScore* utilise quant à lui la régression PLS dans le calcul des modèles externes (ESPOSITO VINZI, RUSSOLILLO, *et al.*, 2010) et a été utilisé afin de garantir une convergence des itérations des calculs des modèles PLS-PM. Après l'obtention des poids, les corrélations entre VM et leur VL associée sont calculées et sont appelées *loadings*.

Le modèle structurel (ou *inner model*) décrit les relations entre différentes VL. Plusieurs schémas internes existent également, mais celui utilisé ici est le *path weighting*. Il considère les relations précédentes dans l'estimation des corrélations et est moins sensible à des variations de signe entre itérations en cas de faible corrélation entre VL par rapport au schéma de type centroïde, principalement utilisé (SANCHEZ, 2013). Un coefficient de détermination R^2 est associé à chaque variable latente devant être expliquée par d'autres VL et exprime la qualité de prédiction de la régression multiple de la VL.

Des simulations par *bootstraps* sont par la suite réalisées afin de déterminer la significativité des relations entre variables latentes : dans le cas où l'intervalle de confiance à 95% de la corrélation n'inclut pas 0, la relation est considérée comme significative.

La qualité des modèles peut être déterminée à l'aide d'un indice de *goodness of fit* (GoF) qui prend en compte les modèles interne et externe. Plus l'indice GoF est élevé, plus le modèle a une forte puissance de prédiction (SANCHEZ, 2013).

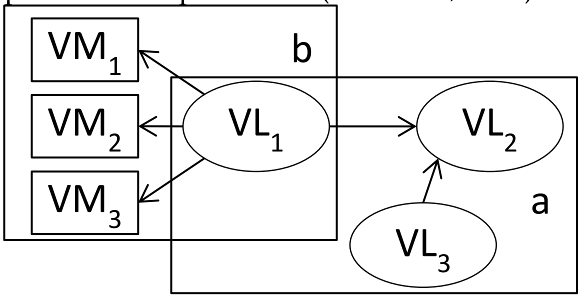

Figure 3 : Représentation schématique d'un modèle PLS-PM.
a : Modèle structurel ou interne
b : Modèle de mesure ou externe

1.5.2. MODELES REALISES

Cinq variables latentes ont été initialement considérées dans cette étude, suivant les relations présentées dans la Figure 4. Les variables paysagères ont été séparées en deux variables latentes afin de permettre une colinéarité des variables manifestes de chacune des VL de paysage.

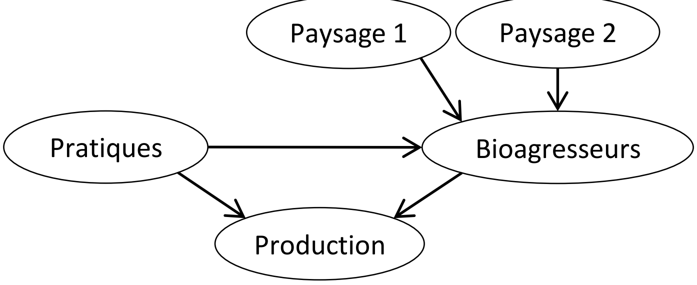

Figure 4 : Modèle interne des PLS-PM.

Le *mode A* (ou réflectif) a été utilisé pour l'ensemble des VL mises à part celles des bioagresseurs, le *mode PLScore* leur ayant été associé. Afin d'obtenir une colinéarité des variables manifestes du Paysage 2, les proportions en cultures, céréales d'hiver et oléagineux ont été modifiées suivant l'opération 100-x (Tableau 4). Ces variables seront notées -(x) dans les représentations graphiques des modèles de PLS-PM.

Cinq modèles généraux ont été réalisés, suivant la culture et les bioagresseurs, avec une sélection de variables manifestes différentielle suivant leur *loading* (Tableau 4). Chacune des variables a été centrée-réduite pour effectuer les modèles de PLS-PM.

Tableau 4 : Liste des variables relevées utilisées dans les différents modèles de PLS-PM et leur variable latente associée.

		Céréales			Colza	
Variables manifestes	Variables latentes	Adv	Puc	Cri	Adv	Dég
IFT fongicides	Pratiques	×				
IFT herbicides	Pratiques	×			×	
IFT insecticides	Pratiques					×
IFT total	Pratiques	×	×	×	×	×
Fertilisation minérale	Pratiques	×	×	×	×	×
Nombre de passages	Pratiques	×	×	×	×	×
Nombre de fertilisations	Pratiques	×	×	×	×	×
Shannon 1	Paysage 1	×	×	×	×	×
Shannon 2	Paysage 1	×	×	×	×	×
% Milieux semi-naturels	Paysage 2	×		×	×	
100-(% Cultures)	Paysage 2	×	×	×	×	×
100-(% Céréales d'hiver)	Paysage 2	×	×	×		
100-(% Oléagineux)	Paysage 2					×
Couvert en Eudicotylédones	Bioagresseurs	×			×	
Couvert en Monocotylédones	Bioagresseurs	×			×	
Abondance des pucerons	Bioagresseurs		×			
Abondance des larves de criocères	Bioagresseurs			×		
Dégâts des larves de criocères	Bioagresseurs			×		
Dégâts des siliques	Bioagresseurs					×
Rendement	Production	×	×	×	×	×

Adv : Adventices ; Puc : Pucerons ; Cri : Criocères ; Dég : Dégâts des siliques

Après avoir réalisé les modèles généraux, des tests de Mantel ont été effectués sur les scores des VL des bioagresseurs afin de vérifier la possibilité d'une autocorrélation spatiale. Seule la variable du modèle des dégâts des siliques présentait une forte autocorrélation ($p < 0{,}001$). De ce fait, une variable latente « Site » composée d'une VM factorielle a été rajoutée à ce modèle et était reliée aux dégâts. L'autocorrélation spatiale des rendements a également été testée et s'est également révélée significative sur l'ensemble des parcelles de chaque culture. Comme dans ce cas, certaines parcelles avaient été échantillonnées les deux années, la VM distinguait les parcelles suivant l'année (« Site Année »). Néanmoins, cette variable ne s'est pas révélée significative et a été supprimée des modèles afin de limiter le nombre des variables latentes.

Des modèles basés sur l'intensité de la pression phytosanitaire appliquée dans les parcelles ont par la suite été effectués (nommés par la suite « sous-modèles »). Le critère de sélection a été la médiane de l'IFT : soit de l'IFT herbicides pour les adventices en céréales et colza (1,39 et 1,59 respectivement), soit de l'IFT total pour les ravageurs en céréales (2,98 pour les pucerons et 2,99 pour les criocères). Comme les dégâts des siliques en colza avaient été relevés dans 26 parcelles, les sous-modèles n'ont pas été réalisés compte tenu du faible nombre d'échantillons. Dans les sous-modèles, l'ensemble des variables manifestes sélectionnées dans le modèle général a été utilisé, malgré le fait que certaines VM ne présentaient plus de *loading* supérieur à 0,7. Ce choix a été fait pour garantir la comparaison entre modèles généraux et sous-modèles. Il est à noter que la suppression de ces variables manifestes modifiait peu les relations internes des PLS-PM, mais augmentaient l'indice de GoF.

1.5.3. AUTRES ANALYSES ET PROGRAMMES UTILISES

Des comparaisons de moyennes ont été réalisées afin de comparer les valeurs de rendement, d'abondances des bioagresseurs et des dégâts entre groupes de fort et faible pression phytosanitaire.

Comme les hypothèses de normalité des données et d'égalité des variances entre groupes n'étaient pas respectées, des tests U de Mann-Whitney ont été utilisés.

L'ensemble des analyses statistiques a été effectuée sur le logiciel R, version 3.3.0 (R CORE TEAM, 2016). Les intervalles de confiance à 95% des moyennes ont été calculés par *bootstraps* à l'aide du package « boot » sur la base de 10 000 simulations (CANTY & RIPLEY, 2016). Les indices de Shannon de la composition du paysage ont été réalisés à l'aide du package « vegan » (OKSANEN et al., 2016). Les tests de Mantel ont été effectués à l'aide du *package* « ade4 » (CHESSEL *et al.*, 2004; DRAY *et al.*, 2007; DRAY & DUFOUR, 2007). Les modélisation de PLS-PM on quant à elles été réalisées en utilisant le package « plspm » (SANCHEZ et al., 2015).

2. RESULTATS

2.1. RELATIONS EN CULTURES DE CEREALES

Le rendement moyen [IC 95%] des 74 parcelles était de 64,86 q·ha^{-1} [60,22–69,39], allant de 20 à 95 q·ha^{-1}. Le couvert moyen en adventices était de 8,08% [4,88–11,71] et variaient de 0 à 76%. Néanmoins, 13 parcelles ne présentaient pas d'adventices. Les couverts en Eudicotylédones et Monocotylédones étaient significativement corrélés (test de corrélation de Spearman, rho = 0,53, p < 0,001).

Un total de 2681 pucerons a été échantillonné dans 62 des 69 parcelles, comprenant 2269 *Sitobion avenae* (FABRICIUS, 1794) et 412 *Metopolophium dirhodum* (WALKER, 1849). L'abondance moyenne était de 0,74 [0,48–1,07] pucerons par plant de blé sur l'ensemble des 69 parcelles, avec des valeurs extrêmes de 0 à 7,98. 348 larves de criocères ont été relevées dans 53 parcelles sur les 68, avec en moyenne 0,10 [0,07–0,13] larves par plante sur l'ensemble des parcelles (de 0 à 0,68). Les dégâts moyens dus aux criocères étaient de 2,11% [1,26–3,15] par plante, variant de 0 à 27,45%, 65 des 68 parcelles ayant subi des dégâts.

Le nombre de larves de criocères et le pourcentage de dégâts étaient significativement corrélés (Spearman, rho = 0,40, p < 0,001). Les abondances en pucerons s'avéraient significativement corrélées avec le nombre de larves de criocères (Spearman, rho = 0,35, p < 0,01), mais ne l'étaient pas avec le pourcentage de dégâts (Spearman, rho = -0,01, p = 0,92). Il n'y avait pas de relation entre les variables des ravageurs et le couvert total des adventices suivant des corrélations de Spearman (abondance des pucerons : rho = 0,06, p = 0,64 ; abondance des larves de criocères : rho = 0,08, p = 0,50 ; dégâts des criocères : rho = -0,14, p = 0,24).

Tableau 5 : Moyennes et IC à 95% des variables de rendement et de bioagresseurs entre groupes de pression phytosanitaire.

	Groupe fort IFT	Groupe faible IFT	U	*p*
Rendement (q·ha^{-1}) $^{(1)}$	76,10 [71,98-80,13]	53,63 [47,37-60,10]	1133	< 0,001
Couvert des adventices (%)	3,57 [1,61-6,54]	12,59 [7,19-19,14]	454	0,01
Abondance des pucerons (nb par plante)	0,49 [0,30-0,71]	1,00 [0,52-1,59]	527,5	0,42
Abondance des larves de criocères (nb par plante)	0,10 [0,06-0,14]	0,11 [0,07-0,15]	562,5	0,85
Dégâts des criocères (% par plante)	1,11 [0,79-1,49]	3,21 [1,53-5,30]	499,5	0,34

$^{(1)}$: Seules les valeurs des parcelles dans lesquelles les adventices ont été échantillonnées sont montrées

Entre les deux groupes de pression phytosanitaire, le rendement des parcelles à faible IFT (herbicides ou total) était systématiquement inférieur à celui du groupe à fort IFT (tests U de Mann-

Whitney, Tableau 5). À l'inverse, les adventices étaient plus abondantes en parcelles à faible IFT, mais les autres bioagresseurs présentaient des valeurs similaires entre groupes.

2.1.1. EFFET SUR LES PLANTES ADVENTICES

L'indice de *goodness of fit* du modèle PLS-PM décrivant les relations entre VL Adventices, Paysage 1 et 2, Pratiques et Production était de 0,55 (Figure 5). La Production était bien expliquée (R^2 = 0,63) par les VL Pratiques et Adventices, avec une corrélation positive des Pratiques (corr = 0,69) et négative des Adventices, non significative (corr = -0,20) quoique en limite de significativité (l'intervalle de confiance à 97,5% peut ainsi être soit légèrement inférieur soit supérieur à 0 lors de 1000 simulations par *bootstraps*). Pour leur part, les Adventices étaient relativement mal expliquées par le modèle (R^2 = 0,18) et étaient impactées significativement par les pratiques (corr = -0,40), tandis que les deux VL du paysage n'avaient que peu d'effet (corr = -0,10 et 0,07 pour Paysage 1 et 2 respectivement). Les Pratiques présentaient également un effet indirect sur le rendement de corr = 0,08, soit près de 12% de sa contribution totale.

Les principales VM participant à la formation de la VL Pratiques étaient les différents IFT et le nombre d'unités d'azote de fertilisation minérale.

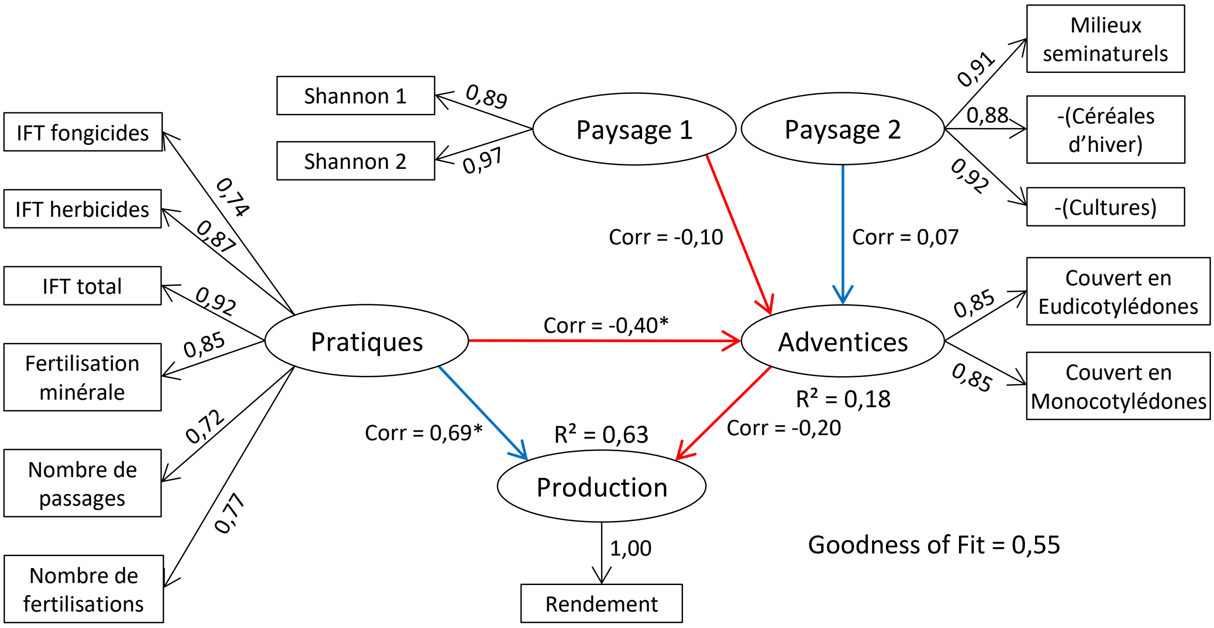

Figure 5 : Modèle de PLS-PM considérant les adventices décrivant les relations entre les variables latentes (VL) en culture de céréales.

n = 74, Corr représente la corrélation entre les différentes VL, les astérisques indiquant des valeurs significativement différentes de 0 basées sur l'intervalle de confiance à 95% calculé à partir de 1000 simulations par *bootstrap*. Le R^2 est le coefficient de la régression des VL endogènes par les VL exogènes associées. Les valeurs des flèches entre les VM et leur VL associée correspondent aux *loadings*.

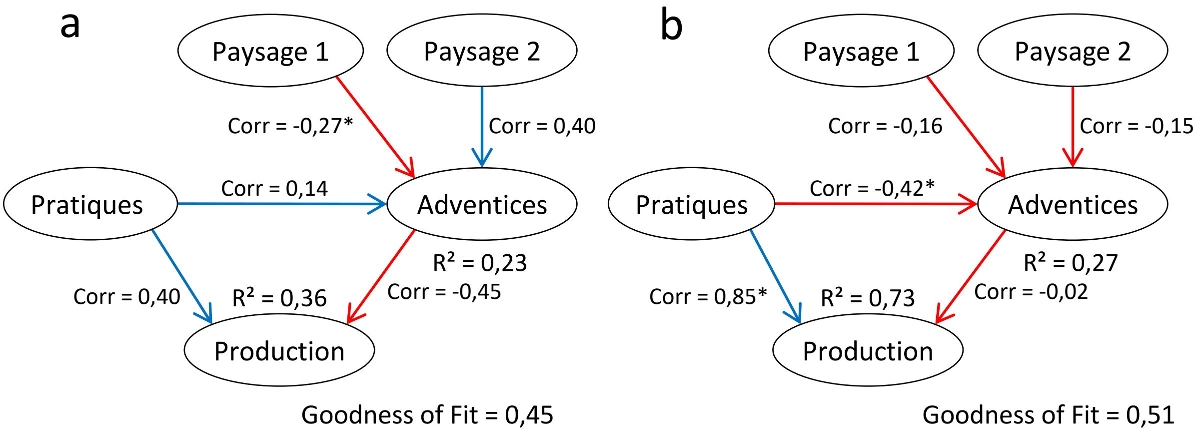

Figure 6 : Modèles PLS-PM considérant les adventices basés sur une sélection de parcelles en céréales suivant la médiane de l'IFT herbicides (1,39).
a : Parcelles à fort IFT herbicides, n = 37 ; b : parcelles à faible IFT herbicides, n = 37

Le modèle du groupe de forte pression phytosanitaire (Figure 6a) était moins prédictif que le modèle général (GoF de 0,45). Le score des Adventices était un peu mieux expliqué que dans le modèle général, avec R^2 = 0,23. Toutefois, le modèle prédisait beaucoup plus faiblement le rendement, à hauteur de 36%, tandis que le modèle général l'expliquait à 63%. Concernant les relations entre variables latentes, celles entre Pratiques vers les Adventices vers la Production ne s'avéraient plus significatives par rapport au modèle avec l'ensemble des parcelles. Mais contrairement au modèle général, les VL du paysage avaient une plus forte influence sur les Adventices : le Paysage 1 diminuait significativement l'abondance en adventices (corr = -0,27), tandis que le Paysage 2 présentait une forte influence (corr = 0,40), mais qui ne se révélait pas significative. Cette relation positive entre le Paysage 2 et les Adventices était principalement liée à une parcelle. Si cette dernière était retirée de l'analyse, la relation s'avérait négligeable (corr = 0,04, modèle complet non montré). La VM qui participait le plus à la construction de la VL Paysage 1 est l'indice de Shannon basé sur les parcelles en cultures annuelles (Shannon 1), ayant un poids de 0,61 contre 0,42 pour l'indice de Shannon des zones cultivées et semi-naturelles.

Le modèle du groupe de faible pression phytosanitaire (Figure 6b) présentait lui aussi un indice GoF plus faible que le modèle général, de 0,51. Néanmoins, la Production et les Adventices étaient mieux expliquées que dans le modèle complet, avec des coefficients de R^2 de 0,73 et 0,27 respectivement, contre 0,63 et 0,18. Ce modèle présentait les mêmes tendances que le modèle général quant aux effets des Pratiques sur les Adventices et la Production (corr = -0,42 et 0,85) qui étaient significatives. Là aussi, les VL du paysage n'influençaient pas significativement les Adventices (corr = -0,16 et -0,15), tandis que ces dernières avaient un effet négligeable sur la Production (corr = -0,02). Toutes les VM de la variable latente Pratiques avaient un poids comparable, mis à part le nombre de passages, qui n'était pas corrélé avec la VL (-0,02). Cela était notamment dû au fait que certaines parcelles en agriculture biologique ont fait l'objet d'un nombre important de désherbages mécaniques. Il est à noter qu'une parcelle en agriculture biologique présentait un fort couvert en adventices (76%) pour un rendement élevé pour ce type de gestion (55 $q \cdot ha^{-1}$ contre 34,67 $q \cdot ha^{-1}$ [30,38–39,06]). Sans cette parcelle, la relation Adventices/Rendement était significativement négative, avec corr = -0,18.

2.1.2. MODELES DES RAVAGEURS

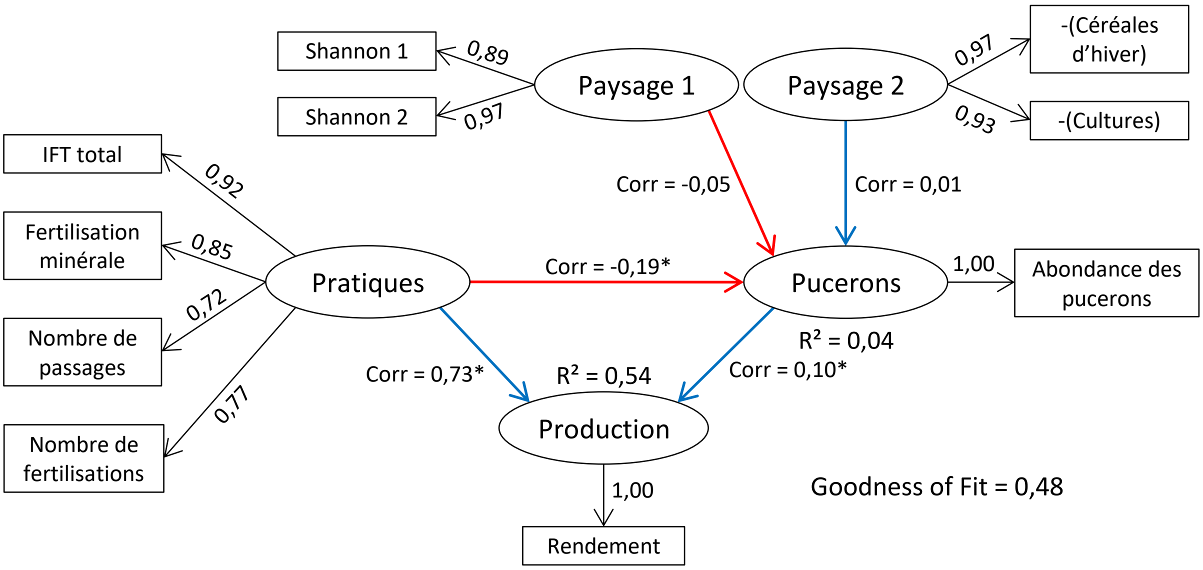

Figure 7 : Modèle de PLS-PM considérant les pucerons décrivant les relations entre les VL en culture de céréales.
n = 69.

L'indice de GoF du modèle PLS-PM intégrant l'abondance des pucerons était de 0,48 (Figure 7). L'explication de la variable Pucerons était très faible, avec un coefficient de R^2 de 0,04. Le R^2 de la Production s'avérait inférieur à celui du modèle général des adventices (0,54 contre 0,63). Les simulations par *bootstraps* ont permis de définir trois relations significatives : entre les Pratiques et les Pucerons et la Production (corr = -0,19 et 0,73) et entre les Pucerons et la Production (corr = 0,10). Les VL du paysage n'avaient quant à elles pas d'effet significatif sur les Pucerons. Les variables participant le plus à la construction de la VL Pratiques étaient l'IFT total et la quantité d'unités d'azote minéral (poids = 0,33 et 0,39 respectivement).

Les modèles des parcelles à fort et faible IFT total (basé sur la médiane = 2,98) ne permettaient pas d'obtenir une plus forte prédiction, avec des GoF de 0,32 pour les parcelles à fort pression et de 0,45 pour celles à faible (modèles complets non montrés). Les abondances de pucerons étaient néanmoins mieux expliqués dans le modèle de forte pression, mais étaient toujours faible, avec R^2 = 0,08. Le rendement était cependant beaucoup plus faiblement expliqué (R^2 = 0,18). Le modèle de faible pression ne permettait pas d'expliquer les abondances de pucerons, avec un coefficient R^2 inférieur à 0,01, mais présentait une meilleure prédiction de la production, de 58%. La seule relation significative pour chacun des deux modèles était l'effet des Pratiques sur la Production, avec une corrélation de 0,44 pour les parcelles à fort IFT et de 0,75 pour les parcelles à faible IFT. Ainsi, la séparation en deux groupes n'a pas permis de distinguer d'effet du paysage sur les pucerons.

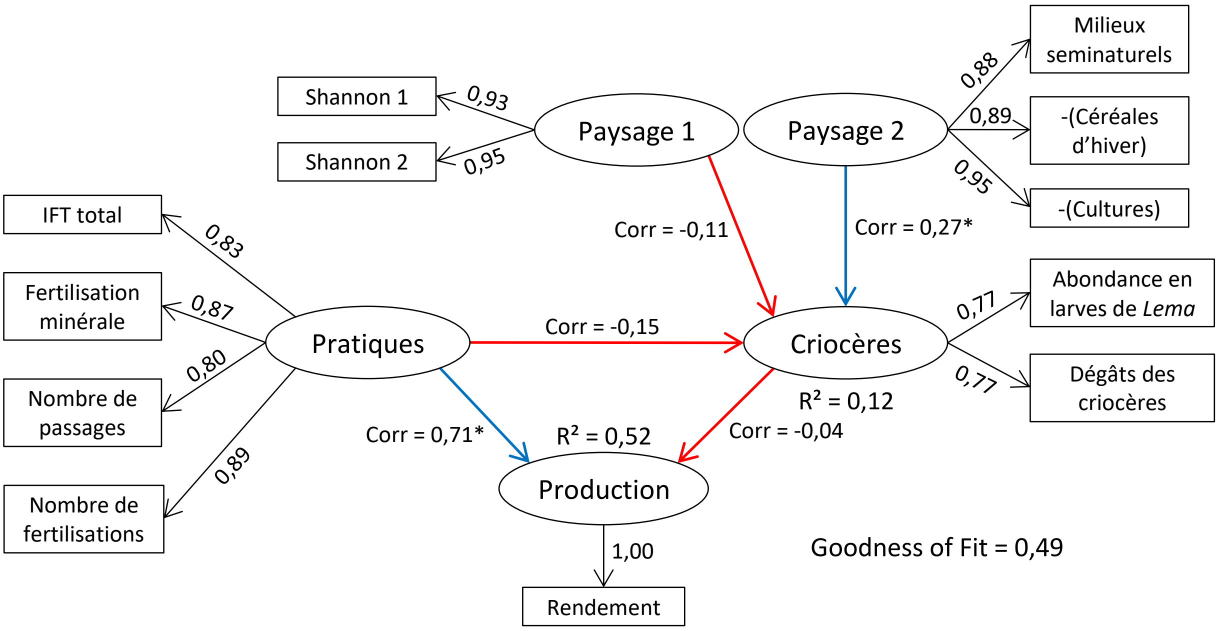

Figure 8 : Modèle de PLS-PM considérant les criocères décrivant les relations entre les VL en culture de céréales.
n = 68.

Le modèle intégrant l'abondance des larves de criocères et leurs dégâts présentait un indice de GoF de 0,49 (Figure 8). Le R² de la Production était similaire à celui du modèle des pucerons (0,52). Néanmoins, la VL Criocères était mieux expliquée, malgré le fait que le coefficient R² restait relativement faible (0,12). Deux relations étaient significatives : entre Pratiques et la Production (corr = 0,71) et entre le Paysage 2 et les Criocères (corr = 0,27). Les principales variables manifestes participant à la construction de la VL Pratiques étaient l'IFT total et la quantité en azote minéral, de façon similaire au modèle considérant les pucerons. La proportion en cultures (sous la forme 100-% en cultures) était quant à elle la principale variable de la VL Paysage 2, avec un poids de 0,43.

La séparation en deux groupes d'intensité de pression phytosanitaire (médiane IFT total = 2,99) n'a pas permis de dégager d'autres effets du paysage. D'autre part, la corrélation entre le Paysage 2 et les Criocères n'était plus significative dans chacun des sous-modèles, bien que la relation avait la même tendance que celle du modèle général. Cela pouvait être lié à la diminution du nombre d'échantillons par groupe, passant de 68 à 34 parcelles, limitant la puissance de détection de cet effet. Seule la relation entre Pratiques et Production était significative, avec une corrélation de 0,41 pour le modèle des parcelles à fort IFT et de 0,76 pour celui des parcelles à faible IFT (modèles complets non montrés).

2.2. RELATIONS EN CULTURES DE COLZA

Le rendement moyen de l'ensemble des parcelles (n = 40) était de 29,37 q·ha^{-1} [26,29–32,39]. Ces parcelles présentaient un couvert moyen en adventices de 11,86% [6,04–18,93], avec 6 parcelles n'en présentant pas. Les couverts en adventices Eudicotylédones et Monocotylédones étaient significativement corrélés (Spearman, rho = 0,38, $p = 0{,}02$).

Au sein des 26 parcelles dans lesquelles les ravageurs avaient été relevés, 22 avaient subi des dégâts pour un pourcentage moyen de siliques touchées de 7,86% [5,21–10,80], pour un rendement de 30,84 q·ha^{-1} [26,38–35,22]. Les dégâts et le couvert en adventices n'étaient pas corrélés (Spearman, rho = 0,02, $p = 0{,}91$)

Les deux groupes de pression phytosanitaire ne présentaient pas de différence significative de rendement suivant un test U de Mann-Whitney (U = 197, $p = 0{,}95$). Les parcelles à fort IFT avaient un rendement de 29,42 q·ha^{-1} [26,20–32,81] contre 29,32 q·ha^{-1} [24,19–34,23] pour les parcelles à faible IFT. Le couvert total en adventices n'était également pas différents entres groupes (Mann-Whitney, U = 219,5, *p* = 0,61), avec un recouvrement de 10,78% [4,10–21,13] en cas de fort IFT herbicides et de 12,94% [4,47–23,31] pour les parcelles à faible IFT.

2.2.1. EFFETS SUR LES ADVENTICES

En colza, le modèle PLS-PM avait un indice GoF de 0,45. Le coefficient de corrélation R^2 de la VL Production était de 0,40, tandis que la VL Adventices était peu expliquée (R^2 = 0,12). Ces valeurs s'avéraient inférieures à celles du modèle général des adventices en céréales (0,63 et 0,18). Deux relations étaient significatives, entre les Pratiques et les Adventices et les Adventices et la Production (Figure 9), avec des corrélations de 0,44 et -0,35 respectivement. Les variables du paysage influençaient peu les Adventices, avec des corrélations de 0,05 et -0,18. Contrairement au modèle en céréales d'hiver, l'IFT herbicides participait relativement peu à la variable latente Pratiques par rapport aux autres VM la composant (poids de 0,15 contre 0,23 à 0,27). D'autre part, les Pratiques augmentait indirectement le rendement à hauteur de corr = 0,11, soit environ 20% de la contribution totale de la VL.

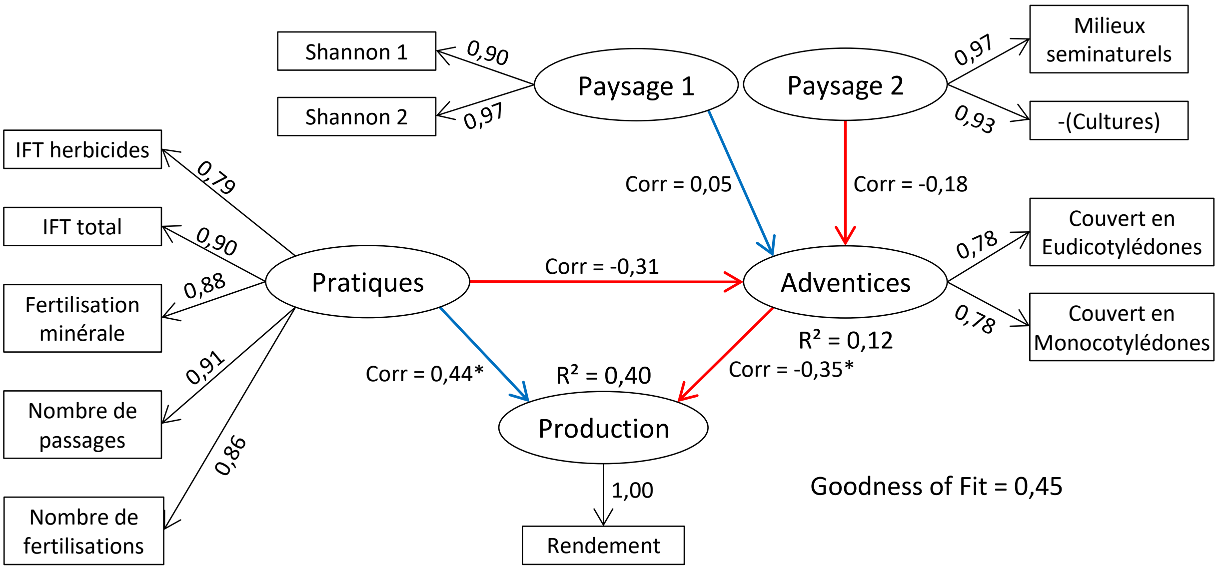

Figure 9 : Modèle de PLS-PM considérant les adventices décrivant les relations entre les VL en culture de colza.
n = 40.

Les modèles des groupes formés suivant la médiane de l'IFT en herbicides (1,59) présentaient des indices de GoF supérieurs au modèle général (Figure 10), avec GoF = 0,48 pour le modèles des parcelles à forte pression en herbicides et de 0,58 pour le modèles des parcelles à faible pression.

Le sous-modèle de forte pression permettait de bien mieux expliquer le couvert des adventices, avec R^2 = 0,35, tandis que le coefficient du rendement était similaire à celui du modèle général (Figure 10a). Ce modèle présentait un effet positif significatif des Pratiques sur la Production (corr = 0,62, Figure 10a), mais contrairement au modèle général, également positif sur les Adventices (corr = 0,61), tandis que les variables du paysage influençaient peu ces dernières (corr = -0,11 et 0,04). Les Adventices n'impactaient par contre plus la Production (corr = -0,02). Dans ce modèle, l'IFT herbicides ne participait pas à la construction de la VL Pratiques, avec un poids de -0,02. Les applications d'herbicides dans ces parcelles avaient également eu lieu en fin d'automne/début d'hiver.

Le modèle des parcelles à faible IFT herbicides présentait les mêmes tendances que le modèle général (Figure 10b). Les deux variables Production et Adventices étaient mieux expliquées que dans le modèle général, avec des R^2 de 0,59 et 0,30 respectivement. Les Pratiques avaient un effet significatif sur la Production et les Adventices (corr = 0,46 et -0,65) et ces dernières impactaient négativement la Production (corr = -0,43). Même si les VL du paysage n'affectaient pas significativement les adventices, le Paysage 1 présentait un effet bien plus important que dans le modèle général (corr = 0,34).

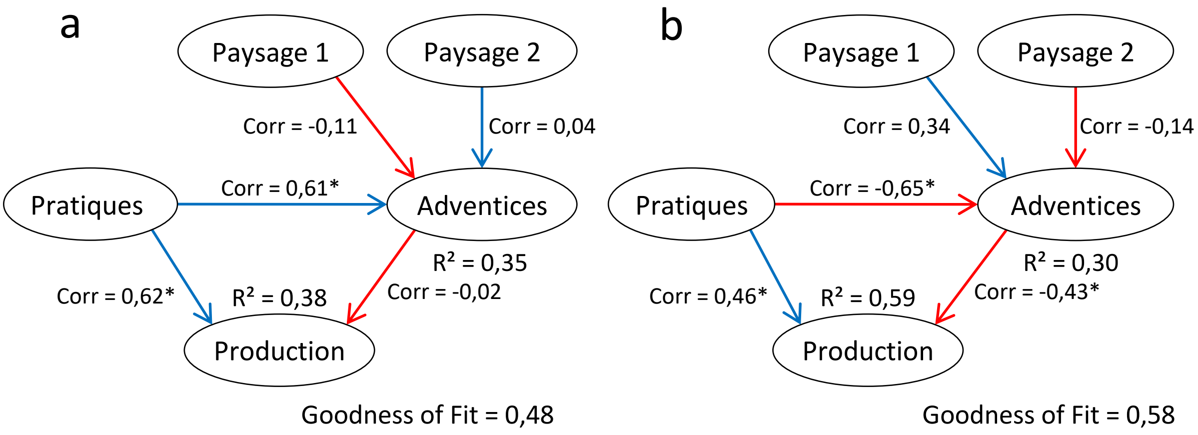

Figure 10 : Modèles PLS-PM considérant les adventices basés sur une sélection de parcelles en céréales suivant la médiane de l'IFT herbicides (1,59).
a : Parcelles à fort IFT herbicides, n = 20 ; b : parcelles à faible IFT herbicides n = 20.

2.2.2. MODELE DES DEGATS DES SILIQUES

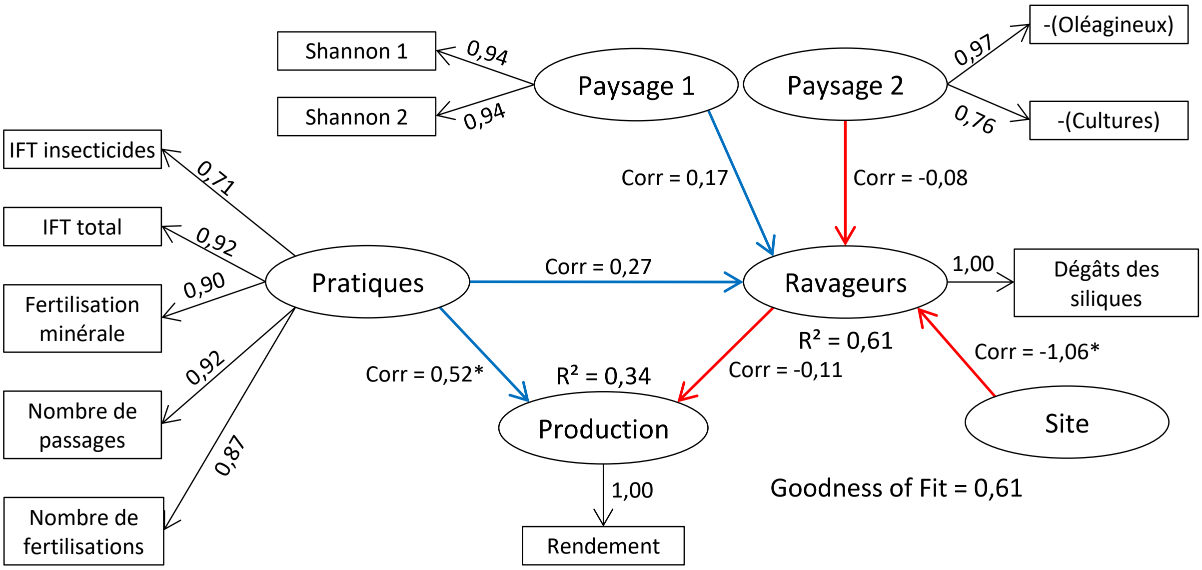

Figure 11 : Modèle de PLS-PM considérant les ravageurs (dégâts des siliques) décrivant les relations entre les VL en culture de colza.
n = 26.

Le modèle PSL-PM intégrant les dégâts des siliques permettait de fortement expliquer les dégâts, d'environ 61%, tandis que le coefficient R^2 de la production était légèrement plus faible que celui du modèle général des adventices ($R^2 = 0,34$, Figure 11). La relation entre les Pratiques et la Production était significative (corr = 0,55). Les dégâts étaient fortement liés au site (corr = -1,06), les parcelles de la zone d'Angers ayant été particulièrement touchées. Ces parcelles présentaient des siliques endommagées en moyenne de 12,16% [9,46–15,32] contre 0,99% [0,16–2,06] sur le site de Dijon (test de Mann-Whitney, U = 160, $p < 0,001$). L'ensemble des autres corrélations ne se sont pas révélées significatives et le paysage ne semblait pas impacter les dégâts.

L'ensemble des résultats des modèles PLS-PM a été résumé dans le Tableau 6

Tableau 6 : Récapitulatif des relations des modèles PLS-PM suivant le bioagresseur considéré

	GoF	R^2 Bioa	R^2 Prod	Bioa → Prod	Pra → Bioa	Pay 1 → Bioa	Pay 2 → Bioa	Pra → Prod
Adventices céréales	0,55 [0,45/0,51]	0,18 [0,23/0,27]	0,63 [0,36/0,73]	– NS	– / + * [NS]	– NS [*/NS]	+ / – NS	+ * [NS/*]
Adventices colza	0,45 [0,48/0,58]	0,12 [0,35/0,30]	0,40 [0,38/0,59]	– NS [NS/*]	– / + *	+ / – NS	– / + NS	+ *
Pucerons	0,47 [0,32/0,45]	0,04 [0,08/0,01]	0,54 [0,18/0,58]	+ * [NS]	– * [NS]	– / + NS	+ / – NS	+ *
Criocères	0,49 [0,34/0,49]	0,12 [0,13/0,10]	0,52 [0,19/0,57]	– NS	– NS	– NS	+ * [NS]	+ *
Dégâts des siliques	0,61	0,61	0,34	– NS	+ NS	+ NS	– NS	+ *

Indice de *goodness of fit* et R^2 des variables latentes Bioagresseurs et Production : modèle général [modèle fort IFT/modèle faible IFT].
Signe des effets suivant la relation considérée, avec en cas de multiples sens : signe du modèle général puis celui possible dans les modèles fort ou faible IFT et significativité.

3. DISCUSSION

Deux autres études menées en milieux agricoles ont utilisé l'approche PLS-PM : PUECH *et al.* (2015) et QUINIO (2016). La première a analysé les effets du paysage sur les communautés d'ennemis naturels (carabes, coccinelles et parasitoïdes de pucerons) et la seconde les effets de la gestion agricole sur les communautés de plantes adventices. Dans notre étude, les indices de *goodness of fit* des modèles généraux étaient d'un peu moins de 0,5 (Tableau 6). Ces valeurs semblent conformes voire supérieures à celles des études précédentes, avec GoF = 0,35 et 0,38 pour les modèles de PUECH *et al.* (2015) et de 0,44 pour le modèle principal de QUINIO (2016).

Toutefois, PUECH *et al.* (2015) avaient obtenus des coefficients de R^2 des communautés d'ennemis naturels de 0,35 à 0,40, contre des R^2 variant de 0,04 à 0,61 ici. Si le coefficient de détermination des dégâts des siliques était très important, il était principalement lié à un effet site. Les autres variables des bioagresseurs s'avéraient bien moins expliquées que les communautés d'auxiliaires. Cette différence pourrait être liée au fait que les ennemis naturels sont connus pour être plus sensibles à la structuration du paysage que les bioagresseurs (CHAPLIN-KRAMER *et al.*, 2011). Néanmoins, les coefficients de R^2 des couverts en adventices étaient supérieurs à ceux obtenus par QUINIO (2016) (0,04 contre 0,18 et 0,12 ici). Cette étude avait également étudié le rendement et avait trouvé un R^2 de 0,13, bien plus faible que ceux obtenus ici pour les modèles généraux (de 0,34 à 0,63).

Certaines variables d'importance pour les bioagresseurs n'ont toutefois pas été considérées dans cette étude, telles que la température ou les précipitations. Comme les échantillonnages ont eu lieu dans différentes régions et sur deux années, il est possible que le climat ou la pression des ravageurs à l'échelle régionale aient pu influencer l'abondance de ces derniers. Cela a pu limiter l'explication des variables des bioagresseurs, mais une variable de site et de l'année avait été intégrée aux différents modèles et ne s'était pas avérée significative.

3.1. INFLUENCE DES PRATIQUES SUR LE RENDEMENT ET LES BIOAGRESSEURS

L'effet direct de la gestion sur le rendement était souvent la relation la plus importante des modèles PSL-PM. Mais sa contribution totale au rendement pouvait être supérieure. L'hypothèse H1 est ainsi globalement confirmée : l'intensité de gestion permettait d'augmenter le rendement de façon directe, mais également dans certains cas indirectement *via* la limitation du couvert des adventices notamment. C'était le cas pour les modèles généraux, que ce soit pour les parcelles en céréales ou en colza. Cette contribution indirecte était de 12% de l'effet total des pratiques pour le modèle des adventices en céréales et de 20% pour celui en colza. L'effet indirect était néanmoins très limité pour les modèles des ravageurs. Les pratiques pouvaient ainsi permettre l'augmentation du rendement, probablement *via* la fertilisation ou les fongicides, tandis que les herbicides ont pu diminuer le couvert en adventices. Ainsi, ces produits devaient limiter l'abondance des plantes adventices de façon directe. Mais ces traitements phytosanitaires peuvent également diminuer la quantité de semences dans la banque de graines (JOSE-MARIA & SANS, 2011). L'application d'herbicides année après année pourrait ainsi conduire en une réduction du nombre de semences, limitant le nombre d'individus et ainsi le couvert les années suivantes (BALL, 1992). L'effet des herbicides pourrait de ce fait être soit direct avec une destruction de l'appareil végétatif, soit indirect dans le cas où une parcelle est traitée à chaque culture en appauvrissant la banque de graines.

Si les plantes adventices devaient être affectées par les herbicides, l'effet des pratiques sur les ravageurs est moins clair. Malgré le fait qu'il n'y avait aucune application d'insecticides en cultures de céréales, l'intensité de gestion impactait significativement les abondances en pucerons et tendaient à diminuer celles des criocères ainsi que leurs dégâts. Une telle relation pourrait-être due à des effets secondaires des autres pesticides utilisés, comme les fongicides et herbicides (NORRIS & KOGAN, 2000). Certaines voies métaboliques auraient ainsi pu être perturbées ou il pourrait s'agir d'un effet négatif subléthal, pouvant limiter la croissance des populations (GUEDES *et al.*, 2016). Toutefois, la gestion ne permettait pas de diminuer les dégâts en colza, voire avait tendance à les augmenter, malgré l'utilisation d'insecticides. Cela peut être dû au fait que ces parcelles pouvaient soient être traitées préventivement, soit de façon curative suivant les densités en ravageurs. De ce fait, une influence des pratiques pourrait être liée à une augmentation de l'utilisation des produits phytosanitaires en réaction à la présence des ravageurs, qui présenteraient de fait une abondance supérieure et auraient causé davantage de dégâts. Néanmoins, le caractère préventif ou curatif des traitements phytosanitaires n'a pu être pris en compte dans les analyses, comme il n'était pas connu pour certaines parcelles.

Les pratiques ont été considérées comme représentant un gradient continu. Néanmoins, les deux grandes typologies de gestion agricole, conventionnelle et biologique, ont des gestions très différentes, avec certains produits proscrits en agriculture biologique. Cela conduit à d'autres stratégies de contrôle des bioagresseurs, comme un plus grand nombre de travaux du sol. Il est alors possible que la comparaison d'un point de vue quantitatif de ces parcelles ne soit pas optimale. En effet, la plupart des études comparent l'effet de la gestion de façon factorielle (*cf.* WINQVIST *et al.*, 2011), mais cette catégorisation peut également être liée à la facilité de distinction de ces deux types d'agriculture, sans nécessiter le détail des pratiques.

3.2. IMPACT DES BIOAGRESSEURS SUR LE RENDEMENT

Globalement, le couvert des plantes adventices avait un impact négatif sur le rendement des parcelles, que ce soit en céréales ou en colza, ce qui confirme l'hypothèse H2 pour ce bioagresseur. Cette relation s'explique par la compétition entre adventices et culture pour les ressources en eau et en lumière, les besoins en nutriments pouvant être moins limitant du fait de la fertilisation minérale ou organique.

Si les adventices réduisaient globalement le rendement, l'impact des ravageurs était moins évident : s'ils tendaient à le diminuer, leurs effets étaient souvent peu prononcés. Cela peut venir du fait que certains ravageurs avaient été relativement peu présents et se situaient sous les seuils de nuisibilité, avec 0,10 criocères par plante pour un seuil de nuisibilité estimé à 2,5 et 0,74 pucerons par plante pour un seuil de 5 (ANONYME, 201X). Étonnamment, les modèles PLS-PM des pucerons montraient un effet positif de leur abondance sur le rendement. Il est possible que la corrélation doive être interprétée comme un effet de la production sur les pucerons, l'effet observé pouvant être lié à des facteurs confondants non pris en compte dans l'analyse. Cela pourrait notamment s'expliquer par une modification de la qualité nutritionnelle des plants de céréales suivant les apports en azote. Ainsi, plus une parcelle est intensive, plus la teneur en azote des plantes serait importante, augmentant par la suite la *fitness* des pucerons pour *in fine* augmenter leur abondance (JONSSON *et al.*, 2015). Cet effet avait été retrouvé dans d'autres études plus contrôlées, avec une augmentation de la fécondité des pucerons suivant l'application d'azote minéral (AQUEEL & LEATHER, 2011).

D'autre part, les abondances de bioagresseurs ont été relevées à un moment considéré comme optimal pour chaque taxon et qu'elles pouvaient être représentatives de l'infestation globale de la culture. Néanmoins, les populations de ravageurs peuvent varier, comme l'abondance des pucerons (BOMMARCO *et al.*, 2007; CHAPLIN-KRAMER *et al.*, 2013) et des larves de criocères (EVANS *et al.*, 2015). Les plantes adventices sont quant à elles sensibles aux dates d'application d'herbicides, qui diminuent leur couvert (ABU-DIEYEH & WATSON, 2007). Compte tenu de cette variabilité, il est possible que les abondances de bioagresseurs relevées ici ne soient pas exactement le reflet de l'infestation des parcelles durant leur mise en culture.

3.3. EFFET DU PAYSAGE

Notre hypothèse H3 était que la composition et l'organisation du paysage affectent les populations de bioagresseurs, avec des effets dépendants des espèces. Notre analyse montre que le paysage influençait globalement peu les abondances de bioagresseurs ou leurs dégâts. Le seul effet détecté sur les modèles généraux concernait les criocères. Leur abondance et leurs dégâts étaient ainsi augmentés par les milieux semi-naturels et, par extension, réduits par la proportion en céréales d'hiver et en cultures. Cela est cohérent avec la biologie de l'espèce la plus abondante généralement, *O. melanopus* (LINNAEUS, 1758). Celle-ci hiverne au stade adulte dans les zones boisées et zones faiblement gérées proches pour ensuite pondre des œufs dans des parcelles de céréales l'année suivante (REAY-JONES, 2010). Les milieux semi-naturels considérés ici semblent ainsi être propices à *O. melanopus*. Néanmoins, il s'avérait que la proportion en céréales d'hiver et celle en cultures participaient davantage à la formation de la variable latente de paysage. Cela dénoterait soit d'un effet de dilution des criocères, soit d'une plus faible abondance régionale du fait d'une plus forte intensité de gestion à cette échelle.

Peu d'études ont étudié l'effet du paysage sur les criocères, mais celle menée par TSCHUMI *et al.* (2015) n'avait pas trouvé d'effet de la proportion en éléments semi-naturel dans le paysage sur les abondances ou sur les dégâts. Néanmoins, cette étude avait considéré une échelle spatiale de 750m autour des parcelles, contre 565m ici, mais avait également analysé l'effet des bandes enherbées sur les criocères. Il s'avérait que ces structures diminuaient l'abondance des larves ainsi que les dégâts, que ce soit en bordure ou à l'intérieur des parcelles. Ces différences de réponse entre les résultats trouvés ici et l'étude de TSCHUMI *et al.* (2015) suggère que l'effet local de certains milieux puisse être différent de celui observé à une échelle régionale. Les milieux semi-naturels à une grande échelle permettraient la dispersion des adultes dans les parcelles de céréales, dépendamment de leurs capacités, tandis qu'à plus faible échelle, les ennemis naturels des criocères seraient favorisés, diminuant l'abondance des ravageurs.

Le fait que le paysage n'influençait pas les abondances de pucerons est en contradiction avec d'autres études ayant étudié ce groupe (AL HASSAN *et al.*, 2012; ALIGNIER *et al.*, 2014). Néanmoins, l'étude menée par ALIGNIER *et al.* (2014) montrait des effets contrastés de la proportion en prairies et en boisements, qui variaient suivant l'échelle spatiale considérée. Dans notre étude, il est possible que le regroupement des éléments semi-naturels (*i.e.* prairies, zones boisées et friches) camoufle un impact différencié de ces milieux. Néanmoins, MARTIN *et al.* (2015) avaient mis en évidence un effet positif de la proportion en milieux semi-naturels sur les abondances de pucerons en cultures de chou (*Brassica oleracea* var. *capitata*). Mais l'augmentation de la densité en ravageurs était néanmoins limitée par la prédation des ennemis naturels, aboutissant à un effet globalement neutre du paysage.

Cependant, les pucerons semblent sensibles au paysage à des échelles régionales qui interagissent avec la composition locale, ne permettant pas toujours la détection de relation (O'ROURKE *et al.*, 2011).

Plusieurs études ont mis en évidence un effet de dilution de la superficie en colza sur les dégâts et les abondances des ravageurs de cette culture (ZALLER *et al.*, 2008a; ZALLER *et al.*, 2008b). Cette relation n'a pas pu être observée dans cette étude, notamment du fait que les dégâts en colza étaient très différents entre les zones d'étude d'Angers et de Dijon. Une très forte variabilité régionale a ainsi pu masquer d'éventuels effets du paysage.

Concernant les communautés de plantes adventices, celles-ci peuvent présenter une importante diversité d'espèces vis-à-vis de leurs traits fonctionnels. Certaines espèces peuvent en effet être davantage impactées par la structure du paysage que d'autres (ALIGNIER *et al.*, 2012). La seule prise en compte du couvert pourrait être insuffisante pour distinguer des effets du paysage. Certaines espèces pourraient être favorisées par une structure ou composition donnée, tandis que d'autres seraient impactées négativement par ce même paysage. La description fine des communautés permettrait probablement de distinguer des effets variés du paysage sur chaque espèce. D'autre part, si les pratiques à l'échelle de la parcelle impactent le couvert en adventices, celles des parcelles adjacentes et au niveau paysager sont susceptibles de modifier la communauté (ALIGNIER *et al.*, 2013; HENCKEL *et al.*, 2015; PETIT *et al.*, 2016), et potentiellement le couvert suivant la compétitivité des espèces présentes.

Les taxons étudiés peuvent également présenter des capacités de dispersion variées, ne permettant peut être de distinguer un effet du paysage qu'à certaines échelles spatiales. Ainsi, le fait d'avoir caractérisé le paysage à 565m de rayon autour des parcelles pourrait empêcher la détection de certaines relations. En effet, certaines études mettent en évidence des effets à des échelles spatiales supérieures (CHAPLIN-KRAMER *et al.*, 2011). Pour les pucerons, il est même possible que les compositions à différentes échelles puissent interagir, avec un effet des parcelles adjacentes à la culture dépendant du contexte paysager à l'échelle régionale (O'ROURKE *et al.*, 2011). De ce fait, l'échelle considérée ici pourrait ne pas être optimale pour l'ensemble des bioagresseurs.

3.4. DES VARIATIONS SUIVANT LA GESTION ?

Nous avons émis l'hypothèse que les relations mises en évidence dans les modèles généraux pourraient potentiellement varier en fonction de l'intensité de la pression phytosanitaire exercée dans les parcelles étudiées. La distinction de groupes basés sur l'IFT (herbicides ou total) a permis de mettre en évidence des effets qui n'avaient pas été détectés dans les modèles généraux ou des différences dans les relations observées. Toutefois, ces résultats ne sont pas généralisables pour l'ensemble des bioagresseurs considérés ici, ou pour un même bioagresseur dans des cultures différentes. D'autre part, les comparaisons entre les modèles de « faible pression » et de forte pression se sont parfois révélées difficiles à interpréter.

Il s'avérait que les pratiques pouvaient augmenter le couvert des adventices, avec pour les groupes à fort IFT un effet non significatif en céréales, mais très fort en colza. Si la relation en céréales pouvait s'expliquer par la présence d'une parcelle à fort couvert en adventices, celle en colza était moins évidente. Néanmoins, pour cette culture, la plupart des parcelles étaient traitée par herbicides à l'installation, pouvant expliquer l'absence de corrélation entre l'IFT et le couvert. En effet, l'IFT herbicides ne participait pas à la formation de la variable latente Pratiques dans le modèle de ce groupe. Ce seraient ainsi les autres variables de gestion qui pourraient expliquer cette corrélation positive, comme la fertilisation.

Les effets des adventices sur les pertes de rendement pouvaient également dépendre de l'intensité de la gestion des parcelles et de la culture. En céréales, les adventices tendaient à réduire le rendement en cas de forte utilisation d'herbicides, tandis que l'effet était très limité pour les parcelles à faible IFT. Il aurait été attendu que les adventices puissent limiter le rendement principalement en cas de faible IFT, ces plantes étant plus abondantes dans ce groupe. Toutefois, une parcelle en agriculture biologique présentait un fort couvert en adventices, pour un rendement supérieur à la moyenne de ce type de gestion, modifiant la relation. En colza, le rendement était significativement réduit par le couvert en adventices dans le groupe à faible IFT, alors qu'il n'y avait pas d'effet dans le groupe à fort IFT.

La séparation des parcelles de céréales a permis la détection d'une relation négative entre la diversité du paysage et le couvert en adventices pour les parcelles à fort IFT. Ce résultat est en contradiction avec l'étude de BOHAN & HAUGHTON (2012) qui avait mis en évidence une augmentation de l'abondance des plantes adventices Eudicotylédones suivant le nombre de milieux adjacents aux parcelles. Cette différence pourrait s'expliquer par l'échelle spatiale utilisée. Dans leur étude, BOHAN & HAUGHTON (2012) ont considéré le nombre de catégories d'occupation du sol adjacentes aux parcelles étudiées, tandis qu'ici, la diversité paysagère a été exprimée *via* un indice de Shannon des parcelles 565m autour des parcelles. Cet effet négatif de la diversité du paysage sur le couvert des plantes adventices en céréales pourrait être indirect, *via* une augmentation de la prédation des carabes granivores notamment (TRICHARD *et al.*, 2013). Comme une plus forte gestion pourrait signifier un plus faible nombre de semences dans la banque de graines, cela permettrait éventuellement d'observer les effets de la prédation sur le couvert. En effet, la proportion de graines consommée par les carabes diminue suivant le nombre de semences disponibles (CARBONNE, 2015). Néanmoins, dans la plupart des modèles, l'analyse des groupes modifiait peu les relations entre variables latentes, voire certaines n'étaient plus significatives. Cela devait être lié à la réduction du nombre d'échantillons, limitant par là-même la puissance de détection d'un éventuel effet.

4. CONCLUSION

Comme cela était attendu, les principales variables impactant les populations de bioagresseurs sont les pratiques agricoles. Celles-ci conduisent généralement à une diminution de l'abondance des bioagresseurs, mais cette relation n'est pas systématique, laissant à penser que certains traitements peuvent ne pas être nécessaires. Pour leur part, les bioagresseurs n'ont pas d'effet extrêmement marqué sur la production, mises à part les plantes adventices qui la réduisent. L'intensité de gestion permet cependant d'augmenter les rendements, que ce soit directement ou indirectement *via* la réduction de l'abondance des bioagresseurs : une diminution de l'utilisation de produits phytosanitaires pourrait *in fine* limiter la production. Le paysage n'a quant à lui qu'un impact limité sur les bioagresseurs, pouvant augmenter leur abondance et dégâts dans le cas des criocères ou réduire le couvert en adventices en céréales en cas de forte pression phytosanitaire. Ces résultats ne permettent pas d'affirmer que le paysage pourrait palier à la diminution de l'usage de produits phytosanitaires en limitant les pertes de rendement. Néanmoins, la description du paysage réalisée ici pourrait ne pas avoir été optimale, notamment en termes d'échelle spatiale. D'autre part, l'utilisation de l'approche PLS-PM ne permet pas d'assigner avec certitude un effet propre aux variables manifestes, pouvant limiter le pouvoir de détection d'éventuelles relations.

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Projet ANR-12-AGRO-006

PEERLESS

Recommendations to optimize the wildflower strip approach

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Recommendations to optimize the wildflower stip approach in combination with different alternative cropping systems
Nature du livrable	Articles
Date	21/02/2018
	Version 4

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Partenaires impliqués	IGEPP, Agronomie, PSH
Tâche associée	Tâche 2, sous-tâche 2-1
Livrables associés	D2.2 et D4.3

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

The objectives of deliverable 2.1 are linked to one of the main objectives of task 2 "Evaluating the pest control service of sown wildflower strips". Based on existing literature and studies realised in the Peerless project, a new mixture was developed that combined high and long-lasting floral resource provisioning under different French climatic conditions. This mixture was tested against grass strips representing a cheaper alternative solution that was found to positively influence generalist predators in previous studies and that is sufficiently competitive to limit the spread of undesirable weed species. Spontaneously emerging vegetation was used as a control treatment. The deliverable objectives were:

- Testing the hypothesis that increased floral resource provisioning improves pest control compared with sown grass strips and spontaneous vegetation
- Evaluating whether potentially positive effects of margin strips are limited to the closest part of the crop field
- Analysing the consistence of regulatory effects at four different sites from NW to SE France

B.2 RESUME

Maximum 1 page en français.

In the multisite core experiment, the cover of flowering entomophilous plant species used as a proxy of floral resource provisioning was consistently higher in wildflower strips whereas differences between grass strips and spontaneous vegetation were not significant. In both tested crops wheat and oilseed rape, a corresponding higher abundance of hoverflies was observed in wildflower strips but also at a distance of 5m within the field whereas differences were not consistently significant at a distance of 30m from the field margin. Effects on other natural enemies and on aphid parasitism were not consistent at different sites. However, a

higher sentinel aphid predation was observed in and close to wildflower strips although the effect size was different between sites. At a part of the sites, higher predation resulted in lower aphid abundance confirming that regulatory effects associated with floral resource provisioning in field margins can be observed down to pest insects. For two test sites (Dijon, Grignon) further analyses is required to evaluate effects on other pest insect groups. At one test site (Avignon), wildflower strips were not planted to wheat/oilseed rape fields but to apple orchards. A complete set of data is available from the Angers/Rennes and Avignon sites. The results of these two sites are part of two separate manuscripts submitted for publication since the joined protocol was extended by several site specific analyses. The major findings are detailed in the following paragraphs.

The first manuscript (in revision) includes results from eight fields between Angers and Rennes obtained for oilseed rape (2014) and wheat (2015). Beyond the common protocol applied at all four sites, the attractiveness of sown and spontaneous plant species to natural enemies was tested by direct observation in the three different margin types. Natural enemy densities were generally higher within and close to wildflower strips within the field. A corresponding effect on aphid predation and aphid infestation was observed. Significant negative correlations between natural enemy abundance in the margin and aphid infestation in the fields confirmed a causal relationship. The sown wildflower strip species were more attractive to natural enemies than spontaneous vegetation. The results demonstrated that improved nectar provisioning increased the regulation of crop herbivores. Further research on spatio-temporal dynamics of interactions is needed to analyse why not all crop herbivores respond to an increase of natural enemies in field margins.

The second manuscript (submitted) details results for three experimental apple orchards in Avignon-Montfavet focussing on the regulation of *Dysaphis plantaginea* in 2014 and 2015. Only hoverflies responded positively to higher resource provisioning by wildflower strips whereas ladybird abundance did not differ between strip treatments. Within the orchards, the presence of parasitoids, hoverflies, and ladybirds in aphid colonies as well as the predation of sentinel aphids were not significantly affected by the adjacent strip treatments. The number of natural enemies observed in aphid colonies was mainly driven by aphid number. Aphid numbers were higher close to the margin strips suggesting that aphid colonization from orchard edges may counteract the positive effect of wildflower strips on natural enemy abundance and on a reduction of aphid infestation. The results confirm the positive influence of floral resource provisioning by wildflower strips on natural enemies within the wildflower strips but they also demonstrate that effects on regulation inside orchards are not always very strong compared with spontaneous vegetation naturally occurring in the margins. A summary of this manuscript was published in IOBC-WPRS Bulletin Vol. 122, 2017, p21-25.

Another study on effects of wildflower strips on pest insect regulation in apple orchards was co-funded by the Peerless project and published in Environmental Entomology (Albert et al. 2017). The study was set up in cider-apple orchards of Brittany and focused on the regulation of *Dysaphis plantaginea*, one of the major pests in European apple orchards. During two years (2014 and 2015), the population dynamics of *D. plantaginea*, its natural enemies and of mutualistic ants were analysed. The influence of the cider-apple cultivar, insecticide use, and distance to hedgerows and flower strips was assessed. The results suggest that flower strips favour natural enemy abundance in the vicinity of the orchards and reduced aphid infestation whereas hedgerows increase infestation due to a higher density of ants protecting aphids.

C PRÉSENTATION DES AVANCÉES

Quatre manuscrits sont annexés à ce livrable :

Pollier, A., Tricault, Y., Plantegenest, M., Bischoff A. (in revision) Sowing of margin strips rich in floral resources improves herbivore regulation in adjacent crop fields.

Odorizzi, L.A., Botelho Costa, M., Lavigne, C., Fernandes, O.A., Bischoff, A., Franck, P. (submitted) Influence of orchard margin vegetation on the control of rosy apple aphid and on the spatio-temporal of natural enemies.

Franck, P., Odorizzi, L.A., Botelho Costa, M., Lavigne, C., Fernandes, O.A., Bischoff, A. 2017 Impact of agro-ecological infrastructures on the control of insect pests in apple orchards. Working Group "Integrated Protection in Field Vegetables". IOBC-WPRS Bulletin 122, 21-25.

Albert, L., Franck, P., Yann, G., Plantegenest, M. (2017) Impact of agroecological infrastructures on the dynamics of *Dysaphis plantaginea* (Hemiptera: Aphididae) and its natural enemies in apple orchards in Northwestern France. Environmental Entomology, 46, 528–537

SOWING OF MARGIN STRIPS RICH IN FLORAL RESOURCES IMPROVES HERBIVORE REGULATION IN ADJACENT CROP FIELDS

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Abstract

1. Field margin vegetation provides resources for natural enemies of crop herbivores. Thus, the design of plant mixtures improving resource provisioning appears to be a promising approach to improve herbivore regulation.
2. We set up a field experiment to assess the effect of a wildflower strip optimised for nectar provisioning, a grass strip and spontaneous vegetation on regulation in oilseed rape and wheat. We also analysed the attractiveness of sown and spontaneous plant species to natural enemies.
3. The cover of entomophilous plant species as a proxy of floral resource provisioning was twice as high in wildflower strips as in the other strip treatments. Natural enemy densities were generally higher within and close to wildflower strips in the field. A corresponding effect on aphid predation and aphid infestation was observed. Significant negative correlations between natural enemy abundance in the margin and aphid infestation in the fields confirmed a causal relationship. The sown wildflower strip species were more attractive to natural enemies than spontaneous vegetation.
4. The results demonstrated that improved nectar provisioning increased the regulation of crop herbivores. Further research on spatio-temporal dynamics of interactions is needed to analyse why not all crop herbivores respond to an increase of natural enemies in field margins.

Key-words: ecosystem service, conservation biological control, plant-insect interactions, natural enemies, wildflower strip, spontaneous vegetation, grass strip

Introduction

Biological control of crop herbivores is an important ecosystem service provided by semi-natural habitats and related biodiversity (Fiedler et al., 2008). Such habitats provide shelter, overwintering sites and floral resources (pollen, nectar) for natural enemies of crop herbivores (Bianchi et al., 2006; Griffiths et al., 2008; Bischoff et al., 2016). Most of these habitat functions are related to the vegetation and its plant species composition. Floral resources may increase the fitness of several natural enemy groups such as hoverflies or parasitoids (Winkler et al., 2009; Araj and Wratten, 2015) resulting in an improvement of pest control efficiency (Blaauw and Isaacs, 2012; Balmer et al., 2014). Predators may also benefit from feeding on alternative prey occurring on field margin plants (Balzan et al., 2014). Such an attraction and resource provisioning to natural enemies by field margin vegetation may reduce herbivore infestation and damage in adjacent crop fields. Most studies on field margin effects have focused on natural enemies without taking into account herbivore infestation within fields (Chaplin-Kramer et al., 2011; Haaland et al., 2011). However, several authors found a positive plant diversity effect on within field regulation of herbivores (Pfiffner and Wyss, 2004; Dassou and Tixier, 2016). In particular, floral resources were shown to increase regulation and/or to reduce the crop damage caused by crop herbivores such as aphids or leave feeders (Bischoff et al., 2016). The potential reduction of crop herbivore abundance and damage by resource provisioning for natural enemies in field margins has resulted in different approaches to improve regulation service by a specific margin management (conservation biological control: Landis et al., 2000; Gurr et al., 2003). The most widespread approach is the use of seed mixtures to establish wildflower strips at the field edge that provide floral resources, shelter and alternative prey for natural enemies (Pfiffner and Wyss, 2004; Haaland et al., 2011; Tschumi et al., 2015). Many studies have confirmed that sown wildflower strips are efficient in increasing the diversity and abundance of natural enemies compared to neighbouring fields. However, few studies demonstrated a corresponding reduction of crop herbivores and their damage on crop plants (Pfiffner and Wyss, 2004; Tschumi et al., 2015). Wildflower strips may also provide resources for pest insects and thus increase crop damage (Koji et al., 2007). Despite an insufficient knowledge on regulation efficiency, sown flower strips have been developed and implemented in agri-environment schemes of several European countries in order to increase biodiversity of agro-ecosystems (Haaland et al., 2011). A second common conservation biological control approach relies on the sowing of grass strips, also known as beetle banks (Collins et al., 2002; Marshall and Moonen, 2002). Such strips provide less floral resources but generalist predators such as ground beetles, rove beetles and spiders may benefit from their shelter function (Collins et al., 2002). Grass strips reduce the spread of problematic weed species compared with spontaneous succession but allow an establishment of perennial herbaceous grassland vegetation (Cordeau et al., 2012) that may also contribute to crop herbivore regulation (Al Hassan et al., 2013). Since seed material comprises few grass and/or legume species – or is even monospecific - the sowing costs are much lower than for wildflower strips. In France, sowing grass strips is mandatory at the edges of crop fields adjacent to water bodies in order to prevent soil erosion and water pollution by fertilizer and pesticide runoff (Cordeau et al., 2012).

In our study, we compared three different field margin types in two successive winter crops. The first margin type was a wildflower strip optimised for floral resource provisioning. The mixture comprised species producing a high quality and quantity of nectar (Hicks et al., 2016), early and late flowering species as well as species with a long-lasting flowering period. Additionally, plant species providing extrafloral nectar which is easily accessible to parasitoids (Jamont et al., 2013; Heil, 2015) were included. The second margin type was a grass strip sown with two species. As a control we used spontaneous vegetation emerging from the soil seed bank. A previous study showed that spontaneous field margins rich in entomophilous flowering species provided an important biological control service without the need to sow expensive seed mixtures (Bischoff et al., 2016). We focused on herbivore regulation within crop fields and correlations between field and margin strip abundance. The main objective of this approach was to evaluate the final outcome of the trade-offs between (1) natural enemy and crop herbivore facilitation and (2) trapping of natural enemies by attractive margins and a spill over to adjacent crop fields. We address the following questions: (i) Do wildflower strips, grass strips and spontaneous vegetation differ in the attraction of natural enemies of crop herbivores? (ii) Does the attraction of natural enemies by field margin vegetation result in higher densities in the field? (iii) Do higher natural enemy densities in field margins result in a better crop herbivore regulation? (iv) Which plant species contribute to crop herbivore regulation?

Material and Methods

Study sites and experimental design

The study sites were located in the Maine-et-Loire and Ille-et-Vilaine, two departments of Western France. We monitored two crops in rotation: oilseed rape in 2014 and wheat in 2015 both sown as winter crops. We selected two taxonomically distant crops to evaluate whether our strip treatments have similar regulating effects on associated crop herbivores and their natural enemies. The study was set up in eight fields of which one was lost in the second year. Otherwise fields were the same in both years. In March 2014, three strip treatments were established in the margins of each of eight oilseed rape fields: (1) a wildflower strip mixture (WS) with 30 flowering vascular plant species (Table S1) optimised for amount and period of nectar production. Apart from nectar provisioning, the life cycle was considered to select plant species. Annuals, biennials and perennials were included to guarantee a sufficient cover in the first and subsequent years and to avoid expensive re-sowing; (2) a commercial grass strip mixture (GS) with the perennial grasses *Lolium perenne* (28%) and *Festuca arundinacea* (72%), a typical combination used in France to protect water bodies from pesticide and fertilizer runoff; (3) an unsown control strip allowing natural colonisation by spontaneous vegetation

(SV). The soil of all treatments was ploughed and harrowed prior to sowing. The strip area was 30m x 3m and the three treatments were randomly assigned to a 90m long field margin of each field.

Vegetation analysis

All vascular plants were recorded in a survey area of 20m x 3m in the centre of the margin strips. Percentage cover of each plant species was visually estimated as the vertical projection of all aboveground organs. At the same, the percentage of flowering plants was evaluated for each species. Survey dates were early June 2014 for oilseed rape and early and late June for wheat. The cover of flowering plants was calculated by multiplying plant cover and flowering percentage of all recorded plant species and adding these products.

Herbivores and natural enemies in field margins and crop fields

All crop herbivores, related damage, parasitism rate and natural enemies were recorded in the margin strips and in the field at a distance of 5 and 30m from the strips. The insect survey dates were close to the dates of the vegetation survey and corresponded to peak abundance and /or of major crop herbivores (aphids, cereal leaf beetles, weevil damage). The observation time was between 10 am and 4 pm under favourable weather conditions (sunny, not windy, no rain).

Oilseed rape was monitored in April and June 2014 at flower bud appearance and early fruiting. In each oilseed rape field and at each sampling date, 20 randomly chosen plants per distance were observed. At both survey dates, aphids (dominant species: *Brevicoryne brassicae*), adult parasitoids (dominant species: *Diaeretiella rapae* and *Tersilochus heterocerus*), hoverflies (Syrphidae sp., adults and larvae) and ladybugs (Coccinellidae sp., adults and larvae) were counted on each plant. In June, pod damage (yes/no) caused by fruit weevils (*Ceutorhynchus assimilis*) and pod midges (*Dasineura brassicae*) were additionally recorded on the main inflorescence. Pollen beetle (*Meligethes aeneus*) adults were captured and counted in April using a suction sampler (Stihl sh 86-d). Within margin strips, all flying and easily visible insects such as pollen beetles, adult parasitoids, ladybugs and hoverflies were first counted from outside the strip to avoid disturbance (observation time: 10 min, at both survey dates). Afterwards insects not visible from outside and less mobile such as aphids (all species), hoverfly and ladybug larvae were recorded in the strips.

Wheat was monitored twice in early and late June 2015 at stages of spikelet emergence and early milk ripening. In each wheat field and for each sampling date, fifty randomly chosen tillers per distance were observed. Cereal leaf beetles (*Oulema sp.*, larvae), cereal aphids (dominant species: *Sitobion avenae* and *Metopolophium dirhodum*), aphid mummies, parasitoids, ladybugs (adults and larvae) and hoverflies (adults and larvae) were counted on each tiller. Aphid mummies indicate parasitoid attack. Aphid parasitism rate was estimated by dividing the total number of mummies by the sum of aphid and mummy numbers. Within the margin strips, leaf beetle larvae, aphids (all species), parasitoids, ladybugs and hoverflies were counted at the same time as in the field. Counting method was the same as in the previous year for oilseed rape.

In both crops and in their margin strips, aphid predation was evaluated using bait aphids glued to sand paper (predation cards). In assuming that natural enemies and attack rates are similar to that of aphids attacking wheat and oilseed rape we used the commercially available pea aphid *Acyrthosiphon pisum* as sentinel prey. Predation cards were prepared by gluing three aphids on 5cm x 5cm black sand paper sheets. The cards were attached to the leaves of oilseed rape and wheat (height= 50cm), respectively. In June 2014 and 2015, we placed one card at each distance (within strips, 5m, 30m) and treatment resulting in a total of nine cards per field and 72 (63 in 2015) cards per crop. Aphid predation was evaluated after 24h. An aphid was considered as predated when damaged or missing.

Under each plant carrying a predation card, we placed a pitfall trap to analyse the abundance and diversity of carnivorous ground beetles in June 2014 and 2015. Trap content was sampled five days after placement to identify beetles to species level (Roger et al., 2012).

Attractiveness of margin plants

In order to evaluate the role of individual plant species in crop herbivore regulation, we counted aphids as the most abundant herbivore species and natural enemies in the margins of winter wheat fields in 2015. We first identified plant species that were visited by aphids, parasitoids, hoverflies or ladybugs. Then we counted insect numbers on all individuals of the selected plant species in each treatment and margin strip. We did not distinguish different aphid species since we were mainly interested in alternative prey provisioning. The counts included sown and spontaneously emerging plant species in order to evaluate the contribution of sown wildflower strip plants to herbivore regulation.

Data analysis

Plant species number (diversity) and cover of entomophilous flowering plants were analysed as a proxy of floral resource provisioning. The biolflor database (Klotz et al., 2002) was used to identify entomophilous plants. Only species flowering at the survey date were included in this category. Herbivores, herbivore damage, natural enemies and parasitism rates were included as response variables in the analyses if present in at least half of the treatment x field combinations (n=24). For response variables occurring at both survey dates, we used the date of highest abundance or damage. Only if this peak abundance was too low data of both survey dates were added (hoverfly and ladybug abundance).

We used generalized linear models (glmer function of lme4 package in R) to test the strip treatment effect on plant diversity, the cover of flowering entomophilous plant species, the diversity of flowering entomophilous plant species, the number of aphids, the aphid parasitism rate, the number and presence of natural enemies, aphid predation (predation cards) and ground beetle abundance. The basic statistical model included strip treatment as a fixed and field as a random effect. Analyses were run separately for the two crop species (wheat, oilseed rape) and the three distances (0m=within strips, 5m, 30m). Vegetation data and aphid parasitism were normally distributed and thus analyzed using a Gaussian distribution and identity link. For count data, we fitted a Poisson distribution with log-link function. When overdispersion was detected, models were fitted using a negative binomial error distribution. The glht function (multcomp package) was used to run multiple comparisons within significant effects.

We additionally tested the influence of herbivores and natural enemy abundances in the field margin on their abundances and damages within crop fields. Using generalised linear models (GLM, R MASS package) margin abundances were used as explanatory and field abundance as response variables. The distributions and link functions were the same as in the basic model. Descriptive statistics was used to compare the attractiveness of different plant species. In order to standardise plant abundance, the insect counts were divided by plant cover. All analyses were run in R, version 03.2.2 (R Development Core Team 2015).

Results

In both years, the number of plant species and the cover of flowering entomophilous species were significantly higher in wildflower strips than in spontaneous vegetation and in grass strips (Fig. 1). The most common spontaneously occurring plants were the grasses *Avena fatua, Bromus sterilis, Festuca arundinacea* and *Lolium perenne*, and the herbs *Chenopodium album* and *Polygonum aviculare*. Sown species represented 37.5% of the total vegetation cover in wildflower strips. The differences in species richness and the cover of entomophilous plants were not significant between spontaneous vegetation and grass strips. In wildflower strips, plant diversity and the cover of flowering entomophilous species increased from 2014 to 2015 corresponding to the development of the sown biennial and perennial species only developing and/or flowering from the second year on. In the other strip treatments, the number of plant species increased but not the cover of flowering entomophilous species.

In oilseed rape fields, the dominant crop herbivores were pollen beetles and aphids (Fig 2). Pollen beetle abundance was not significantly different between the strip treatments. Total aphid number including species not feeding on oilseed rape was higher in wildflower than in the other strips. In the crop field, cabbage aphid infestation was lower close to wildflower strips than close to the other strips. At a distance of 30m, aphid infestation was lower in the wildflower strip treatment than in the grass strip treatment. Aphid predation was higher in the wildflower strip treatment inside margins and at 5m than in other treatments whereas no significant differences occurred at 30m where predation was generally low. Hoverflies were the predominant aphid predators observed in the margin strips. Hoverfly density (larvae and adults) was significantly higher in wildflower strips than in the other strips. A similar difference was also observed at 5m in the crop fields (versus grass strips) as well as at 30m (versus wildflower strips). Ladybug abundance (larvae and adults) was not significantly different between strip treatments. Pod damage was only different at a distance of 30m being higher in the wildflower strip treatment. Carnivorous ground beetles were more abundant in and close to wildflower strips (5m) but at 30m, abundance was higher in the control treatment. Parasitoids as natural enemies of pollen beetles and aphids were less abundant close to wildflower strips at 5m. At 30 m, parasitoid abundance was higher in grass strips than in the control (SV) treatment whereas the difference to the wildflower strip treatment was not significant.

In wheat fields (Fig 3), leaf beetles and aphids were the major crop herbivores. Leaf beetle abundance differed at 30m only being higher in the control than in the grass strip treatment. Contrary to the previous year, total aphid abundance was highest in spontaneous vegetation. Close to the margin (5m), the number of cereal aphids was significantly lower in the wildflower strip treatment than in the control strip whereas at 30m cereal aphid infestation was highest in this treatment. Aphid parasitism was not different between treatments at 5m but highest in the wildflower strip treatment at 30m not explaining the aphid abundance patterns. Corresponding to cereal aphid abundance at 5m, aphid predation was higher in the wildflower strip treatment at 5m than in the grass strip treatment but at 30m no differences were found. However, within margins aphid predation was higher in grass strips than in wildflower strips. Hoverflies and ladybugs were the predominant aphid predators observed in the margin strips. Hoverfly density was significantly higher in wildflower strips treatments both within the strips and at a distance of 5m whereas no differences occurred between the two other treatments (SV and GS). Similar results were obtained for ladybugs showing a significantly higher abundance in the wildflower strip treatment. However, also differences between grass strips (lower abundance) and spontaneous vegetation were significant. Both predators showed no treatment effect at 30m inside the wheat fields. Carnivorous ground beetles occurred in higher numbers in the control with spontaneous vegetation whereas the treatment effect was not significant in the field.

Significant effects of insect abundance in field margins (pooled for treatments) on abundance in crop fields (herbivores and natural enemies) were only found at a distance of 5m (Tab 1). Aphid abundance was negatively influenced by parasitoid and ladybug abundance in margin strips indicating a positive effect of margins on aphid regulation. No correlations were observed between aphids of margin strips and cereal aphids in crops fields suggesting a limited exchange between margins and the field and/or a dominance of non-crop aphid species in the margins. Correlations between hoverfly abundance in field margins and in crops were not significant whereas ladybug abundance of margins and fields was positively correlated.

In wildflower strips adjacent to wheat fields, we found more aphids on spontaneously occurring species than on sown species (Fig 4). The relation is similar when standardised for plant cover indicating that species of the spontaneous vegetation are more attractive to aphids. Most aphids were found on four spontaneous species, *Vicia sativa* (Fabaceae), *Rumex obtusifolius*

(Polygonanceae), *Galium aparine* (Rubiaceae) and *Cirsium vulgare* (Asteraceae) and are thus not cereal aphids (Tab 2). The only host of cereal aphids was wheat (*Triticum aestivum*) accidentally sown into the margin or emerged as volunteer of previous crops. The three analysed natural enemy groups were more abundant on sown plants indicating that selection of plant species was successful in increasing regulatory potential. The difference was even greater when standardised for plant cover since spontaneous vegetation was more abundant than sown plants. Corrected for percentage cover, parasitoids were most attracted by the sown *Leucanthemum vulgare* and *Tanacetum vulgare*, and ladybugs by *Centaurea cyanus* (Asteraceae) and *Dactylis glomerata* (Poaceae). Hoverflies occurred on a higher number of sown than of spontaneous species but two spontaneous species, *Hypochaeris radicata* (Asteraceae) and *Holcus lanatus* (Poaceae), were the most attractive ones.

Discussion

According to our expectations, wildflower strips showed a higher plant diversity and cover of flowering entomophilous plants used as a proxy of floral resource provisioning. The differences were stable for the two study years demonstrating that the mixture of annual and perennial species was efficient without re-sowing and associated soil disturbance. No differences occurred between grass strips and spontaneous vegetation indicating that grass strips did not prevent the development of non-sown species in the first years (Cordeau et al., 2012).

Strip treatment effects on crop herbivores and natural enemies

In agreement with other studies, sown wildflower strips comprised a greater abundance of natural enemies than spontaneous vegetation and grass strips (Pfiffner and Wyss, 2004; Haaland et al., 2011). In particular, hoverflies occurred consistently (both years) in higher numbers in wildflower strips. It is well known that adult hoverflies rely on nectar resources (Wäckers, 2004; Fiedler et al., 2008). A better resource provisioning resulting in higher adult performance increases egg deposition and density of aphidophagous larvae in the field (Laubertie et al., 2012). In other natural enemies such as ground beetles and ladybugs, a positive effect of wildflower strips was only observed in the first year or in the second year, respectively. Both groups do not directly depend on floral resources. However, gut content analyses and observational studies on ladybugs have shown that adults and larvae also consume nectar and pollen contributing to fitness and predation performance (Triltsch, 1999; Ricci et al., 2005). Both ladybugs and ground beetles may have also been attracted by aphids feeding on flower stalks of entomophilous plant species (i.e. *Vicia sativa*) and representing alternative prey (Griffiths et al., 2008). A similar, clearly positive effect of entomophilous plant species on ladybug abundance has also been shown in a correlative study on spontaneous field margin vegetation in the same study area (Bischoff et al., 2016).

Inside the fields, a higher natural enemy abundance was observed close to wildflower strips than close to the other strip treatments at a distance of 5m. Higher densities of hoverflies (both years), ground beetles (2014) and ladybugs (2015) were also observed in the corresponding margins. The results suggest that the attraction of natural enemies by floral resources of field margins had a positive influence on natural enemy densities in the fields and that they are not trapped by more attractive field margin structures (associational resistance: Barbosa et al., 2009). However, the positive wildflower strip effect was not significant any more at a distance of 30m. Such a dilution of field margin resources effects on natural enemies was also observed in several other studies (Collins et al., 2002; Tylianakis et al., 2004).

Effects on crop herbivore abundance and predation corresponded in several cases to natural enemy responses to the strip treatment. In oilseed rape (first year), aphid predation was higher in wildflower strips and at a distance of 5m to these strips, according to a higher hoverfly and ground beetle density. Corresponding to this higher predation, cabbage aphid abundance was always lowest in the wildflower strip treatment at a distance of 5m and 30m. Aphid abundance in the strips did not show such pattern but it has to be taken into account that the majority of aphids counted in the strips do not attack oilseed rape. This is one of the first studies demonstrating a positive effect of wildflower strips on natural enemies, predation rates and aphid abundance in the same field experiment. Similar results for cereal leaf beetles and natural enemies were found (Tschumi et al., 2015, 2016), but they compared wildflower strips with cereal strips as control treatment.

Compared with cabbage aphids in oilseed rape, the wildflower strip effects on cereal aphid regulation in wheat (second year) were less strong but still visible. The positive effect of the wildflower strip treatment on ladybugs and hoverflies resulted in a higher predation but only at a distance of 5m. There was no corresponding effect on cereal aphid abundance suggesting that other factors had a stronger influence on aphid populations. Such a lack of crop herbivore response to an increase of natural enemies and predation rates close to semi-natural habitats seems to be quite common in agro-ecosystems (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Haaland et al., 2011). For example, the proportion of non-crop areas in agricultural landscapes may increase aphid parasitism without reducing aphid densities (Le Guigo et al., 2011).

Similarly, we did not observe consistent treatment effects for other dominant crop herbivores of oilseed rape and wheat. In particular, pollen beetle density as a major oilseed rape herbivore was not influenced by the treatments. Several studies have shown that the high mobility of the beetles increase the importance of large-scale landscape structure compared with relatively small-scale features such as margin strips (Thies et al., 2003; Zaller et al., 2008). Apart from aphids, leaf beetles were the second major crop herbivores in winter wheat. In contrast to (Tschumi et al., 2015), we did not find any evidence for a positive wildflower strip effect on cereal leaf beetle regulation. The magnitude of treatment effects on natural enemies may not have been sufficient to decrease leaf beetle density or the regulatory effect may have been compensated by positive wildflower strip effects on leaf beetles. Cereal leaf beetles also feed on wild grass species and they use semi-natural habitats for overwintering (Evans et al., 2013).

Interactions between strip and crop populations

Comparisons of margin strip and field abundance depend on temporal and spatial dynamics. High mobility may increase spatial scales of interactions between field and non-crop structures beyond field margins as already discussed for pollen beetles (Thies et al., 2003; Zaller et al., 2008). The spread from margins into the field may take some time and after migration into the field insect populations may decline in the margin strips (Collins et al., 2002) for ground beetles) diluting correlations between margin and field abundances. Additionally, the energetic costs of movements and the relative attractiveness of margins may prevent natural enemies from moving into the field (Heimpel and Jervis, 2005; Wanner et al., 2006). In our study, we found a positive correlation between field (at 5m) and margin abundance of ladybugs and a negative correlation between cereal aphid field abundance and margin abundance of ladybugs. The result fits well to the observed positive effect of the wildflower strip treatment on margin and field abundance of ladybugs, on corresponding aphid predation and on a lower aphid abundance in the field (at 5m) confirming a causal relationship between increase of natural enemy and decrease of the crop herbivore population. No correlations were observed between parasitoid abundance and aphid parasitism. There is a time lag of about two weeks between parasitoid attack and mummy development (Le Guigo et al., 2011). It is thus possible that parasitoids that moved from the margins into the field to attack aphids did not occur any more in the field margins when mummies were visible. Relationships between hoverfly populations of margins and fields, and between hoverflies and aphids were not significant suggesting that margins had a relatively small influence on aphid regulation by hoverflies. Hoverflies are highly mobile and their field abundance may not that strongly influenced by field margins (Wratten et al., 2003). However, the consistently higher hoverfly abundance in wildflower strips and at a distance of

5m compared with grass strips and spontaneous vegetation still indicates an influence of margins on hoverfly field populations.

Attractiveness of sown and spontaneous species

In our study, plants used in the wildflower strip mixture were more attractive for the three tested natural enemy groups (hoverflies, ladybugs, parasitoids) than the spontaneous vegetation emerging from the soil seed bank. Thus, our approach to select plant species improving floral resource provisioning was successful in increasing the regulatory potential of the strips. The study highlights the importance of pollen and nectar as resources for natural enemies of crop herbivores also observed in other studies (Wäckers et al., 2005; Wäckers and van Rijn, 2012). In particular, parasitoid abundance was much higher on sown plants. Parasitoids were mainly attracted by the Asteraceae species *Leucanthemum vulgare*, *Tanacetum vulgare* and *Centaurea cyanus*. Their flowers are known to be accessible to parasitoids that have only short mouthparts limiting access to deep flowers with long corollas (Patt et al., 1997; Williams and Hendrix, 2008). *Centaurea cyanus* additionally produces extrafloral nectar easily exploitable by parasitoids (Balzan et al., 2014; Pollier et al., 2016). However, spontaneously occurring species also hosted high numbers of natural enemies. The spontaneous *Hypochaeris radicata* and *Holcus lanatus* showed a higher hoverfly abundance than any of the sown species. *Holcus lanatus* is a grass species not providing any nectar. The high attractiveness may result from pollen provisioning as a second important floral resource (Laubertie et al., 2012) or by the presence of alternative hosts attracting adults for egg deposition. The role of alternative hosts was confirmed by the attraction of ladybugs on a sown grass species *Dactylis glomerata*. Although sometimes feeding on pollen and nectar (Ricci et al., 2005), the high abundance of ladybugs on grass species is more likely the result of alternative host provisioning or other habitat functions (Griffiths et al., 2008). The aphids observed in high numbers on spontaneous plant species also represent alternative hosts not attacking crops. Cereal aphids are specialised on grass species (Poaceae) and cabbage aphids on Brassicaceae (Le Guigo et al., 2012; Evans et al., 2013) both not hosting aphids in our field margins (except for several wheat plants as contaminants). The most attractive plant species for aphids was *Rumex obtusifolius*, a problematic grassland weed. As grass species it is wind pollinated and does not provide any nectar (Cavers and Harper, 1964).

Conclusions

Our study demonstrated that the approach to increase floral resource provisioning by sowing plant species that produce a high quantity and quality of nectar and pollen was successful in attracting natural enemies of crop herbivores. For aphids, the only major crop herbivore group occurring in both tested crops, a corresponding regulatory effect was confirmed down to aphid predation and aphid infestation in the field at least at a distance of 5m from the margin strips. Such efficiency in regulation has rarely been demonstrated so far since most studies on wildflower strips have been limited to natural enemies or have not shown any significant effect on herbivores (Haaland et al., 2011). The negative correlations between natural enemy abundance in margin strips and aphid abundance in the field confirmed the causal relationship between natural enemy attraction by floral resources of the margins and biological control. However, several major crop herbivores did not respond to our treatments despite an increase of natural enemy abundance in wildflower strips. Such an absence of crop herbivore response suggests that other factors than natural enemy abundance determine herbivore population dynamics (Thies et al., 2005; Chaplin-Kramer et al., 2011; Haaland et al., 2011). Further research is needed on regulatory effects down to crop herbivore level and on natural enemy movements between fields and margins, in order to evaluate the potential contribution of field margin management to the control of crop herbivores in the field.

Grass strips did not improve regulation service of margins. Natural enemy densities were in general lower than in wildflower strips and sometimes even lower than in spontaneous vegetation with a corresponding absence of crop herbivore regulation. The more positive evaluation of grass strips in other studies (Collins et al., 2002; Al Hassan et al., 2013) was probably the result of using the complete absence of margin strips as a control. The use of less attractive control treatments (absence of vegetation, crop strips) may also be the reason for stronger effects of wildflower strips on crop herbivore regulation occasionally observed in other studies (Haaland et al., 2011; Tschumi et al., 2015; Hatt et al., 2017). However, we believe that an efficient ecological engineering approach such as wildflower strip sowing needs to demonstrate a better regulatory effect than spontaneous vegetation not requiring any sowing or preparation costs.

Acknowledgements

We thank E. Chenu and F. Braud for their technical assistance and T. Sollet and S. Le Barazer for their help in the field. We also thank all farmers who participated in our study for hospitality and information provided. The project was funded by the French National Research Agency (ANR-12-AGRO-0006, “PEERLESS”) and the chair Ecologically Intensive Agriculture (AEI).

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Tables

Table 1: Relations between crop herbivores and natural enemies observed in field margins (explanatory variables, lines) and in wheat fields at a distance of 5 and 30m from field margins (response variables, columns) in 2015. Estimates and significance levels of explanatory variables are presented for the GLM model. P<0.1 **.** P<0.05 * P<0.01 ** P<0.001 ***, ns: not significant. - : not analysed.

a) Field 5m

Field margin	Cereal aphids	Hoverflies	Ladybugs	Aphid parasitism
Parasitoids	-0.214**.**	-	-	ns
Total aphids	ns	ns	ns	ns
Hoverflies	ns	ns	-	-
Ladybugs	-0.542*	ns	0.577*	-

b) Field 30m

Field margin	Cereal aphids	Hoverflies	Ladybugs	Aphid parasitism
Parasitoids	ns	-	-	ns
Total aphids	ns	ns	ns	ns
Hoverflies	ns	ns	-	-
Ladybugs	ns	-	ns	-

Table 2: Aphid abundance standardised for total vegetation cover (%) and natural enemy abundance standardised for the cover of flowering plants (%) of wildflower strips observed in June 2015 (means +/-SD).

	Plant species	Aphids	Parasitoids	Hoverflies	Ladybugs	Species cover
Sown species	*Achillea millefolium*	0	0	0.14(+/-0.05)	0	1.59(+/-0.27)
	Centaurea cyanus	0	0.71(+/-0.27)	0.14(+/-0.05)	0.14(+/-0.05)	0.29(+/-0.07)
	Dactylis glomerata	0	0	0	0.57(+/-0.22)	8.36(+/-1.15)
	Echium vulgare	0	0	0.05(+/-0.02)	0	1.31(+/-0.17)
	Heracleum sphondylium	0	0.14(+/-0.05)	0.09(+/-0.03)	0	0.71(+/-0.27)
	Hesperis matronalis	0	0	0.01(+/-0.01)	0	3.09 (+/-0.78)
	Leucanthemum vulgare	0	2.98(+/-1.07)	0.03(+/-0.01)	0	9.59(+/-1.24)
	Malva sylvestris	0.09 (+/-0.04)	0	0.33(+/-0.11)	0	1.72(+/-0.19)
	Matricaria recutita	0	0	0.04(+/-0.01)	0	0.74 (+/-0.21)
	Tanacetum vulgare	0	1.43(+/-0.54)	0	0	1.87(+/-0.29)
	Trifolium pratense	0.57 (+/-0.22)	0	0	0	2.9(+/-0.77)
	Trifolium repens	0	0	0	0.01(+/-0.01)	4.93(+/-0.79)
Spontaneous species	*Ammi majus*	0	0.09(+/-0.04)	0	0	0.43(+/-0.16)
	Cirsium vulgare	11.14 (+/-2.14)	0	0	0	1.07 (+/-0.13)
	Euphorbia helioscopia	0	0	0.07(+/-0.03)	0	0.57(+/-0.14)
	Galium aparine	12.57(+/-4.75)	0	0	0	0.51(+/-0.11)
	Holcus lanatus	0	0	1.43(+/-0.54)	0	3.59(+/-1.35)
	Hypochaeris radicata	0	0	2.86(+/-1.08)	0	0.46(+/-0.07)
	Ranunculus repens	0	0	0.05(+/-0.02)	0	2.57(+/-0.8)
	Raphanus raphanistrum	0	0	0	0	0.07(+/-0.03)
	Rumex obtusifolius	15.26(+/-4.08)	0.03(+/-0.01)	0	0.05(+/-0.02)	2.14(+/-0.42)
	Triticum aestivum	1.71(+/-0.65)	0	0	0	0.29(+/-0.07)
	Verbascum thapsus	2.14(+/-0.81)	0	0.07(+/-0.03)	0	0.43(+/-0.11)
	Vicia sativa	22.49(+/-6.09)	0	0	0.06(+/-0.02)	1.66(+/-0.33)

Figure legends

Figure 1: Mean (±SE) number of plant species and percentage cover of entomophilous plants of three field margin types in 2014 (left, oilseed rape) and 2015 (right, winter wheat). WS, wildflower strip; SV, spontaneous vegetation; GS, grass strip; $P<0.05$ (glmer model).

Figure 2: Oilseed rape 2014: pod damage, number of pollen beetles, aphids, parasitoids (adults), hoverflies and ladybugs (larvae and adults), aphid predation (per card), and carnivorous ground beetle abundance (per pitfall trap) within strips and at a distance of 5m and 30m in the field. Abundance in the field was measured in a line of 20 oilseed rape plants per distance. WS, wildflower strip; SV, spontaneous vegetation; GS, grass strip; means ± SD; different letters indicate significant differences with $P<0.05$ (glmer model). **-** : not analyzed.

Figure 3: Winter wheat 2015, number of leaf beetle larvae, aphids, hoverflies and ladybugs (larvae and adults), aphid parasitism, aphid predation (pre card), and carnivorous ground beetle abundance in (per pitfall trap) within strips and at a distance of 5m and 30m in the field. Abundance in the field was measured in a line of 50 wheat plants per distance (one tiller per plant). WS, wildflower strip; SV, spontaneous vegetation; GS, grass strip; means ± SD; different letters indicate significant differences with $P<0.05$ (glmer model). **-** : not analyzed.

Figure 4: Attractiveness of sown and spontaneous species to herbivores and natural enemies in wildflower strips (June 2015). A) Mean number (± SD) of aphids and natural enemies per plot and B) mean number (± SD) of aphids corrected for total cover of each group (sown, spontaneous) and natural enemy abundance corrected for cover of flowering plants.

Figures

Figure 1:

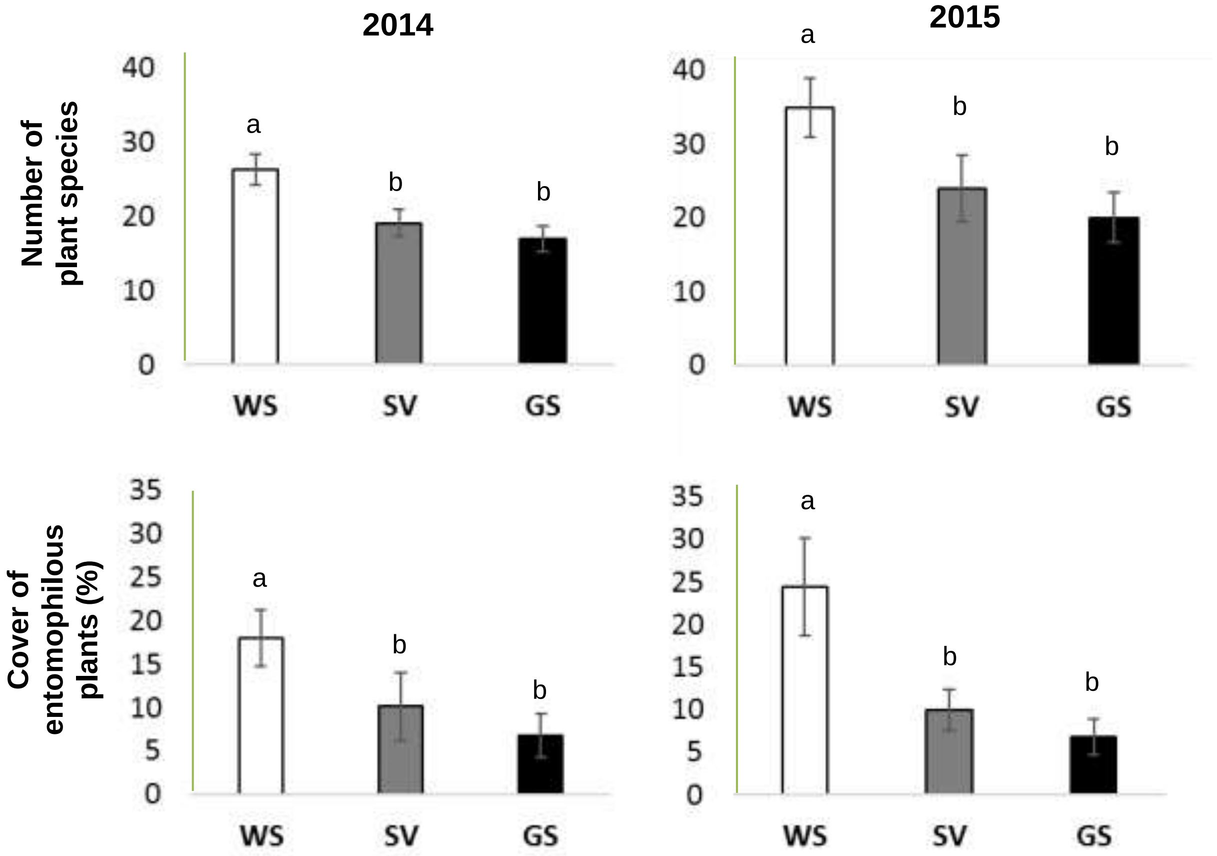


Figure 2:

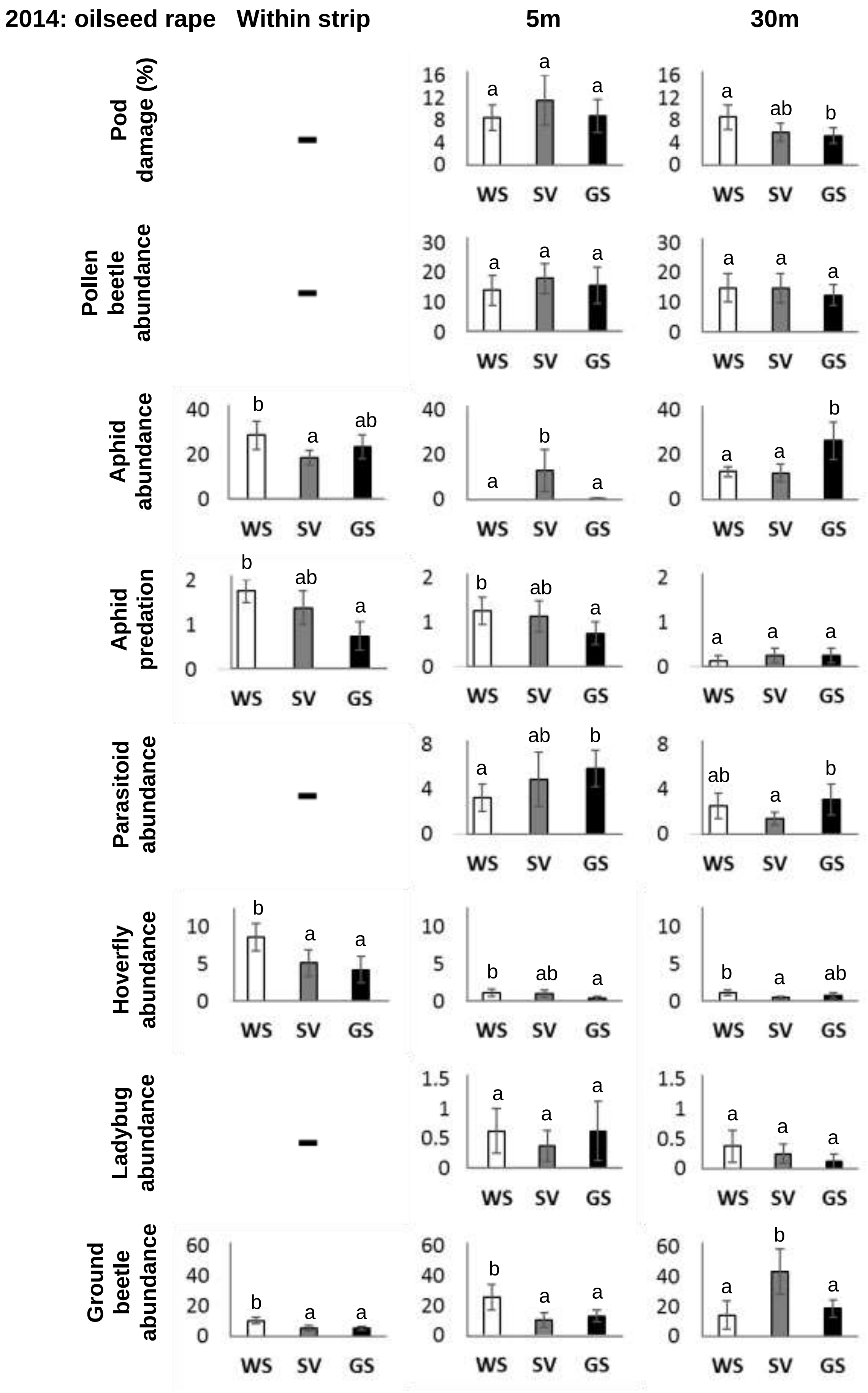

2014: oilseed rape
Within strip
5m
30m
Pod damage (%)
Pollen beetle abundance
Aphid abundance
Aphid predation
Parasitoid abundance
Hoverfly abundance
Ladybug abundance
Ground beetle abundance
–
WS
SV
GS
a
ab
b
0
4
8
12
16
10
20
30
40
1
2
5
0.5
1.5
60

Figure 3:

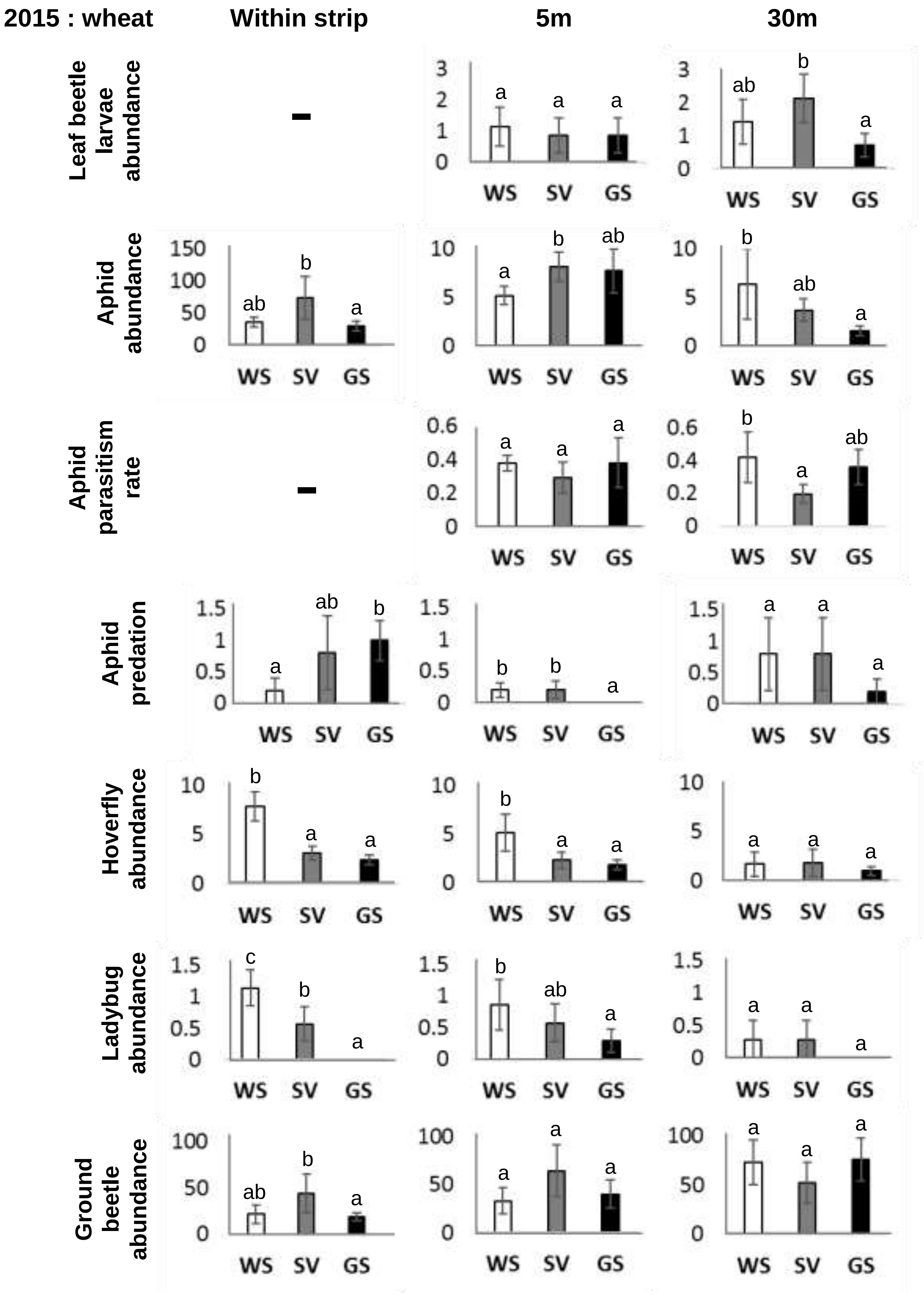
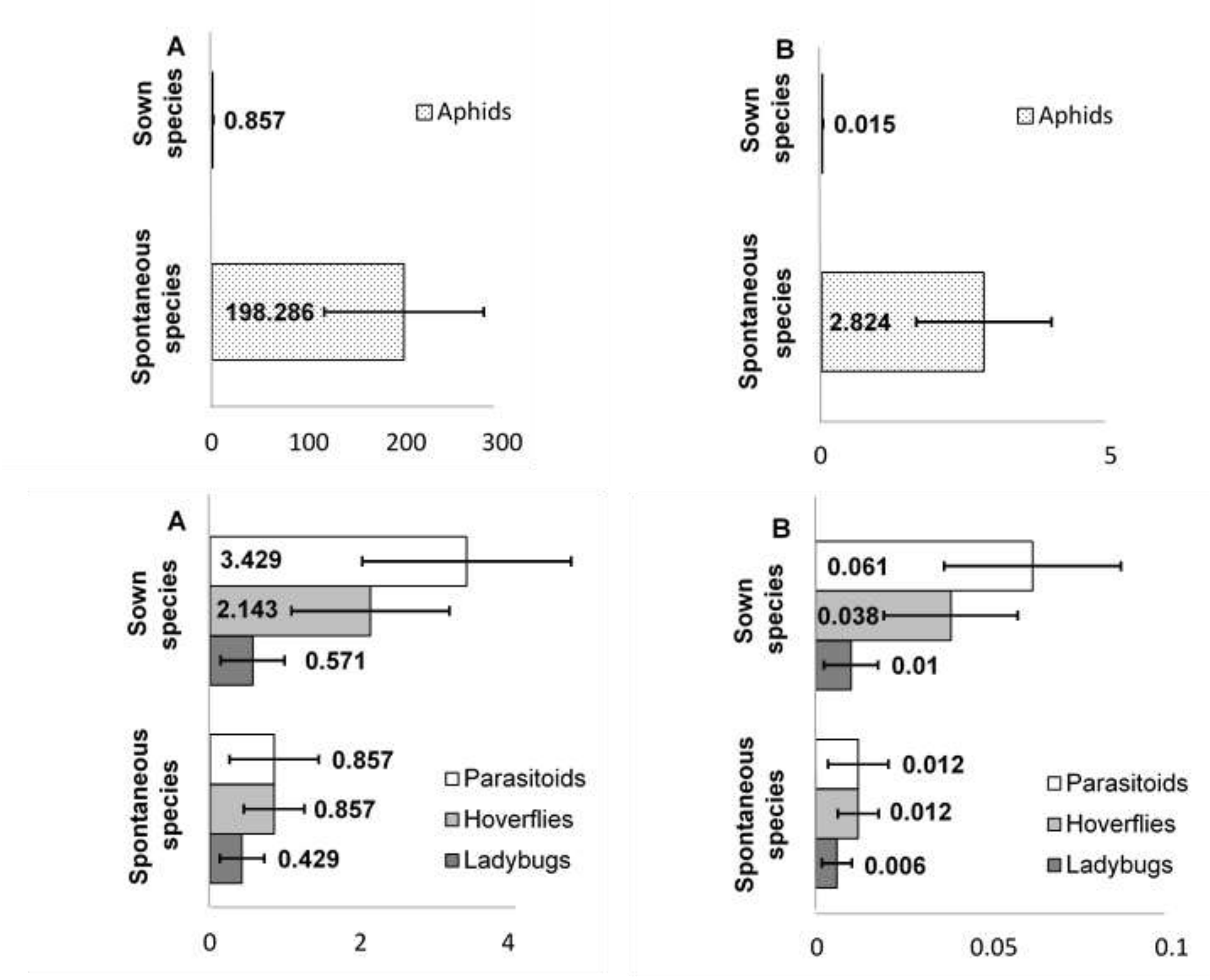

2015 : wheat
Within strip
5m
30m
Leaf beetle larvae abundance
-
3
2
1
0
a
a
a
WS
SV
GS
ab
b
a
Aphid abundance
150
100
50
0
ab
b
a
10
5
0
a
b
ab
b
ab
a
Aphid parasitism rate
-
0.6
0.4
0.2
0
a
a
a
b
a
ab
Aphid predation
1.5
1
0.5
0
a
ab
b
b
b
a
a
a
a
Hoverfly abundance
10
5
0
b
a
a
b
a
a
a
a
a
Ladybug abundance
1.5
1
0.5
0
c
b
a
b
ab
a
a
a
a
Ground beetle abundance
100
50
0
ab
b
a
a
a
a
a
a
a

Figure 4:


A
Sown species
Spontaneous species
0.857
198.286
▨Aphids
0
100
200
300
B
Sown species
Spontaneous species
0.015
2.824
▨Aphids
0
5
A
Sown species
Spontaneous species
3.429
2.143
0.571
0.857
0.857
0.429
□Parasitoids
▨Hoverflies
■Ladybugs
0
2
4
B
Sown species
Spontaneous species
0.061
0.038
0.01
0.012
0.012
0.006
□Parasitoids
▨Hoverflies
■Ladybugs
0
0.05
0.1

INFLUENCE OF THE MARGIN VEGETATION ON THE CONSERVATION OF APHID BIOLOGICAL CONTROL IN APPLE ORCHARDS

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Running title:
Plant diversity to enhance aphid natural control

Abstract

The influence of three margin strip treatments (wildflower strips, grass strips and spontaneous vegetation) adjacent to apple orchards on the biological control of *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) was compared during two consecutive years. The wildflower strips provided the highest amount of floral resources. Within the margin strips, hoverflies responded positively to higher resource provisioning whereas ladybird abundance did not differ between strip treatments. Within the orchards, the presence of parasitoids, hoverflies, and ladybirds in aphid colonies and the predation of sentinel aphids were not significantly affected by the adjacent strip treatments. The number of natural enemies observed in aphid colonies was mainly driven by aphid number. Aphid numbers were higher close to the margin strips suggesting that aphid colonization from orchard edges may counteract the positive effect of wildflower strips on natural enemy abundance and on a reduction of aphid infestation. The results confirm the positive influence of floral resource provisioning by wildflower strips on the conservation of aphid natural enemies, but also demonstrate that effects of wildflower strips on aphid regulation inside orchards are not very strong compared with spontaneous vegetation naturally occurring in the margins.

Key words

Hemiptera; Aphididae; aphidophagous predators; conservation biological control; floral resources; apple orchards

Introduction

The management of non-crop habitats in agricultural landscapes has received a considerable interest during the last decades as a way to conserve biodiversity and agricultural sustainability (e.g. Scheer & McNeely 2008). The semi-natural vegetation in the farmland support shelter and resource provision for many arthropods and it can be manipulated to reinforce pest biological control (e.g. Landis et al., 2000; Gurr et al. 2017). The implementation of wildflower strips optimizing floral resource provisioning have been suggested to improve conservation biological control (Griffiths et al., 2008; Dib et al. 2012; Tschumi et al., 2015). Such wildflower strips have positive effects on natural enemy abundance and associated ecosystem services (Wyss & Pfiffner 2008; Haaland et al., 2011; Balzan et al., 2014). Sugar resources from floral or extrafloral nectars significantly increase the fitness of many parasitoids and hoverfly species and, usually, their efficiency to control insect pests (Wäckers, 2004; Winkler et al., 2006; Laubertie et al., 2012). The choice of plant species for wildflower strips needs to take into account the amount and quality of the qualities and availabilities in pollen and nectar, the floral morphology, and the feeding preference of natural enemies (Sivinski et al., 2011; Campbell et al., 2012; Wäckers & van Rijn 2012). Plants in field margins may also provide resources for insect pests and thus increase crop damage (Koji et al., 2007). Thus, plant species in wildflower strips need to be properly selected to favour natural enemies without increasing pest abundance (Lee & Heimpel, 2005; Lavandero et al., 2006).

The rosy apple aphid (RAA), *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae), is a major insect pest in apple orchards causing considerable damages, in particular fruit deformation (Blommers et al., 2004). Due to economic losses and socio-economic pressure to reduce pesticide applications, an increasing number of studies analyzed the efficiency of naturally occurring parasitoids and predators in controlling RAA populations (e.g. Albert et al., 2017). RAA is attacked by numerous generalist predator species such as spiders and earwigs

(Dib et al., 2016; Lefebvre et al., 2017), and aphidophagous specialists such as hoverflies, ladybirds, and hymenopteran parasitoids (Wyss, 1995; Dib et al., 2010). Among these RAA natural enemies, the most common species observed in south eastern France were the hoverfly *Episyrphus balteatus* (De Geer) (Syrphidae), the ladybug *Adalia bipunctata* L. (Coccinelidae), the parasitoid *Ephedrus persicae* Froggatt (Braconidae) and the earwig *Forficula auricularia* L. (Forficulidae). No evidence of intra- or inter-specific competition on RAA prey was observed so far within this guild (Wyss et al., 1999; Dib et al. 2016). Hoverflies and parasitoids depend on nectar and pollen and it was hypothesized that vegetation providing these resources may improve spring regulation of aphids in apple orchards (Markó et al., 2013; Miñarro & Prida, 2013).

We designed a wildflower strip mixture comprising flowering species with different functional traits and life cycles (early to late flowering, annual to perennial, and various floral morphologies) in order to optimize floral resource provisioning. The effects of this wildflower strip mixture were compared with two different controls, spontaneous vegetation and grass strips. The effect of wildflower strips on the dynamics of the arthropod communities has usually been tested against the complete absence of non-crop vegetation (Pfiffner et al., 2009; Haaland et al., 2011; Tschumi et al., 2016). However, spontaneous vegetation may be as efficient as flower strips in attracting natural enemies of insect pests (Denys & Tscharntke, 2002) without producing costs for seed material and strip management. Sowing of grass strips may be a cost-efficient alternative providing habitat functions for natural enemies (Collins et al., 2002; Al Hassan et al., 2013). They provide less floral resources but generalist predators such as spiders, ground and rove beetles may benefit from their shelter function (Wyss 1995; Collins et al., 2002).

An efficient control of RAA requires a natural enemy movement from the field margins into the apple orchard. Most studies on wildflower strips are limited to observations of natural enemy diversity and abundance within the strips (Haaland et al., 2011; Blaauw & Isaacs 2014). The studies that analyzed the presence of natural enemies both in wildflower strips and within the crops usually confirmed the attraction of natural enemies by flowering plants but not always a corresponding reduction of insect pests (Pfiffner & Wyss 2004; Haaland et al., 2011). The few studies demonstrating a significant contribution of wildflower strips to pest control, showed their contribution to pest control decreased with the distance to field margins (Collins et al., 2002; Tylianakis et al., 2004; Tschumi et al., 2015; Albert et al. 2017). A better understanding of the spatial dynamics of natural enemies is needed to evaluate the efficiency of wildflower strips to mediate a regulation of aphids in orchards.

In this study, we tested the influence of three margin strips (wildflower strips, grass strips, and spontaneous vegetation) on the abundance of RAA and its natural enemies from the margin into apple orchard during two consecutive years in order to answer several questions: (I) Do wildflower strips optimized for nectar and pollen production increase natural enemy abundance in orchard margins in comparison with grass and spontaneous vegetation strips? (II) Does the attraction of natural enemies by the flowering plants in the margins also increase their abundance inside the orchards? (III) Is the decrease in RAA abundance close to orchard margins presenting floral resources due to higher natural enemy density ?; (IV) Do orchard margin effects on natural enemy abundances and aphid control decrease with distance to the edge ?

Materials and methods

Study sites and design

The experiment was set up in three unsprayed mono-cultivar apple orchards located at INRA Saint-Paul, Montfavet, France (43°54'51.57"N, 4°52'56.15"E) and was run from March 2014 to June 2015. The two first orchards comprised five rows of 24 apple trees planted in 1996 (cv Royal Gala or Granny). The third orchard comprised six rows of 48 apple trees planted in 2004 (cv Ariane). A permanent grass sward was regularly mown largely limiting the presence of floral resources within orchards. In March 2014, a 2.5 m wide and 40 to 80 m long margin was ploughed and then harrowed to remove weed seedlings emerging after ploughing. In each orchard, this margin was subdivided into three strips of equal size to establish the following three treatments (Fig. 1): (a) a wildflower strip mixture comprising 30 vascular plant species (WS; Table S1) optimized for a high and long lasting production of floral resources, (b) a grass strip (GS) including two perennial grasses, *Lolium perenne* L. (28%) and *Festuca arundinacea* Schreb (72%), used in France to sow buffer zones between field and water bodies to limit water pollution by fertilizer and pesticide drift, (c) an unsown strip allowing the natural development of spontaneous vegetation (SV). The position of the strip treatments was randomized within each orchard margin and thus each orchard represented a replicate block. The approach to set up all treatments within the same orchard is relatively conservative since mobile arthropods may move between different strip types and the adjacent orchard, which may reduce the probability to find significant treatment differences. However, this design largely limits bias due to orchard differences inherent with the comparison of one field – one treatment situations.

Observations within margin strips

Plant species composition and provision of floral resources were evaluated in spring 2014 and 2015. First, plant richness was estimated based on the number of vascular plant species observed in each margin strip. Second, we calculated the percentage cover of flowering entomophilous plants as a proxy of floral resource provisioning. Percentage cover of all vascular plant species and proportion of vegetative, flowering and fruiting individuals of each plant species were recorded in each strip treatment at each orchard. We considered a plant species as entomophilous if indicated as insect-pollinated in the BiolFlor database (Kühn, et al., 2004). Percentage of each entomophilous plant was multiplied by the estimated proportion of flowering individuals at the respective survey date, which were added for all the entomophilous species to estimate the total percentage cover of flowering entomophilous plants in each margin strip. Survey dates were the 6 June 2014 and the 22 May 2015 corresponding to peaks of RAA abundance.

At the same dates, aphidophagous predators that were visible from outside the strip were counted during 10 min walking along each margin strip to evaluate the abundance of hoverfly and ladybug predators per margin strip. The entomological observations were limited to a period between 10:00 and 17:00 under favorable weather conditions (sunny, no rain, low wind speed).

Observations within apple orchards

Depending on orchard size, observations were performed on 2 or 3 labeled trees per treatment and per distance resulting in a total of 18 or 27 analyzed trees per orchard. According to the position of the apple tree rows, the distances of the observed trees were 1, 5, and 17 m from the margin strips (Fig. 1). The same trees were observed twice a year at the end of April or the beginning of May (session 1) and four weeks later (session 2). Observations were performed at the tree and the RAA colony levels to calculate within the apple orchards estimators of aphid infestations, change in aphid infestations between sessions, numbers of RAA natural enemies, and predation of sentinel aphids.

First, the numbers of terminal growing shoots and of RAA colonies were counted in the canopy of each labeled tree. The terminal growing shoots were counted to take into account the apple tree vigor because only those shoots are attacked by RAA (Simon et al., 2012). Aphid colony infestation per apple tree was calculated as the proportion of terminal growing shoots with a *D. plantaginae* colony. Aphid colony increment per apple tree was defined as the occurrence of tree with higher number of RAA colonies at session 2 than session 1.

Second, six RAA colonies were randomly chosen on the northern and the southern sides of each labeled tree (three colonies at each side). The number of aphids, mummies (dead bodies of aphids parasitized by braconid wasp) and aphid predators (mainly hoverflies, ladybugs, and earwigs) were recorded in each colony. Occurrences per apple tree of each RAA natural enemy (aphid mummy or RAA predators) were estimated as their occurrences in at least one of the six colonies observed per tree.

Finally, sentinel aphids glued to sandpaper cards were used to evaluate at the tree level aphid potential predation (Östman, 2004). Three living aphids were attached to each 5 cm x 5 cm sandpaper card. The cards were fixed at the abaxial leaf surface of the observation trees (1.5 m above the ground) and were removed the following day. Aphid predation was estimated as the proportion of sentinel aphids per card attacked during 24 h.

Statistical analysis

We used generalized linear models (*glmer* function, lme4 package, R version 3.2.4) to test: (1) the effect of the strip treatment on the number of vascular plant species, on the cover of flowering entomophilous plants, and on the abundance of aphid enemies in the orchard margins; (2) the effects of the strip treatment, of the distance to the orchard margin and the treatment x distance interaction on aphid infestation, aphid colony increment between session, occurrences of RAA natural enemies in, and predation of sentinel aphids at the apple tree level; (3) correlations between the number of aphids and the number of aphid natural enemies at the RAA colony level. To take into account temporal variations, year, and session (when relevant) were fitted as additional factors.

The plant species richness (number of vascular plant species) and the cover of flowering entomophilous plants (arcsin square root transformation of the percentage cover) were fitted using a Gaussian error distribution with identity link function. The abundance of natural enemies within margin strips was analyzed using a Poisson error distribution with log link function. Finally, the binary data of aphid infestation, aphid colony increment, predation of sentinel aphids and occurrence of mummies and RAA predators per apple tree were analyzed using a binomial error distribution with a logit function. Linear regressions were calculated to analyze relationships between the number of aphids (ln-transformed) and the total number of natural enemies (ln-transformed) within the RAA colonies.

Strip treatment (WS, GS, SV), distance to the margin strips (1, 5, and 17 m), year (2014 and 2015) and observation dates within year (session 1 and 2) were fitted as fixed factors and orchard was included as a random factor in each model. In the case of over-dispersion, observation tree was included as an additional random factor (Harrison, 2014).

The *Anova* and *glht* functions (car and multcomp R libraries, respectively) were used to test factors and their interactions (Wald's sequential probability likelihood ratio tests) and to compare the effects of a particular strip treatment and distance classes within each significant factor (Z-tests).

Results

Observations within margin strips

In both years, the cover of flowering entomophilous species as a proxy of floral resource provisioning was significantly higher (2.5 fold on average) in wildflower strips than in grass strips and in spontaneous vegetation (Fig. 2 A, B). However, in 2014 the difference was only marginally significant between the wildflower and spontaneous vegetation strips ($|Z|=2.3$, $P=0.059$). No significant difference occurred between spontaneous vegetation and grass strips. In 2014, the sown species represented only 25% of the entomophilous species cover in wildflower strips, whereas their proportion was 90% in 2015. The number of vascular species per strip was also significantly higher in wildflower strips than in grassy and spontaneous vegetation strips (Fig. 2 C, D). On average wildflower strips presented ten more plant species than the other treatments. In 2015, the number of plant species was lower in the grassy than in the spontaneous vegetation strips whereas no such a difference was found in 2014.

Hoverflies and ladybugs, notably *E. balteatus* and *A. bipunctata*, were the most abundant aphid predators recorded in the margin strips. Hoverfly abundance differed significantly between years ($\chi^2=50.2$, $P=1.3\text{x}10^{-12}$) and strip treatments ($\chi^2=11.8$, $P=0.003$). Hoverfly abundance increased from three individuals per strip on average in 2014 to twelve individuals per strip on average in 2015. The significant strip treatment effect was explained by a higher hoverfly abundance in the wildflower strips compared with grass and the spontaneous vegetation strips (in 2014: $|Z|<0.5$, $P>0.62$; in 2015: $|Z|>2.9$, $P<0.008$; Fig. 3 A, B). Ladybug abundance within margin strips (mean= 3.4 ± sd 4.4) did neither differ between years ($\chi^2=0.82$, $P=0.36$) nor between treatments ($\chi^2=0.71$, $P=0.70$).

Observations within apple orchards

Inside orchards, ladybugs, hoverflies, and earwigs were the most frequently observed predators within the RAA colonies (Table 1). Aphid mummies were only observed in the second spring session. Occurrence of all these RAA natural enemies differed significantly between years (χ^2=15.4, P=8.3x10^{-5}) and between spring sessions (χ^2=65.4, P=5.8x10^{-16}), but not among margin strip treatments (χ^2=1.5, P=0.46), or between distance classes to the margin strip (χ^2=0.6, P=0.74). The occurrence of hoverfly larvae doubled between 2014 and 2015 (25% to 54 % of the apple trees; χ^2=13.7, P=2.1x10^{-4}). However, an increase of hoverfly numbers in the wildflower strip treatment observed in the margins was not confirmed by a higher occurrence of hoverfly larvae in RAA colonies inside the orchards (Fig. 3 C, D). Earwigs were frequently observed in 2014 but almost absent in 2015 (42% to 2% of the apple trees; χ^2=77.8, P=2.0x10^{-16}). The occurrence of aphid mummies was higher in 2014 than in 2015 (difference marginally significant: 75% and 56% of the apple trees, respectively; χ^2=3.5, P=0.06).

On average, 18 RAA colonies per tree and date were observed (Table 1). Aphid infestation was estimated as the proportion of terminal growing shoots carrying a RAA colony. Infestation by RAA was significantly different between years, sessions within years and distances from the margin strips (Table 2). Infestation by RAA was three times lower in 2015 than in 2014 (16% and 55% of the growing shoot, respectively). Infestation by RAA was significantly lower at 17 m than at 5 m or 1 m from the margin strips (33%, 37% and 36% of the growing shoots at 17 m, 5 m and 1 m distances, respectively). Although the strip treatment main factor was not significant, the interaction treatment x distance was significant suggesting that the treatment effect depended on distance from the margin. At a distance of 1 m from the orchard margin, aphid infestation was lower close to the wildflower strip (only 33% of the growing shoots) than close to the spontaneous vegetation and grass margin strips (36% and 39% respectively), whereas no significant treatment differences were found at 5 m and at 17 m.

The increment of RAA colonies was measured to evaluate variation of aphid infestation between sessions at the tree level. The proportion of apple trees with more RAA colonies at session 2 than session 1 was marginally higher at the closest distances to the orchard margin strips (71%, 74% and 62% of the apple trees at 1 m, 5 m and 17 m distances respectively; Table 2).

On average, 25% of the sentinel aphids were preyed, but their predation was neither spatially structured within the orchards between distance classes (χ^2=0.4, P=0.810), nor between margin strip treatments (χ^2=0.2, P=0.906), nor temporally structured between sessions (χ^2=0.2, P=0.690) or between years (χ^2=0.1, P=0.799).

Observations within rosy apple aphid colonies

Linear regressions between the number of aphids and the total number of their natural enemies in RAA colony were used to test density-dependence effects of margin strip treatments. Numbers of natural enemies per RAA colony were significantly correlated to numbers of aphids (one natural enemy for 34 aphids on average; slope: χ^2=14.93, P=1.1x10^{-4}; intercept: χ^2=5.04, P=0.025). Separate linear regression for each margin strip treatment was significant for the spontaneous vegetation treatment (slope: χ^2=14.90, P=1.1x10^{-4}) but not for the wildflower and grass strip treatments (Fig. 4). The intercept was only significantly different from 0 in the wildflower strip treatment (intercept: χ^2=4.28, P=0.039; Fig. 4) indicating a higher availability of natural enemies in the absence of aphids.

Discussion

Our results showed that the selected wildflower strip mixture optimized for quantity and duration of nectar production was successful in increasing floral resource provisioning. The cover of flowering entomophilous plants species as a proxy for nectar and pollen production was significantly higher in wildflower strips than in grass and spontaneous vegetation strips. Plant species richness was also higher although not all sown species developed in the wildflower strips. Only small differences occurred between grassy and spontaneous vegetation strips but plant species richness in the grass strips was lower in the second year confirming the suppressive effect of competitive grass mixtures on spontaneously emerging species (Cordeau et al., 2012). Spontaneous vegetation emerging from the soil seed bank considerably contributed to both plant diversity and floral resources in both sown strips reducing the magnitude of treatment effects compared with other studies (Bischoff et al., 2016). Annual plant species were dominant during the first year but were replaced by biennials and perennials in the course of plant succession.

Among the two major aphid predators observed in the strips, only hoverflies responded to the strip treatment. Hoverfly densities were higher in the wildflower strips than in the other strips. Adult hoverflies rely on nectar resources (Wäckers, 2004; Fiedler et al., 2008). Laboratory experiments on the aphidophagous hoverfly *E. balteatus* showed that adult fitness depends on floral resource provisioning (Laubertie et al., 2012). Markó et al. (2013) and Miñarro and Prida (2013) also found a positive effect of the surrounding vegetation on hoverfly abundance in orchards.

Ladybirds did not respond to the strip treatments. Although occasionally feeding on pollen and nectar (Triltsch, 1999), their performance depends much less on floral resources because larvae and adults are predominantly predators (Ricci et al., 2005). Nevertheless, several other studies found a positive effect of floral resources on ladybird abundance (Tschumi et al., 2015; Bischoff et al., 2016).

The effect of strip treatments on natural enemies observed in aphid colonies inside orchards was not significant. The energetic costs and the relative attractiveness of margin strips may have reduced natural enemy movements into the orchard (Heimpel & Jervis, 2005; Wanner et al., 2006). However, hoverflies that strongly responded to the strip treatments are highly mobile insects. Hoverfly movements between the different treatments may have reduced the probability to find significant treatment effects. Additionally, a time lag has to be considered between the measures of hoverfly abundance in wildflower strips and the occurrence of larvae in the orchards. Effects of resource provisioning on adult oviposition occur with a delay since larvae hatch after a couple of days and larvae feed for about three weeks on aphids (Laubertie et al., 2012, van Rijn & Wäckers 2016).

Similarly to natural enemies observed in apple orchards, the overall treatment effect on the aphid infestation was not significant. However, a significant treatment x distance interaction was detected resulting from a lower aphid infestation close to wildflower strips (1 m distance) whereas no such treatment effect was observed at higher distances. Since no corresponding result was obtained with each of the three natural enemy groups observed in RAA colonies (parasitoids estimated from aphid mummies , hoverflies, ladybirds), we hypothesize that a combination of predators, including some non-observed predators coming from the wildflower strips may have contributed to a reduction of aphid infestation close to the wildflower strips. Although floral resources do not necessarily increase ground beetle abundance (Balzan et al., 2014), a positive effect of wildflower strips on this important generalist predator of aphids has been reported (Tschumi et al., 2015). However, we did not find any differences in predation of sentinel aphids glued on predation cards, neither between distances nor between treatments suggesting that this method does not necessary account for predation of RAA colonies.

Aphid infestation and aphid colony increment were higher on the apple trees close to the margin strips than on those that were inside the orchards. RAA secondary host during summer, *Plantago lanceolata* L. (Blommers et al., 2004), is a common species in the study region and was abundant in all strip treatments (up to 13% of the total cover). Thus, it is possible that field margins also represent a source of RAA infestation counteracting potential positive effects of strip treatments mediated by higher natural enemy densities.

In both years, a rapid and significant increase of aphid infestation was observed resulting in a high increment of aphid colonies and suggesting a relatively low natural regulation potential during early spring. Such a strong and rapid increase of aphid infestation was also observed in a previous study of the RAA dynamics in orchards of the same region (Dib et al., 2010). An efficient biological control would require the presence of a sufficient number of natural enemies in March and April when the number of aphids per RAA colony is still low (Lefebvre et al., 2017). Most wildflower strip species started to flower later than April. In order to provide floral resources in time, a higher proportion of early flowering plant species would be necessary for controlling the exponential development of the RAA colonies.

We found a positive relationship between aphid colony size and natural enemy density indicating that natural enemies within orchards mainly responded to the available amount of prey or hosts. However, natural enemy numbers did not significantly depend on aphid numbers in the wildflower strip treatment. In absence of aphids, the regression model predicted higher natural enemy densities for the wildflower strip treatment than for the other treatments (regression intercepts), which may be the result of a higher spill-over of natural enemies from the wildflower strip. A relatively high mobility of natural enemies attacking aphid colonies may compensate for a lower spill-over of natural enemies in the other strip treatments.

In conclusion, we found positive effects of wildflower strips on floral resource provisioning increasing the abundance of hoverflies as an important natural enemies of RAA in apple orchards. However, the effect of wildflower strips on aphid control was less strong than in studies using annual crops as model system (Pfiffner et al., 2009; Tschumi et al., 2015). Such differences may be partially due to differences in the experimental design and the controls used. Most of the studies performed in annual crops have used less attractive controls than we did to evaluate wildflower strip effects (absence of vegetation, crop strips), increasing the probability to obtain significantly positive results (Haaland et al., 2011; Tschumi et al., 2015). However, differences in insect abundances between wildflower strips and other margin types also depend on the age of the wildflower strips and the time of the year (Haaland et al., 2011).

Anyway, we are convinced that a successful conservation biological control approach needs to provide a significantly better control service than spontaneously occurring vegetation to justify higher sowing and management costs. In order to improve pest regulation by wildflower strips, sowing inside orchards should be considered in order to reduce the distance of movements required to reach the target pest species (Albert et al., 2017). Our study also demonstrated the importance of temporal dynamics and the need to provide floral resources at the beginning of the season for an early control of the RAA colonies. Future studies should focus on natural enemy and aphid movements including their temporal dynamics to improve our understanding of interactions between natural enemies and rosy apple aphids and to evaluate efficiency of wildflower planting in orchard margins.

Acknowledgements

This work was supported by the PEERLESS project (ANR-12-AGRO-0006), by the Agropolis Fondation (ANR-10-LABX-0001) and by the “Structure Fédérative de Recherche” TERSYS. We are also grateful to Elise Thenoux, Claire Estellon and Cécile Thomas for field assistance and data compilation.

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Table 1. Mean number of *D. plantaginae* colonies (aphid colonies) and mean occurrence of rosy apple aphid predators (hoverflies, ladybirds and earwigs) or parasitoids (recorded as aphid mummies) per apple tree in 2014 and 2015. Minimum and maximum values per orchard are indicated in brackets.

	2014		**2015**	
	6 May	**3 June**	**24 April**	**19 May**
Aphid colonies	19.9 [15.3-24.6]	41.9 [31.8-56.0]	1.5 [1.5-1.6]	22.3 [11.3-27.4]
Hoverflies	0.3 [0.2-0.5]	0.1 [0.0-0.4]	0.0 [0.0-0.0]	0.7 [0.4-0.9]
Ladybirds	0.1 [0.0-0.2]	0.6 [0,5-0.9]	0.0 [0.0-0.0]	0.5 [0.2-0.7]
Earwigs	0.1 [0.1-0.2]	0.6 [0.5-0.9]	0.0 [0.0-0.0]	0.2 [0.0-0.8]
Parasitoids	0.0 [0.0-0.0]	0.7 [0.5-1.0]	0.0 [0.0-0.0]	0.6 [0.3-0.7]

Table 2. Temporal and spatial variation at the apple tree level of aphid infestation (proportion of terminal growing shoots with at least one *D. plantaginae* colony) and aphid colony increment (occurrence of a higher number of *D. plantaginae* colonies at session 2 than session 1). Temporal and spatial interactions refer to year x session and to margin strip treatment x distance interactions, respectively.

		Aphid infestation		**Colony increment**	
	df	χ^2	***P*-value**	χ^2	***P*-value**
Year	1	102.4	2.2×10^{-16}	0.4	0.548
Session	1	12.3	4.6×10^{-4}	/	/
Temporal interaction	1	21.7	3.2×10^{-6}	/	/
Strip treatment	2	3.1	0.215	0.7	0.704
Distance to margin	2	8.7	0.013	5.1	0.079
Spatial interaction	4	11.2	0.025	5.1	0.279

Figure captions

Fig. 1 Experimental design. Shaded symbols indicate observation trees at three distance classes (1 m, 5 m and 17 m) from the orchard margin treatments.

Fig. 2 Mean (± SE) of the cover with entomophilous flowering plants (A, B) and mean number of plant species (C, D) in each orchard margin treatment in 2014 (A, C) and in 2015 (B, D); WS: wildflower strip, SV: spontaneous vegetation strips; GS: grass strip. Different lowercase letters above columns indicate significant differences at $p<0.05$.

Fig. 3 Mean (± SE) number of hoverflies observed in margin strips (A and B) and in *D. plantaginae* colonies inside the orchards (C and D) in 2014 (A, C) and in 2015 (B, D); WS: wildflower strip; SV: spontaneous vegetation strips; GS: grass strip. Different lowercase letters above columns indicate significant differences at $P<0.05$.

Fig. 4 Relationship between the number of aphids (RAA) and the number of natural enemies (NE) per aphid colony at the second 2015 session (ln-transformed values). Regression lines are presented to illustrate slope and intercept differences between WS (wildflower strip, white circles), SV (spontaneous vegetation strips, grey circles), and GS (grass strip, black circles) treatments. Stars indicate slopes or intercepts that significantly differ from zero (*: $P<0.05$; ***: $P<0.001$).

IMPACT OF AGRO-ECOLOGICAL INFRASTRUCTURES ON THE CONTROL OF INSECT PESTS IN APPLE ORCHARDS

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Abstract: The rosy apple aphid, *Dysaphis plantaginea*, and the codling moth, *Cydia pomonella*, are major insect pests in apple orchards causing high economic losses. A conservation biological control approach using plant species that provide resources for natural enemies may improve natural regulation and reduce insecticide use. In this study, we compared the influence of wildflower strips, grass strips and spontaneous vegetation on the biological control of aphids and moths by their natural enemies (parasitoids, hoverflies, and ladybirds) in three untreated apple orchards in 2014 and 2015. The sown wildflower strip mixture was successful in increasing floral resource provisioning in both years. Among the major natural enemy groups observed in the margin strips only hoverflies responded positively to the increase of floral resources. Within the orchards, the number of aphid colonies per tree was higher close to the margins, but the number of codling moth larvae smaller. The number of natural enemies observed in aphid colonies was largely driven by aphid number. None of the natural enemy groups observed in *D. plantaginae* colonies responded to the adjacent strip treatments. This dynamic response may explain the reduction in aphid numbers close to wildflower strips without finding higher overall natural enemy numbers. Similarly, codling moth parasitism was higher close to the margins. These results suggest a positive influence of floral resource provisioning by wildflower strips on aphid predation and codling moth parasitism but they also demonstrate that effect size may be small if species-rich spontaneous vegetation does already occur in margins or inside orchards.

Key words: conservation biological control, predation, parasitism, codling moth, rosy apple aphid, floral resources

Introduction

Flowering strips significantly increase the local abundance and biodiversity of flying predators and parasitoids in the agroecosystem (Marshall & Moonen, 2002). However, only few studies have demonstrated their role in pest control and their impact on the dynamic of arthropod populations and on trophic interaction within the crop (Lavandero *et al.*, 2006; Géneau *et al.*, 2012).

The objective of this work was to test the effect of biodiversity in flowering strips on the biological control of two major insect pests in apple orchard, the codling moth (CM) and the rosy apple aphid (RAA).

Material and methods

Orchard experimental design

The experiment was carried out in 2014 and 2015 in three untreated apple orchards (480 to 1200 m^2) at INRA Montfavet, France (43 ° 54'51.57 "N, 4 ° 52'56.15" E). Three strip treatments (30 to 70 m^2) were established along the longer edge of each orchard (Fig. 1): (a) a wildflower strip mixture comprising 30 vascular plant species (WS) optimized for high and long lasting productions of floral resources, (b) a grass strip mixture (GS) including *Lolium perenne* (28%) and *Festuca arundinacea* (72%), (c) an unsown strip allowing the natural development of spontaneous vegetation (SV). Grass and wildflower strips were sown in orchard edge in March 2014.

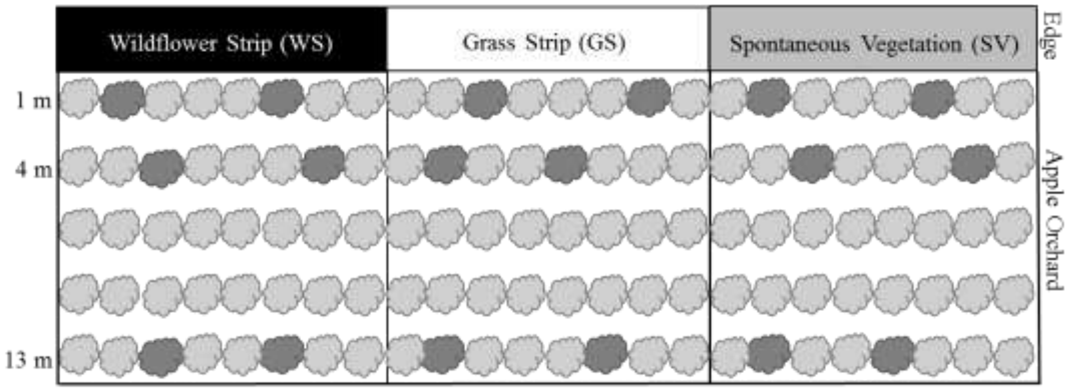

Figure 1. Schema of the experimental design. Shaded symbols indicate the selected trees to monitor apple pests and their enemies in each apple orchard.

Entomological observations

The arthropod communities involved in RAA and CM control were monitored at 18 or 27 apple trees per orchard (Fig. 1). These observation trees were selected at three distances from the margin strips (1 m, 4m and 13 m). The same trees were selected in 2014 and 2015. The number of RAA colonies per apple tree was counted at the end of the RAA growing period (19/05/14 and 03/06/15). The occurrence of predators and aphid mummies were recorded in up to six RAA colonies per tree (Table 1; Dib *et al.* 2016).

Table 1. Mean number of RAA colonies per apple tree and mean proportions of RAA with an observed predator (hoverflies, ladybirds and earwigs) or a mummy

(parasitoids) in 2014 and in 2015. Minimum and maximum values per orchard are indicated in brackets.

	2014	2015
RAA colonies	41.9 [31.8-56.0]	22.3 [11.3-27.4]
Hoverflies	0.1 [0.0-0.4]	0.7 [0.4-0.9]
Ladybirds	0.6 [0.5-0.9]	0.5 [0.2-0.7]
Earwigs	0.6 [0.5-0.9]	0.2 [0.0-0.8]
Parasitoids	0.7 [0.5-1.0]	0.6 [0.3-0.7]

CM larvae were weekly collected from May to October in cardboard band traps wrapped around the tree trunks. The number of CM larvae and adult emergences were recorded to infer the parasitism of diapausing and non diapausing larvae (Table 2; Maalouly *et al.* 2015).

Table 2. Mean number of CM larvae per apple tree, parasitism rates and proportion of parasitoids (*Ascogaster quadridentata, Pristomerus vulnerator* and *Perilampus tristis*) in 2014. A total of 2673 CM larvae were collected (including 927 diapausing). The diapausing samples correspond to the emergences that occurred in 2015. Minimum and maximum values per orchard are indicated in brackets.

	Non-diapausing	Diapausing
CM larvae	27.7 [18.4-33.4]	14.7 [6.9-19.8]
Parasitism rate	0.27 [0.15-0.36]	0.32 [0.15-0.38]
A. quadridentata	0.59 [0.33-0.63]	0.43 [0.21-0.69]
P. vulnerator	0.13 [0.10-0.26]	0.17 [0.00-0.23]
P. tristis	0.27 [0.26-0.40]	0.38 [0.31-0.51]

Furthermore, the percentages of flowering entomophilous plants and the number of predators and parasitoids in each strip treatment were recorded in May of each year to shed light on their respective impact on the control of the apple pests.

Statistical analysis

The occurrence of predators in RAA colonies and CM parasitism were analyzed using generalized linear models assuming a binomial distribution (*glmer* function, lme4 package, R version 3.2.4). The strip treatment, the distance to the orchard margin and their interaction were factors tested. All models also included the observation date as an additional fixed factor to account for temporal variation and a random 'orchard' effect to account for a block factor.

Results and discussion

The percentages of flowering entomophilous plants in the margin strips were significantly higher in WS than in SV and in GS both year (Fig. 2). We mainly observed hoverflies and ladybirds in the margin strips. The number the hoverflies was higher in WS than SV and GS in 2015 (Fig. 2). However, we did not detect significant differences in the number of ladybird and hymenopteran parasitoids among the margin strips.

The abundances of RAA colonies and CM larvae per apple tree were not homogenously distributed within the orchards. RAA infestations were significantly higher at the closest distances from the margin, but infestations were lower close to WS than close to GS and SV strips. Inversely, the number of CM larvae were significantly lower at the lowest distances from margin strips.

The occurrence of predators and parasitoids in RAA colonies and codling moth parasitism within the orchards were not significantly different among the classes of distances to the margin and among the margin strip treatments. However, the arthropod communities involved in RAA and CM control significantly changed within and between years (Tables 1 & 2).

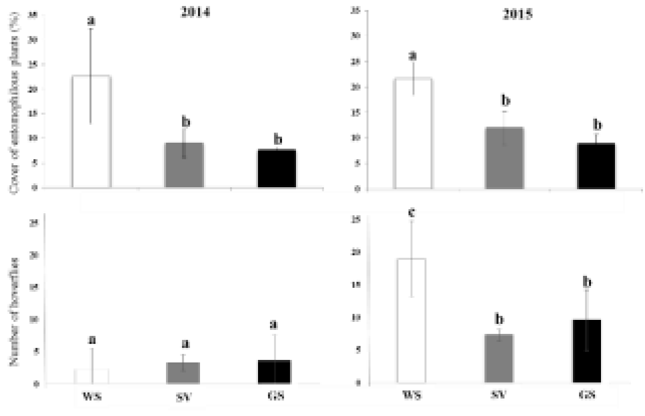

Figure 2. Percentage of entomophilous plants in flower (upper panels) and number of hoverflies (lower panels) in WS (white), SV (grey) and GS (black) margin strips in May 2014 (left panels) and 2015 (right panels).

These results suggest that provisioning of additional flower resources in orchard margins had a limited impact on the abundance of pest natural enemies both within the orchards and their edges if floral resources are already present in the environment. Selection of entomophilous plants according to temporal natural enemy's requirement could additionally enhance RAA and CM controls in the apple orchards.

Acknowledgements

This work was supported by the Agropolis Fondation (ANR-10-LABX-0001) and by the PEERLESS project (ANR-12-AGRO-0006).

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IMPACT OF AGROECOLOGICAL INFRASTRUCTURES ON THE DYNAMICS OF DYSAPHIS PLANTAGINEA PASSERINI (HEMIPTERA: APHIDIDAE) AND ITS NATURAL ENEMIES IN APPLE ORCHARDS IN NORTHWESTERN FRANCE

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Published in Environmental Entomology : 46(3):528-537: doi: 10.1093/ee/nvx054.

ABSTRACT

Apple orchard production is facing new environmental and societal challenges, resulting, in particular, in strong pressure to reduce pesticide use. Cider-apple production, for which the perfect visual aspect of fruits is not a marketability imperative, offers good opportunities to study production systems that are developing new agronomic strategies, which could be subsequently extended to all apple-production types. Agroecological infrastructures play an important role in providing shelter, food resources or reproduction habitats to many arthropods. Consequently, setting-up agroecological infrastructures in the vicinity of or within orchards could increase natural enemy presence and thus improve the biological control of pests. In this study, we focused on *Dysaphis plantaginea* (Passerini), one of the major pests in apple orchards in Europe, which causes important economic production losses. During two years (2014 and 2015), we monitored the population dynamics of *Dysaphis plantaginea*, its natural enemies and mutualistic ants in commercial production cider-apple orchards. The influences of the cider-apple cultivar, insecticide use and distance to agroecological infrastructures (hedgerows and flower strips) were assessed. Our results suggest that flower strips favour an increase in natural enemy abundance in the vicinity of the orchards and could thus play an important role in the production system by improving the biological control of *Dysaphis plantaginea*.

Keywords

Biological control, cider-apple orchard, *Dysaphis plantaginea*, flower strip, hedgerow

In the second half of the 20th century, the green revolution allowed an unprecedented increase in agricultural yields in developed countries. This yield increase was achieved by the generalization of agricultural mechanization and the use of synthetic pesticides and fertilizers. The green revolution resulted in agricultural landscape simplification (Robinson and Sutherland 2002, Benton et al. 2003) and produced numerous negative side effects on biodiversity (Krebs et al. 1999), human health (Lee et al. 2004, Simon et al. 2007) and the quality of soil and water (Moss 2008). Consequently, a change in the current agricultural paradigm and the development of more environmentally friendly agricultural practices are strongly required.

Agroecology proposes to primarily base agricultural production on the mobilization of natural processes and the improvement of ecosystem services (e.g. pollination, nutrient cycling, biological control of pests) rather than on chemical inputs. In particular, promoting the natural control of pests would lead to insecticide use reduction. The resulting reduction of economic and environmental costs would contribute to increase farmer benefits and the environmental sustainability of agriculture (Tschumi et al*.* 2015).

Various approaches have been proposed to improve pest biological control, including changes in practices (e.g. pesticide use reduction, accurate choice of cultivars) and establishing agroecological infrastructures within or in the vicinity of the crop (Haenke et al*.* 2009, Miñarro and Prida 2013). Agroecological infrastructures include hedgerows, flower strips, permanent grasslands and woodlands. They may provide pests and natural enemies with various beneficial functions, including suitable microclimatic conditions and refuge during adverse seasons (Landis et al. 2000). Thus, spiders, beetles and syrphids use them as overwintering areas (Collins et al*.* 2003, Sarthou et al*.* 2005, Pfiffner et al*.* 2013). Agroecological infrastructures also provide pollen and nectar resources that increase the longevity of parasitoids (Wäckers 2001, Berndt and Wratten 2005) and improve the fecundity of other insects (Schmale et al*.* 2001, Wäckers 2001, Winkler et al*.* 2006, Hogg et al*.* 2011, Laubertie et al*.* 2012, Rijn et al*.* 2013). Agroecological infrastructures also provide alternative prey for generalist predators when these resources are not available in the crop (Wyss 1996, Denys and Tscharntke 2002, Lavandero et al*.* 2005).

Northwestern France (i.e. Bretagne, Normandie and Pays de la Loire regions) is the number one cider-apple producing area in Europe. Cider-apple orchard cultivation is thus important in the local economy. The management of apple orchards is based on the intensive use of pesticides to control pests and pathogens (Sauphanor et al*.* 2009). Currently, farmers are under strong pressure to develop environmentally friendly protection strategies to address the new challenges imposed by society, and environmental laws. Because cider-apples are transformed, their perfect visual aspect is not a prerequisite of their marketability and fewer pesticide treatments are applied in cider-apple orchards than in orchards for fresh fruit production (approximately 15 *vs* 35 treatments per year). Consequently, cider-apple orchards offer an opportunity to develop and test protection strategies using less pesticide, which could subsequently be generalized.

Approximately 60 phytophagous arthropod species are considered to be apple pests (Jenser et al*.* 1999). The rosy apple aphid (RAA) *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae), is among the most detrimental pests, causing significant economic losses by reducing yield (Blommers et al*.* 2004). The RAA is problematic not only in organic but also in conventional orchards due to its very low abundance threshold for economic damage, resulting in a low treatment threshold (i.e., as soon as the pest is detected) (Cross et al*.* 2007). As a consequence, an increase in insecticide resistance has been recorded (Delorme et al*.* 1998). Many recent studies have suggested that improving biological control efficiency could be an alternative to insecticides use to limit RAA populations (Hemptinne et al*.* 2003, Dib et al*.* 2010, Miñarro and Prida 2013). RAA is a host-alternating aphid species. Its primary host is the apple tree *Malus domestica* Borkh. (Rosales: Rosaceae), and its secondary hosts are plantain herbs *Plantago spp*, mainly *P. lanceolata* L. (Lamiales: Plantaginaceae) (Blommers, 1999). At the beginning of spring, eggs laid in autumn hatch on apple trees producing parthenogenically reproducing females (Lathrop 1928, Bonnemaison 1959, Blommers et al*.* 2004). Migration to a secondary host occurs from mid-June to July in the North of France. The aphids return to apple trees in autumn, where a sexual generation of oviparous females lays fertilized overwintering eggs on the apple trees. The economic losses caused by this leaf-roller aphid, which develops on the lower side of the leaves, are mainly due to the deformations caused to the fruits and growing shoots, decreasing the yield in the year of infestation, as well as in following years (Bonnemaison 1959, De Berardinis et al*.* 1994, Wilkaniec and Trzcinski, 1997, Blommers et al. 2004).

Several recent studies have focused on the community of natural enemies, which could play a role in the biological control of *D. plantaginea* during spring. In Europe, this community is mostly composed of syrphids, coccinellids, parasitoids (mainly *Ephedrus* sp – Hymenoptera: Braconidae), earwigs, spiders and *Aphidoletes* sp (Diptera: Cecidomyiidae) (Wyss et al*.* 1999, Miñarro et al*.* 2005, Dib et al*.* 2010, Arnaudov et al*.* 2013). The abundance of these natural enemies in orchards depends on the abundance of RAA prey (Dib et al*.* 2016) and on the intra-guild predation pressure (Rosenheim et al*.* 1993, Rosenheim et al*.* 1995, Korenko and Pekár 2010). Thus, while an increase in natural enemy abundance is expected to result in a decrease in RAA abundance, this trend may reverse when intra-guild predation is important (Snyder and Ives 2001). RAA population dynamics also depend on the presence of ants in the colony, as *D. plantaginea* is commonly attended by ants (Bonnemaison 1959, Starỳ 1970). Interactions between the ants and myrmecophilous aphids are beneficial for both arthropods: ants are supplied with sugar through aphids’ honeydew whereas aphids improve their reproductive rate (El-Ziady and Kennedy 1956, Banks and Nixon 1958, Flatt and Weisser 2000) and are protected against natural enemies (Stadler and Dixon 1999, Yao et al*.* 2000, Kaneko 2003). Thus, the relationship between ants and *D. plantaginea* enhances the growth of aphid colonies by reducing aphid predation by their natural enemies (Stewart-Jones et al*.* 2008, Miñarro et al*.* 2010).

Several recent studies noted the potential of agroecological infrastructures to improve the biological control of *D. plantaginea* by favouring the natural enemy community (Dib et al*.* 2012, Miñarro and Prida 2013, Pfiffner et al*.* 2013). Knowledge about the distance at which agroecological infrastructures are operating would help to determine the required density needed to provide an efficient biological control. Indeed, several studies noted that the distance to agroecological infrastructures influenced parasitoids (Corbett and Rosenheim 1996, Lavandero et al*.* 2005), spiders (Miliczky and Horton 2005) and syrphids (Bowie 1999) abundances. Moreover, the link between the distance to agroecological infrastructures and natural enemy abundance is not systematically linear. For instance, Tylianakis et al*.* (2004) have shown that the proportion of the aphid *Metopolophium dirhodum* parasitised by *Aphidius rhopalosiphi* decreased exponentially with the distance to flower resources.

The present project aimed to determine the impact of two types of agroecological infrastructures - flower strips and hedgerows - on the abundance of arthropods interacting with *D. plantaginea* (natural enemies and ants) and its consequences on RAA population dynamics. The influence of the distance to these two types of agroecological infrastructures on arthropod dynamics was assessed in 14 cider-apple orchards in northwestern France, which exhibit a range of farming practices (cultivars, insecticide use). For this purpose, the arthropod populations (aphids, their main natural enemies and their mutualistic ants) were monitored in spring during two successive years.

Materials and Methods

Monitored Cider-Apple Orchards

Experiments were carried out in the spring and early summer in 2014 and 2015 in cider-apple orchards in seven locations in northwestern France (Fig. 1). The orchards were planted between 2010 and 2012 with three different cider-apple cultivars (three consecutive rows of each cultivar: Douce de l’Avent$_{cov}$, Dabinett and Judor) grafted onto MM106 rootstock. The three cultivars differed in their vigour and precocity: Douce de l’Avent$_{cov}$ (DDA) was the most vigorous and precocious cultivar, Dabinett (DAB) was the less precocious cultivar and Judor (JUD) was intermediate.

In each location, two contiguous orchards were studied that differed in regard to insecticide application and in the agroecological infrastructures established (Table 1). Only five out of the seven locations were monitored in 2014 (Fig. 1).

Monitored Trees

Approximately one-third of the trees were systematically monitored in each orchard (63 to 423 contiguous trees, depending on the considered orchard - Table 1). For each apple tree, the distance to the closest hedgerow (ranging from 5 m to 57 m), the distance to the closest flower strip (ranging from 0 m to 63 m) and the insecticide use were recorded, and the arthropod population dynamics were monitored.

The hedgerows were mainly composed of *Carpinus betulus*, *Cornus* sp, *Corylus avellana*, *Viburnum* sp, *Sambucus nigra* and *Quercus pedonculata*. All flower strips, established specifically for the study, included *Centaurea cyanus*, *Silene vulgaris*, *Silene latifolia alba* and *Achillea millefolium*.

Assessment of Insecticide Toxicity to Beneficial Arthropods

Calendars of the insecticide treatments in 2014 and 2015 were collected. The Environmental Impact Quotient (EIQ) was used to estimate the toxicity of each insecticide (https://nysipm.cornell.edu/eiq) to beneficial arthropods. EIQ assigns to each insecticide ingredient a score ranging from 5 to 125 according to its toxicity to beneficial arthropods (Kovach et al. 1992). We calculated the cumulative impact of the insecticides applied during the period of RAA presence in the apple trees (from March to July) in each orchard using the following formula:

$$EIQ_{field\ use\ rating} = \sum(EIQ_i * RT_i * \ \%active\ ingredient_i),$$

where EIQ_i is the EIQ value assigned to the active ingredient contained in the insecticide *i* relative to beneficial arthropods, RT_i, the rate of insecticide *i* use and $\%active\ ingredient_i$ the percentage of active ingredient in the insecticide *i*. The $EIQ_{field\ use\ rating}$ ranged from 0 to 6.61, depending on the year, the orchard and the cultivar (Table 1). The main active ingredients used against RAA in the cider orchard were flonicamid, acetamiprid and lambda cyhalothrin.

Monitoring of Arthropod Population Dynamics

The monitored trees were visually inspected to record the RAA abundance and the abundance of natural enemies and ants within the RAA colonies. The mean height of the monitored trees was 3.4 m (SD 0.49 m). All terminal shoots of each monitored tree were inspected from the lowest branch up to a height of 1.7 m for practical reasons. In 2014 and 2015, the trees were monitored every week from mid-April to the end of June and every two weeks from mid-March to mid-April and during July (except in the two orchards (*4a* and *4b*) located at location *4*, where the RAA populations were recorded every two weeks from April to July).

Dysaphis plantaginea

At each observation date, the total number of RAA individuals was counted on each monitored tree.

Natural Enemies and Ants Observed in RAA Colonies

At each observation date, the number and identity of each natural enemy type and the number of ants found within the RAA colonies were recorded and summed for each monitored tree. We also recorded the developmental stage of all of the observed natural enemies, as not all stages are involved in aphid control. In most cases, natural enemy identification was at the family level. Ants were not identified to the species level. However, we observed only *Lasius niger* and *Formica* sp.

Data Analysis

Dysaphis plantaginea

Three variables were considered to characterize the RAA population dynamics on each monitored tree and for each studied year to assess the different ecological processes:

(i) The presence/absence variable (*PA*), indicating the RAA colonization process, was set to 0 when no RAA was observed at any date or to 1 when at least one RAA was observed on the monitored tree

(ii) The logarithm of the area under the curve (*logAUC*) of the tree population abundance, indicating *in situ* RAA population dynamics (survival and reproduction)

(iii) The presence duration (*PD)*, in days (last date at which at least 1 aphid was observed minus the first date at which at least 1 aphid was observed), indicating the RAA emigration process

Natural Enemies and Ants

Natural enemy dynamics and ants were only assessed on the monitored trees in which at least one RAA was observed (i.e., a monitored tree where the RAA presence/absence was set to 1). The natural enemy dynamics were characterized using the same variables as for RAA (*PA*, *logAUC* and *PD*) for each considered developmental stage (egg, larva, adult) of each taxon. A global variable (*allNE*) was also created by summing the counts of all observed natural enemies for any stage and taxon. The three dynamics variables were also calculated for *allNE*. The ant dynamics were characterized in the same way as those of RAA and their natural enemies (*PA*, *logAUC* and *PD*).

Statistical Analyses

The main purpose of our study was to assess the influence of agroecological infrastructures on the three above variables characterizing RAA population dynamics. First, Generalized Linear Mixed Models (GLMM) were used to assess the influence of each considered factor (distance to the closest hedgerow, distance to the closest flower strip, $EIQ_{field\ rating\ use}$ and cultivar) on each RAA population dynamics variable (*PA*, *logAUC* and *PD*) as well as its significance. Second, to assess in what extent factor effects could result from variations in natural enemy and ant population dynamics, the same GLMMs were fitted to the population dynamics variables associated to each natural enemy taxon and to ants but including as well the rosy apple aphid abundance (*logAUC*) as a supplementary explanatory variable. This allowed assessing how the dynamics of natural enemies and ants are impacted by agroecological infrastructures and other agricultural variables for a given level of rosy apple aphid abundance. Introducing the *logAUC* of RAA as a fixed factor was equivalent to analysing the influence of the factors under study on the abundance ratio between the natural enemies and aphids or between the ants and aphids. In all models two random factors were added, the orchard location and the studied year. All statistical analyses were carried out with the R 3.1.3 software (R core Team 2015) using the tree as the observation unit.

PA were fitted assuming a binomial distribution, *logAUC* were fitted assuming a normal distribution and *PD* were fitted using a Gamma distribution, regardless of the arthropod taxon. The mixed linear models were fitted using the lme4 package, version 1.1-7 (Bates et al. 2015). A significance threshold of p=0.05 was considered.

Results

Aphid Abundance and its Variation in Space and Time

The mean abundance of RAA observed per tree and per sampling date varied widely, depending on the studied year and studied orchard. For instance, in 2014, the mean number of RAA per tree and per sampling date ranged from 0.8 in orchard *3b* to 95.5 in orchard *7a* (Table 2 and Appendix B). Globally, the pest abundance was higher in 2015 than in 2014 in all orchards, except in orchards *4a* and *4b* (Appendix B).

Community of Natural Enemies and its Variation in Space and Time

The composition of the natural enemy community remained fairly stable from one year to the next (Table 2). The natural enemy community was dominated by Syrphidae (45% and 32% of the natural enemies observed in 2014 and 2015, respectively) and Coccinellidae (22% and 36% of the natural enemies observed in 2014 and 2015, respectively), followed by Forficulidae (18% and 15% of the natural enemies observed in 2014 and 2015, respectively) and Araneae (9% of the natural enemies observed in both years). Few Chrysopidae, Hemiptera and Cantharidae were observed in both years and were not retained for the subsequent detailed statistical analyses (Table 2). Similarly few mummies were observed and the ratio of the mummy number to the RAA number never exceeded 0.2% whatever the considered year and orchard.

A large variation in the abundance of RAA, natural enemies and ants was observed among the orchards (Appendix B).

The natural enemy community composition varied strongly during the season. The community was dominated by Syrphidae early in the season and then by Coccinellidae and other natural enemies (Fig. 2). In both years, the RAA populations peaked between mid-May and the end of May.

Influence of Agricultural Practices and Agroecological Infrastructures on the Main Observed Arthropod Taxa

Table 3 provides a synthetic overview of the results of the GLMMs. Aphids and ants appeared to be more abundant in the vicinity of the hedgerows. On the contrary, hedgerows had in most cases no effect on the natural enemies. They only have a positive effect on the presence duration of Syrphidae larvae and of Syrphidae eggs and a negative effect on the presence duration of Coccinellidae larvae. On the contrary, aphids and ants were less abundant in the vicinity of the flower strips, while all of the natural enemies except the Araneae were positively impacted. All arthropods were generally more abundant on the Douce de l'Avent$_{cov}$ cultivar, followed by Judor, and were generally negatively impacted by the insecticide use ($EIQ_{field\ use\ rating}$). However, the insecticide effect on the Syrphidae and Coccinellidae was ambiguous. Indeed, the Syrphidae eggs (*logAUC* and *PD*) and Coccinellidae larvae (*PD*) were positively impacted by the $EIQ_{field\ use\ rating}$ but the Syrphidae larvae (*PA*) and the Coccinellidae eggs were negatively impacted by the $EIQ_{field\ use\ rating}$ (*PA*) (Appendix A). Finally, all natural enemy and ant abundances were positively impacted by aphid abundance. The results were generally consistent regardless of the variables used to describe the arthropod dynamics (*PA*, *logAUC* and *PD*) or the considered natural enemy stage (egg, larva, adult). Detailed results by stage and variables are provided in Appendix A.

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Discussion

Main Findings

This study was carried out under field and farming production conditions. Spatio-temporal variations regarding the abundance of aphids and of their natural enemies have long been reported to depend on farming practices (Marliac et al. 2015) and on climatic conditions (Hemptinne et al. 1994, Roy et al. 2002). Variations among locations and between years in population dynamics of RAA and their natural enemies are not surprising and were modelled as random factors to focus on the effects of farmer practices (insecticide treatment and cultivar choice) and of agroecological infrastructures (distances to the closest hedgerow and to the closest flower strip). All of these factors had an impact on population dynamics of aphids, of natural enemies and of ants. The tested factors appeared to be widely consistent among all natural enemy groups, suggesting that agricultural practices and agroecological infrastructures either favoured or disfavoured the entire community of natural enemies. While the cultivar and insecticide use intensity had a mostly similar influence on all arthropod abundances, the agroecological infrastructures had opposite effects on aphids and ants on the one hand and on natural enemies on the other hand. This result suggests that agroecological infrastructures actually impacted the level of RAA biological control by its natural enemies.

Analyses were carried out using three response variables characterizing arthropod population dynamics: presence probability, logarithm of the area under the curve and presence duration. Our hypothesis was that each variable was related to different ecological processes that could have been differentially influenced by the agricultural practices and agroecological infrastructures. However, in most cases in this study, the three variables were influenced in the same way by the agricultural practices and agroecological infrastructures, suggesting that environmental and agronomical practices had a similar influence on all of the population dynamics components.

Structuration of the Arthropod Community

Regardless of the year and orchard, Syrphidae and Coccinellidae were consistently the two most abundant groups of natural enemies, with Syrphidae being generally present earlier than Coccinellidae. These results are consistent with those of previous studies (Miñarro et al*.* 2005, Dib et al*.* 2010). However, the synchronization between the RAA and natural enemy dynamics varied between the studied years. The lowest RAA infestation level was observed in 2014, when RAA and natural enemy dynamics appeared to be the most synchronized. Indeed, in 2014, the increase of natural enemy abundance was concomitant to the increase of RAA population whereas in 2015, the natural enemy abundance was at its lowest level when the RAA infestation was highest (Fig. 2).

Hymenoptera parasitoids were very rare in both year and in all orchards. The ratio of the number of mummies to the aphid number was much lower (always less than 0.2% in all years and orchards) than in previous surveys conducted in organic apple orchards (*Dib* et al*.* 2010: up to 6.9%; Cruz de Boelpaepe et al*.* 1987: 3.3%). However, other studies similarly reported the absence or a very low abundance of parasitism in RAA colonies (Miñarro et al*.* 2005, Brown and Mathews 2007). The low level of parasitism observed in our study could result from the high sensitivity of the hymenoptera parasitoid to insecticides (Theiling and Croft 1988). Another explanation could be an antagonist effect between ants and parasitoids as evidenced in previous studies (Völkl 1992, Stewart-Jones et al*.* 2008).

As expected, all natural enemies exhibited a positive response to RAA abundance either in their probability of presence (Coccinellidae, Araneae) or in both their probability of presence and abundance (Syrphidae, Forficulidae). This is not surprising, as natural enemies frequently aggregate in places where preys are abundant. In fact, previous studies showed that it is the case for Carabidae and Staphylinidae, (Bryan and Wratten 1984) or for Syrphidae (Tenhumberg and Poehling 1995, Miñarro et al*.* 2005).

Similarly, the presence probability, logarithm of the area under the curve and presence duration of ants responded positively to RAA abundance, which was expected considering the mutualistic relation between *D. plantaginea* and the two species of ants observed (*Lasius niger* L., *Formica* sp.) (Flatt and Weisser 2000, Stewart-Jones et al*.* 2008).

This dependence of ant and natural enemy abundances on RAA abundance supported our choice to include RAA abundance as a factor in the models (through the *logAUC* of RAA). In this way, we were able to analyse the direct effects of farmer practices and agroecological infrastructures on natural enemies and ants.

Practices and Cultivar Influence

Impact of Insecticides on RAA and Natural Enemy Population Dynamics

As expected, we observed a decrease in the probability and duration of RAA presence with an increase of the $EIQ_{field\ use\ rating}$, but the $EIQ_{field\ use\ rating}$ effect on RAA abundance (*logAUC*) was not significant (Table 3 and Appendix A). Such an effect is especially expected in leaf-curling aphids, such as *D. plantaginea*. Indeed, aphids are more vulnerable to insecticides in the first phase of colonization, resulting in a reduction of the colonization success and hence on the presence probability. The aphid vulnerability further decreases while the colony size increases because the rolling-up of leaves provides them with protection against insecticides (Cross et al*.* 2007). Moreover, the negative effect of insecticides on natural enemies might further reduce aphid biological control. A negative effect of insecticide treatments was observed on the presence probability of *allNE* and on their abundance (*logAUC*). This negative effect was significant on the presence probability of Syrphidae larvae, of Syrphidae eggs and of Coccinellidae eggs, as well as on the Forficulidae abundance and on Araneae presence duration. Insecticide treatments applied early in the season seem to be the most efficient to control the development of *D. plantaginea* colonies. Insecticide applications after the leaf curling, would impact more strongly the natural enemies than aphids. High $EIQ_{field\ use\ rating}$ also reduced ant abundance in RAA-infested trees, suggesting that insecticide treatments also negatively impact the ant population.

Effect of Cultivar on RAA and Natural Enemy Population Dynamics

A strong impact of the cultivar was observed in our study and its effect varied whether we considered the presence probability and the presence duration of RAA and natural enemies or the abundance of RAA and natural enemies (except for the Dabinett cultivar, which always exhibited the lowest presence probability, abundance and presence duration of RAA and natural enemies). Douce de l’Avent$_{cov}$ had the highest presence probability and presence duration of RAA and natural enemies (*AllNE*), followed by Judor. For the RAA, this ranking matches cultivars ranked according to precocity. Douce de l’Avent$_{cov}$

was the most precocious cultivar, followed by Judor, with Dabinett being the latest cultivar. Miñarro and Dapena, (2007) still showed that early-leafing apple cultivars were more infested and damaged by RAA than late-leafing ones. We can suppose that the same process operates for natural enemies. However, a different cultivar ranking was obtained when the abundance of RAA and natural enemies was considered, switching between cultivars: Judor had the higher abundance of RAA and of natural enemies (*AllNE*), followed by Douce de l'Avent$_{cov}$. This apparent inconsistency could result from an interaction between the colonization rate and treatment frequency. In fact, the most heavily colonized cultivar (Douce de l'Avent$_{cov}$) was also the earliest one treated with insecticides, resulting in low abundances of both aphids and natural enemies throughout the season.

Hedgerows Favour RAA Populations

Unexpectedly, hedgerows appeared to be consistently beneficial to RAA populations. Indeed, hedgerow proximity had a positive impact on all of the RAA population dynamics parameters. This hedgerow effect may result from either direct effects on the RAA population dynamics, from indirect effects through its influence on mutualistic or antagonist arthropods, or both. The vicinity of the hedgerow may influence the flight behaviour of arthropods by modifying the wind speed and turbulences (Pasek 1988), which could result in the accumulation of insects on the leeward side of the hedgerow (Lewis 1965, Grüebler et al*.* 2008). Such an effect could result in a higher colonization rate by RAA of apple trees situated in the vicinity of hedgerows.

Hedgerows may also indirectly favour aphids by favouring mutualistic ants possibly by providing a suitable nesting habitat. Indeed, the ant presence probability increased with the proximity to the hedgerow in our study. To our knowledge, very few studies have assessed hedgerow influence on ants. Stutz and Entling (2011) found no effect of a woody habitat in the surrounding landscape on ant presence on cherry trees, but Armbrecht and Perfecto (2003) reported a dramatic decrease of twig-nesting ants with an increase in the distance to forest fragments in coffee plantations in Mexico.

Finally, the proximity of hedgerows may modify the arthropods interaction network. For instance, the presence of a hedgerow could reduce RAA biocontrol by increasing the intra-guild predation between natural enemies (Straub et al*.* 2008) or by diverting natural enemies from pests by offering them alternative prey (Kozar et al*.* 1994, Koss and Snyder 2005, Symondson et al*.* 2006). Moreover, as the presence of ants is higher in the hedgerow vicinity, the protection they provide to RAA against their natural enemies could be enhanced. Contrary to previous studies (Altieri and Schmidt 1986, Miñarro and Prida 2013), few hedgerow-distance effects on natural enemy occurrence or abundance in aphid colonies were found in our study. The only significant effects were the decrease of the presence probability and of the presence duration of Coccinellidae larvae and the increase of the presence duration of Syrphidae larvae and Syrphidae eggs in the vicinity of the hedgerow.

Flower Strips Reduce RAA Populations and Increase Natural Enemy Abundance

Contrary to hedgerows, flower strips had a negative impact on the RAA populations in our study. Indeed, the presence probability, the abundance and the presence duration of RAA all decreased with flower strips proximity. A direct effect of flower strips on aphids was very unlikely. We then assumed that flower strips exerted an indirect effect through their influence on the natural enemies and/or on ants. Indeed, Wyss, (1995) and Wyss et al. (1995) showed that introducing flower strips in apple orchards resulted in an increase in natural enemy abundance (Chrysopidae, Coccinellidae, Araneae). Similarly, in our study, the abundance (*logAUC*) and presence duration of natural enemies (*allNE*) increased in proximity to flower strips. More specifically, the presence probability and abundance of Syrphidae (eggs and larvae), presence probability of Coccinellidae (eggs and larvae) and abundance of Forficulidae decreased significantly with the distance to flower strips. This increase of presence and/or of abundance of natural enemies could enhance aphid biological control in the vicinity of flower strips. Hogg et al. (2011) showed that floral resources enhanced aphid suppression by the hoverfly *Eupeodes fumipennis* in a California lettuce field. In addition, the negative influence of flower strips on aphid populations could also be amplified by their negative effect on the ant presence probability. Nagy et al. (2013) showed that applying artificial sugar sources in apple orchards resulted in a reduction of the number of ant-attended *D. plantaginea* colonies and in an increase in natural enemy pressure. Similarly, by providing alternative sugar resources, flower strips could distract ants from aphid attendance. Katayama et al. (2013) showed that extrafloral nectar was more attractive to ants than aphid honeydew. In total, our results suggest that flower strips are beneficial to natural enemies and reduce ant attendance that could account for the observed reduction of *D. plantaginea* infestation in cider-apple trees located in the vicinity of flower strips.

Conclusion

This study showed an impact of the distance to agroecological infrastructures on *D. plantaginea* dynamics in cider-apple orchards. Hedgerows increased the RAA infestation level. This could result from an indirect effect due to modifications in the RAA interactions network with other arthropods. Indeed, our results showed an increase in the presence of mutualistic ants and a decrease in RAA natural enemy abundance in the vicinity of hedgerow. On the contrary, flower strips appeared unfavourable to *D. plantaginea*. Again it could result from indirect effect due to an increase in natural enemy abundance and a decrease of ant presence in the RAA colony. Additionally, we confirmed a strong influence of cultivars and of insecticide use intensity on *D. plantaginea* dynamics.

Acknowledgments

We thank A. Taillade and A. Quero for data collection and the farmers who allowed us to access their orchards. We thank Sylvaine Simon for her help in the characterization of agroecological infrastructure. We thank two anonymous reviewers for their useful comments on a previous version of this manuscript. The work was supported by ANRT, UNICID, Région Bretagne, Région Normandie and the Ministère de l'Agriculture, de l'agroalimentaire et de la forêt (CASDAR). This project is linked to the PEERLESS project (ANR-12-AGRO-0006) and to the "Verger Cidricole de Demain" CASDAR project.

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TABLE

Table 1: Main characteristics of the 14 studied cider-apple orchards. Two contiguous orchards (referred by *a* or *b*) have been monitored in each location (referred by number). In each orchard, 3 cider-apple cultivars were planted (DDA = Douce de l'Avent$_{cov}$ cultivar, DAB = Dabinett cultivar and JUD= Judor cultivar). The Environmental Impact Quotient (EIQ) of each insecticide applied during the RAA presence on the apple trees was used to assess the cumulative toxicity of insecticides used in each orchard each year ($EIQ_{field\ use\ rating}$). *: only 63 trees monitored in 2014; **:only 425 trees monitored in 2014. NA means Not Applicable.

Location		1		2		3		4		5		6		7	
Orchard		1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b
Year of planting		2010	2010	2012	2012	2011	2011	2012	2012	2011	2011	2011	2011	2010	2010
Density of planting by number of trees/ha (planting distance between rows*planting distance within rows)		774 (5.5*2.3)	774 (5.5*2.3)	495 (6.5*3)	774 (5.5*2.3)	774 (5.5*2.3)	774 (5.5*2.3)	495 (6.5*3)	774 (5.5*2.3)	1000 (5.3*2)	1000 (5.3*2)	774 (5.5*2,3)	774 (5.5*2.3)	774 (5.5*2.3)	774 (5.5*2.3)
Number of monitored trees		198	198	153	153	162	162	117*	117*	234	234	279	279	270**	270**
$EIQ_{field\ use\ rating}$ 2014 in (for each apple cultivar)	DDA	0.61	5.58	0	1.20	0.35	0.35	0	0	NA	NA	NA	NA	0	0.29
	DAB	0.61	5.58	0	1.20	0.35	0.35	0	0	NA	NA	NA	NA	0	2.09
	JUD	0.61	5.58	0	1.20	0.35	0.35	0	0	NA	NA	NA	NA	0	0
$EIQ_{field\ use\ rating}$ 2015 in (for each apple cultivar)	DDA	0.67	6.61	0	0	0	2.80	0	1.16	0.087	0.33	0	6.81	0	0.24
	DAB	0.67	6.61	0	0	0	1.60	0	1.16	0.087	0.33	0	4.67	0	0.35
	JUD	0.67	6.61	0	0	0	2.80	0	1.16	0.087	0.33	0	6.61	0	0.35

Mean distance (+SD) of orchard trees to the closest flower strip (in m) (according to the year)	2014	0 (0)	34.5 (14.2)	0 (0)	38.9 (11.3)	1 (0)	43.6 (12.0)	2 (0)	24.9 (4.6)	NA	NA	NA	NA	1.5 (0)	39.8 (13.2)
	2015	0 (0)	34.5 (14.2)	0 (0)	38.9 (11.3)	1 (0)	43.6 (12.0)	2 (0)	31.8 (8.6)	10.8 (6.2)	27.0 (12.9)	11.9 (6.9)	36.9 (14.8)	1.5 (0)	33.4 (11.9)
Mean distance (+SD) of orchard trees to the closest hedgerow (in m) (according to the year)	2014	16.0 (7.2)	21.3 (11.8)	23.9 (12.9)	20.7 (10.4)	21.3 (11.0)	21.3 (11.0)	15.5 (6.0)	13.8 (4.64)	NA	NA	NA	NA	21.5 (11.3)	28.1 (12.9)
	2015	16.9 (7.2)	21.3 (11.8)	23.9 (12.9)	20.7 (10.4)	21.3 (11.0)	21.3 (11.0)	20.8 (10.4)	18.3 (8.2)	14.3 (6.6)	15.2 (6.5)	27.6 (14.1)	27.6 (14.1)	23.7 (12.7)	23.7 (12.7)

Table 2: **Total number of observed arthropods (and range of the mean number for one monitored tree per observation in one studied orchard) by taxonomic group, life stage and year.**

			Year		Total
			2014	2015	
Number of studied orchards			10	14	
Total number of observations (date*orchard)			35 (from 5 to 10)	57 (from 5 to 11)	103
Order	Family	Life stage			
Diptera	Syrphidae	Eggs	1083 (from 5.6^-2 to 0.50)	1122 (from 2.9^-2 to 1.7)	2205
		Larvae	408 (from 1.0^-2 to 0.47)	429 (from 3.0^-2 to 0.51)	838
		Adults	9 (from 0 to 1.0^-2)	51 (from 0 to 5.3^-2)	60
		All	1500 (from 6.6^-2 to 0.71)	1602 (from 6.0^-2 to 2.3)	3103
Coleoptera	Coccinellidae	Eggs	533 (from 0 to 4.7^-1)	1325 (from 0 to 5.2)	1858
		Larvae	141 (from 0 to 2.7^-1)	343 (from 0 to 3.8^-1)	484
		Adults	65 (from 6.3^-3 to 8.8^-2)	161 (from 0 to 3.8^-1)	226
		All	739 (6.3^-3 to 0.79)	1829 (from 0 to 6.4)	2568
	Cantharidae	Adults	17 (from 0 to 1.2^-2)	68 (from 0 to 4.1^-2)	85
Hemiptera	Anthocoridae	-	34 (from 0 to 4.5^-2)	92 (from 0 to 5.0^-2)	126
	Miridae	-	37 (from 0 to 1.2^-2)	114 (from 0 to 1.7^-1)	153
	Nabidae	-	67 (from 0 to 2.4^-1)	0 (from 0 to 0)	67

			Year		
			2014	2015	Total
Number of studied orchards			10	14	
Total number of observations (date*orchard)			35 (from 5 to 10)	57 (from 5 to 11)	103
Neuroptera	Chrysopidae	Eggs	9 (from 0 to 1.2^-2)	0 (from 0 to 0)	9
		Larvae	0 (from 0 to 0)	2 (from 0 to 6.0^-3)	2
		Adults	0 (from 0 to 0)	3 (from 0 to 2.3^-3)	3
		All	9 (from 0 to 1.2^-2)	5 (from 0 to 6.0^-3)	14
Dermaptera	Forficulidae	Juveniles+adults	582 (from 0 to 0.36)	742 (from 2.9^-3 to 0.60)	1324
Hymenoptera		Mummies	33 (from 0 to 3.2^-2)	108 (from 0 5.4^-2)	141
		Adults	12 (from 0 to 3.2^-2)	25 (from 0 to 1.9^-2)	37
		All	45 (from 0 to 6.5^-2)	133 (from 0 to 5.7^-2)	178
Araneae		Juveniles+Adults	296 (from 0 to 0.16)	440 (from 0 to 0.16)	737
AllNE			3326 (from 0.10 to 1.45)	5025 (from 0.30 to 7.4)	8355
Number of RAA			206195 (from 0.77 to 95.5)	554230 (from 21.0 to 182.4)	760425
Ratio (natural enemies per RAA)			0.016 (from 5.0^-4 to 0.18)	0.009 (from 2.4^-3 to 0.21)	0.0109
Ants			9279 (from 2.4^-2 to 3.8)	15578 (from 4.7^-2 to 7.1)	24857

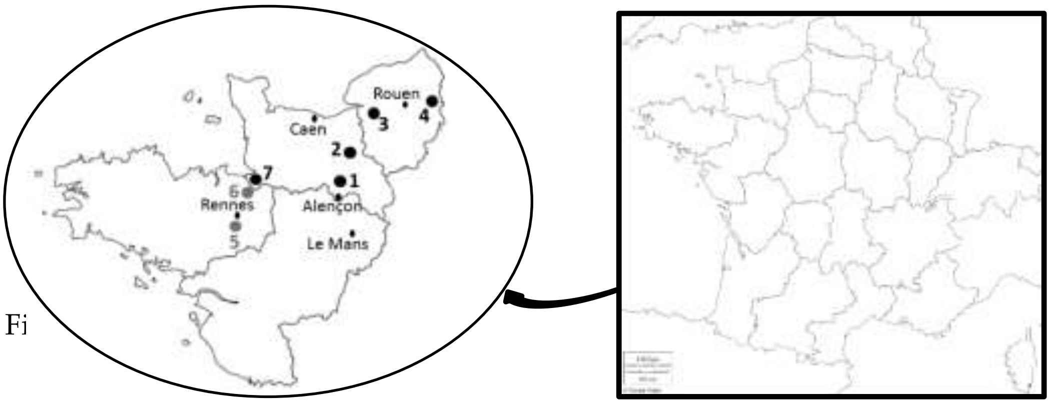
Table 3: Synthetic overview of the Generalized Linear Mixed models results: “+” (resp. “-“) indicates that the factor is favourable (resp. unfavourable) to the considered arthropods. For the distance, a “+” (resp. “-“) indicates that the arthropods are more (resp. less) present in the vicinity of the agroecological infrastructure. For the cultivar factor “∗” means that cultivar has a significant effect on the response variable (*PA*, *logAUC* or *PD)* for at least one arthropod stage. 0 indicates that the factor did not significantly influence the variable. NA: not applicable. See Appendix A for detail.

	RAA	AllNE	Syrphidae	Coccinellidae	Forficulidae	Araneae	Ants
Distance to the closest hedgerow	+	0	+	-	0	0	+
Distance to the closest flower strip	-	+	+	+	+	0	-
Cultivar (*PA*/*logAUC*/*PD*)	∗/∗/∗	∗/∗/∗	∗/0/∗	∗/∗/∗	∗/0/0	∗/0/0	∗/0/0
$EIQ_{field\ use\ rating}$	-	-	-	-	-	-	-
RAA	NA	+	+	+	+	+	+

FIGURE LEGENDS

Fig. 1. Map of the seven studied locations (two orchards per location). Black dots are the locations studied both in 2014 and 2015. Grey dots are the locations studied in 2015.

Fig. 2. Mean number (+ SE) of RAA (black dot), of all natural enemies (grey dotted line with circle mark), of Syrphidae (all stages) (grey dotted line with triangle mark) and of Coccinellidae (all stages) (grey dotted line with square mark) per monitored apple tree in aphid colonies in 2014 (A) and 2015 (B).



Fi

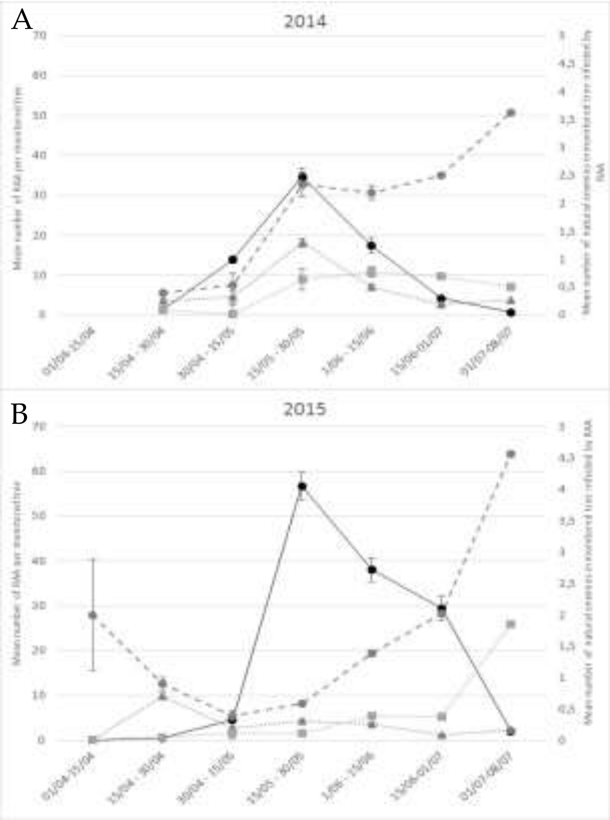

A
2014
Mean number of RAA per monitored tree
Mean number of natural enemies in monitored tree infested by RAA
70
60
50
40
30
20
10
0
5
4,5
4
3,5
3
2,5
2
1,5
1
0,5
0
01/04-15/04
15/04 - 30/04
30/04 - 15/05
15/05 - 30/05
1/06 - 15/06
15/06-01/07
01/07-08/07
B
2015
Mean number of RAA per monitored tree
Mean number of natural enemies in monitored tree infested by RAA
70
60
50
40
30
20
10
0
5
4,5
4
3,5
3
2,5
2
1,5
1
0,5
0
01/04-15/04
15/04 - 30/04
30/04 - 15/05
15/05 - 30/05
1/06 - 15/06
15/06-01/07
01/07-08/07

Fig. 2

Supplementary Material

Impact of Agroecological Infrastructures on the Dynamics of *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) and its Natural Enemies in Apple Orchards in Northwestern France

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Contents

Appendix A: Results of Generalized Linear Models obtained for each arthropod (by taxon and stage) and each variable.

Appendix B: Sum of arthropods observed per orchard each studied year (2014 and 2015) and mean number of arthropods per sampling date per tree infected with rosy apple aphid

Appendix A: Results of Generalized Linear Models obtained for each arthropod (by taxon and stage) and each variable. The first line is the pvalue of the variable, when inferior to 0.05, the second line is the coefficient. NS means no-significant. EIQ means Environmental Impact Quotient. AUC mean Area Under the Curve. DAB means cultivar of Dabinett, DDA means cultivar of Douce de l'Avent$_{cov}$ and JUD means cultivar of Judor.

		Variables studied				
		Log AUC of *D. plantaginea*	Distance to the hedgerow	Distance to the flower strips	Cultivar	EIQ$_{\text{field use rating}}$
Dysaphis plantaginea	Probability of presence (binomial distribution)		**0.002537 -0.0058	*** < 2.2e-16 0.0111	5.348e-12 DAB<JUD<DDA	*** 7.166e-05 -0.057
	Log(Area Under the Curve) (normal distribution)		*** 0.0001546 -0.0171	*0.03814 0.0063	** 0.003741 DAB<DDA<JUD	NS 0.7999
	Presence duration (Gamma distribution)		*** <2.2^-16 -0.0057	*** 7.867e-16 0.0022	*** < 2.2e-16 DAB<JUD<DDA	*** 8.676e-13 -0.019
Global natural enemies	Probability of presence (binomial distribution)	***< 2.2e-16 0.277	NS 0.3227	NS 0.1266	***1.279e-10 DAB<JUD<DDA	*** 4.617e-05 -0.091
	Log(Area Under the Curve) (normal distribution)	***< 2.2e-16 0.194	NS 0.4274	***3.266e-06 -0.0082	***0.0004949 DAB<DDA<JUD	0.005526 -0.051
	Presence duration (Gamma distribution)	*** 2.894e-11 0.0535	NS 0.1892	**0.001459 -0.0029	** 0.003236 DAB<JUD<DDA	NS 0.2187
Eggs of Syrphidae	Probability of presence (binomial distribution)	*** < 2.2e-16 0.185	NS 0.7486	* 0.0366 -0.0048	*** 2.754e-05 DAB<JUD<DDA	0.01154 -0.0586
	Log(Area Under the Curve) (normal distribution)	*** 7.458e-08 0.122	NS 0.8587	** 0.001588 -0.00787	NS 0.1269	NS 0.1041
	Presence duration (Gamma distribution)	*** 4.961e-06 0.0422	*0.04781 -0.0034	*** 6.688e-05 -0.0044	NS 0.6885	*0.03559 0.0225
Larvae of Syrphidae	Probability of presence (binomial distribution)	***< 2.2e-16 0.286	NS 0.8352	** 0.002112 -0.0078	*** 9.99e-06 DAB<JUD<DDA	*** 0.0008589 -0.090
	Log(Area Under the Curve) (normal distribution)	*** 1.125e-07 0.117	NS 0.8032	* 0.03901 -0.00452	NS 0.08464	NS 0.4199
	Presence duration (Gamma distribution)	*** 0.0009433 0.0376	** 0.00516 -0.00536	NS 0.4155 -0.00091	* 0.02581 DAB<DDA<JUD	NS 0.6054
Eggs of Coccinellidae	Probability of presence (binomial distribution)	*** 8.057e-07 0.219	NS 0.1241	0.02953 -0.010	NS 0.2564	** 0.006066 -0.364
	Log(Area Under the Curve) (normal distribution)	NS 0.6864	NS 0.3697	NS 0.1016	** 0.002943 JUD<DAB<DDA	NS 0.8945
	Presence duration (Gamma distribution)	NS 0.06483	NS 0.4644	NS 0.3969	*0.04445 JUD<DAB<DDA	NS 0.3095
Larvae of Coccinellidae	Probability of presence (binomial distribution)	*** < 2.2e-16 0.285	** 0.005793 0.0162	*** 0.000528 -0.011	**0.00986 DAB<DDA<JUD	NS 0.4914
	Log(Area Under the Curve)	* 0.02581 0.122	NS 0.75	NS 0.4144	NS 0.728	NS 0.294

	(normal distribution)					
	Presence duration (Gamma distribution)	NS 0.1201	* 0.03643 0.0057	NS 0.7773	* 0.01121 JUD<DAB<DDA	NS 0.07431
Adults of Coccinellidae	Probability of presence (binomial distribution)	*** 7.437e-15 0.246	NS 0.6654	NS 0.4651	* 0.01922 JUD<DAB<DDA	NS 0.09964
	Log(Area Under the Curve) (normal distribution)	NS 0.491	NS 0.1347	NS 0.895	NS 0.1843	NS 0.5245
	Presence duration (Gamma distribution)	NS 0.8494	NS 0.5724	NS 0.6548	*0.01378 JUD<DAB<DDA	NS 0.4131
Forficulidae (Juveniles and adults)	Probability of presence (binomial distribution)	*** < 2.2e-16 0.223	NS 0.9295	NS 0.8388	*0.01662 DAB<DDA<JUD	NS 0.2327
	Log(Area Under the Curve) (normal distribution)	** 0.001888 0.0892	NS 0.1346	0.04627 -0.005	NS 0.05784	* **0.0006422 -0.097
	Presence duration (Gamma distribution)	*0.03107 0.0304	NS 0.2126	** 0.005847 -0.00534	NS 0.5498	NS 0.9349
Araneae (Juveniles and adults)	Probability of presence (binomial distribution)	*** 4.533e-12 0.146	NS 0.9254	NS 0.1275	*** 1.155e-10 DAB<JUD<DDA	NS 0.08618
	Log(Area Under the Curve) (normal distribution)	NS 0.3479	NS 0.9367	NS 0.3193	NS 0.74	NS 0.1281
	Presence duration (Gamma distribution)	NS 0.1252	NS 0.5216	NS 0.4528	NS 0.1029	** 0.001295 -0.059
Ants	Probability of presence (binomial distribution)	*** < 2.2e-16 0.405	*** 0.000344 -0.0146	0.008168 0.0068	* 0.01761 JUD<DAB<DDA	NS 0.8418
	Log(Area Under the Curve) (normal distribution)	*** < 2.2e-16 0.509	NS 0.5379	NS 0.8873	NS 0.4117	* * 0.006257 -0.049
	Presence duration (Gamma distribution)	*** < 2.2e-16 0.152	NS 0.1676	NS 0.8688	NS 0.6604	NS 0.2145

Appendix B: Sum of arthropods observed per orchard each studied year (2014 and 2015) and mean numb infected with rosy apple aphid

			Diptera				Coleoptera				Dermaptera	Hymenoptera	
			Syrphidae				Coccinellidae				Forficulidae	-	
Orchard	Sampling year	Sum of monitored tree per year	Eggs	Larvae	Adults	Total	Eggs	Larvae	Adults	Total	Nymph +adults	Mummies	adults
1a	2014	1980	246 0.26	102 0.10	0 0	348 0.37	41 0.04	5 5.3^-3	7 7.5^-3	53 0.05	337 0.36	3 3.2^-3	0 0
	2015	2574	294 0.43	63 0.09	3 4.4^-3	360 0.53	13 0.01	1 1.4^-3	4 5.8^-3	18 0.02	411 0.60	0 0	0 0
1b	2014	1980	234 0.29	11 0.01	0 0	245 0.31	0 0	0 0	5 6.3^-3	5 6.3^-3	156 0.19	0 0	0 0
	2015	2574	43 0.04	21 0.03	1 1.4^-3	65 0.09	0 0	2 2.1^-3	8 8.4^-3	10 0.01	211 0.22	0 0	2 2.1^-3
2a	2014	1377	282 0.50	119 0.21	0 0	401 0.71	260 0.46	43 0.07	9 0.01	312 0.55	18 0.03	1 1.7^-3	0 0
	2015	1683	23 0.09	36 0.14	0 0	59 0.23	53 0.21	35 0.13	5 0.01	93 0.37	4 0.01	9 0.03	0 0
2b	2014	1377	148 0.19	84 0.11	0 0	232 0.31	32 0.04	15 0.02	5 6.7^-3	52 0.06	8 0.01	2 2.6^-3	0 0
	2015	1683	13 0.02	39 0.15	1 3.9^-3	53 0.21	126 0.28	125 0.28	7 0.01	258 0.59	4 9.1^-3	5 0.01	3 6.8^-3
3a	2014	810	19 0.06	3 0.01	0 0	22 0.08	15 0.05	1 3.6^-3	6 0.02	22 0.08	3 0.10	0 0	0 0
	2015	972	235 1.79	67 0.51	7 0.05	309 2.35	221 1.68	51 0.38	37 0.28	309 2.35	24 0.18	0 0	2 0.01
3b	2014	810	16 0.05	3 0.01	0 0	19 0.06	0 0	0 0	5 0.01	5 0.01	5 0.01	0 0	0 0
	2015	972	21 0.13	23 0.17	0 0	44 0.33	0 0	0 0	4 0.02	4 0.02	31 0.19	0 0	0 0
4a	2014	378	6 0.07	9 0.11	0 0	15 0.18	19 0.24	21 0.26	4 0.05	44 0.55	0 0	1 0.01	0 0
	2015	819	34 0.65	2 0.03	1 0.01	37 0.71	247 4.75	15 0.28	20 0.38	282 5.43	1 0.01	0 0	1 0.01
4b	2014	378	11 0.16	2 0.02	0 0	13 0.19	32 0.47	16 0.23	6 0.088	54 0.79	7 0.10	0 0	0 0
	2015	819	28 0.35	5 0.09	1 0.019	34 0.65	441 5.58	35 0.44	31 0.39	507 6.41	0 0	1 0.01	0 0
5a	2015	2574	109 0.10	52 0.04	4 3.8^-3	165 0.15	27 0.025	2 1.9^-3	6 5.7^-3	33 0.03	13 0.01	57 0.05	3 2.8^-3
5b	2015	2574	206 0.19	66 0.06	7 6.7^-3	279 0.26	108 0.10	72 0.06	27 0.024	136 0.12	9 8.5^-3	24 0.02	5 4.7^-3
6a	2015	2790	24 0.05	13 0.03	3 6.9^-3	40 0.09	89 0.20	4 9.3^-3	11 0.025	104 0.24	1 2.3^-3	1 2.3^-3	0 0
6b	2015	2790	8 0.03	0 0	6 0.01	14 0.03	0 0	1 3.9^-3	1 3.9^-3	2 7.8^-3	1 3.9^-3	0 0	3 0.01
7a	2014	1875	8 0.12	42 0.45	1 0.10	51 0.54	24 0.25	26 0.27	4 0.04	54 0.58	1 0.10	3 0.03	3 0.03

	2015	2700	26	18	6	50	0	0	0	0	15	0	3
			0.12	0.08	0.02	0.24	0	0	0	0	0.07	0	0.01
7b	2014	1875	47	33	1	81	85	12	8	105	43	20	3
			0.17	0.09	2.8^-3	0.22	0.24	0.03	0.02	0.29	0.12	0.05	8.4^-3
	2015	2700	58	24	11	93	0	0	0	0	17	11	3
			0.17	0.11	0.05	0.44	0	0	0	0	0.05	0.03	9.1^-3

Projet ANR-12-AGRO-006

PEERLESS

Identification of plant species and functional traits that have the potential to improve pest control

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Identification of plant species and functional traits that have the potential to improve pest control
Nature du livrable	Articles
Date	29/06/2016
	Version 2

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Partenaires impliqués	IGEPP, Agronomie
Tâche associée	Tâche 2, sous-tâche 2-1

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

The main objective of the associated studies was to evaluate the role of adjacent non-crop vegetation in the regulation of pest insects in the field. First the existing literature was reviewed for plant traits that may favour natural enemies and thus contribute to biological control. The review was particularly focused on the influence of the community context (plant and animal communities) on arthropod behaviour and performance. Second, a field study was run for three years in the Maine-et-Loire department to identify plant traits and/or plant species that may improve regulation of pest insects in wheat and oilseed rape fields. The design was based on a previous study showing a strong positive influence of flowering entomophilous plants on the regulation of herbivores on phytometer crop plants (*Brassica oleracea*) planted within herbaceous field margins (Bischoff et al. 2016). The objective of the present study was to evaluate whether the strong relationship found in close contact to non-crop vegetation can be confirmed within fields.

B.2 RESUME

Maximum 1 page en français.

In a literature review, it was analysed how a trait-based approach could be used to understand plant-arthropod interactions in agroecosystems. Taking conservation biological control as a case study, we first reviewed the properties of arthropod communities related to biological control. We then synthesised the interaction traits involved in trophic and non-trophic interactions between plants and arthropods. Interaction traits include plant features associated with the provision of trophic resources (attractiveness, accessibility, quality, temporal availability) or with the modification of non-trophic habitat functions (shelter, microclimate).

Progresses have to be made in our understanding of the scaling up from individual to community traits. The extent to which arthropod communities are affected by plant community traits values and their distribution remains widely unexplored. While it can be expected that plant functional diversity and redundancy may be related to a better self-regulation of arthropod communities, this would rather result in an increasing difficulty to predict the effect of plant assemblages.

A trait-based approach to improve our knowledge on relationships between plant assemblages and provided ecosystem services, in particular pest control, is very promising. It would allow providing scientific bases for the design and optimization of agroecological pest management such as optimized plant mixtures for flower strips or an adapted management of semi-natural habitats.

In a field study, the influence of field margin vegetation on the regulation of major pest insects was analysed in wheat and oilseed rape fields of Western France. Altogether 64 fields were analysed, 16 fields of each crop species in each of two years. All pest insects and natural enemies occurring on crop plants were analysed at a distance of 5 and 50 m from the field margin. Additionally, pollen beetle larvae were dissected to evaluate the presence of parasitoids and cereal aphid mummies were counted. The damage caused by cereal leaf beetle and by stem weevils was recorded. At the same time all vascular plants were identified in the adjacent field margin. Plant cover and the percentage of plants flowering at the survey date were estimated.

The study demonstrated a significant effect of the cover of functional groups on crop herbivores and natural enemies indicating an important role in herbivore regulation. In particular, the cover of entomophilous plant species that were flowering at the survey date was positively correlated with natural enemy abundance and action on herbivores. In winter wheat positive correlations were found for hoverflies, ladybugs and aphid parasitism, in oilseed rape a positive correlation was observed for ladybugs and a negative one for aphids. Plant diversity and the cover of taxonomically related plant species that share herbivore species with crop plants had a much smaller influence on regulation. In wheat none of the two variables were significantly correlated to any of the insect groups whereas in oilseed rape several significant correlations were observed. However, only correlations with taxonomically related wild brassicaceae species suggested a potential contribution to herbivore regulation.

Within entomophilous flowering plants, several species could be identified that are linked to a better herbivore regulation such as *Papaver rhoeas* in both crops, *Galium mollugo* and *Rosa canina* in wheat and *Sonchus asper* in oilseed rape. However, correlations were specific for just one herbivore or natural enemy group. So it seems to be impossible to use individual plant species for the regulation of several different pest insect groups. In multivariate ordination techniques analysing plant and insect communities together, the position of natural enemies is often close to their prey/host species (i.e. pest insects). Positive correlations of plant species and natural enemies improving regulation are thus often coupled with positive correlations between the same plant species and pest insects. Therefore, it is difficult to evaluate the causality of plant – natural enemy – pest insect correlations. A better regulation caused by the presence of particular plant species does not necessarily result in lower pest insect abundance or damage.

In conclusion, the field study confirmed that a trait-based approach may be helpful to improve pest insect regulation by non-crop plants favouring natural enemies. In general, entomophilous species that flower at peak infestation of pest insects contribute to a generally higher regulation level. However, the choice of plant species within this group depends on crop species and major pest insects.

C PRÉSENTATION DES AVANCÉES

Deux manuscrits sous-presse sont annexés à ce livrable

Gardarin A., Plantegenest M., Bischoff A., Valantin-Morison M. (2018) Understanding plant-arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. Journal of Pest Science, published online, https://doi.org/10.1007/s10340-018-0958-0.

Pollier A., Guillomo L., Tricault Y., Plantegenest M., Bischoff, A. (2018) Effects of spontaneous field margin vegetation on the regulation of herbivores in two winter crops. Basic and Applied Ecology, published online https://doi.org/10.1016/j.baae.2018.02.004.

Understanding plant-arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics

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Acknowledgements

This work was partially supported by the Agence Nationale de la Recherche PEERLESS project (ANR-12-AGRO-0006). We thank the reviewers for their helpful comments on the manuscript.

Summary

The role of biodiversity in ecosystem services delivery is increasingly addressed via trait-based functional approaches. We reviewed and discussed the contribution of a trait-based approach to understand plant-arthropod interactions and to improve conservation biological control. A stable biological control of multispecies herbivore communities requires functional diversity and redundancy of natural enemies, including specialists and generalists, with reduced antagonistic interactions. Managing these arthropod communities through plant community management implies that plant community support several functions including the provision of diversified trophic resources and of appropriate physical habitats. Many studies have screened plant species in terms of trophic resource and overwintering habitats provisioning to arthropods, but results are often species-specific. Describing communities in terms of trophic and non-trophic interaction traits between plants and animals would allow extrapolating to unstudied species and hence enhancing the generality of the findings. Studies on plant-herbivore and of plant-pollinator interactions identified several important traits related to trophic resource provision, such as resource quantity, accessibility, quality and temporal availability. In contrast, traits related to physical habitat provision and microclimate modification remain less explored. Several metrics describing the community functional composition and diversity have been proposed to extend trait-based approach to plant community level, but the extent to which multitrophic communities are affected by plant traits remains largely unexplored. The step forward will be to identify the combinations of these plant community metrics that best explain their impact on arthropod communities and to disentangle the roles of plant functional composition and diversity.

Keywords: entomophagous arthropods; flower strip; functional diversity; functional trait; interaction trait; natural enemy

Key message

- Managing arthropod communities for conservation biological control implies that plant communities provide diversified trophic resources and physical habitats.
- A trait-based approach would allow producing more generic knowledge.
- Several interactions traits related to resource provision have been identified, while traits related to physical habitat provision remain less investigated.
- At community level, how multitrophic communities are affected by plant traits remains largely unexplored.
- A functional description of plant communities could help manage semi-natural habitats to enhance pest biological control.

Author contribution statement

AG, AB and MP wrote the paper. MVM provided comments on the manuscript.

Introduction

There is increasing evidence that semi-natural habitats provide a wide range of services (Wratten et al. 2012) that depend on ecosystem functioning and on its interactions with the management of these habitats. The role of biodiversity in ecosystem service provisioning is increasingly addressed via trait-based functional approaches relating environmental variables including habitat management to community assembly and structure and to ecosystem functioning. Trait-based approaches are widely developed in plant ecology (e.g. Lavorel et al. 2011) and have been extended to other groups such as soil invertebrates (Birkhofer et al. 2017; Pey et al. 2014), but studies connecting different trophic levels based on their traits remain infrequent (Boukal 2014; but see Moretti et al. 2013).

However, several ecosystem services, such as herbivore regulation, pollination or biogeochemical cycles, depend on multitrophic interactions and there is an urgent need to improve knowledge on the relations between plant and animal communities (Wood et al. 2015). The functioning of species-rich assemblages interrelated through interaction networks has been little studied to date and the underlying mechanisms underpinning the functioning of such assemblage remain poorly understood and quantified (Violle et al. 2014). Recent studies have found correlations between the functional composition of vegetation and the abundance of phytophagous invertebrates in agroecosystems (Storkey et al. 2013) and natural habitats (Frenette-Dussault et al. 2013). Here, we extend the trait-based framework of Lavorel et al. (2013) that focused on trophic interactions, to non-trophic interactions, and we specify how it applies to conservation biological control in agroecosystems.

Our understanding of interactions between plant and animal communities and their effect on biological control of pests remains limited. Conservation biological control aims at increasing the abundance, diversity and efficiency of natural enemies through environmental management and the adoption of accurate agricultural practices. Species-rich habitats such as linear field margins between crop fields support pest natural enemy populations, contribute to the improvement of the biological control of crop herbivores (Bischoff et al. 2016) and their effects are thought to be mediated by plant species composition (Haaland et al. 2011). Plant species found in those habitats provide functions that crop plants do not provide. This is obvious in natural enemies of crop herbivores that depend on specific plant resources at some stage of their life cycle, such as hoverflies and parasitic wasps do. The role of plant species composition is less obvious for natural enemy groups that do not feed on plant. For ground beetles, spiders and other ground-dwelling arthropods, the vegetation cover (Balzan et al. 2016) and structure may be more important than the presence of particular plant species.

Furthermore, the implementation or the management of habitats to enhance functional biodiversity that increases natural enemy abundance does not necessarily result in a significant reduction of crop herbivores. Indeed, biological control efficiency depends on many other factors and interactions (Jonsson et al. 2008), and we are often unable to understand why some plant species mixtures perform better than others. In addition, there is currently no methodology to transfer knowledge on the biological control efficiency of a given plant mixture to help choosing a new set of species adapted to other agronomic and climatic situations. Previous studies on trophic and non-trophic interactions within and between plant and animal communities mainly analysed biological diversity using a taxonomic approach or focused on the global relationship between species diversity and community functioning (Snyder et al. 2006). Their results highly depended on the species composition of the studied plant community (Wilby et al. 2013). A functional description of plant and arthropod communities is then needed to improve the genericity of the findings adapted to different sets of species and to develop predictive agroecology.

Here, we review and discuss the contribution of a trait-based approach to better understand plant-arthropod interactions in agroecosystems, focusing both on trophic (e.g. arthropods feeding on plants, predators feeding on alternative prey) and on non-trophic interactions. We addressed the following questions: (1) What characteristics of entomophagous arthropod communities are related to the regulation of crop herbivore populations? (2) Which functions and which plants traits are involved in plant-arthropod interactions? (3) How to upscale the effects of plants on arthropod assemblages at community and landscape levels, and what are the emerging issues?

To prepare this review, we searched the Web of Science literature database (http://apps.webofknowledge.com) using two search strings in the “topic” search field. The first one was *[(arthropod* or insect* or pest* or prey* or "natural ennem*" or predator* or parasitoid*) and ("biological control" or biocontrol) and diversity and communit*]* and targeted the scientific articles addressing the role of arthropod community structure in biological control. The second search string was *[("food web*" or "trophic network*" or "interaction network*") and (multitrophic or interaction*) and (trait* or morpholog* or characteristic*) and (plant* or arthropod* or insect* or flower*)]* and aimed at finding the articles that identify traits involved in plant-arthropod interactions. Considering references published between 2005 and 2017 (last updated 29th November), the two search strings provided 507 and 528 articles respectively. An analysis of this first set of articles was carried out. New relevant articles cited by the first ones were added to the working set while others being outside the scope of the study were removed. We finally retained 514 articles.

1. The role of natural enemy diversity in controling crop herbivore communities

The main properties of biological control and their relation to the characteristics of entomophagous arthropod communities that emerge from literature are summarized in Fig.1 (first two columns). Crops harbour many herbivore species differing in their identity and relative importance from year to year and from crop species to another. Interannual pest dynamics and crop rotations induced then the interactions of herbivores and natural enemies to be addressed at community level. In general, the control efficiency of a large range of herbivore species increases with the diversity of natural enemies (Jonsson et al. 2017). Studies on predator and prey communities in mesocosms indicate that niche complementarity of predators is the main mechanism leading to higher predation in more diverse predator communities (Northfield et al. 2010; Wilby et al. 2005). Hence, the number and the complementarity of functional groups of natural enemies rather than their taxonomic richness is the major determinant of diversity effect.

In contrast, biological control stability of multi-species herbivores communities requires functional diversity (i.e. the diversity of the provided functions) and redundancy of natural enemies, including specialists and generalists (Gontijo et al. 2015), that do not show antagonistic interactions (Fig. 1). Most relationships between community structure and functioning were inferred from experiments carried out in mesocosms, and their extrapolation to more complex communities under field conditions is problematic. In croplands, habitat management is often used as a tool to support beneficial insects (conservation biological control). It is hypothesised that plant diversity of non-crop habitats favours natural enemies resulting in a decrease in the abundance of herbivores (Letourneau et al. 2011). However, the plant traits favouring biological control and their interactions with arthropod communities are poorly known. In the following section we will review and discuss existing knowledge.

2. A trait-based approach to understand plant – arthropod interactions

2.1 Which functions should plant communities provide to promote herbivore regulation within arthropod communities?

Plant community management to improve the efficiency of natural enemy communities to control herbivore should target several objectives (third column in Fig. 1). Here, we focus our analysis on the neighbouring environment of the field, taken as an example, but our analysis also applies to the within field plant diversity. The surrounding non-crop vegetation fulfils two main functions for natural enemies of pests (detailed in Fig. 1): the provision of trophic resources and the provision of shelter (Griffiths et al. 2008).

The abundance of several insect groups (e.g. Heteroptera, Syrphidae, Pfiffner and Wyss 2004) increases with the total amount of available resources, while others also respond to the diversity of these resources (Carabidae, Harwood et al. 2009). Resources offered by plant communities and required by several natural enemies to complete their life cycle include nectar and pollen for adult herbivorous stages (hoverflies, parasitoids), and alternative prey for larval or adult predator stages. The provision of trophic resources such as floral nectar increases the fecundity and thus the parasitism rate in some parasitoids (Heimpel and Jervis 2005). Food resources need to be abundant, but also accessible and available at different time. The criterion of accessibility, such as the matching of nectar depth in the corolla to the size of arthropod mouthparts, can be used to target specific arthropod natural enemies (Baggen et al. 1999). Plant communities could be designed to improve the regulation of a large range of herbivores through the support of diverse groups of natural enemies. The length of resource provisioning period is also crucial both for maintaining entomophagous communities throughout the year, but also to increase growth rates of specialists during pest outbreaks (Welch and Harwood 2014).

The role of vegetation as shelter has been poorly studied. Perennial plant communities, such as beetle banks, provide refuges against disturbances in the vicinity of cropped habitats (MacLeod et al. 2004). The density and complexity of vegetation architecture and litter are important drivers of microclimate affecting vulnerable life cycle stages of arthropods (oviposition, estivation, hivernation, Griffiths et al. 2008). Vegetation provides attachment points for spider webs (MacLeod et al. 2004). Vegetation structure also determines habitat complexity modifying interactions between natural enemies. It may reduce intraguild predation by providing refuges and shelter, and reduce competition between natural enemies belonging to the same guild (Finke and Denno 2006; Wilby et al. 2013). Studies disentangling the role of resource- and structure-mediated effects suggest, however, that the provision of shelter and favourable microclimate indirectly affect the activity-density of arthropod generalist predators by an increase in weed-borne resources or alternative prey (Birkhofer et al. 2008; Diehl et al. 2012).

Increasing the quantity and diversity of trophic resources may also affect crop pests, as has been demonstrated for several Lepidoptera herbivores (Balzan et al. 2016; Winkler et al. 2010). Plant communities designed to enhance the population of natural enemies should provide them with specific resources and other habitat features not favourable to crop herbivores.

Overall, to promote herbivore regulation, plant communities should therefore supply diversified trophic resources, accessible to various arthropod species differing in the shape and size of their mouthparts, available for a long period and not fostering unwanted herbivores (Fig. 1). A large set of studies has been carried out to screen plant species in terms of floral resource provisioning for parasitoids (e.g. Sivinski et al. 2011; Winkler et al. 2009) and hoverflies (van Rijn and Wäckers 2010) and of overwintering habitats (Bürki and Hausammann 1992). Few of them have shown that specific arthropod groups tended to be associated with particular functional traits of plant resources (e.g. Wäckers and van Rijn 2012). Most of the previously cited studies are species-specific and their results cannot be directly extrapolated to other plant-arthropod pairs. Because of the large number of possible interactions within and between arthropod communities, alternative approaches are required to predict the functioning of these communities.

2.2. Using interaction traits to relate plant and arthropod communities

The mechanisms underlying processes of community assemblage involve morphological, physiological, phenological or behavioural traits (sensu Pey et al. 2014; Violle et al. 2007). The role of morphological traits has been demonstrated in several plant-insect studies. For instance, pollination process depends on the matching between insect proboscis length and nectar holder depth of the corolla (Ibanez 2012; Stang et al. 2006). Grasshopper herbivory is mediated by the compatibility between plant leaf toughness and insect mandibular strength (Ibanez et al. 2013).

To improve resource provisioning to beneficial arthropods, we need to identify pairs of response and effect traits (Lavorel et al. 2013): plants modify arthropod performance via their effect traits and the response of arthropods to the vegetation depends on their response traits. We will use the term “interaction traits” to designate traits mediating interactions between plants and animals.

Interaction traits should not only account for trophic (Lavorel et al. 2013), but also for non-trophic interactions such as shelter functions, all of them finally affecting performance. Non-trophic interactions can modify feeding parameters (escape from predation), non-feeding parameters (mortality, reproduction) and dispersal. A well-known example of a non-trophic interaction is the presence of domatia in some plant species providing specific habitats to arthropods such as ants that increase herbivore predation and plant defence (Agrawal and Karban 1997).

We expect that a trait-based approach, as recently used to predict the effect of various flower strips on hoverflies (van Rijn and Wäckers 2016), may help us better understanding and predicting the assemblages of invertebrate communities as a function of plant community composition (weed communities, semi-natural habitats, flower strips). While numerous studies have screened the attractiveness of individual plant species towards insects, the identification of plant and animal interaction traits would allow an extrapolation to non-tested plant species. Despite the known effects of traits in mediating interactions, most ecological networks are still built on a taxonomical basis. A better understanding of interaction traits will contribute to predict their role in structuring ecological networks and communities (Kissling and Schleuning 2015).

The mechanisms by which invertebrates affect other components of the ecosystem involve several interaction traits (Moretti et al. 2013). This is of great practical importance when the studied organisms are predators or parasitoids of agricultural pests. The relevant effect traits might be related to the diet, foraging behaviour, dispersal ability, shelter requirement and longevity.

2.3. What are the key plant traits involved in plant-arthropod interactions?

We will focus here on some key arthropod functional groups involved in biological control (soil dwellers, nectar and pollen feeders, leaf feeders, vegetation dwelling and flying predators).

107. 2.3.1. Plant traits associated with trophic interactions

Studies on plant-herbivore and of plant-pollinator identified several plant traits implied in the interaction related to resource type, attractiveness, accessibility, quality and availability (Fig. 2).

Resource type: Plants provide various food resources, such as leaves, stems, roots, fruits and seeds, sap, floral and extra-floral nectar and pollen. Additionally, they indirectly provide honeydew and alternative hosts and prey. The role of nectar and pollen has been mainly studied as resources for parasitoids, but these resources are consumed by various other insects and spiders (Chen et al. 2010). The timing, quality and quantity of these resources constitutes interaction traits that vary broadly among plant species (Kühn et al. 2004). Carbohydrate and protein resources provided by plants increase the longevity, reproduction and dispersal of their consumers (Wäckers et al. 2005). There is considerable variation in fitness effects depending on the diet, sex and life-cycle stage of the arthropod consumer (Wäckers et al. 2007). Plant resources may provide occasional and supplementary food sources, but they can also be of crucial importance, in synovigenic species of parasitoids for instance (Jervis et al. 2004) with a strong influence of nectar proteins from pollen on adult performance, and egg maturation.

Attractiveness of the resource: The presence of trophic resources does not always result in consumption. Olfactory, gustatory and visual signals facilitate the recognition of resources and their detection, or may act as repellent, depending on the preferences of arthropod groups. Flowers emit olfactory signals and species are not equally attractive to parasitoids (Belz et al. 2013). Visual signals such as plant height, flowering height, inflorescence size and colour are involved in resource detection and a high visual attractiveness increases the abundance of natural enemies (Fiedler and Landis 2007).

For herbivores feeding on plant tissue, secondary metabolites have a deterrent and defensive effect. In *Brassicaceae*, glucosinolates act as defence compounds against generalist herbivores but they have the opposite effect on specialists (Fahey et al. 2001). The attractiveness to specialists increases with their content in specific glucosinolates (Kos et al. 2014). Chemical traits are often used to predict the relative attractiveness or repellence of plant species and genotypes, even if the effect of secondary metabolites on herbivores largely varies and their role as defence compound has to be questioned (Carmona et al. 2011).

Accessibility of the resource: Flower morphology, in particular corolla shape, plays a crucial role in determining the accessibility of floral nectar and pollen (Heimpel and Jervis 2005). In flower visiting arthropods, the head or body size can physically restrict the access to floral resources if the corolla diameter is small. In such a situation, the plant-arthropod interaction depends on the length of the mouthparts. A correlation between the nectar holder depth and the proboscis length of the flower visitor has been observed in several insect groups, in particular in pollinators. Short corolla flowers favour hoverflies, whereas bumblebees prefer long corollas (Campbell et al. 2012). As a result, flower size is among the most important variables determining the abundance and diversity of flower visitors and their size (Ibanez 2012; Stang et al. 2006; van Rijn and Wäckers 2016). In contrast, extra-floral nectar is generally produced on exposed nectaries and its accessibility is not restricted by size constraints. However, the higher sugar content of extra-floral nectar increases its viscosity compared with floral nectar. This high viscosity facilitates hymenopteran parasitoid feeding due to their adapted mouthparts, but limits access to Lepidoptera that only feed on diluted nectar (Géneau et al. 2012).

In herbivorous insects that provide alternative prey to pest natural enemies, resource provisioning depends on plant palatability, which is related to various morphological (e.g. presence of trichomes, Carmona et al. 2011), biomechanical and chemical traits (e.g. silica content, Massey et al. 2006). Plant resistance to chewing insects is positively related to leaf punch strength, work to shear and work to tear (Peeters et al. 2007). This result in a linkage between the incisor strength of insect mandibles and the traits of the leaves they consume (like leaf dry matter content and carbon:nitrogen ratio, Deraison et al. 2015). Biomechanical properties are associated to several leaf structure traits, such as cuticle thickness, lignin content, specific leaf area and leaf dry matter content (Pérez-Harguindeguy et al. 2003; Schädler et al. 2003). However, the effect of biomechanical properties may be partly confounded with leaf nutrient quality (nitrogen content, carbon:nitrogen ratio, assimilate content), which is negatively correlated to mechanical resistance (Peeters et al. 2007).

Nutritional characteristics of the resource: Floral nectar, extrafloral nectar and honeydew are composed of sugars, while pollen is a source of proteins and free amino acids. The composition in various sugar types, proteins and amino acids is highly variable among plant species (Heimpel and Jervis 2005). Floral nectar predominantly contains sucrose, fructose and glucose (Baker and Baker 1983). The sugar composition of nectar affects pollinator preferences. Parasitoids prefer sucrose-dominated floral nectar (Vattala et al. 2006), partly resulting from a gustatory response (Cocco and Glendinning 2012). Extrafloral nectar generally shows higher sugar concentration, while honeydew is of inferior nutritional quality than nectar (Lee et al. 2004).

Temporal availability of resources: The synchrony between the cycles of plants and of arthropods determines their interaction probability (Welch and Harwood 2014). The circadian rhythm of nectar production has to coincide with the activity period of flowers and extrafloral nectaries visitors. The resource seasonal availability depends on plant phenology. The phenological matching between the flowering period and the period at which arthropods require floral resources is crucial for both herbivores and natural enemies to complete their life cycle.

This synthesis shows that trophic interaction traits are well identified (Fig. 2), and several traits must be simultaneously considered to evaluate trophic interactions between plants and arthropods.

108. 2.3.2. Plant traits associated with non-resource habitat functions

Apart from food provisioning, plants may affect invertebrates by other processes (Fig. 2): physical habitat provision, microclimate modification and habitat provision for all life-stages, including the most critical ones like reproduction.

The structural properties of non-crop vegetation, such as density, height or litter quantity, are known to influence the distribution of soil dwelling arthropods (Griffiths et al. 2008). Plant structural traits such as growth form, height, architecture (density and orientation of ramifications and leaves, leaf morphology) and the presence of domatia contribute to shape arthropod habitats (Parolin et al. 2012). For example, plant morphology influence small-scale invertebrate distribution: plants with complex morphology show a higher invertebrate abundance and biomass than plants with simple morphology (Hansen et al. 2010). At a smaller scale, plant surface properties, such as leaf toughness, epicuticular waxes, pubescence and trichomes affect the attachment and movement of arthropods, with contrasted effects on herbivores and predators, resulting in an increase or reduction of biological control (Mitchell 2016; Petersen 2016).

Plants also provide shelter habitats to epigeic invertebrates, in particular outside the crop growing season. Plant canopy maintains a moist microclimate and reduces wind speed (Norris and Kogan 2005), preventing invertebrates from desiccation and providing favourable aestivation sites. Conversely, relatively dry sites with low temperature variations, such as grass tussocks are favourable overwintering sites for ground beetles (MacLeod et al. 2004). The role of plants in offering suitable overwintering sites has been evaluated for a large range of plant and soil invertebrate species (Bürki and Hausammann 1992), but the corresponding traits have not yet been identified, complicating general conclusions.

Habitat provision for reproduction, such as. the choice of oviposition sites has been mainly analysed in relation to the adult and larval food distribution in the framework of optimal oviposition theory (Wäckers et al. 2007). Olfactory stimuli emitted by plants like kairomones and allomones appear predominant in the long-distance attraction or repulsion of female gravid herbivores, whereas visual stimuli prevail in the choice of specific oviposition sites, limiting oviposition on non-host plants (Hooks and Johnson 2003). Plants that increase egg survival represent suitable oviposition sites for phytophagous and predatory insects and they may differ from plants on which these insects feed (Norris and Kogan 2005). Physical plant characteristics are also important, such as hollow stems of trees and shrubs which determine the selection of nesting sites of sphecid wasps (Bitsch and Leclercq 1993). Nentwig (1992) recorded oviposition preferences of lacewings on a large range of plant species and found that the rate of oviposition was particularly high on *Papaveraceae* and *Boraginaceae* species, which may be related to the pilosity of these species. However, it is still poorly known how plant traits such as architecture or surface (wax, pilosity etc.) affect oviposition behaviour of arthropods.

3. Scaling up to community and landscape levels

3.1. Overcoming the limits of monospecific approaches

A majority of studies on conservation biological control has focused on single or a few plant species in relation to the regulation of one or few herbivore groups by one or few natural enemies (e.g. Langoya and van Rijn 2008; Laubertie et al. 2012). Several studies consisted in plant screening experiments under controlled conditions in order to identify the most appropriate species to increase the biocontrol performance of a targeted natural enemy. The most frequently tested species are *Phacelia tanacetifolia*, *Fagopyrum esculentum* Moench and *Lobularia maritima* (L.) Desv.

However, crops are generally vulnerable to several herbivore species. Moreover, in arable fields where annual crops rotate, a diverse community of natural enemies is required to regulate the associated communities of herbivores. To support a diverse community of natural enemies, surrounding non-crop vegetation should therefore also comprise a mixture of plant species. However, plant effects on arthropod behaviour have been mainly analysed in pure stands and little is known on the effect of plant assemblages (Pontin et al. 2006). In plant communities, attractive plant species may divert herbivores from the less attractive ones reducing their visiting rate compared to monospecific stands. Interactions within arthropod communities may also occur, such as the competition caused by an aggressive species towards a less aggressive one (bee vs. hoverflies, Hogg et al. 2011). Increasing the diversity of plant resources and of plant habitats may reduce competition and other negative interactions between arthropods, promoting a higher arthropod diversity than expected from experimental results obtained on monospecific stands. Interactions advocate the need to develop approaches at community level in order to identify the characteristics of plant communities that (potentially) improve conservation biological control. Up to now, studies are usually focusing on one particular mixture (e.g. Gillespie et al. 2011; Pfiffner et al. 2009) whereas studies comparing different mixtures are less common (eight studies out of 40 synthesized in Haaland et al. 2011).

There is though strong evidence for functional relations among plant and arthropod communities. The abundance of phytophagous invertebrates positively correlated to plant traits related to resistance to disturbance at community level (low leaf dry matter content), suggesting a functional link between both communities (Storkey et al. 2013). Apart from average trait values of plant communities, diversity may also matter. Potts et al. (2004) showed that the diversity of nectar resources was positively related to bee species richness.

3.2. Which metrics relate the effects of plant community structure on arthropod assemblages and what are their limits?

The objective of this section is to review the characteristics of plant communities that are related to arthropod assemblages and to their functioning in terms of herbivore regulation.

Several descriptors can be used to characterize communities. The first one is the species identity. It assumes that the role of a species is idiosyncratic and that the functioning of the community depends on the particular species it comprises. This view might often result from insufficient knowledge or description of the mechanisms underlying the studied processes.

The second type of descriptors relies on the functional composition of the community. Following the biomass-ratio hypothesis, ‘the extent to which the traits of a species affect ecosystem properties is likely to be strongly related to the contributions of the species [...]’ to the community biomass (Grime 1998). This suggests that the effects of plants on ecosystem functions are primarily determined by the mean trait values at community level, weighted by the relative importance of each species. For example, in subalpine grasslands, the mean body mass of grasshoppers responds to the community weighted mean of leaf dry matter content (Moretti et al. 2013). It can be expected that the abundance of nectar and pollen feeding arthropods increases with the amount of accessible resources provided by the whole plant community, possibly modulated by their nutritional value.

However, interactions among the functional components of the community may result in a community functioning that could not be inferred from the sole addition of species effects. The ecosystem impact of organisms of higher trophic levels could be less related to abundance or biomass (Grime 1998) compared with plants. Non-additive diversity effects can result from functional complementarity, which facilitate niche partitioning or from synergistic or antagonistic interactions. Functional diversity is often measured as the diversity of functional traits and can be described by functional trait richness, evenness and divergence (Dias et al. 2013). In plant-invertebrate communities, a high diversity of plant resources and micro-habitats is expected to support a high diversity of invertebrates. Podgaiski et al. (2013) found a positive correlation between functional diversity in plant communities (in terms of size and architecture) and spider functional diversity (morphology and web-building type). This finding was, however, not supported by other recent studies analysing the effects of functional diversity of flower resources on natural enemies (Balzan et al. 2014; Uyttenbroeck et al. 2017). Due to the long generation time of several natural enemies, in particular of generalists, the temporal diversity of resource provisioning (e.g. flowering date and duration) may be more important than the instantaneous diversity of flower resources.

There is no consensus on the relative importance of community species composition and functional structure (Costanzo and Barberi 2014) and the contribution of functional diversity effects to ecosystem functioning remains unclear (Garibaldi et al. 2015; Garnier et al. 2016).

Recent meta-analyses provide evidence that plant species and functional diversity favour generalist predators (Dassou and Tixier 2016) and increase herbivore regulation by natural enemies (Iverson et al. 2014). The future questions to be answered are ‘which functional diversity (i.e. which traits) and which degree of diversity maximises herbivore regulation?’

3.3. How is plant functional diversity related to herbivore regulation?

Determining the level of functional diversity to maximise herbivore control at community level is not trivial. We may expect that biological control of a unique herbivore species could be mainly dependent on the amount of trophic resources and habitats supporting its main natural enemies (dominance effects). The plants traits that support the natural enemies of additional herbivore species may differ, resulting in the needing of diverse plant functions to support the entire natural enemies community required to regulate a community of herbivores. As shown by Isbell et al. (2011), the more ecosystem services are expected from plant communities, the more plants supporting various functions are required. However, in a plant community of fixed size, plant functional diversity cannot be increased independently of modifying other community properties.

First, the generally hump shaped relationship between community weighted mean of traits (CWM) and functional diversity (Dias et al. 2013), means that, for a given trait, functional diversity tends to be the lowest at extreme CWM values. Thus, depending on the plant trait values that are related to biological control, this interdependence may constrain any increase in functional diversity.

Second, evenness, which is a component of functional diversity, reduces dominance effects via a dilution of the role of dominant species in the community. For example, combining plant species according to their flowering period to maintain nectar and pollen provisioning the whole year results in a reduction of the density of plants flowering at the same time. At flowering peak, the amount of available resources is higher in communities with homogeneous phenology than in communities with diverging phenology resulting in a trade-off between the diversity of resources and their instantaneous availability. Thus, increasing the diversity of plant traits to increase the diversity of arthropods may be at the expense of the respective densities of each of these arthropods.

This trade-off between evenness and dominance effects suggests that the functional diversity – biological control relationship may not be monotonous. As long as plant functional diversity promotes complementarity and positive interactions of natural enemies, this should counterbalance the reduction of the plant dominance effects. We therefore expect that the functional diversity – herbivore regulation relationship may not always be positive, and that it could reach a plateau or an optimum value depending on the strength of the synergistic interactions at high functional diversity levels. To determine this relationship, experiments that vary the functional composition and diversity of plant communities are required to test simultaneously the two effects, and to quantitatively relate functional trait diversity, composition and ecosystem functions.

Several traits (Fig. 2) and metrics have been proposed to account for the interactions between species or between restricted taxonomic groups. The next step would be to identify the combinations of metrics of plant communities that account for their effect on arthropod communities, in order to include the effects of functional composition, of functional diversity and of species identity (when effects cannot be related to functional traits). The level of functional redundancy is another important aspect.

3.4. Taking into account the interactions with surrounding landscapes

The management of a given habitat for conservation biological control must be adapted to the characteristics of the neighbouring habitats, such as crop fields and other non-crop structures (Tscharntke et al. 2016). The creation of a new habitat, for example a wildflower strip, provides additional resources and habitats. Hence, plant community management or establishment should be based i) on the assessment of natural enemies requirements and ii) on the assessment of the resources yet provided in the surroundings to provide locally limiting resources or habitats. For instance, the effect of wildflower strips on pollinators is strongly dependent on their complementarity with already available resources at landscape scale (Scheper et al. 2015), in particular in terms of synchrony between flowering period and pollinator requirements. Plant traits have to be adapted to abiotic conditions such as climate and soil. Under arid climates, arthropods may search for moist shelters protecting them from drought stress (tussocks and creeping plants providing shade and a high hygrometry), while under humid climate, open habitats with a rapid warming might enhance arthropod activity. We therefore need to develop a functional characterization of the surrounding landscape (functional landscape ecology) by improving the metrics of landscape description beyond land use (Vialatte 2017 Landscape ecology). To do so, simplified vegetation relevés stratified by habitat type can be used to compute the landscape-wide floral resource availability (Scheper 2015). This approach could be extended to other plant properties, like habitat related traits as well as to other metrics, such as the diversity of plant traits values at a spatial scale. In the future, such a description of the properties of plant communities at landscape scale will enable to adapt habitat creation and management to improve the spatial functional supplementation and complementation instead of implementing standardized greening infrastructures.

Conclusions and implications for conservation biological control

A trait-based approach provides promising perspectives to improve our knowledge on relationships between plant assemblages and conservation biological control. The well-known influence of morphological and biochemical traits on the interaction between plants and pollinators (Stang et al. 2009) suggests that such an approach may also be used to deal with other biotic interactions.

The characteristics of arthropod communities that provide efficient biological control have to be identified. Despite the general finding that a stable biological control of multi-species herbivore communities requires functional diversity and redundancy of natural enemies, the development of accurate management practices is still limited by our poor understanding of the functioning of arthropod communities, in particular of their trophic interaction network.

We suggest further identifying "interaction traits" that are specifically involved in plant-arthropod interactions including the effect traits of plants impacting arthropods and the response traits of arthropods to plants. Interaction traits correlate with plant features related to the provisioning of trophic resources (amount of resource, phenology of production, corolla shape etc.) and habitat (plant architecture) affecting arthropods (Fig. 2). So far, important traits like nectar composition, extrafloral nectar availability, presence of domatia or plant pilosity, are poorly represented in botanical databases. The use of traits would contribute to a better mechanistic understanding of interactions at community level. It may allow quantifying the diversity and redundancy of interaction traits in plant communities and to relate them to natural enemies abundance or to herbivore regulation

Our knowledge of plant-arthropod interactions needs to be scaled up from population to community level. The extent to which arthropod communities are affected by plant traits at community level remains widely unexplored. While we expect that that an intermediate level of plant functional diversity would be more prone to maximise the service of herbivore regulation, experimental designs allowing to compare contrasted plant communities (such as Hatt et al. 2017) will be useful to disentangle the respective roles of plant functional composition and diversity.

The identification of relevant community characteristics should not be limited to additive species traits. They should also include the structure of the interaction network, the species complementarity and the generalist/specialist ratios.

Beyond the identification of relevant plant traits, the high specificity of certain plant-insect and insect-

insect interactions may weaken the trait-based approach. Aphid-parasitoid and plant-aphid interactions are usually species-specific. Consequently, aphid regulation often requires targeting a particular aphid species by favouring a particular parasitoid species. Trade-offs may occur between positive effects of plant traits on one natural enemy group and opposite effects on another. So, it seems to be likely that some sets of traits may be related to herbivore regulation in general but we still cannot exclude that these combinations are highly specific and that finally a trait-based approach is not always more straightforward than a species-based approach. We therefore do not claim that the trait-based approach should be exclusive, and advances in food-web ecology will also contribute to better understand and manage trophic interactions. If interactions are idiosyncratic or poorly understood, and if trait attributes are phylogenetically conserved, phylogenetic parameters may be better predictors of ecosystem functioning than functional traits or groups (Cadotte et al. 2008). However, interaction specificity usually includes a single dimension of a niche, whereas a trait-based approach may still be straightforward for the other dimensions. For generalist predators, a trait-based approach would remain relevant. The difficulty may arise from the number of traits and of their interactions that have to be considered in each situation. If the patterns become too complex and poorly generalizable, the practicability of a trait-based approach will be challenged.

In practice, interaction traits may be used to decide on plant property combinations of seed mixtures for creating or restoring semi-natural habitats, instead of using standard species lists applied to several biogeographical zones. Identifying the plant species of the local flora that meet the desired trait criteria would allow designing seed mixtures with similar functional characteristics, but containing species adapted to local climatic conditions.

The use of functional traits as proxies of communities and ecosystem functioning should not ignore other drivers of plant arthropod interactions such as environmental conditions and habitat management. In addition, the use of plant communities to support biological control must also account for a diversity of ecological, technical and socio-economical criteria, such as a potential loss of diversity during plant succession. Problematic weed species cannot be included in sown mixtures even if they present ideal trait combinations. Local origins of plant species should be preferred to obtain well performing, locally adapted populations and to avoid genetic pollution. Finally, trade-offs with other ecosystem services have to be considered in a multifunctional perspective, including pollination, species conservation and landscape aesthetics.

Conflict of interest: The authors declare that they have no conflict of interest.

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Figure legends

Fig. 1 Outline of the main objectives targeted for efficient conservation biological control (first column), of their corollaries on arthropod community functioning (second column) and on plant community and habitat management (third column) synthesized from the literature

Fig. 2 Overview of the main plant - arthropod interactions traits, recorded from the literature, relevant for managing arthropod communities in conservation biological control. *Heracleum sphondylium* image © Pierre Déom – www.lahulotte.fr

Effects of spontaneous field margin vegetation on the regulation of herbivores in two winter crops

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Keywords: Ecosystem service, plant diversity, floristic composition, natural enemies, biological control, wheat, oilseed rape

Abstract

Non-crop vegetation of field margins provides resources for natural enemies of crop herbivores. However, it is still not well known whether this resource provisioning effect is strong enough to improve herbivore regulation within crop fields and which plant species and functional groups favour this ecosystem service. A better understanding of the interactions between field margin vegetation and herbivore regulation is crucial to evaluate management strategies and to design suppressive plant mixtures. We surveyed 64 wheat and oilseed rape fields of Western France for two years (16 fields per year and crop) in order (1) to identify plant diversity or group effects on herbivore regulation within crop fields and (2) to identify species within plant groups that improve regulation. Herbivores, herbivore damage and natural enemies were monitored on crop plants at a distance of 5 and 50 m from the field margin. At the same time, the cover and phenological stage of all vascular plants were estimated in the adjacent field margin. The study demonstrated a positive relationship between the cover of entomophilous plant species that were flowering at the survey date and response variables related to herbivore regulation. Plant species richness and the cover of plant species taxonomically close to crop plants had a small influence on herbivores and natural enemies in wheat whereas related wild Brassicaceae increased herbivory and decreased herbivore regulation in oilseed rape. Within the entomophilous flowering plants, several species were significantly related to a better herbivore regulation in univariate analyses. Multivariate ordination techniques allowed the identification of plant species influencing several response variables of herbivore regulation at the same time. Our study demonstrated the importance of entomophilous species that flowered at peak infestation of crop herbivores. Spontaneous field margins rich in flowering entomophilous species provide an important ecosystem service without expensive sowing of seed mixtures.

Introduction

Arable ecosystems are relatively species-poor and biodiversity of agricultural landscapes is concentrated in non-cultivated, semi-natural habitats, such as field margins, meadows, hedgerows and woods (Bianchi, Booij, & Tscharntke, 2006; Billeter et al., 2008, Landis 2017). As semi-natural habitats provide shelter and resources for natural enemies, crop herbivore regulation is expected to vary with habitat characteristics driving these functions. While relations between the size and proportion of semi-natural habitats in the surrounding landscape and natural enemy abundance are well documented, our knowledge of the role of habitat quality is still relatively poor (Bianchi et al., 2006; Veres, Petit, Conord, & Lavigne, 2013; Woltz, Isaacs, & Landis, 2012, Begg et al. 2017). Plant species composition may serve as a proxy of habitat quality reflecting variation in plant traits and thereby mediating plant-insect interactions. In a study on semi-natural grasslands and heathlands, the arthropod assemblage composition was better explained by local plant species composition than by the surrounding landscape (Schaffers, Raemakers, Sýkora, & ter Braak, 2008). Plants provide shelter and overwintering sites for natural enemies, and plant species composition determines the herbivore community of field margins representing alternative prey during the absence of crop herbivores (Bianchi et al., 2006; Griffiths, Holland, Bailey, & Thomas, 2008). Floral resources may increase the fitness of natural enemies that change nutrition during their life cycle (Araj & Wratten, 2015; Winkler, Wäckers, Kaufman, Larraz, & van Lenteren, 2009) resulting in an improvement of pest control efficiency (Balmer et al., 2014; Blaauw & Isaacs, 2012; Tylianakis, Didham, & Wratten, 2004). Interactions between plant species and flower-visiting natural enemies are often species-specific (Sivinski, Wahl, Holler, Dobai, & Sivinski, 2011). So it can be concluded that floral resource provisioning for natural enemies strongly depends on plant species composition (Wäckers & Van Rijn 2012, Balzan et al. 2014). Studies testing effects of vegetation composition on pest insect regulation focused on sown wildflower strips (Balmer et al., 2013; Haaland, Naisbit, & Bersier, 2011, Tschumi et al. 2015) and grass strips (Lee, Menalled, & Landis, 2001; MacLeod, Wratten, Sotherton, & Thomas, 2004). Plant species grown in such experimental approaches were selected using expert knowledge of flower attractiveness and results obtained from screening experiments in monospecific stands (Sivinski et al., 2011). However, studies focusing on spontaneous vegetation of semi-natural habitats such as field margins and their plant species composition are rare and limited to natural enemy level as response variable or very simple vegetation proxies such as species richness (Denys &

Tscharntke 2002, Meek et al. 2002, Chaplin-Kramer et al. 2011, Tscharntke et al. 2011, Diehl et al. 2013, Dassou & Tixier 2016).

Analyses including both crop herbivores and natural enemies are needed to test the final outcome of plant-insect interactions in terms of crop herbivore regulation. A meta-analysis by Chaplin-Kramer (2011) demonstrated that landscape complexity involving semi-natural habitats usually increased natural enemy densities but this increase did not necessarily translate into an improved regulation of crop herbivores. Wild relatives of crop plants may for example attract crop herbivores and their natural enemies at the same time. An increase of crop herbivore densities in field margins may increase crop infestation and damage by associational susceptibility (Le Guigo, Rolier, & Le Corff, 2012). Bischoff et al. (2016) showed that wild Brassicaceae species had a predominantly negative influence on herbivore regulation in Brassicaceae crops. In a recent review, beneficial effects of semi-natural habitats on crop herbivores were also cited as a major reason for a failure in enhancing biological control (Tscharntke et al. 2016). Letourneau et al. (2011) still found a better herbivore suppression in agro-ecosystems with higher plant diversity based on 45 published studies but most of the positive results were obtained for intercropping systems and need to be verified for semi-natural habitats outside crop fields.

If crop herbivores are better controlled by a diversity of natural enemies (complementarity hypothesis, Dunning et al. 1992), each being attracted and favoured by particular plant species, then a higher diversity of field margin vegetation may improve crop herbivore regulation. Such a positive plant diversity effect on herbivore regulation has been shown in several studies (Balvanera et al., 2006; Dassou & Tixier, 2016 and citations therein). A better knowledge of spontaneous vegetation effects is required to identify candidate species for designing wildflower strip seed mixtures. Spontaneous vegetation may be natural or spontaneously developing under human management without sowing (semi-natural). Spontaneously occurring species have already proven to be well adapted to local environmental conditions. So, they present an interesting species pool to expand existing wildflower strip mixtures with often similar and limited species combinations.

In this study, we examine the relationships between the spontaneous field margin flora and the abundance of natural enemies, pest insects and crop damage in wheat and oilseed rape. Both commonly grown winter crops succeed each other in typical crop rotations of the study region (Valantin-Morison, Meynard, & Doré, 2007). Due to their taxonomic distance (wheat: Poaceae, monocotyledon; oilseed rape: Brassicaceae, dicotyledon), they show large morphological and physiological differences and do not share major herbivores. We selected these two taxonomically distant crops associated with different herbivore communities to evaluate whether they still share plant species exerting regulatory effects on dominant crop herbivores. The major natural enemy groups regulating herbivores of both crops are parasitoids, hoverflies, ladybugs, lacewings and ground beetles (Tschumi, Albrecht, Entling, & Jacot, 2015; Valantin-Morison et al., 2007). In order to obtain general information on beneficial effects of field margin vegetation on herbivore regulation in both crops, we focus on (1) the cover of entomophilous, nectar-producing plants, (2) the cover of wild relatives of crop plants (same family) and (3) plant species richness.

We address the following questions:

1. Do plant species composition (functional and taxonomic groups) and richness of field margins affect crop herbivores and their natural enemies in the field?
2. Is there a set of plant species or species groups associated with a better regulation of different herbivores?

3. Are relationships between field margin vegetation and crop herbivore regulation similar in two winter crops often grown in succession and are they also detectable at larger distances from the field margin?

Materials and methods

Study sites and experimental design

The study sites were located in the Maine-et-Loire department of Western France (Fig. 1A). The agricultural landscape is dominated by wheat, oilseed rape, maize, vegetable fields and permanent grasslands. We used wheat (*Triticum aestivum* and *Triticum durum*) and oilseed rape (*Brassica napus*) as model systems. Sixteen winter wheat and sixteen oilseed rape fields were monitored in each of two consecutive years (2014 and 2015) resulting in a total of 64 analysed fields (Fig. 1B). Minimum distance between fields of the same year and crop was 1 km. Field management was not standardised and is representative of the study region ranging from organic (2-3 per crop and year) to conventional (13-14 per crop and year). No insecticide treatment was applied to wheat fields during the study period whereas conventional oilseed rape fields were on average treated twice a year against pollen beetles and weevils, respectively. Pollen beetles and weevils were still among the most common crop herbivores in the selected oilseed rape fields allowing a robust analysis of flora effects (Table S1A).

Field margins were > 2 m wide strips of spontaneous herbaceous vegetation, in particular perennial herbs and grasses. Woody field margins and margins dominated by annual weeds or ruderal species indicating recent disturbance were excluded from this study. We only considered the non-cultivated part outside the field as a margin. Usually, margins were managed by cutting once a year during summer.

Vegetation surveys

All vascular plants were recorded in a survey area of 75 m² with a width ranging from 2 m to 5 m (average: 3 m, Fig. 1C). The cover of each plant species was measured as the vertical projection of all aboveground organs using the Braun-Blanquet method (Braun-Blanquet 1964). Instead of applying estimation scales, we directly estimated cover percentage (Damgaard 2014) by first analysing the frequent species from outside the survey area then rarer or less visible species inside. A cover of 0.1% was fixed as detection limit including species covering less than 0.075 m². In order to evaluate floral resource availability, we additionally estimated the percentage of flowering plants for each species. The cover of flowering plants was calculated by multiplying plant cover and flowering percentage of all recorded plant species. The vegetation surveys were conducted during the flowering period of the crop plants, in May for oilseed rape and in June for wheat.

Arthropod observations and surveys

Crop herbivores, related damage and natural enemies were recorded in each field at a distance of 5 and 50 m from the vegetation survey plot in the field margin (Fig. 1C). The survey dates corresponded to the main phenological stages of crops and peak attack of major crop herbivores. Wheat was monitored twice a year in early and late June, at stages of spikelet emergence and early milk ripening. These two stages usually coincide with the peak occurrence of two major pests, cereal leaf beetle larvae (*Oulema ssp.*) and cereal aphids (*Sitobion avenae* and *Metopolophium dirhodum*). In each wheat field and for each sampling date, 50 randomly chosen tillers per distance were observed. The two major pests and their predators (ladybugs, Coccinellidae and hoverflies, Syrphidae) were counted on each tiller (Table S1). Aphid parasitism rate (Hymenoptera, various species) was measured for each of the two distances, by dividing the total number of mummies per tiller by the sum of aphids and mummies. Leaf beetle damage was estimated by visual observation as the mean percentage of removed tissue on all green leaves of each tiller.

Oilseed rape was monitored three times a year in April, May and June at stages of flower bud appearance, flowering peak and early fruiting. These stages characterise peak attack by pollen beetles, aphids and pod midges often following pod weevil attack. In each oilseed rape field and for each sampling date, twenty plants per distance (randomly chosen except for suction sampling) were observed or sampled. In April, pollen beetle (*Meligethes aeneus*) adults were captured along a line of twenty consecutive plants using a suction sampler (Stihl sh 86-d). Suction time was 10 min per distance and field. In May, stem weevil damage (*Ceutorhynchus napi*) was recorded as the number of plants with characteristic symptoms (burst or deformed stems). The main flowering stem of twenty plants was harvested to count pollen beetle larvae and to evaluate parasitism. Samples were frozen before removal and dissection of larvae under a binocular loupe. The head of the larvae was cut and inner organs were removed to check for the presence of parasitoid eggs. In June, aphids (*Brevicoryne brassicae*), adult parasitoids (dominant species: *Diaeretiella rapae*), hoverflies (Syrphidae, larvae and adults) and ladybugs (Coccinellidae, larvae and adults) were counted by visual observation. Aphid parasitism was calculated from aphid and mummy numbers as for wheat. Pod damage caused by fruit weevils (*Ceutorhynchus assimilis*) was recorded on the main inflorescence as the ratio of attacked pods (holes) to total pod number.

Data analysis

The relationships between the explanatory (floristic composition) and response variables (crop herbivores, damage, natural enemies including parasitism, Table S1) were tested using generalised linear mixed models (GLMM). Analyses were run separately for the two crop species (wheat, oilseed rape) and distances (5 m, 50 m). Observation dates within the same year were pooled if the same insects or damage types were observed twice. In order to avoid overparametrisation of statistical models, the analyses were run in two steps. In a first step, plant species number (total species richness), the cover (%) of entomophilous flowering plants and the cover (%) of taxonomically related plants (Poaceae for wheat and Brassicaceae for oilseed rape) were fitted as explanatory variables. The biolflor database (Klotz, Kühn, & Durka, 2002) was used to identify entomophilous plants. In this data base, plant species that are predominantly pollinated by insects are considered as entomophilous. Only species flowering at the survey date were included in this group. Year was fitted as a random factor to account for potential variation between years and sites since fields within crops were not the same in both years. In a second step, we reran the analysis using individual plant species within the plant group providing the best model fit in the first step which was the entomophilous species group in both crops. The cover of each species within this group was fitted as explanatory variable. Again to avoid overparametrisation, rare plant species occurring in less than one third of the field margins were omitted from this analysis. In both steps, we applied a stepwise backward procedure to identify the best models using Akaike’s Information Criterion (AIC). Explanatory variables were removed one by one, and the model with fewer variables was tested against the more complex one. The reduced model was retained if the AIC was lower or if models were not significantly different. GLMMs on normally distributed data and residuals were fitted using an identity link function. The percent damage of cereal leaf beetle was arcsin[sqrt(x/100)]-transformed to achieve normality of residuals. Count data such as the abundance of crop herbivores or their natural enemies were analysed using a Poisson distribution with log link function. When overdispersion was detected models were fitted using a negative binomial distribution. All GLMM were run in the lme4 package (R, version 03.3.1, R Development Core Team (2013)).

All plant species included in the second step of the univariate GLMM were also used to build up multivariate models analysing relations between plants (explanatory variables) and the entire set of response variables. This approach allows a synthetic evaluation of potential plant species effects on herbivore regulation in order to analyse whether (and which) plant species have a positive effect on several regulation parameters at the same time. In order to decide whether a linear or a unimodal approach is better adapted to the data set, a Detrended Correspondence Analysis (DCA) was run on response variables (Canoco 5). The gradient length was quite small (1.3 SD for wheat, 1.6 SD for oilseed rape), advocating for a linear approach (ter Braak & Smilauer, 2012). We finally used a Redundancy Analysis (RDA) as a method constraining explanatory variables in a linear model. The method also accounts for the different response variable types and units requiring an adjustment to zero mean and unit variance. Count data were additionally log-transformed and percentage values were arcsin[sqrt(x/100)]-transformed prior to analysis in order to homogenise variances and to obtain similar scales of response variables. The effect of explanatory values on response variables was evaluated by calculating the cumulative explained variation of all axes and using Pseudo-F statistics (ter Braak & Smilauer, 2012).

Results

Effects of plant species richness and plant groups

We found altogether 260 plant species in the field margin survey of which 134 species occurred in the margins of both crops and 126 were specific to one of the crops. The vegetation can be characterised as disturbed *Arrhenaterum elatius* grassland with a dominance of the perennial grasses *A. elatius*, *Elytrigia repens*, *Festuca arundinacea*, *Lolium perenne* and *Poa trivialis*. The most common herbs were *Galium aparine*, *Papaver rhoeas*, *Sinapis arvensis* and *Urtica dioica*. Plant species richness was similar in both years and crops whereas the cover of entomophilous species was a little higher in the 2015 surveys and in oilseed rape margins (Fig. 2). There was huge variation in the cover of entomophilous species among fields within years and crops ranging from less than 1% to more than 50% (Fig. 3). The cover of crop-related plants was much higher in wheat field margins (Poaceae) than in oilseed rape margins (Brassicaceae). The dominant crop herbivores in wheat fields were cereal aphids and leaf beetles. Cereal aphid infestation was much higher in 2014 than in 2015 due to the more favourable weather conditions (warmer, less rainfall during peak infestation) but aphid parasitism was also lower in 2014 (Appendix A. Table 1A). Oilseed rape was mainly attacked by pollen beetles, cabbage aphids. Furthermore, stem and fruit weevils caused considerable damage in both years (Appendix A. Table 1B). In both crops (Tables 1 and 2), more significant effects of plant groups and species richness were observed close to the margins (5 m) than inside the fields (50 m). However, for five response variables (ladybug abundance in wheat, stem damage, aphid and hoverfly abundance, pollen beetle parasitism in oilseed rape), such effects occurred at a distance of 50 m. Most of the significant relationships had a $P<0.05$ at 5 m and a $P<0.1$ only at 50 m. In both crops, the cover of entomophilous species best explained crop herbivore regulation with predominantly positive relations to natural enemy abundance and negative relations to crop herbivore abundance and damage (Tables 1 and 2; Fig. 3). In winter wheat, plant species richness had only a weak influence on response variables and no significant effect was found for the cover of wild crop relatives. In oilseed rape, plant species richness and the cover of wild crop relatives showed some significant relationships with response variables. In particular, effects of wild Brassicaceae species on crop herbivore regulation were negative.

In winter wheat, the cover of entomophilous flowering plants was positively related to aphid parasitism and hoverfly abundance at 5 m and to ladybug abundance at 50 m suggesting a better control of aphids (Table 1, Fig 3A). However, aphid abundance was not significantly related to any of the tested plant groups. In oilseed rape, the cover of entomophilous flowering plants was negatively related to aphid abundance at 5 m and to stem damage at 50 m. The correlation to pollen beetle larvae parasitism at 5 m and to hoverfly abundance at 50 m was negative (Fig. 3B). Relationships were significant at 5 m but only marginally significant at 50 m. Stem damage and pollen beetle larvae increased with the cover of wild Brassicaceae species and pollen beetle parasitism decreased (all at 5 m). Plant species richness was positively related to leaf beetle damage (5m) in wheat, and to aphid abundance and pollen beetle parasitism in oilseed rape (50 m, Appendix A. Fig. 1).

Identification of plant species related to herbivore regulation

Since the cover of entomophilous flowering plants was best related to herbivore regulation in both crops, we tested which species within this group contributed most to regulation. Wheat and oilseed rape margins shared five species among the most frequently surveyed ten species in total. *Papaver rhoeas* and *Vicia sativa* cover significantly influenced response variables in both crops (Table 3). However, both species showed positive and negative effects on crop herbivore regulation. *P. rhoeas* flower cover was positively related to hoverfly abundance in wheat and negatively to aphid abundance but also negatively to hoverfly abundance and pollen beetle parasitism in oilseed rape. *V. sativa* cover was negatively related to aphid parasitism in wheat but positively to pollen beetle parasitism. Positive (hoverflies) and negative effects (ladybugs) were also observed for *Galium mollugo in wheat. Leucanthemum vulgare* had a strong positive effect on regulation in wheat (highly significant effect on ladybugs and aphid parasitism) while *Sonchus asper* cover was positively related to regulation in oilseed rape (negatively with aphid abundance, positively with pollen beetle parasitism).

The multivariate analyses testing effects on all response variables did not clearly identify plant species that have a general positive influence on the regulation of crop herbivores. Significant relationships obtained by the univariate analysis (Table 3) were also visible in the RDA biplots (Fig. 4). However, the RDA did not always separate explanatory variables that were positively from those that were negatively related to crop herbivore regulation. For example, in winter wheat aphid and ladybug abundance as well as hoverfly and leaf beetle abundances occurred together in the explanatory – response variable biplot. At a distance of 5 m, plant species as explanatory variables accounted for 30% of variation in wheat (Pseudo F=0.9, P=0.578) and for 38% in oilseed rape (Pseudo F=1.3, P=0.078). At a distance of 50 m (biplots not shown) these values were 29% for winter wheat (Pseudo F=0.9, P=0.710) and 35% for oilseed rape (Pseudo F=1.1, P=0.202). Due to the better model fit, we focus in the following paragraph on the 5 m data.

In winter wheat, a group of three species increased aphid parasitism and reduced aphid abundance (but also ladybug abundance) at the same time: *Galium mollugo*, *Trifolium pratense* and, to a lesser degree, *Leucanthemum vulgare*. *Papaver rhoeas* was positively related to hoverfly abundance and negatively to leaf beetle damage (but also to ladybugs). In oilseed rape, the overlap of response variables representing crop herbivory with those representing natural enemies was even stronger than in winter wheat. A group comprising *Veronica persica*, *Galium aparine*, *Silene latifolia* and *Geranium molle* favoured aphid parasitism and was negatively correlated with pollen beetle abundance (larvae and adults). The influence on parasitoids and pollen beetle parasitism was, however, negative. *Papaver rhoeas* correlated negatively to three major crop herbivores: pollen beetles (larvae), stem weevils (damage) and aphids.

Discussion

Plant species richness and plant groups

In field margins of both crops, we found a high plant species richness but large variation in plant species composition between fields. The total number of plant species was as high as in a previous study on field margins of the same region but bordering brassicacean vegetables (Bischoff et al., 2016). Margin vegetation is often bordered by different habitats such as wetlands, woodlands or meadows but also by the arable fields with different plant communities (Bischoff et al. 2016, Cordeau, Petit, Reboud, & Chauvel, 2012). This ecotone character of margins explains the high species richness compared to adjacent non-ecotone habitats.

Plant species richness, taxonomic and functional groups of field margin vegetation significantly influenced insect communities (natural enemies, crop herbivores, parasitism and damages) in the adjacent fields covering the typical variety of cultural practices in the study region. In agreement with (Schaffers et al., 2008), the results showed that the local plant community is an important predictor of arthropod communities although our study was limited to crop herbivores and natural enemies. Fewer significant relationships were found at a distance of 50 m than close to the margins at 5 m. Such a decline of vegetation effects on arthropods and on crop herbivore regulation was also found in other studies (Collins, Boatman, Wilcox, Holland, & Chaney, 2002; Tylianakis et al., 2004). It may be explained by the energetic costs of movements and the relative attractiveness of margins preventing natural enemies from moving into the field (Heimpel & Jervis, 2005; Wanner, Gu, Hattendorf, Günther, & Dorn, 2006). However, some correlations only occurred at a distance of 50 m. Indirect effects, such as competition with other natural enemy groups, resulting in a lower availability of prey, may have contributed to the absence of significant effects close to the field margin.

Entomophilous plant species flowering at the survey dates showed the strongest correlations with the tested response variables. Relations to crop herbivores and damage were negative and those to natural enemy abundance or attack (parasitism) were generally positive except for pollen beetle parasitism. These results confirmed the findings of Bischoff et al. (2016) obtained for phytometer crop plants placed into the field margins. The present study showed that positive effects of entomophilous plant species on the regulation of crop herbivores can also be detected within the crop fields. In wheat fields, positive relationships were found between entomophilous plant cover and aphid parasitism and the abundance of two major groups of aphid enemies, hoverflies and ladybugs. It is well known that adult hoverflies rely on nectar resources (Fiedler, Landis, & Wratten, 2008; Wäckers, 2004). A better resource provisioning resulting in higher adult performance increases egg deposition and density of aphidophagous larvae in the field

(Laubertie, Wratten, & Hemptinne, 2012). Recently, similar results were obtained for parasitoids also feeding on nectar. Adult longevity and parasitism rates were found to depend on nectar provided by entomophilous plant species (Araj & Wratten, 2015; Géneau, Wäckers, Luka, Daniel, & Balmer, 2012; Jamont, Dubois-Pot, & Jaloux, 2014; Pollier et al., 2016). In contrast to hoverflies and parasitoids, adult ladybugs are predominantly predators. However, gut content analyses and observational studies have shown that adult and larval ladybugs also consume nectar and pollen contributing to fitness and predation performance (Ricci, Ponti, & Pires, 2005; Triltsch, 1999). In oilseed rape fields, entomophilous plant cover had a negative influence on herbivory (aphid abundance, weevil stem damage) but not on predators and parasitism. Pollen beetle parasitism and hoverfly abundance (although only at $P<0.1$) were even negatively related to entomophilous plant cover. It seems quite likely that the observed reduction in herbivory was still the result of a positive regulatory effect by natural enemies but that higher predation occurred before survey dates or that generalist natural enemies not analysed in this study such as ground beetles regulated herbivores (Collins et al., 2002; Valantin-Morison et al., 2007).

Taxonomically related plant species had no influence on herbivore regulation in wheat but increased herbivore attack and damage in oilseed rape. Pollen beetles and stem weevils may have been attracted by wild Brassicaceae species of the field margin switching afterwards to the crop plants. Such an associational susceptibility was also observed in previous studies on different brassicacean crops (Bischoff et al., 2016; Le Guigo et al., 2012). In wheat, associational resistance due to a higher attractiveness of wild relatives (Poaceae grasses) may have counteracted the spill over of herbivores into the field (Barbosa et al., 2009; Le Guigo et al., 2012).

Against our expectations, we found few and predominantly negative correlations between plant species richness and crop herbivore regulation. In most studies of a recent meta-analysis, predators responded positively to plant diversity, and specialist herbivores showed a corresponding negative response (Dassou & Tixier, 2016). Niche complementarity may explain such a positive relationship. Flower visiting natural enemies of crop herbivores often use different plant species as a resource (Heimpel & Jervis, 2005; Stang, Klinkhamer, & Van Der Meijden, 2006) and higher plant species richness results in a higher natural enemy diversity increasing the regulation potential (Campbell, Biesmeijer, Varma, & Wäckers, 2012). In our study, the quantity of flowering entomophilous plants clearly overruled diversity effects in a multifactorial analysis.

Identification of plant species related to herbivore regulation

Within entomophilous flowering plants, several species could be identified that were linked to a better herbivore regulation such as *L. vulgare* in wheat and *S. asper* in oilseed rape. *P. rhoeas* (both crops) and *G. mollugo* showed positive and negative effects on regulation suggesting negative interactions between different natural enemy groups (competition). Relationships with plant species were often specific for just one or two herbivore or natural enemy groups. Positive effects of *L. vulgare* on natural enemies have already been shown in previous studies. A screening experiment testing 52 plant species in monospecific stands close to winter wheat revealed a good overall score of the species hosting generalist and specialist enemies of wheat herbivores (Frei & Manhart, 1992). A recent study comparing the resource provisioning for pollinators showed that this species produces high pollen and nectar sugar quantities (Hicks et al., 2016). Different *Sonchus* species are also highly nectar rewarding, and in particular *Sonchus asper* considerably contributed to the total nectar production of the tested plant community

(Hicks et al., 2016). So there is some evidence that positive interactions between crop herbivore regulation and flowering plants are mediated by the provisioning of floral resources.

The multivariate analysis allowed drawing more general conclusions on plant species effects in a plant and animal community context. In winter wheat, positive effects of three already mentioned plant species (*P. rhoeas*, *G. mollugo*, *L. vulgare*) on several response variables linked to aphid regulation (aphid and hoverfly abundance, aphid parasitism) were identified in RDA biplots. Additionally, *Trifolium pratense* was related to higher aphid parasitism rate and lower aphid number. Focussing on damage and crop herbivore abundance as response variables closely linked to crop yield, some general trends were also visible in oilseed rape. *P. rhoeas* cover was negatively related to aphid infestation and stem damage, and a group of four species (*V. persica, G. aparine, S. latifolia, G. molle*) negatively to pollen beetle (adult and larvae) abundance and pod damage. As *L. vulgare, S. latifolia* is known to produce high amounts of nectar and pollen that may attract natural enemies of pollen beetles and pod weevils whereas the other three plant species do not seem to be very attractive to insects depending on floral resources (Frei & Manhart, 1992, Hicks et al. 2016).

However, natural enemies and crop herbivores or damage were not always separated in RDA biplots limiting conclusions on plants that may improve the general level of regulation over several herbivores. In winter wheat, aphid parasitism and leaf beetle damage as well as aphid and hoverfly abundance occurred closely together. In oilseed rape, a similar proximity was observed for pollen beetle larvae and pollen beetle parasitism, for aphids and aphid parasitism and again for aphids and ladybugs. These correlations complicate the interpretation of results, in particular the evaluation of causality. A higher abundance of natural enemies may result from better resource provisioning by the adjacent vegetation but also from a higher prey (crop herbivore) density.

Conclusions

Our study demonstrated the importance of entomophilous species that flower at peak infestation of crop herbivores, suggesting that the amount of floral resources is a key factor in herbivore regulation. Contrary to previous studies, this effect could be demonstrated inside crop fields and was not limited to field margins (Bischoff et al., 2016; Frei & Manhart, 1992; Sivinski et al., 2011). In oilseed rape, significant results were obtained down to the trophic level of crop plants and their herbivores whereas in winter wheat effects were limited to natural enemies. Within the group of entomophilous plants, we identified individual species that improved herbivore regulation but in most cases effects were limited to one or two response variables. This result highlights the importance of plant diversity offering complementary floral traits although relationships between total species richness and herbivore regulation were relatively weak or negative.

A correlative approach relating vegetation characteristics and herbivore regulation is useful to identify candidate species for designing seed mixtures improving regulation services. Contrary to classical wildflower strip studies using monospecific stands or early successional stages of sown mixtures (Haaland et al., 2011; Sivinski et al., 2011; Tschumi et al., 2015), it allows testing plant species and group effects in a late-successional, semi-natural community context. Our study showed that spontaneous field margins rich in flowering entomophilous species provide an important biocontrol service without expensive sowing of seed mixtures. Likewise, Denys and Tscharntke (2002) found that arthropod species richness and predator-prey ratios were as high in spontaneous field margin vegetation as in sown wildflower strips. The high regulation potential of spontaneous field margin vegetation needs to be better supported in agri-environmental schemes currently focussing on wildflower strips (Haaland et al., 2011). Therefore, financial support should be linked to an appropriate management protecting margins from early cutting (until peak infestation of crop herbivores), shrub encroachment, fertiliser input and pesticide drift.

Acknowledgements

We thank E. Chenu for her technical assistance and T. Sollet, A. Saphore and S. Le Barazer for their help in the field. We also thank all farmers who participated in our study for hospitality and information provided. The project was funded by the French National Research Agency (ANR, “PEERLESS”) and the chair Ecologically Intensive Agriculture (AEI).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX."

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Tables

Table 1. Results on wheat fields: relations between plant species composition (species richness, entomophilous flowering plants, Poaceae) of field margins as explanatory variables and crop herbivore abundance/damage and predator abundance/parasitism at a distance of 5 m and 50 m from field margins. GLMM estimates and significance levels of explanatory variables are presented for the best model (lowest AIC). -: not retained by AIC, + P<0.1 P<0.05 * P<0.01 ** P<0.001 ***, ns: not significant.

Distance: 5 m	**Plant species**	**Entomophilous plant cover**	**Poaceae cover**	**Family**
Herbivores and damage				
Aphids	-	ns	-	Gaussian
Leaf beetle larvae	ns	ns	ns	Neg binomial
Leaf beetle larvae	0.002*	ns	ns	Gaussian
Predators and parasitism				
Ladybugs	-	ns	ns	Neg binomial
Hoverflies	ns	0.076*	-	Neg binomial
Aphid parasitism	-	0.007+	-	Gaussian
Distance: 50 m	Plant species	Entomophilous plant cover	Poaceae cover	Family
Herbivores and damage				
Aphids	ns	ns	-	Neg binomial
Leaf beetle larvae	ns	ns	-	Neg binomial
Leaf beetle larvae damage	ns	ns	ns	Gaussian
Predators and parasitism				
Ladybugs	-	0.068***	ns	Poisson
Hoverflies	ns	ns	ns	Neg binomial
Aphid parasitism	ns	ns	-	Gaussian

Table 2. Results on oilseed rape fields: relationships between plant species composition (species richness, entomophilous flowering plants, Brassicaceae) of field margins as explanatory variables and crop herbivore abundance/damage and predator abundance/parasitism at distances of 5 m and 50 m from field margins as response variables. GLMM estimates and significance levels of explanatory variables are presented for the best model (lowest AIC). -: not retained by AIC, + P<0.1 P<0.05 * P<0.01 ** P<0.001 ***, ns: not significant.

Distance: **5 m**	Plant species richness	Entomophilous plant cover	Brassicaceae cover	Family
Herbivores and damage				
Pollen beetles	-	ns	ns	Neg binomial
Pollen beetle larvae	-	ns	0.026+	Neg binomial
Aphids	ns	-0.062*	-	Neg binomial
Pod damage	-	-	ns	Gaussian
Stem damage	ns	ns	0.013*	Gaussian
Predators and parasitism				
Ladybugs	-	ns	-	Neg binomial
Hoverflies	ns	ns	-	Poisson
Pollen beetle parasitism	ns	-0.004*	-0.007*	Gaussian
Aphid parasitism	ns	ns	-	Gaussian
Distance: **50 m**	Plant species richness	Entomophilous plant cover	Brassicaceae cover	Family
Herbivores and damage				
Pollen beetles	-	ns	ns	Neg binomial
Pollen beetle larvae	ns	ns	ns	Neg binomial
Aphids	ns	ns	-	Neg binomial
Pod damage	ns	ns	ns	Gaussian
Stem damage	ns	-0.003+	-	Gaussian
Predators and parasitism				
Ladybugs	-	ns	-	Neg binomial
Hoverflies	ns	-0.027+	-	Neg binomial
Pollen beetle parasitism	0.004*	-	ns	Gaussian
Aphid parasitism	ns	ns	ns	Gaussian

Table 3. Relationships between entomophilous flowering plants species, natural enemy abundance and parasitism rate in wheat (A) and oilseed rape (B) fields. The model was only applied to response variables significantly correlated to the total cover of flowering entomophilous species. GLMM estimates and significance levels of explanatory variables are presented for the best model (lowest AIC). -: not retained by AIC, + P<0.1 P<0.05 * P<0.01 ** P<0.001 ***, ns: not significant.

A) Wheat	*Galium aparine*	*Galium mollugo*	*Geranium dissectum*	*Papaver rhoeas*	*Vicia sativa*	*Bellis perennis*	*Leucanthemum vulgare*	*Ranunculus bulbosus*	*Rosa canina*	*Trifolium pratense*
Hoverflies 5 m	ns	0.256+	-	0.837+	-	-	ns	-	-	-
Ladybugs 50 m	-	-0.314*	ns	-	-	-	8.261***	-	-	-
Aphid parasitism 5 m	-	-	ns	-0.088+	-0.262*	-	1.547***	-	-	-

B) Oilseed rape	*Galium aparine*	*Galium mollugo*	*Geranium dissectum*	*Papaver rhoeas*	*Vicia sativa*	*Geranium molle*	*Silene latifolia*	*Sinapis arvensis*	*Sonchus asper*	*Veronica persica*
Aphids 5 m	-	ns	-	-0.445+	-	-	-	ns	-0.424+	-
Hoverflies 50 m	-	-	-	ns	-	-	-	ns	ns	ns
Pollen beetle parasitism 5 m	-0.123*	-	0.016*	-0.035**	0.059*	-	-	-	0.032**	-
Stem damage 50 m	-	ns	ns	ns	-	-	-	-	-	ns

Figure legends

Fig. 1. (A) Geographical position of the study area in France, (B) the analysed fields within the study area and (C) the survey design.

Fig. 2. Total species richness (top) and cover of plant groups (bottom; CEFP: entomophilous flowering plants, CPO: Poaceae, CBR: Brassicaceae) measured in field margins (75 m^2) of (A) wheat and (B) oilseed rape fields in 2014 (black bars) and 2015 (grey bars); means ±SD.

Fig. 3. Relationships between the cover of flowering entomophilous plants and significantly affected response variables ($P<0.1$) using parameter estimates of Generalized Linear Mixed Models (GLMM) for (A) wheat and (B) oilseed rape.

Fig. 4. Ordination biplots (first and second axis) of Redundancy Analysis (RDA) showing relations between explanatory (entomophilous plant species) and response variables (crop herbivores, crop damage and natural enemies) for (A) wheat and (B) oilseed rape.

Figures

Figure 1:

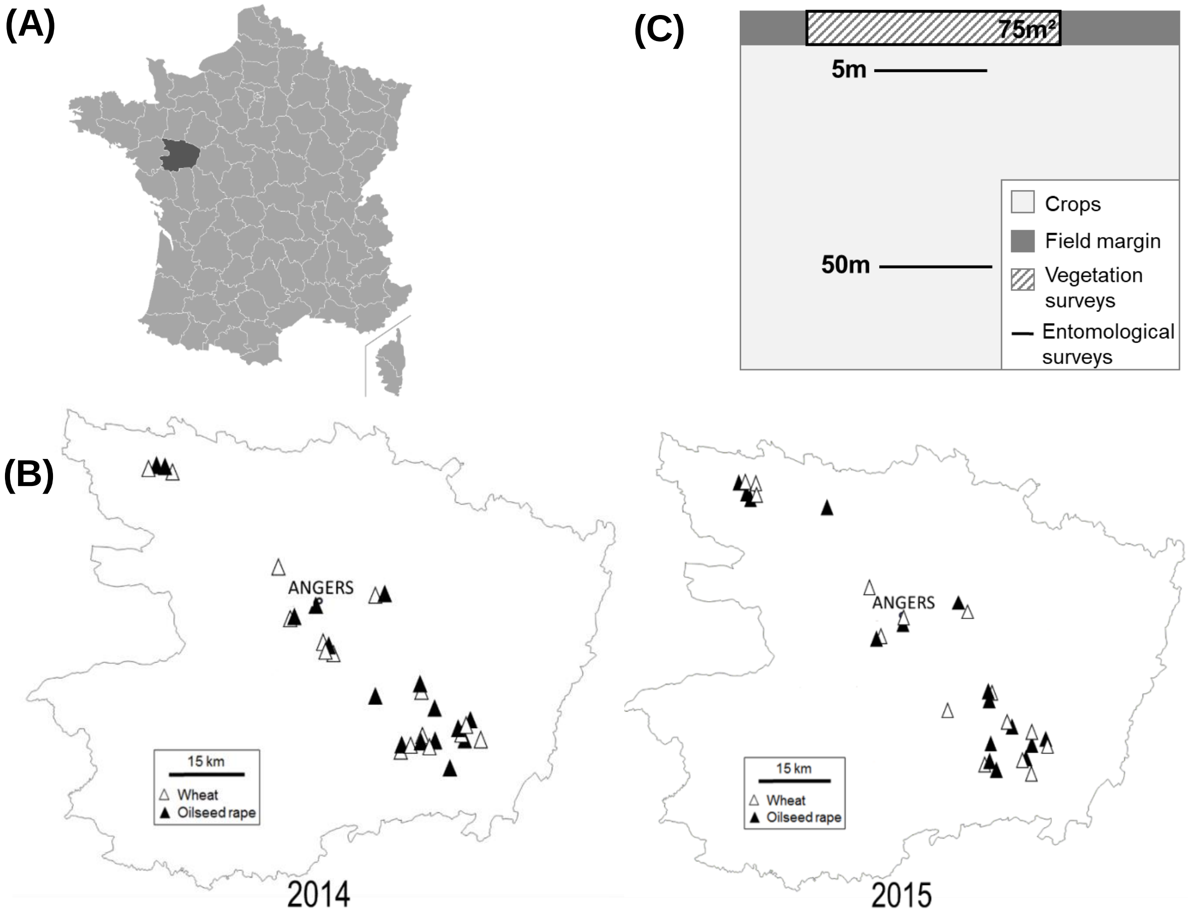


Figure 2:

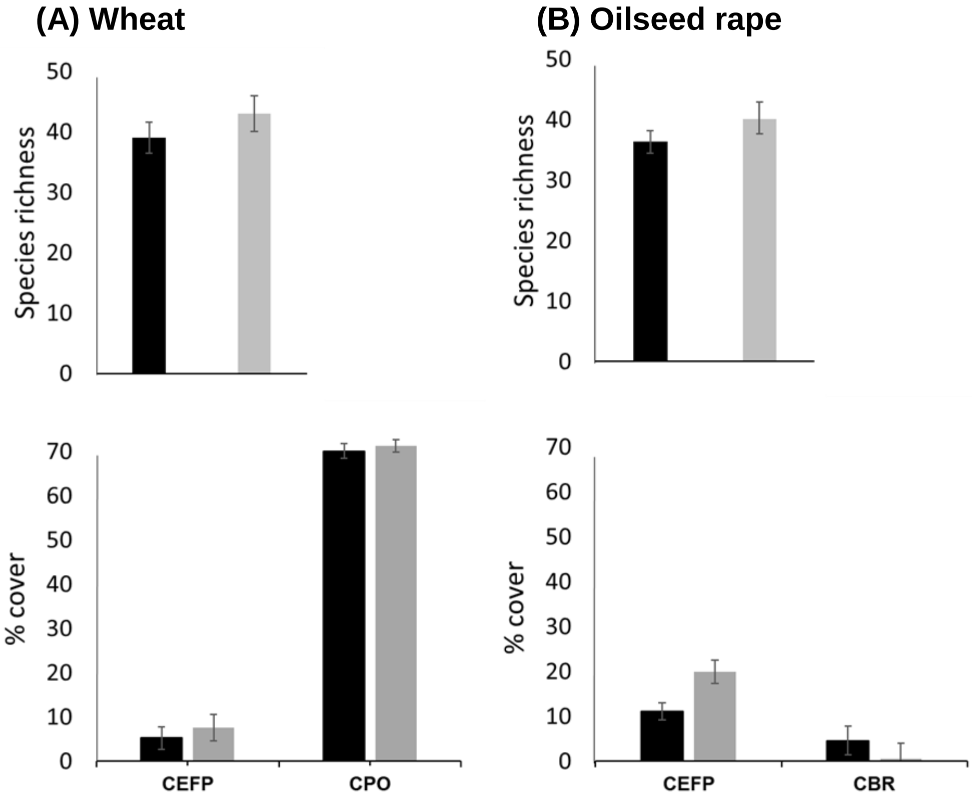

(A) Wheat
(B) Oilseed rape
Species richness
0
10
20
30
40
50
% cover
0
10
20
30
40
50
60
70
CEFP
CPO
CBR

Figure 3:

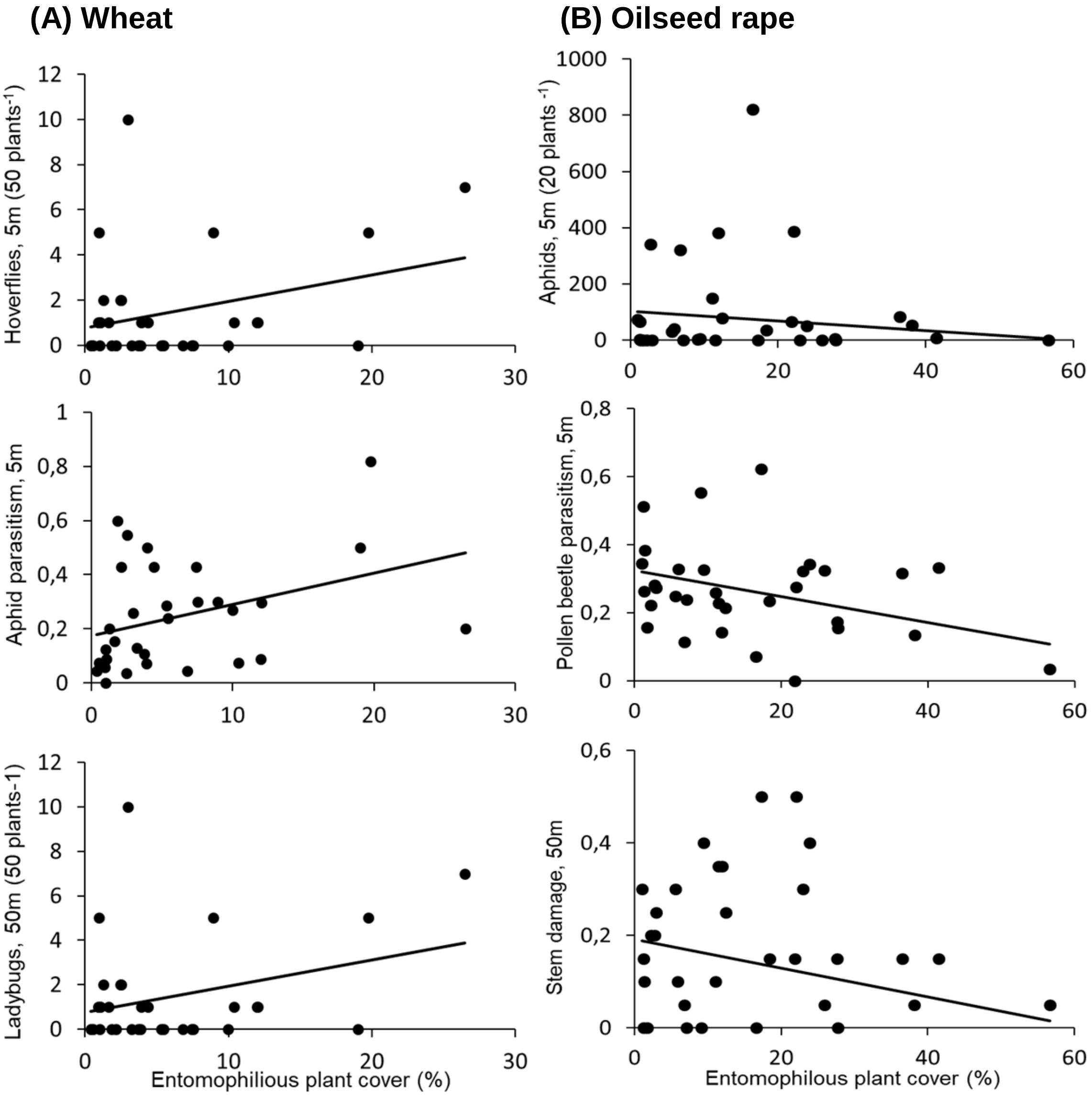
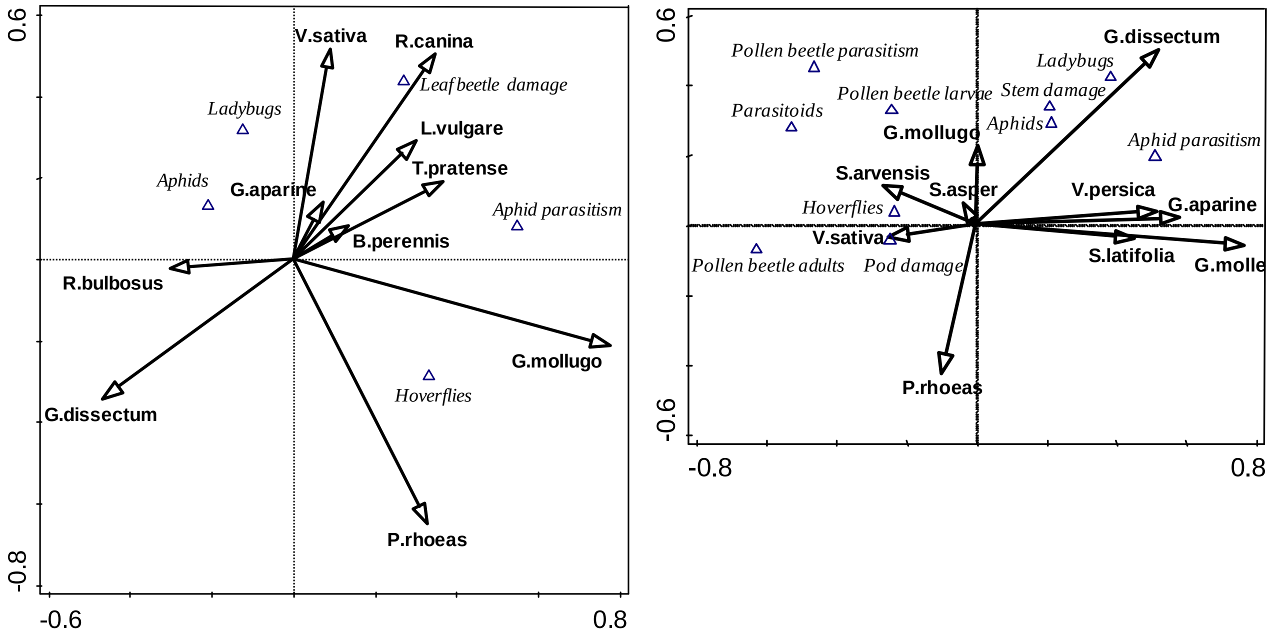

(A) Wheat
(B) Oilseed rape
Hoverflies, 5m (50 plants^{-1})
0
2
4
6
8
10
12
0
10
20
30
Aphids, 5m (20 plants $^{-1}$)
0
200
400
600
800
1000
0
20
40
60
Aphid parasitism, 5m
0
0,2
0,4
0,6
0,8
1
0
10
20
30
Pollen beetle parasitism, 5m
0
0,2
0,4
0,6
0,8
0
20
40
60
Ladybugs, 50m (50 plants-1)
0
2
4
6
8
10
12
0
10
20
30
Entomophilious plant cover (%)
Stem damage, 50m
0
0,2
0,4
0,6
0
20
40
60
Entomophilous plant cover (%)

Figure 4:



(A) Wheat

(B) Oilseed rape

Projet ANR-12-AGRO-006

PEERLESS

Toolbox for the analysis of carabids' food webs in agricultural landscapes

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Toolbox for the analysis of carabids' food webs in agricultural landscapes
Nature du livrable	
Date de publication	20/07/15
	Version 2

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Partenaires impliqués	IGEPP
Tâche associée	tâche 3, sous tâche 3-1

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

Recently developed powerful technological tools (DNA metabarcoding, next-generation sequencing, multiplex PCR) added to older ones (stable isotope analyses) provide preliminary data for a detailed description of trophic networks. Purposes of this livrable are to perfect, compare and combine those various approaches and their resolutive ability on a wide range of environmental samples (from feces to gut contents and whole insect tissues). The ultimate and directly applicable goal of this livrable is the development of a methodological framework and a « ready-to-use » toolbox for the study of invertebrate trophic networks in agricultural context.

B.2 RESUME

Maximum 1 page.

This deliverable presents the diet assessment of the most commonly encountered carabid species in intensively managed wheat and oilseed rape crop fields in typical Bretton agricultural landscape (« bocage »). We combined two approaches: 1) DNA identification from animal and plant prey remains in carabids' faeces and gut contents using molecular barcoding and next-generation sequencing (i.e. metabarcoding) ; 2) Estimation of trophic position using carbon and nitrogen stable isotope analyses.
Obtained results allowed us to set up a standard protocol for the study of trophic interactions of carabid generalist predators in agricultural context. We show that the most successful protocol implies working in stringent conditions such as bleach cleaning of carabids' carapaces and dissection of gut contents. Moreover we demonstrate that specific blocking of predator's DNA with costly blocking probes is not particularly needed nor recommended. Finally, we encourage the combination of several animal and plant markers that are complementary in their amplification success and taxonomic resolution capacity.
Detailed information about main methodological caveats is presented below.

C PRESENTATION DES AVANCEES

C.1 PRINCIPAUX RESULATS

- *DNA & High-throughput Sequencing Approach*

Using sequence data generated by 454 GS Roche and MiSeq Illumina high-throughput sequencing we compared the validity of different protocols for estimating diet of naturally-occurring insect generalist predators (carabid beetles) collected in agricultural fields. More specifically, we compared (i) the nature of the samples (feces vs gut contents vs whole individuals) ; (ii) the validity of using cleaning procedure prior molecular analyses ; (iii) the relevance of using blocking probes and (iv) the amplification efficiency and taxonomic resolution of animal and plant markers (see Table 1).

Very few prey DNA sequences were recovered from feces, the majority of sequences originating from the predator itself or accidental contaminations (e.g. human, pollen, etc.). Sequencing from carabids' gut contents gave more consistent results with about 28 % of individuals being positives for at least one animal or plant prey taxon. More than 30 prey items were recovered including several insect, arachnid and earthworm taxa as well as several weed plant families (Asteraceae, Fabaceae, Papaveraceae, etc.) present in the study area. No accidental contaminations with environmental DNA were observed, probably as a result of the cleaning protocol (immersion in 1.5 % bleach solution for 20 mn, see Greenstone et al. 2012), applied on carabids' carapaces before dissection and DNA extraction. However, carabid DNA sequences accounted for > 90 % of the total number of sequences (compared to only 18 % in feces) as no blocking probe was used and more carabid tissue is present in gut contents compared to feces. Several carabid sequences were recovered in PCR blank controls, assigned mostly to two species, *Metallina lampros* and *Phyla obtusa.* Given their small size (1-2 mm) the whole individuals from these two species were homogenized rather than dissected before the molecular analyses resulting in very high concentrations of carabid DNA (> 200 ng/uL compared to 20-100 ng/uL for gut contents).

Specific blocking of carabid DNA amplification resulted in a highly reduced diversity of prey sequences amplified with this primer set. Nevertheless, the combination of animal and plant molecular markers allowed covering for the first time the full spectrum of carabids' diet. Particularly, the use of universal plant primers revealed a relatively high proportion of plant material consumed by the carabid beetles (> 50 % of all individuals positive for at least one prey). The combination of several universal 16S and COI animal markers with different coverage and resolution allowed the simultaneous quantification of pest and non pest consumption with an adequate precision.

- *Stable Isotopes Approach*

We first evaluated the effect of two major variables affecting the discrimination factor of carbon (C) and nitrogen (N) isotopic ratios namely the tissue type and the lipid content. For this, we compared for two carabid species (i) whole individuals vs dissected tissues (muscle, head) ; (ii) non delipidated vs delipidated individuals (chlorophorm-methanol protocol and mathematical correction). Globally, results suggest that any particular manipulation of insect tissues (e.g. dissection, lipid correction) introduced artificial noise and bias in data as increased intra-specific variability and enrichment with heavy isotopes for nitrogen. Therefore, we recommend processing whole individual insects without delipidation for C and N isotope analyses.

Second, we applied this protocol for analyzing carbon and nitrogen isotope ratios of more than 60 carabid species collected from wheat and oilseed rape fields. Despite an apparent overlapping of carabids' trophic niches, our results demonstrate several distinct trophic positions (nitrogen) and spatially structured resource partitioning (carbon), with carabid species dependent on local resources, and others who seem to be mobile foragers.

- *Coupling molecular and isotopic data*

For the most commonly encountered carabid species (> 10 individuals collected per field and per date at the LTER "Armorique" in Brittany), we compared the consistency of molecular and isotopic trophic data. Detection rates with molecular approach were low (about 28 % of analyzed individuals were positive for at least one prey) but rather congruent with carbon isotopic data. Thus, results indicate that mobile foragers most likely consume various trophic resources as weeds and detritivorous species (e.g. dipterans, springtails or earthworms) whereas local foragers mainly feed on crop plants or crop associated pest species (e.g. *Meligethes aeneus, Delia spp*). However, further integration of data generated with these two different methods seems difficult, as no reliable isotopic references exist for the range of prey consumed by the carabid beetles.

C.2 PRINCIPALES RECOMMANDATIONS D'UTILISATION

1) Development of high-throughput sequencing approach for the description and for the quantification of trophic interactions in invertebrate generalist predators in agricultural landscapes. Successful protocol implies:

(i) Working with dissected gut contents rather than feces or whole individuals as it is the best compromise between samples' preservation, contamination risk and data quality. From our experience, a tremendous effort was necessary for collecting several hundreds of individual insect feces in a delay compatible with the average digestion rate (≈24 h in carabid beetles). Moreover, the presence of feces did not guarantee the presence for a prey inside, whereas using dissected gut contents allowed the optimization of the number of analyzed samples by visual control for the presence/absence of digested prey. In cases where species are too small to dissect, whole individuals could be analyzed. However, we caution that an increased risk of cross-contaminations with highly concentrated DNA is possible especially if no blocking primers are used.

(ii) Cleaning carabids' carapaces with adequate and standardized protocol (Staudacher et al. 2011; Greenstone et al. 2012) for minimizing risk of environmental DNA contaminations. Clearly, the impossibility of cleaning carabids' bodies before defecation severely compromised upstream results as a high number of contaminating DNA was amplified which were absent when a cleaning protocol was applied.

(iii) Relaxing the necessity of using blocking probes for insects because (i) their cost is about 6 times higher compared to a classical primers for the same number of samples processed; (ii) the risk of blocking target prey DNA increases substantially; (ii) the number of currently generated sequences guarantees the successful detection prey DNA even with high concentrations of predator DNA. However, it is possible to complement the high-throughput sequencing approach (using universal primers) with multiplex PCR approach (using a range of group-specific primers) to improve detection accuracy, especially for rare prey DNA.

(iv) Using a combination of universal primer sets that are complementary in their amplification and resolution capacity. For example, the use of 16S and COI primers allowed a double checking of the number of different prey taxa amplified with both 16S and COI, whereas COI marker allowed to improve the taxonomic assignation of prey sequences by taking advantage of the comprehensive barcoding public database (BOLD). We discourage using of the 16S marker MAV (see table below) because of its capacity of efficiently amplifying mammal DNA (i.e. human contaminations). Moreover, because of the small fragment size (37 bp), the taxonomic information obtained is very restricted (generally, at the order level).

2) Development of stable isotope approach for the analysis of carbon and nitrogen isotopic ratios in carabid beetles that implies:

(i) Using a homogenized mixture of all tissues for isotopic analyses. Dissecting guts for molecular analyses thus avoiding bias in isotopic signature in case if a undigested prey is present in the gut. Yet, dissection protocol is not suitable for small-size species (1-3 mm) which are analyzed with their gut contents.

(ii) Precluding any delipididation step (either chemical, either mathematical correction) as important bias in nitrogen ratios are observed in the case of carabid beetles.

(iii) Analyzing, for each sampling location, carbon and nitrogen isotopic signatures of at least one basal resource (e.g. the soil or the dominant crop species) as local variations impede direct comparisons of trophic niches between species from different locations.

3) Coupling of molecular high-throughput sequencing and isotopic analyses on the same individuals allowing the acquisition of complementary and rather congruent trophic data.

Table 1. General features of the animal and plant markers used to inform carabid diet (bibliographical data only). In brackets the % of taxa resolved at the species level in our study (MiSeq Illumina sequencing of 700 gut contents from 15 carabid species, collected in LTER "Armorique", Brittany).

Primer name	**Primer sequence**	**Amplicon size (bp)**	**Target gene**	**Target group**	**Taxonomic coverage** *Type of samples tested*	**Amplification success (% amplified species)**	**Taxonomic resolution (% taxa resolved at the species level)**	**Reference**
ewB ewE	CAAGAAGACCCTATAGAGCTT CTGTTATCCCTAAGGTAGCTT	120	16S	Oligochaeta	Lumbricidae (15 taxa) *In silico PCR* *Environmental DNA (soil samples)*	93 %	100 % (57%)	Bienert et al. 2012
16SMAV-F 16SMAV-R	CCAACATCGAGGTCRYAA ARTTACYNTAGGGATAACAG	37	16S	Mollusca Arthropoda	Data no provided	Data no provided	30 % (11 %)	de Barba et al. 2014
ZBJ-ArtF1c ZBJ-ArtR2c	AGATATTGGAACWTTATATTTTATTTTTGG WACTAATCAATTWCCAAATCCTCC	157	COI	Arthropoda	Insecta & Arachnida (14 taxa) *In vitro PCR* *Environmental DNA (bat faeces)*	6 %	96 % (31 %)	Zeale et al. 2011
Ins16S_1short-F Ins16S_1short-R	TRRGACGAGAAGACCCTATA ACGCTGTTATCCCTAAGGTA	156	16S	Insecta	Insecta & Arachnida (11 taxa) Artificial blend of different clans *In silico & in vitro PCR*	90 %	85 %	Clarke et al. 2014
G H	GGGCAATCCTGAGCCAA CCATTGAGTCTCTGCACCTATC	10 – 200 bp	trnL	Viridiplantae	*Wide range of plant taxa* *Environmental DNA (animal faeces, soil, sediments)* *In silico & in vitro PCR*	92 %* 66 %*	19 – 78 % (12.5 %)	Taberlet et al. 2007

*Expressed as % of variation at the priming sites for a range of plant taxa

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Projet ANR-12-AGRO-006

PEERLESS

Actual food ranges and their variation for several arthropods considered to provide important pest control services

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Actual food ranges and their variation for several arthropods considered to provide important pest control services
Nature du livrable	Database
Date de publication	13/02/2018
	Version 2

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Tâche associée	Tâche 3

B OBJECTIFS DU LIVRABLE

The objectives of deliverable 3.2 are linked to one of the main objectives of task 3 "Develop efficient tools for the identification, description and analysis of interactions networks" linking pests and natural enemies in agricultural fields. Based on the development of new molecular technologies, notably high-throughput sequencing, new tools are offered to carry out the characterization of large food webs in actual field conditions. However, many questions are still under debate concerning the efficacy and reliability of those new approaches. Here, we compared two different approaches (diagnostic multiplex PCR *vs* DNA metabarcoding approach) to describe the food range of two generalist carabid predators (*Poecilus cupreus* and *Pterostichus melanarius*) collected from experimental plots of four cropping systems differing in the frequency and the intensity of agrochemicals applications and tillage. The deliverable objectives were:

- Assessing the food range of the two predators in each cropping system using diagnostic multiplex PCR on predator gut contents
- Assessing the food range of the two predators in each cropping system using DNA metabarcoding approach by high-throughput sequencing of amplicons obtained by amplifying the DNA from predator gut contents using a set of universal primers
- Analysing the consistency of the food ranges identified by the two approaches
- Analysing the effect of species identity and the type of cropping system on the food range exhibited by the two carabid predators

C DESCRIPTION DES DONNÉES

Carabid beetles were sampled within the long-term experimental station "La Cage" near Versailles, France. "La Cage" is an agronomic trial of four contrasted cropping systems whose main objective is to assess the economic and environmental performances of typical production systems in the agricultural context of the Paris Basin. Four cropping systems were repeated twice: (i) high-yield high-input intensive farming (PRO); (ii) high-yield moderate-input integrated farming (INT); (iii) no-input organic farming (BIO); (iv) cropping system under permanent plant cover with no tillage (NTS).

Between 24 and 30 empty pitfall-traps were placed in a regular grid within each field and filled with clay beads to limit interactions between predators within the trap. Pitfall traps were left open for 24h at 4 occasions during May-June 2014. Field-collected carabid beetles were immediately freeze-killed at -20°C, identified to the species level and subsequently stored at -80° prior molecular analyses. Beetles selected for molecular analyses were individually cleaned-up from prospective environmental DNA contaminations following Staudacher et al.

(2013). Their gut contents were dissected and again individually stored at -80° prior molecular analyses. Prey DNA from the gut contents was extracted using the NucleoSpin Tissue kit (Macherey-Nagel, Germany) following the manufacturer's instructions.

For each species a total of 178 (*P. melanarius*) and 278 (*P. cupreus*) individual gut contents were selected for further molecular analyses.

Mutliplex diagnostic PCR:

We employed three 'ready-to-use' multiplex PCR assays (for details see Staudacher et al. 2016) targeting a range of invertebrate prey taxa commonly found in temperate cereal crops: cereal aphid species (*Rhopalosiphum padi*, *Sitobion avenae*, and *Metopolophium dirhodum*), as well as non-aphid extraguild prey such as earthworms and dipterans, and intraguild prey including ground-dwelling generalist predators (beetles and spiders) and aphidophagous specialist predators (ladybeetles). The practical applicability of this approach has already been approved by screening several thousand carabid beetles collected in cereal fields (Staudacher et al. 2016; Roubinet et al. 2017).

A higher proportion of *P. melanarius* individuals (66%) tested positive for at least one prey category compared to only 29% in *P. cupreus*. The likely explanation is that *P. melanarius* is usually more strictly carnivorous than *P. cupreus*. For both species, aphids were the most frequently detected prey (50% in *P. melanarius*, 21% in *P. cupreus*). Spider consumption was also frequent in both species (12% in *P. melanarius*, 8% in *P. cupreus*). The food range of *P. melanarius* appeared more diversified compared to *P. cupreus*. We also observed differences in carabid food ranges according to the cropping system from which they were collected with intra-guild predation being the weakest in organic farming system.

DNA metabarcoding:

Each DNA extract was simultaneously amplified with four general primer pairs by following the original PCR conditions specified in the corresponding reference papers: Clarke et al. 2014 (Insects, *16S*), Zeale et al. 2011 (Arthropods, COI), Bienert et al. 2012 (Earthworms, *16S*) and Taberlet et al. 2007 (Plants, *trnL*). High-throughput pair-end sequencing was carried out on the Illumina MiSeq platform. All sequences were taxonomically assigned using the *ecoTag* program (Boyer et al. 2016) and the EMBL sequence reference database (release 123; http://www.embl.de/). A unique taxon was assigned to each sequence. When several matches between the query sequence and the reference database were possible, the sequence was assigned to the taxon corresponding to the last common ancestor node of all the taxa in the NCBI taxonomic tree that best matched against the query sequence. A species name was accepted only if the identity score strictly equaled 1.00, a genus name in cases where the best match was ≥ 0.98, and a family name if the maximum identity was ≥ 0.95. No filtering on the number of sequence reads per specimen was applied, the presence of a prey was considered whenever at least a single read per sequence was present.

For primers targeting animal prey, the vast majority of obtained sequences were assigned to carabid beetles. With the 16S Insect primers, one in a *P. cupreus* individual was identified to contain *Apis mellifera* sequences, while eight *P. melanarius* beetles contained non-carabid sequences: *Lumbricus castaneus* (1 individual), *L. terrestris* (2), *Phalangio opilio* (3), *Bombus lapidarius* (2). It can be noticed that the 3 individuals who contained earthworm DNA were also positive with *16S* Earthworm primers. Very few non-carabid sequences were amplified with the COI Arthropod primers and sequence reads were always low. Two *P. cupreus* individuals contained few sequences of *Pardosa prativaga*. Those two individuals were also positive for the Lycosidae family with the diagnostic multiplex PCR approach. Finally, the highest prey detection frequencies were obtained with the *16S* Earthworm primers. Despite being designed for targeting Oligochaetes, those primers also amplified considerable amount of carabid DNA. However, ten carabids (eight *P. melanarius* and two *P. cupreus*) showed to be positive for earthworm DNA compared to the twenty with the diagnostic PCR approach. With the DNA metabarcoding approach, four earthworm species were identified: *Lumbricus castaneus* (1 individual), *L. terrestris* (4*), Apporectodea longa* (2), *Allobophora chlorotica* (3). Among those ten positive individuals, seven have been found also positive using the diagnostic PCR approach. Finally, using the *trnl* primers, plant sequences belonging to as much as 30 families were detected in all carabid individuals.

Database availability: doi:10.15454/DYARY6

The database corresponds to an excel spreadsheet including the results of the diagnostic multiplex PCR detections and the corresponding high-throughput sequence counts and their taxonomic assignment for the 178 *P. melanarius* and 278 *P. cupreus* individuals analysed.

D PRÉSENTATION DES AVANCÉES

Prey detection rates were much higher using diagnostic PCR than using DNA metabarcoding. Especially, no aphid sequences were amplified with the latter. However, despite the absence of aphid DNA, DNA metabarcoding results were fairly consistent with the results from the diagnostic PCR approach. All earthworm and spider taxa amplified using the 16S and COI primers have been also detected using the diagnostic PCR method. Similarly, among the ten individuals in which earthworms DNA was amplified using the *16S* Earthworm primers, seven have also showed to be positive using diagnostic PCR. Moreover, the three *P. melanarius* in which earthworm sequences have been detected using the 16S Insect primers were also positive for earthworm DNA using the 16S Earthworm primers. The species-level taxonomic identifications were similar in all those three cases. Three other prey species were identified with the 16S Insect primers (*Apis mellifera*, *Bombus lapidarius* and *Phalangio opilio*). These three prey taxa were not identified using diagnostic PCR as our diagnostic multiplex PCR primers did not target Apidae nor Opiliones. In all cases, DNA metabarcoding allowed the species-level identification of the prey taxa detected by the non-specific diagnostic PCR. The most puzzling case concerns aphid species, detected in half of all carabid individuals but for which not a single sequence was amplified using DNA metabarcoding. The most likely explanation is the existence of a mismatch between the Aphidoidea and the *COI* Arthropod and *16S* Insect primers leading to an amplification bias for this group.

All in all, our results suggest that diagnostic PCR and DNA metabarcoding appear to be consistent, the first method being far more sensitive. The low amplification success of using the general primers seemed to be due to the overwhelming predominance of carabid DNA in the samples. This result advocates for the necessity to increase sequencing depth in comparable studies.

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Projet ANR-12-AGRO-006

PEERLESS

Description of the food web structure based on pests and weeds, the factors influencing it and its influence on pest control service

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS: Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Description of the food web structure based on pests and weeds, the factors influencing it and its influence on pest control service
Nature du livrable	Articles
Date de publication	01/07/2016
	Version 3

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B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

Methods for inferring interaction networks from data, 'machine learning', to reconstruct food webs from existing ecological data-sets have recently been developed. The generated trophic links should be thought of as hypotheses and will be tested using molecular-based approaches. The learning methodology used available data (FarmScale Evaluations, Firbank et al 2003; Bohan et al 2005) and data gathered during the PEERLESS project. The learning approach will ask three complementary questions: 1) can we link the invertebrates and plants within agricultural systems to understand better the effects of trophic behaviour, including generalists/omnivores; 2) can we simplify the network structure to functional descriptions that more closely ally to functionally-based ecosystem services; and, 3) can we include primary plant productivity in the networks?

Des méthodes d'apprentissage, « machine learning », permettant d'inférer des réseaux d'interaction, à partir de données écologiques existantes ont récemment été développées. Les liens trophiques générés doivent être considérés comme des hypothèses qui demandent à être testés en utilisant des approches moléculaires. La méthodologie d'apprentissage a utilisé les données disponibles et les données recueillies au cours du projet PEERLESS. L'approche d'apprentissage vise à répondre à trois questions complémentaires: 1) pouvons-nous lier les invertébrés et les plantes dans les systèmes agricoles pour mieux comprendre les effets du comportement trophique, y compris les généralistes / omnivores ? 2) pouvons-nous simplifier la structure du réseau en fonction de descriptions fonctionnelles plus proches des services écosystémiques fonctionnels ? et, 3) pouvons-nous inclure la productivité des plantes dans les réseaux?

B.2 RESUME

Maximum 1 page en français.

This deliverable examines whether ecological networks have value for examining and understanding agro-ecosystems. Specifically, we ask a series of complementary nested questions: 1) can we link the invertebrates and plants within agricultural systems to understand better the effects of trophic behaviour, including generalists/omnivores; 2) can we simplify the network structure to functional descriptions that more closely ally to functionally-based ecosystem services; and, 3) can we include primary plant productivity in the networks? To answer the question - *Can we link the invertebrates and plants within agricultural systems to understand better the effects of trophic behaviour, including generalists/omnivores?* – we developed a methodology that brought together machine learning of existing data, behavioural approaches specifically targeted at the foraging behaviour of carabid beetles (and similar model species), Next-Generation Sequencing (NGS) approaches for testing specific network links and statistical approaches for the analysis of highly replicated networks of the sort that machine learning can provide. To ask - *Can we simplify the network structure to functional descriptions that more closely ally to functionally-based ecosystem services?* – we developed a modified version of the learning process to build functionally based networks. The second component of this question was to ask whether the functional networks that were built had similar structural elements to species based networks, and had similar explanatory power and parsimony. For the final question - *Can we include primary plant productivity in the networks?* – the goal was to build explicit networks that included arable plants. We started this process using a highly replicated carabid sub-network with feeding links to slugs and arable plants. This subnetwork was then used to demonstrate the importance of including plants by analysing the interaction of two potential ecosystem services – weed seed regulation and slug control. The subnetwork was also used to argue that the prediction and management of ecosystem services could be done better by fusing ecological networks to social and economic networks.

Ce livrable examine si les réseaux écologiques aide à comprendre le fonctionnement des agro-écosystèmes. Nous posons une série de questions complémentaires : 1) pouvons-nous lier les invertébrés et les plantes dans les systèmes agricoles pour mieux comprendre les effets du comportement trophique, y compris les généralistes / omnivores; 2) pouvons-nous simplifier la structure du réseau en fonction de descriptions fonctionnelles plus proches des services écosystémiques fonctionnels? et, 3) pouvons-nous inclure la productivité des plantes dans ces réseaux?
Pour répondre à la question « Pouvons-nous relier les invertébrés et les plantes dans les systèmes agricoles pour mieux comprendre les effets du comportement trophique, y compris les généralistes / omnivores? », nous avons développé une méthodologie qui combine : i) l'apprentissage automatique des données existantes ; ii) des approches comportementales spécifiquement ciblées sur le comportement alimentaire des carabes (et des espèces similaires) ; iii) des approches de séquençage nouvelle génération (NGS) pour tester des liens spécifiques du réseau ; et, iv) des approches statistiques pour analyser les réseaux répliqués du type que l'apprentissage automatique peut fournir. Poser la question « Pouvons-nous simplifier la structure du réseau pour des descriptions fonctionnelles plus proches des services écosystémiques fonctionnels? », nous avons développé une version modifiée du processus d'apprentissage pour construire des réseaux fonctionnels. Le deuxième élément de cette question consistait à se demander si les réseaux fonctionnels construits avaient des éléments structuraux similaires à ceux basés sur les espèces, et avaient le même pouvoir explicatif et la même parcimonie. Pour la dernière question « Pouvons-nous inclure la productivité des plantes primaires dans les réseaux? » l'objectif était de construire des réseaux explicites incluant toutes les plantes présents dans les champs agricole. Nous avons commencé ce processus en utilisant un sous-réseau de carabes très répété avec des liens d'alimentation vers les limaces et les plantes arables. Ce sous-réseau a ensuite été utilisé pour démontrer l'importance d'inclure les plantes en analysant l'interaction de deux services écosystémiques potentiels - la régulation des graines de mauvaises herbes et le contrôle des limaces. Le sous-réseau a également été utilisé pour faire valoir que la prévision et la gestion des services écosystémiques pourraient être mieux faites en fusionnant les réseaux écologiques aux réseaux sociaux et économiques.

C PRESENTATION DES AVANCEES

Can we link the invertebrates and plants within agricultural systems to understand better the effects of trophic behaviour, including generalists/omnivores?

i) Using logic-based Machine learning approaches we have demonstrated that it is possible to reconstruct ecological networks, by linking invertebrates, and test trophic networks using classically-sampled agro-ecological data (Bohan et al. 2013; Tamaddoni-Nezhad et al. 2013).

ii) Foraging behaviours of a model species of tenebrionid beetle were shown to conform to highly efficient Lévy Flight movements, but also provided the first test that Lévy

Flight and random walks are aspects of the same movement patterns (Reynolds et al. 2013).

iii) Some carabid beetles were found both to become less choosy about their weed seed food and to eat more weed seed when placed in situations of predation stress (Charalabidis et al. 2017). This feeding behaviour was limited to facultative omnivores that typically specialised upon weeds and took few animal prey. This work suggests that there may be a behaviourally-based biodiversity-ecosystem function relationship among the carabids, with carabids increasing their rate of weed seed predation in situations of high carabid species diversity, but is contingent upon the composition (mix of predators, omnivores and generalists) of the carabid community.

iv) A recently submitted paper, based upon the network learnt in i), above, shows that it is possible to analyse highly replicated networks to detect the effects of agricultural management (Ma et al. submitted). This paper shows that changes in herbicide regimes have a lower effect on network structure and function than changes in crop species, such as happen across a rotation.

v) Using Next Generation Sequencing approaches, we have demonstrated that it is possible to empirically reconstruct a part of the agro-ecological food web, linking carabid beetles to prey plants, earthworms, collembolan, other insects and spiders (Vacher et al. 2016). This molecular network illustrates similar links to the learnt networks, providing a validation of the learning methodology.

vi) We have demonstrated that, in principal, machine learning approaches could be applied to NGS data to build ecological networks much more rapidly and cheaply than currently (Vacher et al. 2016). This paper has recently led to the funding of the project "ANR-17-CE32-0011 Next Generation Biomonitoring (NGB) of change in ecosystem structure and function".

Can we simplify the network structure to functional descriptions that more closely ally to functionally-based ecosystem services?

vii) We have demonstrated that learning approaches can be used to produce ecological networks based upon function (Tamaddoni-Nezhad et al. 2013). Statistical comparison of the functional networks with the pre-existing species-based networks showed them: to have similar explanatory power to species-based networks; to have common patterns and similarities of structure; and, to have greater parsimony.

Can we include primary plant productivity in the networks?

viii) Using a learnt sub-network of carabids feeding on weed seed (primary producer plants) and slugs we have analysed how the ecosystem service of plant regulation (weed seed regulation) and slug predation interact (Gray et al. submitted, Figure 1.). This work demonstrates that ecosystem services interact and that the consequent changes in network structure affect primary plant regulation – slug predation interferes with weed seed regulation (Figure 2).

ix) Building upon this multi-service network, we advocated that ecological network approaches could be merged with social and economic network approaches to better predict ecosystem service provision (Bohan et al. 2016).

x) Pocock et al. (2016) argued that ecological networks, should they become available in sufficient quantities could be used as tools for engagement, advocacy and management of ecosystems.

Figure 1. The ‘master’ food web encompassing all species and their interactions across all the food webs used in this study. Carabid (black circles), weed (green circles) and gastropod (red circles) species nodes are sized proportionally to their ranked relative to how often they were found across all food webs. Link colour intensity and thickness is proportional to the strength of the interaction across all food webs.

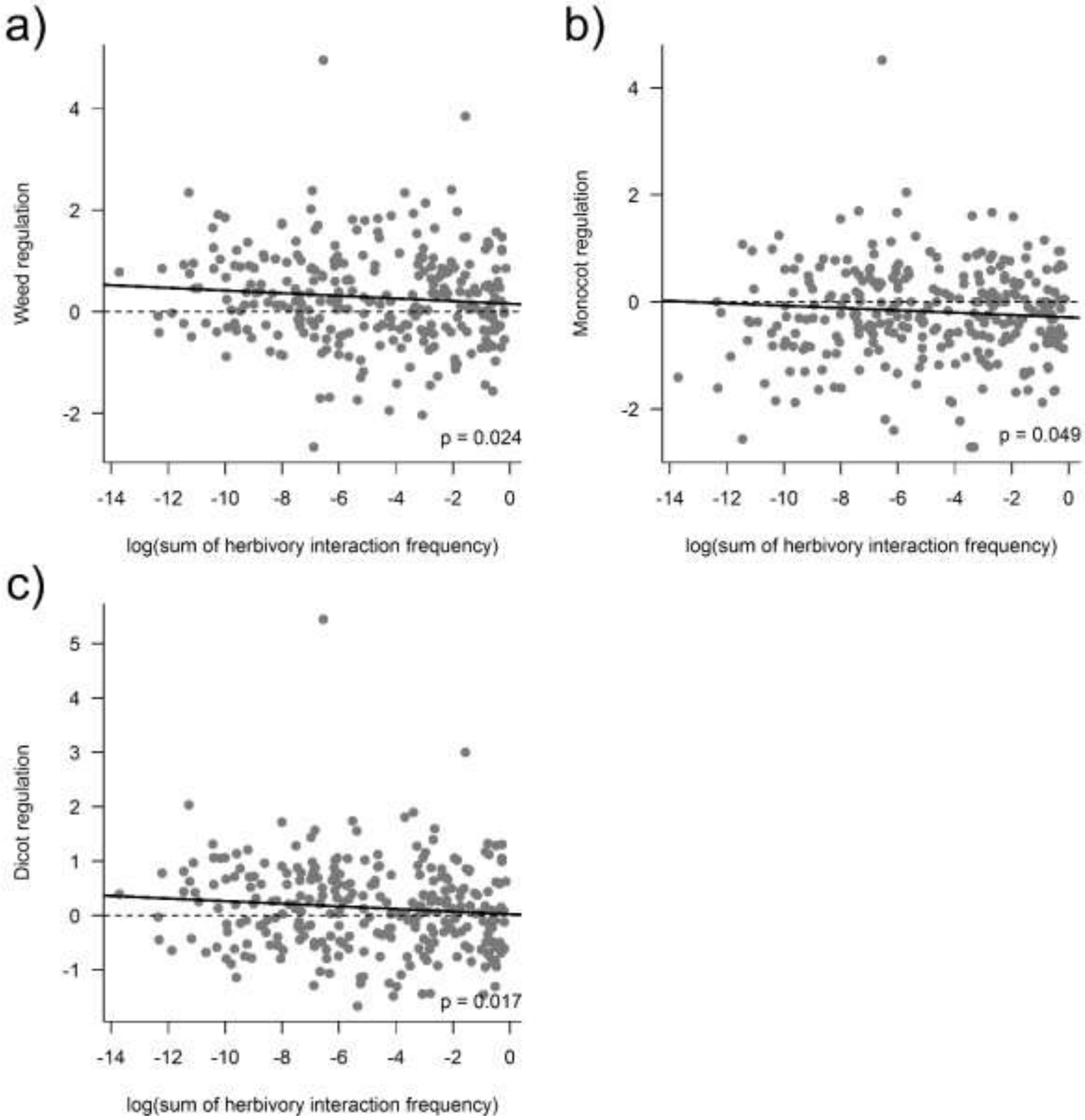

Figure 2. The level of total weed seed regulation (a), monocot seed regulation (b) and dicot seedregulation (c) related to the sum herbivory interaction frequency for each network. The weed regulation was calculated as the log of the ratio of the number of weed seeds in the seed bank between two crop sowings. Herbivory interaction frequency encompassed interaction with herbivorous and omnivorous carabid.

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Projet ANR-12-AGRO-006

PEERLESS

Molecular ressources to analyse population genetic structure of several pest and beneficial species

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	
Nature du livrable	Articles
Date de publication	01/06/2016
	Version 3

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Tâche associée	Tâche 4, sous-tâche 4.1
Livrables associés	D4.2

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

La tâche 4 a pour objectif de mesurer l'influence des pratiques agronomiques et des caractéristiques du paysage sur les dynamiques de populations d'insectes ravageurs et celles de leurs ennemis naturels. Les méthodes de marquage-recaptures utilisées classiquement en écologie pour estimer la dispersion et les effectifs de populations sont souvent difficiles à mettre en place chez les insectes notamment lorsqu'on souhaite estimer les variations démographiques associées à l'hétérogénéité des habitats. Des approches de génétique du paysage et de démo-génétiques ont été envisagées pour pallier ces difficultés. Ces approches reposent sur des inférences généalogiques (classification d'individus en fonction de leur population d'origine, relations de parenté entre paires d'individus) et nécessitent le développement de marqueurs de la variabilité génétique dans les populations (au moins 10 marqueurs polymorphe par espèce). Des marqueurs microsatellites ont été développés pour des ravageurs inféodés aux cultures du colza ou aux vergers de pommiers pendant une longue période de leur cycle de vie et pour leurs principaux hyménoptères parasitoïdes.

B.2 RESUME

Ce rapport synthétise les marqueurs microsatellites développés pour sept espèces d'insectes : les 2 principaux ravageurs Tortricidae sur la pomme (*Cydia pomonela* et *Grapholita molesta,* Lépidoptère Tortricidae), et 3 de leurs parasitoïdes (*Asgogaster quadridentata, Pristomerus vulnerator* et *Perilampus tristis*), le méligèthe en colza (Meligethes aeneus) et son principale parasitoïde (*Tersilochus heterocerus*). Les marqueurs ont été développés à partir de banques génomiques enrichies en séquences d'ADN répétées pour chacune des 7 espèces. Les mêmes protocoles ont été utilisés pour le design des amorces d'amplification PCR et la validation des marqueurs. Moins de 20%, 30% et plus de 40% des marqueurs développés s'avère utilisables pour des analyses de génétique des populations chez les Tortricidae (11 et 3 marqueurs polymorphes pour *C. pomonella* et *G. grapholita*), chez le méligèthe (19 marqueurs) et chez leurs parasitoïdes (au moins 18 marqueurs), respectivement. Les niveaux de polymorphisme varient entre 3 et 5 allèles en moyenne par marqueur et par espèce. Les niveaux de polymorphisme chez *G. molesta*, *A. quadridentata* et *T. heterocerus* sont relativement faibles et sans doute insuffisants pour des analyses d'apparentements compte tenu du nombre de marqueurs développés*.* Ces résultats soulignent la grande variabilité (quantitative et qualitative) des marqueurs obtenus pour les différentes espèces pour un même investissement initial.

C PRESENTATION DES AVANCEES

C.1 SYNTHESE DES RESULTATS

Les méthodes suivis pour constituer les banques enrichies en ADN microsatellites et pour obtenir des séquences nucléotidiques (454 GS-FLX Titanium pyrosequencing) sont présentées dans le papier de Malausa *et al* (2011). Le tableau 1 fait une synthèse des données de pyroséquencage et des marqueurs microsatellites développés pour chacune des espèces. Le nombre de séquences différentes obtenus variait selon les espèces entre 8 000 et 100 000. 0.3% à 5.5% de ces séquences étaient exploitables pour le développement de marqueurs microsatellites (design de paires d'amorces PCR, Meglécz *et al* 2010). Pour chaque espèce, 40 à 60 marqueurs ont été développés à partir des séquences présentant *i)* au moins 5 répétitions d'un même motif microsatellite et *ii)* des régions flanquantes à la zone répétée qui n'étaient pas elle-même répétées parmi l'ensemble des séquences obtenues dans la banque. Les marqueurs développés ont finalement été testés sur un échantillon d'une trentaine d'individus collectés dans un même site. Les marqueurs polymorphes et à l'équilibre de Hardy-Weinberg pour cet échantillon de référence ont été retenus pour de futures analyses de génétique des populations. Moins de 20%, 30% et plus de 40% des marqueurs testés ont été respectivement retenus chez les deux tordeuses, le méligèthe et leurs parasitoïdes. Les rendements relativement faible obtenus chez les tordeuses sont principalement lié à l'instabilité des région répété dans ce groupe et de fortes proportions d'allèles nuls au locus testé (Meglécz *et al* 2010) Plus de la moitié des marqueurs polymorphes testés chez les tordeuses présentaient de forte proportion d'allèle nuls (>10%).

Tableau 1 : Synthèse des marqueurs microsatellites développés et testés dans une population de référence pour chaque espèce. L'indice de polymorphisme de Nei (*PIC*) correspond à la probabilité que deux individus aient un génotype différent en moyenne à un locus dans la population de référence.

	Cydia pomonella	*Grapholita molesta*	*Ascogaster quadridentata*	*Perilampus tristis*	*Pristomerus vulnerator*	*Meligethes aeneus*	*Tersilochus heterocerus*
Number of NGS sequences	8146	26716	50216	9094	8770	93675	16899
Number of microsatellite markers	370	646	199	498	314	255	307
Number of marker tested	58	48	43	37	39	60	40
Number of marker valided	12	3	18	18	19	19	18
Mean number of alleles per marker	5,8	2,7	3,3	5,9	5,1	5,4	3,3
PIC	0,54	0,37	0,36	0,56	0,48	0,54	0,33

C.2 CARACTERISTIQUES DES MARQUEURS DE CHAQUE ESPECE

Ce paragraphe présentent les marqueurs qui ont été développés et testés dans une population de référence pour chacune des espèces.

- *Cydia pomonella* L. (Lepidoptera, Tortricidae)

Parmi les 27 marqueurs microsatellites polymorphes nouvellement développé chez le carpocapse des pommes, 13 sont utilisables pour des analyses de génétique des populations (Tableau 2). Plus de la moitié des marqueurs polymorphes testés n'étaient à l'équilibre de Hardy-Weinberg. Ces marqueurs s'ajoutent aux marqueurs précédemment développés chez cette espèce (Chen & Dorn 2010 ; Franck *et al.* 2005 ; 2007).

Tableau 2 : Caractéristiques des 27 marqueurs microsatellites polymorphes développés chez *C. pomonella*. T_a correspond à la température optimale d'hybridation des amorces PCR. N_a correspond au nombre d'allèles observés pour un échantillon de 28 carpocapses capturés dans un verger de pommiers en Basse vallée de la Durance. H_p et H_d correspondent respectivement à la proportion d'hétérozygotes et à la diversité génétique de Nei estimés dans cet échantillon. *HW* correspond aux écarts d'hétérozygotie par rapport à l'hypothèse d'équilibre de Hardy-Weinberg (Test exact de Fisher : *** : $p<0.001$; ** : $p<0.01$; * : $p<0.05$; NS: $p>0.05$).

Locus	Primer sequences (5'-3')	Repeat motif in the sequenced allele	T_a	Size of the sequenced allele (bp)	N_a	Allele size range (bp)	H_p	HW
			(°C)				H_d	
CP-GF2ON	F : AGTTTCACTCATCGCTTCC	(CT)9	50	276	8	226 -276	0.23	***
(cons112)	R : CTCGACACAAAGGCATATAAC						0.85	
CP-GMENS	F : GTCGCTCCGTATGAGG	(GAA)6	51	310	2	301-304	0.39	NS
(cons51)	R : CAACATCAACCGTCTGG						0.32	
CP-GWVG0	F : GCTCGCCACACTATTGC	(AC)7	52	292	5	284-292	0.75	NS
(cons7)	R : GGGAAGTTGGAGTTTGG						0.73	
CP-GOU1O	F : GGGAAGTTGGAGTTTGG	(GA)8	50	152	4	144-150	0.42	*
(cons92)	R : ACGGTAATATGACTTGGTAGG						0.63	
CP-F25BU	F : AAAGTTCAGCATACGGCTC	(GT)7	51	137	10	141-183	0.43	***
	R : TGCGAGACAAATTGACG						0.68	
CP-F26NZ	F : CCACATCTGCCTATTGTC	(GATA)9	50	167	2	143-159	0.04	-
	R : GTGGTCTCAATATAAGTCTTGC						0.04	
CP-F29K4	F : CATGTTTGATTCGGACTTATC	(TC)8	50	212	4	210-216	0.50	*
	R : GACAGGCGACCACAATATC						0.59	
CP-FNJA4	F : TCGTCAGTCTGTGGACC	(CA)8	50	176	6	264-276	0.13	***
	R : GCACGAATAAAGGTAAATAATG						0.77	
CP-FZGVC	F : GTTTCCCTGAATTGGCATC	(TA)7	54	294	8	294-350	0.32	***
	R : TAGTGTGCTAACACGCTTTGC						0.69	
CP-GOARQ	F : GTCGGAATGAGTATTGACG	(AC)7	50	215	4	205-215	0.71	NS
	R: TTTAGATTCAGACAGCACTAGC						0.56	
CP-G1ULO	F : CCTTCTCTGATGGAAAGC	(CT)13	50	147	4	141-147	0.27	***
	R: CTATGTCTTTACTAAGGTATGTGC						0.64	
CP-G3PA3	F : TGACTACCATCCACAATACG	(TG)8	52	266	19	262-342	0.89	NS
	R: CGACTGTGCTGAAACTAATACC						0.91	
CP-G5WU5	F : TTAAAGAGTATGTTAGTTCATCG	(TG)11	48	142	7	134-152	0.57	NS
	R: CGCCTCAGACCTATCC						0.74	
CP-GAO94	F : CTTGGAAAGATCCTCATACTG	(TC)10	50	144	4	126-140	0.16	*
	R: ACCACAAATGATCCGTAAAG						0.29	
CP-GHC8W	F : GACCAATGCTAAAGATAATGAC	(AC)10	50	230	12	204 -236	0.75	**
	R: CGTTTGTCCCTGTCTGAG						0.90	
CP-GHYJE	F : TACATCGGGAAAGTCAATC	(CT)7	51	162	3	160-164	0.64	NS
	R: GTTGAAGTCTGCCAGTGC						0.55	
CP-GZNC4	F : TAAGATCGCCCTTGTGG	(TC)6	51	176	4	176-182	0.57	NS
	R: ATGTTGCTTTGGGTTCG						0.63	
CP-HB4HC	F : GATTTGAAAGCAATTTGAGG	(TG)8	50	252	7	220 -266	0.64	NS
	R: AGTCAGCTACACGACTACAGC						0.81	
CP-HGPXE	F : GTCTGTAAGGTATTTGTAATATGG	(CA)11	48	264	8	250-270	0.81	NS
	R: ATTGACATGCCTATTTCC						0.86	
CP-F2DV5	F : GCAGACTTCAATAAGTTCAACAG	(AAC)11	54	207	4	192-207	0.54	*
	R: GGTTGTGTTCCTTTTAATGC						0.59	
CP-GUS6W	F : GCTGTAAGGGAGGTGTGG	(GATA)9	52	179	2	179-187	0.00	***
	R: TGTGGCAAACAAATAAACG						0.39	
CP-FODQY	F : CCCTCATAGTCCTTTCCTG	(AG)8	54	178	3	176-180	0.36	NS
	R: AGCAGACAAATGCCGTAG						0.30	
CP-GVCLU	F : TTAACCTAAACACGGTCAGAG	(CA)10	54	224	5	222-230	0.68	NS
	R: TTAACTTTCCTTGTGACATCC						0.61	
CP-FIL46	F : CGGCATTTGAGTATCAGC	(AG)9	54	149	10	151-195	0.48	***
	R: GAATGACTTACTAGGTAATCTCG						0.88	
CP-GN5DV	F : CCCAAACGTCATAATATCC	(AC)9	54	165	4	161-167	0.33	NS
	R: AGAACATAGTGAGAGTAAAGTGTC						0.49	
CP-FTGHG	F : CATCCTCACACCCTAGCC	(AC)8	55	293	5	285-297	0.37	NS
(cons39)	R: CCAATCGAGAACCAATCC						0.41	
CP-FS9VN	F : GAATTAGCTTGTATCACGACC	(AC)7	55	198	9	190-224	0.71	*
	R: ATGTGCGTCCAGTAATATCC						0.83	

- *Grapholita molesta* (Busck) (Lepidoptera, Tortricidae)

Parmi les 17 marqueurs microsatellites polymorphes nouvellement développé chez la tordeuse orientale du pêcher, 3 sont utilisables pour des analyses de génétique des populations (Tableau 3). 25% des marqueurs testés dans la population de référence était monomorphes et 80% des marqueurs polymorphes n'étaient pas à l'équilibre de Hardy-Weinberg. Le marqueur *CP-F29K4* développé pour *C. pomonella* est également polymorphe et à l'équilibre de Hardy-Weinberg chez *G. molesta (*5 allèles observés dans la population de référence analysée). Ces marqueurs s'ajoutent aux marqueurs précédemment développés chez cette espèce (Torriani, *et al.* 2010).

Tableau 3 : Caractéristiques des 17 marqueurs microsatellites polymorphes développés chez *G. molesta.* T_a correspond à la température optimale d'hybridation des amorces PCR. N_a correspond au nombre d'allèles observés pour un échantillon de 28 tordeuses orientale capturés dans un verger de poiriers. H_p et H_d correspondent respectivement à la proportion d'hétérozygotes et à la diversité génétique de Nei estimés pour cet échantillon. *HW* correspond aux écarts d'hétérozygotie par rapport à l'hypothèse d'équilibre de Hardy-Weinberg (Test exact de Fisher : *** : *p*<0.001 ; ** : *p*<0.01 ; * : *p*<0.05 ; NS: *p*>0.05). Les marqueurs notés *cons* ont été développés sur la base d'une séquence consensus établie à partir de plusieurs séquences de la base.

Locus	Primer sequences (5'-3')	Repeat motif in the sequenced allele	T_a	Size of the sequenced allele (bp)	N_a	Allele size range (bp)	H_p	HW
			(°C)				H_d	
GM-BWBSE	F : CAGGCAAATGCTGAGG	(GA)8	50	248	4	139-157	0.52	**
	R : CATACTTGGATGATACTTTTACG						0.64	
GM-CG2BT	F : GTAATCGGGTAAGGGAGAC	(TGA)16	50	214	5	194-218	0.57	*
	R : ACAATTATCGTCATCTAGCC						0.78	
GM-CHEBK	F : GTTCAAGAGTAAACCTCTAATCC	(GT)6	51	259	6	259-323	0.43	***
	R : TCTAACCAACGCCAAGG						0.68	
GM-BTV8Y	F : CTGCGTTACCCTTGTCTAC	(GT)9	50	142	2	138-142	0.21	**
(cons327)	R : TCACTATAGGAAATCAGAAGTATG						0.51	
GM-CB1LP	F : GCAATGAGGATACGACTGG	(AA)6	53	135	2	113-135	0.54	NS
(cons452)	R : CAAGTGCGGGTAGTTCG						0.43	
GM-CFPYL	F : GTGGCAGAGAGGGACATGG	(CA)7	56	150	4	144-156	0.42	**
	R : GTGCGAATCGTGATAAAAGC						0.66	
GM-BXGYL	F : TAGAACGGGACACATTTGG	(GTT)6	54	150	5	213-321	0.46	***
	R : GAGAATATCGCCATTTACACC						0.67	
GM-B6T1D	F : ATCTGCAAGTGGTCTGTAGC	(GA)13	55	146	2	146-148	0.11	*
	R : CGGTCCTGATCTACTCTCTTC						0.22	
GM-CGTU7	F : CCCATCCGCCTAAATC	(CA)9	55	120	3	112-122	0.46	*
	R: TAAAGATGAACCGTGAAATTG						0.61	
GM-BTRXV	F : GTGGCAACATGGAAAAGG	(GT)8	52	141	3	139-145	0.61	NS
	R: CATTACTATTGAAATCCAAACG						0.55	
GM-BXD6R	F : CTCTCAAAGTGATAAACACATCC	(CA)7	52	215	7	203-231	0.29	***
	R: GAAATGAAAATGTGGCAAAG						0.67	
GM-CFAIN	F : GGGACTAATTGATGAACTGC	(AC)7	52	153	3	135-153	0.07	***
	R: CTCAAACGAAACCGAACTC						0.48	
GM-B0G3L	F : TGCTCCTATAACATCAACG	(CTT)6	52	188	2	182-188	0.04	-
(cons158)	R: AATTTCTGAGTCAAGTATTTCG						0.04	
GM-B7EYM	F : CCCTCACCTGGACTTTCG	(ATC)15	52	236	3	209-236	0.11	*
	R: CTTCTTGGGTCGTTCTGG						0.17	
GM-B802U	F : TGCAAGTTGTGATAGAAAGC	(TG)8	52	235	3	231-235	0.39	NS
(cons63)	R: ATAACCTATCGTCGGGAAAC						0.34	
GM-BVWP4	F: AGTTATTCTTGCGTTTATTGG	(AG)12	50	197	4	195-221	0.15	***
(cons395)	R: AGTAGGAGCGACTTACAACC						0.67	
GM-CAQ2O	F: GGCTAACCTCAAAGGATGTC	(CA)7	55	147	2	145-147	0.04	-
	R: GGTCCCTAGATGAGTAATATGC						0.04	

- *Meligethes aeneus* F. (Coleoptera, Nitidulidae)

Parmi les 19 marqueurs microsatellites polymorphes nouvellement développé le méligèthe du colza, 17 sont utilisables pour des analyses de génétique des populations (Tableau 4). Les marqueurs *Ma-C89XX* et *Ma-ESV1Z* sont également polymorphes chez *Meligethes viridescens* (5 extraits d'ADN testés).

Tableau 4 : Caractéristiques des 19 marqueurs microsatellites polymorphes développés chez *M. aeneus*. T_a correspond à la température optimale d'hybridation des amorces PCR. N_a correspond au nombre d'allèles observés pour un échantillon de 24 méligèthes capturés dans champ de colza. H_p et H_d correspondent respectivement à la proportion d'hétérozygotes et à la diversité génétique de Nei estimés pour cet échantillon. *HW* correspond aux écarts d'hétérozygotie par rapport à l'hypothèse d'équilibre de Hardy-Weinberg (Test exact de Fisher : *** : $p<0.001$; ** : $p<0.01$; * : $p<0.05$; NS: $p>0.05$). *PIC* correspond à l'espérance que deux individus aient un génotype différent au locus considéré dans la population de référence

Name	Primers sequences (5'-3')	Motif	Size of the sequenced allele (bp)	Ta (°C)	Na	Alle size range (bp)	Alle size range (bp)	H_p	HW	PIC
								H_d		
Ma-D3QFM	F: GGAGCACGTAGCAGGAC	(AC)8	103	54	6	116-132	6	0,43	NS	0,418
	R: GCTGCTGCGTAATTATAGTG							0,45		
Ma-ESV1Z	F: GTCAGTTGTTTGGCTTATTG	(GAA)7	110	54	7	124-136	7	0,50	NS	0,492
	R: CAGGAACTCGAACAAAGC							0,55		
Ma-ESPVQ	F: GTTAGGATATGAATGTTTCTGC	(CA)8	227	54	9	139-159	9	0,86	NS	0,763
	R: CATATGCGACATCGTTGG							0,80		
Ma-C89XX	F: ACGGAAAGGTAGAGACAGG	(CA)11	117	54	6	125-139	6	0,58	NS	0,551
	R: CCTAACCCAACGGAGATG							0,59		
Ma-D8RH8	F: GAGCTTGAGAACGGAAAGG	(CA)7	160	54	4	179-187	4	0,61	NS	0,559
	R: GATCTGTTTTGATGTGCTCTTAC							0,63		
Ma-EPL2N	F: CCGACTTATCAGGTGTATGG	(GGA)11	171	54	8	177-198	8	0,70	NS	0,740
	R: CGTTCGACGTTGTGTTACC							0,77		
Ma-DM3QY	F: CATGTAAGCTATTTTGGGACG	(AC)12	134	54	7	204-218	7	0,61	NS	0,732
	R: CTATTTGCTTTGCTTGGATGC							0,79		
Ma-Cons147	F: CATTACCAGTGACAAAAGCC	(GAA)6	195	54	6	277-292	6	0,73	NS	0,660
	R: GTAAGTGAGAACCCAGAGC							0,73		
Ma-EIS2M	F: CTTTATCTCCCTGAATCTCC	(TACA)7	264	54	2	213-223	2	0,35	NS	0,246
	R: GAATGAACATCGACACACG							0,29		
Ma-3C4QRG	F: AAGAGTATAAGTCGTCGAGC	(CT)6	305	54	5	320-332	5	0,50	NS	0,590
	R: AGTGGATGTAGAGAAATAGTGG							0,67		
Ma-DCH30	F: CGCAGATCTAAATTCGTGTG	(AC)7	128	54	5	130-145	5	0,87	NS	0,673
	R: GTATAGCGAAACAACAAGTGC							0,73		
Ma-DDEYS	F: GTACACCGAGAGGCTTTGTC	(CA)7	132	54	5	142-154	5	0,67	NS	0,576
	R: GACTGTTCGGCTAGTTTTTATG							0,63		
Ma-DPXHQ	F: GGAATTTTGCAGGTACG	(GT)7	297	54	2	148-150	2	0,13	NS	0,110
	R: CACTTGCACAACATCACC							0,12		
Ma-DQM5T	F: GGGAGAGTGATGTACCTTTG	(TG)9	153	54	5	163-173	5	0,52	NS	0,596
	R: GGCAAGATAACTCAGATCC							0,67		
Ma-Cons13	F: AATGCCAAAATCTGTCATG	(CTT)6	214	54	5	222-234	5	0,81	NS	0,608
	R: GTTTCGCCGCTTTATTTGAG							0,68		
Ma-3CEALQ	F: TTTCATTAAGCAACCTGTCG	(TC)6	222	54	4	230-240	4	0,18	NS	0,162
	R: GTGAGAGTAAGTTAAAGGCG							0,17		
Ma-Cons390	F: CAGGATGATTTCAGTGGAG	(GGA)8	190	54	4	202-211	4	0,71	NS	0,523
	R: CGGAAGAGTTGTTTTGTATG							0,59		
Ma-Cons501	F: CTTACTCGCTCGTCCTATATC	(AC)7	237	54	8	227-251	8	0,70	NS	0,826
	R: CACCTATCGTGCAGATCAC							0,86		
Ma-Cons173	F: ATAAAGTACAAACCTGGTGC	(TCT)6	117	54	4	302-314	4	0,50	NS	0,520
	R: GATACAACACACAAGAAATCG							0,60		

- *Ascogaster quadridentata* Wesmael. (Hymenoptera, Braconidae)

18 marqueurs utilisables pour les analyses de génétique des populations ont été développés chez le Braconide *A. quadridentata*, un parasitoïde primaire de *C. pomonella* et *G. molesta* (Tableau 5). Les tests d'amplification réalisés sur 12 extraits d'ADN de larves de carpocapse parasitées étés concluant pour les 2 locus testés (*Aq-cons259* et *Aq-cons491*). Les niveaux de polymorphisme observés chez cette espèce sont relativement faibles (3 allèles et *PIC*<0.33 en moyenne par marqueurs)

Tableau 5 : Caractéristiques de 18 marqueurs microsatellites polymorphes développés chez *A. quadridentata*. T_a correspond à la température optimale d'hybridation des amorces PCR. N_a correspond au nombre d'allèles observés pour un échantillon de 28 parasitoïdes capturés dans un verger de pommier en Basse vallée de la Durance. H_p et H_d correspondent respectivement à la proportion d'hétérozygotes et à la diversité génétique de Nei estimés pour 11 femelles de cet échantillon. *HW* correspond aux écarts d'hétérozygotie par rapport à l'hypothèse d'équilibre de Hardy-Weinberg (Test exact de Fisher : NS: $p>0.05$; / non analysé). *PIC* correspond à l'espérance que deux individus aient un génotype différent au locus considéré dans la population de référence.

Name	Primers sequences (5'-3')	Motif	Size of the sequenced	Ta (°C)	Na	Alle size range (bp)	H_p	HW	PIC
							H_d		
Aq-C3NJQ	F:CTAAGGATTTGAAACATATAAAGG	(AG)7	161	50	3	155-161	0,39	NS	0,326
	R:GTGGCAAGGATTCAGTC						0,46		
Aq-cons231	F: GCACAAATCCCAAGTTAATG	(GAA)6	196	50	3	193-211	0,49	NS	0,356
	R: AAGGTGTTTCTCCAAGACG						0,55		
Aq-cons259	F: ATACAACAAGCTCAACAACG	(CAA)9	141	50	5	132-144	0,65	NS	0,574
	R: TGATGTAACATTAACTGAATATGG						0,91		
Aq-cons331	F: GTTATCGTGGCTAGTTTATCG	(GAA)6	183	50	3	177-183	0,17	NS	0,152
	R: GAAAAGCAATATCAAGTAATCG						0,18		
Aq-cons379	F: CGTATTCGTTCACTCTACAGG	(TC)7	222	50	3	220-224	0,18	NS	0,163
	R: GATACAAATGACGCAATCG						0,18		
Aq-cons381	F: TATCCCGACATCTGTATTAGG	(AC)7	207	50	4	187-199	0,37	NS	0,29
	R: ACTGTTCTCAATTACGTTTGC						0,27		
Aq-cons393	F: AGTCTTTCGCACTCAAACC	(GTT)9	258	52	2	252-255	0,17	NS	0,152
	R: AGTCATTCGCACTTTACACC						0,18		
Aq-cons433	F: GCTCGTTAAACTTTGAGTCTCG	(ACG)8	223	54	2	220-223	0,46	NS	0,34
	R: AAGGGTGTGACTGGATGC						0,46		
Aq-cons491	F:GACATTCTCAGCATTCAGTTATC	(TC)9	146	50	9	136-154	0,72	NS	0,651
	R:CGTGTATTCTGCATCTCATAGC						0,64		
Aq-cons55	F: CCCTTCTCACTCTCAATCC	(CT)7	176	52	2	172-174	0,42	NS	0,318
	R: AAGCTGAGTTGCCAGTTG						0,55		
Aq-CZL2L	F: GCGTGACCTTGATTGCTC	(CT)7	186	52	4	182-188	0,77	NS	0,682
	R: CGACGAGAATGTAATAAACG						0,64		
Aq-DFUXY	F: GTGGGATAAGTAACAGTGAACG	(AG)10	252	52	4	244-250	0,64	NS	0,526
	R: CGAGAGCACCTTGTATTCC						0,61		
Aq-DJN61	F: GACATAGTCTGTTGGCAAGG	(TC)7	200	52	3	196-200	0,60	NS	0,484
	R: CGAGCATATAAGGGAGTAGC						0,36		
Aq-DLVQO	F: CTTCCATTAAATTATTGTTCTCC	(GTT)9	196	50	2	196-199	0,51	NS	0,367
	R: GTTCTCAACATCAACTTTATCAAC						0,46		
Aq-C475D	F: CAAACCAGACTCATCTTGACG	(TC)8	264	54	2	262-264	0,25	NS	0,208
	R: CTCTACCCACCTCCTACCG						0,27		
Aq-C8VW2	F: TGGTTCGGTGTTGTGG	(TGT)12	227	52	3	224-230	0,18	NS	0,163
	R: CCACCTCCTGCTTATTACC						0,18		
Aq-DD45O	F: CCTTCGTCACTTTCATTGG	(TCT)6	168	50	3	165-171	0,09	/	0,083
	R: CAATCATAGAATAAATGAGGTAGC						0,09		
Aq-DL0ZC	F: TTCCTTTGTCCTAGTTGTCG	(ACG)9	245	52	3	245-260	0,09	/	0,083
	R: TGGATATAGTTACTGGTGTTGC						0,09		

- *Pristomerus vulnerator* (Panzer). (Hymenoptera, Ichneumonidae)

19 marqueurs utilisables pour les analyses de génétique des populations ont été développés chez *P. vulnerator*, un parasitoïde primaire de *C. pomonella* (Tableau 6).

Tableau 6 : Caractéristiques de 19 marqueurs microsatellites polymorphes développés chez *P. vulnerator*. T_a correspond à la température optimale d'hybridation des amorces PCR. N_a correspond au nombre d'allèles observés pour un échantillon de 28 parasitoïdes capturés dans un verger de pommier en Basse vallée de la Durance. H_p et H_d correspondent respectivement à la proportion d'hétérozygotes et à la diversité génétique de Nei estimés pour 11 femelles de cet échantillon. *HW* correspond aux écarts d'hétérozygotie par rapport à l'hypothèse d'équilibre de Hardy-Weinberg (Test exact de Fisher : NS: $p>0.05$). *PIC* correspond à l'espérance que deux individus aient un génotype différent au locus considéré dans la population de référence.

Name	Primers sequences (5'-3')	Motif	Size of the sequenced allele (bp)	Ta (°C)	Na	Alle size range (bp)	H_p	HW	PIC
							H_d		
Pv-A05ZL	F: GGCACAAGGGATACATTCTC	(TC)9	140	57	6	130-146	0.702	NS	0.649
	R: GATCCAACTCTGAACACCTG						0.692		
Pv-AOQHG	F: GTGGGAAGAGCAGAAGG	(AG)10	124	54	4	108-122	0.625	NS	0.500
	R: GAGAAGGAAATACCGAAGC						0.462		
Pv-A4FF7	F: GGATTTTCGTGGACTGG	(TC)9	148	53	4	144-150	0.452	NS	0.399
	R: CTGACGTGTATTCGTAAAGC						0.538		
Pv-A4GZ2	F: GCCGAAAACCAATTAGC	(AG)10	145	52	4	143-163	0.545	NS	0.474
	R: CAGCACGAACTCTCACG						0.615		
Pv-AIRF4	F: CCTATACCAGAGCCCACC	(CA)9	177	55	3	175-179	0.542	NS	0.447
	R: GGCAAAGATGAGGCACC						0.615		
Pv-AM3IS	F: GATGGAGAAAGCTGTGAGG	(TC)10	138	57	5	130-144	0.566	NS	0.526
	R: GAGAGTCGAGGGGTTGG						0.615		
Pv-AQNDF	F: GACAGGCTTTGACGAACC	(AG)10	153	56	5	149-175	0.280	NS	0.285
	R: GAGAGTCGAGGGGTTGG						0.308		
Pv-AQTME	F: GTGTAGTTCGTGTGAGCC	(AG)10	181	52	8	159-199	0.732	NS	0.739
	R: CCAAAATCAAGTGTGACC						0.692		
Pv-ASJDZ	F: GGATACGAGATTTCCGATACG	(GA)10	163	57	6	159-173	0.760	NS	0.690
	R: CGTTTTTGTCTTTCGTCTAATGG						0.769		
Pv-AW23T	F: CAAGCATCGGAGAGTCG	(GA)11	146	55	13	140-168	0.886	NS	0.850
	R: GCGGGAAGTATGGAGG						0.769		
Pv-B6Z55	F: CTTCGACTTGCATTGAGC	(TC)10	313	54	5	309-325	0.609	NS	0.499
	R: CGTGTGGACGATGAACC						0.615		
Pv-BCNV5	F: CACTTACTCCATCCTTCACC	(CT)9	147	57	3	141-145	0.385	NS	0.271
	R: GAAGTAGAGAAGCGGAACG						0.385		
Pv-BDXXD	F: CCTTCAGAGATTACGATTACG	(TCG)9	271	52	6	244-277	0.532	NS	0.582
	R: CTGTTATTATTGTGCATTTCG						0.615		
Pv-BJJHP	F: CGGAGTATTGGCAGAGC	(TC)11	258	55	3	252-256	0.532	NS	0.485
	R: GGAAGCTGAGGGTTGC						0.462		
Pv-Cons150	F: CGTGGCTGAGTTGTTCC	(TC)9	250	56	3	248-254	0.480	NS	0.421
	R: CGTGGCTGAGTTGTTCC						0.462		
Pv-Cons17	F: GTCACTTGCGTCAGAGTTG	(GA)12	140	56	5	132-142	0.646	NS	0.621
	R: GTCACTTGCGTCAGAGTTG						0.538		
Pv-Cons 347	F: CGATACACATTCACAAAAGC	(GA)11	227	54	3	221-225	0.271	NS	0.305
	R: CCTTTTCTTGCTAAATCTCG						0.154		
Pv-Cons58	F: CTCGATCTTATACCCGTTC	(CT)10	136	54	2	138-140	0.148	NS	0.126
	R: CCATCAGCCAAGTTATCC						0.154		
Pv-BPKA2	F:GGTGAATCGAGAGAAAAGG	(TCT)12	172	57	8	160-199	0.818	NS	0.759
	R:GGAAAAGGAAGAGCAGAGG						0.692		

- *Perilampus tristis* Mayr. (Hymenoptera, Perilampidae)

19 marqueurs utilisables pour les analyses de génétique des populations ont été développés chez *P. tristis*, un parasitoïde secondaire de *C. pomonella* (Tableau 7).

Tableau 7 : Caractéristiques de 19 marqueurs microsatellites polymorphes développés chez *P. tristis*. T_a correspond à la température optimale d'hybridation des amorces PCR. N_a correspond au nombre d'allèles observés pour un échantillon de 25 parasitoïdes capturés dans un verger de pommier en Basse vallée de la Durance. H_p et H_d correspondent respectivement à la proportion d'hétérozygotes et à la diversité génétique de Nei estimés pour 13 femelles de cet échantillon. *HW* correspond aux écarts d'hétérozygotie par rapport à l'hypothèse d'équilibre de Hardy-Weinberg (Test exact de Fisher : * : $p<0.05$; NS: $p>0.05$). *PIC* correspond à l'espérance que deux individus aient un génotype différent au locus considéré dans la population de référence.

Name	Primers sequences (5'-3')	Motif	Size of the sequenced allele (bp)	Ta (°C)	Na	Alle size range (bp)	H_p	HW	PIC
							H_d		
Pt-C3PJJ	F: ATACCTCTATCGCACTCTCG	(CGA)9	159	52	7	150-174	0.846	NS	0.768
	R: CGATTTATTTCGCTCTCG						0.843		
Pt-C6YDA	F: CCAACGATACCATAGTGACC	(GTT)8	282	56	7	282-372	0.846	NS	0.631
	R: ATCCAGAGTCCGAGAAGC						0.671		
Pt-Cons52	F: TCCAGGGCATCACAGC	(AT)6	188	54	3	183-188	0.231	NS	0.216
	R: GCGTGTGCAATTTATGAGC						0.212		
Pt-D28UZ	F: CTCCACTATATCACACTTCACG	(AC)6	195	57	4	193-199	0.462	NS	0.432
	R: GACTGACCTCCAAATCTCG						0.406		
Pt-D73HD	F: CAACAGCAGAGGGTTATAGG	(AG)13	150	56	5	140-150	0.769	NS	0.731
	R: GGAAGAAGGCATGAGAGG						0.766		
Pt-DEVQL	F: GATCGGTCAGAGACTAAGG	(AC)18	166	55	10	148-190	0.615	*	0.712
	R: AAACGACGACTAGAGAAACC						0.735		
Pt-DJZJA	F: CCCATTTACATATCCAATCC	(GA)10	162	52	4	158-164	0.769	NS	0.576
	R: GGCAACGATAATTCAACC						0.689		
Pt-DKFK8	F:TTCGTGTAGGGCAATCG	(GA)8	168	53	3	162-166	0.308	NS	0.261
	R:ATTTCTCATGCTACCTGTCG						0.283		
Pt-DPQP1	F: TAAAGGTGCGGTATTCTCC	(AG)9	233	53	6	228-238	0.846	NS	0.702
	R: AATCTTATCGTTCAATTTCTCC						0.785		
Pt-DNPXW	F: CATACTCACGCATTAAGAACC	(GA)9	173	56	15	169-239	0.923	NS	0.850
	R: GCTCTCCCACATTTCTCG						0.831		
Pt-DPPIT	F: GGCTTTCGGCTTATTCG	(ACG)8	208	54	3	202-208	0.385	NS	0.257
	R: AGAGAAACACGGATCTTATACC						0.342		
Pt-DSDSI	F: GGAGACAGGAATGTGTAAGG	(GA)10	208	51	8	194-234	0.692	NS	0.661
	R: TGCTTTGCGATGTTGG						0.702		
Pt-DU7XG	F: CACCGAACCGTGATACC	(GT)8	160	54	4	152-166	0.538	NS	0.443
	R: CAATACCATCGTCACAAGC						0.502		
Pt-DWGHH	F: CTAATAAAGCGTCTCCTTCG	(AC)11	230	55	6	224-244	0.846	NS	0.647
	R: TTCCTTCTGGTCTCACTCG						0.702		
Pt-EEPMQ	F: CATTCATTCGGCTTCG	(GA)9	156	50	3	150-154	0.615	NS	0.574
	R: CTAAACGCAACCATGACG						0.665		
Pt-EOMB7	F: CTCTCACAAGGAGGCTACG	(CT)8	193	55	12	195-231	0.692	NS	0.829
	R: AGCAACAGCAGCACTGG						0.889		
Pt-EFB2E	F: TGACAACACTCTAATCCCTACC	(TCC)7	146	56	5	134-146	0.923	NS	0.640
	R: GACATGAGAAATGAGAAGACG						0.692		
Pt-DOX83	F: GGAGTTGGGTGTTTATTATGG	(TA)6	172	56	2	172-176	0.462	NS	0.357
	R: TGTGAATACAGCAGAAAGAGC						0.517		

- *Tersilochus heterocerus* Latreille. (Hymenoptera, *Tersilochus heterocerus*)

19 marqueurs utilisables pour les analyses de génétique des populations ont été développés chez *T. heterocerus,* le principal parasitoïde de *M. aeneus* (Tableau 8).

Tableau 8 : Caractéristiques de 19 marqueurs microsatellites polymorphes développés chez *T. heterocerus*. T_a correspond à la température optimale d'hybridation des amorces PCR. N_a correspond au nombre d'allèles observés pour un échantillon de 25 parasitoïdes capturés dans un verger de pommier en Basse vallée de la Durance. H_p et H_d correspondent respectivement à la proportion d'hétérozygotes et à la diversité génétique de Nei estimés pour 13 femelles de cet échantillon. *HW* correspond aux écarts d'hétérozygotie par rapport à l'hypothèse d'équilibre de Hardy-Weinberg (Test exact de Fisher :* : p<0.05 ; NS: p>0.05). *PIC* correspond à l'espérance que deux individus aient un génotype différent au locus considéré dans la population de référence.

Name	Primers sequences (5'-3')	Motif	Size of the sequenc	Ta (°C)	Na	Alle size range (bp)	H_p H_d	HW	PIC
Th-ACRH8	F: CATAATTGTCGGCAGAAACG	(AG)11	289	54	296-304	4	0,25	NS	0,281
	R: ATCTTGTCATTGTCCGTCC						0,30		
Th-AOD81	F: TTGGTGTTGGGATGATATCG	(CT)9	235	54	275-283	3	0,27	NS	0,224
	R: TCAAAGGTCCTAAGTTCGTC						0,24		
Th-ARXDT	F: ATGTAGCCATTAACCAATCC	(CT)10	226	54	224-236	3	0,15	NS	0,193
	R: ACCGTTGAAGTTTTTAGTCG						0,21		
Th-AXWOA	F: GCTTCCATTCACAAGTTTACG	(AG)11	157	54	171-185	4	0,50	NS	0,428
	R: AGTGCTGAAGTTTATTTCCC						0,54		
Th-B2M3A	F: ACACTAGAATAATTGCACGC	(AG)10	239	54	255-257	2	0,63	NS	0,374
	R: GTAGCTGAATGACGACAAAC						0,51		
Th-B7116	F: GAACATTGTTGGCTTATAACCC	(GT)14	238	54	248-260	5	0,52	NS	0,434
	R: GATCGTAAAGAAAAGAAATAAC						0,51		
Th-BBCFN	F: CTGACGCACATTCGTAAAGG	(AG)9	189	54	207-211	2	0,12	NS	0,159
	R: CAGTGATGTTTAACCGAACTTGGC						0,18		
Th-BXXGG	F: GCCCGAATCTCATTAACG	(GA)9	344	54	358-268	4	0,38	NS	0,305
	R: GTTCACAGCCTTAATAAGAACC						0,34		
Th-C3H5G	F: ACCTTCATTCACTCTCCATC	(CT)9	244	54	247-259	7	0,73	NS	0,738
	R: GTTGAGCTGATAATTGTGGC						0,79		
Th-C56FP	F: GAAGACCGGAAACAGAGC	(CT)11	229	54	247-249	2	0,48	NS	0,352
	R: CGGATTTCGCTTCAGG						0,46		
Th-CIET7	F: TGACGTGGGAGAAACAGAG	(GA)10	163	54	181-185	3	0,33	NS	0,269
	R: GCTTTGCCACCTCGTTC						0,30		
Th-cons47	F: CAGAGCAACGACGTGG	(CA)15	209	54	227-263	6	0,42	NS	0,443
	R: CATAGGGCAAAAGACTAGCG						0,48		
Th-cons521	F: TTCTATATTTTGGGCTGTGC	(GA)13	331	54	339-349	2	0,50	NS	0,365
	R: ACGTCATACAAGCACTATCC						0,49		
Th-Cons651	F: TTTCCCTTCGACGTGTCC	(TC)10	289	54	303-305	2	0,44	NS	0,375
	R: ATTAGAGTTTACGACCATTTGTG						0,51		
Th-CTURT	F: GTCTTTCCAATTCTCTGCAC	(TG)9	150	54	169-161	2	0,15	NS	0,178
	R: ACTATCTCGCCCATTTTCAC						0,20		
Th-CWJY8	F: GCTGTTTTAAGTGCTTTGAAC	(CA)9	198	54	215-217	2	0,41	NS	0,362
	R: GATGGCGAATCGTGCG						0,48		
Th-DAXQK	F: TTAGAATAGCGGTTTGAATC	(CT)10	209	54	224-234	4	0,15	NS	0,137
	R: TGTATCATGGGAAGTACGTC						0,14		
Th-DB9SW	F: CCCTTTGATCGTTAACTCCC	(CT)12	248	54	264-268	3	0,44	NS	0,375
	R: CCTCGGTATTCCCCATTTAC						0,42		

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Projet ANR-12-AGRO-006

PEERLESS

Identification of habitats in the agricultural mosaic that affect the dynamic and the genetic structure of pest populations

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Identification of habitats in the agricultural mosaic that affect dynamic and genetic structure in several pest and natural enemy populations
Nature du livrable	
Date de publication	Décembre 2017
	Version 2

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Partenaires impliqués	PSH, BioSP, Agronomie
Tâche associée	Tâche 4
Livrables associés	D4-1 et D4-3

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

Les ravageurs et de surcroit, leurs ennemis naturels, sont présents le plus souvent dans les cultures que pendant une partie de leurs cycles. Les dynamiques de leurs populations dans les paysages agricoles dépendent donc d'un ensemble d'habitats dont il convient de déterminer les effets sur la recolonisation des cultures. Un des objectifs de la tâche 4 est de déterminer les effets des principales caractéristiques de paysages et les pratiques agricoles associées sur la structuration des populations de ravageurs et de leurs ennemis afin de préciser les dynamiques de recolonisation des cultures.

B.2 RESUME

Maximum 1 page en français.

Le livrable 4-2 est une synthèse des principaux résultats obtenus sur le carpocapse, *Cydia pomonella*, et une araignée prédatrice de carpocapses, *Cheiracanthium mildei* dans les vergers de pommiers de la Basse vallée de la Durance et le méligèthe, *Brassicogethes aeneus* et un parasitoïde du méligèthe, *Tersilochus heterocerus* dans les cultures de colza sur le plateau et la vallée de l'Eure. Cette synthèse repose à la fois sur des études publiées d'hétérogénéités d'abondances et des analyses plus préliminaires de structuration génétique des populations dans les paysages agricoles. Les analyses ont confirmées le fort impact des pratiques de protection phytosanitaire sur les hétérogénéités d'abondance de carpocapse et de l'araignée *C. mildei* dans les vergers. La distance des colzas aux bois est un facteur déterminant des abondances de méligèthes dans les colzas. Ce serait plutôt les densités de colza dans le paysage qui détermineraient le taux de parasitisme des larves de méligèthe par *T. heterocerus.*

A l'échelle des paysages étudiés, aucune structuration génétique des populations de méligèthe n'a été détectée. La structuration génétique des populations de carpocapse étaient faible en basse vallée de la Durance et variable spatialement entre années. La diffusion des carpocapses dans le paysage serait également variable selon les usages avec une plus forte dispersion dans les zones urbanisées et de prairie que dans les cultures et les bois.

Les données de variabilité génétique dans les populations de *Cydia pomonella* et *Brassicogethes aeneus* et de leurs parasitoïdes sont disponibles au lien suivant : doi:10.15454/THTFH0.

C PRESENTATION DES AVANCEES

C.1 DYNAMIQUE DES POPULATIONS CARPOCAPSES EN VERGERS DE POMMIERS

Les effets de la mosaïque paysagère sur les populations du carpocapse des pommes et de certain de ses prédateurs comme l'araignée *Cheiracanthium mildei* ont été étudiés dans une importante zone de vergers en Basse vallée de la Durance. 25 à 50 vergers de pommiers ont été échantillonnés chaque année depuis 10 ans dans la zone. Ces vergers ont été choisis selon un double gradient de densité de vergers et d'habitat semi-naturel dans le paysage les environnants [4]. Les suivis de populations ont été réalisés par piégeage à l'automne des larves de carpocapse et des araignées sur le tronc des pommiers à l'aide de bandes cartonnées. Les pratiques de phytoprotection dans les vergers ont été enregistrées parallèlement [4, 5].
Les abondances de larves de carpocapse en verger de pommiers dépendent avant tout des traitements insecticides locaux. Les effets du paysage ne sont pas les mêmes selon l'intensité des traitements phytosanitaires dans les vergers. Dans les vergers les plus traités, les abondances de carpocapse augmentent quand la proportion de verger dans le paysage augmente. C'est l'inverse qui est observé dans les vergers les plus faiblement traité [4, 5].
C. mildei est majoritairement présente dans les vergers couverts de filets de protection contre le carpocapse et entourés de nombreuses haies. L'occurrence de *C. mildei* est également renforcée dans les vergers en agriculture biologique et dans les vergers en protection intégrée les moins traités. Par contre, les occurrences de *C. mildei* et celles de larves de *C. pomonella*, ne sont pas corrélées suggérant que la dynamique de l'araignée ne dépend pas directement de la densité du ravageur dans les vergers [6].
Les analyses génétiques d'échantillons de larve collectés au cours de deux années consécutives ont montré que les populations des vergers été globalement peu structurées en Basse vallée de la Durance. La différentiation génétique moyenne entre les vergers était de l'ordre de 1% de Fst chaque année. Quand bien même les échantillons collectés ont pu être classés dans une dizaine de groupes génétiques qui étaient structurés spatialement, la structuration spatiale de ces groupes dans la zone variait sensiblement entre années [11]. Ces données de structuration génétique ont été utilisé pour estimer avec l'appui d'un modèle mécanico-statistique [8] la diffusion des populations de carpocapse en fonction de l'hétérogénéité du paysage [7, 11]. Les résultats préliminaires obtenus suggèrent que la diffusion des populations de carpocapse varierait en fonction des usages avec une forte dispersion dans les zones urbanisées et de prairies en comparaison aux zones de bois et de cultures (pérennes et annuelles).

C.2 DYNAMIQUE DES POPULATIONS MELIGETHES DANS LES CULTURES DE COLZA

La colonisation des cultures annuelles par les insectes nuisibles et la gravité des dommages qui en découlent dépendent pour beaucoup des déplacements des nuisibles entre les champs et les zones non-cultivées. Le coléoptère, *Brassicogethes aeneus*, est l'un des ravageurs les plus importants du colza d'hiver. L'abondance du coléoptère a tendance à augmenter dans les champs de colza le plus proches des zones boisées. Des suivis abondances du coléoptère au printemps pendant quatre semaines consécutives dans 24 champs de colza du département de l'Eure choisi par rapport à leur distance au bois le plus proche. Ces suivis d'abondance ont permis d'estimer à l'aide de modèle mécanico-statistique, la dispersion du méligèthe des bois vers les champs de colza [2]. Les résultats obtenus montrent que les méligèthes colonisent en moyenne les champs colza distant de 1.2km des bois. La colonisation au printemps débute par les champs de colza des champs les plus proches des bois, la colonisation des champs les plus éloignés des bois arrivant plus tardivement [2].
Les abondances de *Tersilochus* dans les champs de colza dépendent principalement des abondances *B. aeneus.* Ce serait plutôt les densités de colza dans le paysage qui détermineraient le taux de parasitisme des larves de méligèthe par *T. heterocerus* [10].

C.3 STRUCTURATION GENETIQUE DES POPULATIONS DE PARASITOÏDES

Le nombre d'échantillons réduit de récolte de parasitoides du carpocapse (*Ascogater quadridentata*) et du méligèthe (*T. heterocerus)* n'a pas permis l'analyse de la structuration de leurs populations à l'échelle des deux zones d'étude. Les analyses génétiques des populations de ces 2 espèces de parasitoïdes ont été conduites indépendamment en regroupant des échantillons de populations de différents bassins de production en France et en Europe, ainsi que des populations qui ont été introduites au siècle dernier aux Etat-Unis [3, 9].

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La bibliographie correspond aux principales productions du livrable D4-2 pour partie en lien avec les productions du livrable D4-3. Ces productions comprennent des articles scientifiques et des présentations à des colloques. Les résultats obtenus sont également détaillés dans plusieurs mémoires de master et la thèse d'Amandine Juhel.

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Projet ANR-12-AGRO-006

PEERLESS

Identification of agronomic practices and vegetation that affect pest and natural enemy population dynamics

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Identification of agronomic practices and vegetation that affect pest and natural enemy population dynamics
Nature du livrable	Articles
Date de publication	16/03/2018
	Version 1

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Partenaires impliqués	IGEPP, Agronomie, AE, PSH
Tâche associée	Tâche 4, sous-tâche 4-2
Livrables associés	D4.1 et D5.1

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

Semi-natural vegetation introduced in crop margins may enhance pest biocontrol by attracting beneficial species from the surrounding landscape. Mark-capture experiments and directional trapping that are classical tools in ecology have been used to assess the movement of pest and beneficial species among semi-natural habitat patches, among contiguous crop fields and between both. Furthermore, some of the collected individual were genotyped for sibship inferences to estimate the progeny size distribution and population sizes at the field level of a couple of pests and their associated parasitoids. The objective was to compare temporal samples within a field and among fields accounting for the presence of semi-natural habitats and floristic management.

B.2 RESUME

Maximum 1 page en français.

First, the movement of natural enemies from margin strips into the field were analysed using isotopic or immune-marking techniques.

At the Angers site, a new method of nectar labelling was tested that based on the injection of ^{13}C labelled sugar solution into the plant stem in order to analyze the nectar uptake by parasitoids (cotton wick method). The experiment was published in Entomologia Experimentalis and Applicata (Pollier et al. 2016). The cotton wick method was successful in labelling extrafloral cornflower nectar (*Centaurea cyanus*). The uptake of labelled nectar by parasitoids was first tested under laboratory conditions, and second in an oilseed rape field. About 2/3 of the parasitoids were identified as marked after 96 h exposure to labelled plants in the laboratory. Labelled parasitoids were also detected inside the field, but the detection rate was only 1%. The experiments clearly demonstrated that the cotton wick method is appropriate to label extrafloral nectar and parasitoids feeding on this labelled nectar. Further research is needed on the amount of labelled extrafloral nectar required to obtain a sufficient number of marked individuals to track parasitoid movements in the field.

At the Avignon site, ovalbumin protein (5% white egg solution) was sprayed on adjacent wildflower strips or hedgerows to the apple orchards in order to analyse the movement of various predators potentially involved in the control of two apple pests (*Cydia pomonella* and

Dysaphis plantaginae). In a first experiment, we placed pitfall traps at different distances from the flower strips to capture during the summer ground beetles and spiders that are major generalist predators of the *C. pomonella* larvae. An ELISA test was used to analyse the presence of ovoalbumin mark of the captured predators. In total, 37 out of 490 individuals were marked by the egg protein. The labelled predators were found all over the orchards suggesting a high mobility of the captured predators. We conclude that among the ground arthropods that were associated in the regulation of *C. pomonella*, only few crossed the flower strips during the experiment. In a second experiment of immunomarking, the spring movements of the arthropod predators between the orchards and their adjacent hedgerows were analysed. The results of this second experiment were published in Basic and Applied Ecology (Lefebvre et al. 2017). Canopy and ground predators were captured using beating and pitfall traps, respectively, and about 20% of the 1272 captured arthropods were marked by the egg protein. Here again, most of the ground arthropod species preferred staying in the orchard habitat, but the canopy insects mainly moved between the orchards and the hedgerows. Movement also depended on the environment surrounding the orchard, the canopy insects staying more in the orchard habitat than in the hedgerow when those hedgerow were the thickness.

Second, the activity density and the nutritional status of three weed seed-eating carabid species, *Poecilus cupresus*, *Amara similata* and *Pseudoophonus rufipes,* were analysed in oilseed rape and in winter cereal fields adjacent to another crop field or to a grassy field margin to infer the functional role of different habitat types and their combinations. Part of the results of this experiment were published in Agriculture Ecosystem and Environment (Labruyère et al. 2016). Grassy field margins were used by the three species at least during a part of their activity period. However, during the peak of activity of *Poecilus cupresus*, *Amara similata* in spring, no positive effect of the adjacency of a grassy field boundary could be detected on the abundance and the nutritional state of individuals in the adjacent crop. Conversely, grassy field margins had a positive effect on *P. rufipes* which peak of activity occurred after crop harvest in summer. This study highlights the importance of complementation and spillover processes in the functioning of populations living in agricultural shifting mosaics.

Kinship inferences were performed on population samples from oil seed rape fields or apple orchards of both *Brassicogethes aereus* and *C. pomonella* and their main hymenopteran parasitoids, *Tersilocus heterocerus* and *Ascogaster quadridentata,* respectively. Effective size of the parent population in a field was estimated based on the proportions of sibs inferred in the sample of their offsprings. Effective population sizes of the two pests varied from a few decade to a few thousand parents per field (up to 350 *C. pomonella* and up to 2700 *B. aereus* parent per field). Effective population sizes in *B. aereus* differed among fields; the lowest effective population size was estimated in the farthest field from the forest (less than 40 *B. aereus* parents). Comparatively, effective population sizes in the parasitoid species ranged from a few decade to a hundred parents per field (up to 150 *A. quadridentata* and up to 25 *T. heterocerus* parents per field). Effective population sizes died not significantly differ among fields or between generations in the same field.

C PRÉSENTATION DES AVANCÉES

The following manuscripts and theses constitute this deliverable:

Juhel, A., Barbu, C., Morison-Valentin, M., Olivares, J. Franck, P. 2017. Sibship assignments and effective population size measure of an oilseed rape pest in Juhel A.'s PhD thesis. Chapter 2, pp 73-88.

Juhel, A., Barbu, C., Morison-Valentin, M., Olivares, J. Franck, P. 2017. Using microsatellite markers to improve knowledge on the dispersal of a crop pest parasitoid, *Tersilochus heterocerus* in Juhel A.'s PhD thesis. Chapter 5, pp 157-171.

Labruyère, S., Ricci, B., Lubac, A., Petit, S. (2016). Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes. Agriculture Ecosystem and Environment. 231, 183-192. 10.1016/j.agee.2016.06.037.

Pollier, A., Dosdat, S., Tricault, Y., Bischoff, A., Plantegenest, M., Jaloux, B. (2016) Using the stable isotope marker ^{13}C to study extrafloral nectar uptake by parasitoids under controlled conditions and in the field. Entomologia Experimentalis et Applicata 161, 131-140.

Lefebvre, M., Papaix, J., Mollot, G., Deschodt, P., Lavigne, C., Ricard, J.M., Mandrin, J.F., Franck, P., 2017. Bayesian inferences of arthropod movements between hedgerows and orchards. Basic and Applied Ecology 21, 76-84.

Teles dos Santos, R., 2015. Structure génétique des populations du parasitoïde du carpocapse des pommes, *Ascogaster quadridentata* (Hymenoptera, Braconidae). Master thesis. SupaAgro, Montpellier, p. 25.

Bayesian inferences of arthropod movements between hedgerows and orchards

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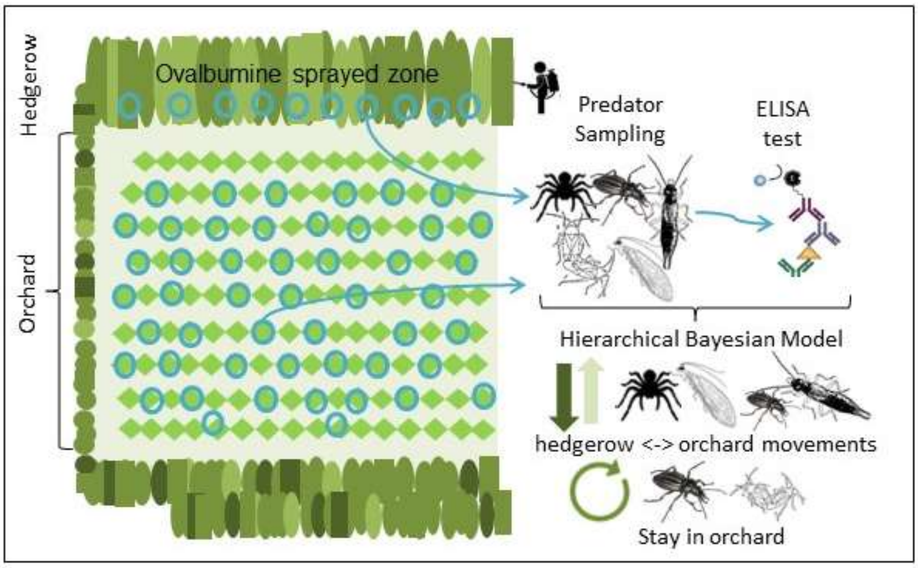
Running title:

Assessment of arthropod movements based on immunomarking

Highlights

- Samples of immunomarked arthropods were analyzed using a Bayesian model.
- Mobility and habitat preferences differed according to the arthropod taxa.
- The most abundant ground arthropod species preferred the orchard habitat.
- Canopy insects mainly move from the hedgerows to the orchards.

Graphical abstract



Abstract

Hedgerows are agro-ecological infrastructures that are assumed to enhance biodiversity in an agro-ecosystem and the control of crop pests. However, local movements of arthropod predators from hedgerows to crops remain poorly understood. In this research, these movements were analysed in eleven commercial apple orchards over two weeks in the spring of 2014. Predators were indirectly marked by spraying ovalbumin on the hedgerows. Canopy and ground predators were captured using beating and pitfall traps, respectively, in both the orchards and the hedgerows, and individuals marked by ovalbumin were detected using ELISAs. Approximately 20% of the 1,272 captured predators were identified as marked. Movements between the orchards and the hedgerows of the most abundant predator taxa (*Forficula auricularia*, *Chrysoperla sp*, *Philodromus spp*, *Cheiracanthium mildei*, and *Nebria brevicollis*) and of four guilds (ground spiders, ground beetles, canopy spiders and canopy insects) captured across the eleven locations were estimated using a Bayesian model. On one hand, canopy insects and ground spiders were less likely to stay in the hedgerows than were the canopy spiders and ground beetles. On the other hand, the canopy spiders and ground beetles were less likely to stay in the orchard than were the canopy insects and ground spiders. However, there were exceptions within these groups: *F. auricularia* and *N. brevicollis* exhibited a high probability of staying in the hedgerow and in the orchard, respectively. Overall, these results demonstrate the frequent movements that occurred between the orchard and the adjacent hedgerow in a diverse range of predator taxa. The probabilities of movement were further affected by the characteristics of the orchard for most taxa. Therefore, agro-environmental measures that focus on hedgerow management require consideration of the local arthropod predator communities and their characteristics to enhance pest control in apple orchards.

Keywords:

Earwig, ELISA, ground beetles, hierarchical Bayesian model, lacewing, mark-recapture, mobility, spiders

Introduction

Hedgerows are hot spots of arthropod diversity in agricultural landscapes. They host natural pest enemies and may provide pest control services for crops (Haenke et al. 2014; Morandin, Long & Kremen 2014). The enhancement of such services requires understanding of the routine movement (Van Dyck & Baguette 2005) of these pest enemies between semi-natural elements and crops (Rand, Tylianakis & Tscharntke 2006; Schellhorn, Bianchi & Hsu 2014; Tscharntke, Rand & Bianchi 2005).

In orchards, the abundance and diversity of arthropod predators may be high within the crop areas close to hedgerows or woodlands (*e.g.,* Debras et al. 2008; Sackett, Buddle & Vincent 2009), and the distribution of insect pests may be affected by hedgerows (Ricci et al. 2011). However, only a few studies have directly investigated predator movements between hedgerows and their adjacent orchards (Debras et al. 2007; Moerkens et al. 2010 for the earwig). Orchards are particularly interesting for addressing questions about routine predator movements in agricultural landscapes. First, hedgerows and orchards share numerous ground- and canopy-dwelling predator taxa, which are likely to move between the two habitats (Boreau de Roincé et al. 2012; Debras et al. 2007; Maudley, Seeley & Lewis 2002; Miñarro & Dapena, 2003; Miñarro & Prida 2013; Pollard & Holland 2006). Second, the low contrast in vegetation structure between an orchard and a hedgerow should enhance predator movements between the two habitats (Inclan et al. 2016; Schellhorn, Bianchi & Hsu 2014; Rand, Tylianakis & Tscharntke 2006). Third, hedgerow and orchard habitats may differ in terms of the amount of trophic resources, depending on their management and characteristics; the availability of phytophagous prey for generalist predators is, for example, expected to vary in orchards because of insecticide treatments and to vary in hedgerows because of their floristic composition (Miñarro & Prida 2013) and structure (Maudsley 2000). Predator foraging movements into or out of the orchard are likely to vary depending on the environmental context (Maudley, Seeley & Lewis 2002; Polis, Anderson & Holt 1997; Van Dyck & Baguette 2005) and the movement capacity across arthropod taxa (Schellhorn, Bianchi & Hsu 2014; Sorribas et al. 2016).

In the present study, we investigated the movement of ground and canopy dwelling predators within eleven apple orchards and their adjacent northern hedgerows using an immunomarking approach (Jones et al. 2006;

Horton, Jones & Unruh 2009). A hierarchical Bayesian model was developed to model the mark and capture process for each predator taxon. The movements of the most abundant taxa between orchards and hedgerows were deduced from the Bayesian estimations. Orchard and hedgerow characteristics modulating this movement were also assessed.

Materials and methods

Orchards and their environmental characteristics

This study was conducted in south eastern France (from 43°46’27”N to 43°51’23”N and from 4°51’12”E to 4°57’34”E), a region where apple orchards account for 22% of the land cover, and windbreak hedgerows and small woodlots account for approximately 8%. We selected in this region eleven commercial orchards comprising 8-15 apple tree rows (approximately 100 m long), which were protected by a parallel windbreak hedgerow on the north side of the orchard (hereafter named hedgerow). At each location, the environmental characteristics of the orchard and its hedgerow were measured using four variables (Table A1). The *Management* variable described whether the orchard management was organic or conventional. The *Shannon* index (Shannon & Weaver 1949) characterized the floristic diversity in the hedgerow based on the occurrence frequency of all perennial plant species observed at ten positions along the hedgerow (Table A2; Ricci et al. 2011). The *Thickness* variable described the hedgerow area (in m^2) and was calculated based on height, width and optical porosity (Lazzaro, Otto & Zanin 2008) of the vegetation as height x width x (1-porosity). The *Thickness* mainly depended on hedgerow width and porosity because hedgerow height varied little among locations (height = 9.5 ± 1.0 m). The *WoodyIndex* (in m) was defined as the area of natural woody habitat adjacent to the orchard, including hedgerows, divided by the perimeter of the orchard.

A principal component analysis (factorial analysis of mixed data, *FAMD*) was performed to summarize the four environmental characteristics at each location (package FactoMineR, R version 3.3.2) (Table A1). The first dimension (*Dim1*, 55% of the total variance) increased with organic *Management* (which accounted for 30% of *Dim1*), the *Shannon* diversity of the hedgerow (accounting for 24%) and the *WoodyIndex* (accounting for 33%). The second dimension (*Dim2*, 22% of the total variance) increased with the *Thickness* of the hedgerow (accounting for 81% of *Dim2*) (Tables A3 and A4). Spring damages caused by the two main apple insect pests (*Cydia pomonella* and *Dysaphis plantaginea*) were very low at each location and were not included in the *FAMD* (Tables A1 and A4). However, *D. plantaginea* damages were positively correlated with the *WoodyIndex* (Table A3) and *Dim1* coordinates (Spearman's correlation; $r_s = 0.8$, $P < 0.01$).

Marking and assessment of the immunological marks

Hedgerow marking with ovalbumin

Ovalbumin was used to mark predators in the hedgerow on the north side of the orchard. The hedgerow was sprayed on 13 May, 2014, with a 4% solution of ovalbumin (eggNERGY© egg white powder). A total of 5 L of this solution was applied with a backpack sprayer (Stihl SR 450©) to the entire length of each hedgerow, from the ground to 2.5 m high, i.e., 20 mL/m² on average.

Predator capture

Arthropods, which were considered potential predators of *C. pomonella* and *D. plantaginea*, hereafter called 'predators', were collected 2, 6 and 13 days after ovalbumin application. Capture occurred at 10 equidistant positions in each hedgerow, and at up to 50 apple trees evenly distributed in each orchard (Table 1). The capture sites within the orchard were 5-62 m from the hedgerow (Tables C1 and C2). Two modes of capture were used at each position and at each time: pitfall traps and beating. The pitfall traps (diameter: 5.3 cm, height: 10 cm) were located at 20 cm on the north side of the apple tree trunk or on the south side of the hedgerow border. They were opened 24 hours before sampling. Five branches at 1.50 m above the ground on the south side of each apple and hedgerow tree were selected for beating. Branches were struck three times with a wooden bat and the arthropods that fell down were captured onto a 40 cm x 50 cm tray. Each location was sampled at a different time of day for the three different capture sessions (between 8:00 AM and 3:00 PM).

To prevent ovalbumin contamination among the collected predators (Horton, Jones & Unruh 2009), we used disposable gloves and Horiver® sticky yellow traps to cover the beating plate. The gloves were changed at each capture position. One beating bat was used for the hedgerow capture and another was used for the orchard. Each predator was individually transferred into a 1.5 mL microtube with a disposable wooden toothpick that was changed between each sample. Each predator was stored dry at -18°C in this microtube until immunological analysis.

Indirect ELISA

Each predator was soaked in 1 mL of a phosphate saline buffer solution (PBS). A total of 80 µL of this solution was transferred into microplates to assess the presence of the ovalbumin antigen using indirect ELISA, following Jones et al. (2006). In each well, 100 µL of diluted commercial SIGMA© antibodies were used: anti-chicken egg albumin antibody produced in rabbit (C6534) was diluted to obtain a concentration of 10^{-3} mg/mL, and anti-rabbit IgG-peroxidase antibody produced in goat (A0545), was diluted to a concentration of 10^{-2} mg/mL. Each individual sample was tested twice on different plates. The optical densities (ODs) were measured at 450 nm with a microplate reader (TECAN© infinite M200). The raw OD readings were corrected (*correctOD)* for each plate by removing the mean OD values of 10 wells that contained only PBS and no antigen.

Detection of the marked predator*s*

The individual predators were considered marked or not based on a threshold value that was defined with a set of negative controls. Among the individual predators that were captured in the mid-south orchard areas (the farthest from the hedgerow), the 50% that exhibited the lowest *correctOD* were used as negative controls (Appendix B). The thresholds were defined as the mean *correctOD*+4sd values of the negative controls (Jones et al. 2006; Sivakoff, Rosenheim & Hagler 2011). An individual predator was considered marked if both of the *correctOD* values on the two ELISA plates were above the threshold (0.32 and 0.10 for the pitfall and beating samples, respectively).

Predator identification and grouping

All predators were identified with a binocular loupe (Appendix C). Among the 1,272 captured predators, 814 were collected by beating (194 in hedgerows and 620 in orchards), and 458 were collected in pitfalls (61 in hedgerows and 397 in orchards). The number of captures also varied among the locations (Table A1).

Only a few predator species were captured in sufficient numbers across the eleven locations to deduce their movement (Table 1). Thus, an initial analysis was performed on four broad predator guilds: 'ground spiders', ‘ground beetles’, ‘canopy spiders’ and ‘canopy insects’. Then, a second analysis was performed on the eight most abundant predator taxa (i.e., species or genera with more than 10 individuals captured per location in more than half of the 11 locations, Tables C1 and C2). These eight predator taxa were captured in both the orchards and the hedgerows, but *Forficula auricularia*, *Pterostichus spp*., *Cheiracanthium mildei*, and *Trochosa hispanica* were hardly ever captured in the hedgerows (Table 1).

Hierarchical Bayesian model

For each predator guild and the most abundant taxa, the model estimated the probabilities $p^{(\alpha)}$ of not entering the orchard and $p^{(\beta)}$ staying in the orchard during one time step of 24 hours. Both probabilities were linked by the latent structure of the model, which takes into account the localization and possible movements of the predator. We assumed that the large majority of arthropods caught in the orchard or its hedgerow were already in the orchard or in the hedgerow during the marking; thus, their movements occurred only within or between the hedgerow and the orchard and $p^{(\alpha)}$ could be interpreted as the probability of staying in the hedgerow (but see Appendix E). We also assumed that the predator individuals were only marked during the first 24 hours following the protein treatment and that the marked individuals had not lost their mark on the thirteenth day of capture (Hagler et al. 2014; Jones et al. 2006).

Movement process

The movements were described from the unobserved latent variable $Y_{i,t} \sim \text{Bern}(p_{i,t})$, indicating whether individual i was in the orchard ($Y_{i,t} = 1$) or not ($Y_{i,t} = 0$) at time t.

At time $t = 1$ (marking session), the probability of individual i being in the orchard is $p_{i,t} = m\,(1 - M_i)$. $p_{i,t}$ depends on whether individual i was marked ($M_i = 1$) or not ($M_i = 0$) and on the probability m that an unmarked individual (but later captured) was in the orchard during the marking session. The probability m depends on the marking probability and on immigration from non-sampled habitats during the survey. However, because of high marking efficiency in the hedgerow (Hagler et al., 2014), the high values of m represent situations in which most captured individuals were initially in the orchard or in the hedgerow.

At time $t > 1$, the probability $p_{i,t}$ of individual i being in the orchard is defined as the probability of individual i to enter the orchard given that it was not in the orchard before and the probability of individual i to stay in the orchard given that it was in the orchard the time before. It is defined as follows:

$$p_{i,t} = X_{i,t}\left(\left(1 - Y_{i,t-1}\right)\left(1 - p_i^{(\alpha)^{Ndays_{t-1}}}\right) + Y_{i,t-1}\, p_i^{(\beta)^{Ndays_{t-1}}}\right), \forall t \in \{2,3,4\},$$

where $p^{(\alpha)}$ and $p^{(\beta)}$ respectively refers to the probability of staying in the hedgerow and of staying in the orchard for one time step of 24 hours and $Ndays_{t-1}$ is the number of days between the times $t-1$ and t. The value $X_{i,t}$ indicates whether individual i is alive ($X_{i,t} = 1$) or not ($X_{i,t} = 0$) at time t.

Effects of the orchard environment

The effects of the environment on the mobility of each predator taxon were estimated by means of logistic regressions on $p^{(\alpha)}$ and $p^{(\beta)}$ using the coordinates at the two first *FAMD* axes to summarize the environmental characteristics of the orchards at each sampling location as follows:

$$\begin{cases} \text{logit}\left(p_i^{(\alpha)}\right) = \alpha_{sp_i}^{(0)} + \alpha_{sp_i}^{(1)} Dim1 + \alpha_{sp_i}^{(2)} Dim2 \\ \text{logit}\left(p_i^{(\beta)}\right) = \beta_{sp_i}^{(0)} + \beta_{sp_i}^{(1)} Dim1 + \beta_{sp_i}^{(2)} Dim2 \end{cases}$$

where sp_i represents the taxon to which individual i belongs and *Dim1* and *Dim2* represent the scaled and centred coordinates at the two first *FAMD* axes. Each coefficient was estimated separately for each predator guild and each predator taxon.

Observation process

For each time t and individual i, the observations were described through the categorical random variable, $Y_{i,t}^{(obs)} \sim Cat(pobs_{i,t}^{(1)}, pobs_{i,t}^{(2)}, pobs_{i,t}^{(3)})$, with the following three values: uncaptured ($Y_{i,t}^{(obs)} = 1$), captured in the hedgerow ($Y_{i,t}^{(obs)} = 2$) or captured in the orchard ($Y_{i,t}^{(obs)} = 3$).

There was no observation at time t=1 (marking session); thus, we determined the following:

$$\begin{cases} pobs_{i,1}^{(1)} = 1 \\ pobs_{i,1}^{(2)} = 0 \\ pobs_{i,1}^{(3)} = 0 \end{cases}$$

Following the marking session, the probability of capture depends on the trapping effort, $Ntraps_{i,t}$, deployed at time t and based on the probability of capture in a single trap, $q_{i,t}$:

$$\begin{cases} pobs_{i,t}^{(1)} = 1 - pobs_{i,t}^{(2)} - pobs_{i,t}^{(3)} \\ pobs_{i,t}^{(2)} = X_{i,t}\left(1 - Y_{i,t}\right)\left(1 - \left(1 - q_{i,t}\right)^{Ntraps_{i,t}}\right) \\ pobs_{i,t}^{(3)} = X_{i,t}Y_{i,t}\left(1 - \left(1 - q_{i,t}\right)^{Ntraps_{i,t}}\right) \end{cases}$$

Indeed, $\left(1-q_{i,t}\right)^{Ntraps_{i,t}}$ is the probability for individual i at time t of not being captured, and is the $1-\left(1-q_{i,t}\right)^{Ntraps_{i,t}}$ probability of being captured. The value of $q_{i,t}$ is assumed to vary across taxa and between the hedgerow and orchard positions (Appendices D2 and D3).

A priori

No a priori information was assumed to be available for the parameters, and non-informative prior densities were used: the capture probabilities q were defined as being uniformly distributed on [0, 0.1], and the regression coefficients $\alpha^{(0)}$, $\alpha^{(1)}$, $\alpha^{(2)}$, $\beta^{(0)}$, $\beta^{(1)}$, and $\beta^{(2)}$ were defined as being normally distributed with a mean of 0 and variances of 1000. Parameter m could not be estimated properly and was set to fixed values in {1, 0.95, 0.90, 0.85, 0.80}. Assuming a marking efficiency of 1, this corresponds to assuming that between 0% (m = 1) and 20% (m = 0.8) of the caught individuals came from somewhere other than the hedgerow or the orchard.

Markov Chain Monte Carlo computation

Inferences about the parameters were performed using Bayesian statistical methods resulting in a joint posterior distribution (Gelman, Hwang & Vehtari 2014). This posterior distribution was computed via a Markov Chain Monte Carlo (MCMC) method using JAGS (version 4.2.0) call in R (Plummer 2003). Three MCMC-chains of 100,000 iterations were computed. The burn-in was set to 50,000, and thinning was applied every 50 iterations, which resulted in acceptable mixing and convergence ($\hat{R}$ < 1.1 for all of the parameters, Gelman, Hwang & Vehtari 2014).

Data fitting

The fit of the model to the data was assessed using posterior predictive checking (Gelman, Hwang & Vehtari 2014) and proved to be adequate (Appendix D1).

Analyses of the model outputs

We first characterized the average mobility of each taxon based on the estimations $\alpha^{(0)}$ and $\beta^{(0)}$. The higher the logit^{-1}($\alpha^{(0)}$) (respectively, logit^{-1}($\beta^{(0)}$)), the higher the probability that the taxon stayed in the hedgerow (respectively, in the orchard) over 24 hours. A 0.5 threshold was used to classify the taxa according to four main categories of behaviour in terms of habitat preference and mobility (Table 2).

Second, we determined the effects of the environmental characteristics of the orchards on the mobility of each taxon by calculating the median and the credibility interval [0.025, 0.975] of the estimations of $\alpha^{(1)}$, $\alpha^{(2)}$, $\beta^{(1)}$, and $\beta^{(2)}$. The estimations that significantly differed from 0 were interpreted as a positive (or negative) effect of *Dim1* ($\alpha^{(1)}$, $\beta^{(1}$) or *Dim2* ($\alpha^{(2)}$, $\beta^{(2)}$) on the probability of staying in the orchard ($\beta^{(1)}$, $\beta^{(2)}$) and staying in the hedgerow ($\alpha^{(2)}$, $\alpha^{(2)}$).

Results

Among the 1,272 captured predators, 19% were identified as marked with ovalbumin; 25% and 17% of the predators that were collected in the hedgerows and in the orchards, respectively (Table 1). The proportions of marked predators in the orchards increased slightly, from 15% to 18%, between the first and the third capture sessions. The estimations of the daily probability of staying in the hedgerow ($\alpha^{(0)}$) or within the orchard ($\beta^{(0)}$) varied little with the probability m of a predator not being initially marked when guilds were considered. However, these probabilities could not be estimated accurately for individual species for the lowest values of m because the numbers of marked individuals were too low (Appendix E). Consequently, the results section only presents estimations for the case $m = 1$.

Habitat preference and mobility

Figure 1 displays $\alpha^{(0)}$ and $\beta^{(0)}$ logit^{-1} estimates for each taxon, which were interpreted using Table 2. 'Ground beetles' had a logit$^{-1}(\alpha^{(0)}) > 0.5$ and a logit$^{-1}(\beta^{(0)}) \approx 0.5$, but *Nebria brevicollis* had a logit$^{-1}(\alpha^{(0)}) \approx 0.5$ and a logit$^{-1}(\beta^{(0)}) > 0.5$. 'Ground beetles' stayed in the hedgerow rather than in the orchard, with little mobility from the hedgerow to the orchard, and *N. brevicollis* stayed in the orchard rather than in the hedgerow, with little mobility from the orchard to the hedgerow. The ground predators *Pterostichus spp.* had a logit$^{-1}(\beta^{(0)}) >> 0.5$, but they were hardly captured in hedgerows, and $\alpha^{(0)}$ could not be estimated. 'Canopy insects', including the green lacewing *Chrysoperla sp.,* had a logit$^{-1}(\alpha^{(0)}) \leq 0.5$ and a logit$^{-1}(\beta^{(0)}) > 0.5$; thus, they had a preference for the orchard and frequently moved from the hedgerow to the orchard. Unlike most of the 'canopy insects', *F. auricularia* had a logit$^{-1}(\alpha^{(0)}) > 0.5$ and a logit$^{-1}(\beta^{(0)}) \approx 0.5$. Therefore, it had a preference for the hedgerow and preferentially moved from the orchard to the hedgerow. 'Ground spiders' and 'canopy spiders,' including *Philodromus spp.,* had a logit$^{-1}(\alpha^{(0)}) > 0.5$ and logit$^{-1}(\beta^{(0)}) > 0.5$. Therefore, they had low mobility and no habitat preference. *C. mildei* had a logit$^{-1}(\alpha^{(0)}) \approx 0.5$ and a logit$^{-1}(\beta^{(0)}) \approx 0.5$; thus, they were more mobile. The canopy web spider *Theridion varians* had a logit$^{-1}(\alpha^{(0)}) > 0.5$ and a logit$^{-1}(\beta^{(0)}) << 0.5$ and thus did not stay in the orchard.

Effect of the environmental characteristics of the orchards

The covariables *Dim1* and *Dim2* affected the probabilities of the predator taxa staying within the hedgerow (i.e. not entering in the orchard) ($\alpha^{(1)}$ and $\alpha^{(2)}$) or staying within the orchard ($\beta^{(1)}, \beta^{(2)}$) (Table 3). The covariable *Dim1,* which was positively correlated with the organic management of the orchards, the presence wood in orchard borders, and diversified perennial plants in the hedgerows (Table A4), significantly increased the probability of the 'canopy insects' and *N. brevicollis* entering the orchard ($\alpha^{(1)} < 0$) and staying within the orchard ($\beta^{(1)} > 0$). To a lesser extent, *Dim1* also increased the probability of the 'canopy spiders' staying in the orchard ($\beta^{(1)} > 0$) and of *Philodromus spp.* entering the orchard ($\alpha^{(1)} < 0$). The covariable *Dim2,* which was positively correlated with the thickness of the hedgerows (Table A4), significantly decreased the probability of the 'ground beetles' entering the orchard ($\alpha^{(2)} > 0$) and staying in the orchard ($\beta^{(2)} < 0$). Furthermore, *Dim 2* decreased the probability of the *Philodromus spp.* entering the orchard ($\alpha^{(2)} > 0$) and *Dim 2* increased the probability of the 'canopy insects' entering the orchard, notably for *Chrysoperla sp.* ($\alpha^{(2)} < 0$).

Discussion

An immunomarking study coupled with a hierarchical Bayesian model was used to investigate the routine movements of arthropod predators in spring. Almost all captured arthropod taxa included marked individuals in the orchard, which suggests numerous movements from the hedgerow to the orchard. The arthropod communities were very different among the studied locations, with few taxa being abundant at one location only (e.g. *Pilophorus spp.*), which limited our ability to infer movement at the species level with a Bayesian model. The estimations of the movements between hedgerows and their adjacent apple orchards were robust for five abundant taxa that were regularly distributed among the eleven sampling locations: *Philodromus spp.*, *C. mildei*, *F. auricularia, Chrysoperla sp.* and *N. brevicollis.* These taxa are all important predators of insect pests in apple orchards (Solomon et al. 2000).

The *Philodromus spp.* and *C. mildei* canopy spiders did not show a preference for the orchard or hedgerow habitats. *Philodromus spp.* were mostly sedentary in each habitat, whereas *C. mildei* displayed relatively higher mobility between both habitats, which is in agreement with previous observations (Lefebvre et al. 2016). The mobility of the *Philodromus spp.* was mainly impacted by the quality of the hedgerow. They preferentially stayed in the thickest hedgerows and preferentially left the hedgerows at the woodiest locations, including in the organic orchard. This is consistent with the fact that *Philodromus spp.* is a very generalist predator (Michalko & Pekar 2015) that moves either when local trophic resources are insufficient or when it is disturbed by pesticide treatments (Pekar & Haddad 2005; Rezac, Pekar & Stara 2010). Inversely, the mobility of *C. mildei* between the hedgerow and the orchard habitats was not significantly impacted by the environmental characteristics of the orchard, which is in agreement with the lack of habitat specificity of this agrobiont predator (Hogg et al. 2010).

The European earwig, *F. auricularia*, displayed a preference for the hedgerow and mainly moved from the orchard to the hedgerow regardless of the environmental characteristics of the orchards, which is in agreement with the conclusions of previous mark and release experiments (Debras et al. 2007; Moerkens et al. 2010), their semi-social and relatively sedentary behaviours (Burnip et al. 2002; Lamb 1975) and previous results indicating that hedgerow characteristics had little impact on *F. auricularia* abundances in apple orchards (Malagnoux et al. 2015; Moerkens et al. 2010).

The green lacewing, *Chrysoperla sp.*, displayed a preference for the orchard and mainly moved from the hedgerow to the orchard, notably where the hedgerows were thickest. Lacewing adults are very mobile (Liu, McNeil & Wu 2011) and actively forage in crops using herbivore-induced-plant volatiles to detect their prey (Jones et al. 2011). The hedgerow thickness may increase lacewing movement by buffering climatic conditions and reducing wind speed, thus enhancing flight activity and the detection of kairomone cues.

Lastly, the European gazelle beetle, *N. brevicollis*, displayed a very strong preference for the orchard and mainly moved from the hedgerow to the orchard, notably at the woodiest locations. These movements are consistent with the fact that this species is frequently found in apple orchards (Miñarro & Dapena 2003). This observation is also consistent with the fact that hedgerows constitute significant barriers to *N. brevicollis* dispersal between fields (García, Griffiths & Thomas 2000; Joyce et al. 1999).

All estimations of movement reported in the present study should be considered qualitative rather than quantitative because of model assumptions and methodological limitations. The main simplifying model assumption was that the individuals caught during the study were initially in the orchard or in the hedgerow (i.e. m was assumed to be equal to one). This assumption is consistent with a certain stability of predator assemblages during the 13 days of the study and the recognition that the local scale is relevant for conservation biological control (Begg et al. 2017). Relaxing this assumption by assuming that up to 20% of the caught individuals were not in the orchard or the hedgerow initially (Appendix E) did not qualitatively modify inferences of movements between hedgerows and orchards for the four arthropod guilds, although movements could not be properly assessed for the individual taxa because of the lack of observations. Relaxing the assumption on high m values could be pertinent for the most mobile taxa, such as *Chrysoperla* spp. To go further in the inference of movements between habitats, the Bayesian model would have to be modified to explicitly consider additional habitats. This would also require arthropod sampling in the different habitats.

Defining an optical density (OD) threshold to assess marked individuals also proved difficult when comparing various predator taxa. The OD of unmarked individuals may vary among predator taxa and during the development of these taxa because of differences in size or frequency of moulting. The OD of the marked individuals may also depend on the duration and the path of their movement into the marked habitat. We found that 15-18% of the captured predators in the apple orchards were marked with ovalbumin. Although we cannot exclude overestimation of the number of marked predators as a result of the chosen criteria to infer the immunological marks (Sivakoff, Rosenheim & Hagler 2011), the marking bias was likely independent of the habitat of capture (Hagler et al. 2014; Horton, Jones & Unruh 2009), and the results were comparable to those from a study assessing predator movements from cover crops to tree canopies using the same immunomarking method (17-29% of marked arthropods were in the tree canopy; Horton, Jones & Unruh 2009). Furthermore, lowering the OD marking threshold did not change the Bayesian estimations of predator guilds staying in the hedgerow or in the orchards. There were some changes for individual taxa in the direction of a higher mobility, notably for *Philodromus spp*. (Appendix F).

This study focused on routine movement in springtime, when colonies of rosy apple aphids were still present on the apple trees and when the first generation of codling moths was laying eggs on apple tree leaves. Consequently, the observed movements between hedgerows and orchards were likely to be foraging movements or movements to escape from insecticide spraying. We could not disentangle the effects of insecticide pressure and food amount in the present study. Nevertheless, we confirmed the impact of local hedgerow structures on the movement of canopy insects, notably lacewings, into orchards (Sorribas et al. 2016). Furthermore, we found that a woody environment, together with less intensive management, enhanced the probability that the ground beetle *N. brevicollis* and the canopy insects and spiders stayed in or entered the orchard.

Although it remains difficult to generally predict the effects of hedgerows based on the movements of a few arthropod predators and to advise farmers on hedgerow management strategies to enhance pest biocontrol, our study provides evidence that hedgerows have a large influence on the presence of numerous predators in apple orchards. Efficient hedgerow management strategies at the orchard level should take into account both the local singularity of the arthropod communities and the agro-ecological context.

Acknowledgements

This work was supported by the PEERLESS project, in the ANR-agrobiosphere programme [ANR-12-AGRO-0006], and the RéPARe project, in FRB-Ecophyto programme. ML's PhD was supported by the CTIFL and RéPARe. GM's postdoctoral fellowship was granted by the 'Fondation de France' agroforestry programme.

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Tables

Table 1. Total numbers of individuals of ground and canopy arthropods captured (N) and numbers of individuals marked with ovalbumin (OV) in the orchards and hedgerows (see Appendix C for taxonomic details). Values in each ecological group include the numbers of individuals of single species/genera.

	Hedgerow		Orchard	
Taxa	N	OV	N	OV
		Pitfall		
Ground spiders	29	8	171	23
Trochosa hispanica (Lycosidae)	6	3	81	8
Ground beetles	31	7	227	32

Nebria brevicollis (Carabidae)	20	4	52	10
Pterostichus spp. (Carabidae)	4	0	61	8
		Beating		
Canopy spiders	143	36	264	34
Cheiracanthium mildei (Eutichuridae)	8	3	26	6
Philodromus spp (Philodromidae)	27	7	67	9
Theridion varians (Theridiidae)	15	3	36	11
Canopy insects	51	13	356	79
Chrysoperla sp. (Chrysopidae)	17	5	54	9
Forficula auricularia (Forficulidae)	8	5	114	51

Table 2. Ecological interpretation of logit^{-1}($\alpha^{(0)}$) and logit^{-1}($\beta^{(0)}$) values when *m* tends toward 1.

logit^{-1}($\alpha^{(0)}$)		<0.5 Does not stay in hedgerow		>0.5 Stays in hedgerow	
logit^{-1}($\beta^{(0)}$)		<0.5 Does not stay in orchard	>0.5 Stays in orchard	<0.5 Does not stay in orchard	>0.5 Stays in orchard
Most likely process	Mobility	High	High, hedgerow to orchard	High, orchard to hedgerow	Low
	Habitat preference	None	Orchard	Hedgerow	None

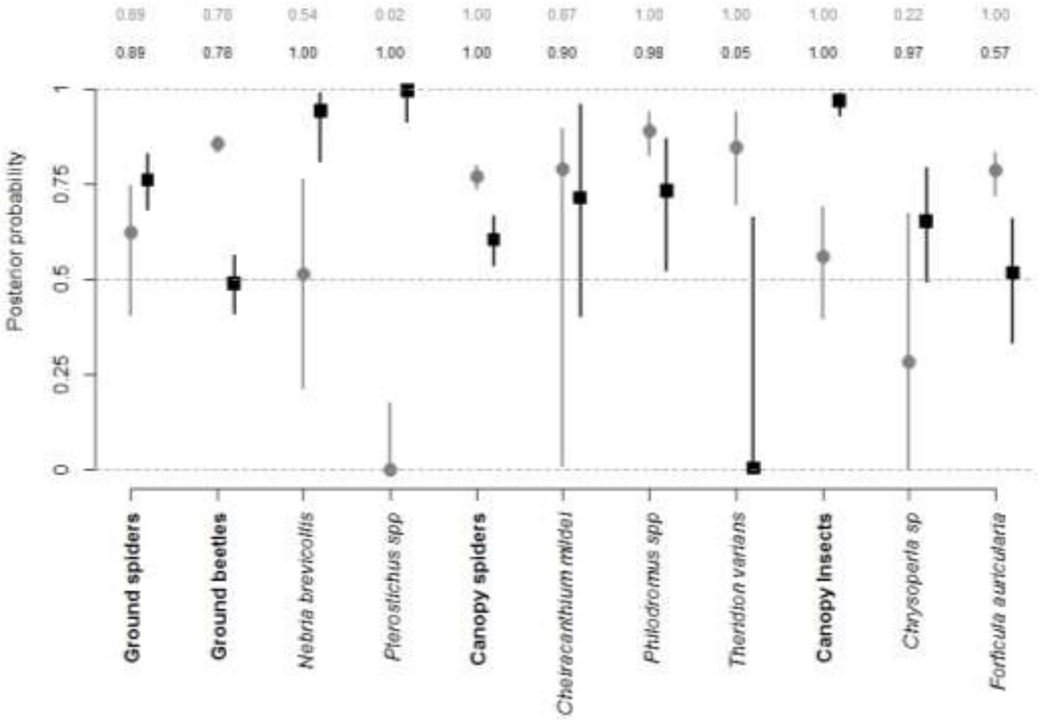
Table 3. Median and credibility intervals [0.025, 0.975] of the estimations of the effects of *Dim1* and *Dim2* on the probability that each taxon stays over 24 h in the hedgerow and within the orchard (α and β, respectively). The *p*-values are the probabilities that each estimation is positive. Significant results are reported in bold. '/' refers to a parameter that was not estimated (i.e. when parameter distribution did not differ from the prior distribution).

	α(1)	*β(1)*	*α(2)*	*β(2)*
Ground spiders	0.24 p= 0.86	-0.30 p= 0.05	0.02 p= 0.53	0.14 p= 0.78
	[-0.18 ; 0.85]	[-0.69 ; 0.08]	[-0.71 ; 0.55]	[-0.19 ; 0.53]
Ground beetles	-0.05 p= 0.30	-0.01 p= 0.48	0.26 p= 1.00	-0.46 p= 0.00
	[-0.23 ; 0.13]	[-0.26 ; 0.25]	[0.07 ; 0.45]	[-0.82 ; -0.15]
Nebria brevicollis	**-1.64 p= 0.00**	**1.99 p= 1.00**	-0.06 p= 0.43	-0.17 p= 0.31
	[-3.08 ; -0.66]	**[0.76 ; 3.89]**	[-0.97 ; 0.53]	[-1.08 ; 0.46]
Pterostichus spp	/	4.28 p=1.00	/	0.36 p=0.76
	/	[1.05 ; 10.34]	/	[-0.62 ; 1.67]
Canopy spiders	0.13 p= 0.92	**0.44 p= 1.00**	0.05 p= 0.73	-0.22 p= 0.06
	[-0.04 ; 0.29]	**[0.18 ; 0.73]**	[-0.12 ; 0.23]	[-0.5 ; 0.06]
Cheiracanthium mildei	0.20 p= 0.67	0.19 p= 0.60	0.20 p= 0.66	-0.84 p= 0.06

	[-0.64 ; 1.56]	[-1.1 ; 2.35]	[-0.82 ; 1.47]	[-2.29 ; 0.23]
Philodromus spp	**-0.61 p= 0.02**	-0.75 p= 0.05	**0.62 p= 1.00**	-0.45 p= 0.08
	[-1.31 ; -0.02]	[-1.55 ; 0.14]	**[0.15 ; 1.14]**	[-1.14 ; 0.19]
Theridion varians	-0.09 p= 0.38	0.77 p=0.89	-0.37 p= 0.19	/
	[-0.79 ; 0.52]	[-0.43 ; 2.39]	[-1.23 ; 0.51]	/
Canopy insects	**-0.87 p= 0.00**	**2.13 p= 1.00**	**-0.42 p= 0.01**	-0.15 p= 0.20
	[-1.51 ; -0.33]	**[1.23 ; 3.27]**	**[-0.82 ; -0.04]**	[-0.55 ; 0.20]
Chrysoperla sp	0.34 p= 0.67	0.03 p= 0.53	**-1.67 p= 0.00**	0.08 p= 0.61
	[-2.09 ; 2.21]	[-0.71 ; 0.92]	**[-4.03 ; -0.41]**	[-0.69 ; 0.69]
Forficula auricularia	0.17 p= 0.84	0.29 p=0.79	0.19 p= 0.95	-0.19 p=0.25
	[-0.16 ; 0.48]	[-0.45 ; 1.18]	[-0.04 ; 0.44]	[-0.88 ; 0.50]

Figures

Fig. 1. Estimations of the posterior probability (median and 95% credibility intervals) of staying in the hedgerow (logit^{-1}($\alpha^{(0)}$); grey circles) and staying in the orchard (logit^{-1}($\beta^{(0)}$); black squares) over 24 h for four predator guilds and six predator taxa. The probabilities of logit^{-1}($\alpha^{(0)}$) > 0.5 (in grey) and logit^{-1}($\beta^{(0)}$) > 0.5 (in black) are indicated above each estimation. Estimates were not reported for the ground spider *Trochosa hispanica* because the posterior distributions of the estimations for this taxon did not differ from the prior distributions.



Appendices

Appendix A: Environmental and orchard characteristics

The apple orchards at each location were characterized according to environmental covariables (*WoodyIndex*, *Shannon*, *Thickness,* and *Management*) and damages caused by the two main insect pests, *Cydia pomonella* (CM) and *Dysaphis plantaginae* (RAA). CM damages were measured on 1000 apple fruits per location collected on 50 trees (20 apples per tree). RAA damages were measured on 100 randomly chosen shoots per location (2 shoots per tree). Damages were measured at each location either on the 16 or the 17 June 2014. Environmental covariables were measured at each location and summarized using the coordinates of the two main axes of the Factorial Analysis of Mixed Data (FAMD). Table A1 summarizes the characteristics of each orchard location. Table A2 presents the floral composition of the hedgerow at each location, which were used to calculate the *Shannon* covariable. Table A3 presents the correlations between the covariables. Table A4 refers to FAMD results.

Table A1. Sampling, damage and environmental characteristics in each orchard location: the number of trap positions (#trap), the total number of captured arthropods (#arthropods) for each trapping method (beating or pitfall), the percentages of damages caused by the codling moth (CM) and the rosy apple aphid (RAA), environmental measures (*Management*, *Shannon*, *Thickness*, *WoodyIndex*) of orchard and hedgerow characteristics and the coordinates at the two main axes (*Dim1* and *Dim2*) of the principal component analysis (FAMD).

Location		#arthropods		Damages		Orchard		Hedgerow	Environment	FAMD axes	
No.	#traps	beating	pitfall	CM	RAA	*Management*	*Shannon*	*Thickness*	*WoodyIndex*	*Dim1*	*Dim2*
81	50	84	65	12‰	0%	conventional	0.00	12.00	0.04	-1.69	1.39
55	34	30	35	3‰	0%	conventional	1.34	2.25	0.04	-1.41	-1.59
214	40	28	25	4‰	0%	conventional	0.93	7.00	0.05	-1.33	-0.25
216	34	56	42	1‰	1%	conventional	1.36	6.75	0.04	-1.00	-0.54
179	51	50	28	1‰	1%	conventional	0.94	13.20	0.04	-0.78	1.20
28	36	55	24	1‰	9%	conventional	0.69	6.50	0.15	-0.77	-0.22
191	52	27	41	0‰	0%	conventional	1.79	9.00	0.08	-0.12	-0.26
194	42	63	45	0‰	2%	organic	1.60	9.00	0.06	0.79	-0.83
190	40	92	60	11‰	11%	conventional	1.91	17.00	0.13	1.14	1.55
35	40	120	61	0‰	9%	organic	1.60	11.20	0.21	2.26	-0.30
170	55	209	32	11‰	23%	organic	1.93	12.60	0.24	2.92	-0.16

Table A2. Floral composition of the hedgerows at the eleven studied locations. Plant species were recorded at 10 observation points along each hedgerow. Numbers in the table refer to the number of times each plant species was recorded over the 10 observation points.

Locations → Species ↓	*28*	*35*	*170*	*179*	*181*	*190*	*191*	*194*	*214*	*216*	*55*
Cypresses											
Cupressus sempervirens	10				10	10			10	10	
Cupressus leylandii		10		7							10
Cupressus arizonica				10			10	10			
Creepers											
Hedera helix		8	9	2		10	10	9	10	10	
Rubus ulmifolius		4	1			2	1				5
Vitis vinfera		2	2							1	
Rubia peregrina			1				1	1		3	
Bryonia dioica	2	1					1			1	
Vitis alba	1						2	5		1	
Rosa canina			1								
Deciduous trees											
Crataegus monogyna			5			4		3			3
Fraxinus augustifolia			7								
Prunus spinosa							3				2
Prunus laurocerasus			2			2		1			
Ligustrum vulgare						3					
Ostrya carpinifolia						7	4				
Quercus ilex									2		1
Cornus sanguinea		1	1			4					
Juglans regia								1			
Corylus avellana			1								

Prunus avium							1				
Laurus nobilis		2									

Table A3. Correlations between covariables measuring the orchard environmental characteristics and damages caused by the main insect pests: the codling moth (CM) and the rosy apple aphid (RAA). Spearman's correlation coefficients (in black in the up right-hand corner) and p-values (in grey in the down left-hand corner) between the quantitative covariables describing hedgerow and orchard characteristics. In the last line, *p*-values of the Wilcoxon-Mann-Whitney test between the qualitative variable *Management* and the quantitative variables.

	WoodyIndex	*Shannon*	*Thickness*	CM	RAA
WoodyIndex		**0.61**	0.25	-0.28	**0.69**
Shannon	**0.05**		0.4	-0.35	0.48
Thickness	0.46	0.22		-0.09	0.27
CM	0.40	0.30	0.80		0.02
RAA	**0.02**	0.14	0.41	0.95	
Management	0.08	0.12	0.54	0.60	**0.02**

Table A4. Coordinates, contribution and square-cosinus of the 4 covariables contributing to the two first axes of the FAMD (*Dim1* and *Dim2*).

	coordinates		Contribution (%)		cos²	
	Dim1	*Dim2*	*Dim1*	*Dim2*	*Dim1*	*Dim2*
Shannon	0.54	0.08	24.15	9.28	0.29	0.01
WoodyIndex	0.75	0.00	33.67	0.00	0.56	0.00
Thickness	0.27	0.71	11.97	81.57	0.07	0.50
Management	0.67	0.08	30.21	9.15	0.45	0.01

Appendix B: ELISA Optical Density and threshold

Threshold values of Optical Density that discriminate marked and unmarked arthropods with ovalbumin were defined separately for the arthropods collected in pitfall trap and by beating. Each threshold value was defined as the mean Optical Density plus four times the standard error of control arthropods collected within the orchard area (Figure B1). These negative controls represented 140 and 169 predators captured in the pitfall traps and by beating respectively. Figure B2 represents the distribution of the Optical Density measured on all the collected predators

Figure B1. Organization of a sampled location. Positions of arthropod captures by pitfall and beating are represented by circles in the apple orchard and the northern hedgerow. The orchard area where the predator individuals used as ELISA controls were captured is indicated.

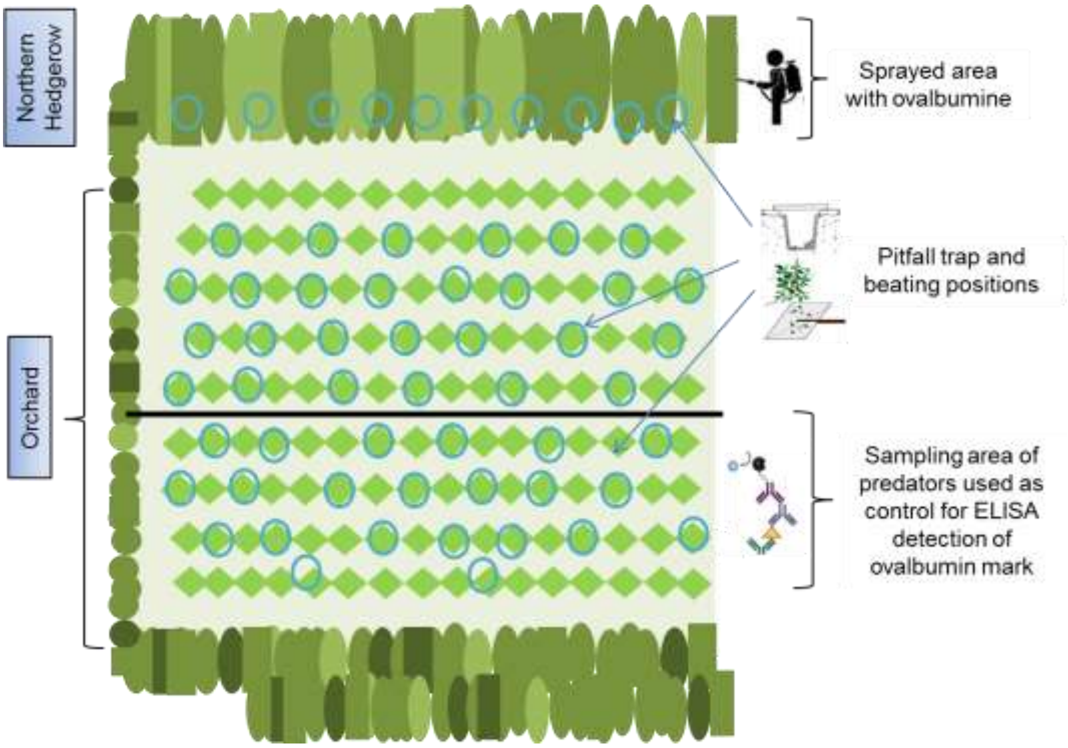
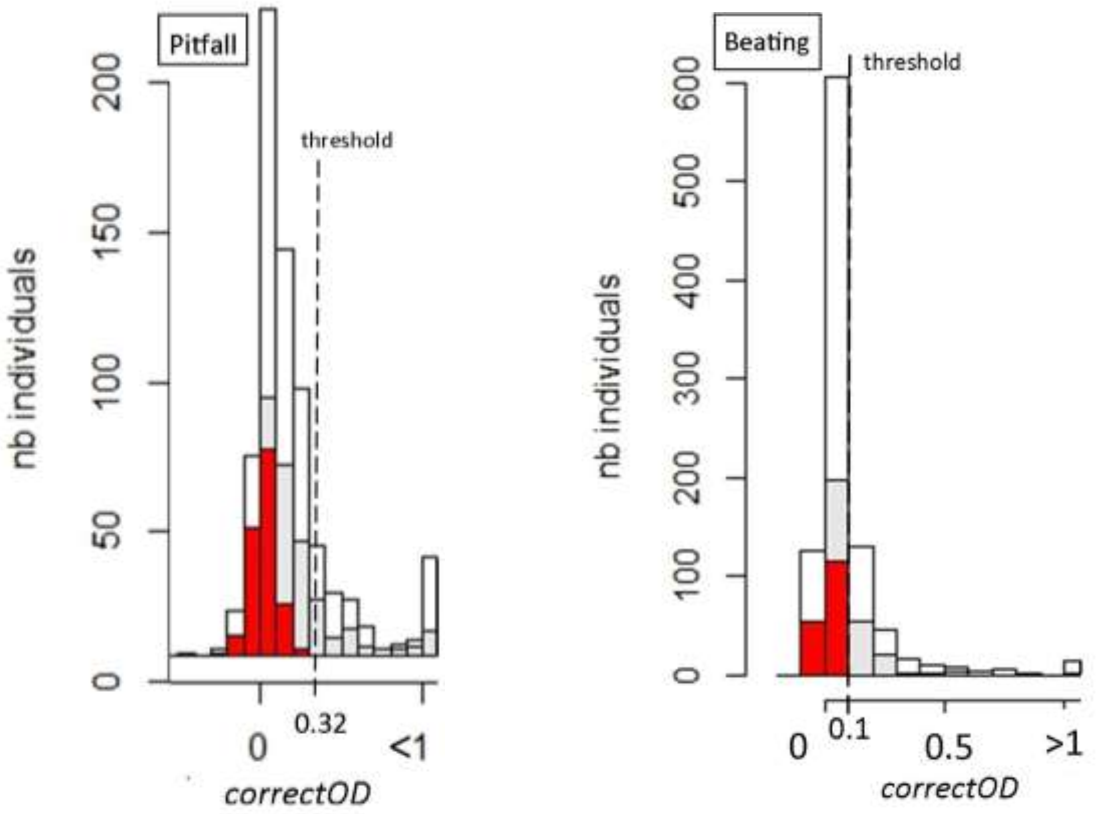


Figure B2. Distribution of the Optical Density (*correctOD*) measured on the arthropods collected in pitfalls (left) and by beating (right). *CorrectOD* of the arthropod samples that were captured in the 2nd part of the orchard (the mid-part the farthest from the northern hedgerow) and, among them, those of arthropods considered as controls (in each orchard, the 50 % that exhibited the lowest *correctOD* values) are respectively represented in grey and in red.



Appendix C: Taxonomy of the captured and marked arthropods in the hedgerows and orchards

Table C1. Taxonomy of the canopy spiders and insects collected by beating. The numbers of individuals captured (N) and marked by ovalbumin (OV) in the hedgerows and in the orchards were reported. The first column (n) corresponds to the number of locations (out of 11) where 95% of the individuals of each taxa were collected. The total number of traps across the 11 locations was 73 in hedgerows and 403 in orchards. The last two columns indicate the highest and the smallest distances from the hedgerow (in meters) where the marked individuals were captured in the orchard. The most abundant and equally distributed arthropod taxa among locations are reported in bold. These taxa were analyzed independently from the guild they belong to.

Family	*Species*	n	hedgerow		orchard		distance	
			N	OV	N	OV	min	max
Canopy spiders								
Anyphanenidae	*Anyphaena accentuata*	2	4	1	4	0		
Araneidae	*Araneus spp.*	5	5	1	4	2	18	31
	Araniella cucurbitana	6	8	2	23	2	11	29
	Gibaranea bituberculata	1	0	0	1	0		
	Larinoides sp.	1	0	0	1	0		
	Nuctenea umbratica	1	0	0	1	0		
Clubionidae	*Clubiona spp.*	2	9	2	17	1	25	
Coreidae	*Gonocerus sp.*	1	1	0	2	0		
Dictynidae	*Dictyna sp.*	1	1	0	0	0		
	Lathys humilis	3	3	1	2	2	11	25
	Nigma puella	1	0	0	1	1	47	
Eutichuridae	***Cheiracanthium mildei***	**11**	**9**	**4**	**28**	**9**	**6**	**43**
Gnaphosidae	*Aphantaulax trifasciata*	4	1	0	4	0		
	Drassodes sp.	2	2	1	0	0		
Linyphiidae	*Didectoprocnemis sp.*	1	1	0	0	0		
	Tenuiphantes sp.	1	7	0	17	0		
Oxyopidae	*Oxyopes lineatus*	1	0	0	1	0		
Philodromidae	***Philodromus spp***	**8**	**30**	**10**	**73**	**7**	**12**	**52**
	Thanatus spp.	3	5	3	3	0		
Salticidae	*Ballus chalybeius*	5	12	1	1	0		
	Carrothus xantogramma	4	5	1	4	0		
	Evarcha sp.	1	1	0	0	0		
	Icius hamatus	1	2	0	1	0		
	Saitis barbipes	4	7	2	2	0		
	Salticus zebraneus	4	0	0	4	0		
Segestridae	*Segestria senoculata*	2	2	1	2	0		
Theridiidae	*Dipoena melanogaster*	1	1	0	0	0		

	Euryopis sp	1	1	0	0	0		
	Theridion spp	**6**	**15**	**2**	**36**	**6**	**11**	**29**
Thomisidae	*Diaea dorsata*	1	1	1	0	0		
	Ebrechetella tricuspidata	1	1	0	3	0		
	Misumena vatia	1	1	0	1	0		
	Runcinia grammica	4	1	1	4	1		
	Synaema globosum	1	1	1	2	0		
	Thomisus sp	3	0	0	5	0		
	Tmarus piger	1	0	0	1	0		
	Xysticus sp	6	3	0	8	1	16	
Zodariidae	*Zodarion sp*	0	0	0	1	0		
Not determined		4	4	1	7	2		
			Canopy insects					
Cantharidae	*Cantharis rustica*	4	1	0	10	2		
Chrysopidae	***Chrysoperla sp.***	**9**	**17**	**3**	**54**	**3**	**12**	**36**
Coccinellidae	*Adalia bipunctata*	1	0	0	5	1		
	Chilocorus bipustulatus	3	1	0	9	0		
	Vibidia duodecimguttata	1	1	0	0	0		
	Harmonia axyridis	2	0	0	3	0		
	Oenopia conglobata	3	0	0	3	0		
	Propylea quatuordecimpunctata	2	1	1	2	0		
	Scymnus sp.	4	1	0	3	0		
	Coccinella septempuctata	2	0	0	3	0		
	Vibidia duodecimguttata	1	1	0	2	0		
Forficulidae	***Forficula auricularia***	**6**	**8**	**7**	**114**	**56**	**10**	**61**
Hemerobiidae	*Hemerobius sp.*	1	1	0	0	0		
Miridae	*Daerocoris ruber*	4	4	0	38	0		
	Heterotoma planicornis	1	0	0	28	4	18	25
	Ligus sp.	1	0	0	2	0		
	Pilophorus spp.	1	1	0	69	11	14	45
	Not determined	3	0	0	5	1		
Raphidiidae	Not determined	6	14	2	6	1		

Table C2. Taxonomy of the ground spiders and insects collected in pitfall traps. The numbers of individuals captured (N) and marked by ovalbumin (OV) in the hedgerows and in the orchards were reported. The first column (n) corresponds to the number of locations (out of 11) where 95% of the individuals of each taxa were collected. The total number of traps across the 11 locations was 73 in hedgerows and 403 in orchards. The last two columns indicate the highest and the smallest distances from the hedgerow (in meters) where the marked individuals were captured in the orchard. The most abundant and equally distributed arthropod taxa among locations are reported in bold. These taxa were analyzed independently from the guild they belong to.

			Hedgerow		Orchard		Distance	
Family	Species	n	N	OV	N	OV	min	max
		Ground spiders						
Lycosidae	***Trochosa hispanica***	**7**	**6**	**3**	**81**	**8**	**16**	**48**
	Alopecosa cuneata	2	5	1	16	3	8	28
Araneidae	*Araneus sp.*	1	0	0	1	0		
Dysderidae	*Dysdera erythrina*	1	0	0	2	0		
Gnaphosidae	*Drassodes sp.*	3	2	1	5	1	29	
	Gnaphosa lucifuga	4	1	1	15	1	25	
	Zelotes sp.	6	7	0	11	1	31	
Hahniidae		1	1	0	1	0		
Linyphiidae	*Tenuiphantes sp.*	1	0	0	2	1	61	
Pisauridae	*Pisaura mirabilis*	4	1	0	9	1	14	
Salticidae	*Ballus chalybeius*	1	0	0	1	1		
Thomisidae	*Xysticus sp.*	3	0	0	3	1	48	
Titanoecidae	*Titanoeca tristis/hispana*	4	1	1	6	3	32	43
Zodariidae	*Zodarion italicum*	6	6	1	11	1	40	
Not determined		1	0	0	1	0		
		Ground Insects						
Carabidae	***Pterostichus sp.***	**16**	**4**	**0**	**61**	**6**	**6**	**32**
	Nebria brevicollis	**6**	**20**	**4**	**52**	**10**	**14**	**43**
	Amara aenea	1	0	0	1	0		
	Anchomenus dorsalis	2	0	0	5	0		
	Badister bullatus	2	0	0	3	0		
	Bembidion quadrimaculatum	1	0	0	1	0		
	Brachinus chrepitans	5	0	0	19	7	5	50
	Calathus melanocephalus	1	1	0	1	0		
	Diachromus germanica	2	0	0	26	0		
	Harpalus spp.	5	0	0	18	1	35	
	Metallina sp.	4	0	0	5	0		
	Ophonus spp.	4	1	1	6	0		
	Pseudoophonus rufipes	4	3	1	3	1	22	

Not determined	8	2	1	31	6	18	62

Appendix D: Bayes estimations

Fit of the model to the data: posterior predictive checking

Table D1. Percentages of individuals captured in the hedgerow, in the orchard and not captured (over the three collecting sessions) as function of the predictions given by the Bayesian model. The worse prediction was for the captures in the hedgerow, 1/3 of which being predicted as unseen.

Observation↓/Prediction→	unseen	hedgerow	orchard
not captured	90.1%	6.2%	3.7%
hedgerow	32.5%	67.5%	0.0%
orchard	17.2%	0.0%	82.8%

Probability of capture of a single trap.

Table D2. Medians and credibility intervals [0.025; 0.975] of the probability of capture of a pitfall trap in the hedgerow or in the orchard for each taxon (parameter *m*=1). Estimations of the posterior probabilities were not reported (-) when the Markow chains did not converge.

	hedgerow	orchard
Ground spiders	0.07	0.02
	[0.05; 0.09]	[0.01; 0.02]
Trochosa hispanica	0.05	0.01
	[0.02; 0.09]	[0.01; 0.02]
Ground beetles	0.09	0.02
	[0.07; 0.10]	[0.02; 0.03]
Nebria brevicollis	0.26	0.02
	[0.15; 0.44]	[0.01; 0.03]
Pterostichus spp	-	0.01
	-	[0.01; 0.02]

Table D3. Medians and credibility intervals [0.025; 0.975] of the probability of capture for a beating in the hedgerow or in the orchard for each taxa.

	hedgerow	orchard
Canopy spiders	0.06	0.02
	[0.05; 0.07]	[0.01; 0.03]
Chieracanthium mildei	0.06	0.03
	[0.03; 0.12]	[0.01; 0.07]
Philodromus spp	0.09	0.02
	[0.06; 0.12]	[0.01; 0.04]
Theridion varians	0.08	0.02
	[0.04; 0.10]	[0.01; 0.04]
Canopy insects	0.17	0.02
	[0.11; 0.26]	[0.01; 0.03]
Chrysoperla sp	0.10	0.02
	[0.06; 0.18]	[0.01; 0.03]
Forficula auricularia	0.05	0.00
	[0.04; 0.07]	[0.00; 0.01]

Appendix E: Influence of *m* variations on α(0) and β(0) estimations

Parameter *m* could not be estimated properly and was set to fixed values. The value of *m* depends on the marking probability and on possible immigration from habitats that were not sampled. Assuming a high marking probability, the value of *m* is mainly driven by immigration. The results presented in the main text assume no immigration (*m*=1). To test the robustness of our conclusions, we varied *m* in {1.00, 0.95, 0.90, 0.85, 0.80} and estimated the model parameters for each value.

We illustrate the values of α(0) and β(0) according to the value of *m* for guilds only because the estimation failed for the species level when *m*<1, because of a lack of data. Indeed, as the value of *m* decreases, the capture of non-marked individuals is less and less informative because of an increasing uncertainty of their localization before the capture. Figures E1 and E2 show that the estimation of α(0) and β(0) varied little according to *m*. However, estimation of β(0) was not possible for canopy arthropods for the lowest values of *m*. High levels of immigration may not be compatible with the behavior of canopy spiders and insects.

Figure E1: Median and credibility interval 95% of the estimates of Logit^{-1}(α(0)), for the four guilds, and different values of *m*.

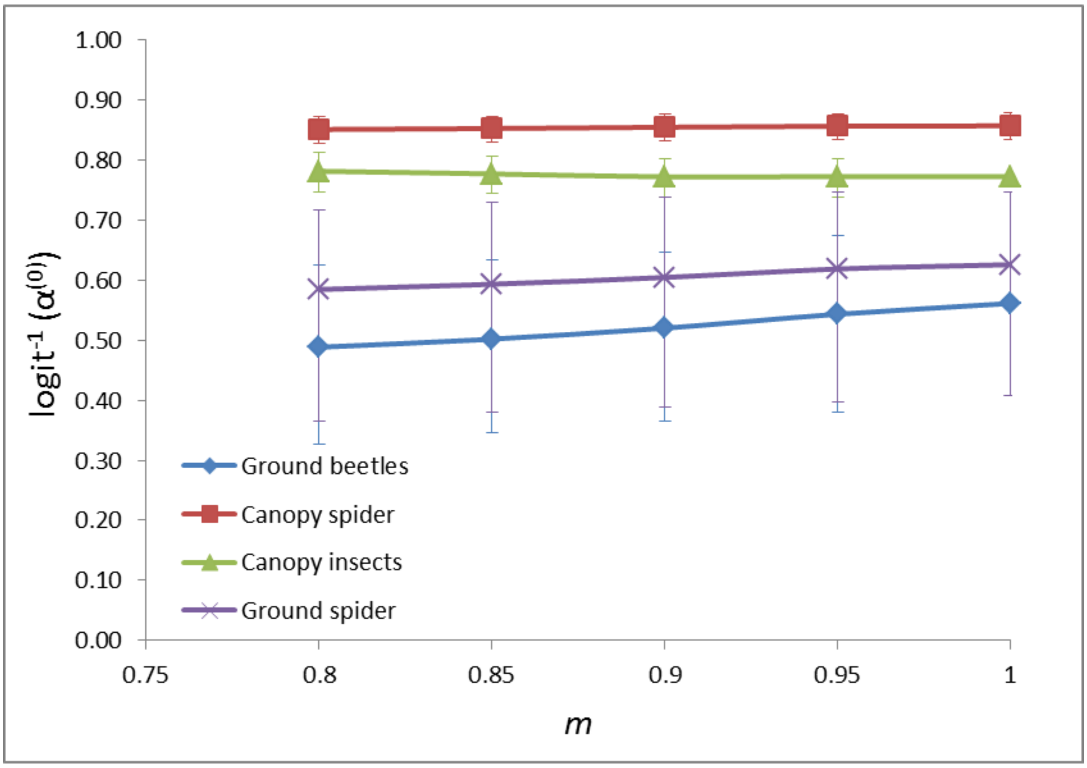
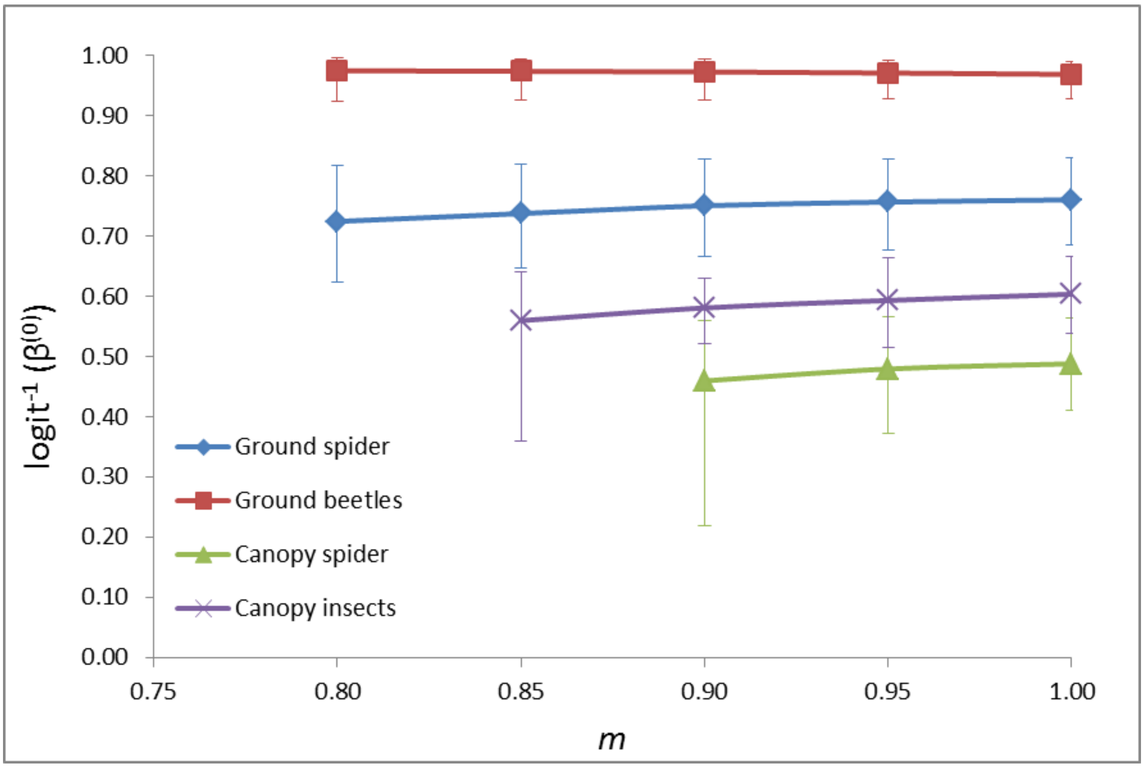


Figure E2: Median and credibility interval 95% of the estimates of Logit^{-1}(β(0)), for the four guilds, and different values of *m*. Estimations are not displayed in the cases when convergence was not achieved.



Appendix F: Influence of to the threshold used to determine marked and unmarked individuals on α(0) and β(0)

Figure F2 presents results of the hierarchical Bayesian model for a threshold chosen to determine marked and unmarked individuals that is lower than the threshold used in the main text (Fig. F1). Black squares indicate the posterior probability (median and 95% credibility intervals) to stay in the hedgerow, i.e. $\text{logit}^{-1}\left(\alpha^{(0)}\right)$ and grey dots indicate the posterior probability (median and 95% credibility intervals) to stay in the orchard, i.e. $\text{logit}^{-1}\left(\beta^{(0)}\right)$. This figure can be compared to Figure 1 in the main text where thresholds were 0.10 for canopy arthropods and 0.32 for ground arthropods. Results are very stable for guilds. Differences can be observed for some individual taxa. Most differences are that the MCMC chains did not converge: $\text{logit}^{-1}\left(\alpha^{(0)}\right)$ were not estimable for *F. auricularia, C. mildei* and *T. varians*, $\text{logit}^{-1}\left(\beta^{(0)}\right)$ was not estimable for *Pterostichus spp.* Further *Philodromus spp* appeared more mobile than with a higher threshold, *N. brevicollis* still showed high probability to stay in the orchard but its probability to enter the orchard was higher, as were those of *T. varians* and *F. auricularia*.

Figure F1: Thresholds of the *correctOD* : canopy = 0.10 and ground= 0.32 (*m*=1) (as in main text). Estimations are only displayed in the cases convergence was achieved. Number of individuals marked: 230.

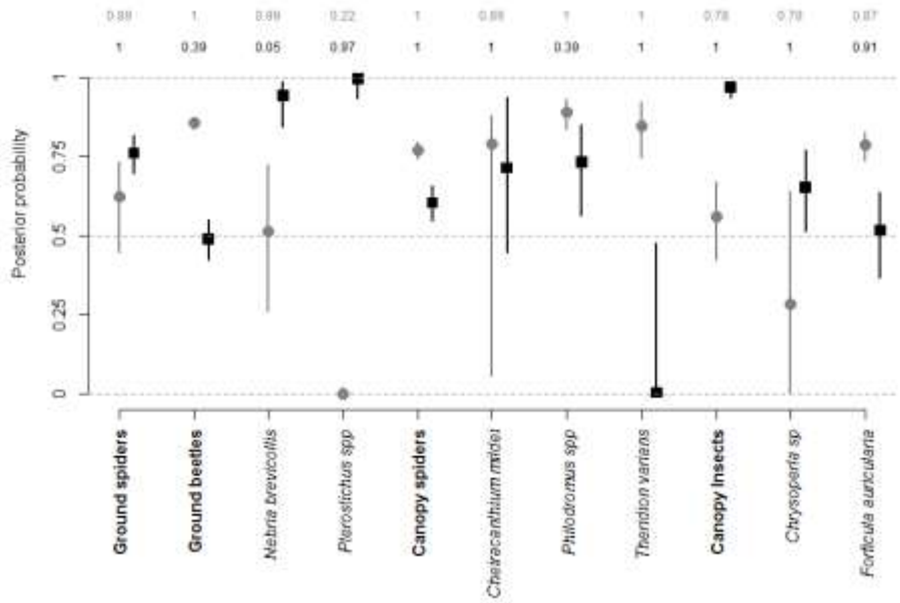
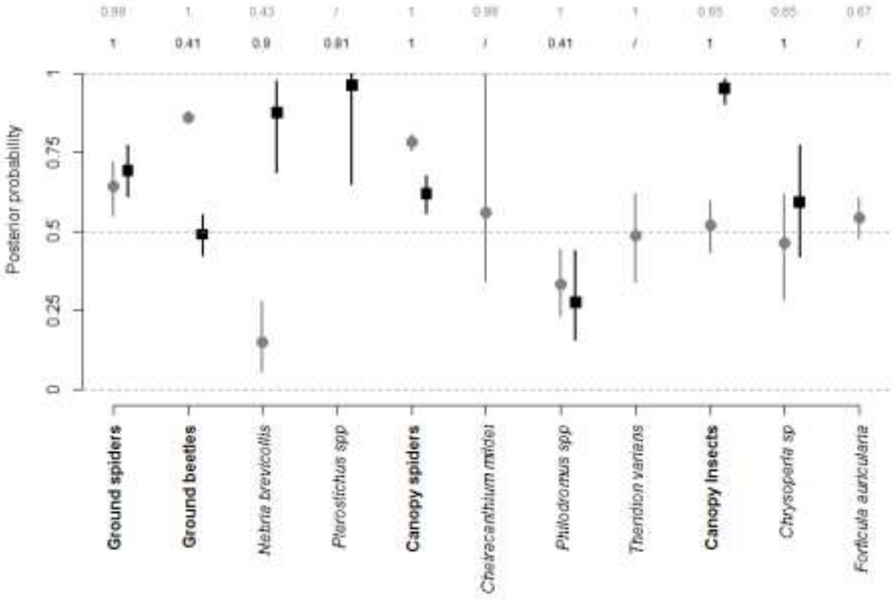


Figure F2: Thresholds of the *correctOD* : canopy = 0.08 and ground= 0.15 (*m*=1). Number of individuals marked: 462.



Using microsatellite markers to improve knowledge on the dispersal of a crop pest parasitoid, *Tersilochus heterocerus*

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Abstract

One of the possible ways to reduce pesticide use is to improve the pressure from natural enemies on insect pests. Parasitoids are important biological control agents in agroecosystems. *Tersilochus heterocerus* (Thomson) is one of the most abundant and widespread parasitoid species of the pollen beetle (*Brassicogethes aeneus* F.) but nothing is known about the genetic structure of its populations. To shed light on their genetic patterns, we developed microsatellite markers. Sixteen out of the 40 designed loci turned out to be polymorphic on *T. heterocerus* and were relevant for population genetic studies. The 16 loci cross-amplified and seemed to be polymorphic in some other Ichneumonidae species such as *Phradis intersticialis.* Parasitoids from five population samples in Europe: Austria, Sweden, Estonia, and France (Eure and Ille & Vilaine departments) and from two successive generations of *T.heterocerus* collected in many oil seed rape fields in the Eure department were analyzed at these 16 loci to reveal the genetic structure between populations and sibship between individuals.

The genetic variability was similar among population samples except for the Swedish population. The genic differentiation was significant over population samples in Europe, which were structured in two clusters. We found similar proportions of full sibs and half sibs among the population samples. The effective population sizes were similar among the population samples and between generations for a population from the Eure.

These polymorphic microsatellite markers could be used in future population genetics studies of *T. heterocerus* and showed a strong population structure among European populations. These results highlight the importance of a better understanding of biology and dynamic of natural enemies of crop pests and that the management can be thought in the same scheme in European countries.

Introduction

Natural enemies are one of the major control of crop pests. Parasitoids wasps are one of the main biological control agents in agroecosystems (Hawkins et al 1997). *Tersilochus heterocerus*, is one of the main parasitoids of pollen beetles, *Brassicogethes aeneus* (formerly named *Meligethes aeneus*), a pest of oilseed rape (OSR) (Ulber et al., 2010). The female parasitoid lays his eggs into pollen beetles larva, the larva drop and pupate in the soil. Then the parasitoid egg develops within the pollen beetle larvae and overwinter within it in the soil until the following spring (Williams, 2006).

T. heterocerus is impacted by the landscape structure, indeed this wasp is more abundant in complex sites with high proportion of non-crops areas (Thies & Tscharntke, 1999) such as woodlands and grasslands (Rusch et al., 2012a). The effect of landscape complexity has been explained by difficulties for parasitoids to move in high open fields (Thies et al., 2008). It can also be explained by the number of flowers that can be found in semi-natural habitats there, which are sources of nectar and pollen for parasitoid young adults (Rusch et al., 2013). However, these habitats could also have an indirect effect on the parasitoids because of an effect on their host, the pollen beetle. Indeed, pollen beetles use woodlands for overwintering (Rusch et al., 2012b) and the grasslands as feeding sites (Juhel et al., 2017).

T. heterocerus are to some extent difficult to observe in the fields (Bernays & Chapman, 1994), but genetics tools might improve our knowledge on *T. heterocerus* (MacDonald & Loxdale, 2004). The microsatellite loci are codominant and highly variable genetic markers, two important criteria for assessing genetic variability in populations and relatedness between individuals (Sunnucks, 2000). These markers have already been used to study the population structure of parasitoids of crop pests, particularly of introduced species (Hufbauer et al., 2004). They have also been used on endemic parasitoids to analyze their breeding strategies (Tentelier et al., 2008) or their population structure (Jourdie et al., 2010).

In the present study, we developed microsatellite markers for a parasitoid *Tersilochus heterocerus* of the main OSR pest, *Brassicogethes aeneus*. We tested the efficiency of this newly developed set of microsatellite loci in describing the genetic structure of this wasp in Europe. Moreover we searched to measure the dispersal of this species with these markers using sibship analysis.

Materiel and methods

Study sites and insect sampling

First, *T. heterocerus* adults were caught by beating in one OSR field per country in Estonia, Sweden, Austria and France (Ille & Vilaine) in 2015 (Fig 1A). Second, both *T. heterocerus* adults and *B.*

aeneus larvae were sampled in 97 OSR fields in May 2016 by beating 15 OSR plants per field in the Eure department, France (Fig 1B). *T. heterocerus* adults from one of these fields were analyzed with the four other population samples in Europe to describe the population genetic structure of this species. All the parasitoids were used in the sibship analysis described below. All the parasitoid adults were identified by their wing and antennae according to Osborn (1960). The genus *Tersilochus* have 16 antennal segments with the fourth shorter than the third or the fifth whereas genus *Phradis* have 15-16 antennal segments without length differences. The forewing vein 2-m-cu leaves vein M at the junction of veins forming the ariolet for *Phradis* whereas the forewing vein 2-m-cu leaves the vein M after the junction for *Tersilochus*. Finally, we distinguished for T. heterocerus males and females: the ovipositor of *T. heterocerus* female is particular, smoothly curved, clearly toothed dorsally and shallowly toothed ventrally. The ovipositor is visible, the females were distinguished from males with this detail.

We identified the pollen beetles larvae that were parasitized: the larvae are sufficiently transparent to see the dark eggs under a binocular magnifier (Osborn 1960). We then extracted *T. heterocerus* eggs from these larvae. The adult parasitoids were found in 39 of the 97 fields fields (Table 1).

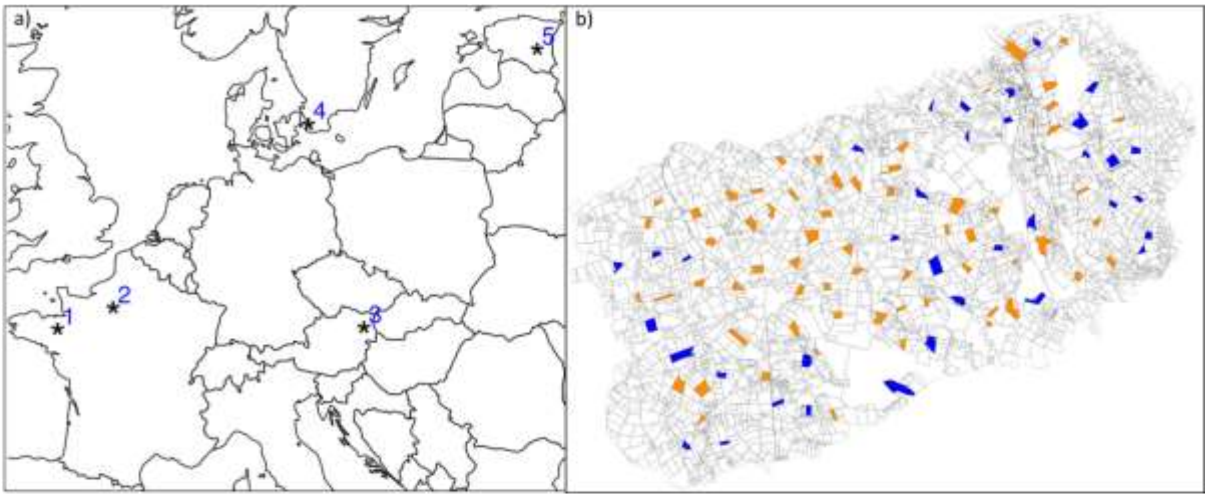

Figure 1: Geographical positions of the a) five *T. heterocerus* European population samples b) of the fields sampled with adults parasitoids (Orange) and without adults parasitoids (Blue). 1: France (Ille & Vilaine), 2: France (Eure), 3: Austria, 4: Sweden, 5: Estonia

Microsatellite development

To develop and characterize markers, *T. heterocerus* were sampled, in the soil of oilseed rape crops in the Eure French department, in autumn 2014. Total DNA of the 21 *T. heterocerus* sampled, was extracted following the DNeasy® Blood & Tissue Kit (Qiagen) DNA extraction protocol modified as follows: 180 µl of Buffer ATL was added to each sample, then they all were ground using 3.15 mm steel beads on a 1600 MiniG (Spex® SamplePrep) tissue homogenizer at 1500 strokes/min for 1 minute. Extraction was then continued following the "Animal Tissues Spin-column Protocol"

(DNeasy® Blood & Tissue Kit Handbook, p. 28-30). Microsatellite library development was based on the pool of the DNA of the 15 parasitoids and performed by GenoScreen (Lille, France), involving Roche 454 GS-FLX Titanium pyrosequencing of enriched DNA libraries (Malausa et al. 2011). A total of 40 microsatellite markers were selected out of the 5,368 microsatellite sequences available based on the number of repeated motifs, the size of amplified fragments and the presence non-repeated sequences flanking microsatellite array longer than 20 pb each. Specific primer pairs were designed for each marker using Primer3 (Rozen & Skaletsky 2000).

CR amplifications were attempted at these loci on six individuals. Each forward specific primer was conjugated with a 5'-GTTGTAAAACGACGGCCAGT-3' M13-tail at its 5' end as in Juhel et al., (2017b). 21 microsatellite loci out of 40 amplified on the six *T. heterocerus* specimens tested. These loci were chosen to estimate the polymorphism in a population of 25 individuals collected in one field of oilseed rape crop in France (Ille & Vilaine) (location 1, Figure 1). The number of alleles per locus, heterozygote proportion (H_O) and gene diversity (H_E) were estimated and departure to Hardy-Weinberg equilibrium were tested using exact test implemented in Genepop, version 4.2.2 (Rousset, 2008). We selected the polymorphic loci with less than 10% of null allele and that were at HWE. The selected microsatellite loci were combined in PCR multiplex, labelling each forward primer with a fluorescent dye at their 5′-end, either *6-FAM* (6-carboxyfluorescein), or *HEX* (hexachloro-fluoresceine), or *TAMRA* (carboxy-tetramethyl-rhodamine), or *ATTO 565* (Rhodamine dyesclass) (Table S1). These loci were also tested on five *Phradis interstitialis* individuals to check for interspecific cross-amplification.

Population structure and diversity analysis

Microsatellite analysis

DNA extractions were performed in a 96-well format plate as in Juhel et al. (2017b). First, tissues of each parasitoid adults were ground in 50 µL of H_2O using a 2 mm steel bead using a 1600 MiniG (Spex® SamplePrep) homogenizer at 1500 strokes/min for 30 seconds. Second, tissues were digested at 56°C for 14 hours in a 100 µl solution including 10% Chelex® 100 (Biorad) and 3% proteinase K using a Mastercycler thermocycler (Eppendorf). The tissue digestion was stopped by a final thermocycler step of 30 min at 98°C. Finally, the supernatant of this solution was used as a DNA template for the PCR reactions. A simplified protocol was applied for the eggs: we discarded the ground step and only added 30 µl of the Chelex/proteinase K solution. PCR amplifications were done as in Juhel et al., (2017b).

Analysis of the genetic data

A total of 1 111 parasitoids individuals were genotyped at the selected microsatellite loci and we analyzed the genetic diversity in the 5 European population samples (Table 1). We calculated at each locus in each population sample, the proportion of heterozygote, H_O, in female parasitoids (males being haploids) and gene diversity, H_E, based on allele frequencies estimated on both males and females. Allelic richness in each population sample was estimated using a rarefaction method (Hurlbert, 1971), as implemented in the HP-RARE program (Kalinowski, 2005). As we had populations with few females, we did not permed FST tests (Weir & Cockerham 1984). Exact test for departure from the Hardy-Weinberg equilibrium (HWE), genic differentiations and linkage disequilibrium between pairs of loci were performed using Genepop version 4.2.2 (Rousset et al 2008).

Table 1: Number of sampled OSR fields and number of genotyped males and females in each population samples.

Population	Instar	OSR field	Females	Males	Total
Austria	Adult	1	10	10	20
Estonia	Adult	1	10	12	22
France (Eure)	Adult	1	1	25	26
France (Ile & Vilaine)	Adult	1	25	/	25
Sweden	Adult	1	/	18	18
France (Eure total)	Adult	1	9	119	128
France (Eure)	Eggs	39	40	52	92

To detect clusters among the sampled parasitoids, we used the Bayesian clustering method implemented in Structure version 2.3.4 (Pritchard *et al.*, 2000). We selected the optimal number of groups *K* in which individuals should be assigned by testing the likelihood of models with values of *K* from 1 to 10. For each model, we performed 10 runs of 500 000 iterations after a 'burn-in' period of 200 000 iterations. Individual assignations were computed assuming admixture among the *K* groups. As recommended by Wang (2016), the geographical locations of the sampled individuals and non-equal contribution of the *K* sources to the admixture were used as priors for the structuration. We performed this analysis on the males and females from the five European populations.

Statistics for sibship assignment

WTo determine if they were similarities between European populations in terms of proportion of full sibs and half sibs per field. This analysis was conducted using the program COLONY version 2.0.6.3 (Jones and Wang 2010). Sibship assignments were based on likelihood ratio tests. The mating behavior in *T. heterocerus* is not known; we supposed that both sexes are polygamous. We used models accounting for haplo-diploidy. We used the Full-Likelihood and Pair-Likelihood combined method (FPLS). We used the percentage of null alleles estimated at each locus in the reference population from Ile & Vilaine to set up genotype errors. We did not update allele frequency and did not use the sibship scaling. All other parameters were set as default. We ran the model 10 times with a different seed and kept only full sibs and half sibs (maternalship and paternalship) pairs found in each of the 10 replicates. We performed these models on diverse data sets with males and females. We performed 1) kinship assignments among parasitoids in an OSR field to estimate Ne (independently in the five European population samples), 2) kinship assignment among parasitoids from several fields in the Eure department to estimate dispersal between fields, and 3) parentage assignment of parasitoid eggs.

The program COLONY permit also to estimate the effective population size (Ne) based on the sibship assignments (Wang, 2009). We estimated Ne with this method for the 7 different models of assignment, based on the full sibs and half sibs (paternal ships and maternal ships) kept by the 10 models.

Results

Design and selection of microsatellite markers

We analysed the genetic variability at each microsatellite locus on 25 *T. heterocerus* females from the Ille & Vilaine population used as reference. Among the 21 loci genotyped in this population, three were monomorphic (*Th-AFT3B*, *Th-B95QV*, *Th-cons698*) and two did not amplify in several individuals (*Th-B7116*, *Th-ARXDT*). The 16 remaining loci showed a large range of polymorphism (2 to 7 alleles per locus): proportion of heterozygotes ranged from 0.14 to 0.77 and gene diversity ranged from 0.12 to 0.73 (Table 2). None deviated from the HWE or had a frequency of null alleles lower than 10 %. Cross-amplifications of these 16 *T. heterocerus* microsatellite loci on *P. interstitialis* were successful but few loci were polymorphic in this species (Table S2).

Table 2: Characterization of 16 polymorphic microsatellite loci in *Tersilochus heterocerus*. Locus Name, forward (F) and reverse (R) primer sequences, repeat in sequenced clone, sizes of the PCR products, number of alleles (*N*a), proportion of heterozygotes (*H*p) and gene diversity (*H*d), frequency of null alleles, expected and observed heterozygosity (He and Ho). Polymorphism statistics were performed on 25 individual females collected in the same OSR field in Ille & Vilaine, France.

Locus	Primer sequences (5’-3')	Repeat motif	Size (pb)	Size range	N_a	H_E	H_O	Null Alleles
Th-ACRH 8	F: CATAATTGTCGGCAGAAACG	(AG)11	289	276-284	2	0.30	0.25	0.06
	R: ATCTTGTCATTGTCCGTCC							
Th-AOD8 1	F: TTGGTGTTGGGATGATATCG	(CT)9	235	255-283	2	0.24	0.27	0.00
	R: TCAAAGGTCCTAAGTTCGTC							
Th-AXWO A	F: GCTTCCATTCACAAGTTTACG	(AG)11	157	151-165	2	0.53	0.50	0.00
	R: AGTGCTGAAGTTTATTTCCC							
Th-B2M3 A	F: ACACTAGAATAATTGCACGC	(AG)10	239	235-237	2	0.50	0.63	0.01
	R: GTAGCTGAATGACGACAAAC							
Th-BBCF N	F: CTGACGCACATTCGTAAAGG	(AG)9	189	187-191	2	0.17	0.12	0.00
	R: CAGTGATGTTTAACCGAACTTGGC							

Th-BXXG G	F: GCCCGAATCTCATTAACG	(GA)9	344	338-248	3	0.33	0.38	0.00
	R: GTTCACAGCCTTAATAAGAACC							
Th-C3H5 G	F: ACCTTCATTCACTCTCCATC	(CT)9	244	227-239	3	0.77	0.73	0.00
	R: GTTGAGCTGATAATTGTGGC							
Th-C56F P	F: GAAGACCGGAAACAGAGC	(CT)11	229	227-229	3	0.46	0.48	0.00
	R: CGGATTTCGCTTCAGG							
Th-CIET 7	F: TGACGTGGGAGAAACAGAG	(GA)10	163	161-165	3	0.29	0.33	0.02
	R: GCTTTGCCACCTCGTTC							
Th-cons4 7	F: GAACATTGTTGGCTTATAACCC	(CA)15	209	207-243	4	0.47	0.42	0.00
	R: CATAGGGCAAAAGACTAGCG							
Th-cons52 1	F: TTCTATATTTTGGGCTGTGC	(GA)13	331	319-329	4	0.48	0.50	0.03
	R: ACGTCATACAAGCACTATCC							
Th-Cons65 1	F: TTTCCCTTCGACGTGTCC	(TC)10	289	283-285	4	0.50	0.44	0.00
	R: ATTAGAGTTTACGACCATTTGTG							
Th-CTUR T	F: GTCTTTCCAATTCTCTGCAC	(TG)9	150	149-141	4	0.20	0.15	0.07
	R: ACTATCTCGCCCATTTTCAC							
Th-CWJY 8	F: GCTGTTTTAAGTGCTTTGAAC	(CA)9	198	195-197	5	0.48	0.41	0.05
	R: GATGGCGAATCGTGCG							
Th-DAXQ K	F: TTAGAATAGCGGTTTGAATC	(CT)10	209	204-214	6	0.14	0.15	0.00
	R: TGTATCATGGGAAGTACGTC							
Th-DB9S W	F: CCCTTTGATCGTTAACTCCC	(CT)12	248	244-248	7	0.41	0.44	0.00
	R: CCTCGGTATTCCCCATTTAC							

Genetic variability in T. heterocerus populations

The mean number of alleles ranged from 3.00 to 3.38 (mean = 3.27), the gene diversity (H_E) ranged from 0.36 to 0.44 (mean = 0.40) and proportion of heterozygotes (H_O) ranged from 0.32 to 0.41 (mean = 0.37) (Table 3). We estimated *HWE* and LD on the females of Austria, Estonia and France (Ile & Vilaine). The three populations did not deviated from *HWE* and no significant LD was detected for the 359 microsatellite pairs (p<0.00014).

Table 3: Genetics characteristics of *T. heterocerus* in the five European populations (mean [SE]). Ar: Allelic richness.

	N males/females	H_E	H_O	N alleles	A_R
Austria	10/10	0.45 [±0.23]	0.38 [±0.24]	3.19	3,00 [± 1.54]
Estonia	12/10	0.36 [±0.21]	0.35 [±0.21]	2.88	2,68 [± 0.88]
France (Eure)	25/1	0.32 [±0.21]	0.33 [±0.21]	3.13	2,51 [± 1.10]
France (Ille & Vilaine)	0/25	0.39 [±0.15]	0.38 [±0.16]	3.19	2,65 [± 0.90]
Sweden	18/0	0.19 [±0.24]	-/	1.94	1,81 [± 0.99]

Population structure of *T. heterocerus*

The genic differentiation was significant for all the population pairs ($p < 0.05$). The global F_{ST} was of 0.15 ($p < 0.001$). Based on their microsatellite genotypes, the number of clusters, *K*, to which the 111 individuals (males and females) could be assigned was estimated using the software Structure assuming a uniform prior and for *K* between 1 and 10. The model that best described the genetic data was with *K* = 2.

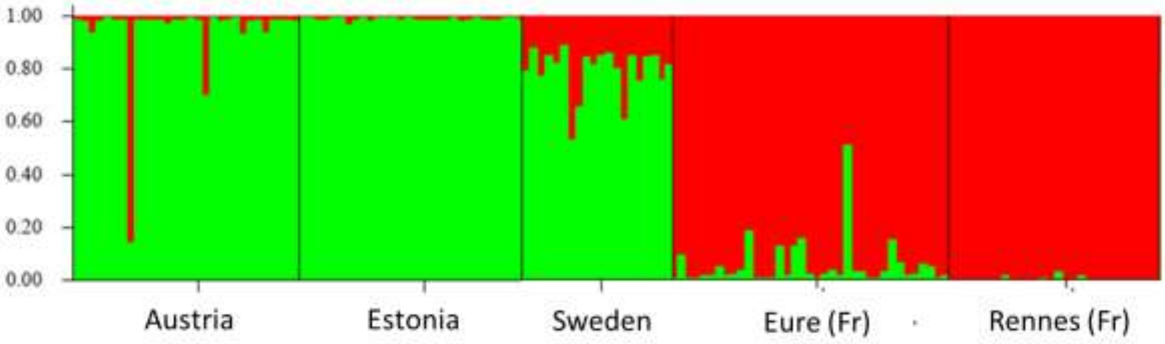

Figure 2: Bayesian assignment of *T. heterocerus* individuals from 5 populations to each of the *K* = 2 identified clusters using Structure software on micro-satellites.

Sibship assignments and distances

e performed 5 models of sibship assignments with the software COLONY, one for each of our population samples (Austria, Estonia, Sweden and France (Eure and Ille & Vilaine). The number and percentage of full sibs was similar in all the populations (Table 4). The percentage of half sibs was also similar across populations, varying from 11 to 24 %. We also compared the number of full sibs and half sibs found in the adults from the Eure region (N = 128) and in all the eggs (N = 93). We found in this region 22 (0.27 % of the possible pairs) and 16 (0.37 %) full sibs and respectively 68 (0.83 %) and 90 (2.10 %) half sibs.

The effective population size Ne was similar among European populations except for the Austrian population which had a much higher Ne and Sweden with a lower Ne (Table 4). Ne calculated from all individuals collected in Eure was 268 with the adults and 35.2 [20, 62] with the eggs.

Table 4: Mean number of half sibs (HSm maternal ship and HSp paternal ship) and Full sibs (FS) by population of *T. heterocerus*, and percentage within pairs of FS and HS possible with the by sites analysis.

Population	N	Possible dyads	FS nb	HSm nb	HSp nb	FS %	HSm %	HSp %	Ne
Austria	20	190	2	37	4	1.05%	19.47%	19.47%	13
Estonia	22	231	5	46	4	2.16%	19.91%	19.91%	13
France (Eure)	26	325	4	36	2	1.23%	11.08%	11.08%	23
France (Ille & Vilaine)	25	300	3	47	28	1.00%	15.67%	15.67%	12
Sweden	18	153	8	35	9	5.23%	22.88%	22.88%	9
France (Eure total)	128	8128	22	51	18	0.20%	0.60%	0.22%	268
France (Eure Eggs)	93	4278	16	45	33	0.37%	1.05%	0.01%	137

We also ran COLONY on the eggs considering the adults as putative parents. Out of the 92 eggs genotyped, seven were assigned to four different males among the 128 genotyped adults. These putative fathers were found at distances between 6,200 m and 16,700 m. This analysis showed also 6 pairs of full sibs: 3 from the same field and 3 in different fields.

In our samples, seven cases of super-parasitism (two parasitoid eggs in the same larva) were detected. One of the pair was detected as full sibs.

Discussion

Microsatellite markers are mainly used in the characterization of the population structure of non-model species (Sunnucks, 2000). Here, we have developed 16 microsatellite markers on the Ichneumonid wasp, *Tersilochus heterocerus*. From a total of 5,368 microsatellite markers sequences, 40 were selected based on the number of repeated motifs and the size of amplified fragments. Less than a half of these selected sequences were kept as microsatellite markers as a lot of markers did not amplify or were monomorphic. We developed a consequent number of microsatellite loci compared to other ichneumonidae species. Indeed, in *Neotypus melanocephalus*, only nine polymorphic microsatellite were developed (Anton et al. 2006) but with a higher number of alleles (2 to 10). We tested if, even if the microsatellites markers were not very polymorphic, they were useful in population genetic analysis and sibship analysis.

The 111 adult parasitoids of the five European populations were assigned to 2 clusters *K*. The two populations from France were separated from populations from other countries in Europe. As our species is haplo-diploid, we used differentiation genic and it was significant for all the population pairs. This result was in agreement with the results of STRUCTURE but more precise as we differentiated all populations. The genetic structure of this species seems to be weak in France but stronger in Europe than its of his host, *B. aeneus* (Juhel et al., 2017b). The genetic diversity of the European populations was similar except for the Swedish population, in which it was lower. This could be explained by the absence of females on our sample.

We used sibship assignment analysis based on the micro-satellite genetic markers we developed. Such sibship assignments depend on four assumptions (Jones and Wang, 2010): no deviation from the *HWE* in the populations, unlinked and selectively neutral loci, knowledge of population allele frequencies and no genotyping errors. Here, the HWE could be calculated only on populations with females, as these populations not deviating from the HWE, we considered that the other populations did not deviate either. Significant LD was not detected either in these populations. The other assumptions were assumed to be met.

The proportion of full sibs and half sibs was low but similar between European fields except for Swedish population. In this population, only males were genotyped and the assignment of males is easier than females this could explain the higher proportion of full sibs found. The proportion of half sibs was also low and similar between European populations. These results shows that the demographic patterns of this species are similar in Europe. The effective population size, Ne, was also significantly similar across populations, except for the Swedish population. As we had only males, the diversity was lower and this could explain the low Ne. Moreover the genetic diversity was similar across populations and this normally suggests similar Ne in the field (Schneider et al., 2015), this is in agreement with our results.

We found couples of fathers and theirs sibs at long distances: 6 and 16 km. This distance seems to be high for a parasitoid. For example, the *Pleolophus basizonus* can travel 0.400 km in 2 days (Price, 1970). Moreover, on the path between fathers and theirs sibs there were woodlands and parasitoids are expected to have difficulties to pass through this type of habitat. Nevertheless, parasitoids can use upwind anemotaxis for host-habitat location facilitating long distance dispersal (Williams et al., 2007). Other parasitoids of OSR are attracted by the oilseed rape volatiles (Jonsson & Anderson, 2008), we suppose it is the same for *T. heterocerus*. However, the distance at which parasitoids can detect these odors is still unclear. In any cases, as we detected only seven pairs of father-sibs, these distances have to be considered with caution.

Seven cases of super-parasitism were detected. One of the pair was detected as full sibs. Even if we have a weak occurrence of super-parasitism, this result suggests females lay their eggs in diverse larvae and tends to avoid competition between their own sibs but also between their own sibs and other ones. This phenomenon is common in nature to avoid kin competition and inbreeding (Motro, 1991).

In this study, we extracted the DNA of adults parasitoids but also of eggs. The amplification of microsatellite markers was successful for 86 % of the adults but only for 49 % of the eggs. This result could be explained by a better conservation of DNA for adults than eggs and an easier extraction. The eggs were kepts in the larvae of pollen beetles for three months in 90 % ethanol and then kept alone in 90 % ethanol for one month. Eventually, the eggs had to be extracted from the larva less time before the DNA extraction. Detection of DNA of parasites in their host is often used (Zhu & Williams, 2002) but the extraction of DNA from small individuals is rarer and harder.

Despite the low polymorphism of the 16 newly developed microsatellite loci, they were useful for measuring genetic variations within populations of *T. heterocerus*. This markers were also useful in the sibship assignment though a little weak. These polymorphic microsatellite markers could be used in future population genetics studies of *T. heterocerus* but for sibship assignments, adding more markers could be helpful to detect full sibs.

Acknowledgments

We would like to thank the participating farmers for their interest in the project and A. Butier and M. Bazot for their technical assistance.

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Supplementary Material

Table S1: Polymorphic microsatellite loci selected in this study with reference to the labelled dye of the forward primer and the molar concentration (C) of each locus each multiplex. 6-FAM (6-carboxyfluorescein), HEX (hexachloro-fluoresceine), TAMRA (carboxy-tetramethyl-rhodamine), ATTO 565 (Rhodamine dyesclass).

Multiplex 1	Dye	C (nM)
Th-B2M3A	6-FAM	0.050
Th-cons651	6-FAM	0.100
Th-CIET7	Tamra	0.500
Th-DAXQK	Tamra	0.500
Th-C56FP	Hex	0.250
Th-Cons521	Hex	0.100
Th-CTURT	Hex	0.074
Th-AOD81-R	Atto-565	0.100
Th-BXXGG	Atto-565	0.200
Multiplex 2		
Th-BBCFN	6-FAM	0.074
Th-ACRH8	Tamra	0.400
Th-C3H5G	Hex	0.300
Th-CWJY8	Hex	0.150
Th-AXWOA	Atto-565	0.150
Th-cons47	Atto-565	0.250
Th-DB9SW	Atto-565	0.200

Table S2: Characterization of 16 polymorphic microsatellite loci in 8 *Phradis interstitialis* samples collected in a seed in the Eure French department.. Sizes of the PCR products, number of alleles.

Loci	Alleles	Size range
Th-ACRH8	2	280-286
Th-AOD81	1	255
Th-AXWOA	2	157-165
Th-B2M3A	1	235
Th-BBCFN	1	187
Th-BXXGG	4	338-352
Th-C3H5G	2	227-237
Th-C56FP	2	225-227
Th-CIET7	2	163-165
Th-cons47	2	209-241
Th-cons521	1	317
Th-Cons651	2	281-283
Th-CTURT	1	147
Th-CWJY8	3	191-195
Th-DAXQK	1	208
Th-DB9SW	1	246

Sibship assignments and effective population size measure of an oilseed rape pest

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Abstract

Pollen beetles, *Brassicogethes aeneus* (formerly named *Meligethes aeneus*) is one of the most significant pest of the oilseed rape crop in Europe. We used sibship assignment methods to better understand the local dynamics of pollen beetles in the Eure department, France. To describe the dilution of the proportion of sibship found over a given surface over a generation, we sampled pollen beetles of the same generation at different time from their birth in OSR fields in 2015 to their breeding in OSR fields in 2016. We also sampled them at their overwintering places (woodlands) and potential feeding places (grassland) in which they might stop before reaching their reproduction places. On each date, we sampled pollen beetles at different locations spread in a same area of 6 x 8 km. Based on sibships assignments, we estimated 1) the proportion of full sibs and half sibs at each of the locations, 2) the proportion of full sibs and half sibs captured over the whole generation across sites, 3) the effective population size in each site. Here we show that the effective population size Ne decrease with time within a generation. These variables were similar among locations in the same dates. We found dyad of full sibs at more than 2 km between locations suggesting that both dispersal phase were over long distances. These results confirm the dispersal capacities of pollen beetles over several kilometers.

Introduction

Pesticide use is a major threat for biodiversity and human health (Geiger et al., 2010) and a wide variety of alternatives strategies have been sought, in particular to deal with insect pests of field crops. These strategies go from the use of repellent (Mauchline et al., 2017), to the use of trap crops (Cook et al., 2004) or resistant cultivars (Herve et al., 2014). The implementation of these strategies requires a good knowledge of the biology of the pests and in particular their dispersal. A way to approach it is to use sibship methods based on individual pairwise assignment (Thompson, 1976).

The pollen beetles, *Brassicogethes aeneus* (Fabricius, 1775) (formerly *Meligethes aeneus*) (Coleoptera: Nitidulidae) is one of the most significant pest of oilseed rape (OSR). As the OSR receive a large amount of pesticides and as pollen beetles are resistant to pyrethroids (Hansen, 2003), other means of control against this species have to be found. To elaborate these alternatives strategies, a good knowledge of the biology of *B. aeneus* is needed for example on their dispersal. Dispersal is indeed key for this species at it lives in different landscape elements at different points of its life cycle. First, the adults lay their eggs in the buds of the OSR in the spring. Then, the larvae develop in the buds and drop to the ground to pupate when the OSR flowers fade. A few weeks later, the adults of this new generation emerge and seek overwintering sites such as woodlands. They emerge in the spring when temperatures reach 12°C and seek breeding sites (i.e new OSR fields), possibly stopping before at feeding sites such as the edges of grasslands or fields (Juhel et al., 2017a, Taimr et al., 1967). This species is supposed to have high dispersal capacities, it can travel up to ten kilometers in two days in the spring (Taimr et al., 1967) with a mean dispersal distance of 1.2 km (Juhel et al., 2017b) and up to three kilometers in the summer (Stechmann and Schütte, 1976). These distances were confirmed by a low genetic differentiation in Europe (Juhel et al., 2017c, Kazachkova et al., 2008) but also within countries (Juhel et al., 2017c, Kazachkova et al., 2007).

Here, we want to confirm and precise these estimates of dispersal by identifying distances at which siblings might be found and by measuring the effective population size in pollen beetles populations. We performed a genetic analysis over one pollen beetle generation collecting adults between their emergences in OSR field to their breeding site in OSR field the next year. We also sampled them in several locations at each of the four different dates. Based on sibship assignment method, we estimated the number of full sibs and half sibs and the effective population size Ne in each of these locations.

Materiel and Methods

Study site and sample collections

Pollen beetle adults were sampled in the valley of the Eure River (Fig 1, Table 1). Pollen beetle were collected on different dates and at different locations on each date. First, pollen beetles were caught when they emerged from four OSR fields in June 2015 using emergence traps (four emergence tents per field). Then, overwintered individuals were caught in woodlands from February to April 2016 using emergence traps (53 emergence traps in different locations along woodland edges). Finally, in April 2016, pollen beetles were caught by beating plants in seven grassland plots (five 60 cm x 60 cm quadrats in each plot either in grasslands or along road borders) and in five OSR fields (10 OSR plants from 10 different points in each of five different fields). All the sampled insects were stored in 90° ethanol solution until DNA extraction. We selected all the individuals sampled in the grasslands, roadsides and woodlands. We kept 50 individuals from each of the OSR tents (or less if we had less than 50 individuals) and 10 individuals from each of the beating in the OSR samples. Distances between pairs of pollen beetle were calculated based on the geographical coordinates at the various sampling points. We used the coordinates transformed in UTM to calculate them. Each field in 2015 and 2016, each grassland and all the woodlands were considered as a population as all the tents for the genetic differentiation analysis.

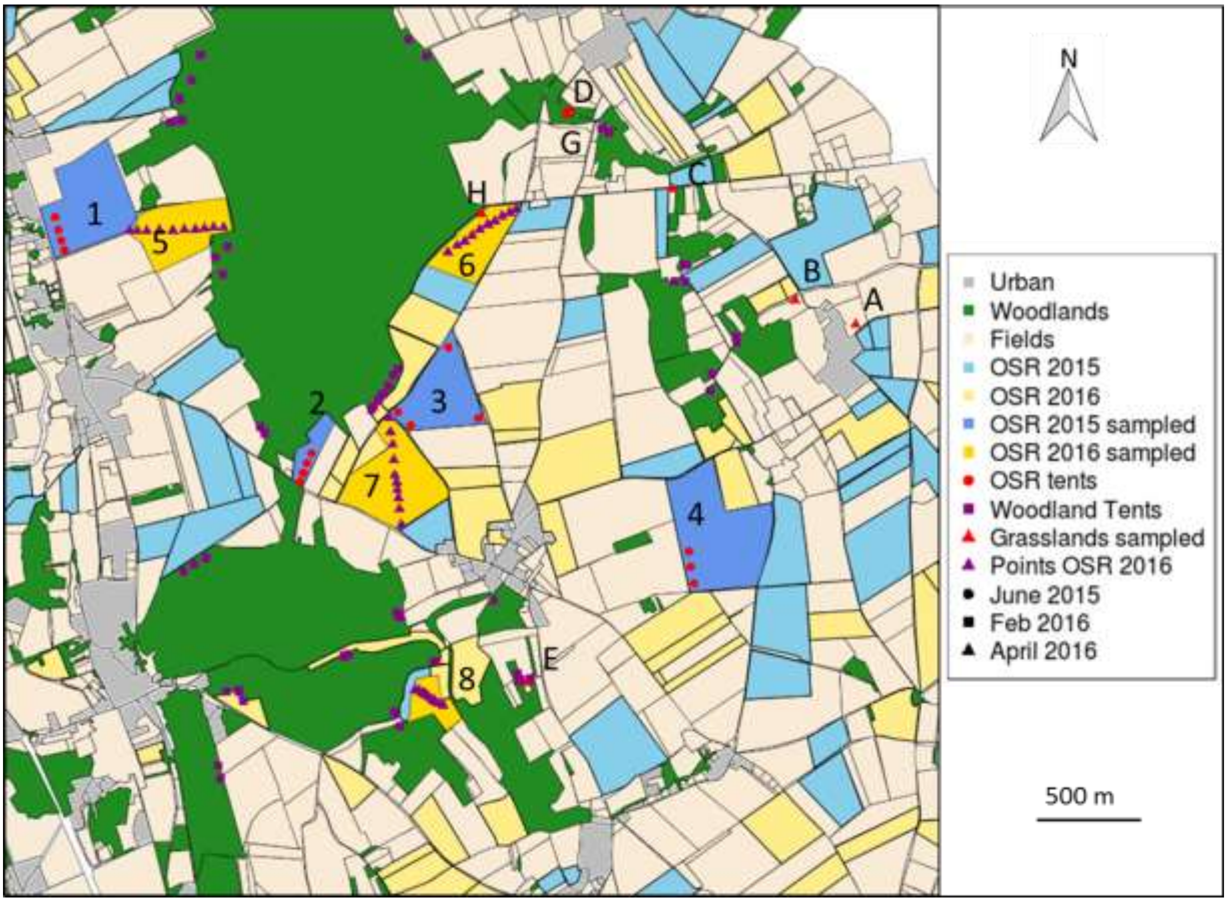

Figure 1: Map of the study sites in Normandy, France including the sampling points. Blue field: OSR 2015, Dark blue fields (1-4): OSR 2015 sampled. Yellow field: OSR 2016, Dark yellow fields (5-8): OSR 2016 sampled. Green fields: woodlands. Purple squares: woodland tents. Red points: OSR tents. Red triangles: grassland and roadside sampling points. Purple triangles: OSR sampling points. A-G: grasslands sampled

Table 1: Characteristics of sampled sites

Site types	Sampling dates	Sampling modes	Locations	Number of sampling points	Number of genotyped individuals
OSR crops	June 2015	Tent	4 Fields (1- 4)	16	621
Woodland	Feb-March 2016	Tent	Several woods	53	129
Grassland	April 2016	Beating	6 Grasslands (A-G)	35	172
OSR crops	April 2016	Beating	5 Fields	50	360

Microsatellite analysis

Thirteen microsatellite loci (*Ma-C4QRG, Ma-CEALQ, Ma-CVT0N, Ma-EL7YR, Ma-EB7XX, Ma-D3QFM, Ma-DCH30, Ma-DDEYS, Ma-DM3QY, Ma-DQM5T, Ma-EPL2N, Ma-ESPVQ, Ma-ESVIZ,* Juhel et al. 2017c) were scored for a total of 1,397 adults. We extracted the DNA by grounding each individual in 50 µl of water using 2 mm steel beads on a 1600 MiniG (Spex® SamplePrep) tissue homogenizer at 1500 strokes/min for 30 seconds. At each sample were added 50 µl of 20% Chelex 100 (Biorad) solution and 6% of 10 mg/ml proteinase K (Eurobio). Tissues were digested 14 hours at 56°C Mastercycler thermocycler (Eppendorf) with a final temperature step of 30 minutes at 98°C, supernatant was used as DNA template for PCR reaction. PCR amplifications were carried out with a Mastercycler thermocycler (Eppendorf) in a 10 µl reaction volume containing 5 µl of master-mix (QIAGEN), 2µl of primer-mix (primers concentration ranging from 0.13 to 2.5 µM), and 2 µl of DNA template. The PCR conditions were: 15 minutes at 95°C followed by 35 cycles at 94°C for 30s, 54°C for 90s, and 72°C of elongation for 1 min with a final extension step at 72°C for 20 min. Each PCR multiplex products was diluted in 40 µl H20. 2µl of this dilution with 7.8 µl of HiDi formamide, and 0.2 µl GeneScan™- 600 LIZ® Size standard (Applied Biosystems) was injected on an ABI 3730xl DNA Analyzer (Applied Biosystems) using POP7 polymer (Applied Biosystems). Genotypes were visualized using GeneMapper®, version 4.1 (Applied Biosystems).

Population genetic variability

Basic statistics for microsatellite loci were performed on predefined population samples considering either the individuals sampled in one tent in OSR field, or the individual sampled at one location on the same date (OSR fields or grassland or woodland locations). We estimated heterozygote proportion, gene diversity, and proportion of null alleles at each microsatellite locus in each population sample, together with their standard deviation, presented hereafter with ± within square brackets, using GENEPOP version 4.1 (Rousset 2008). We computed exact tests for Hardy-Weinberg Equilibrium (HWE) and linkage disequilibrium (LD). Allelic richness in each population sample was estimated using a rarefaction method (Hurlbert, 1971), using the HP-RARE program (Kalinowski, 2005) parameterized with the smallest population sample size.

Sibship assignment

Sibship analysis was conducted using COLONY version 2.0.6.3 (Jones and Wang 2010). Sibship assignments were based on likelihood ratio tests assuming pollen beetle of both sexes are polygamous and using the Full-Likelihood and Pair-Likelihood score combined method (FPLS). Sibship assignment based on the FPLS method is more accurate in the detection of sibs than the pairwise likelihood method and is computationally much more efficient than the full-likelihood method (Wang, 2012).

Previous estimate of null allele frequencies (Juhel et al., 2017), were used to set up allelic dropout error at each locus, which ranged from 0 to 0.09. Other genotyping error rate was set at 0.001 for all the loci. We did not update the allele frequency and did not used the sibship scaling. All other parameters were set as default. We ran the model 10 times with a different seed and considered the full sib and half sib dyad that came out in all of the 10 replicates to get a more accurate assignment.

We ran these models on groups sampled at the same period : 1) all the individuals sampled in OSR in June 2015, 2) all the individuals collected in the woodland in February to April 2016, 3) all the individuals collected in the grassland or in roadsides in April 2016 4) all the individuals collected in OSR fields in April 2016. We separated the samples from grasslands and from OSR fields even if they were sampled on the same date as these habitats provide different resources for the pollen beetles. We then ran these models splitting groups based on the location of the sampling when the number of individuals collected per location was large enough (more than 20 individuals): 1) each tent in OSR field in 2015, 2) 3 grasslands separately in April 2016, 3) each OSR field separately in 2016. Finally, to detect links between individuals from all the locations and dates, we ran another model including all the 1282 genotyped individuals.

The contemporary effective population size (Ne) was inferred using the sibship assignment result provided by COLONY based on the estimated proportions of full-sib and half-sib dyads (Wang 2009). Among the many genetic methods available for estimating Ne (Luikart et al. 2010), the sibship assignment method was chosen because it allows population size estimation based on samples from a single cohort (Wang 2009). We estimated Ne in each of the 6 different models with the method of Wang but using only full sibs and half sibs selected in the 10 replicates.

Spatial genetic structure

We analyzed how kinship between individuals was spatially structured. We first computed the ratio of siblings over sampled pairs of individuals by bins of distance of 250 m. We tested the impact of the distance on the ratio of siblings in the pairs using a binomial general model. In addition we used semi-variograms (Wagner et al., 2005) as implemented in the package ggene (Rossi, 2016) tosummarize the spatial genetic structure in the population given the coordinates of the sampled individuals.

Results

We sampled a total of 7 458 pollen beetles in all our sample sites. We genotyped 621 individuals out of the 1 312 pollen beetles in OSR fields in 2015, all the 129 individuals collected in the woodlands, all the 172 individuals collected in the grasslands and roadsides and 360 individuals out of the 5816 caught by beating in the OSR in 2016.

Genetic diversity

The mean number of alleles ranged from 4.54 to 7.69 (mean = 6.08 [±0.89]), the gene diversity (H_E) ranged from 0.56 to 0.63 (mean = 0.60 [± 0.02]) and proportion of heterozygotes (H_O) ranged from 0.58 to 0.64 (mean = 0.61 [± 0.01]). The mean allelic richness was of 4.24 [± 0.15]. The proportions of null allele did not exceed 0.09 (mean = 0.03). HWE was rejected for 7 of our 26 populations or sub-populations (3 OSR tents from the field 1, OSR fields 1, 3 and 4 and grassland 3). Significant LD were detected for 4 dyads of microsatellite loci ($p>0.000024$).

Sibship assignments and effective population size

We ran with COLONY the model on the 18 different data sets on diverse levels: spatial and temporal (Table 2). The model was performed 10 times for each dataset but with a different seed. Here we present only the full sibs and half sib dyads that came out in the 10 repetitions to increase confidence in our assignments. The percentage of these full sibs and half sibs dyads compared to all the dyads found in the 10 replicate was low (Table 2).

Temporal analysis

The percentage of full sib dyads found in each of the four temporal models was low (<0.007%). Surprisingly, the higher percentage of full sib dyads was found for the samples collected in grasslands. The effective population size Ne decreased with time. Ne estimates in OSR were about twice lower in 2016 than in 2015.

Spatial analysis

At the same date, the percentages of full sib and half sib dyads were highly variable between locations. There was no significant differences between tents of the same field of OSR in 2015. The level of sibship was low given that the larvae were on a few neighbor plants suggesting that the females spread their eggs over multiple plants. The estimated effective population size was similar between tents (Table 2).

In each of the 4 OSR fields sampled in 2015, the percentage of full siblings was close to zero. The same result was found for the half sibs, except for the field 4, in which we found 6 % of half sibs. The effective population sizes were similar in all fields, but about four time lower in field four, which was the more distant to woodland. Ne between these fields was variable and decreased with the distance to the woodlands.

In the grasslands, we also found a percentage of full sibs close to zero and the percentage of half sibs varied between 2 % to 4 % with a higher value for the grassland E with 16 %. Ne were significantly different between grasslands.

No full sibs were found in the OSR fields of 2016 and a low number of half sibs, less than 1% in each of the sites. As for the other comparisons, Ne were similar between OSR fields in 2016.

Table 2: Number of half sibs (HS) and full sibs (FS) dyads by models, and percentage within dyads of FS and HS possible with the by sites analysis. Ne: mean effective size [min, max]. N= sample size. Prop FS10 and prop HS10: percent of full sibs and half sibs found in the 10 repetitions compared to all the dyads found. Tents 1-4 were tents from the field 1.

Sample	Time	N	Pairwise possible	nb FS	nb HS	%FS	%HS	prop FS10	prop HS10	Ne
Temporal datasets										
OSR 2015	June 2015	621	192510	4	41	0.00	0.02	2.2	0.4	8556
Woodlands	Feb-Mar 2016	129	8256	0	11	0.00	0.13	0.0	0.5	1501
Grasslands	April 2016	172	14706	1	42	0.01	0.29	4.3	2.4	684
OSR 2016	April 2016	363	65703	0	28	0.00	0.04	0.0	0.4	4693
Spatial datasets										
Tent 1	June 2015	50	1225	1	45	0.08	3.67	4.3	7.4	53
Tent 2	June 2015	28	378	2	47	0.53	12.43	5.0	14.8	15
Tent 3	June 2015	32	496	2	68	0.40	13.71	6.7	19.4	14
Tent 4	June 2015	38	703	1	37	0.14	5.26	2.9	7.7	37
Field 1	June 2015	148	10878	2	27	0.02	0.25	3.6	1.2	750
Field 2	June 2015	220	24090	0	18	0.00	0.07	0.0	0.4	2677
Field 3	June 2015	213	22578	2	24	0.01	0.11	2.2	0.6	1737
Field 4	June 2015	40	780	1	48	0.13	6.15	3.1	8.8	32
Grassland B	April 2016	36	630	0	31	0.00	4.92	0.0	6.6	41
Grassland C	April 2016	57	1596	1	27	0.06	1.69	2.4	3.4	114
Grassland E	April 2016	31	465	3	74	0.65	15.91	5.3	18.3	12
Field 5	April 2016	75	2775	0	21	0.00	0.76	0.0	1.2	264
Field 6	April 2016	89	3916	0	10	0.00	0.26	0.0	0.6	783
Field 7	April 2016	99	4851	0	20	0.00	0.41	0.0	1.2	485
Field 8	April 2016	96	4560	0	18	0.00	0.39	0.0	1.3	507
Global model										
All samples	2015-2016	1283	822403	10	84	0.00	0.01	4.5	0.5	17498

Distances between sibships

A total of 94 dyads were assigned as kind (10 dyads as full sibs and 84 dyads as half sibs) in the global model performed with COLONY (Table 2). About half the full sib dyads were detected between individuals collected in the same plot at the same date (Figure 2): 4 dyads were between individuals from the same tent in OSR field and one dyad was detected between individuals collected in the same grassland. Another pair was between an individual sampled in a woodland and an individual sampled in an OSR field in 2016. There were 1 660 m between these two locations. Two other dyads of full sibs were found between individuals found at 2 300 m between each other and were sampled in an OSR of 2015 and the second individuals in OSR of 2016. Finally the ultimate pair was found at 2 600 m between two individuals from tents in OSR of 2015. Three of these 10 dyads were also found in the temporal models. The other were not tested in the temporal models.

Figure 2: Distribution of the full sibs found in the whole dataset.

For each date we evaluated the effect of distance on kinship. The ratio between the counts of full sibs or half sibs and the counts of sampled dyads for each distance class did not vary significantly with the distance. We did not find either any correlation between physical and genetic distance using variograms as implemented in ggene R package.

Discussion

Here, we attempted to estimate the effective population size of pollen beetle populations and seasonal dispersal based on kinship assignment. The proportions of full sibs and half sibs were similar and low between sites of collection at the same date but not between sampling dates. Dispersal between dates seems to be high, at 2 kilometers.

For all the sampled populations, we found a similar genetic diversity, showing there is no bias between our populations and sites, this is in agreement with results found at the regional, national and continental scales (Juhel et al., 2017c). Sibship inferences require four major assumptions about the genetic markers that are used (Jones and Wang, 2010): no departure from the HWE in the population, unlinked and selectively neutral loci, knowledge of population allele frequencies and no genotyping errors. The set of microsatellite was developed in order to conform to these four assumptions (Juhel et al., 2017c). Nevertheless, the presence of a high level of null alleles could affect the efficiency of sibling assignments.

The number of loci and their polymorphism are significant elements in the sibship assignment analysis (Jones & Wang, 2010). Here, we had only 13 microsatellite loci but they were polymorphic with a mean number of alleles of six. A higher assignment error rate of half sibs than full sibs is known in this kind of analysis (Van Horn et al., 2008). Here to avoid this bias, we performed our models 10 times and kept only dyads selected in each of the 10 repetitions. Only a small proportion of all the dyads found were selected by the 10 models but we found the same full sibs with all models, confirming the robustness of our analysis.

In the temporal models we found few related individuals whether full sibs or half sibs. This result could be explained by the high number of individuals in the populations. Indeed, we sampled around 7 500 individuals in all our samples. In a field, there are possibly 2 million of adult pollen beetles (Juhel et al., 2017c). The possible combinations of parents are huge and could explain a very small number of full sibs and half sibling dyads. The effective population size decreased with time, except for the last date, when pollen beetles returned in the OSR fields. This decrease between OSR fields in 2015 and woodlands, perhaps we found some individuals of the same clutch. We found a lower Ne in grasslands, showing that less parents were involved in the breed for the individuals caught in grasslands. The grasslands could host the individuals from the new generation which emerge from the OSR fields of 2016 and were from the same clutch but did not disperse a lot. In these fields, the Ne was higher than in grasslands and woodlands as they were a higher number of individuals potentially descendent of a bigger set of parents.

In the spatial models, the proportion of full and half sibs was highly variable. Between tents of the same OSR field, the proportion of full sibs and half siblings dyads was similar. The effective population size was also similar between tents showing that a similar number of parents was at the origin of the sibs. The pollen beetles which emerge in the same site of oviposition have different parents. The females seems to disperse their clutch. Pollen beetles females are known to lay their eggs in small groups of six eggs (Hopkins & Ekbom, 1999) and perhaps can lay these groups on diverse plant of the field. Disperse the clutch is common in nature to avoid kin competition (Godfray, 1992).

Indeed, many studies give as the maximum number of eggs produced by a *B. aeneus* female around 100 - 300 (Blunck, 1921; Scherney, 1953, Hopkins & Ekbom1999). If a female lay all it's eggs on the same plant, their sibs will destroy the plant and will not have sufficient resources to survive. Here we did not detect the groups of six siblings. Perhaps we did not genotyped enough individuals, or there is a high mortality rate in the ground. Some ground beetles were known to be their predators at this stage (Schlein, & Büchs, 2004).

Between OSR fields in June 2015, the proportion of full sibs and half sibs was similar except for the field 4, in which we found more sibs. The effective population size was also similar among these fields except for field 4 in whitch the Ne was smaller. This field was the farthest from woodlands, perhaps parents were less numerous in this fields than others, and because of that the sibs were less mixed with others. This hypothesis is probable as pollen beetles are less abundant in fields farthest from woodland than the others (Juhel et al., 2017a). This result is also confirmed by the proportion of sibs and Ne similar between OSR fields in 2016, without field far from woodlands.

Finally, two of the three grasslands, had similar proportions of half and full sibs. The last one had a higher proportion of sibs. The three grasslands had a high Ne similar to the Ne found in the OSR fields. One of the grasslands was encircled by woodlands; the emerging pollen beetles from woodlands may have been concentrated in this grassland and could stay in the grassland if there were wild brassicacea. We saw pollen beetles on *Sinapis arvensis*, a wild brassicacea and other studies confirmed we can found pollen beetles on it (Free & Williams, 1978). Another explanation could be that the individuals found in the grasslands were from the new generation which just emerged from OSR fields and have more chances to be siblings.

With the global model we found 10 dyads of full sibs distributed across time and space. These dyads were confirmed in the other models. We found dyads of full sibs in June 2015, the emerging siblings were found in the same trap but also in different fields. This could suggest that females were able to lay their eggs on different plants both within and between OSR fields. This is in agreement with the hypothesis of spread of the clutch by females. We also found one dyad within the grassland E, the same as in the local sampling, confirming the effect of woodlands as a barrier on the individuals from this grassland. Two dyads were found between OSR fields in 2015 and OSR fields of 2016, showing that individuals can travel at least 1 km between their birth place and their breeding place. We also found a pair of full sibs between a woodland tent and an OSR field of 2016 at 1 600 m. This is in agreement with the mean dispersal distance of 1 200 m found with statistical methods (Juhel et al., 2017a) and the mean distance traveled by pollen beetles between woodlands and OSR fields by capture marking recapture of 1 000 m (Taimr et al., 1967). Nevertheless, these distances are only minimums as we did not found an effect of the distance on kinship structures, up to 4 kms.

We used sibship inference to estimate pollen beetles demographic parameters within and between diverse sites from a French department, the Eure, in a context of low population genetic structure. We showed that the proportion of full sibs and half sibs between sites is stable but can be affected by the presence or absence of woodlands. The effective population sizes were similar between sites but low, suggesting a high larvae mortality. Full sibs of one generation were found at more than 2 000 m of their birth place highlighting the difficulties to manage *B. aeneus*.

Acknowledgements

We would like to thank the participating farmers, A. Butier and M. Bazot for their field work and V. Vivet for its field and lab work.

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Using the stable isotope marker C-13 to study extrafloral nectar uptake by parasitoids under controlled conditions and in the field

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Abstract: Parasitic wasps are prominent natural enemies of crop pests. They usually feed on floral resources during the adult stage (nectar, pollen, or honeydew). Extrafloral nectar is an alternative source of sugar easily accessible to adult parasitoids. We developed an original method of nectar labelling based on the injection of labelled sugar solution into the plant stem in order to analyse the nectar uptake by parasitoids (cotton wick method). This method was used to artificially enrich extrafloral cornflower, Centaurea cyanus L. (Asteraceae), nectar with the stable isotope C-13. We analysed (1) the transfer of C-13 from the sugar solution into extrafloral nectaries, (2) the uptake of labelled nectar by parasitoids under laboratory conditions, and (3) the ability of the method to discriminate, in an oilseed rape (Brassica napus L., Brassicaceae) field, between labelled parasitoids (i.e., those who have fed on labelled cornflowers located adjacent to the field) and unlabelled parasitoids to track parasitoid movements from the margin into the field. The extrafloral nectar of all test plants was C-13-labelled. Most (66%) of the parasitoids were identified as marked after 96h of exposure to labelled plants in the laboratory. We could also detect labelled parasitoids inside the field, but the detection rate was only 1%. The experiments clearly demonstrate that the cotton wick method is appropriate to label extrafloral nectar and parasitoids feeding on this labelled nectar. Further research is needed on the amount of labelled extrafloral nectar required to obtain a sufficient marker level to track parasitoid movements in the field.

Keywords : agroecosystem; flower strips; labelling method; Diaeretiella rapae ; Centaurea cyanus ; Brassica napus ; Hymenoptera ; Braconidae ; Asteraceae ; oilseed rape ; EFN

Journal: Entomologia Experimentalis Et Applicata 161, 131-140.

DOI 10.1111/eea.12495

Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes

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Abstract: Promoting the ecosystem service of crop pest biological control requires to understand the drivers of the spatio-temporal distribution of natural enemies in agricultural landscapes. In this study, we analysed the functional role of different habitat types that are widespread in mosaics of arable farmlands for three abundant weed seed-eating carabid species (*Poecilus cupreus* (L.), *Amara* similata (Gyll.) and *Pseudoophonus rufipes* (DeG.)) Carabids were sampled in an experimental design of 5 replicates for each of three habitat combinations, i.e. oilseed rape fields adjacent to winter cereal fields, oilseed rape fields adjacent to grassy field margins and winter cereals fields adjacent to grassy field margins. The effect of habitat type (crop type and semi-natural habitat), habitat management (insecticide use) and of the adjacency to a grassy field boundary on the activity-density and the nutritional state of were tested for the three species. Our results indicate that oilseed rape is of prime importance for the two spring breeders *P. cupreus* and *A. similata* in terms of activity density and nutritional state, although high levels of insecticide use had a detrimental effect on the nutritional state of individuals. Grassy field margins were used by the three species at least during the beginning of their activity period but, during the peak of activity of the two spring breeders, no positive effect of the adjacency of a grassy field boundary could be detected on the abundance and the nutritional state of individuals in the adjacent crop. Conversely, grassy field margins had a positive effect on *P. rufipes* which peak of activity occurred after crop harvest. This study highlights the importance of complementation and spillover processes in the functioning of populations living in agricultural shifting mosaics. Particular attention should thus be paid to the spatial distribution of cropping systems at various spatial scales if we are to enhance populations of organisms of benefit to agriculture.

Keywords : Carabidae; Condition factor; Activity density; Habitat quality ; Habitat ; adjacency ; Grassy field margin ; Oilseed rape

Journal: Agriculture Ecosystem & Environment 231, 183-192.

DOI : 10.1016/j.agee.2016.06.037

Projet ANR-12-AGRO-006

PEERLESS

Demographic parameters and landscape features affecting population dynamics

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Statistical inferences of the demographic parameters and landscape features affecting population dynamics
Nature du livrable	Articles
Date de publication	01/07/2016
	Version 1

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Tâche associée	tâche 4, sous-tâche 4-3
Livrables associés	D4.2 et D5.1

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

The goal of this deliverable is to develop and test statistical methods to infer ecological processes in link with landscape features in order to estimate demographic and dispersal parameters in the populations of pests and their natural enemies. The methods of inferences are based on computational approaches that optimize the parameters of a mechanistic model that simulate the population dynamics with spatio-temporal ecological observation in the landscape. The objective was to combine reaction-diffusion and integro-differential models with count or genetic data in order to analyse dispersal variations in heterogeneous landscapes.

B.2 RESUME

Maximum 1 page en français.

The deliverable is based on two published papers that used reaction-diffusion equations for modelling a species dynamics coupled with a probabilistic model to fit on observation data. The first paper used annual observations on the presence of an invasive mosquito species to estimate its diffusion in two dimensional space and along motorway corridor. The second paper used observations on captured and genotyped individuals to estimate variation of the diffusion according to landscape heterogeneities. The methodology was tested as a proof of concept on genetic data in codling moth populations from apple orchards in the Basse-Durance valley.

C PRÉSENTATION DES AVANCÉES

Two papers have been published for this deliverable:

Roques, L., Bonnefon, O., 2016. Modelling Population Dynamics in Realistic Landscapes with Linear Elements: A Mechanistic-Statistical Reaction-Diffusion Approach. PLoS ONE 11, e0151217.
We propose and develop a general approach based on reaction-diffusion equations for modelling a species dynamics in a realistic two-dimensional (2D) landscape crossed by linear one-dimensional (1D) corridors, such as roads, hedgerows or rivers. Our approach is based on a hybrid 2D/1D model, i.e, a system of 2D and 1D reaction-diffusion equations with homogeneous coefficients, in which each equation describes the population dynamics in a given 2D or 1D

element of the landscape. Using the example of the range expansion of the tiger mosquito *Aedes albopictus* in France and its main highways as 1D corridors, we show that the model can be fitted to realistic observation data. We develop a mechanistic-statistical approach, based on the coupling between a model of population dynamics and a probabilistic model of the observation process. This allows us to bridge the gap between the data (3 levels of infestation, at the scale of a French department) and the output of the model (population densities at each point of the landscape), and to estimate the model parameter values using a maximum-likelihood approach. Using classical model comparison criteria, we obtain a better fit and a better predictive power with the 2D/1D model than with a standard homogeneous reaction-diffusion model. This shows the potential importance of taking into account the effect of the corridors (highways in the present case) on species dynamics. With regard to the particular case of *A. albopictus*, the conclusion that highways played an important role in species range expansion in mainland France is consistent with recent findings from the literature.

Roques, L., Walker, E., Franck, P., Soubeyrand, S., Klein, E.K., 2016. Using genetic data to estimate diffusion rates in heterogeneous landscapes. Journal of Mathematical Biology 73, 397–422.

http://dx.doi.org/10.1007/s00285-015-0954-4

Having a precise knowledge of the dispersal ability of a population in a heterogeneous environment is of critical importance in agroecology and conservation biology as it can provide management tools to limit the effects of pests or to increase the survival of endangered species. In this paper, we propose a mechanistic-statistical method to estimate space-dependent diffusion parameters of spatially-explicit models based on stochastic differential equations, using genetic data. Dividing the total population into subpopulations corresponding to different habitat patches with known allele frequencies, the expected proportions of individuals from each subpopulation at each position is computed by solving a system of reaction–diffusion equations. Modelling the capture and genotyping of the individuals with a statistical approach, we derive a numerically tractable formula for the likelihood function associated with the diffusion parameters. In a simulated environment made of three types of regions, each associated with a different diffusion coefficient, we successfully estimate the diffusion parameters with a maximum-likelihood approach. Although higher genetic differentiation among subpopulations leads to more accurate estimations, once a certain level of differentiation has been reached, the finite size of the genotyped population becomes the limiting factor for accurate estimation.

Projet ANR-12-AGRO-006

PEERLESS

Population Dynamic model to optimize pest control

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Population dynamic model to optimize pest control
Nature du livrable	
Date de publication	15/02/2016
	Version 2

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Tâche associée	Tâche 5
Livrable associé	D5-3 et D6-1

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

The goal of this deliverable was to adapt and develop population dynamics models capable of reproducing how the landscape composition and its structure influence the population dynamics of some specific pests and of their natural enemies, and their inter-trophic level interactions.

B.2 RESUME

Maximum 1 page en français.

This note proposes a modeling approach for assessing the effectiveness of pest biocontrol by natural enemies in diversified agricultural landscapes including several pesticide-based management strategies. Our approach combines a stochastic landscape model with a spatially-explicit model of population dynamics. It enables us to analyze the effect of the landscape composition (proportion of semi-natural habitat, non-treated crops, slightly treated crops and conventionally treated crops) on the effectiveness of pest biocontrol. Effectiveness is measured through environmental and agronomical descriptors, measuring respectively the impact of the pesticides on the environment and the average agronomic productivity of the whole landscape taking into account losses caused by pests.

The effectiveness of the pesticide, the intensity of the treatment and the pest intrinsic growth rate are found to be the main drivers of landscape productivity. The loss in productivity due to a reduced use of pesticide can be partly compensated by biocontrol. However, the model suggests that it is not possible to maintain a constant level of productivity while reducing the use of pesticides, even with highly efficient natural enemies. Fragmentation of the semi-natural habitats and increased crop rotation tend to slightly enhance the effectiveness of biocontrol but have a marginal effect compared to the predation rate by natural enemies.

C PRESENTATION DES AVANCEES

The note can be downloaded from arcXiv with the following link : https://arxiv.org/abs/1602.06584.

Projet ANR-12-AGRO-006

PEERLESS

Dynamic landscape patterns for controlling pest mediated plant epidemics

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Dynamic landscape patterns for controlling pest mediated plant epidemics
Nature du livrable	Article
Date de publication	01/06/2018

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Tâche associée	tâche 5, sous tâches 5-2 et 4-3

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

To assess landscape properties that could mitigate the impacts of pests or weeds on crop production, we need to generate realistic landscapes to be used as input data to explore spatial organizations that differ from the current existing landscapes in combination with population dynamics models. In a first study, focusing on carabid population dynamics, we adapted available landscape simulation frameworks to create landscape controlling for crop plots density and shapes; and that allow to spatially distribute agronomical practices according to pre-defined rules. In a second study dedicated to annual weed species, we generated dynamical landscapes to compare landscape scenarios, varying semi-natural habitat proportion and fragmentation, in terms of weed infestation level in crops.

B.2 RESUME

Maximum 1 page en français.

Pour minimiser les impacts environnementaux et sanitaires, l'agriculture moderne devrait réduire sa dépendance aux utilisations systématiques d'intrants. Pour satisfaire aux compromis vis à vis de la production, une stratégie alternative pour une agriculture durable est de renforcer les services écosystémiques de régulation.

Le premier article décrit une approche méthodologique fondée sur les données pour proposer des réarrangements de paysages agricoles améliorant ces services. S'appuyant sur des relevés entomologiques spatialisés et des données cartographiques associées, nous avons développé un modèle de réaction-diffusion parcimonieux décrivant la dynamique des populations d'un auxiliaire des cultures. L'estimation des paramètres s'appuie sur une approche bayésienne hiérarchique intégrant le type d'observations et leurs incertitudes. Définit par un problème de satisfaction de contraintes, démarrant d'un paysage réel, un ensemble de paysages est générée en respectant les spécificités d'un paysage donnée. La population d'auxiliaire est ensuite simulée sur chaque paysage et une métrique de proxy vers le service nous permet de les ordonner. Cet ordonnancement est ensuite comparé à un trie effectué via une métrique de type proxy a-spatialisé. Comme preuve de concept, notre méthode a été appliquée à un auxiliaire carabique régulateur potentiellement important d'adventices. Ce travail met en lumière des différences dans les ordonnancements par métriques (spatialisé ou non) confirmant ici l'importance de proposer plusieurs réarrangements spatialement explicites alternatifs pour améliorer les services de régulation.

Le second article présente le développement d'un modèle de dynamique des espèces adventices annuelles à l'échelle du paysage. Le paysage support à la simulation est constitué d'un parcellaire simulé, ayant quatre types possibles d'occupation du sol qui traduisent des effets différents des pratiques sur les adventices : agriculture conventionnelle (forte intensité de traitement herbicides), agriculture biologique (désherbage mécanique et recours plus fréquent aux cultures de printemps dans la rotation), agriculture en semis direct (absence de labour) ou habitats semi-naturels (peu de perturbation mais habitat peu favorable à la germination des espèces adventices inféodées aux cultures). Associé à ce modèle, un module de génération de paysage permet de générer des paysages dynamiques (avec rotation des cultures) et de comparer des scénarios contrastés d'allocations spatiale des différentes occupations du sol sur un parcellaire donné. Avec ce modèle, nous avons étudié l'effet sur les abondances des différents types d'espèces annuelles de l'introduction d'habitats semi-naturels constitués par des prairies permanentes défavorables aux adventices (i) pour différentes proportions dans le paysage et (ii) pour différents niveaux d'agrégation spatial de cet habitat. Il apparait que les densités d'adventices annuelles dans les cultures diminuaient quand la proportion d'habitats semi-naturels mais que cet effet était particulièrement faible en comparaison avec les effets locaux liés aux cultures et aux pratiques. Par ailleurs, le niveau d'agrégation spatiale des habitats semi-naturels n'influençait pas les abondances dans les champs. Ces résultats s'expliquent d'une part par les faibles distances de dispersion des espèces adventices et d'autre part par la grande longévité des graines adventices induisant un stock de semence persistant qui tend à gommer les variations spatio-temporelles du paysage.

C PRESENTATION DES AVANCEES

Les travaux réalisés pour ce livrable correspondent à deux articles publiés :

Parisey, N., Bourhis, Y., Roques, L., Soubeyrand, S., Ricci, B., Poggi, S., 2016. Rearranging agricultural landscapes towards habitat quality optimisation: In silico application to pest regulation. Ecological Complexity 28, 1113-1122 (accepté le 10/06/16 ; document de 29 pages).

Ricci, B., Petit, S., Allanic, C., Langot, M., Parisey, N., Poggi, S., 2018. How effective is large landscape-scale planning for reducing local weed infestations? A landscape-scale modelling approach. Ecological Modelling 384, 221-232 (accepté le 26/06/18 ; document de 40 pages).

Rearranging agricultural landscapes towards habitat quality optimisation: *in silico* application to pest regulation

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Abstract

Modern agriculture suffers from its dependence on chemical inputs and subsequent impacts on health and environment. Alternatively, protecting crops against pests can be achieved through the reinforcement of regulation ecological services. Our work propounds a data-driven methodological framework to derive relevant agricultural landscape rearrangements enhancing populations of beneficial organisms regulating pests.

Building on spatialised entomological and geographic data, we developed a parsimonious reaction-diffusion model describing the population dynamics of beneficial organisms. Parameter estimation was carried out in a Bayesian framework accounting for uncertainty in the measurement.

Thousands of agricultural landscapes were generated under agronomic specifications dealt with as constraint satisfaction problems. Population dynamics was simulated on each landscape with the fitted reaction-diffusion model mentioned above, and two metrics of abundances allowed the assessment of the regulation performance of the landscape spatial arrangements. One metric is a mean field performance criterion assessing the regulation performance from the landscape composition only, the other is a spatial performance metric assessing the performance resulting from the whole landscape spatial configuration. The former is computed with a non-spatialised form of the population dynamics model, the latter results from the reaction-diffusion model of the population dynamics. Comparing these metrics enabled to quantify the impact of spatial arrangements, hence allowing arrangements proposals.

This framework was applied to the case study of a ground beetle species involved in the biological regulation of weeds. The arrangement proposals abides by the productive agronomic constraint that is the

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landscape composition, while they allow for significant habitat quality enhancement (as well as deterioration) for the beneficial organism. Minor adaptations of our integrated data-driven approach would suit numerous situations ranging from the provision of enhanced ecosystem services to land management for conservation.

Keywords: population dynamics; landscape management; reaction-diffusion model; ecological intensification; crop protection; conservation biological control

2010 MSC: 35Q92, 92D25

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1. Introduction

A main concern in modern agriculture lies in reducing its dependence on chemical inputs and limiting its impact on health and environment. Alternative strategies for a sustainable agriculture converge towards the reinforcement of ecological processes suitable to protect crops against pests. Landscape has been described as a relevant scale to manage most pests and airborne plant diseases as numerous studies have highlighted the link between landscape complexity and biological control (Thies & Tscharntke, 1999; Bianchi & Van der Werf, 2003; Tscharntke et al., 2007; Chaplin-Kramer et al., 2011). Developing ecologically based agricultural production systems requires to identify and understand key pest suppression drivers. In particular, it is crucial to understand how the spatial configuration of landscape features impacts the dynamics of natural enemies and thus potential biological regulation services (Bianchi & Van der Werf, 2003). In this regard, rearrangement of the landscape in terms of habitat structure might efficiently contribute to pest regulation.

Habitat management, that aims at conserving or enhancing beneficial organisms, can potentially improve pest management (Landis et al., 2000). Also, Jonsson et al. (2010) reviewed how habitat manipulation has improved biological control of invasive pests over the years 1998-2009, and discussed under what circumstances different types of habitat management are likely to be effective, and how the likelihood of success can be improved. Yet, most of the cited experiments had been conducted at a local scale (*e.g.* field scale). Studies at the landscape scale are rarer (SESAME, 2015), notably due to the difficulty to experiment at such spatial scale, thus emphasising the relevance of developing frameworks that enable *in silico* experiments.

Indeed, although landscape-scale effects on pest natural enemies in agroecosystems are numerous, as evidenced by many studies (Gámez-Virués et al., 2012; Veres et al., 2013), the underlying mechanisms are only partially known. In particular, we still have a limited understanding of the optimality in spatial and temporal arrangements of habitat structures, and even less of the management measures required to improve biological control (Gámez-Virués et al., 2012). Despite some recent papers heading towards that direction (Jonsson et al., 2014), landscape planning applied to agricultural landscape has not become a standard tool against pests and diseases. As a whole, landscape planning addresses the integrated analysis of land-use change in relation to socio-economic and biophysical driving factors (Verburg et al., 2002; Polasky et al., 2008).

In our study, we propose a data-driven methodological framework to derive apposite agricultural landscape rearrangements that might enhance pest regulation. As such, our framework is intended to be part of a landscape planning process coerced with other requirements and concerns, *e.g.*, for multiple pest dynamics or socio-economic factors. Our incentive is that, in order to cope with possible trade-offs between ecosystem services, we should (i) capture spatial dependencies of ecological processes underlying a given service and (ii) be able to provide many acceptable solutions, *i.e.* landscape rearrangements, enhancing the service under consideration. We addressed the first point by fitting a parsimonious, mechanistic and spatially explicit population dynamics model to observation data. Such a flexible tool allows to explore the effects of landscape management scenarios on the insect population and its seasonal field colonisation process. Secondly, combining a search heuristic and a constraint satisfaction problem, we generated candidate landscape rearrangements that abide by landscape composition constraints. Combining these two elements, we investigate the effects of the spatial configurations, looking for the best land-cover arrangements for each given composition (*i.e.* setting aside the non-spatial effects of the land-cover proportions). The initial conditions of the mechanistic model were assessed from field observations. We then investigated the effects of spatial arrangements on pest regulation conditionally on these agronomic constraints.

We demonstrate the relevance of our data-driven approach by applying it to the case study of carabid beetles, an arthropod family involved in weed regulation through seed predation (Bohan et al., 2011) and that has been shown to depend both on local (*i.e.* field) and landscape characteristics (Trichard et al., 2013; Labruyere et al., 2015).

2. Materials and methods

2.1. Study area and experimental data

2.1.1. Study area and landscape characterisation

The study area (Fig. 1) consists in an agricultural landscape of approximately 130 km^2 located in north-western France (origin at 48° 29' N 1° 34' W.). This area, called "Zone Atelier Armorique" (ZAA), belongs to the International Long Term Ecological Research Network (ILTER, 2015) and, as such, its land-use has been assessed every summer over the last 25 years using aerial photographs, field observations and manual cartography. It is characterised by a SW-NE gradient of landscape structure—from hedged farmland, woodlands and permanent grasslands, to open fields (see Baudry et al. (2000) for more details). In 2010 (the season under study here), the ZAA comprised 36% grasslands, 38% cultivated areas (essentially wheat and corn in summer), 14% woodland, and the rest corresponded to roads and built areas. As it will be made explicit later, we focused our investigation on two sub-domains of the ZAA, hereafter referred to as Ω_1 and Ω_2 (Fig. 1), spanning respective areas of 3 km^2 and 2.3 km^2, and mapped at a 10-meter resolution. In 2010, the landscapes Ω_1 and Ω_2 were characterised by 37% (resp. 54%) of grasslands, 47% (resp. 31%) of cultivated areas and 7% (resp. 5%) of woodland.

2.1.2. Sampling design of entomological data

The activity-density of carabid beetles was assessed using pitfall traps installed in 25 agricultural fields spread across the whole study area. In each sampled field, 3 pitfall-traps were set at random places within crop limits. Experiments were then carried out during five weeks between the 6th of May and the 8th of July 2010 resulting in the monitoring of 75 traps. At the end of each week, trapped carabids were removed, identified and counted. Around 17000 individuals from more than 70 carabid species were thus identified in 2010. Stating the trade-off between the weed seed predation ability (Bohan et al., 2011) and the relative species abundance in the region under study (Al Hassan et al., 2013), we focused on the species *Poecilus cupreus* (L.). Although this species is omnivorous with a relatively low individual rate of seed consumption, it is still a potentially high contributor to weed seed regulation given its high level of abundance in agricultural fields (Petit et al., 2014). Each of the selected sub-domains Ω_1 and Ω_2 comprised 12 pitfall-traps located in 4 fields. These landscapes were chosen *a posteriori* for their pitfall-traps affluence. Indeed, while their cumulated surface represented only 4% of the study area, they provided a third of the collected data.

2.2. Parsimonious spatially explicit models of population dynamics

Reaction–diffusion models have been widely used in ecology and evolution for a long time (Fisher, 1937; Turing, 1952) and they provide an appropriate framework for studying many agroecosystem processes from pest outbreaks (Ciss et al., 2013; Soubeyrand & Roques, 2014; Bourhis et al., 2015) to conservation (Cantrell & Cosner, 2003; Berestycki et al., 2005; Pereira & Daily, 2006; Roques & Hamel, 2007). To capture the dynamics of carabids, we derived a simple model in line with *P. cupreus* life cycle in the studied region. This species is univoltine, *i.e.* it has one generation per year and therefore exhibits a single peak during its activity season (see Fig. 2 for the seasonal population measurements). It is also known to react differently to crop and non-crop habitat types (Marrec et al., 2015), in this case semi-natural habitats, grasslands and cereal fields. We also considered the first trapped carabid adults to be a good proxy for a previous small and stable population emerging from overwinter a few days before the first trapping.

Thus, the model for a population density $P(x, y, t)$ in a spatial domain Ω_i $(i \in \{1, 2\})$ representing a sub-domain of the study area (ZAA) writes for any $(x, y) \in \Omega_i$ and $t > 0$:

$$\frac{\partial P(x,y,t)}{\partial t} = D\Delta P(x,y,t) + P(x,y,t)r(x,y)e^{-\beta t} - \mu P(x,y,t), \tag{1}$$

with a growth rate at $t = 0$

$$r(x,y) = \begin{cases} r_C \text{ if } (x,y) \text{ in a crop field} \\ r_S \text{ if } (x,y) \text{ in a semi-natural habitat} \\ r_G \text{ if } (x,y) \text{ in a grassland} \\ 0 \;\; \text{otherwise} \end{cases}$$

Here, $\Delta = \partial_{xx} + \partial_{yy}$ is the two-dimensional Laplace diffusion operator. This operator describes the uncorrelated random walk movements of the individuals. This means that the individuals travel at random, with no drift in any particular direction; the diffusion coefficient D measures the mobility of the individuals (for general results on reaction-diffusion models, see Grindrod (1996); Shigesada & Kawasaki (1997); Turchin

(1998); Murray (2002); Roques (2013)). The parameter $\beta > 0$ measures the exponential speed at which the birth rate decays during the activity season, and the parameter μ is the death rate; in other words, $\mu = 1/\text{life expectancy}$.

We assumed reflecting (*i.e.*, Neumann) boundary conditions, which mean that either the individuals crossing the boundaries are reflected inside the domain or the inward and outward fluxes are equal at the domain boundaries. The mathematical formulation of these boundary conditions is: $\frac{\partial P(x,y,t)}{\partial \boldsymbol{n}}\Big|_{\partial\Omega_i} = 0$, where $\boldsymbol{n}$ is a unit vector normal to the frontier $\partial\Omega_i$.

The initial time $t = 0$ corresponds to the day of the first observation. The initial conditions are based on the number of individuals trapped during the week preceding the first observation, that we denote by $Q(\boldsymbol{x}_i, 0)$ at each census point $\boldsymbol{x}_i$. Assuming a constant population density $P(x, y, t)$ during the first week $t \in (-\tau, 0)$, we can derive a relationship between $P(\boldsymbol{x}_i, 0)$ and $Q(\boldsymbol{x}_i, 0)$:

$$Q(\boldsymbol{x}_i, 0) = \alpha\tau P(\boldsymbol{x}_i, 0), \tag{2}$$

where τ is the time between the beginning of the experiment and the first observation and $\alpha \sim 10^{-4}$ is the surface ratio of a trap over a space discretisation (the traps are supposed to be non-attractive).

Using an Inverse Distance Weighting (Press et al., 2007), the initial population density can then be interpolated over the whole spatial domain:

$$P(\boldsymbol{x}, 0) = \frac{\sum\limits_{i=0}^{N-1} Q(\boldsymbol{x}_i, 0)\phi(\|\boldsymbol{x}_i - \boldsymbol{x}\|)}{\alpha\tau \sum\limits_{i=0}^{N-1} \phi(\|\boldsymbol{x}_i - \boldsymbol{x}\|)}, \text{ for } \boldsymbol{x} \neq \boldsymbol{x}_i, \tag{3}$$

with $\phi(d) = d^{-\rho}$ and $d = \|\boldsymbol{x}_i - \boldsymbol{x}\|$. N is the number of population census points, $\boldsymbol{x}_i$ the location of each census point, $\boldsymbol{x}$ each location of the discretised space and $\tau = 5$ days, the traps opening duration. The parameter ρ was determined by means of a cross-validation procedure (Press et al., 2007; Borra & Di Ciaccio, 2010). Remaining parameters from equation (1), namely D, β, μ, and $r(x, y)$ were estimated using a mechanistic-statistical framework as described below.

2.3. Parameter estimation in a heterogeneous landscape

State-space models offer an efficient framework to link process models and observation processes (Clark, 2004). They have become a widespread approach to link mechanistic population dynamics with statistical methods for inference (Soubeyrand & Roques, 2014; Hostetler & Chandler, 2015; Beeton et al., 2015). They combine the flexibility of modelling mechanistic ecological processes with the ability to exploit the information within field data while tackling with observation uncertainty.

For the purpose of inferring the parameters $\boldsymbol{\theta} = (r_C, r_S, r_G, D, \mu, \beta)$ from equation (1), we applied a mechanistic-statistical approach where (i) the prediction for the species activity-density is computed from numerical simulations of the model described in (2.2) (using the same numerical scheme as in Bourhis et al. (2015)), and (ii) the observed abundances of *P. cupreus* within pitfall-traps are random variables which depend on the population density.

We modeled the trapping process with a probabilistic approach. First, we computed the expected number of trapped individuals at each trap location $\boldsymbol{x}_i$ and each observation time t_j, given the population density $P_{\boldsymbol{\theta}}$ (we use the notation $P_{\boldsymbol{\theta}}$ for the population density P to emphasise the dependence of P with respect to the set of parameters $\boldsymbol{\theta}$):

$$\overline{Q}_{\boldsymbol{\theta}}(\boldsymbol{x}_i, t_j) = \alpha \int_{t_j-\tau}^{t_j} P_{\boldsymbol{\theta}}(\boldsymbol{x}_i, t)dt, \tag{4}$$

where the integration over time represents the duration of the weekly openings of the traps during $\tau = 5$ days (from Monday to Friday; traps were closed for week-ends). Second, we assumed that the number of individuals trapped during the previous τ-day period followed a Poisson distribution with the expected number of trapped individuals as mean value:

$$Q(\boldsymbol{x}_i, t_j) \sim \text{Poisson}\left\{\overline{Q}_{\boldsymbol{\theta}}(\boldsymbol{x}_i, t_j)\right\}. \tag{5}$$

As the individuals are removed at each observation time, the random variables $Q_{\boldsymbol{\theta}}(\boldsymbol{x}_i, t_j)$ conditional on the population densities $P(\boldsymbol{x}_i, t)$ for $t \in (t_j - \tau, t_j)$ can be considered as independent observations. We can then compute the likelihood function:

$$\mathcal{L}(\boldsymbol{\theta}) = p(Q|\boldsymbol{\theta}) = \prod_{j=1}^{J}\prod_{i=1}^{I} e^{-\overline{Q}_{\boldsymbol{\theta}}(\boldsymbol{x}_i,t_j)} \frac{\overline{Q}_{\boldsymbol{\theta}}(\boldsymbol{x}_i,t_j)^{Q(\boldsymbol{x}_i,t_j)}}{Q(\boldsymbol{x}_i,t_j)!}, \tag{6}$$

where J is the number of observation times and I the number of traps.

Finally, we used a Markov chain Monte Carlo (MCMC) algorithm for inference (Roques et al., 2011) over sub-domains Ω_1 and Ω_2, choosing non informative uniform priors for all parameters. This algorithm computes the likelihood of the parameters sets depending on the agreement between the model predictions and the field observations. Maximising the likelihood, the MCMC converges towards the more likely parameters set, which is used for the subsequent simulations. The geomatic and population data of both domains were used to ensure an efficient parameters identification.

2.4. Proxies for pest regulation efficiency in spatial and non-spatial contexts

In view of predicting the outcome of agroecosystem rearrangements, we defined a metric characterising the regulation potential of the beneficial organism: the integral of population P over time (*i.e.* along the course of the activity season) and space (*i.e.* one spatial sub-domain: Ω_1). This metric is a proxy for the habitability (embedding indistinctly survival and reproductive efficiency) of a given landscape for the beneficial organism and hence, a proxy for the pest regulation efficiency. In order to assess the impact of the spatial configuration of a landscape being given its composition, we also needed the equivalent of a "null model". We thus defined a mean field model (Morozov & Poggiale, 2012), comparable to our previous population model, as such: given p_k the proportion of the cultural type k ($k \in \{C, S, G, O\}$ and $\sum p_k = 1$, with C, S, G, O respectively standing for *Crop*, *Semi-natural*, *Grassland* and *Other* land-covers) and r_k the associated growth rate we have

$$\frac{dP(t)}{dt} = P(t)\sum_k p_k r_k e^{-\beta t} - \mu P(t), \tag{7}$$

hence

$$P(t) = P(0)\exp\left(\frac{1}{\beta}(1-e^{-\beta t})\sum_k p_k r_k - \mu t\right). \tag{8}$$

So, for the set of population parameters $\boldsymbol{\theta} = (r_C, r_S, r_G, D, \mu, \beta)$, the mean field performance criterion (MFP) simply writes:

$$MFP = \int_t P(t)dt. \tag{9}$$

It only depends on land-cover proportions that form the landscape composition, while the spatial performance criterion (SP), depending on the composition and spatial organisation of the landscape, writes:

$$SP = \int_t \int_x \int_y P(x, y, t)dxdydt. \tag{10}$$

2.5. Pest regulation performances of the spatial arrangements

Manipulating landscapes can rely on several kinds of operation. Agricultural landscapes can be altered in the spatial configuration of their land-cover units (through crop rotation), or in the shape and size of these units (through fields merging or splitting). One can also simply modify the landscape composition (*i.e.* the land-cover proportions), or combine those operations to result in further alternative topologies. Here we consider the topology of a landscape as an emerging property resulting from the structure (*sensu* polygonal meshing), the composition and the spatial configuration of the different land-covers impacting the process under study (here, the population dynamics).

In this study, we defined a simple crop allocation problem (CAP) where, starting with the landscape Ω_1, we considered its structure as immutable and focused on crop rotations to alter its topology. We first explored the local compositions throughout the study area (ZAA), focusing on 60 landscapes of 1 km^2 from which we computed the compositions in crops and grasslands. This way, we derived 60 realistic sets of land-cover proportions. Through sequential crop rotations, these compositions were applied on the polygonal meshing of Ω_1 by reassigning the land-covers of arable lands (*i.e.* crops and grasslands; woodlands, built areas and the hedgerows network were left unchanged).

Having defined a CAP, we treated it as a decision-making problem (Akplogan et al., 2013) and we proposed a simple yet robust Constraint Satisfaction Problem (CSP) (Russell & Norvig, 2009) approach to solve this. A CSP is a triplet $(\mathcal{X}, \mathcal{D}, \mathcal{C})$ where :

- $\mathcal{X}$ is a finite set of variables, $\{X_1, \ldots, X_n\}$.

- $\mathcal{D}$ is a finite set of domains, $\{D_1, \ldots, D_n\}$, one for each variable. Each domain D_i consists of a set of allowable values, $\{v_1, \ldots, v_k\}$ for variable X_i.
- $\mathcal{C}$ is a set of constraints that specify allowable combinations of values.

To translate our CAP into a CSP, we defined a set of variables $\mathcal{X} = \{X_1, \ldots, X_n\}$ representing fields (polygons of arable lands) forming the landscape. The corresponding land-cover choice for each variable is a domain $D_i = \{C, G\}$, C means crop allocation while G means grassland allocation. One can note that we worked here on a subset of the k possible land-covers, using only those commonly available for crop rotations (*i.e.* crops and grasslands) which, here, were associated with the highest estimated growth rates for *P. cupreus* (see 3.1). Function $S(X_i)$ returns the area of the field X_i normalised on the total area of arable lands (*i.e.* available for crop rotations). The set of constraints $\mathcal{C}$ was defined so that:

$$\begin{aligned} (1-\epsilon) * p_C^{target} &\leq \sum_{i \text{ s.t. } X_i = C} S(X_i) \leq p_C^{target} * (1+\epsilon), \\ (1-\epsilon) * p_G^{target} &\leq \sum_{j \text{ s.t. } X_j = G} S(X_j) \leq p_G^{target} * (1+\epsilon), \end{aligned} \tag{11}$$

where ϵ is a tolerance threshold ($\epsilon = 10^{-2}$), and ($p_C^{target}, p_D^{target}$) are the desired proportions of crops (C) and grasslands (G) in the landscape.

A solution to our CSP is a consistent (*i.e.* all constraints are satisfied) and complete assignment (*i.e.* every field has a land-cover). This numerical optimisation problem was solved using a genetic algorithm with a population size of 500 individuals (*i.e.* 500 landscapes here). Optimisations were considered successful (and stopped) when at least a third of the population found a solution to the CSP. Subsequently, for each of the 60 optimisations (1 optimisation per set of land-cover proportions), few hundreds of different landscapes were expected to fulfil the compositional requirements.

In order to assess the impact of the topologies produced on the Ω_1 structure we compared the two metrics defined in §2.4:

- the mean field performance criterion (MFP), proxy towards the mean fitness of the carabid population computed on a mean field simulation of the population dynamics model depending only on composition (*i.e.* the land-cover proportions),

- the spatial performance criterion (SP) which has the same meaning but is derived from the spatialised simulation and is therefore impacted by the topology.

The MFP criterion was computed on every set of land-cover proportions (*i.e.* 60 computations), while the SP criterion was computed for every generated landscape (*i.e.* 60 × few hundreds computations). Therefore, each value of the MFP criterion is compared to a distribution of values of the SP criterion. Comparing those two metrics offers a quantification of the topology effect on the population density $P(x, y, t)$ of beneficial organisms, and hence on the putative pest regulation service.

3. Results

3.1. Parameter estimation in a heterogeneous landscape

All the posterior distributions of model parameters were greatly different from the priors. Reasonably satisfying chains convergence was attested by the multivariate potential scale reduction factor (PSRF) $\hat{R} = 1.11$ (Brooks & Gelman, 1998). We used the median values (reported in Table 1) of the parameter posterior distributions for subsequent simulations in this study. Using these punctual values instead of the whole posterior parameters estimates was consistent regarding their low dispersion tendencies (*cf.* the 95% confidence intervals in Table 1). These parameters lead to a viable coefficient of determination $r^2 = 0.53$ when comparing the model predictions with the mean abundances in pitfall-traps at each sampling date on sub-domains Ω_1 and Ω_2. Figure 3 shows the simulation of the population density at 5 sampling dates (see online Supplementary Materials for a video of this simulation). The estimated growth rates were consistent with the habitat preferences of *P. cupreus* which is known to be a cultural beetle (Thiele, 1977). The diffusion parameter was also in agreement with the rare mobility measurements encountered in the literature (Allema et al., 2012) for very similar species.

3.2. Pest regulation performances of the spatial arrangements

In the non-spatial context (*i.e.* mean field model), the simulated regulation efficiency only depends on the proportions and quality of the different habitat types, expressed here in terms of land-cover dependent growth rates. Table 1 ranks crops as the most favourable habitat ($r_C = 2.14$), followed by grasslands ($r_G = 1.64$), and hedges ($r_S = 0.68$), all other land-covers (mostly represented by woodlands and built areas) being assigned a null growth rate. Therefore, the landscapes containing more crop surfaces are expected to be the most highly populated, at least in a non-spatial context. As aforesaid, this ranking is consistent with the known preferences of *P. cupreus* for cultural habitats (Thiele, 1977).

The land-covers of Ω_1 were reassigned sequentially to reach the 60 sets of proportions of crops and grasslands, keeping the original tessellation (the polygonal meshing) as immutable as well as the hedgerows network. As previously mentioned, the Constraint Satisfaction Problem (CSP) was solved by a genetic algorithm (GA) with a population size of 500 individuals (*i.e.* landscapes here). The stopping condition of the GA optimisation was reached when at least a third of the population felt within a $\pm 1\%$ interval around the 60 sets of proportions. Only 4 optimisations out of 60 failed to reach this threshold. For each of the remaining set of compositions, between 231 and 314 landscapes answered successfully to the CSP with alternative configurations. Consequently, the population dynamics model was simulated 15988 times, on 15988 different landscapes.

All the performances values were normalised over the initial performances of the original Ω_1 landscape. Figure 4 displays the landscapes spatial performances (SP) as a function of the mean field performance (MFP) of their respective set of compositions. Both performances strongly correlated with the crops and grasslands proportions figured here by the gradients of respectively sizes and colors of the circles. The variability around the mean SP appears fairly important, which is highlighted by the black dots indicating the best (above the circles) and worst (below the circles) spatial arrangements. The original landscape's performances (the red cross) occur to be very standard, with a rather poorly performing spatial arrangement.

Figure 5 shows the best, mean and worst spatial arrangements (assessed by the SP metric) encountered for 3 contrasted compositions (best, central and worst MFP). From left to right, the colour gradient from green to yellow distinctly reflects the composition shift inducing the MFP improvement. We found no obvious and apparent gradient explaining the change in the spatial performance (*i.e.* along each column in Figure 5). Shedding light on any relationship between topology and spatial performance would call for a complementary analysis which is beyond the scope of this study.

4. Discussion

Promoting a sustainable agriculture calls for innovative strategies relying on ecological intensification (Wezel et al., 2014). Landscape has been evidenced as a relevant scale to address such challenge and, in particular, habitat manipulation at the landscape scale appears as a promising lever for conservation biological control (Landis et al., 2000; Woltz et al., 2012; Gámez-Virués et al., 2012). In this study, we propose a methodological framework to investigate and quantify the effect of landscape rearrangements on the pest regulation ecosystem service. To demonstrate its relevance, we applied it to the case study of a carabid beetle, a relevant natural enemy family, notably for the biological regulation of weeds (Bohan et al., 2011).

For this purpose we defined two simple metrics as proxies for pest regulation efficiency. The mean-field performance (MFP) assess the performance based solely on the landscape composition (proportions of crops, grasslands, woodlands and built areas), which is known to influence the activity-density of carabidae (Gardiner et al., 2010). Besides, the spatial performance (SP) appraises the performance taking the spatial organisation of land-covers into account, given the composition. These metrics directly rely on georeferenced data informing the activity-density of the beneficial ground beetle. They integrate a population dynamics model describing the mechanisms underpinning the ecosystem service under consideration. Interestingly, as this approach supports ecosystem services assessments by a mechanistic understanding of the relationships between drivers and services, it allows the consideration of multiple ecosystem services simultaneously (Bennett et al., 2009).

Our framework includes a search heuristic to explore numerous spatial organisations of land-covers satisfying agronomical constraints (*i.e.* here constraints on the landscape composition), providing candidate landscapes that improve the SP metric. This provides a set of solutions to stakeholders and decision makers. Being given the complexity of the landscape, the performance global optima are very unlikely to be identified. Moreover, as the performance is assessed *a posteriori* on the landscapes, their generation by the genetic algorithm is a blind process only heading towards the suitable compositions. Nevertheless, the solutions appear to provide significant improvements of the spatial performance (see Fig. 4). The ability to provide numerous good solutions instead of the only best one appears as one of the strength of the framework. As every ensuing landscape management decision would be made accounting for other constraints (being ecological or not), providing some degree of freedom with the solutions seems mandatory to us.

The mechanistic model of our framework embed habitat quality by means of a spatialised growth rate. This is a common approach (Okubo, 1980; Shigesada & Kawasaki, 1997; Kinezaki et al., 2010; Soubeyrand & Roques, 2014). Although it is apparently simplistic, it reveals itself as sufficiently responsive to catch an important part of the spatial complexity of the agricultural landscape and to result in contrasted population dynamics. As shown in Fig. 4, a given landscape composition can give rise to a diversity of spatial arrangements, and ensuing pest regulation performances. Here, arrangements were generated by means of a search heuristic (the genetic algorithm) and the landscapes habitability for the beneficial ground beetles was assessed *a posteriori* with a deterministic population dynamics model. For some compositions, the spatial arrangements resulted in a 50% spatial performances (SP) variation (between the best and the worst SP), while the mean SP variation for the 56 compositions exceeded 30%. These are very significant contrasts, especially when compared to the ±1% each specific arrangement was allowed to vary around its targeted composition. Those variations are symmetrical and either improving or declining the global habitat quality seems in the range of the framework. While we focused here on improving the habitat quality of a beneficial organism, the habitat degradation can nonetheless be an interesting objective when applied directly on a pest population.

Several theoretical works on reaction-diffusion models have focused on the optimal arrangements of habitat for species conservation or resilience to external perturbations (Berestycki et al., 2005; Roques & Chekroun, 2007; Roques & Hamel, 2007). All of these works demonstrate that the optimal landscape arrangement is a compromise between lessening the detrimental habitat edge effects—which means that the perimeter of the most suitable habitat (the crops in the current study) has to be minimal—and taking advantage of the domain boundary (in the case of reflecting boundary conditions). Thus, the optimal arrangement of the landscape should look like a quarter of disc, concentrated in a corner of the domain. In the current study, the main difference with the previous approaches is that we do not focus on a specific metric of species conservation, but rather on cumulated population size, and we consider time-dependent mortality rates. Because of these assumptions, the initial conditions, which had no effect on the results of the above-mentioned theoretical studies, play a critical role here. Here, the initial conditions can been seen as an additional agronomic constraints resulting from the previous seasonal population dynamics (year $n-1$) and impacting the landscape spatial performance (year n). They need to be accounted for to efficiently dispose land-covers across the landscape. As shown in Fig. 5, the mean field performance is solely a matter of composition which is obviously rendered by the horizontal colour gradient. On the other hand, this figure fails to depict the source of the SP discrepancy that we know occurs along the vertical gradient. The possibly numerous causes of such discrepancy are likely to be complex polygonal structures, resulting in significant topological effects. Given that we are dealing with an initial value problem (*i.e.* our spatial population dynamics model), it is plausible, as expressed above, that this sensitivity to landscape topology is linked to spatial heterogeneity of initial conditions. In further work, a sound landscape analysis *via* Landscape Pattern Indices (LPI, see *e.g.* Riitters et al. (1995); Leitao et al. (2006)) might help shedding some light on the performances of the emerging topologies. In addition, there are also available tools (Rubner et al., 2000; Potts et al., 2014) that would enable us to assess these landscape performances given strong mechanistic hypothesis (*e.g.* initial condition sensitivity).

We believe that all sub-parts of this framework might be refined depending on the research question and the knowledge of the system under study. For example in our case we built a simple and parsimonious population dynamics model and inferred parameters from entomological georeferenced samples (activity-density collected in traps). Additional mechanisms can be considered (*e.g.* genetic processes) and the observation process can be adapted to different kinds of data (*e.g.* presence/absence or relative occurrence rate) and/or several kinds of observation (*i.e.* heterogeneous data).

Overall, objectives for close future research are twofold: (i) better integrate anthropic effects, *e.g.* by considering land-use instead of land-covers in order to take cultural practices into account, which are known to affect the natural enemies at the landscape scale (see *e.g.* Puech et al. (2015)), (ii) understand the nature of the topological effect on our simple population dynamics model in order to alter the topology (by means of a set of spatial operations on the landscape), not only the spatial organisation of land-covers.

5. Acknowledgments

This research was funded by the ”Sustainable Management of Crop Health” INRA metaprogramme, the PAYOTE INRA network, and two French ANR projects ”Landscaphid” (ANR-09-STRA-05) and ”Peerless” (ANR- 12-AGRO-0006). The authors are also grateful to Zone Atelier Armorique for providing access to experimental facilities and GIS data, Jonathan Potts for usefull scientific inputs and the ModStatSAP INRA network for insightful methodological assistance.

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6. Table

Parameters	Values	SD	CI 95%	Units
ρ	1.12	-	-	-
r_S	0.155	0.0304	(0.154, 0.156)	day^{-1}
r_G	0.304	0.0212	(0.303, 0.305)	day^{-1}
r_C	0.385	0.0174	(0.385, 0.386)	day^{-1}
β	0.123	0.0105	(0.122, 0.123)	-
μ	0.210	0.0181	(0.210, 0.211)	day^{-1}
D	76.1	7.11	(75.7, 76.4)	$\text{m}^2.\text{day}^{-1}$

Table 1: Median estimates of the model parameters obtained with a MCMC procedure. The parameter ρ related to the interpolation of initial conditions (Equation 3) was identified by cross-validation. Simulations in Figure 3 rely on this set of parameter estimates.

7. Figures

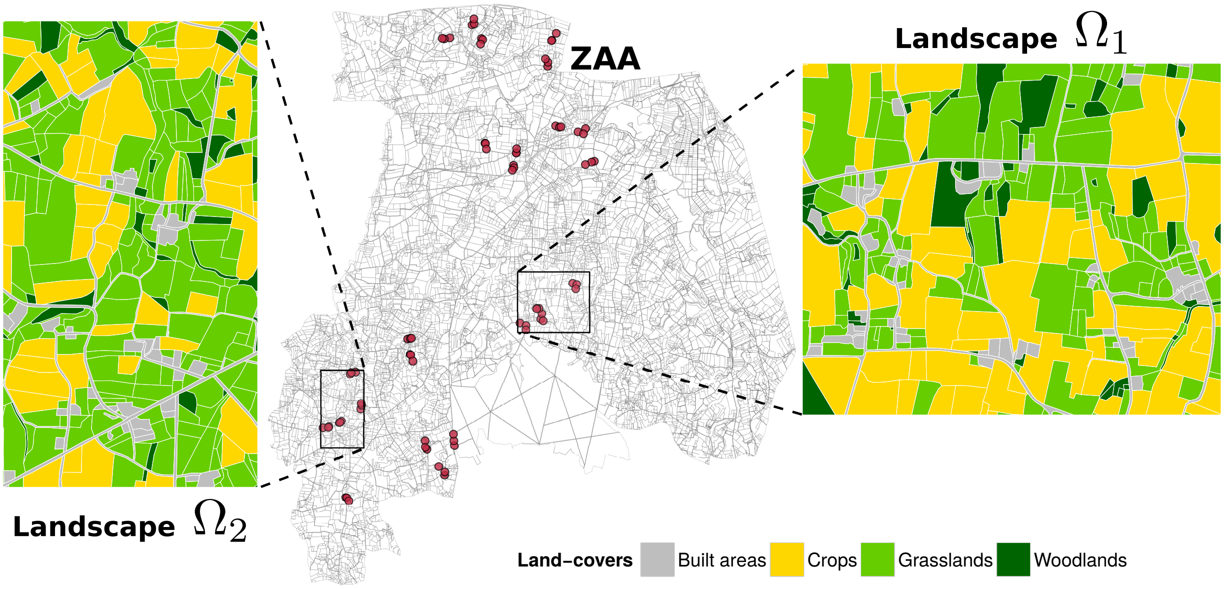

Figure 1: Map of the study area showing the locations of the sampled fields (red circles), the sub-domains under investigation (Ω_1 and Ω_2) and the land-covers of interest (colour legend).

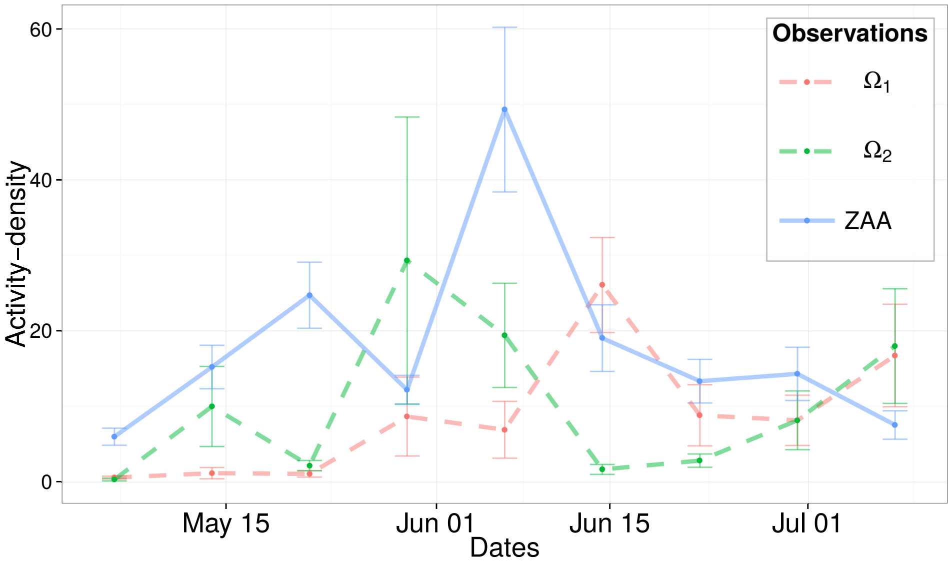

Figure 2: Activity-density of carabids (*P. cupreus*) trapped over the full study area (ZAA), and sub-domains Ω_1 and Ω_2.

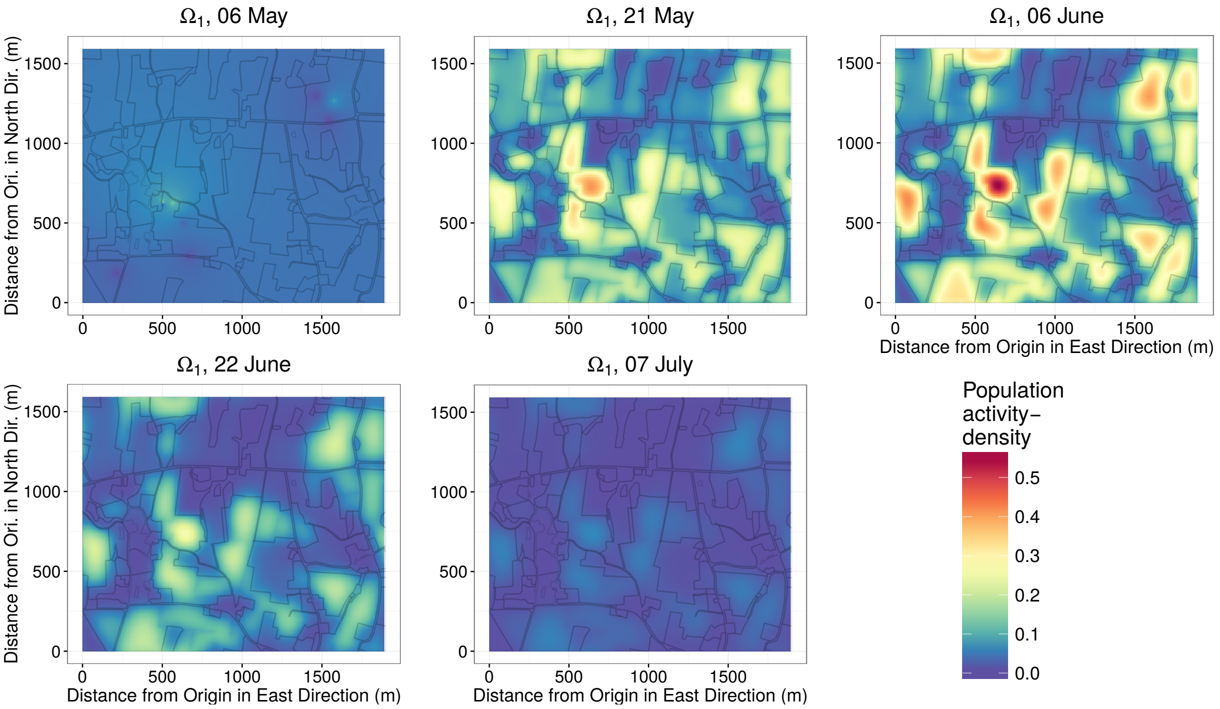

Figure 3: Simulation of the dynamics of the density of *P. cupreus* carabid population in the sub-domain Ω_1 obtained with the model (1) and parameter values in Table 1.

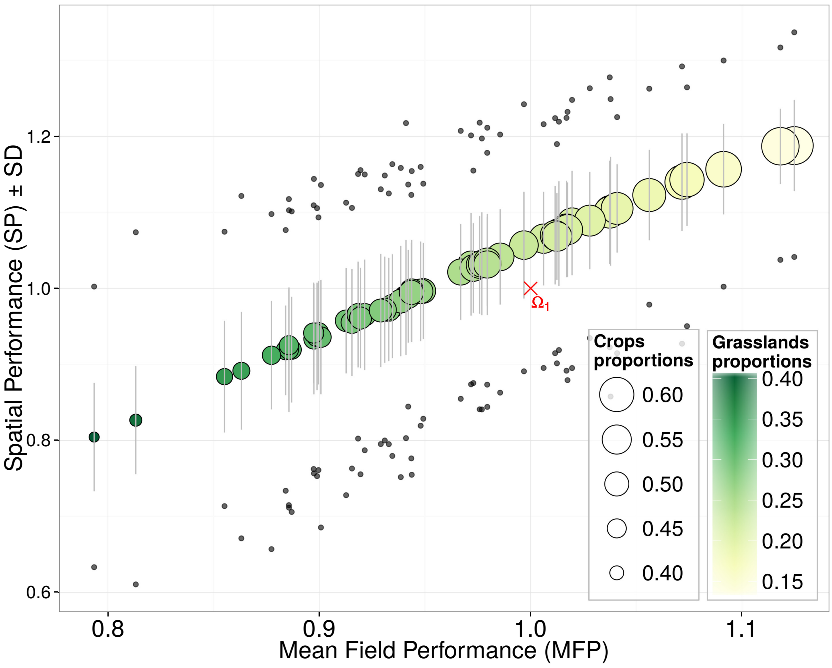

Figure 4: The spatial performances (SP) of the 15988 landscapes (in ordinate) is reported over the mean field performance (MFP) of their respective compositions (in abscissa). The 56 circles represent the mean SP with the grey segments figuring the standard deviation of SP, and the black dots point the extreme values. Both metrics are normalised over the performances of the original landscape Ω_1, pointed here by a red cross. The gradients of crops and grasslands proportions are respectively figured by the circles sizes and colours.

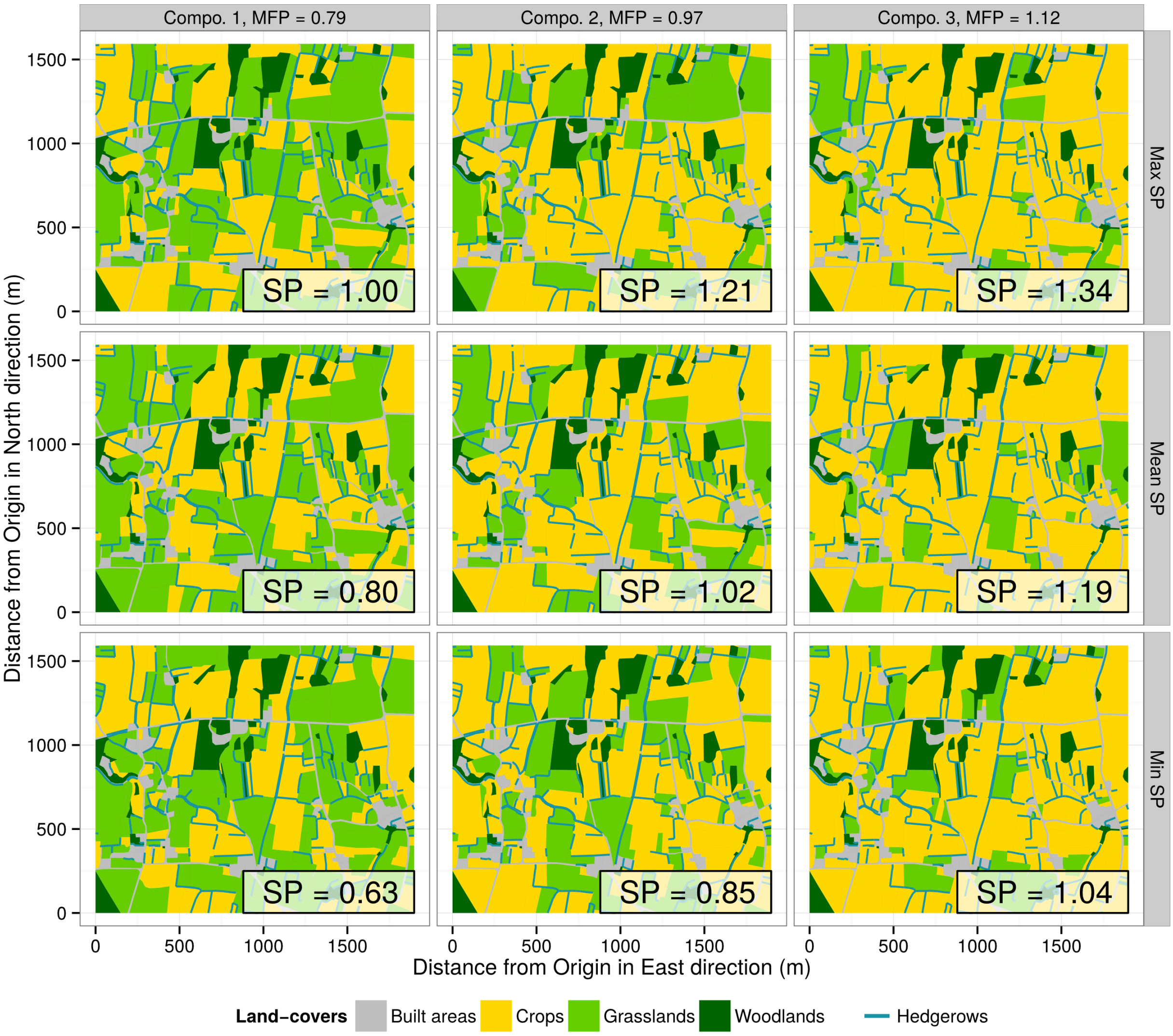

Figure 5: Representation of 9 of the 15988 generated landscapes taken from 3 different compositions. From left to right: the worst, central and best landscape mean-field performance (MFP). For each composition, from top to bottom: the best, mean and worst landscape spatial performance (SP). Origin $(0, 0)$ is located at 48° 29' 21" N 1° 34' 3" W.

How effective is large landscape-scale planning for reducing local weed infestations? A landscape-scale modelling approach

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Abstract

Finding efficient and environmentally sustainable methods for arable weed management is a current challenge in agroecosystems. Weed species disperse over scales larger than the field. Landscape-scale management could, therefore, reinforce field-scale strategies for innovative cropping systems. In particular, the introduction of semi-natural habitats, such as permanent meadows, which are unsuitable habitats for annual arable weeds, could potentially reduce weed densities in crops. We developed a spatially explicit, landscape-scale model of annual arable weed population dynamics including the main components of weed management at cropping system level: crop rotation, tillage regime, intensity of herbicide use and mechanical weeding. The variability of responses to these factors for different weed species functional types was considered by modelling four functional response groups. We used this model to investigate the effects of increasing the proportion of permanent meadows in the landscape and of the spatial arrangement of meadows on weed density in crops. With this model, increasing the proportion of permanent meadows significantly decreased mean seed density of weeds in crops. Furthermore, weed density in crops was found to be lower for landscapes in which the meadows were scattered, rather than clustered together in large zones. However, these spatial and landscape-scale effects were much weaker than the local effect of cropping systems. Weed density in permanent meadows was more sensitive to the proportion of meadows and to their spatial arrangement than weed density in crops, although the absolute value of weed density remained low in this unfavourable habitat.

Keywords

Virtual landscape, population dynamics, crops, rotation, tillage, herbicides

1. Introduction

In agroecosystems, the management of weed populations in crops is challenging, due to the need to limit weed impact on production whilst conserving weed contribution to biodiversity (Marshall *et al*., 2003; Mézière *et al.,* 2015). The limitation of crop yield by weeds is often related to local infestations, which may occur in a given year due to weed management failure. The control of weed abundance in cropped fields is mostly achieved through field-scale management, which can be highly reliant on herbicide use or more integrated, i.e. mobilizing cropping practices that have an impact on weed population dynamics, e.g. crop rotation, sowing time management and mechanical weeding (Chikowo *et al.,* 2009). However, annual arable weeds disperse beyond the edge of the field (Benvenuti, 2007; Alignier and Petit, 2012) and therefore, it is questionable whether weed management should not be thought at multiple scales, from the field to the wider landscape (Petit *et al.,* 2011; 2013).

There is strong empirical evidence that the characteristics of the landscape surrounding a cropped fields affects its in-field weed richness and composition (Gaba *et al*., 2010; Alignier *et al.*, 2013; Henckel *et al.*, 2015) but the effect of landscape scale drivers on weed abundance is much less documented. Studies that have simultaneously explored the contribution of field management and landscape context on weed abundance suggest that the impact of landscape scale factors is marginal compared to the effect of local field management (Ekroos *et al.*, 2010; Hawes *et al.*, 2010; Petit *et al.*, 2016). Recent national-scale British analyses provide correlative evidence that weed abundance is positively affected by field size (Alignier *et al.*, 2017), the diversity of landscape elements surrounding arable field (Bohan and Haughton 2012) and the proportion cover of cropped area in the wider landscape surrounding the field (Alignier *et al.*, 2017). The existence of such correlative patterns raises the question of the contribution of weed dispersal processes to the local dynamics of weed populations in arable fields.

Annual arable weed species are characterised by high levels of seed production and long-term seed viability (Baker, 1974) and this temporal dispersal explains that modelling approaches are often adopted to assess the long-term effect of field management on weed abundances (Sester *et al.*, 2007, Colbach *et al.*, 2014). In such models, the level of herbicide use, the nature of soil tillage operations and the crop rotation are among the key field management factors that drive weed dynamics (Gardarin *et al.,* 2007; Gardarin *et al.*, 2012). Weeds response to these management factors depends on some of their biological characteristics, mainly germination period seed size (Buhler, 1995; Gunton *et al.,* 2011).

Addressing the potential contribution of weed dispersal to local annual arable weed abundance would require to expand existing modelling frameworks in space (in order to account for weed spatial dispersal) but also to explicitly consider the temporal dynamics of the landscape (dynamic landscapes). Few studies have adopted spatially explicit modelling approaches to assess the dynamics of annual arable weeds at the landscape scale. Existing studies considered only one species and a small number of agricultural practices (Perry and Gonzalez-Andujar, 1993; Gonzalez-Andujar and Perry, 1995; Dauer *et al*., 2009; Gonzalez-Diaz *et al*., 2012; Gonzalez-Diaz *et al*., 2015) or focused exclusively on the effects of neighbouring fields (Gonzalez-Andujar *et al*., 2001) and none of these models specifically represented cropping systems. In these models, crop type directly determined the set of population dynamics parameters, with, at best, the possibility of varying herbicide use intensity, whereas tillage regime which is known to impact the local weed dynamics was never taken into account. There is thus a need for a modelling framework that simultaneously considers dispersal processes over a large landscape-wide scale and realistic cropping system, with a balance between simplicity and realism, to prevent the final model becoming too complex and intractable (Holst *et al*., 2007).

In this paper, we propose a modelling framework to address the question of the relative contribution of weed dispersal to annual arable weed abundances in contrasted scenarios of landscape composition and configuration. Weed abundance is modelled for four types of annual arable weed species (or virtual species) that differ for their germination period and seed size, two characteristics that are related both to intrinsic demographic parameters (Bond, 2008; OdERA-Systèmes, 2014) and to weed response to cropping systems (Buhler, 1995; Gunton *et al.,* 2011). Cropped areas in the landscape are three types of realistic cropping systems (no tillage systems with high level of herbicides, systems including tillage and non-chemical weeding and classical systems including both tillage and herbicide applications). We consider a fourth habitat type, permanent meadows, considered to be much less suitable than arable crops for the annual arable weeds modelled here (Moonen *et al*., 2001; Meiss *et al*., 2010; Cordeau *et al*., 2012). The framework is then used to explore contrasting scenarios to test the following hypotheses: (i) increasing the proportion of unsuitable habitat in the landscape significantly decreases weed infestation in crops; (ii) this effect is magnified if the unsuitable habitat is scattered (fragmented) throughout the landscape rather than clustered together.

2. Materials and Methods

2.1. Agronomical practices

We focused on three main management options that drive weed population dynamics (sowing time, soil tillage regime and herbicide use intensity) and modeled functional species types that respond differently to these three determinants.

Sowing time is a determinant factor in the selection of the weed species able to grow in a given crop, resulting in contrasting weed floras in winter and spring crops (Milberg *et al*., 2001). A trait-based analysis revealed that crop sowing period was a better predictor of the composition of weed communities than crop type (Gunton *et al.,* 2011). Similarly, the dichotomy between winter and spring crops has been identified as the most explanatory and predictive variable in species distribution models, outcompeting the full crop list and other more detailed classifications of crop types (Alignier *et al.,* 2013).

The type of mechanical operations applied to the soil has a major impact on the weed seed bank. In particular, inversion tillage is designed to aerate the soil and to improve its structure. It involves turning over the uppermost 20 to 40 cm of the soil with a plough and has major consequences for the distribution of seeds in the soil (Yenish *et al*., 1992; Cardina *et al*., 2002; Sester *et al.,* 2006) and for germination rate. Gardarin *et al*. (2010) showed that the maximal shoot and root lengths of weeds, which determine the maximum depth from which a seed can germinate, are positively related to seed weight. Species with low or high seed weights would therefore be expected to respond differently to inversion tillage. Large seed would be expected to have better germination rates at greater depths (Gardarin *et al.*, 2011; Cordeau *et al.,* 2015), whereas small seeds preferentially germinate close to the soil surface. This hypothesis was confirmed by the observation that tillage reduction is followed by a decline in weed species with large seeds (Buhler, 1995). In addition, seed production (the quantity of seed produced by a given plant) and seed mortality are also related to seed weight (Bond, 2008; OdERA-Systèmes, 2014).

Finally, we considered that the herbicide use intensity (often characterized through the Treatment Frequency Index, an indicator which quantifies the number of recommended doses applied to each hectare, OECD, 2001) directly modulates the plant mortality rate.

2.2. Species functional types

We considered four functional types of weed species, defined according to their preferential germination in winter or spring crops and seed size: *WinterSmall*, *WinterLarge*, *SpringSmall* and *SpringLarge*. Doing this, we distinguished (i) between winter weed species (those growing preferentially in winter crops) and spring weed species that differ in terms of germination rate (proportion of germinating seeds) and (ii) between small seed species (< 5 mg) and large seed species (> 5 mg) that differ in terms of germination rate, seed mortality (OdERA-Systèmes, 2014) and seed production (Bond, 2008). Examples of species of each functional types are: WinterSmall: *Alopecurus myosuroides*, *Capsella bursa-pastoris* and *Viola arvensis*; WinterLarge: *Veronica hederifolia*, *Fallopia convolvulus* and *Galium aparine*; SpringSmall: *Chenopodium album*, *Persicaria maculosa and Solanum nigrum*; SpringLarge: *Convolvulus arvensis,* and *Ambrosia trifida*.

2.3. Agricultural systems and response of the species functional types

In real agricultural landscapes, the above described agronomical practices (sowing time, soil tillage regime and herbicide use intensity) are not determined separately but are rather part of an agricultural system. We here combined these three drivers of weed dynamics to define three contrasted and realistic cropping systems observed in agricultural landscapes of Europe and North-America: crops with tillage and herbicide use (*Herbi-Till*), crops without herbicide use (*noHerbi-Till*), and crops without tillage and with herbicide use (*Herbi-noTill*). The following paragraph describes their detailed characteristics based on real combination of practices in French commercial farms.

The *HerbiTill* system was considered to have a crop succession with mainly winter crops (3 years out of four) and few spring crops, with a frequent use of tillage. Half of winter crops and one fourth of spring crops in *HerbiTill* system are tilled each year. In this system, herbicide use combined with possible mechanical weeding operations were considered to remove 75% of the weed species with a phenology similar to that of the crop (i.e. *WinterSmall* and *WinterLarge* in winter crops and *SpringSmall* and *SpringLarge* in spring crops). Conversely, the *noHerbi-Till* system was considered to have half of spring crops in their crop succession, spring crops being systematically tilled and winter crops never tilled. Weed management of this system, based solely on mechanical weeding, was considered less efficient (mortality: 60%). In both *noHerbi-Till* and *HerbiTill* systems, weed plants with a phenology different from that of the crop were considered to be largely destroyed by sowing (for winter weeds in spring crops) or harvesting (for spring weeds in winter crops) operations before seed production (mortality: 90%). *Herbi-noTill* were considered to have an intermediate use of spring crops (one year out of three) and to never use tillage. In this system, the absence of mechanical operations in *Herbi-noTill* fields was considered to be compensated by greater herbicide use, killing 95% of all weed plants (Table 1).

Finally, unlike the three crop land uses, permanent meadows (*PM*) were assumed to be long-term, stable, and unsuitable habitats for annual arable weeds, because the well-established dense grass cover and successive mowing should limit the growth rate of weed populations, by decreasing plant growth (e.g. Teasdale and Frank, 1983) *and* seed production (e.g. Mertens and Jansen, 2002), and through interception of the seed rain (e.g. Doisy *et al*., 2014).

2.4. Landscape definition and dynamics

In the modelling framework developed, a landscape is defined as a mosaic of polygonal field plots, each assigned a land-use type, either *Herbi-Till, noHerbi-Till*, *Herbi-noTill*, or *PM*. The first three land uses are considered to be 'crop land uses'. Each year, every field which is assigned one of the three types of crop land uses is defined as either spring crop or winter crops and either tilled or not according to the definition of the land uses (Table 1). Thus, for a given landscape, the map of land uses is constant over time whereas the maps of spring versus winter crops and of tilled field are changing each year. Between-field zones were considered to be homogeneous and are referred to as the landscape 'matrix'.

2.5. Population dynamics model

The population dynamics model is based on a raster representation of the landscape with a resolution of 3 m. Using a one-year time step, the local dynamics (population growth) for each pixel of the raster is dependent on ecological parameters that are in turn dependent on land use in the pixel and the type of weed species. Newly produced seeds disperse further over the landscape, according to a dispersal kernel.

Local weed population dynamics depends on five parameters: seed mortality rate (*sm*), germination rate (*gr*), plant mortality rate (*pm*), seed production (*sp*, number of seeds produced per plant), and carrying capacity *K* (maximal adult plant density). Each year, a proportion 1-*sm* of viable seeds either germinates (with a proportion *gr*) to produce plants or remains in the seed bank (with proportion 1-*gr*). As a result of natural mortality and weed management practices, a proportion *pm* of plants dies and the surviving plants (proportion 1-*pm*) each produce *sp* new seeds that disperse according to a bivariate Student's distribution (2Dt, Clark *et al.,* 1999), to enter the seed bank (Figure 1). Plant density is limited by carrying capacity (*K*). Therefore, over a raster corresponding to a domain $A=\{(x',y')\}$, the local densities (number per m²) of seeds S_t and plants P_t at year *t,* at the pixel location (*x*,*y*), are driven by the following equations:

$$P_{t,x,y} = \min\{K_{t,x,y}, (1 - sm_{t,x,y}) gr_{t,x,y} (1 - pm_{t,x,y}) S_{t-1,x,y}\} \quad (1)$$

$$S_{t,x,y} = \left(1 - sm_{t,x,y}\right)\left(1 - gr_{t,x,y}\right)S_{t-1,x,y} + \iint_{(x',y')\in A}\left(P_{t,x',y'}sp_{t,x',y'}\right)F_{2Dt}(x - x', y - y') \quad (2)$$

$$F_{2Dt}(x,y) = \frac{b-1}{\pi a^2}\left(1 + \frac{x^2+y^2}{a^2}\right)^{-b} \quad (3)$$

Eq. 1 corresponds to number of plants that emerge from the seed bank, left after weeding and limited by the carrying capacity. The first part of Eq. 2 describes the number of seeds that remains alive in the seedbank while its second parts corresponds to the dispersal. In the 2Dt distribution (Eq. 3), *a* is a scale parameter and *b* is a parameter that determines the weight of the distribution tail.

To ensure that the density limitation of weed plants also depend on the effects mentioned above, the carrying capacity *K* was defined as a function of the species functional type *s*, the land use *l*, the crop type *c* and the presence/absence of tillage *n*:

$$K_{s,l,c,n} = K_{max}GR_{s,l,c,n}/GR_{max} \quad (4)$$

with $GR_{s,l,c,n}$ the growth rate with equations (1) and (2) in non-equilibrium and without dispersal:

$$GR_{s,l,c,n} = \left(1 - sm_{s,l,c,n}\right)\left(1 - gr_{s,l,c,n}\right) + \left(1 - sm_{s,l,c,n}\right)gr_{s,l,c,n}\left(1 - pm_{s,l,c,n}\right)sp_{s,l,c,n} \quad , \quad (5)$$

GR_{max} the highest population growth rate overall *s*, *l*, *c* and *n* values:

$$GR_{max} = \max_{s,l,c,n}\left\{GR_{s,l,c,n}\right\} \quad (6)$$

and K_{max} the maximal weed plant density realistically observed in a crop or a pasture.

2.6. Parameterization

In the model, the habitat suitability of a given pixel of the landscape for a given species functional type, and, thus, its local demographic parameters, are completely determined by (i) land use (*Herbi-Till*, *noHerbi-Till*, *Herbi-noTill* or *PM*), (ii) crop type (winter or spring) and (iii) the presence or absence of tillage. A reference value for each of the demographic parameters *sm*, *gr*, *pm* and *sp,* for each of the four species functional types, was obtained through a literature survey (Infloweb, 2014; OdERA-Systèmes, 2014; Gardarin *et al.,* 2012 ; Gonzalez-Diaz *et al.*, 2012; Gardarin *et al.,* 2011; Gardarin *et al.,* 2010; Bond, 2008; Fumanal *et al.,* 2007; Sester *et al.,* 2006; Grundy *et al.*, 2003; Freckleton and Watkinson, 1998 ; Perry and Gonzalez-Andujar, 1993; Robert and Feast, 1972; see

Table A1 in Appendix A) and adapted according to land use, crop type and the presence or absence of tillage, to represent the effects described above (Table 1). Because the local dynamics is determined by field properties, at a given time step all the pixels of a given field have the same land use type, crop type, and tillage value, and therefore the same values of demographic parameters. Conversely, the plant and seed densities could vary over the pixels of a given field as a result of the dispersal process.

Dispersal was parameterized using established relationships between plant traits (maximal plant height and seed mass) and dispersal distances (Thomson *et al.,* 2010; 2011) to 15 current weed species either anemochorous or zoochorous. Over this set of species, the calculated average mean and maximal distances were respectively 1.3 m and 71.1 m (Table A2 in Appendix A). To fit with this order of magnitude, the 2Dt dispersal function (Eq. 3) was parametrized with a = 0.01 and b = 0.72 which corresponded to a mean dispersal of 1.5 m and 99% of dispersal events occurring over distances of less than 66 m.

2.7. Initialization

For each of the four land uses, we first ran the local demographic model (without dispersal) over 150 years (with 10 replicates per land uses), with an initial seed density of 2 seeds.m^{-2} of each species functional type. Convergence was reached after less than 100 years. As a result of the definition of local parameters, mean densities of plants and seeds converged to a non-zero value, except for *WinterLarge* and *SpringLarge* species functional types in meadows, which is consistent with experimental studies showing that weed species with large seeds are not favoured in habitat without tillage and/or with permanent cover (Cordeau *et al.,* 2015). For all subsequent simulations, the initial seed density of each land use was chosen as the mean seed density over the last 50 years of this initialization run. The spatial distribution of initial seed density is thus determined by the spatial distribution of land uses.

2.8. Landscape generation and simulation plan

2.8.1. Field structures

We used a set of five maps with contrasting spatial patterns of field plots (hereafter referred to as ‘field structures’) to account for sources of variability associated with field-size distribution, the spatial distribution of fields within the landscape and the geometric properties of fields. These structures covered the gradients of mean field area and total number of fields (Figure 2). Each field structure corresponded to a 4 × 4 km sample from the “Land Parcel Identification System” (official European geographic database for payments to farmers in the framework of the Common Agricultural Policy) for the Côte d’Or area, France. With these field structures, three sets of land use maps were produced.

2.8.2. Land use maps

The first set of maps consisted of homogeneous maps in which all the fields are assigned the same land use (20 maps corresponding to each of the four land uses over the five field structures). This corresponded to a reference situations with either 0% or 100% of permanent meadows.

The second set of maps was dedicated to studying the effect of the proportion of permanent meadows. We used a simulated annealing algorithm (SAA) to generate spatial configurations with either 3%, 10%, 25% or 50% area of permanent meadows (10 replicates each, see Figure 3 for some map examples). The lowest proportion corresponds to the minimum area under meadow for a farm to receive conditional subsidiaries through the ecological framework of the European Common Agricultural Policy (MEDDE, 2012). Then, for each spatial configuration, three maps were produced in which all fields non-selected as permanent meadows were set as either *HerbiTill*, *noHerbi-Till* or *Herbi-noTill* (thus a total of 600 maps corresponding to the five field structures, the four *PM* proportion, the 10 replicates and the three crop land uses).

With the third set of maps, we explored the effect of the spatial fragmentation of meadows. As described by Roques and Stoica (2007), the level of fragmentation was defined by considering the ratio of neighbours with a similar land use to the maximum possible number of similar neighbours. For each field structure, spatial configurations were generated using a SAA with two simultaneous targets: 50% area under meadows and either a low (*LowFrag* configurations) or a high (*HighFrag* configurations) fragmentation value, with ten replicates of each case (100 spatial configurations, see Figure 4 for some example of maps). Because the fragmentation also depends on fields shape and distribution, specific low and high fragmentation values were used for each field structure (see details in Appendix A for the definition of the fragmentation value). For 19 of the 100 cases, the SAA did not converge to the desired fragmentation value and the corresponding spatial configurations were discarded. In the 81 remaining cases, the low fragmentation value was 0.160 ± 0.004 (mean±SD) and the high fragmentation value 0.243 ± 0.006. Zonal configurations (*Zones*) were also generated by dividing the field structure into two equal parts by latitude (or longitude), with a complete spatial segregation of the meadows (20 spatial configurations exploring the four possible configurations for each field structure, Figure 4). The exact position of the rectilinear separation was defined with a SAA to respect 50% area under meadows. The mean fragmentation value for these segregated maps was 0.104 ± 0.030. Then, for each spatial configuration, three maps were produced in which all non-meadow fields were set as either *HerbiTill*, *noHerbi-Till* or *Herbi-noTill* (303 maps). Figure 5 presents a schematic representation of the land use map generation procedure, with the example of the zonal configurations.

2.8.3. Simulations

The three crop land uses (*HerbiTill*, *noHerbi-Till* or *Herbi-noTill*) correspond to dynamical agricultural systems (see sections 2.3 and 2.4). For each field defined as *HerbiTill*, *noHerbi-Till* or *Herbi-noTill* by the land use map generation procedure, the model determines each year if it is a spring or a winter crop and if it is as tilled or not, according to the definition of its land use (Table 1). Thus, although the map of land uses is constant over time, the maps of spring versus winter crops and of tilled field are changing each year. To account for this stochastic component, ten simulation runs were performed for each one of the generated land use maps, with a 50 years simulation duration (Figures A1 in Appendix A).

2.9. Statistical analyses

For each simulation and each weed species functional type, seed and plant densities were averaged over the last 10 years of the run and over all pixels for each land use. Similar calculations were performed on the cumulative number of seeds and the cumulative number of plants for all four species functional types together, to generate two summary variables for weed abundance (‘total seed density’ and ‘total plant density’). Therefore, each simulation simplified output corresponded to one value for each one of the following 10 response variables: the seed and plant densities of the four species functional types considered separately and the total seed and plant densities, together referred to as ‘weed density’ for simplicity. All subsequent analyses were performed on these 10 response variables.

We used linear models to analyse how land use type and field structures affected weed density in reference situations. We then analysed the effect of the proportion of permanent meadows on weed density in crops, by fitting linear models including the *PM* proportion, crop land use (*HerbiTill*, *noHerbi-Till* or *Herbi-noTill*) in the landscape and field structure as qualitative explanatory variables. For graphical representation of the *PM* proportion effect on weed density, we calculated centred partial regression coefficients (sum-to-zero contrasts) to allow for the interpretation of main effects in the presence of interactions (Schielzeth, 2010). In addition, the large number of simulations would make the detection of significant relationships likely even in the case of small effects. We therefore also calculated an effect size as the ratio of weed density for each *PM* proportion over weed density in the reference situation without *PM*. Similarly, we analysed the effect of the proportion of *PM* in the landscape on weed density in *PM* fields; the effect size was calculated using 100% *PM* simulations as the reference.

We then assessed the effect of the spatial distribution of meadows on weed density for each land use, with linear models including the different fragmentation levels (three-level factor: *Zones*, *LowFrag* and *HighFrag*), the crop land use present in the landscape and field structure as explanatory variables, and calculated centred partial regression coefficients to represent the effect of the fragmentation levels. We also calculated an effect size as the ratio of weed density in *LowFrag* and *HighFrag* situations relative to weed density in *Zone* situations. Similarly, we analysed the effect of the fragmentation level on weed density in *PM* fields.

The model implementation (Appendix B), the landscape generation procedure and all statistical analyses were performed with R software version 3.2.5. (R Development Core Team, 2016).

3. Results

In homogeneous landscapes (reference situations with either 0 or 100% *PM*), the spatial seed dispersal process did not modify the relative weed densities between land uses defined by the local demographic parameters values (Figure 6). Crops without herbicide (*noHerbi-Till*) had the highest densities, followed by crops with herbicide and tillage (*HerbiTill*), and then crops without tillage (*Herbi-noTill*); the permanent meadows habitat had a very low mean weed density (less than one plant per m²). Between-land use density patterns were similar, for both seeds and plants and for the four species functional types (Figure A2 in Appendix A). Finally, plant density of *WinterSmall* and *SpringSmall* species functional types always converged to one plant m^{-2} in *PM* land use.

3.1. Effect of the proportion of permanent meadows in the landscape

Increasing the proportion of permanent meadows significantly reduced total mean seed density in crops, as a result of a significant reduction in seeds of *WinterSmall* and *WinterLarge* species functional types (Table 2, Figure 7a). However, this variation was much smaller than the differences between crop land uses with an effect size always close to 1 (Table 3). There was no significant effect of increasing *PM* proportion on mean plant density in crops (Table 2, Figure 7c).

Conversely, decreasing the proportion of *PM* (i.e. increasing the proportion of crop land uses) significantly increased both seed and plant densities for all weed species functional types within *PM* fields (Table 2, Figure 7b and 7d). This effect size on seed density ranged between 1.2 and 2.2 whereas the absolute plant density value in *PM* fields was less affected than seed density, with a maximal effect size of 1.1 (Table 3). The field structure also significantly affected weed densities in *PM*.

3.2. *Effect of spatial aggregation of land uses*

The spatial aggregation of land uses had no significant effect neither on seed nor on plant densities in crops (Table 4, Figure 8a and 8c). By contrast, increasing the level of fragmentation significantly increased both seed and plant densities in permanent meadows (Table 4, Figure 8b and 8d). The effect size comparing weed seed density in *HighFrag* and *LowFrag* situations to the *Zones* reference situation ranged between 1.1 to 1.7 (Table 5). The effect size for weed plant density was smaller, with a maximum value of 1.1. In addition, the variability of plant density in meadows increased with the level of fragmentation (Figure A5 and A6 in Appendix A), indicating that the pattern of assignment of fields to land uses in different simulations affected the impact of crop habitats on semi-natural habitats. Both seed and plant densities in meadows were also significantly affected by the field structure.

4. Discussion

We evaluated the contribution to annual arable weed management of including semi-natural habitats in agricultural landscapes, by implementing a spatially explicit landscape-scale model of annual weed population dynamics taking cropping systems into account, including the crop rotation, tillage regime, mechanical weeding and herbicide use. This model showed that changing the proportion of permanent meadows or their spatial arrangement in the landscape only slightly modified the seed density of annual weeds in crops and had no effect on annual weed plant density. Yet, the range of meadow proportions was large, with a highest value of 50%. This confirms empirical studies that have shown a marginal effect of landscape characteristics compared to that of local-field management (Ekroos *et al.*, 2010; Hawes *et al.*, 2010; Petit *et al.*, 2016). As expected, weed seed density in crops decreased with increasing meadow proportion, as this semi-natural habitat is unsuitable for the annual arable weeds modelled here (Moonen *et al.*, 2001; Meiss *et al.*, 2010; Cordeau *et al.*, 2012). There was no significant effect of the spatial aggregation of meadows on annual weed densities in crops. Weed density in meadows was more strongly affected by the reciprocal effects of crop proportion and spatial arrangement, although absolute values were always low in this habitat unfavourable for annual weed species.

Arable weeds are characterised by a short dispersal range relatively to the landscape scale that we considered (e.g. Bischoff, 2005), which may explain why weed population dynamics is only weakly affected by such large-scale landscape properties. However, even a step-by-step dispersal may produce spatial pattern at large scale (Ricci *et al.*, 2013), and indeed our model generated significant spatial effects in terms of composition (*PM* proportion), spatial organisation of fields (field structure effect), and spatial organisation of land uses. Concerning the field structure effect, there was no apparent link between weeds density and field structure properties, in terms of field number or field shape, although the limited number of field structures considered precluded the formal testing of such relationships.

The low effect size associated to landscape composition and configuration may also reflect the rapid temporal dynamics of agricultural landscapes, for which habitat suitability maps vary continuously over years (Benoit *et al.*, 2012). This may counteract the effect of the spatial dissemination process, particularly for weed species that have adapted to these rapid temporal changes by developing temporal dispersal through a large seed bank. The role of the seed bank was tested in this model, with simulations including very small seed bank (i.e. 90% germination rate and 99% mortality of non-germinated seeds; results not shown): the effects on plants were of the same intensity as those on seeds. The presence of a seed bank seems to smooth effects between years, with a semi-natural habitat having a strong effect on some fields, due to the crop type and practices present, but with smaller effects in other years.

The weed density of the four species functional types in crops did not react equally to landscape modifications, with only *WinterSmall* and *WinterLarge* weed density in crops exhibiting a response to landscape composition, namely species functional types more adapted to winter crops (Figure A3, A4, A5 and A6 in Appendix A). Indeed, the observed effects mainly resulted from situations where the non-*PM* land use type was either *HerbiTill* or *Herbi-noTill*, two land uses defined with respectively 75% and 66% of expected winter crops in the temporal crop sequence. Thus our model suggests that species that are more adapted to a crop type frequent in the crop successions would be more sensitive to spatial effect than species adapted to a less frequent crop type.

In analyses of field data, the major determinants of weeds communities are the local crop characteristics and weed abundance, which respond principally to local factors (Petit *et al*., 2016). Some known landscape effects on weed abundances are “near landscape” effects (Bohan and Haughton, 2012), corresponding to the specific effects of neighbouring fields or border types (Alignier *et al*., 2013), which were not modelled here. Larger-scale landscape properties were frequently related to weed community structure. For example, the proportion of a crop in the landscape was shown to be negatively related to weed diversity, suggesting that the introduction of semi-natural habitats might increase diversity (Petit *et al*., 2013).

Even if the effect on the relative mean seed density was often small or insignificant, increasing *PM* proportion increased the between-simulation variability of annual weed abundance in crops (Figure 10). Situations in which land uses are more scattered may therefore increase the effect of one land use on the other one. However, weed seed abundance was also more variable in fragmented landscapes than in landscapes in which land uses were totally segregated spatially. Thus, the exact spatial position of the fields assigned to each land use may be at least as important as the level of aggregation. This effect may reflect the impact of the matrix (an extremely unfavourable habitat), which depends on field size and shape, two factors determining the length of the interface between the field habitat and the matrix habitat, a well-known landscape effect (Ricketts, 2001). A similar mechanism may account for the effect of field structure on annual weed abundance in homogeneous landscapes.

5. Conclusion

In this model-based study, we found that introducing permanent meadows into the landscape decreased annual arable weed densities in crops to a much lesser extent than the adoption of particular cropping systems. For weed species already widespread over the entire landscape, even with effective seed dispersal, the spatial dispersal process appeared to have a smaller effect on population dynamics than local factors and temporal dispersal, suggesting that the spatial organisation of cropping systems and semi-natural habitat would not be a major lever to manage weed abundances in crops. We focused here on mean annual arable weed densities over large scales. However, given the production of large amounts of weed seeds and the persistence of the seed bank (Baker, 1974), weed management strategies in arable crops also aim to control the temporal variability of weed densities and, particularly, the risk of high level of infestation in a particular field (Colbach *et al.*, 2001), a component which merits additional investigations with the present landscape-scale model (i.e. the spatiotemporal variability of weed densities in a given cropping system). For widespread species, we suggest, as an interesting complementary approach, that the effects of nearby landscape features, such as sown grass strips, grass margins or hedgerows on the risk of infestation should be modelled for different types of cropping systems and annual arable weed management strategies. The model described here could also be used for studies of newly introduced species, the spread of which may be more influenced by landscape composition and arrangement at a large scale (Von der Lippe *et al.*, 2013).

Acknowledgements

This work was carried out with financial support from "ANR- Agence Nationale de la Recherche - The French National Research Agency" under the AGROBIOSPHERE program, project "ANR-12-AGRO-0006, PEERLESS" and from "Région Bourgogne". We thank Bruno Chauvel, Stéphane Cordeau and Martin Lechenet for providing expertise about weed responses to cropping systems and the description of cropping systems, Nathalie Colbach for her advices about dispersal modelling, and Fabrice Dessaint and Guillaume Adeux for their help on statistical analyses. This work also beneficiated from the INRA PAYOTE research network.

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Tables

Table 1. Values of local demographic parameters for the four species functional types as a function of land use, crop type and the presence/absence of tillage.

Parameter	Land use	Crop type	Tillage	Small seeds		Large seeds	
				Spring weeds	Winter weeds	Spring weeds	Winter weeds
sm	All	-	-	0.35	0.35	0.5	0.5
gr	noHerbi-Till/HerbiTill	Spring/Winter	Yes	0.05	0.05	0.25	0.25
		Spring/Winter	No	0.075	0.075	0.2	0.2
	Herbi-noTill	Spring	No	0.1	0.01	0.15	0.1
		Winter	No	0.01	0.1	0.1	0.15
	PM	-	-	0.001	0.001	0.01	0.01
	Matrix	-	-	0.001	0.001	0.01	0.01
pm	noHerbi-Till	Spring	Yes	0.6	0.9	0.6	0.9
		Winter	No	0.9	0.6	0.9	0.6
	HerbiTill	Spring	Yes or No	0.75	0.9	0.75	0.9
		Winter	Yes or No	0.9	0.75	0.9	0.75
	Herbi-noTill	Spring/Winter	Yes or No	0.95	0.95	0.95	0.95
	PM	-	-	0.3	0.3	0.3	0.3
	Matrix	-	-	0.9	0.9	0.9	0.9
sp	PM	-	-	1000	1000	50	50
	Others	-	-	5000	5000	250	250
K	HerbiTill	Spring	Yes	42	4	8	2
			No	63	4	7	2
		Winter	Yes	4	42	2	8
			No	4	63	2	7
	noHerbi-Till	Spring	Yes	67	4	13	2
		Winter	No	4	100	2	11
	Herbi-noTill	Spring	No	17	2	1	1
		Winter	No	2	17	1	1
	PM	-	-	1	1	1	1
	Matrix	-	-	1	1	1	1

sm: seed mortality rate; *gr*: germination rate; *pm*: plant mortality rate; *sp*: seed production (number of seeds produced per plant). *Herbi-Till*: crops with tillage and herbicide use; *noHerbi-Till*: crops without herbicide use; *Herbi-noTill*: and crops without tillage; *PM*: permanent meadows; *Matrix*: between-field zones.

Table 2. ANOVA table with relative omega squared (rω²) for simulation with various *PM* proportions. Bold values indicates effects corresponding to a proportion of explained variance rω² > 10%.

Variable	Effect	df	F value				
			WinterSmall	*WinterLarge*	*SpringSmall*	*SpringLarge*	Total weed
Seed density in crops	*PM* prop.	3	5.1 **	5.4 **	1.9 ns	2.0 ns	8.7 ***
	Crop land use	2	$9.7.\times10^5$ ***	1.8×10^6 ***	1.7×10^5 ***	4.8×10^5 ***	1.1×10^7 ***
	Field structure	4	0.9 ns	0.9 ns	0.4 ns	0.4 ns	4.0 **
	PM prop. x Crop land use	6	1.4 ns	2.6 *	1.2 ns	1.4 ns	1.1×10^1 ***
	PM prop. x Field structure	12	2.0 ns	1.7 ns	1.7 ns	1.6 ns	0.7 ns
Plant density in crops	*PM* prop.	3	2.4 ns	2.1 ns	2.8 *	2.2 ns	0.8 ns
	Crop land use	2	5.9×10^5 ***	1.2×10^6 ***	1.2×10^5 ***	3.7×10^5 ***	9.3×10^8 ***
	Field structure	4	0.5 ns	0.3 ns	0.5 ns	0.3 ns	0.3 ns
	PM prop. x Crop land use	6	0.9 ns	0.7 ns	0.7 ns	0.8 ns	1.1 ns
	PM prop. x Field structure	12	1.4 ns	0.9 ns	1.2 ns	1.2 ns	1.1 ns
Seed density in *PM*	*PM* prop.	3	3.2×10^2 ***	4.7×10^2 ***	2.7×10^2 ***	2.4×10^2 ***	3.2×10^2 ***
	Crop land use	2	8.3×10^3 ***	9.0×10^3 ***	7.8×10^3 ***	9.1×10^3 ***	8.4×10^3 ***
	Field structure	4	5.5×10^2 ***	5.1×10^2 ***	5.7×10^2 ***	5.2×10^2 ***	5.7×10^2 ***
	PM prop. x Crop land use	6	4.3×10^2 ***	4.7×10^2 ***	4.0×10^2 ***	4.7×10^2 ***	4.4×10^2 ***
	PM prop. x Field structure	12	5.2×10^1 ***	4.8×10^1 ***	5.2×10^1 ***	4.8×10^1 ***	5.3×10^1 ***
Plant density in *PM*	*PM* prop.	3	-	7.1×10^2 ***	-	9.4×10^1 ***	4.8×10^2 ***
	Crop land use	2	-	3.2×10^3 ***	-	2.3×10^3 ***	5.1×10^3 ***
	Field structure	4	-	5.2×10^1 ***	-	1.4×10^2 ***	1.7×10^2 ***
	PM prop. x Crop land use	6	-	2.9×10^2 ***	-	5.0×10^2 ***	5.2×10^2 ***
	PM prop. x Field structure	12	-	5.3×10^1 ***	-	4.2×10^1 ***	2.4×10^1 ***

* *P*< 0.05; ** *P*< 0.01; *** *P*< 0.001; ns: not significant. *Herbi-Till*: crops with tillage and herbicide use; *noHerbi-Till*: crops without herbicide use; *Herbi-noTill*: and crops without tillage; *PM*: permanent meadows

Table 3. Effect size of PM proportion on the total weed density with situations without PM as reference situation.

Variable	Landscape composition	Reference situation	*PM proportion*			
			0.03	0.10	0.25	0.50
Seed density in crops	*HerbiTill / PM*	*PM* prop. = 0	1.0011	1.0000	0.9997	0.9987
	noHerbi-Till / PM		1.0002	1.0000	0.9993	0.9980
	Herbi-noTill / PM		0.9997	0.9995	0.9988	0.9977
Plant density in crops	*HerbiTill / PM*	*PM* prop. = 0	1.0006	1.0000	1.0001	1.0004
	noHerbi-Till / PM		1.0007	1.0007	1.0008	1.0007
	Herbi-noTill / PM		1.0000	1.0000	1.0000	1.0000
Seed density in *PM*	*HerbiTill / PM*	*PM* prop. = 1	1.7631	1.6387	1.5396	1.3517
	noHerbi-Till / PM		2.2321	2.0313	1.8709	1.5677
	Herbi-noTill / PM		1.2492	1.2087	1.1763	1.1149
Plant density in *PM*	*HerbiTill / PM*	*PM* prop. = 1	1.0600	1.0450	1.0400	1.0100
	noHerbi-Till / PM		1.1000	1.0850	1.0800	1.0300
	Herbi-noTill / PM		1.0000	1.0000	1.0000	1.0000

Herbi-Till: crops with tillage and herbicide use; noHerbi-Till: crops without herbicide use; Herbi-noTill: and crops without tillage; PM: permanent meadows. *PM* prop.: proportion of permanent meadows.

Table 4. ANOVA table with relative omega squared (rω²) for simulation with various levels of fragmentation. Bold values indicate effects corresponding to a proportion of explained variance rω² > 10%. Plant density of *WinterSmall* and *SpringSmall* species functional types always converged to one plant m^{-2} in *PM* land use.

Variable	Effect	df	F value				
			WinterSmall	*WinterLarge*	*SpringSmall*	*SpringLarge*	Total weed
Seed density in crops	Frag. level	2	0.5 ns	0.3 ns	0.3 ns	0.8 ns	1.5 ns
	Crop land use	2	4.0×10^5 ***	7.2×10^4 ***	7.0×10^4 ***	1.9×10^5 ***	4.8×10^6 ***
	Field structure	4	1.0 ns	1.1 ns	1.1 ns	0.9 ns	1.2×10^1 ***
	Frag. level x Crop land use	4	1.1 ns	0.9 ns	0.9 ns	1.3 ns	5.9 ***
	Frag. level x Field structure	8	0.7 ns	1.4 ns	0.8 ns	0.9 ns	2.0 *
Plant density in crops	Frag. level	2	0.3 ns	0.2 ns	0.2 ns	0.3 ns	1.0 ns
	Crop land use	2	2.4×10^5 ***	4.7×10^5 ***	5.0×10^4 ***	1.5×10^5 ***	4.0×10^6 ***
	Field structure	4	0.4 ns	0.7 ns	0.8 ns	0.5 ns	0.5 ns
	Frag. level x Crop land use	4	0.8 ns	0.6 ns	1.0 ns	0.7 ns	0.7 ns
	Frag. level x Field structure	8	0.8 ns	1.0 ns	0.9 ns	1.0 ns	1.0 ns
Seed density in *PM*	Frag. level	2	1.6×10^3 ***	2.2×10^3 ***	1.3×10^3 ***	1.1×10^3 ***	1.5×10^3 ***
	Crop land use	2	1.1×10^4 ***	1.2×10^4 ***	1.0×10^4 ***	1.2×10^4 ***	1.1×10^4 ***
	Field structure	4	8.4×10^2 ***	7.7×10^2 ***	8.0×10^2 ***	7.3×10^2 ***	8.5×10^2 ***
	Frag. level x Crop land use	4	1.8×10^3 ***	1.9×10^3 ***	1.7×10^3 ***	1.9×10^3 ***	1.8×10^3 ***
	Frag. level x Field structure	8	2.0×10^2 ***	1.8×10^2 ***	2.0×10^2 ***	1.8×10^2 ***	2.1×10^2 ***
Plant density in *PM*	Frag. level	2	-	1.4×10^2 ***	-	2.6×10^1 ***	3.7×10^1 ***
	Crop land use	2	-	1.8×10^3 ***	-	4.5×10^2 ***	1.9×10^3 ***
	Field structure	4	-	5.6×10^2 ***	-	1.9×10^2 ***	6.7×10^2 ***
	Frag. level x Crop land use	4	-	6.0×10^2 ***	-	1.6×10^2 ***	6.5×10^2 ***
	Frag. level x Field structure	8	-	1.9×10^2 ***	-	6.7×10^1 ***	2.3×10^2 ***

$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns: not significant. Frag. level: level of landscape fragmentation.

Table 5. Effect size of the fragmentation level on the total weed density with Zones configuration as reference situation.

Variable	Landscape composition	Reference situation	Fragmentation level	
			LowFrag	*HighFrag*
Seed density in crops	*HerbiTill / PM*	*Zones*	0.9976	0.9979
	noHerbi-Till / PM		0.9977	0.9989
	Herbi-noTill / PM		0.9972	0.9988
Plant density in crops	*HerbiTill / PM*	*Zones*	1.0003	0.9996
	noHerbi-Till / PM		1.0003	1.0003
	Herbi-noTill / PM		1.0000	1.0000
Seed density in *PM*	*HerbiTill / PM*	*Zones*	1.3611	1.1708
	noHerbi-Till / PM		1.5688	1.2691
	Herbi-noTill / PM		1.1212	1.0574
Plant density in *PM*	*HerbiTill / PM*	*Zones*	1.0200	1.0000
	noHerbi-Till / PM		1.0500	1.0000
	Herbi-noTill / PM		1.0000	1.0000

Herbi-Till: crops with tillage and herbicide use; *noHerbi-Till*: crops without herbicide use; *Herbi-noTill*: and crops without tillage; *PM*: permanent meadows.

Figure captions

Figure 1. Structure of the weed population dynamics model. Seed mortality (*sm*), plant mortality (*pm*), germination rate (*gr*), seed production (*sp*) and carrying capacity (*K*) vary over space and time, and differ between weed species functional types and land uses.

Figure 2. Maps of the five field structures (FS 1, …, FS 5) used in the simulation plan and their position along the gradients of number of fields per field structure and mean field area (error bars correspond to standard errors).

Figure 3. Example of some of the maps generated, with various proportions of permanent meadows in the field structure 1. a: 3%; b: 10%; c: 25%; d: 50% of permanent meadows (*PM*). Light grey: crop land use; dark grey: *PM* fields.

Figure 4. Example of some of the maps generated, with different spatial arrangements of the field structure 5. a: zonal landscape; b: low level of fragmentation; c: high level of fragmentation. Light grey: crop land use; dark grey: permanent meadows (*PM*).

Figure 5. Schematic representation of the land use map generation procedure illustrating the case of the zonal configurations. For each field structure, different spatial configuration of the permanent meadows (*PM*) positioning are produced; then, for each spatial configuration, land use maps are generated by assigning either *HerbiTill*, *noHerbi-Till* or *Herbi-noTill* crops to non-*PM* fields.

Figure 6. Mean total seed density and mean total plant density for each land-use type in homogeneous landscapes (error bars correspond to the standard deviation)

Figure 7. Centred partial regression coefficients of the effect of the proportion of permanent meadows on weed density (average over the last 10 years of the run) and 95% confidence intervals.

Figure 8. Centred partial regression coefficients of the effect of the level of fragmentation of permanent meadows on weed density (average over the last 10 years of the run) and 95% confidence intervals. *Zones*: zonal landscapes with total spatial segregation between meadows and the other land use type; *LowFrag* and *HighFrag*: low and high levels of meadow fragmentation, respectively.

Figure1

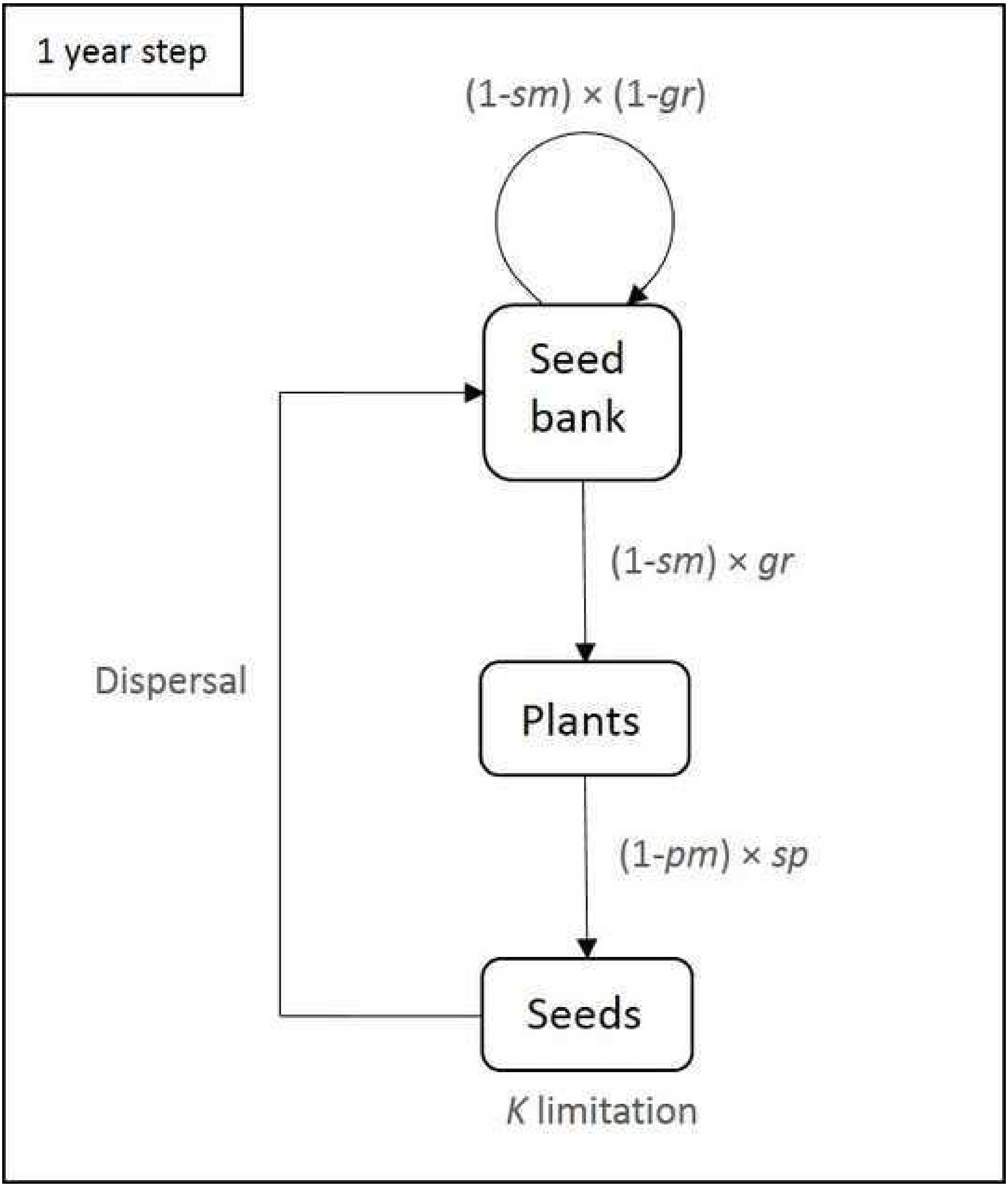
1 year step
(1-*sm*) × (1-*gr*)
Seed bank
(1-*sm*) × *gr*
Dispersal
Plants
(1-*pm*) × *sp*
Seeds
K limitation

Figure2

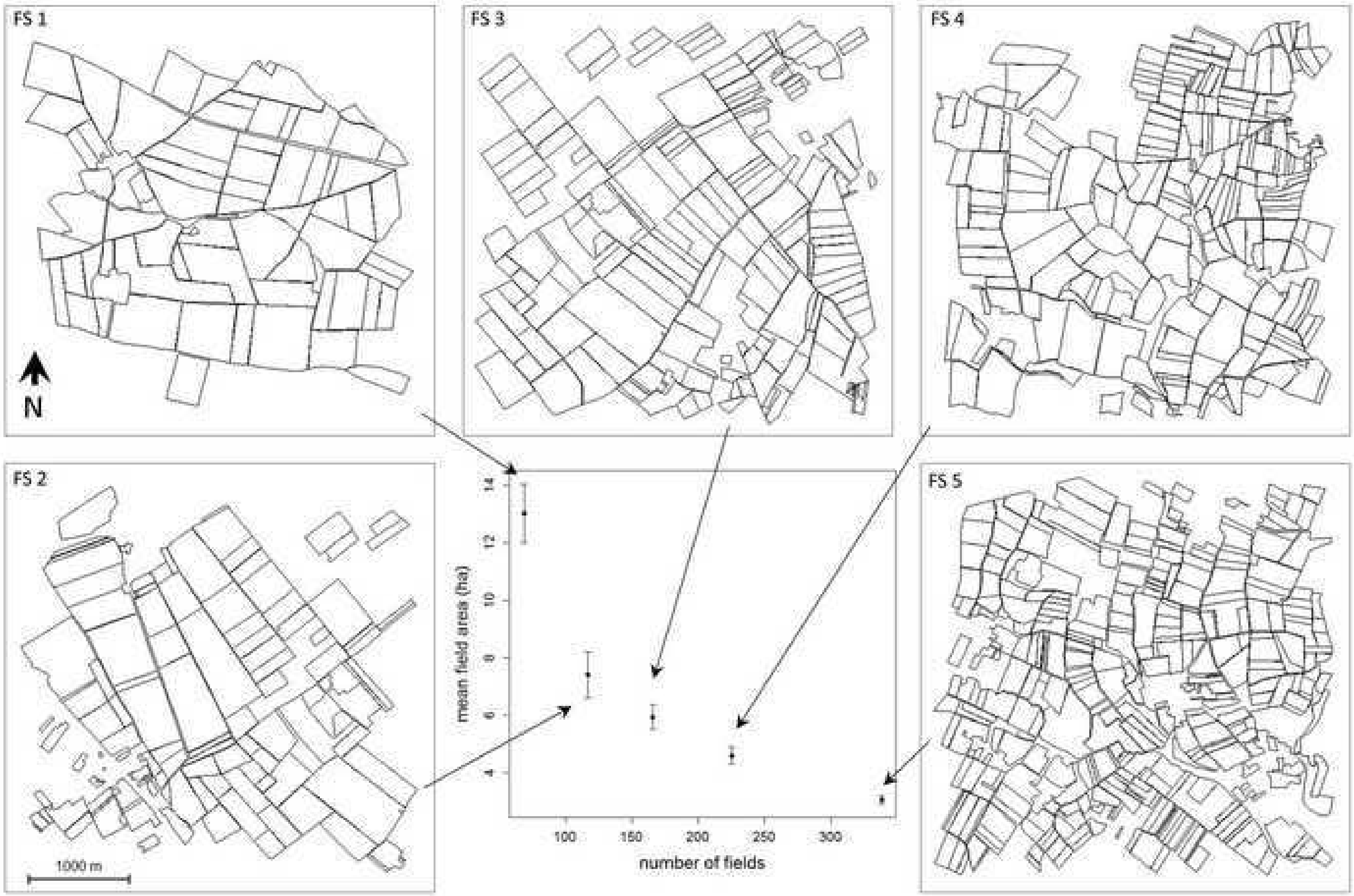
FS 1
N
FS 3
FS 4
FS 2
1000 m
FS 5
mean field area (ha)
4
6
8
10
12
14
100
150
200
250
300
number of fields

Figure3

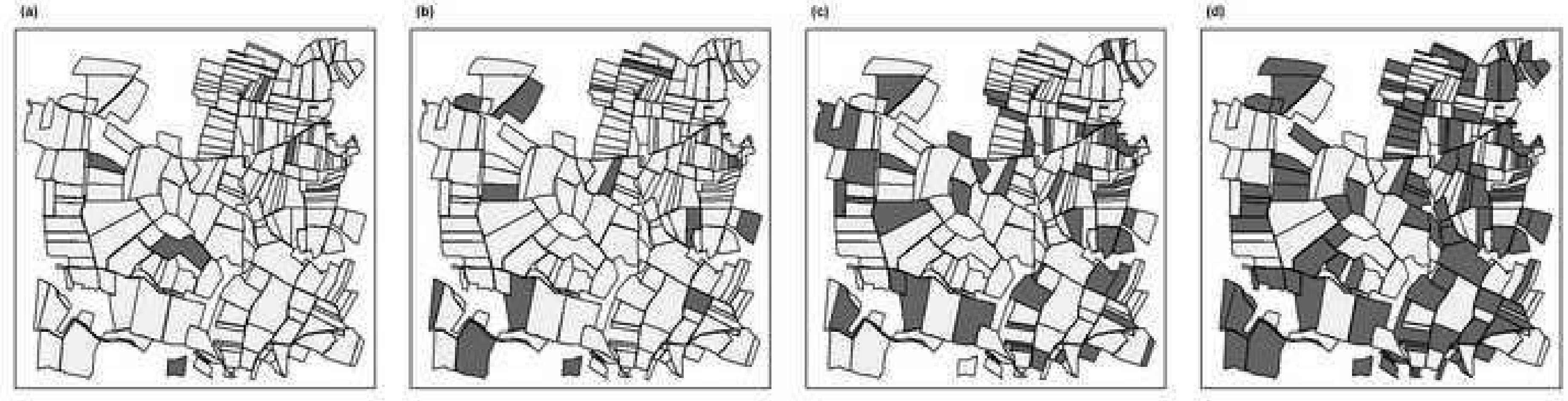

Figure4

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Figure5

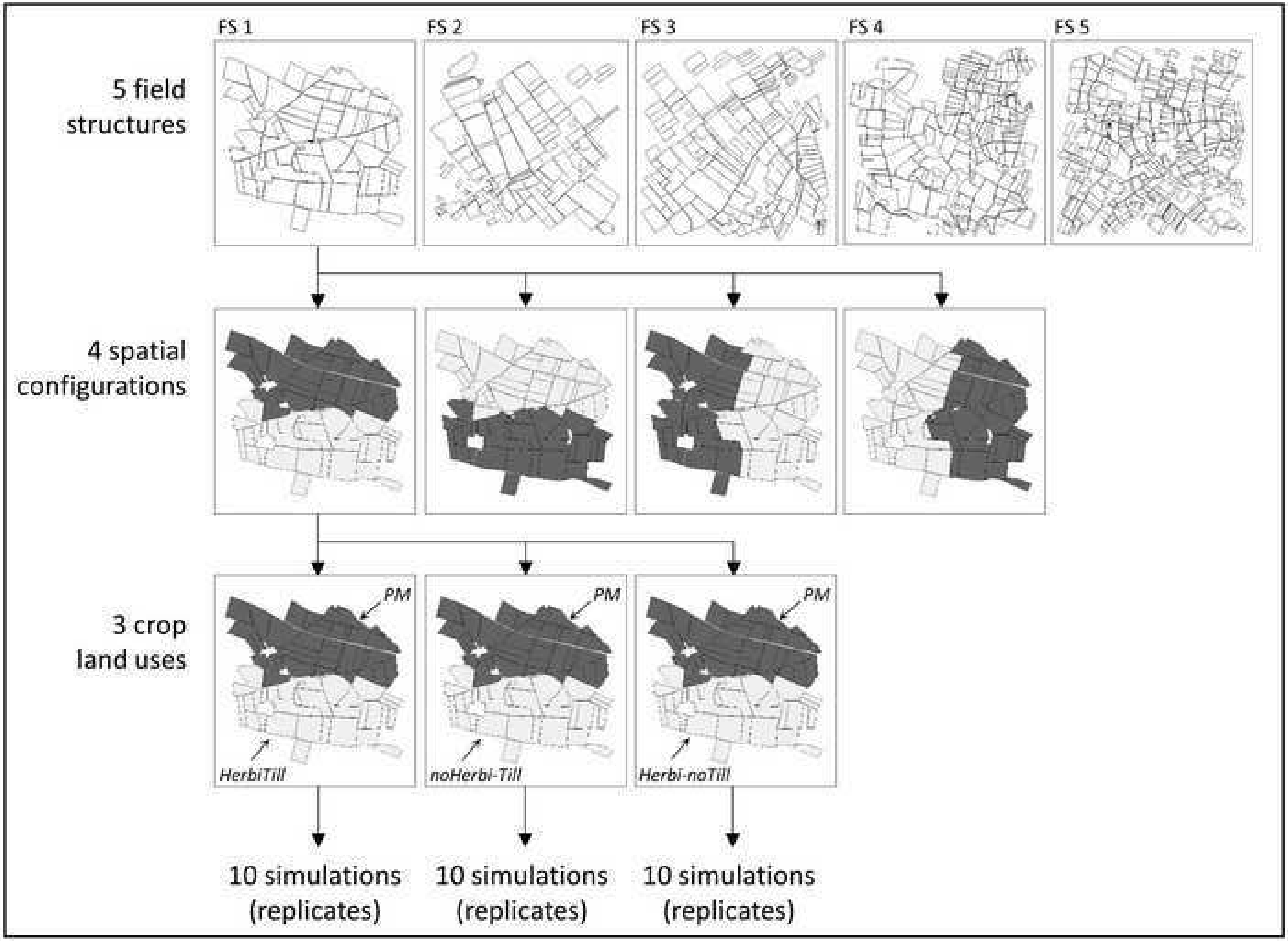

5 field structures
FS 1
FS 2
FS 3
FS 4
FS 5
4 spatial configurations
3 crop land uses
PM
PM
PM
HerbiTill
noHerbi-Till
Herbi-noTill
10 simulations (replicates)
10 simulations (replicates)
10 simulations (replicates)

Figure6

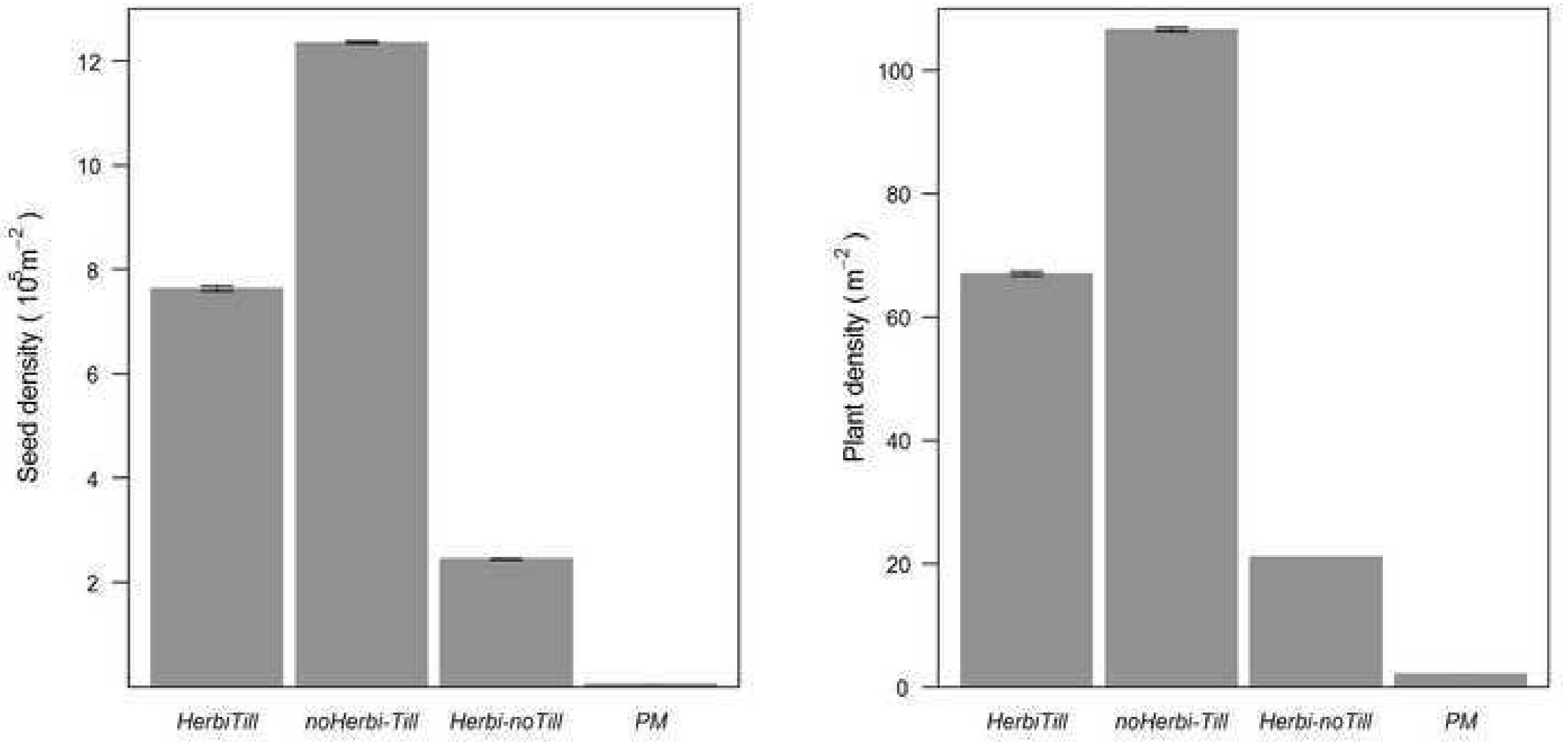

Seed density (10^5m^{-2})
2
4
6
8
10
12
HerbiTill
noHerbi-Till
Herbi-noTill
PM
Plant density (m^{-2})
0
20
40
60
80
100
HerbiTill
noHerbi-Till
Herbi-noTill
PM

Figure 7

Click here to download high resolution image

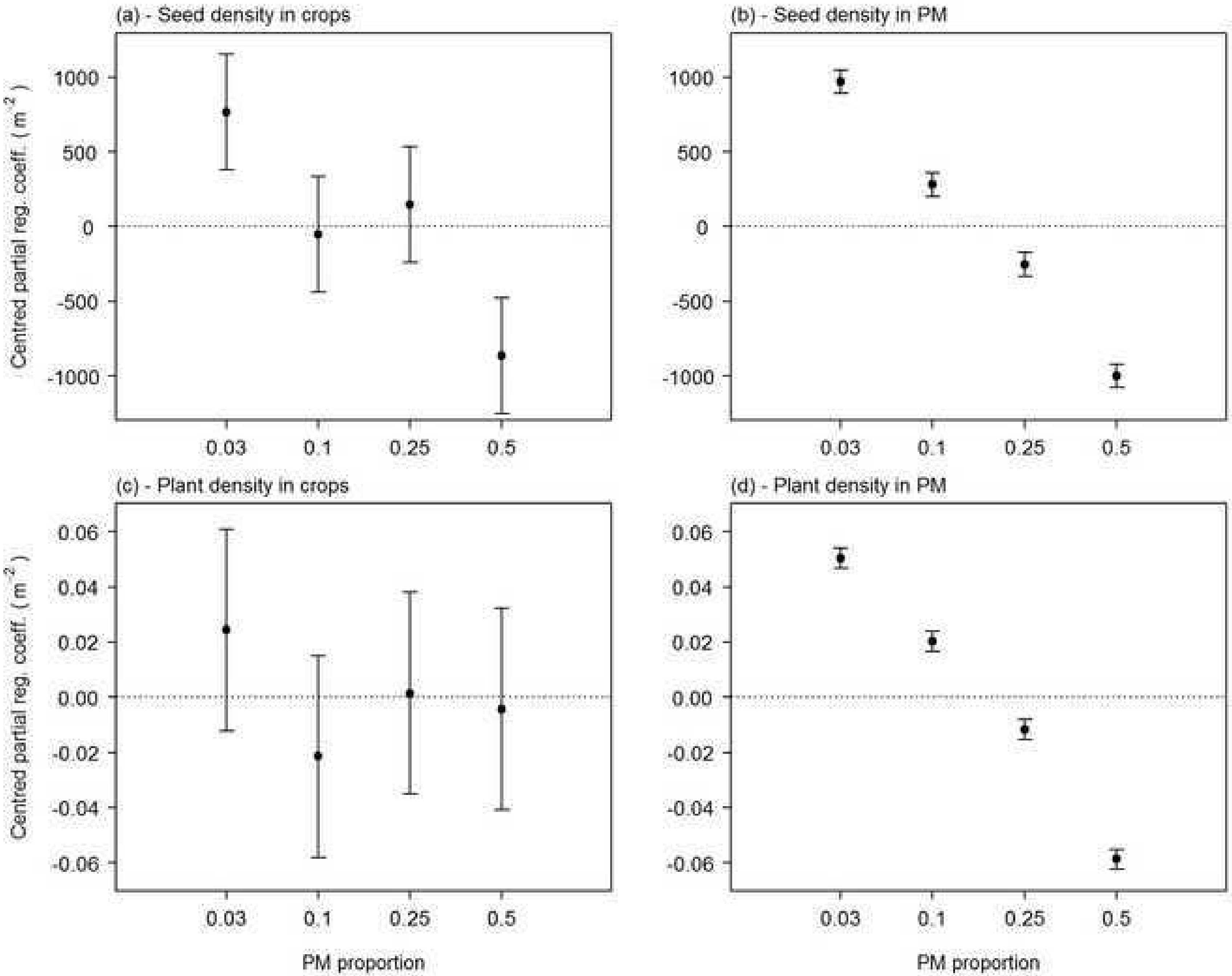
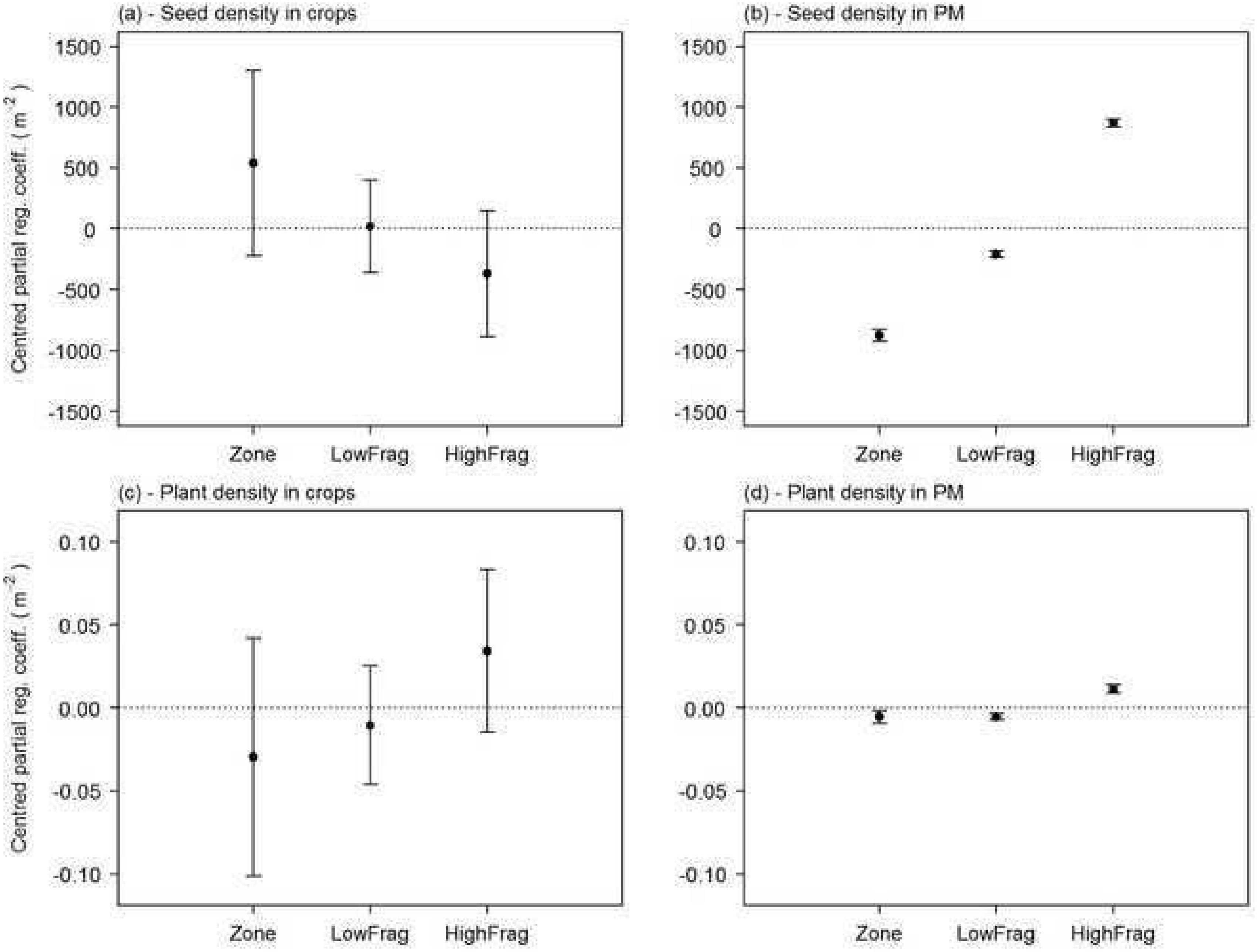


Figure 8


(a) - Seed density in crops
(b) - Seed density in PM
(c) - Plant density in crops
(d) - Plant density in PM
Centred partial reg. coeff. (m^{-2})
1500
1000
500
0
-500
-1000
-1500
0.10
0.05
0.00
-0.05
-0.10
Zone
LowFrag
HighFrag

Projet ANR-12-AGRO-006

PEERLESS

Analyse de l'éco-efficacité agro-écologique et économique de paysages:

Modèle Proie-Prédateur-Paysage avec décisions économiques

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Analyse de l'éco-efficacité agro-écologique et économique de paysages: Modèle Proie-Prédateur-Paysage avec décisions économiques
Nature du livrable	Rapport interne : méthodologie et analyses préliminaire de résultats
Date de publication	02/02/2018

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B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

L'objectif de ce livrable est de présenter la méthodologie adoptée pour générer les ensembles de productions possibles des paysages, en prenant en compte les productions agronomiques (rendement, dégâts aux cultures), économiques (profit) et écologiques (IFT, densité des ravageurs et de leurs ennemis naturels). Nous avons pour cela développé un modèle « Paysage, proie, prédateur » dynamique et spatialement explicite permettant de simuler la performance des paysages selon ces différentes dimensions, sous différents scénarios d'usage des sols.
Le livrable présente le modèle, le plan de simulation, les données générées, et les questions de recherche qui exploiterons ces données.

B.2 RESUME

Maximum 1 page en français.

Dans une approche interdisciplinaire, nous avons construit un modèle économique-agronomique-écologique représentant un paysage agricole (1 km²), dont l'usage des sols et les pratiques (fertilisation, usage de pesticides) dépendent du contexte économique, agronomique et écologique, et en particulier de la présence de ravageurs et de leurs ennemis naturels.

La dimension économique du modèle décrit comment les agriculteurs allouent les terres entre différents usages en fonction

- des conditions agronomiques : qualité de leur sol
- des conditions économiques : prix de la production, coûts des intrants et des pratiques, instruments de politique publique (taxes, subventions, bonus de prix pour les productions sans pesticides)
- des conditions écologiques : la présence de ravageurs et de leurs prédateurs
- de leurs préférences : utilité du profit et désutilité des pesticides (effet ``santé'')

Leurs décisions portent sur

- l'allocation des sols entre cultures et habitats non cultivés
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Le modèle a été utilisé pour générer une grande base de données de simulation, qui sera exploitée pour des publications interdisciplinaires.

Les valorisations prévues à ce stade sont:

- Un *data paper* présentant le modèle, le plan de simulations et les données générées
- Un article décrivant l'influence du contexte agronomique et écologique sur l'efficacité du contrôle biologique
- Un article discutant de la manière de définir le contrôle biologique par différentes proxy (paysagères et écologiques) et des biais que cela induit.
- Un article analysant l'effet des instruments de politique publique sur le contrôle biologique.

C PRESENTATION DES AVANCEES

Voir rapport ci-joint.

Analyse de l'éco-efficacité agro-écologique et économique de paysages : Modèle Proie-Prédateur-Paysage avec décisions économiques

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Projet PEERLESS (Tâche 5 - Tâche 6)

12 février 2018

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1 Introduction

Ce livrable décrit les travaux menés conjointement par les unités Economie Publique et BioSP dans le cadre des tâches 5 et 6 du projet PEERLESS. Dans une approche interdisciplinaire, nous avons construit un modèle économique-agronomique-écologique représentant un paysage agricole ($1km^2$), dont l'usage des sols et les pratiques (fertilisation, usage de pesticides) dépendent du contexte économique, agronomique et écologique, et en particulier de la présence de ravageurs et de leurs ennemis naturels.

Le modèle a été utilisé pour générer une grande base de données de simulation, qui sera exploitée pour des publications interdisciplinaires.

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- Un article analysant l'effet des instruments de politique publique sur le contrôle biologique.

2 Modèle écologique-économique

La dimension économique du modèle décrit comment les agriculteurs allouent les terres entre différents usages en fonction

- des conditions agronomiques : qualité de leur sol
- des conditions économiques : prix de la production, coûts des intrants et des pratiques, instruments de politique publique (taxes, subventions, bonus de prix pour les productions sans pesticides)
- des conditions écologiques : la présence de ravageurs et de leurs prédateurs
- de leurs préférences : utilité du profit et désutilité des pesticides (effet "santé") [1]

Leurs décisions portent sur

- L'allocation des sols entre cultures et habitats non cultivés [2]
- L'utilisation de fertilisants sur les cultures
- L'usage de pesticides sur les cultures, avec trois modalités : pas de traitement, traitement moyen et traitement fort.

La dimension écologique du modèle décrit l'évolution des populations de ravageurs et de prédateurs en fonction de l'utilisation des sols et des pratiques phytosanitaires.

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[1] Cet effet n'est pas représenté dans les simulations car il est équivalent à la taxe lorsque la désutilité des pesticides est linéaire.

[2] Il est possible de considérer ces HNC comme des prairies de fauche dont le produit serait vendu, mais nous retenons dans les simulations l'option plus simple consistant à dire que ces HNC ne génèrent pas de revenu privé.

Des indicateurs permettent d'estimer les performances locales (champs) et régionales (paysage) en termes économiques, agronomiques et environnementaux / écologiques, à chaque date.

2.1 Choix de modélisation

Le modèle décrit la dynamique des paysages ainsi que la dynamique des ravageurs et de leurs prédateurs en fonction des décisions d'usage des sols agricoles. Nous utilisons pour cela un modèle écologique proie-prédateur en temps continu avec décisions discrètes à intervales réguliers. L'instant initial est noté 0. Nous supposons qu'il n'y a pas de ravageurs dans le paysage initialement. L'optimisation économique donne les conditions initiales du payage. Chaque période de temps discret t, appelée année, correspond à l'intervalle continu $]t-1;t]$. Ainsi, la première année se termine à l'instant 1, et l'année t se termine à l'instant t (description du temps de type “calendaire”). L'introduction des ravageurs dans le paysage se fait à un temps $T_{intro} \in \mathbb{N}^+$. Cela représente une invasion du paysage par le nuisible.

Le modèle écologique est défini en temps continu. Le modèle agroéconomique est tel que les décisions d'usage des sols (choix des cultures) se font en début de période en fonction des anticipations sur les variables d'intérêt à partir des conditions terminales de la période précédente. Les performances de l'année sont calculées en fin de période, qui correspond à la récolte. Les performances agronomiques et économiques de l'année t sont donc calculées en fonction des valeurs des variables à l'instant t.

2.2 Contexte agronomique

Un territoire correspond à un ensemble de parcelles réparties dans l'espace. Le territoire est modèlisé par une lattice Q de dimension $n \times n$. Chaque cellule $(i,j) \in [1:n]^2$ représente un hectare[3] et a une qualité inhérente $Q_{i,j}$ qui représente le rendement potentiel maximal de la parcelle si elle est mise en culture, lorsqu'il n'y a pas de facteurs limitants (fertilisation maximale), et en l'absence de dommages liés aux ravageurs. Cette qualité varie entre des valeurs $Y_{\min} = 0$ et $Y_{\max} = 12$ (tonnes par hectare) qui correspondent à des rendements minimum et maximum réalistes pour des régions tempérées sur des grandes cultures (Martinet, 2013). La qualité de chaque cellule prend une valeur entre ces bornes. La qualité de cellules proches dans l'espace peut être plus ou moins corrélée. Le paysage est ainsi décrit par une distribution des qualités des sols dans l'intervalle $[Y_{\min}; Y_{\max}]$ et une autocorrélation des qualités dans l'espace.

Les bornes des rendements régionaux $Y_{\min}$ et $Y_{\max}$, la distribution des qualités $Q_{i,j}$ sur cet interval, et la répartition spatiale des qualités sont générées de manière aléatoire pour chaque simulation, pour représenter une diversité de configuration

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[3] Cette représentation permet de modéliser des choix d'allocation des sols à une échelle plus fine que celle de la parcelle, par exemple pour représenter la mise en jachère écologique d'une partie de parcelle.

pédoclimatiques. Cela donne une carte régionale de qualité des sols spécifique à chaque simulation. Il y a donc des régions de qualités agronomiques plus ou moins bonnes, plus ou moins hétérogènes, et dont les qualités sont plus ou moins agrégées dans l'espace. Cela permet d'étudier une diversité de contexte agricoles, ainsi que l'effet de l'agrégation des usages des sols sur la performance de l'agroécosystème et des politiques publiques.

2.3 Usages de sols et production agricole

Nous considérons deux types d'usage des sols les cultures (C), et les Habitats Non Cultivés (HNC) générant un profit différent. Nous considérons des frais de changement d'occupation des sols $\mathcal{C}$ asymétriques, avec un surcoût pour le passage de la culture à l'HNC, i.e., $\mathcal{C}_{C\to HNC} > \mathcal{C}_{HNC\to C} > 0$. Cela représente le fait que les coûts d'implentation d'une infrastructure écologique ou d'une jachère (semis et entretien) sont supérieurs au coûts de retournement de celle-ci (travail du sol et désherbage).

Habitats non cultivés Les habitats non-cultivés (e.g., prairies semi-naturelles) rapportent une éventuelle subvention s_{HNC}. Une version alternative du modèle consiste à leur attribuer également un revenu donné p_{HNC} supposé homogène dans l'espace (i.e., ne dépendant pas de la qualité des sols).[4] Si la parcelle était cultivée l'année précédente, un coût de conversion $\mathcal{C}_{C\to HNC}$ vient diminuer le profit. On a donc :

$$\pi^{HNC}(t) = p_{HNC} + s_{HNC} - \mathbf{1}_{C\to HNC}\mathcal{C}_{C\to HNC} \tag{2.1}$$

où l'opérateur $\mathbf{1}_{C\to HNC}$ est égal à 1 si la parcelle était en culture à la date $t-1$ et zéro sinon.

Cultures Les parcelles cultivées offrent des rendements $Y_{i,j}$ hétérogènes dans l'espace, qui dépendent de la qualité locale du sol $Q_{i,j}$, du niveau de fertilisants appliqué $f_{i,j}$ et des dommages L proportionels à la population locale de ravageurs $P_{i,j}$. Les populations de ravageurs dépendent des décisions locales (pesticides) mais aussi de l'utilisation des terres et des traitements phytosanitaires sur l'ensemble du paysage, et de la présence de prédateurs (voir description du modèle écologique).

Production Le rendement est donné, pour l'année de production t, par une fonction de rendement de type “Mitscherlich-Baule” prenant en compte les ravages des cultures :

$$Y_{i,j}(Q_{i,j}, f_{i,j}(t), P_{i,j}(t)) = Q_{i,j}\left(1 - c_1 e^{-c_2 f(t)}\right)\left(1 - L\left(P_{i,j}(t)\right)\right). \tag{2.2}$$

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[4] Un raffinement consisterait à introduire un système de vente de la production de la prairie, avec une hétérogénéité spatiale de la production. Les paramètres pour cela sont disponibles. PAr ailleurs, lorsuqe l'on considère un revenu constant, son rôle est parfaitement substituable à une subvention. Dans les simulations, nous fixerons donc le revenu à 0 et ferons varier le niveau de subvention, qui sera interprété comme un revenu global de l'habitat non cultivé.

Le paramètre c_1 représente la part du rendement perdue quand aucun fertilisant n'est appliqué et le paramètre c_2 représente l'effet marginal des fertilisants sur le rendement. Ces deux paramètres sont fixés de manière exogène.

Le terme $L(P_{i,j})$ correspond à la perte de rendement liés aux domages causés par les ravageurs présents dans la parcelle au moment de la récolte.[5] On remarquera que le niveau d'utilisation des pesticides n'entre pas explicitement dans l'équation. Il influence par contre la population de ravageurs et donc les dégats qu'ils provoqueront.

Profit Le profit des cultures dépend

- des rendements obtenus $Y_{i,j}$
- du prix[6] de vente du produit p. Pour prendre en compte une possible différence de qualité du produit en fonction du mode de production (présence ou absence de pesticides), le prix des productions réalisées sans pesticides est majoré d'un bonus $\beta \geq 0$. (Fonction indicatrice $\mathbf{1}_{no\_pesticide}$).
- des coûts des intrants λ_f et λ_φ, ainsi que de potentielles taxes sur ces intrants θ_f et θ_φ.
- d'un coût fixe ν
- d'éventuels coûts de conversion $\mathcal{C}_{HNC \to C}$ si la parcelle a changé d'usage en début d'année.

Le profit s'exprime donc comme suit :

$$\begin{aligned} \pi^C_{i,j}(t) = p(1 + \mathbf{1}_{no\_pesticide}\beta)Y_{i,j}(Q_{i,j}, f_{i,j}(t), P_{i,j}(t)) - (\lambda_f + \theta_f)f_{i,j}(t) \\ - (\lambda_\varphi + \theta_\varphi)\varphi_{i,j}(t) - \nu - \mathbf{1}_{HNC \to C}\mathcal{C}_{HNC \to C} \end{aligned} \tag{2.3}$$

2.4 Préférences des agriculteurs, rationalité, anticipations et décisions

Chaque agricultueur possède une seule parcelle, de telle sorte que le modèle peut s'apparenter à un modèle mutli-agent (ou un automate cellulaire). La fonc-

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[5] Plusieurs types de fonctions de dommage ont été utilisées dans la littérature. Par exemple, Mitchell (2001) utilise la forme $L(P) = \frac{aP}{1+bP}$, les paramètres a et b caractérisant la virulence des ravageurs. Cette fonction de dommage peut être caractérisée par les paramètres L_{max} (correspondant au dommage maximum) et $P_{1/2}$ (densité de ravageurs provoquant des dégats égals à $L_{max}/2$) avec $a = L_{max} \times (1 - P_{1/2})/P_{1/2}$ et $b = (1 - 2 \times P_{1/2})/P_{1/2}$. L'inconvénient de ce type de fonction de dommage est qu'elle ne prend pas en compte les liens entre production, capacité de charge de la parcelle pour le ravageur et dommages. En faisant l'hypothèse que la capacité de charge du ravageur dépend de la production, et que sa capacité de charge est atteinte lorsque la récolte est totalement détruite, on peut supposer que les dommages sont proportionnels à la densité de ravageur (i.e., $L(P) \propto P/Q$, où Q est la capacité de charge exprimée comme le rendement potentiel de la parcelle.). Dans cette représentation des dommages, la virulence des ravageurs est liée directement à leur taux de croissance. Ceci est rendu possible dans notre approche par le représentation explicite des dynamiques écologiques.

[6] Les prix sont dans une première version supposés fixes mais les fluctuations de marchés peuvent être modélisées en utilisant un système dynamique avec des prix autocorrélés et des chocs aléatoires. Les agriculteurs anticipent alors ces fluctuations de façon rationelle (Barraquand and Martinet, 2011).

tion objectif de chaque agriculteur dépend du profit de l'usage de sa parcelle et du mode de conduite phytosanitaire, afin de représenter une possible aversion à l'usage de pesticides, par exemple pour des questions de santé. Cette aversion est représentée par un niveau de pénalisation de l'usage des pesticides σ caractérisant le contexte régional des préférences, qui définit une préoccupation de santé liée à l'exposition individuelle au pesticide lors de l'épandage local $\varphi_{i,j}$.

Pour des raisons de simplicité, nous ne considérons pas un objectif intertemporel. L'utilité que l'agriculteur tire d'un usage des sols $LU = \{C; HNC\}$ au temps t est donnée par :

$$U_{i,j}(t) = \pi_{i,j}^{LU}(t) - \sigma\varphi_{i,j}(t) \tag{2.4}$$

Cela permet d'étudier l'effet de levier informationnels liés au risque santé sur le comportement des acteurs.[7]

On suppose que les agents sont rationels et maximisent leur utilité. Les décisions d'utilisation des sols dépendent donc du profit relatif lié à chaque mode d'utilisation ainsi que de l'exposition aux pesticides que chaque usage entraine.

On considère trois niveaux de traitement phytosanitaires : pas de traitements, traitement moyen, et traitement élevé. Cela se justifie par l'aspect discret des choix de traitement et des nombres de doses associées. Etant donné ce nombre discret de choix de conduite de culture, en début d'année, l'agriculteur fait face à quatre options d'usage des sols : prairie, culture sans pesticides, culture avec niveau de pesticides moyen, culture avec niveau de pesticides élevé. Il peut anticiper un profit pour chacune de ces options, en fonction d'une anticipation du nombre de ravageurs associé à chacune, et choisir celle qui maximise son utilité.

La rationalité individuelle est cependant limitée par la connaissance des dynamiques écologiques et des décisions des autres acteurs du paysage. Les décisions se font donc à partir d'anticipation des densités de ravageurs au moment des dommages (voir description du modèle écologique). On note cette densité anticipée $\tilde{P}_{i,j}(t)$. Différents modèles d'anticipation sont envisagés plus loin.

A partir de ces anticipations, le décideur va déterminer la quantité d'intrant optimale dans chaque option de culture.

Optimalité dans l'usage des fertilisants Nous considérons que les agriculteurs optimisent leurs revenus au regard de leur niveau de fertilisation. Cela permet de trouver la forme de la quantité de fertilisants optimale

$$f_{i,j}^{*}(t) = \frac{-1}{c_2} ln \left(\frac{\lambda_f + \theta_f + \sigma\varphi_{i,j}}{p(1 + \mathbf{1}_{no\_pesticide}\beta) c_2 c_1 Q_{i,j} \left(1 - L(\tilde{P}_{i,j}(t))\right)} \right) \tag{2.5}$$

Ensuite, cela permet de définir les rendements et profits anticipés avec chaque type d'utilisation des sols. En choisissant l'usage qui maximise le profit, nous

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[7] Techniquement, cela revient à imposer une taxe sur les pesticides. Les deux instruments sont confondus dans l'implémentation informatique du modèle. La seule différence sera dans l'interprétation et dans le calcul d'un éventuel revenu fiscal de la taxe.

obtenons ainsi pour chaque année t une lattice d'utilisation des sols. C'est sur cette lattice que la dynamique des populations est simulée.

Remarque 2.1 *Toutes les valeurs économiques sont exprimées à l'hectare pour éviter les effets d'échelle. On considère donc implicitement des rendements d'échelle constants sur tous les facteurs de production autres que la qualité des sols.*

2.5 Modèle écologique

La description de dynamiques multi-espèces dans des environnements spatialement et temporellement variables repose souvent sur des modèles dits de réaction-diffusion (Turchin, 1998; Murray, 2002; Cantrell and Cosner, 2003; Roques, 2013). L'approche adoptée ici pour la description des dynamiques de populations de ravageurs et de leurs ennemis naturels utilise un système dynamique sur grille (Weinberger, 2002; Guo and Wu, 2012), qui est le pendant des modèles de réaction-diffusion pour des espaces discrets, le temps restant une variable continue. Chaque élément de la grille correspond à une parcelle, la dynamique sur cette parcelle dépendant de son usage (culture ou habitat non cultivé) et de l'utilisation de pesticides.

Le temps continu est décrit par une variable $\tau \geq 0$, qui coïncide avec le temps discret t décrit dans les sections précédentes quand $\tau \in \mathbb{N}$. Nous notons $\mathbf{x} = (i,j)$ les positions des parcelles appartenant à la lattice de dimension $n \times n$. Le système dynamique décrivant l'évolution des populations de ravageurs ($P_\tau(\mathbf{x})$) et de leurs ennemis naturels ($N_\tau(\mathbf{x})$) est le suivant :

$$\left\{ \begin{array}{l} P'_\tau(\mathbf{x}) = D_P \mathcal{D}[P_\tau(\mathbf{x})] + g_P(\tau, \mathbf{x}, P_\tau(\mathbf{x})) - \varphi_\tau(\mathbf{x}) P_\tau(\mathbf{x}) - \alpha_1 \, P_\tau(\mathbf{x}) N_\tau(\mathbf{x}), \\ N'_\tau(\mathbf{x}) = D_N \mathcal{D}[N_\tau(\mathbf{x})] + g_N(\tau, \mathbf{x}, P_\tau(\mathbf{x})) - \varphi_\tau(\mathbf{x}) N_\tau(\mathbf{x}) + \alpha_2 \, P_\tau(\mathbf{x}) N_\tau(\mathbf{x}). \end{array} \right. \tag{2.6}$$

Les déplacements des individus sont décrits par l'opérateur discret de Laplace : pour $\mathbf{x} = (i,j)$,

$$\mathcal{D}[U(i,j)] = \frac{U(i+1,j) + U(i-1,j) + U(i,j+1) + U(i,j-1) - 4\,U(i,j)}{\delta_x^2}, \tag{2.7}$$

où $\delta_x = L/n$, L étant la longueur des côtés du site d'étude, dont la valeur est ici normalisée à $L = 1$. Ainsi, à chaque pas de temps de longueur infinitésimale δ_t, une proportion $4\,D_P\,\delta_t/\delta_x^2$ de la population de ravageurs située en chaque point $\mathbf{x}$ se répartit sur les parcelles adjactentes (idem pour les ennemis naturels, en remplaçant D_P par D_N). Les paramètres D_P et D_N, appelés coefficients de diffusion, contrôlent donc la mobilité des individus. Pour le calcul de $\mathcal{D}[U(i,j)]$ aux bords du domaine, nous choisisons des conditions périodiques.

Les fonctions g_P et g_N décrivent la croissance (ou décroissance) de P et N respectivement, en l'absence d'intéractions entre les espèces et en l'absence de traitements. La fonction g_P prend la forme suivante :

$$g_P(\tau, \mathbf{x}, P_\tau(\mathbf{x})) = \left\{ \begin{array}{l} 0 \text{ si } \tau \in [t, t+1/2[\\ R_{P,\tau}(\mathbf{x}) P_\tau(\mathbf{x}) \left(1 - \frac{P_\tau(\mathbf{x})}{Q(\mathbf{x})}\right) \text{ sinon,} \end{array} \right. \tag{2.8}$$

où

$$R_{P,\tau}(\mathbf{x}) = \left\{ \begin{array}{l} g_P > 0 \text{ sur culture,} \\ 0 \text{ sur prairie.} \end{array} \right. \tag{2.9}$$

Nous supposons ainsi que la fonction de croissance est nulle durant la première partie de l'année, correspondant aux mois qui suivent la récolte. Durant l'autre partie de l'année, $R_{P,\tau}(\mathbf{x})$ est taux de croissance intrinsèque du ravageur P, qui dépend de l'usage du sol à la position $\mathbf{x}$ au temps τ ; $Q(\mathbf{x})$ est la qualité du milieu, comprise entre $Y_{\min}$ et $Y_{\max}$. Nous supposons que la capacité de charge du milieu pour le ravageur est propotionnelle à la qualité du milieu (rappelons que la qualité correspond elle-même au rendement potentiel maximal d'une parcelle). A une renormalisation près, nous pouvons donc supposer que capacité de charge et qualité du milieu sont deux quantités identiques.

La fonction g_N est décrite par :

$$g_N(\tau, \mathbf{x}, N_\tau(\mathbf{x})) = \left\{ \begin{array}{l} -N_\tau(\mathbf{x})/\gamma \text{ sur culture,} \\ r_N N_\tau(\mathbf{x})\,(1 - N_\tau(\mathbf{x})) \text{ sur prairie.} \end{array} \right. \tag{2.10}$$

Ici, γ correspond à l'espérance de vie des ennemis naturels sur culture, en l'absence de proies et r_N à leur taux de croissance intrinsèque dans les prairies. A une renormalisation près, la capacité de charge du milieu pour N dans les prairies est ici fixée à 1.

Dans le système (2.6), le coefficient $\varphi_\tau(\mathbf{x})$ correspond au taux de mortalité induite par le pesticide. La valeur du coefficient dépend de l'efficacité du traitement ainsi que du type d'usage du sol :

$$\left\{ \begin{array}{l} \varphi_\tau(\mathbf{x}) = \rho > 0 \text{ sur culture faiblement traitée,} \\ \varphi_\tau(\mathbf{x}) = 2\,\rho \text{ sur culture fortement traitée,} \\ \varphi_\tau(\mathbf{x}) = 0 \text{ sur culture non-traitée et sur prairie.} \end{array} \right. \tag{2.11}$$

Enfin, les termes $-\alpha_1\, P_\tau(\mathbf{x}) N_\tau(\mathbf{x})$ et $\alpha_2\, P_\tau(\mathbf{x}) N_\tau(\mathbf{x})$ correspondent à l'impact des interactions entre le ravageur et son ennemi naturel sur leurs dynamiques respectives.

Remarque 2.2 *Notons qu'un passage à la limite $\delta_x \to 0$, c'est à dire pour des grilles dont les mailles deviennent infiniment fines, permet d'obtenir un système de réaction-diffusion. Ainsi, le modèle développé ici peut très facilement s'adapter à des environnements continus ou définis sur des grilles non rectangulaires.*

Valeurs des paramètres

Des gammes de valeurs réalistes pour les coefficients D_P, D_N, g_P, r_N, γ, ρ et α_1, α_2 peuvent être obtenues selon la logique suivante.

Termes de croissance g_P, r_N. Considérons un modèle malthusien $U' = r\,U$, correspond à la dynamique d'une population en l'absence d'intéractions intra et interspécifiques, de dispersion et d'utilisation de pesticides. Sur 1/2 année (période entre l'émergence des ravageurs et la récolte), cette population est multipliée par $e^{r/2}$. Un taux de multiplication compris entre 2 et 100 correspond donc à des valeurs de r entre $\ln(4)$ et $\ln(10^4)$. Nous supposons que $r_N \in (\ln(4), \ln(10^4))$ et que le prédateur a un dynamique plus lente, correspondant à un doublement annuel (sur prairies) : $r_P = \ln(2)$.

Coefficients de diffusion D_P, D_N. Considérons une prairie isolée avec des conditions absorbantes (les prédateurs qui quittent la prairie meurent). La survie de la population de prédateurs dans cette prairie isolée correspond à l'instabilité de l'état $N = 0$, soit $r_N > 4\, D_N/\delta_x^2$, correspondant à une valeur de D_N vérifiant $D_N < r_N\, \delta_x^2/4$, soit avec $\delta_x = L/n = 1/n$, $D_N < \dfrac{r_N}{4\, n^2}$.

Notons qu'à chaque pas de temps δ_t une proportion $4\, D\, \delta_t/\delta_x^2$ de la population (nuisible et prédateur) située en chaque point $\mathbf{x}$ se répartit sur les parcelles adjactentes (où $D = D_P$ ou D_N). Prenons $\delta_t = 1$ jour ; la valeur $r_N/(4\, n^2)$ calculée ci-dessus correspond à une proportion d'environ 0.2% de la population migrant sur les parcelles voisines par jour. Dans nos simulations, nous supposons qu'entre 0.1% et 1% de la population migre sur les parcelles voisines pendant cet intervalle de temps, correspondant approximativement aux valeurs

$$D \in \left[\frac{1}{10\, n^2}, \frac{1}{n^2}\right].$$

Niveau de traitement φ. Nous supposons que la valeur de φ induit une mortalité dans le même intervalle que la croissance des populations de ravageurs : $\rho \in (\ln(4), \ln(10^4))$.

Espérance de vie γ du prédateur sur culture. Nous supposons que l'espérance de vie du prédateur est de $\gamma = 1/2$ soit 6 mois sur culture. A titre d'exemple, les carabidæ ont une espérance de vie souvent comprise entre un et quatre ans *dans leur milieu naturel.*

Termes d'interactions α_1, α_2. Considérons, sur une culture $\mathbf{x}$, les intéractions ravageur/prédateur en l'absence de dispersion et de traitement, et dans le cas $R_{P,\tau}(\mathbf{x}) = g_P > 0$ (présence de ressource pour le ravageur). Le système (2.6) devient :

$$\begin{cases} P_\tau' = g_P\, P_\tau \left(1 - \dfrac{P_\tau}{Q(\mathbf{x})}\right) - \alpha_1\, P_\tau N_\tau, \\[2ex] N_\tau' = -N_\tau/\gamma + \alpha_2\, P_\tau N_\tau. \end{cases} \tag{2.12}$$

Les états stationnaires de ce système sont $(0,0)$, $(Q(\mathbf{x}), 0)$ et $\left(\frac{1}{\gamma\, \alpha_2}, \frac{r_N}{\alpha_1}\left(1 - \frac{1}{\alpha_2 \gamma Q(\mathbf{x})}\right)\right)$. Ce dernier état, correspondant à une coexistence ravageur/prédateur, n'existe (et n'est stable) que si $\alpha_2\, \gamma\, Q(\mathbf{x}) > 1$. On choisit ici α_2 de telle sorte que N se stabilise à une valeur stationnaire comprise entre 25% et 75% de $Q(\mathbf{x})$ quand

$Q(\mathbf{x}) = (Y_{\min} + Y_{\max})/2$, soit

$$\alpha_2 \in \frac{2}{\gamma(Y_{\min} + Y_{\max})} \left(\frac{4}{3}, 4\right). \tag{2.13}$$

Le changement de variables $\tilde{P} = \alpha_1 P$ permet de voir facilement que la dynamique des ravageurs dans (2.12) ne dépend pas de α_1. Nous pouvons donc poser, sans perte de généralité sur la dynamique de N,

$$\alpha_1 = \alpha_2 = \alpha. \tag{2.14}$$

Remarque 2.3 *L'unité de N étant renormalisée par rapport à la capacité d'accueil $Q(\mathbf{x})$, il est normal de voir apparaître une dépendance entre les valeurs prises par le coefficient α_2 et les bornes $Y_{\min}$ et $Y_{\max}$ pour $Q(\mathbf{x})$.*

2.5.1 Anticipation des populations de ravageurs

Afin de prévoir les dégats engendrés par les ravageurs sur le rendement, nous supposons que les agriculteurs anticipent l'évolution future de ces populations à partir des indications dont ils disposent au temps $t-1$. Cette prévision dépendra donc du niveau d'information et du degré de rationalité du décideur.

Pour calculer ces populations anticipées par les agriculteurs suivant différents degrés de rationalité, nous utilisons une version dégradée du modèle de dynamique des populations (2.6). Nous considérons trois niveaux d'anticipation :

- Anticipation de la croissance des ravageurs sans prise en compte de la prédation et de la diffusion (Proie)
- Anticipation de la croissance des ravageurs avec prise en compte de la prédation mais pas de la diffusion (Proie_Prédateur)
- Anticipation de la croissance des ravageurs avec prise en compte de la prédation et de la diffusion (Proie_Prédateur_Paysage)

Ces trois options correspondent à la connaissance de la part des agriculteurs des interactions trophiques et des phénomènes spatiaux.

Pour des questions de simplicité (et parce que la solution du problème avec interactions stratégiques ne peut être obtenue dans un modèle aussi complexe)[8] nous considèrons que les agriculteurs appliquent ce raisonnement sur le paysage actuel, en prenant en compte les changements induits par leurs options d'usage des sols, mais en faisant comme si les autres agriculteurs n'allaient pas changer leur usage des sols.

$$\begin{cases} P'_\tau(\mathbf{x}) = g_P(\tau, \mathbf{x}, P_\tau(\mathbf{x})) - \varphi_\tau(\mathbf{x}) P_\tau(\mathbf{x}) \underbrace{-\alpha_1 P_\tau(\mathbf{x}) N_\tau(\mathbf{x})}_{si\ predation} \underbrace{+D_P \mathcal{D}[P_\tau(\mathbf{x})]}_{si\ diffusion} \\ N'_\tau(\mathbf{x}) = \underbrace{g_N(\tau, \mathbf{x}, N_\tau(\mathbf{x})) + \alpha_2 P_\tau(\mathbf{x}) N_\tau(\mathbf{x}) - \varphi_\tau(\mathbf{x}) N_\tau(\mathbf{x})}_{si\ predation} \underbrace{+D_N \mathcal{D}[N_\tau(\mathbf{x})]}_{si\ diffusion}, \end{cases} \tag{2.15}$$

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[8] Rajouter des interactions stratégiques spatiales et dynamiques est trop complexe dans ce modèle mais fera l'objet de travaux théoriques sur un problème plus stylisé par ailleurs.

2.6 Indicateurs de performances

Le programme calcule et stocke, chaque année et pour chaque cellule, des indicateurs primaires de performance (fonction matlab Performances.m) à partir desquels nous pourrons calculer différents indicateurs plus agrégés.

Performance économique individuelle La performance économique d'une parcelle est mesurée par son profit $\pi_{i,j}$.

Performance économique sociale La performance économique d'une parcelle peut être corrigé en tenant compte des instruments de politiques publiques pour calculer le bénéfice économique social $\pi_{i,j} + \theta_f f_{i,j} + \theta_\varphi \varphi_{i,j} - \mathbf{1}_{HNC} s_{HNC}$.

Performance agricole Pour mesurer la performance agricole, nous utilisons le rendement $Y_{i,j}$.

Performance environnementale Pour mesurer la performance environnementale, nous utilisons la quantité de pesticides épandus $\varphi_{i,j}$.[9]

Performance écologique Pour mesurer la performance écologique du système (services et disservices écosystémiques), nous utilisons deux indicateurs :
- le niveau de dommage infligé aux culture $Q_{i,j}\left(1 - c_1 e^{-c_2 f}\right) L\left(P_{i,j}(t)\right)$
- le taux de prédation effectif donné par la différence de densité de ravageur entre le niveau actuel et un niveau de référence calculé en "annulant" l'effet de prédation pour l'année en cours.

Performance paysagère Les usages de sols sont stockés afin de calculer différents indices paysagers relatifs à la composition et à la fragmentation du paysage.

3 Algorithme global pour la simulation de scénarios

3.1 Gestion du temps

Dans ce modèle, les décisions d'usage des sols sont prises à chaque temps discret t. Ces décisions s'appliquent pendant la période $]t; t+1]$ correspondant à

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[9] Nous aurions pu retenir la quantité maximale de pesticides étendue pendant une année ou leur accumulation dans l'environnement en calculant une quantité de pesticide finale présente dans l'environnement à la fin de la période, en prenant en compte un taux d'absorption naturelle. Toutefois, la persistence des pesticides dans l'environnement est très variable (Kerle et al., 1994) et choisir une valeur de temps de demi-vie aurait été compliqué. De plus, étant donné les temps de demi-vie relativement faibles des pesticides dans l'environnement à l'échelle d'une année (Kerle et al., 1994), l'accumulation est faible et cette mesure aurait donné trop de poids à la fin de période. La moyenne spatiale inter-temporelle semble donc mieux reflèter le risque et l'exposition dus à l'utilisation des pesticides dans chaque scénario.

la durée d'une campagne de culture. Le module de dynamique des populations calcule ensuite en temps continue la croissance et la diffusion des populations de ravageurs et de prédateurs entre t et $t+1$. A la fin de chaque campagne, au temps $t+1$, le module de performance, calcule des indicateurs sur la campagne passée puis le module de décision intervient à nouveau pour décider des LU de la campagne suivante.

3.2 Vue globale de l'algorithme

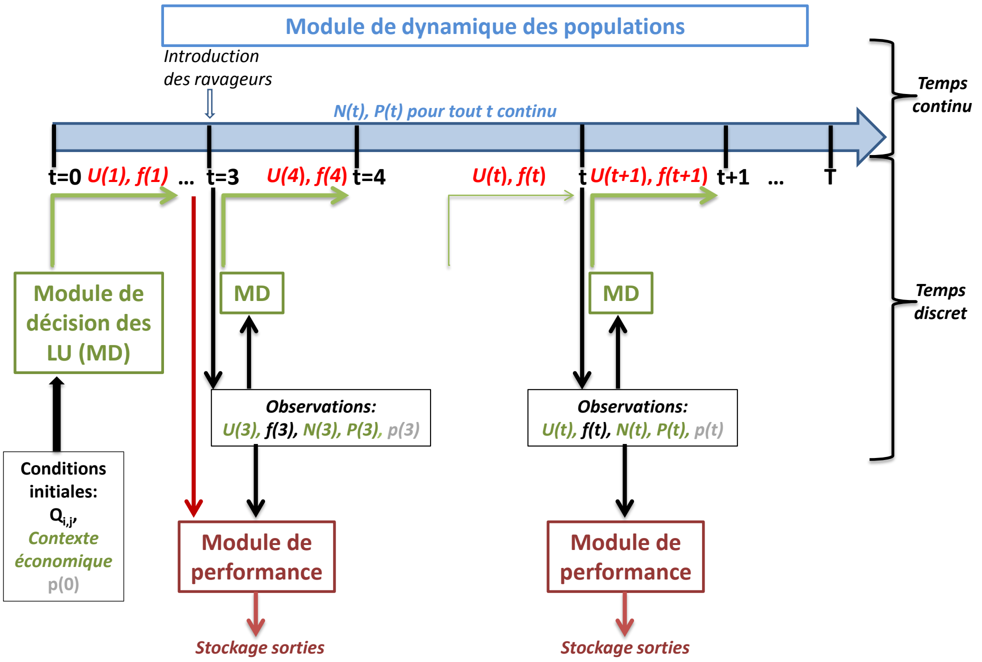

FIGURE 1 – Articulation des différents modules

Pour un jeu de paramètres donné (paramètres agronomiques, écologiques et économiques) et un mode d'anticipation, les différentes fonctions Matlab s'articulent comme suit pour générer un paysage dynamique et les dynamiques des populations associées.

1. La fonction "LUini.m" génère l'usage des sols initial. Cet usage des sols sera stable tant qu'il n'y a pas de ravageurs étant donné que le contexte économique est stable. Cela nous donne une référence "économique" pour le contexte agroéconomique en l'absence de problème de ravageurs.
2. La population des prédateurs est fixée à la capacité de charge dans les prairies. La dynamique des populations donne l'évolution des prédateurs dans l'espace, pour avoir leur densité dans les cultures à l'équilibre
3. A chaque date, les variables agronomique, économiques et écologiques sont stockées.

4. Le nuisible est introduit à une date (e.g., $T_{intro} = 3^+$ soit la période 4), uniformemment dans le paysage.
5. Une des fonctions d'anticipation est utilisée pour générée la matrice tridimensionnelle des scénarios de ravageurs (fonction "PS_Pest... .m" selon le mode d'anticipation de la simulation)
6. La fonction "LandUse.m" détermine l'usage des sols en fonction de ces scénarios ravageurs.
7. La dynamique des populations donne l'évolution des ravageurs et des prédateurs
8. Possibilité de faire une étape intermédiaire de révision des croyances en ajustant l'usage des pesticides en fonction de la densité des ravageurs à mi-temps
9. La population des ravageurs en fin de période est utilisée pour calculer les productions et profits réalisés (stoqués)
10. La population des ravageurs est utilisée par la fonction "LandUse.m" pour déterminer l'usage des sols pour la période suivante... [RETOUR A L'ETAPE 5]

3.3 Plan d'expérience

Nous souhaitons évaluer
- la multiperformance de différents paysages agricoles
- l'influence de la diversité de situations agronomiques et écologiques sur cette performance
- la valeur des Services Ecosystémiques de contrôle biologique des ravageurs
- l'influence d'instruments de politiques publiques
- l'effet du niveau de rationalité des agriculteurs sur les performances des paysages

Pour cela, nous réalisons des simulations avec une diversité de jeux de paramètres biologiques et de lattices de qualité qui correspondent ainsi chacun à un paysage potentiel.

La première étape consiste à générer un contexte agronomique :

1. Tirage d'**une distribution de qualité des sols** (100 valeurs de rendement potentiel plus ou moins concentrées). Cette distribution donne le potentiel agronomique de la région.[10] Elle a pour moyenne une valeur parmi $Y_{\max} * \{0.3; 0.5; 0.7\}$, et pour écart-type une valeur parmi $Y_{\max} * \{0.05; 0.1; 0.3\}$.
2. Génération de plusieurs paysages dans lesquelles les qualités des sols sont plus ou moins corrélées spatialement. Cela permet d'étudier le rôle de

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[10] En l'absence d'effets spatiaux, notamment dans les dynamiques écologiques, tout territoire avec la même distribution aura la même performance.

l'agencement spatial des parcelles sur la performance (donc l'effet "paysage").

Pour chaque contexte agronomique ainsi généré, on fait varier le contexte écologique et économique.

Les paramètres biologiques qui varient (et les valeurs associées) sont : **A corriger en fonction des notations de la partie écologie corrigée, et des valeurs prises dans le programme informatique**

— g_P : le taux de croissance du ravageur (Valeurs : $\{ln(4); 2ln(10); 4ln(10)\}$)

— α : le taux de prédation (Valeurs : $\frac{4}{(Y_{\min}+Y_{\max})}\{0; 1; 2.5; 4\}$)

— D_P : le paramètre de diffusion du ravageur (Valeurs : $\{\frac{1}{n^2}; \frac{1}{n^2}\}$)

— D_N : le paramètre de diffusion du prédateur (Valeurs : $\{\frac{1}{n^2}; \frac{1}{n^2}\}$)

— φ : le taux de mortalité induit par les pesticides (Valeurs : $\{ln(4); 2ln(10); 4ln(10)\}$)

Cela correspond à 144 contextes écologiques.

Les paramètres économiques qui varient sont :

— θ_φ : le niveau de taxation des pesticides (Valeurs : $\{0; 10; 30; 50\}$)

— s_{HNC} : le niveau de subvention des prairies (Valeurs : $\{0; 100; 200; 300; 400; 500\}$)

— β : le niveau de valorisation du produit "sans pesticide" (Valeurs : $\{0; 0.2; 0.5\}$)

Cela correspond à 72 contextes économiques.

Toutes les combinaisons de paramètre sont étudiées pour chaque contexte agronomique.

La combinaison Contexte agronomique × Contexte écologique × Contexte économique constitue un scénario contextuel. Pour chaque scénario contextuel, trois modes d'anticipation sont examinés (scénarios comportementaux).

Ces différentes simulations permettront d'évaluer à la fois les bénéfices apportés par les prédateurs, dans l'esprit du travail de Chambers et al. (2010), ainsi que l'effet de la prise en compte ou non des prédateurs dans les anticipations des agriculteurs mais également les coûts de prévention et de dégats dues à la présence de ravageurs.

4 Paramètres fixes du modèle

Symbole	Description	Valeur	Unité	Source
n	Largeur de lattice de territoire	10		
T	Durée d'une expérience	10	années	
p	Prix de base	150	$Euro.t^{-1}$	RICA 2014 (blé tendre)
$Y_{\min}$	Rendement régional minimum	0	$t.ha^{-1}$	
$Y_{\max}$	Rendement régional maximum	12	$t.ha^{-1}$	Agreste (hétérogénéité départements)
c_2	Effet marginal des fertilisants	0.015	$[t.ha^{-1}]/[kg.ha^{-1}]$	Monod et al. (2002)
c_1	Effet basal des fertilisants	0.38		Monod et al. (2002)
ν	Montant des coûts fixes	110	$Euro.ha^{-1}$	(semences, assurances, produits pétroliers)
λ	Coût d'une unité de fertilisants	1.62	$Euro.unit^{-1}$	AGRESTE 2014 (mix Nitrate d'ammonium 33% + engrais binaire (K,P), ratio (N,K,P)=(3,1,1))
λ_φ	Prix d'une unité IFT de pesticides	33	$Euro.IFT^{-1}$	Butault et al. (2010)
$\bar{\varphi}$	IFT en culture avec pesticides intermédiaire	3	IFT	Butault et al. (2010)
$\underline{\varphi}$	IFT en culture avec pesticides intensifs	6	IFT	Butault et al. (2010)
p_{HNC}	Profit prairie (hors subvention)	0	$Euro$	Habitat non cultivé
$\mathcal{C}_{C\to HNC}$	Coût de conversion de culture vers HNC	219.4	$Euro.ha^{-1}$	Miao et al. (2013) (référence = prairie d'intérêt écologique)
$\mathcal{C}_{HNC\to C}$	Coût de conversion d'un HNC vers culture	27.4	$Euro.ha^{-1}$	Miao et al. (2013)

Table 1 – Paramètres du modèle

5 Eléments d'analyse

A partir des simulations de tous ces scénarios contextuels croisés aux scénarios de politiques publiques, nous allons aborder les questions suivantes :

— Quelles sont les conditions agroécologiques qui favorisent un rôle significatif du biocontrôle ?

— Quel est le rôle des instruments de politique publique sur le biocontrôle et sur l'efficacité des paysages agricoles en termes de profit / de production et de pollution (IFT) ?

— Quel est le rôle des anticipations (connaissances de la dynamique écologique par les agents) sur ces performances ?

5.1 Rôle du contexte agroécologique

L'analyse vise ici à identifier les combinaisons de paramètres agronomiques (type de région agricole : production moyenne, écart-type, agrégation spatiale) et écologique (type de couple ravageur-prédateur, effet des pesticides) pour lesquels le contrôle biologique joue un rôle significatif. Nous nous plaçons pour cela dans un contexte économique de référence, avec $(\theta_\varphi; s_{HNC}, \beta) = (0, 300, 0)$, et examinons l'effet de la présence du prédateur sur le **profit social**, ainsi que sur l'IFT. Cet effet est mesuré par le gain de profit économique pour la société (i.e., corrigé des incitations) lié à la présence du prédateur, et par la variation d'IFT permise par sa présence.

Le gain de profit peut être exprimé en valeur ajoutée absolue, par rapport à une situation sans prédateur :

$$SE^{abs} = \pi(\alpha > 0) - \pi(\alpha = 0) \tag{5.16}$$

ou en valeur ajoutée relative (exprimée en pourcentage), représentant le gain lié à la présence du prédateur :

$$SE^{rel} = \frac{\pi(\alpha > 0) - \pi(\alpha = 0)}{\pi(\alpha = 0)} \tag{5.17}$$

Un valeur absolue s'apparente à la mesure classique du service écosystémique de biocontrôle et c'est cette mesure que nous retenons.

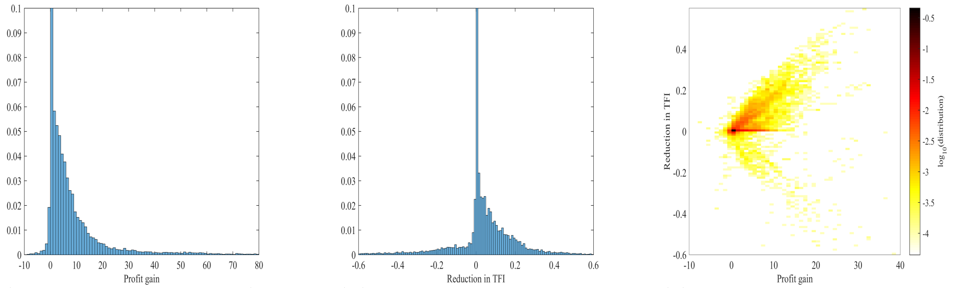
Un indice moins économique serait l'efficacité du contrôle biologique, définie comme

$$SE^{eff} = \frac{\pi(\alpha > 0) - \pi(\alpha = 0)}{\pi(Pest = 0) - \pi(\alpha = 0)} \tag{5.18}$$

et qui correspond au pourcentage du diservice qui est régulé biologiquement.

Il s'agit là de différentes mesures du service écosystémique de contrôle biologique. Pour être plus complet, on peut également compter le gain social lié à la diminution des pesticides dans l'environnement, en rajoutant le terme approprié partout dans ces définitions (mais cela repose sur une hypothèse concernant le coût social des pesticides).

Les performances obtenues au niveau du paysage sont présentés dans les figures 2 ci-dessous, montrant la distribution des performances économiques et environnementales.



(a) Gain économique (variation de profit en Euro par ha)

(b) Réduction de l'IFT

(c) Distribution bi-variée

FIGURE 2 –

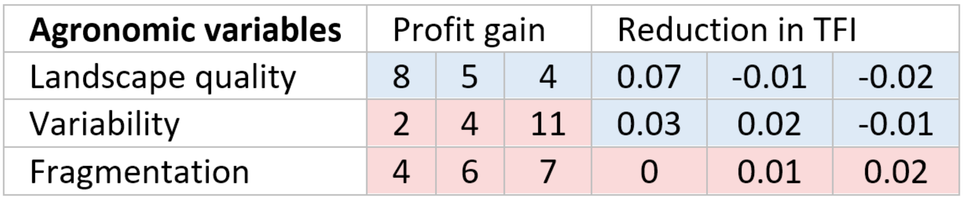
Premiers éléments d'analyse Résultats qualitatifs obtenus à partir de l'analyse des données montre que le contrôle biologique a un effet négligeable dans une moitié des configurations étudiées, et que l'effet est globalement positif dans l'autre moité des configurations, avec des effets plus ou moins marqués.

- L'effet du biocontrôle est d'autant plus fort que la mortalité liée aux pesticides ρ est faible (pas d'effet notable pour ρ important).
- Dans le cas d'une mortalité pesticide ρ faible, le gain lié au biocontrôle est d'autant plus important que la mortalité par prédation est importante.
- La virulence du ravageur (g_P) joue sur le gain, avec peu de gain au biocontrôle pour des valeur faibles ou fortes de g_P mais des gains plus importants pour les valeurs intermédiaires.
- Les paramètres de diffusions jouent en interaction avec la fragmentation du paysage. La diffusion du ravageur a toujours un effet positif sur le biocontrole (plus de ravageurs arrivent dans des HNC). La diffusion du prédateur dépend de l'aggrégation du paysage. Sur des paysages très désagrégés, il vaut mieux un coefficient de diffusion faible dans un contexte fragmenté (car se déplace des HNC vers les cultures voisines) et un coefficient de diffusion plus fort dans un contexte agrégé (pour sortir des gros patchs d'HNC). Ces premiers éléments d'analyse spatiale doivent être complétés par une analyse des indicateurs de paysage (notamment sur les proportions d'HNC).

Ces résultats sont synthétisés dans les tableaux ci-dessous.

5.2 Effet des politiques publiques

Il s'agira d'examiner, séparemment dans un premier temps, l'effet de chaque instrument de politique publique sur la distribution des performances économiques (profit) ou agronomiques (production) vs environnementales (IFT).

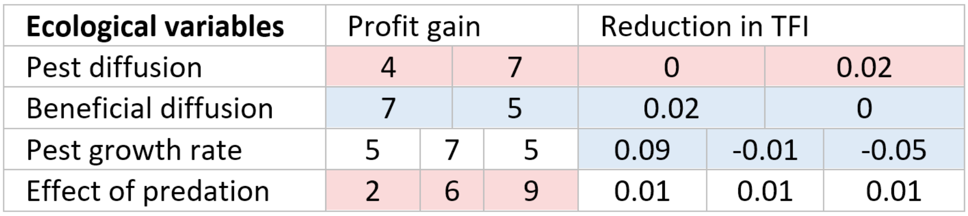


Agronomic variables	Profit gain			Reduction in TFI		
Landscape quality	8	5	4	0.07	-0.01	-0.02
Variability	2	4	11	0.03	0.02	-0.01
Fragmentation	4	6	7	0	0.01	0.02

Figure 3 – Effet des variables agronomiques

Pesticide	Profit gain			Reduction in TFI		
Effect of pesticide	11	3	3	-0.04	0.04	0.03

Figure 4 – Effet des paramètres écologiques



Ecological variables	Profit gain			Reduction in TFI		
Pest diffusion	4		7	0		0.02
Beneficial diffusion	7		5	0.02		0
Pest growth rate	5	7	5	0.09	-0.01	-0.05
Effect of predation	2	6	9	0.01	0.01	0.01

Figure 5 – Effet des paramètres économiques

Ces analyses peuvent être faites sur l'ensemble des contextes agroécologiques, pour examiner l'effet moyen, ou sur les contextes qui favorisent le plus le biocontrôle, afin d'examiner l'effet d'une politique ciblée sur ces zones.

Enfin, cela peut nous donner des pistes d'analyses des effets croisés des politiques.

5.3 Effet des anticipations

Dans un second temps, nous examinerons comment les résultats précédents sont modifiés lorsque les hypothèses d'anticipation des populations biologiques des agriculteurs varient.

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Projet ANR-12-AGRO-006

PEERLESS

Methodology for field/landscape efficiency measurement

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Methodology for field/landscape efficiency measurement
Nature du livrable	Rapport interne
Date de publication	15 juillet 2015

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Partenaires impliqués	Economie Publique
Tâche associée	T6.2

B OBJECTIFS ET RESUME DU LIVRABLE

B.1 OBJECTIFS

Maximum 10 à 20 lignes. Positionner le livrable par rapport à la tâche à laquelle il se réfère et les livrables associés.

Ce rapport interne présente les méthodologies utilisables pour évaluer l'efficacité de pratiques agroécologiques d'une part, et de paysages d'autre part, selon les dimensions de performance économiques, agronomiques, écologiques et environnementales. Ces méthodologies sont associées à des métriques (outils de mesure) permettant de mesurer la distance de la performance d'une parcelle ou d'un paysage à une frontière d'efficience composée de l'ensemble des parcelles/paysages pour lesquel(le)s il n'est pas possible d'améliorer la performance sur une dimension sans la détériorer sur une autre.

Ces méthodologies seront appliquées, dans le cadre de la tâche 6.2, aux données issues de la tâche 6.1. L'objet de la tâche 6.1 est de générer des *ensembles de productions possibles* (sur les différentes dimensions de performance), i) à l'échelle paysagère à partir des modèles élaborés conjointement avec la tâche 5 du projet (modélisation) ; et ii) à l'échelle parcellaire en utilisant les données issues des tâches 1 (suivi terrain) et 2 (expérimentation) du projet lorsque ces données « terrain » le permettent [D6-1 prévu en décembre 2016]. Le résultat de l'analyse de la tâche 6.2 alimentera la tâche 6.3 en identifiant les pratiques agroéclogiques ou les structures paysagères les plus efficaces. Celles-ci fourniront des objectifs pour la définition d'instruments incitatifs pour la régulation de l'usage des sols et le contrôle biologique des ravageurs (tâche 6.3).

B.2 RESUME

Maximum 1 page.

Le rapport se compose en cinq parties.
La première partie correspond à une introduction qui reprend les objectifs du projet PEERLESS et l'articulation entre le travail décrit dans ce livrable et le reste du projet. Ainsi, le document produit peut être lu indépendamment du descriptif du projet. L'objectif global de la tâche 6 du projet y est décrit, ainsi que l'insertion des travaux faisant l'objet de ce rapport. La deuxième partie propose un état des lieux assez formalisé des concepts utilisés en économie pour mesurer l'(in)efficacité. La troisième partie décrit les méthodes d'estimation des frontières d'efficacité et les outils de la mesure de l'efficacité associés. La quatrième partie décrit la manière dont ces instruments de mesure peuvent être étendus et utilisés pour mesurer l'efficacité environnementale de processus de production. Elle permet de faire le lien entre les cadres économiques théoriques décrits dans les parties 2 et 3, et les objectifs précis du travail de recherche mené dans la tâche 6.2 du projet. Cette partie se base sur une revue de la littérature sur la manière dont les outils de mesure de l'efficacité ont été utilisés pour mesurer l'efficacité environnementale, en particulier dans le domaine de l'agriculture, avec un focus sur la réduction des pesticides. La cinquième partie présente la manière dont les outils développés seront utilisés dans le programme de recherche. Elle présente des résultats préliminaires sur la construction de frontières de paysages efficaces en termes de production, de pollution et de lutte contre les ravageurs. Les résultats définitifs du projet feront l'objet du délivrable 6.1 dont le rendu est prévu en fin de projet.

C PRESENTATION DES AVANCEES

Etant donné le caractère technique du contenu du rapport (présence d'équations et de figures), celui-ci a été réalisé sous un logiciel d'édition scientifique et est placé en annexe.
Le document fait XX pages.

Peerless Deliverable report 6-2: MEASURING ENVIRONMENTAL EFFICIENCY

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July 29, 2015

1 Introduction

1.1 Context

Humanity faces unprecedented challenges arising from the scale of human activity and its impacts (Millennium Ecosystem Assessment 2005). Human actions are important drivers of global change, including changes in land use and bio-geochemical cycles, emergent diseases, invasive species, biodiversity loss and climate change that could irreversibly affect the well-being of current and future generations. Predicting the trajectory of global change and human well-being requires an integrated analysis of the dynamics of socialecological systems (Polasky et al., 2011). Agriculture is one important driver of this global change and among the most serious threats to biodiversity (Krebs et al., 1999; Tylianakis et al., 2008). Large-scale modern farming has seen great increases in nutrient and pesticide uses and the simplification of the agro-system by reduction and fragmentation of semi-natural habitats to support agricultural profitability. Higher intensity of land use has also led to conicts between crop production and other ecosystem services provision: examples include water surface pollution, the evolution of pesticide resistance, and loss of biodiversity and of linked ecosystem services (Devine and Furlong, 2007; Krebs et al., 1999). Pressure on limited resources due to human population growth poses a critical challenge to the maintenance of sustainable food supply with a

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minimal loss of biodiversity. Such a *perfect storm*[1] of challenges requires that we change our global paradigm of pure intensification to one based on landscape sustainable development (Rifkin, 2011), through maximizing the benets of ecosystem services provided by farmland biodiversity, such as the control of pest populations by predators and parasitoids Bianchi et al. (2006) supported by ‘ecoagriculture’ landscape management (Scherr and McNeely, 2008; Kareiva et al., 2011).

With the shift towards a reduced reliance on external inputs in agriculture, identifying management options that enhance the provision of ecosystem services has become a critical issue. National- and European-level public policies currently promote alternative methods of crop protection, notably based on pesticide reduction and ecological services. Regulation for plant protection products (EC 1107/2009 and directive 2009/128/EC) establishes a new framework to “achieve a sustainable use of pesticides by promoting the use of integrated pest management and of alternative approaches including the utilization of ecological infrastructures inside and outside production sites.” Overlying these European directives, the French law “Grenelle de lenvironnement” defined the “Ecophyto 2018” goal to reduce pesticide use to 50% of the 2008 level within 10 years (Butault et al., 2010). Pest control resulting from the activity of natural predators and parasitoids is frequently cited as an important service that could reduce pesticide use as targeted by the French 2018 Ecophyto governmental action. However, the link between management options, pest control level and ultimately crop yield is poorly understood. An issue is to understand if each farmer should dedicate a minimum percentage of their farmland area to semi-natural habitats in order to promote pest regulation, or if the effort can be concentrated spatially. This issue has created an urgent requirement for landscape engineering methods. How should our agricultural landscapes, containing both crop and semi-natural habitats, be structured and plant protection products and pest management be employed within them to maximize ecosystem service provision?

1.2 Related economic issues

There are two important economic dimensions to consider when discussing the pros and cons of alternative land use to control insect and weed pests. First, form a macro-economic point of view, better environmental or ecological outcomes may be associated with lower economic outcomes. There may be trade-offs between the different dimensions of sustainability in agriculture. Such trade-offs at the regional or landscape levels have been examined in Polasky et al. (2005, 2011). By means of modeling and selection of

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[1] Global crisis ‘to strike by 2030’ `http://news.bbc.co.uk/2/hi/uk_news/7951838.stm`

optimal land uses, a production possibility frontier of biodiversity and economic profit is constructed by maximizing an outcome under a constraint on the other (e.g., maximizing the economics outcome under an ecological outcome constraint). By varying the level of the ecological constraint, one obtains a set of feasible productions - in a broad sense, including economic and ecological dimensions - whose frontier is usually decreasing. Society has to arbitrate between the two objectives on the efficiency frontier, where it is not possible to improve one outcome without reducing the other. It is, however, important to emphasize that current land uses may be far from efficiency, within the set of possible production situation. Adopting eco-efficient practices may then result in an increased economic outcome ("win-win" situation).

Second, from a micro-economic point of view, it is necessary to assess the cost of improving the agricultural practices from an ecological point of view. This cost is related to the socio-economic acceptance of the alternative practices, and the economic viability of the underlying production patterns. Usually, landscapes are the result of the interaction of numerous individual decisions by private land owners. In such a context, implementing a given land-use pattern is made difficult for two reasons. On the one hand, one has to define proper incentives to modify the individual behaviors in favor of the desired land uses. As the agents are usually heterogeneous and the decision maker does not know their Willingness To Accept (WTA - the amount required to adopt the practice), such policy instruments may be costly as many farmers may be over-paid (Jack et al., 2008). On the other hand, the spatial effect of the incentives has to be consistent with the spatial pattern of the ecological objectives. This requires developing "smart spatial incentives" (Hartig and Drechsler, 2009). If the desired ecological pattern to conserve is expected to last over time, it is of crucial importance to also investigate the sensitivity of economic models to the choice of the time horizon or time preference (Hartig and Drechsler, 2008).

1.3 Peerless project overview

The Peerless project follows three objectives:

1. Identify farming systems and landscape patterns in which functional biodiversity enhances crop productivity through improved provision of ecosystem services of biocontrol.

2. Identify ecological mechanisms linked with spatio-temporal heterogeneity in densities of agronomic pests and their natural enemies that enhance ecosystem services of biocontrol.

3. Design viable deployments of alternative crop systems and semi-natural habitats in spatially explicit landscapes to improve biolog-

> ical pest control. Landscape scenarios based on simulation models of populations dynamic of both pests and their enemies are used to optimize crop productivity, pest control, pesticide reduction and farmers' income.

The PEERLESS project focuses on the functional biodiversity that supports crop protection ecosystem services against important agricultural pests, to elaborate predictive, integrated strategies of crop management at both local- and landscape-scales in both perennial and annual cropping systems to reflect the scales of policy-making and the diversity of agricultural landscapes across France. It aims at identifying alternative management strategies that enhance the crop protection service provided by functional biodiversity and ultimately to optimize agricultural systems, at local and landscape scales, for economic viability and sustainability. The project combines: (i) an empirical assessment of naturally occurring crop protection from weed and insects pests in annual (Wheat/Oil Seed Rape rotations) and perennial (apple orchards) systems across a broad range of landscape and agronomic situations; (ii) ecological engineering with an assessment of alternative plant protection system to improve crop protection at the local scale; (iii) an in-depth study of the structure of trophic networks; and, (iv) population dynamics of key pests and their regulators in case study areas. These components will support the parametrization of spatially-explicit, predictive models to (v) test the effect of landscape patterns of alternative local and landscape management strategies on pesticide use, pest control, crop yield and farmer income and (vi) identify landscape scale viable management strategies to control insect and weed pests. The project is divided in six Tasks, corresponding to the six items above. Part of Task 5 is aimed at designing landscape patterns for pest control, by determining the effect of landscape attributes (e.g. spatial distribution of crops, agronomic practices, pest resistance, etc.) on landscape suppressiveness. Landscape heterogeneity, in itself, can dampen epidemic spread or, at least, involve a privileged direction for the epidemic wave. The objective is to identify spatial patterns that could help in designing suppressive landscape. The system formed by the population dynamics of pests and their natural enemies, on one hand, and the landscape dynamics (Burel and Baudry, 2003), on the other hand, is complex. Indeed, this system is (i) nonlinear (both in time and space) (ii) susceptible to initial conditions and (iii) showing many feedback loops. While more complex to assess, the spatio-temporal patterns that could be extracted from such study would be invaluable in the context of Integrated Pest Management (IPM). These patterns could explore the importance of crop rotation; pesticides use reduction, and many other time-dependent, spatially heterogeneous agronomic practices. Both 'static' and 'dynamic' landscape suppressiveness will be explored using models coupled with multi-objective optimization algorithms e.g. evolutionary algorithm and particle swarm. Such algorithms aim at minimizing or maximizing simultaneously several criteria (for example minimizing the amount of pest damage on crops) with respect to a set of constraints on the decision variables (for example by respecting realistic landscape patterns with a given utilized agricultural area). These algorithms are known to be suitable to a wide range of model types as long as they can provide numerical output, which is the case of all our models.

The objective of task 6 is to provide a socio-economic analysis of the management strategies proposed to control insect and weed pests. On the one hand, this task describes the trade-offs between the various dimensions of agricultural production at the landscape scale. On the other hand, this task develops analytical tools to evaluate the social interest of implementing given management strategies. In this task, the focus of the analysis is reduced to four important dimensions of the performance of the agro-ecosystems at the landscape level: the produced quantity, the gross margin, an environmental index (e.g., the IFT) and an ecological index (e.g., the predation rate, or the avoided pest damage).

Task 6 is divided into three interconnected sub-tasks.

Sub-task 6.1 uses the simulation results of task 5 to build the eco-efficiency production possibility frontier. This frontier is a representation of the necessary trade-offs between the considered criteria. The agro-ecological data generated by the models of task 5 is completed with economic data to provide multidimensional outcomes for each landscape scenario. Efficient points (points on the eco-efficiency frontier, for which it is not possible to improve an outcome without reducing another one) may correspond to land-use patterns not easily achievable. Realistic land-use patterns would lie strictly within the set of feasible outcomes. Therefore, sub-task 6.2 defines instruments to measure the distance of a given land use pattern to the frontier, and to assess the performance of the associated scenario. Different measurement tools are examined. This analysis reveals how far from the efficiency frontier the current (business-as-usual) agricultural land-use is, and what could be the gains of improving eco-efficiency. **This aspect of the project is detailed in the present report.** Sub-task 6.3 defines incentive instruments to reach land-use patterns that are more eco-efficient. This requires assessing the cost of adoption of some innovative agro-ecologic practices, and the interactions of private agents over the landscape. Cost-Benefit analysis will be used to assess the social interest of these public policies. This Cost-benefit analysis will take into account the heterogeneity of farmers profits/preferences regarding the program.

2 Measuring (in)efficiency

2.1 Different approaches to efficiency

Production frontier models seem a natural tool for measuring environmental performance as the objective of minimizing the environmental impact of agricultural activity can be thought of as an efficiency problem. Therefore, in order to properly understand the measurement of environmental efficiency, it is necessary to be familiar with several production theory concepts.

Decision units are efficient if they have produced as much as possible with the actual level of inputs, resources used and if they have produced that level of output at minimum cost. Farrell (1957), drawing upon the previous work of Koopmans (1951) and Debreu (1951), argued that the overall, or economic, efficiency could consist of two components:

- Allocative efficiency: it refers to the ability to combine outputs and inputs in optimal proportions in the light of current prices and tecnology.
- Technical efficiency: it refers to the ability to obtain the maximum level of output given the level of inputs. In the literature there are two main definitions of technical efficiency:
    - Debreu (1951) and Farrell (1957) defined technical efficiency as "*one minus the maximum equiproportionate reduction in all inputs that still allows the production of given outputs, a value of one indicates technical efficiency and a score less than unity indicates the severity of technical inefficiency*". This measure of technical efficiency is known as the Debreu-Farrell measure.
    - Koopmans (1951) indicates that "*a producer is technically efficient if an increase in an output requires a reduction in at least on other output or an increase in at least one input, and if a reduction in any input requires an increase in at least one other input or a reduction in at least one output*".

Therefore, allocative and technical efficiency can be measured following two approaches:

- The input approach: it considers the ability to minimize the level of inputs used while keeping the outputs constant.
- The output approach: it considers the ability to maximize the level of output produced while keeping the inputs constant.

In the following section we will discuss further on these two approaches, beginning with Farrell's example that had an input-reducing focus.

2.1.1 Input efficiency

Figure 1 represents a production technology based on two inputs (x_1 and x_2) through an isoquant curve (yy')[2]. At the optimal production level, the tangent to the production function is equal to the ratio of the costs of production factors (isocost curve). The input mix in $C$is thus optimal for the given level of output. Firms located in A, C and D are technically efficient, whereas that in B is not. Technical efficiency is Farrell's sense is measured as the distance to the frontier for a given ratio of production factors x_1/x_2. In this example, ratio $0S/0B$ measures the technical efficient of firm B (it is between 0 and 1). Although the technology in S is technically efficient, it is more costly that input mix C. This difference provides a way to measure price-efficiency, by the ratio $0R/0S$. One can then measure overall efficiency of firm B as the by the ratio $0R/0B$, which is the product of the two efficiency components:

$$0R/0B = 0S/0B \times 0R/0S. \tag{1}$$

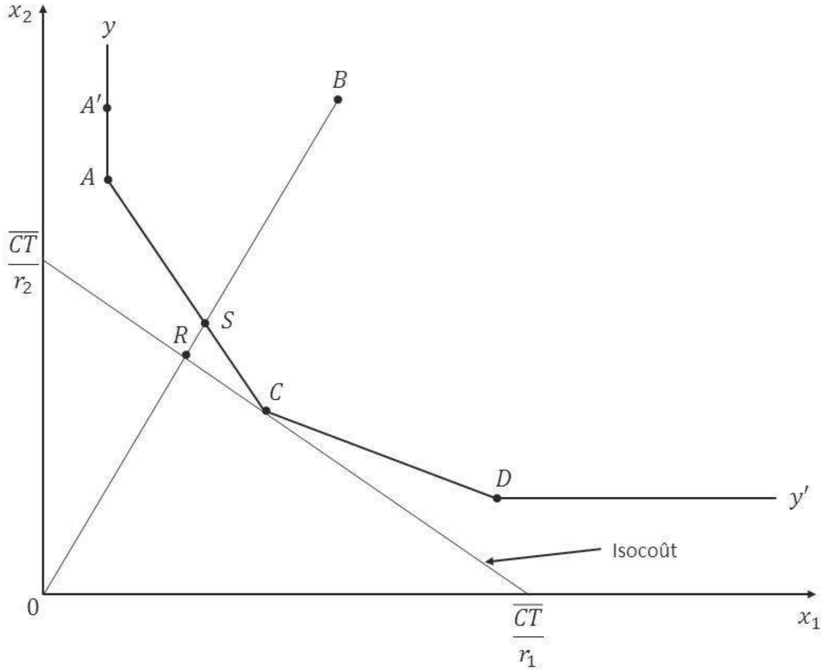

Figure 1: Farrell's efficiency measure

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[2] A single isoquant curve is sufficient to represent the technology under constant returns to scale.

Note that, on figure 1, point A', which is located just above point A, is technically efficient in Farrell's sense, but not in Koopmans' sense, as one could diminish the quantity of input x_2 without diminishing the output level. This difference is usually called the "*input slack*"). Technical efficiency is thus necessary but not sufficient to define overall efficiency.

According to Lovell (1993) this "drawback" of Farrell's efficiency has received to much emphasize, at least because this distinction vanishes in the case of parametric frontiers, but also because it is always possible to measure efficiency and "*slacks*" separately when defining non-parametric frontiers. Nevertheless, many authors have proposed alternative approaches to "solve the problem", without providing a perfect solution. We shall present here the approach of Färe and Lovell (1978), to emphasize the direction taken by these researches.

For Färe and Lovell (1978), x is an efficient input vector if and only if it belongs to the efficient subset Eff $L(y)$ defined as follows :[3]

$$\text{Eff } L(y) \equiv \{x : x \in L(y),\ x' \leq x \Rightarrow x' \notin L(y)\} \text{ pour } y > 0. \tag{2}$$

They also define the property that an efficiency indicator should satisfy :

P1 (x, y) is efficient f and only if x belongs Eff$L(y)$ (Pareto-efficiency) ;

P2 x and x' cannot be compared if they belong to Eff$L(y)$;

P3 An efficiency indicator should be homogeneous of degree -1 ;

P4 An efficiency indicator should be monotonic.

On figure 2, efficiency in Farrell's sense would recommend to move from A to B, whereas for Färe and Lovell, any point on the curve between points C and D could be considered, and in particular C would be chosen if one applies "Russell's measure", which satisfies properties 1 to 4.

Definition (Russell's measure)**.**

$$\mathcal{R}(x, y) \equiv \min \left\{ \frac{1}{k} \sum_{i=1}^{k} \lambda_i : (\lambda_1.x_1, \lambda_2.x_2, \ldots, \lambda_k.x_k; \ldots) \in L(y), \right.$$
$$\left. \lambda_i \in \,]0, 1]\ (i = 1, 2, \ldots, k),\ k \in \{1, 2, \ldots, n\} \right\},\ y > 0. \tag{3}$$

This measure is a weighted mean of k coefficients that one seeks to minimize. Farrell's efficiency is a particular case, with $\lambda_i = \lambda$, $i = 1, 2, \ldots, k$. Note that this measure can be non radial, and does not require equiproportionality. The example on figure 2 gives, with Farrell's definition : $\lambda = 0.8$ (16/20), whereas that of Russell gives : $\lambda_1 = 0.4096$ (8.192/20) and $\lambda_2 = 1$, corresponding to a mean value lower than 0.8 ($\frac{1+0.4096}{2} = 0.7048$).

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[3] $x' \leq x$ means that, for all elements of the vector, one has $x'_i \leq x_i$, and for at least one element, one has $x'_j < x_j$.

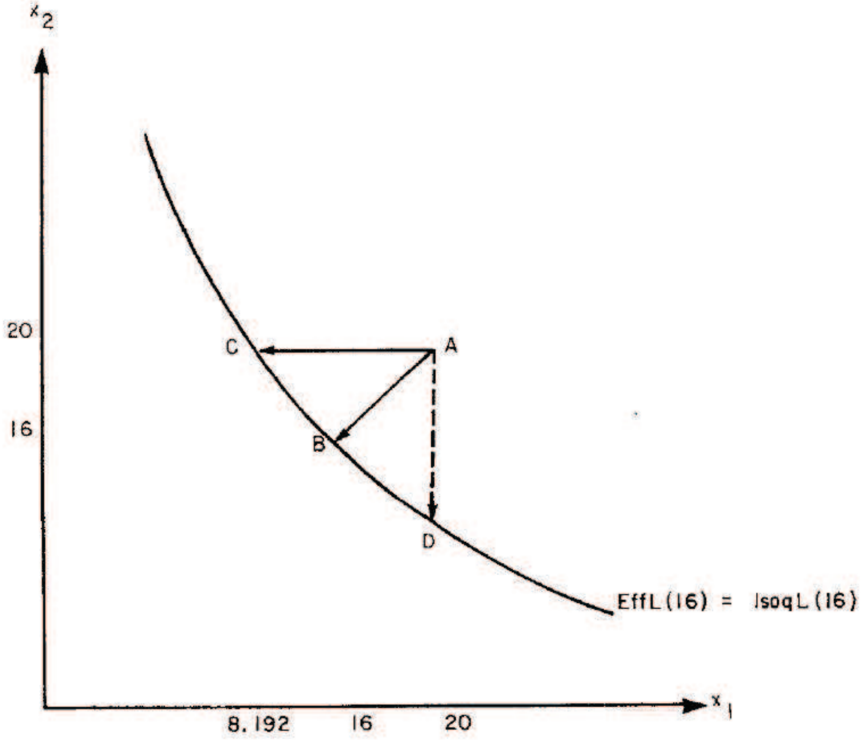

Figure 2: Non radial efficiency measure (Färe and Lovell, 1978)

2.1.2 Output efficiency

Farrell also proposed a product efficiency measure based on the same idea. It is defined as the ration of observed output over optimal output, at given input levels. This measure is illustrated on figure 3 for a single-input and single output production, with non-increasing (a) and constant (b) returns to scale.[4] In the latter case, the two approaches are strictly equivalent ($AB/AP = CP/CD$).

2.1.3 Distance functions

An approach for measuring efficiency and productivity is the distance function, that was introduced by Malmquist (1953) and Shephard (1953). Distance functions are very useful in the case of multi-input, multi-output production technology as there is no need to specify an objective function such as profit or cost maximization. Instead, output (input) distance function characterizes the technology by computing the maximal (minimal) proportional expansion (contraction) of the output (input) vector, given an

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[4] NIRTS : "*Non Increasing Returns To Scale*" and CRTS : "*Constant Returns To Scale*".

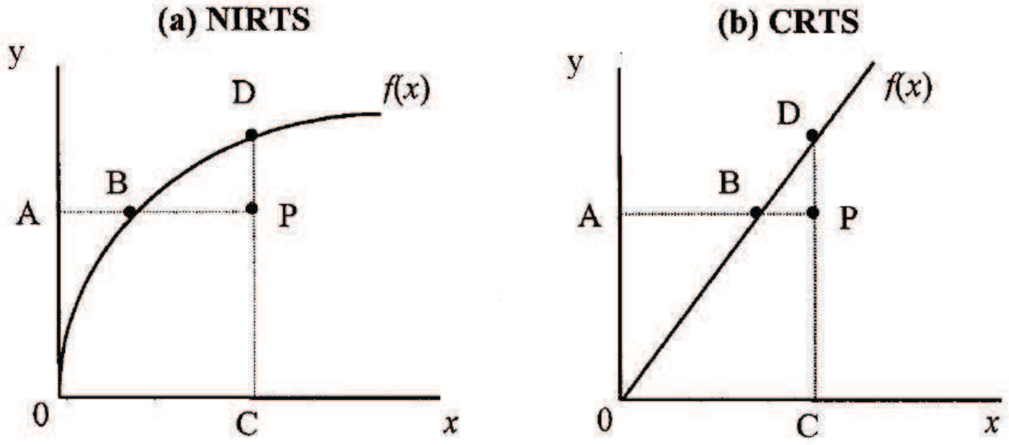

Figure 3: Input and output oriented efficiency depending on the returns to scale (from Coelli et al., 2005)

input (output) vector.

In a single-output technology, the output distance function can be written as:

$$D_o(x, y) \equiv \inf_{\theta}\{\theta : f(x) \geq y/\theta\}, \tag{4}$$

$$\Rightarrow \quad D_o(x, y) \equiv y/f(x). \tag{5}$$

The ratio CP/CD in figure 3 (p. 10) is then identified.

The general case (multi-output, multi-input technology) can easily be deduced from (4) :[5]

$$D_o(x, y) \equiv \inf\{\theta > 0 : (y/\theta) \in P(x)\} \leq 1, \ \ \forall x \in \mathbb{R}^n_+, \tag{6}$$

that represents the proportional expansion of all the outputs, given the level of inputs.

Therefore, the input distance function is defined as: :[6]

$$D_i(y, x) \equiv \sup\{\lambda > 0 : (x/\lambda) \in L(y)\} \geq 1, \ \ \forall y \in \mathbb{R}^m_+, \tag{7}$$

that represents the proportional contraction of all inputs, given the level of outputs.

2.1.4 Directional distance functions

Directional distance functions have recently received increasing attention as they allow for simultaneous expansion of desirable outputs and contraction

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[5] y/θ represents ${}^t(y_1/\theta, \ldots, y_m/\theta)$

[6] These two measures are inversely equal for a constant returns to scale technology.

of undesirable outputs. Therefore, this type of functions is very useful in modeling production processes in which desirable outputs are obtained with undesirable by-products such as toxic wastes or air pollution. Directional distance functions generalize the Shephard's input and output distance functions to adequately represent a joint production process.

Following Chambers et al. (1998), the directional distance function is defined as:

$$\overrightarrow{D}_T(x, y; -g_x, g_y) = sup\,\{\beta : (x - \beta g_x, y + \beta g_y)\ \ \epsilon\ \ T\} \tag{8}$$

where $g = (-g_x, g_y)$ is a directional vector in which the input-output vector (x, y) is projected onto the boundary of T as can be seen in Figure 4, that is it simultaneously expands output y and contract input x.

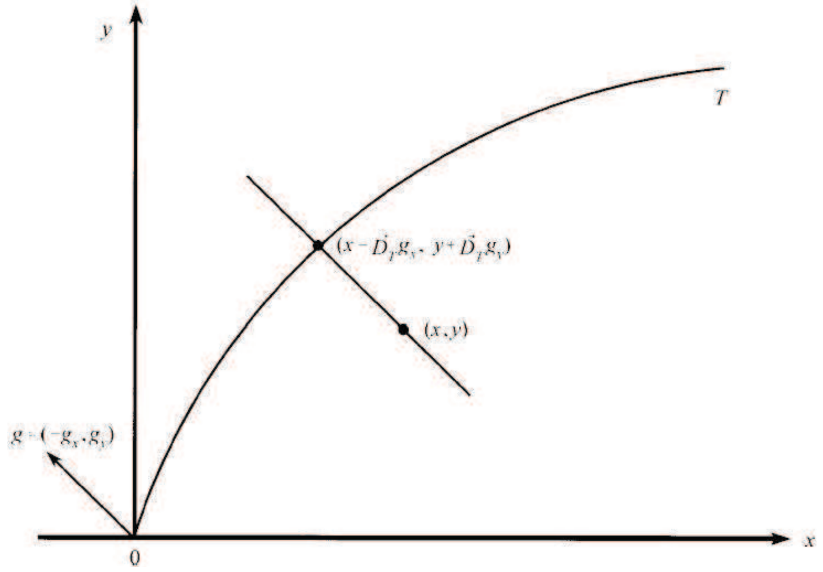

Figure 4: Directional Distance Function (Färe and Grosskopf, 2000)

In the presence of undesirable output, the directional distance function can be written as:

$$\overrightarrow{D}_T(x, y, b; -g_x, g_y, -g_b) = sup\,\{\beta : (y + \beta g_y, b - \beta g_b) \epsilon P(x - \beta g_x)\} \tag{9}$$

being the directional vector $g = (-g_x, g_y, -g_b)$. That is, Equation (9) seeks for the largest feasible expansion of desirable output y in the direction g_y, and the maximum attainable contraction of input x and undesirable output b in the direction $-g_x$ and $-g_b$, respectively (Picazo-Tadeo et al., 2005).

3 Estimation of production frontiers

There are two main methodologies for the assessment of efficiency, namely the mathematical (nonparametric) approach and the econometric (parametric) approach. These two methods to envelop data primarily differ in the accommodation for random noise and the flexibility in the structure of production technology.

3.1 Econometric approaches

Stochastic frontier analysis (SFA) is a methodology for the estimation of a frontier production function, which is "an extension of the familiar regression model based on the theoretical premise that a production function, or its dual, the cost function, or the convex conjugate of the two, the profit function, represents an ideal, the maximum output attainable given a set of inputs, the minimum cost of producing that output given the prices of the inputs, or the maximum profit attainable given the inputs, outputs, and prices of the inputs" (Greene, 2008). In this sense, the frontier production function is estimated consistent with the theoretical constraint that all the observations in the analysis lie below the frontier. The efficiency measurement is computed after the estimation of the frontier production function as the distance between an observation and the estimated theoretical ideal.

In this context, we permit a decision unit to be technically inefficient by allowing it to operate beneath its stochastic production frontier. The decision unit's production technology is characterized by a production function of the form:

$$y_i = a \prod_{i=1}^{n} x_i^{\alpha_i} e^{\epsilon_i} \tag{10}$$

where y_i is the output, x_i is the vector of inputs, ϵ is a random disturbance and a and α_i are the parameters to be estimated. The functional form needs to be specified, being the most common ones the linear and Cobb-Douglas forms (as first-order flexible), and the quadratic, normalized quadratic, translog, generalized Leontief and Constant Elasticity of Substitution (as second-order flexible) (Coelli et al., 2005).

Following Aigner et al. (1977) and Meeusen and van den Broeck (1977), the disturbance is assumed to be:

$$\epsilon_i = v_i - u_i \tag{11}$$

where v_i is distributed as $\mathcal{N}(0, \sigma_v^2)$ and captures the random variation in output due to unobserved factors that are outside the control of the decision unit such as weather, and u_i is the inefficiency term that is equal to $\sigma_u \eta_i$, being $\sigma_u \geq 0$ and $\eta_i \mathcal{N}^+(0,1)$.

Once the frontier production function is estimated, the Debreu-Farrel output-oriented technical efficiency can be obtained:

$$TE_i = \frac{y_i}{[f(x_i, \beta)\mathrm{e}^{v_i}]} = \mathrm{e}^{u_i}. \tag{12}$$

There are two main ways to estimate β. The simplest is to assume that $v_i = 0$ and to estimate a deterministic production frontier. The second consists in assuming that $v_i \neq 0$, having a stochastic frontier.

Deterministic frontiers can be estimated through three main methods :

1. Corrected Ordinary Least Squares (COLS) : without assuming any special functional form for the u_i, one estimates the equation (10) by OLS[7], then “translating” the regression line until satisfying $u_i \leq 0$ and $u_j = 0$ for at least one observation ;

2. Modified Ordinary Least Squares (MOLS) : an hypothesis is made on the functional form of the inefficiency error term (semi-normal) before estimating the regression line through OLS. The line is then translated until the mean of the error terms u_i becomes negative ;

3. Maximum Likelihood (MLE) : a functional form is assumed for the error term, but it is estimated jointly with the estimation of the technological parameters, so that the regression line “encompasses” all observations.

These regression methods are illustrated on figure 5.

When estimating stochastic frontiers, COLS can no longer be used, but MOLS and MLE can. The process is roughly the same, except that the residuals, which contain both the noise and the inefficiency, must be decomposed. Jondrow et al. (1982) propose a functional form for the u_i, and derive a conditional distribution $(u_i | v_i + u_i)$.

Equation (10) is used for the estimation of technical efficiency for the one-output, multiple-input cross-sectional model. However, it is also possible to estimate technical efficiency for panel data by using fixed effect models (FE) and random effect models (RE).

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[7] OLS : *Ordinary Least Squares*

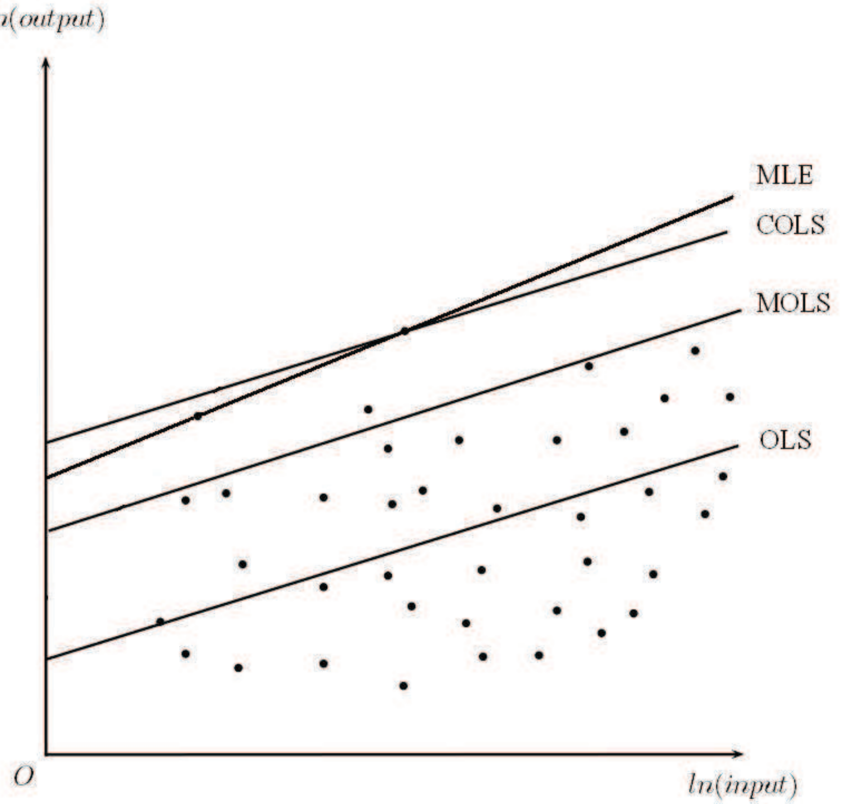

Figure 5: Different regression methods to estimate production frontiers (Lovell, 1993)

3.2 Linear programming

Data Envelopment Analysis (DEA) is a linear programming methodology to construct a nonparametric piecewise surface that envelops the data as tightly as possible. The term was coined by Charnes et al. (1978), and since then, numerous studies have applied and extended this methodology.

3.2.1 *Data envelopment analysis*

This method consists in "enveloping" observation piecewise, by treating each observation individually in the optimization process. This corresponds to the search of the points minimizing a input/output ratio (input-oriented approach) or that maximizing the output/input ratio (output-oriented). These points are then linked to form the production frontier. Constraints are used to make sure that the envelop encompasses all points.

The model proposed by Charnes et al. (1978) is input-oriented and assumes constant returns to scale (CRS). Subsequent papers have extended this approach, however, we begin with the input-oriented CRS model, since it is the basic model. This model can be defined as the ratio of M outputs over N inputs for each of the I firms:

$$\begin{aligned} \max_{u,v} \quad & uy_j/vx_j \\ \text{tels que} \quad & uy_i/vx_i \geq 1, \ i = 1, \ldots, j, \ldots, I, \\ & u, v \geq 0, \end{aligned} \tag{13}$$

where u and v are vectors of outputs and inputs weights respectively, (y_j, x_j) is the output-input vector of the producer evaluated, and (y_i, x_i) is the output-input vector of the Ith producer in the sample.

The problem can be expressed as a linear optimization problem in the following form :

$$\begin{aligned} \max_{u,v} \quad & uy_j \\ \text{tels que} \quad & vx_j = 1, \\ & uy_i - vx_i \leq 0, \\ & u, v \geq 0. \end{aligned} \tag{14}$$

The constraint $vx_j = 1$ is set to avoid an infinite number of solutions[8].

Using the duality of linear programming, we can rewrite eq (14) as follows :

$$\begin{aligned} \min_{\theta,\lambda} \quad & \theta \\ \text{tels que} \quad & -y_j + Y\lambda \geq 0, \\ & \theta x_j \leq Y\lambda, \\ & \lambda \geq 0, \end{aligned} \tag{15}$$

where θ is a scalar and λ is a $Ix1$ vector of constants.

This optimization problem defines I couples (θ, λ). If $\theta^* = 1$, the producer is technically efficiency, whereas if $\theta^* > 1$, it is possible to decrease the level of inputs while maintaining constant the outputs.

The hypothesis the most often relaxed is that of constant returns to scale. Non-increasing returns to scale are obtained by imposing ${}^tE\lambda \leq 1$ (E being a vector of 1) and variable returns to scale can be obtained by assuming ${}^tE\lambda = 1$. The difference between these three frontiers is illustrated on figure 6. The measure of efficiency is strongly influenced by the type of technology assumed.

The convexity assumption is barely relaxed, even if it is assumed more for mathematical ease than for realism. A "*free disposal hull*"[9] (FDH)

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[8] If (u^*, v^*) is solution $(\alpha u^*, \alpha v^*)$, $\alpha \in \mathbb{R}$, is too.

[9] This concept was applied to frontier analysis by Deprins et al. (1984) (see Lovell, 1993).

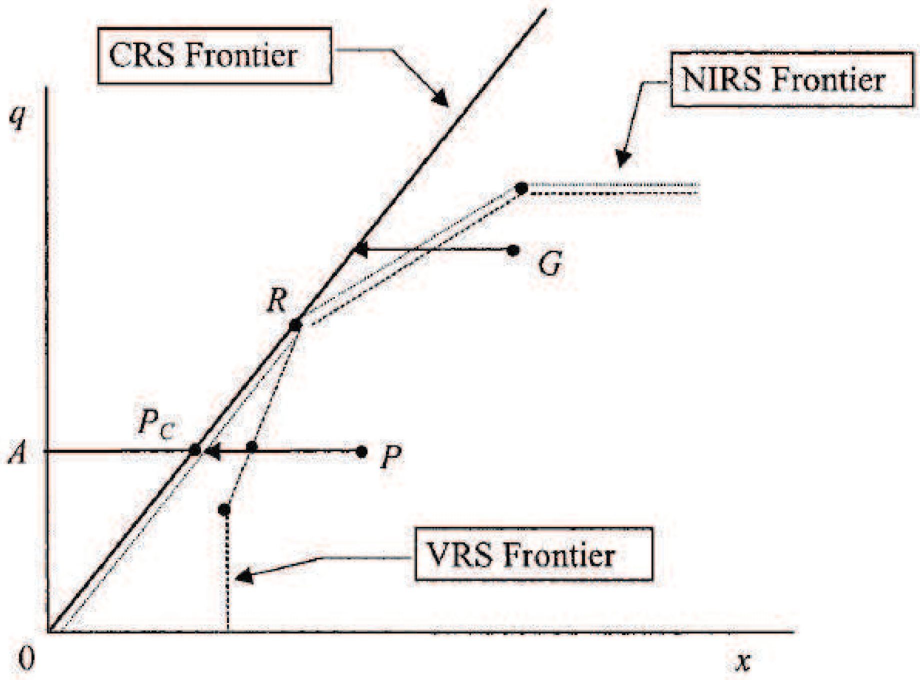

Figure 6: DEA and returns to scale (Coelli et al., 2005)

allows to drop convexity. It is obtained by adding the condition ${}^tE\lambda = 1$ (constant returns to scale) with $\lambda_i \in]0;1[$, $i = 1, \ldots, I$ to equation (15). The FDH frontier (dashed line on figure 8) is a step function. This frontier has the advantage to envelop the observations more tightly, and leads to a more restrictive definition of dominance, since (“*slacks*”notwithstanding) producers are directly compared to each others.

The standard DEA model has been extended to measure income-efficiency and deduce allocative (output) efficiency from the residual.

3.2.2 Stochastic DEA approach

The standard DEA approahc suffers from many limitations: omitted variables, errors in measures, other sources of statistical noise. The stochastic version makes it possible to fix some of these problems. One considers that the constraints in equation (15) may not be respected with some probabil-

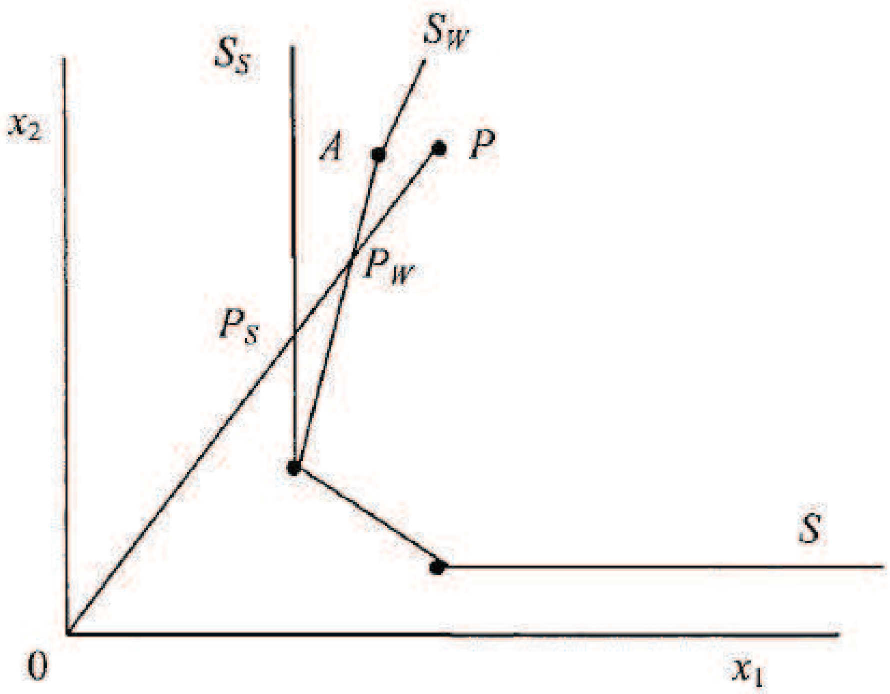

Figure 7: DEA and weak input disposal (Coelli et al., 2005)

ity.

$$
\begin{aligned}
\max_{\theta,\lambda} \quad & \theta & (16)\\
\text{tels que} \quad & \Pr\left(\sum_{i=1}^{I} x_{is}\lambda_i \leq x_{js}\right) \geq P_s,\ s = 1,\ldots,n,\\
& \Pr\left(\theta y_{jt} \leq \sum_{i=1}^{I} y_{it}\lambda_i\right) \geq P_t,\ t = 1,\ldots,m,\\
& \lambda \geq 0.
\end{aligned}
$$

This problem is interpreted as the maximal increase in output which can be realized with some probability, given the established frontier. The counterpart of this result is that this approach requires more information to define the probabilities.

3.3 Heterogeneity in frontier models

An important assumption of frontier models is that the underlying production technology is common to all decision units, that is, they operate within homogeneous environments. However, if decision units use different

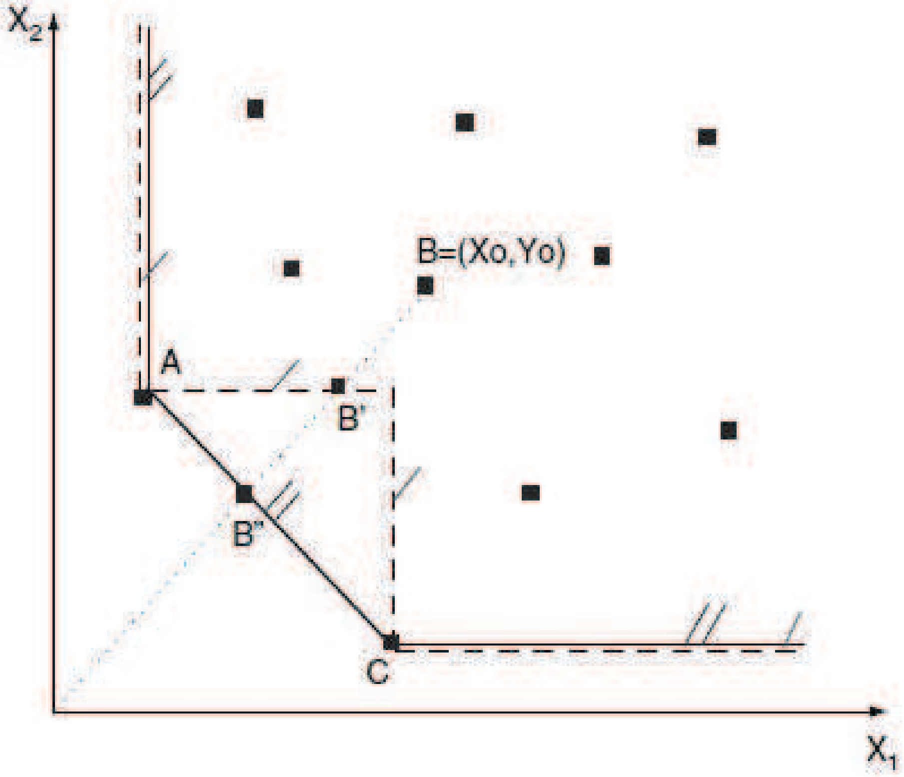

Figure 8: Technical efficiency measurement : DEA and FDH frontiers (Daraio and Simar, 2007)

technologies, the estimation of a common frontier may be misleading and the estimated frontier may not represent the "true" technology (Orea and Kumbhakar, 2004). Moreover, if heterogeneity is not taken into account, the omitted environmental differences would be inaccurately considered as inefficiency (Orea and Kumbhakar, 2004).

The different approaches to control for heterogeneity in the operating environment can be classified into separation models and single and multiple stage models. In separation models, the sample is divided based on *a priori* knowledge and then frontier models are estimated for each group, whereas one stage and multiple stage models include exogenous variables in the analysis to adjust efficiency scores based on the influence of these variables. As discussed by Yang and Pollitt (2009), the first type of models are easy to implement if *a priori* information to distinguish the groups is available. However, in the case of no firm *a priori* knowledge about the operating environment, the other type of models are preferred.

Several approaches aiming at controlling for heterogeneity in the operational environment are detailed below.

3.3.1 Separation Models

3.3.1.1 Metafrontier Models

The concept of metaproduction was introduced by Hayami (1969) and defined by Hayami and Ruttan (1971) as "the envelope of commonly conceived neoclassical production functions". The stochastic metafrontier function operationalises the metaproduction function approach (Battese and Rao, 2002) by including a non-negative technical inefficiency term and a symmetric random error term.

In a metafrontier model, we assume that the technology set includes all possible input-output combinations:

$$T = \{(x, y) : \quad x \geq 0; y \geq 0; \texttt{x can produce y}\} \tag{17}$$

The nonnegative inputs and outputs for decision units in a particular sector are such that the stochastic frontier production function model fits the technology for J different groups in that sector (Battese et al., 2004). The stochastic frontier model for the j^{th} group is given by:

$$\begin{aligned} &y_{it}(j) = f(x_{it}(j), \beta(j))e^{v_{it}(j)-u_{it}(j)} \\ &i = 1, ..., N; t = 1, ..., T; j = 1, ..., J \end{aligned} \tag{18}$$

where $y_{it}(j)$ and $x_{it}(j)$ are the output and a vector of inputs for the ith decision unit belonging to group j in the period tth, $\beta(j)$ is the parameter vector to estimate for the jth group $v_{it}(j)$ is the random term that is identically and independently distributed as $N(0, \sigma^2_{v(j)}$ and $u_{it}(j)$ is the inefficiency term distributed as $N(\mu_{it}(j), \sigma^2(j))$.

A metafrontier production function can be defined as a deterministic parametric function with values that are not lower than the deterministic components of each stochastic frontier production functions. This function envelops all the stochastic frontier functions and is expressed by:

$$y*_{it} = f(x_{it}, \beta*) = e^{x_{it}\beta*}; \quad i = 1, ..., N; t = 1, ..., T \tag{19}$$

The technical efficiency for the jth group is computed as:

$$TE_{it} = \frac{y_{it}}{e^{x_{it}\beta(j)+v_{it}(j)}} = e^{-u_{it}(j)} \tag{20}$$

Moreover, a technology gap ratio can be also calculated as:

$$TGR_{it} = \frac{e^{x_{it}\beta(j)}}{e^{x_{it}\beta*}} \tag{21}$$

A metafrontier function and three stochastic frontier models are presented in Figure 9. The stochastic frontier outputs are indicated by the

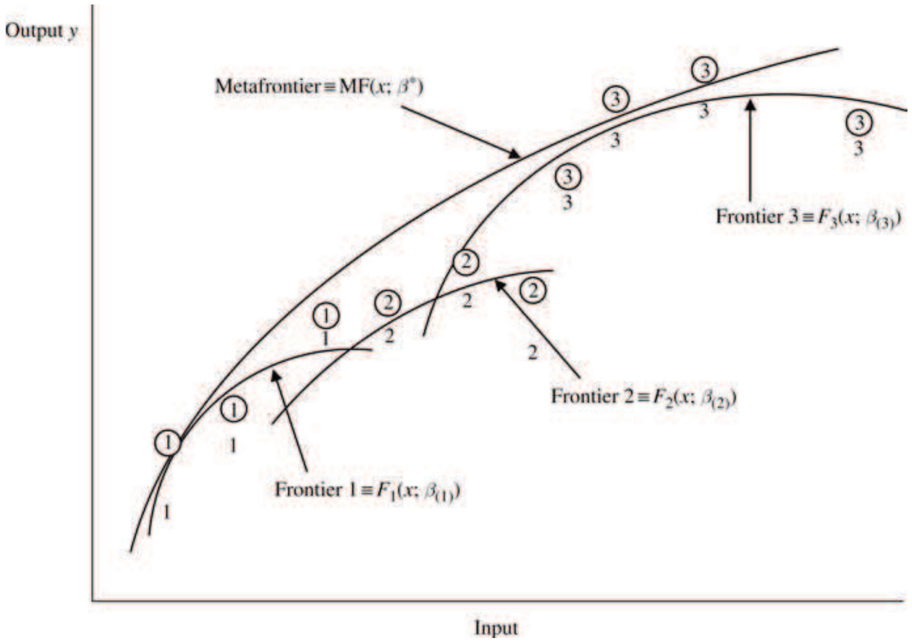

Figure 9: Metafrontier and stochastic frontier functions (Battese et al., 2004)

numbers in circles whereas the deterministic outputs are the numbers below the former. Therefore, the metafrontier function has values no less than the deterministic functions and some of the stochastic frontier outputs even exceed the metafrontier.

The main limitation of this methodology is that it is more susceptible to sample misclassification caused by a potential arbitrary grouping criterion.

3.3.2 Single and multiple stage approaches

3.3.2.1 Latent Class Stochastic Frontier Model

The latent class stochastic frontier model estimates a mixture of technologies or frontier functions by combining the stochastic frontier approach with the latent class analysis, as the researcher may not be able to identify *a priori* which decision unit is using what technology (Orea and Kumbhakar, 2004).

In this single-stage approach, the technology for the jth class can be written as:

$$y_{it} = f(x_{it}(j), \beta(j))|_j e^{v_{it}|_j - u_{it}|_j} \tag{22}$$

where $u_{it}|_j$ is the non-negative inefficiency term modeled following the standard approach in the literature.

Therefore, the log density for decision unit i if it belongs to the jth class, can be written as:

$$l(it|j) = \frac{2}{\sigma_j}\phi\left\{\frac{\epsilon(it|j)}{\sigma_j}\right\}\Phi\left\{-\frac{\lambda_j\epsilon(it|j)}{\sigma_j}\right\} \tag{23}$$

where $\sigma_j^2 = \sigma_{uj}^2 + \sigma_{vj}^2$, $\lambda_j = \sigma_{uj}^2/\sigma_j^2$ and $\epsilon(it|j) = lny_{it} - lnf(x_{it}(j), \beta(j))$.

The unconditional likelihood for decision unit i is the weighted sum of the j-class likelihood functions:

$$l(it) = \sum_{j=1}^{J} l(it|j)\pi_{ij}, \quad 0 < \pi_{ij} < 1 \tag{24}$$

The posterior probabilities of class membership can be furthered parametrized, for instance, as a multinomial logit model:

$$\pi_{ij}(\delta_j) = \frac{exp(\delta_j' q_i)}{\sum_{j=1}^{J} exp(\delta_j' q_i)}, \qquad j = 1, ..., J \tag{25}$$

where q_i is a vector of decision unit-specific and time-invariant variables and δ_j is the vector of parameters to estimate. The q_i “separating variables” are proxies for the environment where decision units operate, that sharpen the prior probabilities.

In the estimation of a standard stochastic frontier model, the efficiency scores are computed relative to the unique estimated frontier. However, in the latent class stochastic frontier model, the number of estimated frontiers is equal to the number of classes identified. Therefore, it is possible to assign observations to a particular class based on the highest membership probability, and then compute efficiency scores relative to the frontier estimated to that particular class. This method is not taking into account the fact that the probability of belonging to the other classes is not zero. In order to avoid *ad hoc* class selection, efficiency scores can be computed following the approach by Greene (2002):

$$lnEF_{it} = \sum_{j=1} JP(j|i)lnEF_{it}(j) \tag{26}$$

where $P(j|i)$ is the posterior probability of decision unit i to belong to the j_{th} class and $EF_{it}(j)$ is the efficiency score computed using the technology of class j as the reference technology.

One limitation of this methodology is that, since it is a probabilistic model, it is not possible to assign a particular decision unit to one and only one class or operational environment (Llorca et al., 2014). In this sense, class membership probabilities may help to understand the uncertainty about the different environments and, therefore, the true partition of the sample.

3.3.2.2 Four stage procedure to adjust environmental impacts

In the four stage model, efficiency scores are adjusted based on the influence of the operational environment. In the first stage, each input is regressed on a set of exogenous variables that may represent this operational environment using a Tobit model as in Hof et al. (2004) and Macpherson et al. (2013):

$$x_{il} = \alpha + \sum_{j=1}^{J} \beta_{ij} z_{ijl} + \epsilon_{il} \tag{27}$$

where x_{il} represents input l for decision unit $i = 1, ..., N$, z_{ijl} is the exogenous variable j for each decision unit i andϵ_{il} is the error term.

The input adjustment is obtained by predicting input $\hat{x_{il}}$ using the exogenous variables at their mean value $\bar{z_{ij}}$.

$$\hat{x}_{il} = \hat{\alpha} + \sum_{j=1}^{J} \hat{\beta}_{ij} \bar{z}_{ij} + \bar{\epsilon}_{il} \tag{28}$$

Once the inputs are adjusted, efficiency scores are computed using DEA. In order to check that the effect of the exogenous variables was actually removed, the input slacks are regressed against the exogenous variables.

This approach may be useful if the researcher has no firm *a priori* assumption about the importance of the operational environment in the model. However, it also has some limitations. Some relevant variables defining the environment may be observed and, therefore, sources of heterogeneity would not be captured in the model. Moreover, as noted by Simar and Wilson (2007), using Tobit models in multiple-stage DEA may not be appropriate due to the serial correlation of efficiency scores and input slacks.

3.3.2.3 Semiparametric Smooth-Coefficient Stochastic Frontier Model

Another possibility for modeling environmental factors in frontier analysis is the use of Semiparametric Smooth-Coefficient Stochastic Frontier Models. Environmental factors are included in frontier models by considering the impact of the operational environment on technical efficiency and also in the actual frontier. That is, intercept and slope coefficients are expressed as unknown functions of variables that represent this environment, allowing the frontier to shift non-neutrally. Meanwhile, the environmental factors are also considered determinants of technical efficiency as in parametric stochastic frontier models proposed by Simar et al. (1994) and Alvarez et al. (2006). Therefore, this model can be written as:

$$y_{is} = \alpha_s(z_{is}) + x'_{is}\beta_s(z_{is}) + v_i - u_{is}(z_{is}) \tag{29}$$

where y_{is} is the log of production, x_{is} is a vector of l inputs, z_{is} is a vector of environmental factors, $\beta_s(z_{is})$ is a vector of unspecified smooth functions of z_{is}, α_{is} is the intercept and is also an unspecified function of z_i and the subscript s denotes the state. v_{is} is the noise term, a standard normal random variable, and $u_{is}(z_{is})$ is the inefficiency term that is multiplicatively decomposed into a scaling function of the z environmental factors. Following Simar et al. (1994), the efficiency term is assumed to be $u_{is} = \sigma_u(z_{is})\eta_i$ where $\eta_i \sim iidN^+(0,1)$ and $\sigma_u(z_{is}) = exp(\delta_0 + {\delta_1}' z_{is}) > 0$. This assumption implies that $E[(u_{is}(z_{is})|z_{is}] = \sqrt{2/\pi}\sigma_u(z_{is}) = \sqrt{2/\pi}exp(\delta_0 + {\delta_1}' z_{is})$. Thus, equation (29) can be rewritten as:

$$\begin{aligned} y_{is} &= \alpha_s(z_{is}) + {x_{is}}'\beta_s(z_{is}) + v_i - (u_{is}(z_{is}) - E[(u_{is}(z_{is})|z_{is}] + E[(u_{is}(z_{is})|z_{is})]) \\ &= \theta(z_{is}) + {x_{is}}'\beta_s(z_{is}) + \epsilon_{is} \end{aligned} \tag{30}$$

where $\theta(z_{is}) = \alpha_s(z_{is}) - E[u_{is}(z_{is})/z_{is}]$ and $\epsilon_{is} = v_i + u_{is}(z_{is}) + E[u_{is}(z_{is})/z_{is}]$. This simple transformation allows one to estimate the frontier using the semiparametric smooth-coefficient model proposed by Li et al. (2002).

Once the frontier is estimated, technical efficiency is analyzed in the second stage. Recalling the assumption on the efficiency term and obtaining the residuals from the frontier estimation as $\hat{\epsilon}_{is} = y_{is} - \hat{\theta}(z_{is}) - x'_{is}\hat{\beta}(z_{is})$, define $R_i = \hat{\epsilon}_{is}$, the estimation equation is given by:

$$\begin{aligned} R_i &= \sqrt{2/\pi}\sigma_u(z_{is}) + v_i - \sigma_u(z_{is})\eta_i \\ &= \sqrt{2/\pi}exp(\delta_0 + \delta'_1 z_{is}) + v_i - exp(\delta_0 + \delta'_1 z_{is})\eta_i \\ &= \sqrt{2/\pi}exp(\delta_0 + \delta'_1 z_{is}) + \epsilon^*_i \end{aligned} \tag{31}$$

where $\epsilon^*_{is} = v_i - exp(\delta_0 + \delta'_1 z_{is})$. Following Sun and Kumbhakar (2013), in this second stage, a parametric stochastic frontier estimation technique is applied. The log-likelihood function is written as:

$$lnL = constant - \frac{1}{2}\sum_i ln[\sigma^2_u(z_{is}) + \sigma^2_v] + \sum_i ln\Phi\left(-\frac{\epsilon^*_{is}\gamma_i}{\sigma_{is}}\right) - \frac{1}{2}\sum_i \frac{\epsilon^*_{is}}{\sigma^2_{is}} \tag{32}$$

where $\sigma^2_{is} = \sigma^2_v + \sigma^2_u(z_{is}) = \sigma^2_v + exp[2(\delta_0 + \delta'_1 z_{is})]$ and $\gamma_i = \sigma_u(z_{is}/\sigma_v)$. By maximizing this log-likelihood function, δ_0, δ_1 and σ^2_v are estimated and then, the rest of the unknown parameters can be obtained.

Finally, in order to obtain the efficiency scores, the Battese and Coelli (1988) point estimator is computed:

$$TE_i = E(exp\left\{-u_{is}\right\}|\epsilon^*_{is}) = \left[\frac{\Phi(\mu_{*is}/\sigma_* - \sigma_{*is})}{\Phi(\mu_{*is}/\sigma_*)}\right] exp\left[-\mu_{*is} + \frac{1}{2}\sigma^2_*\right] \tag{33}$$

where $\mu_{*is} = -\epsilon_{is}\sigma^2_u/\sigma^2$ and $\sigma^2_* = \sigma^2_u\sigma^2_v/\sigma^2$.

4 A review on environmental efficiency measurement

4.1 Environmental efficiency measurement

As discussed above, Efficiency Analysis is a useful tool for the assessment of environmental performance. Since the late 1980's, a vast literature has used different frontier techniques to measure environmental efficiency, specially in the agricultural sector.

However, as indicated by Lauwers (2009), there exist two main approaches depending on how environmental effects are included into frontier models. In the first approach, known as " environmentally adjusted production efficiency" (EAPE), efficiency models are estimated using Stochastic Frontier Analysis (SFA) or Data Envelopment Analysis (DEA) including for environmental pressures either as an undesirable output or as an environmentally detrimental input. The second approach, labeled as "frontier eco-efficiency" (FEE), analyzes the relation between ecological outcomes and economic outcomes rather than conventional inputs and outputs.

4.1.1 Environmentally adjusted production efficiency

The earliest studies adjusting efficiency measures to include environmental effects follow the paradigm of costly environmental regulation (Lauwers, 2009), despite the fact that in standard efficiency analysis all efficiency improvements, including environmental ones, imply cost reductions. Färe et al. (1989) develop the hyperbolic efficiency measure and incorporate pollution as a bad output introducing the concept of weak disposability of undesirable outputs so that a reduction in the production of bad outputs also implies a reduction in the production of good outputs and, therefore, is costly. Several studies use output distance functions, allowing also for weak disposability of bad outputs, and a dual Shephard's lemma applied to those functions to generate shadow prices of undesirable outputs (Färe et al., 1993; Coggins and Swinton, 1996), however, they do not compute environmental efficiency measures. Alternatively, Seiford and Zhu (2002) propose modeling bad outputs using data translation instead of the weak disposability assumption. However, this approach computes DEA scores that are not intuitively interpreted (Asmild and Hougaard, 2006) and it does not resort to ad hoc treatment of bad outputs as inputs (Färe and Grosskopf, 2004).

Weak disposability of bad outputs is also assumed in applications to agricultural production. Piot-Lepetit and Vermersch (1998) measure technical efficiency including organic nitrogen from animal breeding as a bad output and compute the shadow price of organic price for a sample of 107

French pig farms in 1991. Ball and Norton (2002) develop an environmental performance index in terms of agricultural pesticide used that may pollute ground and surface water and affect both human and fish health. This index, which is based on distance functions, is computed using data on the U.S. agricultural sector for 48 states for the period 1960-1996. Berre et al. (2014) consider greenhouse gas emissions and nitrogen surplus as environmental bads in the analysis of the relation between milk production and its environmental impact for dairy farms from Reunion Island. Environmental efficiency is computed using directional distance functions and then, four scenarios are proposed to evaluate future sustainable intensification.

As discussed above, another possibility in EAPE modeling is to consider pollution as strongly disposable detrimental inputs. Haynes et al. (1993) consider undesired environmental residuals for chemicals concern as inputs in their DEA-based efficiency measure. Hailu and Veeman (2001) also treat pollution as inputs in a DEA model to measure efficiency in pollution prevention activities in the Canadian pulp and paper industry for the period 1959-1994. There are also interesting applications in the agricultural sector as in Reinhard et al. (1999) who treat nitrogen surplus as an environmentally detrimental input in the estimation of technical and environmental efficiency of Dutch dairy farms. Output-oriented technical efficiency is estimated using a translog production frontier, whereas environmental efficiency is estimated as the input-oriented technical efficiency when only considering nitrogen surplus as input. Shaik et al. (2002) computes direct and indirect shadow price estimates of nitrogen pollution abatement using data from the Nebraska agricultural sector for the period 1936-1937. Shadow price estimates are obtained treating pollution as an undesirable output and as an input, concluding that the difference in the disposability assumptions generates higher shadow price estimated when treating pollution as a bad output.

4.1.2 Frontier Eco-efficiency models

OECD (1998) defines Eco-efficiency as “the efficiency with which ecological resources are used to meet human needs”. This measure is considered as the ratio of the value of products and services produced and the sum of environmental pressures generated in the production process. Kuosmanen and Kortelainen (2005) used the frontier method, in particular DEA, for the operationalisation of this concept, as DEA allows to aggregate environmental pressures without any a priori weight. The “pressure-generating technology set” is proposed representing all feasible combinations of economic value and environmental pressures.

In this context, the eco-efficiency is also measured as the distance to a frontier, and therefore, the eco-efficiency score represents the maximum equiproportionate possible reduction in the environmental pressures. Figure 10 represents the eco-efficiency frontier in the case of two environmental pressures (z_1 and z_2) that are obtained in the production process that generates economic value added. As explained before, the frontier represents the estimated best practice technology, and therefore, the possible trade-offs between economic value added and environmental pressures.

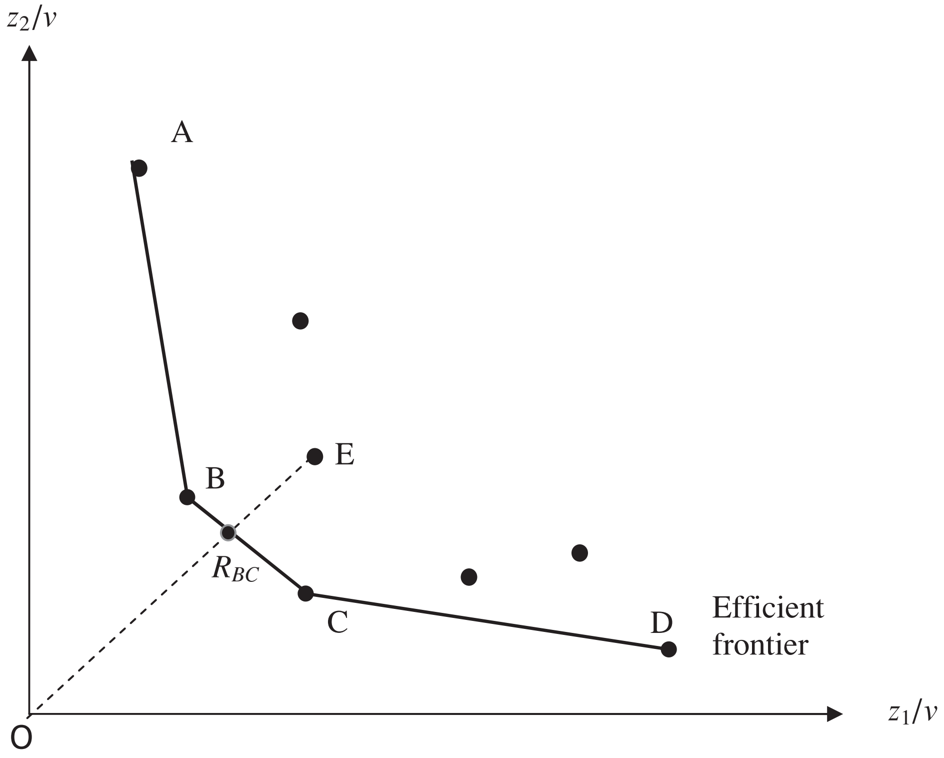

Figure 10: Eco-efficiency frontier, Kuosmanen and Kortelainen (2005)

The points A, B, C, D and E represent different decision units. A, B, C and D lie in the frontier, that is, those decision units are eco-efficient. However, the decision unit E is above the frontier, so it is considered to be eco-inefficient. In order to obtain a measure of this eco-inefficiency, we compute the radial distance from E to the point R_{BC} in the frontier, where the two environmental pressures would be reduced in the same proportion. Therefore, the eco-efficiency score is equal to the following ratio:

$$EE = \frac{|OR_{BC}|}{|OE|} \tag{34}$$

Kortelainen (2008) generalizes the method by Kuosmanen and Kortelainen (2005) from a static to a dynamic perspective, so that environmental performance can be analyzed through time. To do so, an environmental performance index is constructed and decomposed into the relative eco-efficiency change components and environmental technical change.

FEE models have been recently applied for the assessment of environmental performance in the agricultural sector.

For instance, Picazo-Tadeo et al. (2011) aim at analyzing agricultural sustainability for a sample of Spanish farmers operating in a rain/fed agricultural system. Considering the ecological features of the agricultural system in the analysis, there are five relevant environmental indicators related to pressures generated jointly with agricultural production. The first indicator is Specialization, since a high level of specialization may have a negative impact on biodiversity related to the existence of different crops. Nitrogen and Phosphorus balance indicators quantifying the amount of these two pollutant elements released into the ecosystem by this agricultural system are also considered in the analysis. Pesticide risk is another important environmental indicator that informs about the overall toxicity generated through the pesticide used. The last environmental pressure included in the analysis is an indicator of Energy Balance that accounts for the proportion of energy consumed to generate the inputs to the energy fixed by crops and exported by the output. In order to calculate a composite indicator of environmental efficiency, it is necessary to aggregate the environmental indicators using a weighting scheme. Therefore, DEA techniques, and in particular the approach proposed by Kuosmanen and Kortelainen (2005), are used as weights are generated at farm level without any *a priori* subjective valuation. This approach is a measure of eco-efficiency in a Farrell-Debreu sense, that is, it computes the maximal equiproportional reductions of all the environmental pressures given the economic value. Picazo-Tadeo et al. (2011) also compute pressure-specific potential reductions that could be still possible after attaining the equiproportional reduction of all pressures, that allow them to calculate a pressure-specific eco-efficiency measure following the approach by Koopmans (1951).

Gómez-Limón et al. (2012) obtain radial eco-efficiency scores for olive farms in Andalusia (Spain) also following the approach by Kuosmanen and Kortelainen (2005) for three different types of olive growing systems. The environmental pressure indicators considered in the study are Erosion, Energy balance, Nitrogen balance, Pesticide risk, a Biodiversity indicator that reflects the degree of implementation of agricultural practices that improve biodiversity in olive farming, and a water use indicator quantifying the water extracted from the ecosystem that has been used for olive production.

Beltrán-Esteve et al. (2014) also analyses different types of olive producers but using a metafrontier approach to differenciate between traditional mountain and traditional plain growing systems. As indicated in the previous section, this methodology allows one to assess technical efficiency and technological gaps between different production systems. Moreover, directional distance functions are used to compute eco-efficiency at pressure level for each type of production system, so that it is possible to evaluate the advantages and disadvantages of the two different production technologies regarding the level of eco-efficiency related to a specific environmental pressure.

4.1.3 Measuring efficiency of pesticides

Although pesticides have several benefits such as reducing crop losses to pests, they may cause damages on the environment and human health such as contamination of water and soil, and biodiversity and human poisonings.

In this context, it is important to measure how much pesticides could be reduced while maintaining production levels. However, few studies have assessed the level of efficiency of pesticides. Lansink and Silva (2004) analyzes the productivity of pesticides using DEA on specialized Dutch cash crop farms, and the results show a substantial under-utilization of pesticides. Wossink and Denaux (2006) compare the level of efficiency in pesticide use in for producers of transgenic cotton and conventional cotton using data from a survey of cotton growers in North Carolina, USA. Efficiency scores are computed by means of DEA and then, efficiency determinants are investigated using a Tobit model. Skevas et al. (2012) include pesticides as an input and, the impact of pesticides on water organisms and biological controllers as outputs to measure technical efficiency controlling for pesticides' dynamic effects and production uncertainty. To do so, a dynamic DEA is applied to data on Dutch specialized arable farms covering the period 2002-2007.

4.2 Explaining environmental efficiency

Participants at the 1995 OECD workshop in Rosendal, Norway, identified eco-efficiency as a flexible and pragmatic concept related to sustainable consumption and production. However, they also indicated that "the term eco-efficiency was insufficient on its own as a basis for policy making. A wider understanding would be needed of the links between economic activity and environmental damage, driving forces of change, and the psychological and ethical motives of producer and consumer behaviour" (OECD, 1998). However, as noted by Lansink and Wall (2014), the determinants of environmental efficiency have received much less attention than the measurement of this indicator.

There are few studies analysing the efficiency determinants for environmentally adjusted production efficiency models. Reinhard et al. (2002) use a two-stage approach to analyse differences in environmental efficiency for Dutch dairy farms. Technical and environmental efficiency are estimated in the first stage using stochastic frontier analysis and, in the second stage, the estimated environmental efficiency scores are regressed against several factors such as physical environment, technology and management indicators. Galdeano-Gómez et al. (2006) study environmental performance in the Spanish horticultural sector over the period 1994-2002 by estimating an environmental productivity index applying stochastic frontier analysis. In a second stage, improvements in labour quality and productivity, growth of capital intensity and environmental spillovers have a positive effect on the environmental performance in this sector.

The determinants of efficiency have been also examined in environmentally adjusted production efficiency models implementing nonparametric methods. For instance, Wossink and Denaux (2006) investigate the determinants of environmental efficiency scores previously obtained using a Tobit regression. However, this approach may be inappropiate because the serial correlation of the first stage DEA efficiency estimates is not taken into account, as shown by Simar and Wilson (2007). Skevas et al. (2012) implement the Simar and Wilson double-bootstrap procedure to expalin Dutch farmer's performance in pesticide use.

Regarding the frontier eco-efficiency models, only a few studies have focused on the agricultural sector. Picazo-Tadeo et al. (2011) examine the eco-efficiency scores computed for Spanish farmers in the rain-fed agricultural system of Campos country, including socioeconomic determinants such as farmers' age, income, education and training. Pérez Urdiales et al. (2015) extend the analysis for a sample of dairy farms in Asturias, Spain, by also including information on farmers' attitudes towards the environment such as environmental habits or attitudes towards environmental regulation. Both studies use the Simar and Wilson double-bootstrap procedure to perform the analysis.

5 Research perspectives

5.1 Modeling landscape outputs and their efficiency

In the PEERLESS project, we aim at analyzing the trade-offs between agricultural production and environmental performance at landscape level. For this purpose, we developed a model in which landscape is generated by individual (field) land use decisions.[10] Each landscape is composed of 100 agricultural fields and, for each field, there are four potential land uses. Land can either be allocated to extensive grassland or to cropland with three levels of pesticide intensity: none, medium and high. The landscape is thus composed of a proportion of grassland, cropland with no pesticide, cropland using a intermediate level of pesticides and cropland using a high level of pesticides. Ecological dynamics at the field and landscape levels determine global and local populations of pests and their predators (metapopulation model), which generate damages and agricultural losses.

Pesticide use influences negatively the pest dynamics, which may have a positive impact on the agricultural production by reducing pest damage. However, pesticides also generate adverse effects on the environment and human health, justifying public policies to reduce their use. A set of public policies is thus considered to promote reductions in pesticide use. The public policies are taxes on pesticide use (four different levels), subsidies on grassland (six different levels), as well as a price bonus for production without pesticides. In this context, land use decisions depend on the farmers' information level (i.e., their degree of knowledge of the ecological dynamics, which influence their anticipations of damages and thus the associated treatment), their expectations on the field's performance, and the public policies implemented.

By varying the policy instruments, we obtain a set of potential landscape and measure their performance with respect to three outcomes: the production level, the pesticide use and the generated profit. We examine if the landscape composition and structure makes it possible to reduce pesticide use and thus to improve the environmental performance of the production system. To do so, we analyze the efficiency of the simulated landscapes.

5.2 Measuring efficiency in pesticide use

In order to measure the trade-offs between agricultural production and environmental damage caused by the use of pesticides, we use Data Envelopment Analysis to construct a nonparametric frontier that identifies the

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[10] More details on this generic model "Proie-Predateur-Paysage" will be available in Deliverable report D6-1, as well as in the outputs of Task 5.

most efficient landscapes in terms of pesticide use. The following linear program determines the optimal proportions of land use within landscapes to obtain the minimum pesticide use:

$$\begin{aligned} &\min_{\lambda_i x_{ij}} \sum_{j=1}^{4} p_j x_{ij} \\ &s.t. \sum_{i=1}^{n} \lambda_i x_{ij} - x^*_{nj} \leq 0 \\ &\sum_{i=1}^{n} \lambda_i Y_i - Y_n \geq 0; \sum_{i=1}^{n} \lambda_i = 1 \end{aligned} \tag{35}$$

where x_{ij} is the proportion of fields devoted to each j land use for landscape i, p_j is the level of pesticide use for each j land use, Y_i is the output for landscape i and λ_i is the non-negative weights for landscape i.

The level of efficiency is then calculated using the following equation:

$$PE_i = \frac{\sum_{j=1}^{4} p_j x^*_{ij}}{\sum_{j=1}^{4} p_j x_{ij}} \tag{36}$$

5.3 Explaining efficiency in pesticide use: truncated regression

As stated in section 4.2, the serial correlation of DEA efficiency scores should be taken into account in a second stage analysis of efficiency determinants. Therefore, we apply the methodology proposed by Simar and Wilson (2007). Specifically, we implement the Algorithm #2 which consists on a truncated regression and a double bootstrap.

In order to apply the methodology proposed by Simar and Wilson (2007), it is necessary that the dependent variable follows a distribution with left-truncation at 1, so we transform the efficiency estimates obtained using equation (36) by taking its inverse so that the transformed efficiency scores range from 1 to infinity. Once the transformation is performed, the truncated regression of the efficiency in pesticide use scores on a set of explanatory variables can be written as:

$$\varepsilon_i = z_i\beta + \epsilon_i \geq 1 \tag{37}$$

where ε_i represents (the inverse of) the efficiency scores.

The double bootstrap procedure described below performs bias correction and improves on inference, therefore, leading to consistent estimates of β:

1. Use maximum likelihood to obtain estimates of β and σ_ϵ for the regression of the inverse of the efficiency in pesticide use scores on the environmental variables or determinants using (37).

2. Loop over the following steps L times to obtain a set of bootstrap estimates for the parameters β and σ_ϵ:

$$\mathrm{B}_1 = \left\{ (\widehat{\beta}^*, \widehat{\sigma}^*_\epsilon)_b \right\}_{b=1}^{L} \tag{38}$$

    (a) For each observation draw ϵ_i from the $\mathrm{N}(0,\sigma_\epsilon)$ distribution with left-truncation at $(1 - z_i\widehat{\beta})$.

    (b) Compute for each observation $\varepsilon_i^* = z_i\widehat{\beta} + \epsilon_i$

    (c) Define $p_i^* = p_i$ and $v_i^* = v_i \frac{\widehat{\varepsilon}_i}{\varepsilon_i}$ for each observation.

    (d) Compute the DEA efficiency scores using equations (35) and (36) again by replacing v_i and p_i with v_i^* and p_i^* and take again the inverse of the obtained efficiency scores.

3. Calculate for each observation the bias-corrected estimator defined as $\widehat{\widehat{\varepsilon}}_i = \widehat{\varepsilon}_i - \widehat{\mathrm{BIAS}}(\widehat{\varepsilon}_i)$ using the original inverse of the efficiency and the bootstrapped estimates obtained in Step 2.

4. Use maximum likelihood again to estimate the truncated regression, but using $\widehat{\widehat{\varepsilon}}_i$ as the dependent variable. Obtain estimates of $\widehat{\widehat{\beta}}$ and $\widehat{\widehat{\sigma}}_\epsilon$

5. Apply the following steps L times to obtain a set of bootstrap estimates:

$$\mathrm{B}_2 = \left\{ (\widehat{\beta}^*, \widehat{\sigma}^*_\epsilon)_b \right\}_{b=1}^{L} \tag{39}$$

    (a) For each observation draw ϵ_i from the $\mathrm{N}(0,\sigma_\epsilon)$ distribution with left-truncation at $(1 - z_i\widehat{\widehat{\beta}})$.

    (b) As done in Step 2.b , compute for each observation $\varepsilon_i^{**} = z_i\widehat{\widehat{\beta}} + \epsilon_i$.

    (c) Use maximum likelihood to estimate the truncated regression with ε_i^{**} as dependent variable and z_i as explanatory variable. Obtain estimates of $\widehat{\widehat{\beta}^*}$ and $\widehat{\widehat{\sigma}^*_\epsilon}$

6. Finally, construct estimated confidence intervals for β and σ_ϵ by using the original estimates of $\widehat{\widehat{\beta}}$ and $\widehat{\widehat{\sigma}}_\epsilon$ and the bootstrap values obtained in B_2.

5.4 Data description

The dataset comprises a sample of landscapes simulated using the economic-ecological model described in Section 5.1. On average, the *Profit* is 543.86 €/hectare, the *Production* is 5.12 tons/hectare and the level of *Pollution* or pesticide, expressed using the Treatment Frequency Index (TFI), is 2.15 TFI (also expressed per hectare).

Table 1: Descriptive Statistics of the production variables

	Mean	Std. Dev	Min	Max
Profit	543.86	58.18	370.42	648.77
Production	5.12	1.20	2.26	6.77
Pollution	2.15	0.71	0.55	3.20

Moreover, as can be seen in Table 2, there are significant differences between those landscapes which take into account predation into the expectations on pests populations and those which do not. The mean score of the three indicators, *Profit* , *Production* and *Pollution*, is significantly higher in the case of landscapes with expectations of predation.

Table 2: Mean differences in terms of predation anticipation

	No Mean	V2	T-statistic	p-value
Profit	562.95	524.77	15.22	0.00
Production	5.39	4.85	9.97	0.00
Pollution	2.32	1.97	11.29	0.00

Figure 11 depicts the combinations of production and pollution obtained with the actual proportions of land uses. It can be seen that, for low levels of production, there is high heterogeneity in terms of pollution. This indicates that the amount of pesticides could be reduced while keeping production constant. However, the potential for reductions in terms of pollution is smaller for higher production levels.

Regarding the distribution of land uses, Table 3 shows the descriptive statistics of the proportion of land uses and the aggregation index for each type of land use. The type of land use with the highest average proportion is *Cropland 2* – moderately treated field (an average of 60 fields per landscape), followed by *Grassland* (in average 28 fields with grassland per landscape). The two remaining types of land uses, *Cropland 1* – untreated fields, and *Cropland 3* – heavily treated fields, represent, in average, only 7 and 6% of the fields per landscape, respectively.

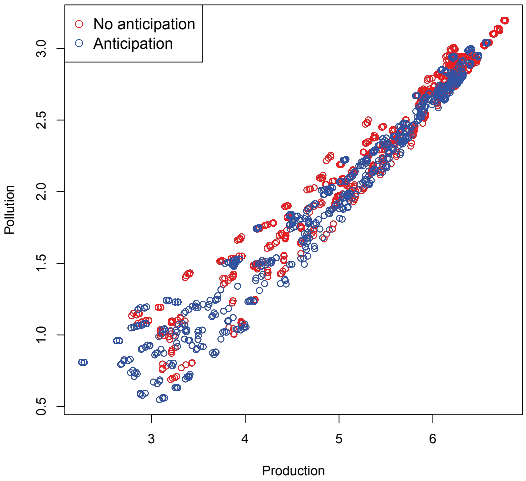


Figure 11: Production vs Actual Pollution

Table 3: Descriptive Statistics for land uses and aggregation patterns

	Mean	Std. Dev	Min	Max
Grassland	0.28	0.21	0.02	0.73
Cropland 1	0.07	0.09	0.00	0.43
Cropland 2	0.60	0.25	0.02	0.95
Cropland 3	0.06	0.09	0.00	0.43
Aggregation 1	0.58	0.46	0.00	1.00
Aggregation 2	0.18	0.21	0.00	0.72
Aggregation 3	0.77	0.33	0.00	1.00
Aggregation 4	0.15	0.20	0.00	0.69

5.5 Efficiency in pesticide use

Using the linear program in Equation (35) we obtain the optimal proportions of different land uses. A test of mean differences between the proportions in actual and optimal land uses is shown in Table 4. There is a significant positive difference between the optimal and the actual Grassland and Cropland 1 proportions. As expected, the optimal average proportions for these land uses, in which pesticides are not applied, are higher. The difference in the case of Cropland 2 is negative, although is not statistically significant, whereas this difference is negative and significant for Cropland 3, that is, the land use that receives the most intensive application of pesticide.

These preliminary results can be interpreted as follows. Environmental efficiency (i.e., quantity of pesticide use for a given production level) can be

Table 4: Mean differences in actual and optimal Land use

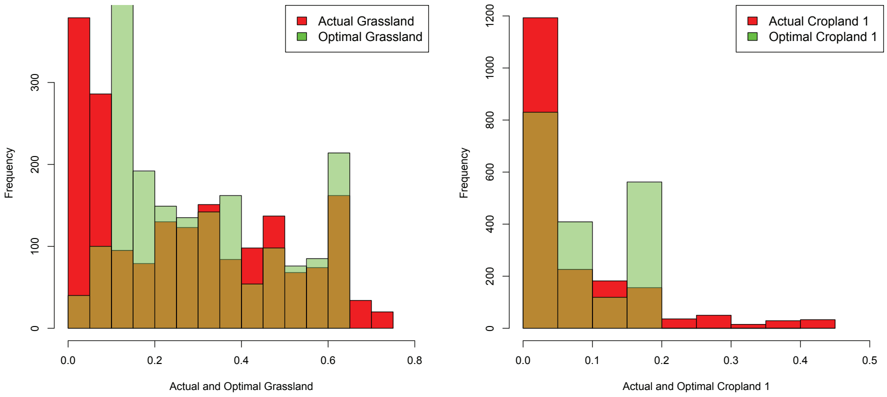
	Actual Mean	Optimal Mean	Change	T-statistic	p-value
Grassland	0.28	0.30	0.08	-3.47	0.00
Cropland 1	0.07	0.09	0.26	-7.67	0.00
Cropland 2	0.60	0.59	-0.01	1.00	0.32
Cropland 3	0.06	0.03	-0.87	15.69	0.00

increased by strongly reducing the most intensive croplands (Cropland 3 is reduced by 87% in mean) and increasing non-treated cropland (Cropland 1) along with grassland. This suggests that, over all the generated landscapes, grassland has a positive, indirect effect on production and could serve as a substitute for pesticides.

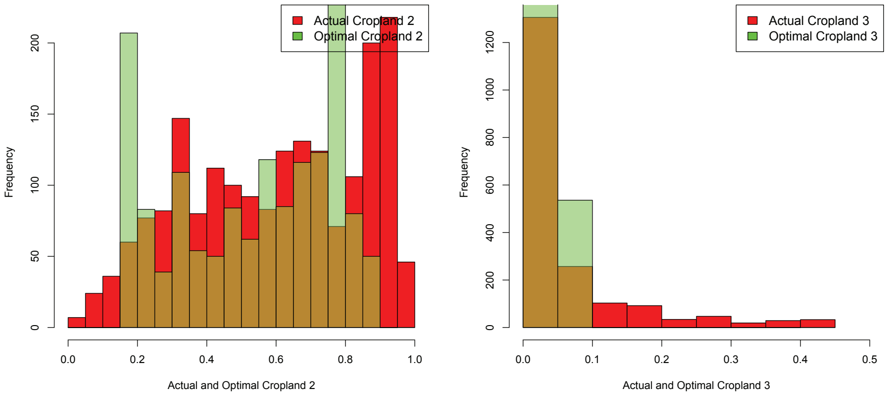
These mean results can be examined in further details by considering the optimal land allocation for different production configurations (production levels, landscape types).

Figure 12 shows the distributions of actual and optimal land uses proportions. It can be seen that the distribution of the actual grassland proportions is right-skewed, being this proportion less than or equal to 7.1% for 25% of the landscapes. However, the distribution of optimal grassland proportions is less skewed, and the percentage of landscapes with less than or equal to 7.1% (the first quartile for the actual grassland proportion) is only 3.65%. This means that the suggested increase of grassland mainly occurs in landscape with low grassland proportions ("cropland oriented landscapes").

A similar pattern can be observed in the case of the distribution of Cropland 1 proportions, that is, the proportion of actual Cropland 1 is concentrated at low levels and a less skewed distribution of optimal Cropland 1. The distribution of actual Cropland 2 proportions is characterized by being asymmetric with a heavy upper tail. In the case of its optimal proportions, we observe that the minimum and the maximum values are less extreme. Although, it continues to be the most commonly used type of land for the majority of the landscapes. Regarding the remaining land use, Cropland 3, the distribution of actual proportions is concentrated at low levels, but with a maximum value of 0.43, whereas for the optimal proportion, the maximum value is reduced to 0.086. This suggests that the share of treated corplands (Cropland 2 and Cropland 3) should be reduced in "cropland oriented landscapes." Note that all these results have to be confirmed by a more detailed analysis.



Production vs Grassland Production vs Cropland 1



Production vs Cropland 2 Production vs Cropland 3

Figure 12: Production vs Land Use

5.5.1 Efficiency scores

The efficiency in pesticide use scores are computed using the estimator in Equation (36). These scores, presented in Table 5, represent the potential radial reduction of the level of pesticide use while maintaining the level of production constant. The mean efficiency in pesticide use score is 0.8554, that is, pesticides could be reduced by an average of around 14% while maintaining the level of production by optimally allocate land to certain uses. The most inefficient lanscape cold reduce its pesticide use in more than 54%, as it has an efficiency score of 0.4586, however the number of landscapes that are fully efficient, that is, whose efficiency score is equal to 1, represents only 1.25% of the landscapes.

Table 5: Descriptive Statistics of Efficiency in Pesticide Use

Mean	Min	1^{st} Q	Median	3^{rd} Q	Max
0.8554	0.4586	0.7861	0.9174	0.9658	1

5.5.2 Efficiency determinants

Once efficiency in pesticide use at landscape level has been assessed, we perform an analysis of the efficiency determinants using truncated regressions and bootstrap procedures as described in Section 5.3. The estimated coefficients and their bootstrapped confidence intervals[11] from the truncated regression are presented in Table 6. Given that the dependent variable is defined as the inverse of the efficiency in pesticide use scores, a positive estimated coefficient indicates a positive impact on inefficiency and hence lower efficiency, whereas a negative estimated coefficient indicates a negative impact on inefficiency and therefore a higher level of efficiency.

Moreover, the interpretation of the boostrapped confidence intervals is the same as in the case of habitual ones, that is, if both the upper and lower bound are positive (negative), the estimated coefficient is positive (negative) and statistically significant at the 5 or 10% level, that is, the coefficient is significantly different from 0.

With this in mind, and beginning with the variables related to land uses aggregation, the positive estimated coefficient for Grassland Aggregation indicates that the more aggregated fields allocated to grassland within a landscape, the more inefficient in pesticide use, that is, this variable has a negative effect on the level of efficiency in pesticide use. This result indicates that it is preferable to allocate grassland disperse through the landscape. This reinforces the intuition that grassland have a positive (local) spatial externality on pest reduction. On the other hand, the effect of aggregation of fields that apply pesticides is not statistically significant, implying that there is no spatial effect of these treatments.

As might be expected, the estimated coefficient for pesticide tax variable

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[11] We use bootstrap estimates and the original estimates $\widehat{\widehat{\beta}}$ and $\widehat{\widehat{\sigma_\sigma}}$ to construct confidence intervals. Habitual 95% and 90% confidence intervals can be constructed from:

$$Pr[-b_\alpha \leq (\widehat{\widehat{\beta}}_j - \beta_j) \leq a_\alpha] = 1 - \alpha \tag{40}$$

being α equalto 0.5 and 0.1. However, the distribution of $(\widehat{\widehat{\beta}}_j - \beta_j)$ is unknown. We can use the j^{th} element of $\widehat{\widehat{\beta}}_j$ to obtain a^*_α and b^*_α from:

$$Pr[-b^*_\alpha \leq (\widehat{\widehat{\beta^*_j}} - \widehat{\widehat{\beta}}_j) \leq -a^*_\alpha] = 1 - \alpha \tag{41}$$

From equation 41 we can obtain the boostrapped confidence intervals $[\widehat{\widehat{\beta}}_j + a^*_\alpha, \widehat{\widehat{\beta}}_j + b^*_\alpha]$.

is negative, implying that those landscapes that have been subjected to a higher tax are more efficient in pesticide use. The subsidy to promote grasslands has a positive coefficient, indicating that the higher the subsidy, the lower the level of efficiency in pesticide use. This would seem to suggest that this type of subsidies could encourage a reduction in the amount of pollution only if the production level is reduced in a higher proportion. The interactions between the two effects will be studied further.

Finally, the negative coefficient for the variable related to anticipation indicates that landscapes which take into account the level of predation into the expectations on pests populations are more efficient in pesticide use.

Table 6: Truncated regression and bootstrapped confidence intervals

		(95% confidence)		(90% confidence)	
	Parameter	lower bound	upper bound	lower bound	upper bound
Intercept	1.2425	1.0399	1.3190	1.0617	1.3001
Anticipation	-0.0498	-0.0571	-0.0171	-0.0530	-0.0211
Grassland Aggregation	0.1970	0.1220	0.1986	0.1279	0.1933
Pesticide Intensity	-0.1427	-0.2118	0.1070	-0.1880	0.0874
Pesticide Tax	-0.0004	-0.0022	-0.0004	-0.0021	-0.0006
Grassland Subsidy	0.0005	0.0004	0.0006	0.0004	0.0006
Sigma	0.1315	0.1286	0.1431	0.1295	0.1420

5.6 Concluding remark

This preliminary results emphasize the usefulness of this type of economic tools to analyse the efficiency of agricultural production systems. More detailed analysis will be conducted in the second half of the PEERLESS project, and should lead to interesting results.

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Projet ANR-12-AGRO-006

PEERLESS

Scientific publications in peer-reviewed international economics and environmental journals in collaboration with other tasks

A IDENTIFICATION DU LIVRABLE

Titre du projet	PEERLESS:Predictive Ecological Engineering for Landscape Ecosystem Services and Sustainability
Titre du livrable	Scientific publications in peer-reviewed international economics and environmental journals in collaboration with other tasks
Nature du livrable	Liste de productions scientifiques de la tâche 6 du projet
Date de publication	02/02/2018
	Version 2

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Partenaires impliqués	Idem
Tâche associée	T6

B OBJECTIFS

Les travaux de la tâche 6 ont donné lieu à la rédaction d'articles scientifiques qui ont été présentés en conférences et seront soumis pour publication prochainement. Le livrable présente un résumé des différents travaux qui ont été présenté.

C PRESENTATION DES AVANCEES

1. Memmah, M.-M., Lescourret, F., Yao, X. et Lavigne, C. (2015) Metaheuristics for agricultural land use optimization. A review. *Agronomy for Sustainable development* 35, 975-998.

Résumé:

Agricultural landscapes presently cover about 46 % of earth terrestrial surface. This cultivated area is decreasing, whereas the global food demand is projected to increase up to 70 % in 2050. The intensification of agriculture is not a solution to this food issue because intensive agriculture has often resulted in pollution and loss of biodiversity. On the other hand, mechanistic models with optimization algorithms can be used to design alternative land uses for sustainable agriculture. Here, we present a review of metaheuristics for land use optimization reported in 50 articles including 38 case studies carried out in 16 countries. Our main conclusions are: 1) the success of metaheuristics is problem-dependent. In general, metaheuristics enable search to escape from local optima and find a good global approximation solution. 2) The choice of a given metaheuristic for solving a given problem seems to be driven by its historical use in a research team and by its popularity outside the metaheuristics research community, rather than by the characteristics of the problems to be solved and by the latest results from the metaheuristics research community. 3) Stakeholders of land use are increasingly involved at different levels of the land use optimization procedure and multi-actors decision-making methods are necessary to find trade-offs between their competing interests. 4) A future challenge is the use of parallelization techniques along with the hybridization of different metaheuristics or of metaheuristics with other optimization methods.

2. Pérez-Urdiales M. et Martinet V. (2017) Pesticide use reductions at landscape level: efficient allocation of land uses. Working paper. Présenté en conferences internationales en 2016 et 2017. Soumission prévue au printemps 2018.

- VII Congreso Internacional de Eficiencia y Productividad EFIUCO, 19-20 mai 2016 Cordoba, Spain
- *3ème Conférence annuelle de la FAERE – 08-09 Septembre 2016 – Bordeaux*

Résumé :

There is an increasing conflict of interest between food security and environmental and health issues that may be caused by pesticide use. Biological control of pests by natural enemies could provide a substitute for pesticides, but it is intimately related to the ecological dynamics of pests and their natural enemies at landscape level. There is, however, a potentially efficient composition of the landscape into cropland and non-crop habitats, which would leave the production constant, while reducing the use of pesticides. In this paper, we aim at identifying this efficient allocation of land and at computing the reduction in the amount of pesticides. To do so, we use data at landscape level simulated from an ecological-economic model and nonparametric frontier techniques that allow us to identify the pesticide-efficient landscape composition. Moreover, we analyze the effect of some agronomic characteristics and economic incentives on the efficiency in pesticide use. Our results show that pesticides could be reduced by 7% on average without affecting the agricultural output. Dispersed non-crop habitats within the landscape and a tax on pesticide use are the variables that reduce pesticide use at landscape level.

3. Dakpo H., Boussemart J.-P., et Martinet V. (2018) Spatial aggregation of land uses allocation and pesticide efficiency at landscape level A Multi-ware production approach. Working paper. Sera présenté en conférences internationales en 2018. Soumission prévue en mai 2018.

- *DEA40 : International Conference on Data Envelopment Analysis. Aston University, UK, April 16-18, 2018*

Résumé:

We extend the single-stage framework of damage-control inputs like pesticides to a multi-ware framework where four technologies are considered. The economic technologies describe the production and the damages due to pests while the ecological technologies represent the dynamics of pests and predators' populations. To account for the possibilities of spatial effects of land uses (crop and non-crop habitats), we consider an analysis at the landscape level and try to find the optimal allocation of the land uses that help minimizing pesticides. To this aim we rely on a prey-predator simulation model. We assess pesticides performance considering nonparametric production frontier techniques. Our results indicate that pesticides can be reduced by 7.7% without reducing the landscape production. In terms of land uses we found that grasslands areas should be increased by more than twice and croplands with medium levels of pesticides unchanged. Croplands with zero and high levels of pesticides should be reduced. In terms of trade-offs between pesticides and the landscape production we found that the spillover effect is very high and result in a negative trade-off because of the destruction of predators by pesticides. Pesticides inefficiency can be reduced when treated areas are spatially aggregated and when grasslands are subsidized.

4. David M., Chèze B. et Martinet V. (2018) Farmers’ motivations to reduce their use of pesticides: a choice experiment analysis in France. Working paper. Présenté en conferences internationales en 2017 et 2018. Soumis à *European Review of Agricultural Economics.*

- *4ème Conférence annuelle de la FAERE – 12-13 Septembre 2017 – Nancy*

Résumé :

Reducing the use of pesticides has become a major challenge in developed countries’ agriculture. Public policies have developed for the last ten years and some farming practices have proven efficient to maintain yields while reducing the use of chemicals (Lechenet et al. 2017). However, farmers' consumption of chemical inputs has increased in Europe between 2008 and 2016. What are the main obstacles that prevent farmers from adopting low-pesticides practices that could be win-win strategies?

We use a discrete choice experiment (DCE) to measure the relative weight of various factors that determine farmers’ choice in this field. We also estimate farmers' willingness to pay (WTP)/ willingness to accept (WTA) for changes in these factors. Only very few DCE contributions have looked into the role of risk in farmers' choices whereas price-risk and harvest-risk are two factors that can drastically affect farmers' revenues. Using pesticides can be interpreted as an insurance behavior as it limits income variability by reducing harvest losses, without necessarily increasing the total mean income. Our analysis is a first attempt to include, besides other attributes, the role of the harvest-risk in 89 French farmers' decisions to reduce -or not - their use of pesticides.

Using a Conditional Logit, a Random Parameter Logit and a Latent Class Model, we find that the risk of poor harvest is a prominent obstacle for farmers' reduction of pesticides use. All else being equal (in particular, for a given mean yearly profit), farmers need to receive in average 101 euros per year and per hectare to accept one additional year of poor harvest every ten years. Another factor that influences farmers' behavior is the administrative framework that may come along with the practices' change, which is not seen by farmers as an opportunity for support or integration in a network but rather as a burden. For example, all else being equal, farmers need to receive 86 euros per year and per hectare to accept to sign an agri-environmental contract. Another noteworthy result is that the impact of pesticides on health and the environment does not seem to be a significant criterion.