



Influence des activités agricoles et des éléments permanents sur la biodiversité : l'exemple des coléoptères carabiques et des papillons rhopalocères dans les paysages agricoles bocagers

Stéphanie Aviron

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THÈSE

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DEVANT L'UNIVERSITÉ DE RENNES 1

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Mention : BIOLOGIE

PAR

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UFR Sciences de la Vie et de l'Environnement

**EFFETS DES ACTIVITES AGRICOLES ET DES ELEMENTS
PERMANENTS SUR LA BIODIVERSITE : L'EXEMPLE DES
CARABES ET DES PAPILLONS RHOPALOCERES DANS
LES PAYSAGES BOCAGERS**

Composition du jury :

Jacques BAUDRY	Directeur de Recherche, INRA, Rennes	Président du Jury
Michel BAGUETTE	Professeur, Université de Louvain	Rapporteur
Hervé JACTEL	Directeur de Recherche, INRA, Cestas	Rapporteur
Françoise BUREL	Directrice de Recherche, CNRS, Rennes	Directrice de thèse
Félix HERZOG	Ingénieur de recherche, FAL, Zurich	Examineur
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INTRODUCTION GENERALE

INTRODUCTION GENERALE

1. Cadre général : la conservation de la biodiversité dans les paysages agricoles

1.1. Intensification agricole et modifications de la biodiversité

L'augmentation de la pression des activités humaines depuis la seconde guerre mondiale a entraîné des modifications importantes des paysages agricoles au niveau planétaire (Turner II et Meyer, 1994). Dans ce travail, nous définirons l'intensification de l'agriculture selon Brookfield (1972, dans Lambin *et al.*, 2000) comme « *the substitution of inputs of capital, labour and skills for land, so as to gain more production from a given area, use it more frequently, and hence make possible a greater concentration of production* »¹. L'intensification de l'agriculture en Europe a consisté en une spécialisation et une concentration de la production, permises par la modernisation du machinisme agricole, l'introduction de nouveaux produits phytosanitaires (engrais chimiques, pesticides), de nouvelles cultures et d'animaux d'élevage (Hietala-Koivu, 2002 ; Robinson et Sutherland, 2002). En Bretagne, le système de polyculture-élevage présent avant 1950 a évolué vers une agriculture spécialisée dans la production animale et caractérisée par des systèmes de production simplifiés (Canévet, 1992). Ces modifications se sont accompagnées d'une concentration de la production (forte réduction du nombre d'exploitations, augmentation de leur surface, forte croissance des cheptels en particulier concernant les élevages hors sol) (Canévet, 1992). Les pratiques culturales se sont profondément modifiées pendant cette période. Le nombre et l'étendue des applications de pesticides a augmenté (Robinson et Sutherland, 2002), la plupart des champs recevant des traitements multiples. Les engrais organiques ont peu à peu été remplacés par des engrais chimiques, plus concentrés (Robinson et Sutherland, 2002). En outre, avant l'utilisation massive de pesticides, le contrôle des mauvaises herbes en champ était réalisé par labour et par l'utilisation de rotations culturales incluant des cultures autres que céréalières ; l'utilisation massive de produits chimiques, en particulier des herbicides, a alors conduit à de la culture plus continue de céréales (Robinson et Sutherland, 2002). La spécialisation de la production, l'élargissement des exploitations, la simplification des rotations culturales et la réduction des milieux permanents ont conduit à une homogénéisation des paysages (Fjellstad et Dramstad, 1999 ; Hietala-Koivu, 2002; Robinson et Sutherland, 2002). La fragmentation des habitats pour la faune et la flore et l'utilisation croissante d'intrants ont entraîné le déclin de nombreuses espèces (Wilcove *et al.*, 1986 ; Solbrig, 1991 ; McLaughlin et Mineau, 1995 ; Jongman, 2000 ; Stoate *et al.*, 2001).

Depuis ce constat, la conservation de la biodiversité dans les paysages agricoles est devenue un enjeu majeur et de nombreux programmes de recherches ont été développés afin d'identifier les facteurs de la dynamique de la biodiversité dans les paysages agricoles. **La problématique de mon travail de thèse s'inscrit dans cette perspective générale d'évaluation des relations entre agriculture et biodiversité.**

¹ « Changements de capitaux, de travail et de compétences liés à l'utilisation des terres, ayant pour objectif un accroissement de la production dans une zone donnée, son utilisation plus fréquente et une plus grande concentration de la production ».

1.2. La biodiversité : une notion complexe

Le terme de biodiversité a fait l'objet de nombreuses définitions, la plus simple étant « la variabilité du vivant ». **La définition que nous retenons est celle de Noss (1990), qui propose une définition hiérarchique de la biodiversité, articulée autour de trois attributs fondamentaux, la composition, la structure et le fonctionnement** : « *Biodiversity is not simply the number of genes, species, ecosystems, or any other group of things in a defined area...More useful than a definition, perhaps, would be a characterization of biodiversity that identifies the major components at several levels of organization ... Composition, structure, and function ... determine, and in fact constitute, the biodiversity of an area. Composition has to do with the identity and variety of elements in a collection, and includes species lists and measures of species diversity and genetic diversity. Structure is the physical organization or pattern of a system, from habitat complexity as measured within communities to the pattern of patches and other elements at a landscape scale. Function involves ecological and evolutionary processes, including gene flow, disturbances, and nutrient cycling* ». La biodiversité peut être alors décomposée en différents niveaux d'organisation allant du gène à l'écosystème, en passant par les individus, les populations et les communautés. Cette définition inclut la notion de complexité croissante des êtres vivants et des systèmes écologiques.

1.3. L'importance des éléments (semi-)permanents

Dans les paysages agricoles actuels, les éléments permanents ou semi-permanents, tels que les bois, les bords de champs ou les prairies permanentes, sont relativement stables dans le temps, et jouent de ce fait un rôle essentiel dans le maintien de la biodiversité. Ils servent d'habitat à certaines espèces spécialistes (Forman et Baudry, 1984 ; Paillat et Butet, 1996), de refuges saisonniers aux espèces qui utilisent en alternance les zones cultivées et les milieux permanents (Morvan *et al.*, 1994 ; Delettre *et al.*, 1998). Il jouent également le rôle de refuge temporaire lorsque les parcelles cultivées sont perturbées (Ouin *et al.*, 2000) et fournissent des ressources pour les organismes (Dennis et Fry, 1992). Enfin, certains milieux permanents tels que les haies sont utilisés comme corridor de dispersion entre îlots boisés par certaines espèces (Duelli *et al.*, 1990 ; Petit et Burel, 1998b).

Les paysages agricoles de l'ouest de la France sont caractérisés par la présence d'un réseau bocager (Baudry *et al.*, 2000a) qui abrite une flore et une faune variée (Hooper, 1974 ; INRA *et al.*, 1976). La diversité animale et végétale des haies a été reliée à des facteurs locaux tels que les conditions abiotiques (Burel, 1996 ; Maudsley *et al.*, 2002), la structure de la haie (profondeur du fossé, hauteur du talus, largeur de la bordure, perméabilité des strates herbacées, arbustives et arborescentes) (Pollard *et al.*, 1974 ; Delettre et Morvan, 2000 ; Moonen et Marshall, 2001) et sa composition (espèces végétales, origine de la haie) (Forman et Baudry, 1984 ; Thomas et Marshall, 1999). Le bocage a atteint sa densité maximale à la fin du 19^{ème} et début du 20^{ème} siècle. Son évolution a été caractérisée par une grande instabilité, consistant en des périodes d'importantes modifications, édifications ou arasement, liées au bouleversement des techniques agricoles. L'intensification agricole de l'après-guerre a conduit à une réduction particulièrement importante du linéaire de haies dans ces paysages. La mécanisation des travaux des champs a nécessité des structures adaptées, ce qui a conduit à de nombreuses opérations individuelles ou collectives de suppression des haies et d'augmentation de la taille des parcelles cultivées (Morant, 1999 ; Baudry et Jouin, 2003). En outre, les modes de gestion des haies ont changé avec l'évolution récente de l'agriculture et ne

cessent de se modifier (Baudry et Jouin, 2003), conduisant à une réduction de la végétation arborescente et arbustive des haies et une diminution de leur capacité d'accueil pour les espèces (Baudry *et al.*, 1998). La reconnaissance du rôle écologique du bocage, en plus de son importance d'un point de vue esthétique et patrimonial, a conduit à une sensibilisation des politiques, de l'opinion publique et des agriculteurs à l'importance des haies dans les paysages agricoles. **Dans ce travail de thèse, les haies et autres milieux (semi-) permanents des paysages agricoles bretons ont constitué un objet d'étude central.**

2. Vers une approche holistique des relations biodiversité – agriculture

2.1. Les apports de l'écologie du paysage

En application des concepts de la théorie biogéographique des îles (McArthur et Wilson, 1967), de nombreuses recherches se sont centrées sur l'étude de la biodiversité dans les milieux boisés (Milne et Forman, 1986 ; van Dorp et Opdam, 1987). Le paysage agricole a alors été représenté comme une matrice neutre, stable et homogène dans laquelle étaient imbriqués les bois et éléments linéaires boisés, considérés comme des îlots forestiers (van Dorp et Opdam, 1987 ; Bennett, 1990). Depuis, l'hétérogénéité et la variabilité de la mosaïque a été reconnue comme un facteur déterminant pour le fonctionnement des paysages.

Dans ce travail de thèse, réalisé au sein de l'équipe Ecologie du paysage de l'UMR 6553 Ecobio, **l'étude des haies et autres éléments (semi-) permanents est réalisée en considérant l'hétérogénéité et la dynamique de la mosaïque agricole.** Notre approche, qui considère le paysage comme le produit des activités humaines, s'inscrit dans le cadre conceptuel et méthodologique de l'écologie du paysage (Forman et Godron, 1986). La première définition du paysage de l'écologue a été celle de Bertrand (1975), pour lequel « *le paysage est un médiateur entre la nature et la société ayant pour base une portion d'espace matériel qui existe en tant que structure et système écologique, donc indépendamment de la perception* ». Plus tardivement, Forman et Godron (1986) ont donné une définition similaire : « *a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout* »². Enfin, la définition que j'ai retenue est celle de Burel et Baudry (1999), qui ont proposé une définition faisant la synthèse des deux précédentes : « *le paysage est un niveau d'organisation des systèmes écologiques, supérieur à l'écosystème ; il se caractérise essentiellement par son hétérogénéité et par sa dynamique gouvernée en partie par les activités humaines. Il existe indépendamment de la perception* ».

Parmi les différentes idées développées pour définir l'écologie du paysage, nous retiendrons trois points qui nous semblent essentiels à la compréhension des conséquences écologiques des transformations des paysages agricoles et particulièrement pertinents dans le cadre du présent travail :

- la prise en compte de l'hétérogénéité spatiale et temporelle comme composante essentielle des processus écologiques,
- la prise en compte des activités humaines comme facteurs d'organisation et de dynamique des paysages,
- la reconnaissance du paysage comme une échelle pertinente pour les gestionnaires.

² « Portion de territoire hétérogène composée d'ensembles d'écosystèmes en interaction qui se répètent de façon similaire dans l'espace ».

Hétérogénéité spatiale et processus écologiques

L'hétérogénéité spatiale du paysage, qui reflète la diversité et l'arrangement spatial de la mosaïque du paysage (Baudry et Baudry-Burel, 1982), a été reconnue comme une composante essentielle de la biodiversité à plusieurs niveaux (Hushton, 1995), allant des individus aux communautés en passant par les populations.

Dans les paysages agricoles, la mobilité est un processus clé de la survie des espèces, que ce soit en terme de dispersion au sein des populations fragmentées (Taylor, 1990 ; Johnson *et al.*, 1992 ; Fahrig et Merriam, 1994 ; Hanski *et al.*, 1996 ; Szacki, 1999), ou en terme de déplacements journaliers ou saisonniers pour l'exploitation des ressources (Wiklund, 1977 ; Dunning *et al.*, 1992 ; Brommer et Fred, 1999). La connectivité du paysage, définie comme « *the degree to which the landscape facilitates or impedes movement among resource patches*³ » (Taylor *et al.*, 1993), est alors un concept clé pour traduire les interactions entre les caractéristiques du paysage et le déplacement des individus (les caractéristiques du paysage sont sa composition (nature et abondance des éléments présents dans le paysage) et sa structure (arrangement spatial de ces éléments)). Les interactions entre le mouvement des individus, les caractéristiques du paysage et sa dynamique déterminent alors la distribution et le maintien des espèces à plus ou moins long terme (Wiens *et al.*, 1993a ; Wiens *et al.*, 1997 ; McIntyre et Wiens, 1999) et la dynamique des communautés (Gutzwiller et Anderson, 1992). Bien que le paysage ait longtemps été considéré comme une matrice neutre et homogène, l'hétérogénéité spatiale de la mosaïque agricole a depuis été reconnue comme un facteur déterminant du mouvement des organismes (Schippers *et al.*, 1996 ; Martin *et al.*, 2001 ; Ricketts, 2001) et de la dynamique des communautés (Burel *et al.*, 1998 ; Romero-Alcaraz et Avila, 2000 ; Millán Peña *et al.*, 2003 ; Benton *et al.*, sous presse). Désormais, l'élément permanent n'est plus considéré comme déconnecté de son environnement (Ouin *et al.*, 2000 ; Le Coeur *et al.*, 2002) : la faune et la flore d'une haie ne dépendent pas seulement des conditions locales mais également des caractéristiques du paysage environnant, qui déterminent les possibilités d'échanges avec les taches voisines et la présence des espèces au sein de la haie (Baudry, 1985 ; Petit et Burel, 1998b ; Millán Peña, 2001 ; Le Coeur *et al.*, 2002).

La prise en compte des activités humaines comme facteurs d'organisation et de dynamique des paysages

La volonté d'identifier les processus impliqués dans l'organisation et la dynamique des paysages a conduit à considérer la mosaïque agricole dans son ensemble et à relier les cultures et usages locaux au territoire d'exploitation agricole dans lequel ils s'inscrivent. Ainsi, l'hétérogénéité spatiale du paysage est liée à la diversité des systèmes de production agricole (diversité des utilisations du sol et de pratiques), qui se traduisent par une diversité de couverts végétaux. La répartition des usages par l'agriculteur au sein du territoire d'exploitation agricole participe à l'organisation de la mosaïque (Thenail et Baudry, sous presse). La dynamique des paysages agricoles est liée aux activités agricoles à différentes échelles : la mosaïque des ressources change en fonction du stade phénologique des cultures et des pratiques culturales au cours de la saison ; les successions culturales et de pratiques associées modifient l'organisation spatiale de cette mosaïque sur plusieurs années ; à plus long terme, les changements des systèmes de production entraînent des modifications plus durables des paysages, en terme d'utilisation des terres, de taille des parcelles cultivées ou

³ « La capacité du paysage à faciliter ou au contraire freiner les déplacements des individus ».

d'importance des éléments (semi-) permanents (Thenail, 2002). Les modifications des paysages sont spécifiques des systèmes de production et de leur dynamique (Poudevigne *et al.*, 1997 ; Millán Peña *et al.*, 2003). Il apparaît alors fondamental de prendre en compte la nature des systèmes de production impliqués dans les processus d'intensification du fait qu'ils conduisent à différentes trajectoires d'évolution des paysages. Certains travaux se sont intéressés aux effets des transformations des paysages agricoles liés aux changements d'utilisation des terres sur la biodiversité (Chamberlain et Fuller, 2000 ; Siriwardena *et al.*, 2001), mais peu d'auteurs ont considéré de façon explicite les relations entre les changements des systèmes de production agricole et la dynamique des paysages et de la biodiversité (Baudry *et al.*, 2003 ; Millán Peña *et al.*, 2003).

2.2. Vers une approche holistique et hiérarchique des activités agricoles

Dans les paysages, les processus écologiques se déroulent à des échelles d'espace et de temps qui leur sont propres. Les activités agricoles opèrent également à plusieurs niveaux allant du champ, aux exploitations agricoles et aux politiques agricoles à l'échelle régionale (Balent, 1987). La mise en relation des activités agricoles et des systèmes écologiques nécessite donc d'adopter une approche holistique et hiérarchique (Naveh et Lieberman, 1994 ; Reenberg et Baudry, 1999). Dans ce contexte, la théorie de la hiérarchie (Allen et Star, 1982 ; O'Neill *et al.*, 1986) apporte un cadre conceptuel approprié (Baudry *et al.*, 2000b).

La théorie de la hiérarchie prédit que les systèmes écologiques peuvent être décomposés en plusieurs niveaux, chaque niveau opérant à des échelles d'espace et de temps distinctes (Allen et Star, 1982 ; O'Neill *et al.*, 1986). Les facteurs explicatifs de la biodiversité interviennent ainsi à différentes échelles (Auger *et al.*, 1992) : la qualité des ressources et les conditions physiques à l'échelle locale, les caractéristiques du paysage à l'échelle du paysage, et les facteurs biogéographiques à l'échelle régionale. Les activités agricoles peuvent également être décomposées de façon fonctionnelle selon différentes échelles (Baudry *et al.*, 2000b). Le champ ou le bord de champ constituent, en tant qu'unité de gestion⁴, le premier niveau de la hiérarchie : au niveau de la parcelle, l'agriculteur met en œuvre un certain nombre de pratiques en relation avec l'usage parcellaire au cours de l'année ou d'une saison ; le bord de champ est géré par l'agriculteur en fonction de l'utilisation du sol adjacente (Baudry *et al.*, 1998). Au niveau de l'exploitation agricole, l'agriculteur décide de la répartition annuelle des usages (utilisations du sol, pratiques) au sein de son territoire d'exploitation. Au dernier niveau de la hiérarchie, le paysage peut être vu comme un ensemble de territoires d'exploitations caractérisés par divers systèmes de production qui évoluent au cours du temps en fonction de décisions individuelles des agriculteurs, de contraintes naturelles (pente, nature des sols, etc.) ou politiques (économie, aménagements).

Cette approche apparaît comme essentielle à l'étude des relations entre biodiversité et agriculture dans le sens où elle identifie des échelles pertinentes pour appréhender les interactions entre activités agricoles et biodiversité (Baudry *et al.*, 2000b). Le territoire d'exploitation, souvent discontinu dans l'espace, ne peut être considéré comme un paysage à part entière ni comme une entité écologique fonctionnelle (Baudry *et al.*, 2000b ; Thenail et Baudry, sous presse). Lorsque l'on se situe dans une même région biogéographique comme

⁴ L'unité de gestion est définie pour 1) la parcelle, par la portion de territoire soumise une utilisation définie par l'agriculteur et 2) le bord de champ, par le segment de haie délimité par deux parcelles (Baudry *et al.* 2000b).

c'est le cas ici, l'échelle de l'unité de gestion par l'agriculteur et celle du paysage constituent des échelles appropriées pour l'étude des relations entre biodiversité et agriculture.

2.3. Evaluation de l'importance relative des facteurs de la biodiversité dans les paysages agricoles

Les recherches développées sur les interactions entre biodiversité et agriculture se sont le plus souvent restreintes à une échelle d'étude, échelle locale **ou** échelle du paysage. Les études écologiques ou agronomiques des effets des activités agricoles sur la biodiversité ont le plus souvent été réalisées à l'échelle locale, la parcelle le plus souvent. Elles ont été centrées sur l'impact de l'utilisation intensive de certaines pratiques, telles que la fauche, le pâturage, l'utilisation de pesticides et de fertilisants, considérées individuellement (Freemark et Boutin, 1995 ; McLaughlin et Mineau, 1995 ; Fuhlendorf *et al.*, 2002a ; Kruess et Tscharntke, 2002) ou comme partie de systèmes de production (Dritschilo et Erwin, 1982 ; Weibull et Östman, 2003 ; Weibull *et al.*, 2003). Ces travaux ont permis de montrer que les effets de ces pratiques peuvent être une mortalité directe dans le cas de la fauche (Gibson *et al.*, 1993), du labour (Basore *et al.*, 1986), ou de l'utilisation de pesticides (Thacker et Hickman, 1990 ; Freemark et Boutin, 1995), ou indirects dans le cas du pâturage ou de l'utilisation d'herbicides, via la modification des ressources alimentaires, des sites de reproduction ou des refuges offerts par la végétation (Maudsley, 2000 ; Kruess et Tscharntke, 2002). Cependant, une telle approche revient à considérer que la dynamique de la biodiversité peut être expliquée par les seuls effets des pratiques agricoles et que les processus observés à l'échelle locale peuvent être extrapolés à une échelle plus globale. Plus récemment, quelques auteurs ont considéré de façon explicite les relations entre la dynamique des paysages, les changements des systèmes de production agricole et la biodiversité (Baudry *et al.*, 2003 ; Millán Peña *et al.*, 2003), sans toutefois considérer l'effet des pratiques agricoles ou la qualité des ressources à l'échelle locale.

Il apparaît alors difficile d'évaluer l'importance relative des facteurs qui interviennent sur la dynamique de la biodiversité aux différentes échelles. Les études ayant adopté une approche hiérarchique pour estimer l'importance relative de la qualité des habitats à l'échelle locale et des caractéristiques du paysage ont, au mieux, considéré l'effet des pratiques agricoles à l'échelle locale sans prise en compte des activités agricoles à l'échelle du paysage (Freemark, 1995 ; Alard et Poudevigne, 1999 ; Jeanneret *et al.*, sous presse). La compréhension des effets de l'intensification de l'agriculture et de la dynamique des paysages agricoles sur la biodiversité nécessite de considérer simultanément les activités agricoles comme facteur d'organisation et de dynamique du paysage mais également comme facteur de qualité des ressources à l'échelle locale.

3. Problématique de la thèse

L'objectif du présent travail est d'identifier l'importance relative de la structure et la dynamique du paysage et de la qualité des ressources sur la dynamique de la biodiversité, en considérant les processus impliqués dans la structuration des communautés et dans la distribution et la dynamique des populations. **Il se démarque des précédents par la prise en compte explicite des activités agricoles à plusieurs échelles dans l'étude de la biodiversité dans les paysages agricoles.**

Nous avons ainsi considéré :

- les pratiques agricoles comme facteurs déterminant, à court ou plus long terme, la qualité des ressources à l'échelle locale,
- les activités agricoles comme facteurs d'organisation et de dynamique des paysages agricoles : dynamique à court terme sous l'effet de pratiques agricoles, dynamique à plus long terme sous l'effet des changements des systèmes de production.

Notre problématique s'intègre dans une réflexion commune à l'équipe Ecologie du Paysage de l'UMR 6553 « Ecobio » et l'unité de recherche INRA SAD Armorique de Rennes depuis plusieurs années, sur les relations entre agriculture et biodiversité. La mise en place de notre démarche de travail a été permise par les unités d'observation communes à ces deux unités de recherche (unité de gestion, paysage) et par la mise en place d'observations sur le long terme dans le site Atelier de Pleine Fougères et dans un site des Côtes d'Armor.

D'un point de vue institutionnel, le présent travail s'insère dans le cadre de deux programmes de recherche pluri-disciplinaires impliquant l'équipe Ecologie du paysage et l'unité INRA SAD Armorique : le programme GREENVEINS « *Vulnerability of biodiversity in agroecosystems as influenced by land-use intensity and green veining* » initié par la Communauté Européenne et le programme DIVA, « *Diversité et agriculture : analyse agronomique et écologique des unités spatio-temporelles pertinentes pour la gestion de la biodiversité* », initié par le Ministère de l'Environnement et du Développement Durable. Les principaux objectifs de ces programmes de recherche sont :

- de décrire la relation entre structure des paysages, intensité de l'agriculture et biodiversité,
- de développer des méthodes d'estimation de la vulnérabilité de la biodiversité dans les paysages agricoles,
- de définir des unités spatio-temporelles pertinentes en terme de gestion et d'aménagement.

La réponse des espèces ou groupes d'espèces aux perturbations locales ou aux modifications du paysage varie en fonction de leurs exigences écologiques (Burel, 1991 ; Burel *et al.*, 1998 ; Morris, 2000). Pour aborder la question des relations entre agriculture et biodiversité, nous avons choisi deux groupes d'insectes comme modèles biologiques, les coléoptères carabiques et les papillons de jour (rhopalocères). Deux approches ont été privilégiées, l'une étant axée sur l'étude empirique des facteurs d'organisation et de dynamique des communautés (coléoptères carabiques), la deuxième consistant en une approche d'observation et de modélisation des flux d'individus et de la dynamique des populations (papillon rhopalocère). Dans les paragraphes suivants, nous expliquons le choix des modèles biologiques considérés, justifions la complémentarité des approches empiriques et de modélisation, et notre approche du paysage.

3.1. Le choix des modèles biologiques

Dans le cadre de ce travail, nous avons choisi le groupe des insectes comme modèle biologique car ils ont été profondément touchés par l'intensification agricole. Ils sont particulièrement sensibles aux modifications des habitats à l'échelle locale et aux modifications du paysage (Burel *et al.*, 1998).

La première partie de la thèse s'est intéressée aux effets respectifs du paysage et des activités agricoles sur la structuration et la dynamique des communautés. C'est en effet à ce niveau que les effets de l'intensification agricole sont les plus facilement observables en terme d'apparition, diminution ou extinction d'espèces. Le groupe des coléoptères carabiques (Coleoptera, Carabidae) a été retenu car leur biologie est bien connue (Thiele, 1977 ; Kromp, 1999).

Dans la deuxième partie, nous avons testé les effets des pratiques agricoles et du paysage sur les mouvements d'individus et la distribution des populations d'un papillon rhopalocère, le Myrtil (*Maniola jurtina* L., Satyridae). Contrairement aux coléoptères carabiques, les papillons sont appropriés pour l'étude de leurs mouvements *in situ*. Les papillons de jour sont particulièrement sensibles aux modifications des ressources et relativement faciles à échantillonner *in situ*. Le Myrtil est une espèce relativement commune dans nos sites d'étude, rencontrée dans des milieux herbeux variés. Cette espèce a fait l'objet de nombreuses études et sa biologie est bien connue (Dowdeswell *et al.*, 1957 ; Brakefield, 1982a ; Brakefield, 1982b ; Brakefield, 1987).

3.2. La complémentarité des approches empiriques et de la modélisation

Les méthodes développées jusqu'à présent pour comprendre la dynamique de la biodiversité dans les paysages agricoles sont de deux ordres. Les approches dites empiriques consistent en des expérimentations ou des observations *in situ* du mouvement des individus, de la distribution et la dynamique des populations, et de la dynamique des communautés. Cependant, les observations de terrain sont parfois lourdes à mettre en œuvre, en particulier pour le suivi du mouvement d'organismes. La répétition de ces études à l'échelle du paysage reste également difficile. La modélisation constitue alors un outil complémentaire qui permet de formaliser des hypothèses concernant le fonctionnement des populations (Fahrig, 1991) et de répliquer les expériences sur une gamme variée de paysages (Turner *et al.*, 1995). Les hypothèses posées sont ensuite validées au moyen d'observations de terrain. Une telle approche nécessite des connaissances préalables sur la biologie et le comportement des espèces *in situ*.

Dans ce travail, les deux approches ont été adoptées. L'étude des communautés de carabiques a été réalisée de façon empirique, par observation et expérimentation. Une approche de modélisation complétée par des observations *in situ* a été adoptée pour étudier le mouvement du Myrtil, les données disponibles sur cette espèce permettant la mise en œuvre d'une démarche de modélisation.

3.3. Caractérisation du paysage : approche fonctionnelle

Wiens et Milne (1989) affirment que les espèces peuvent percevoir le paysage d'une manière différente de l'homme, et de façon différente les unes des autres. Différentes espèces peuvent ainsi répondre à des échelles spatiales distinctes en fonction de leur capacité de dispersion (Kareiva, 1990 ; Keitt *et al.*, 1997). Baudry et Merriam (1988) ont distingué la connectivité spatiale de la connectivité biologique en soulignant le fait que la relation entre structure du paysage et colonisation des milieux dépend du mode de dispersion des espèces.

Dans les paysages bocagers, les communautés de carabes sont caractérisées par la présence simultanée d'espèces forestières dans les bois et les haies, et d'espèces de champs

(Pollard, 1968 ; Thiele, 1977 ; Burel, 1991 ; Petit et Usher, 1998). Ces différentes espèces sont susceptibles de ne pas répondre aux mêmes descripteurs du paysage, ni aux mêmes échelles du paysage. Nous avons donc utilisé une approche pluri-échelles, dans laquelle le paysage est décrit dans des fenêtres de taille variable correspondant aux différentes échelles de perception des espèces étudiées. Chaque fenêtre est caractérisée par sa composition (occupation du sol, haies) et son hétérogénéité spatiale. Pour caractériser la connectivité du paysage pour le Myrtil, nous sommes partis de l'hypothèse que certains éléments du paysage peuvent être plus ou moins perméables pour un individu en déplacement, en fonction de sa mobilité et de ses exigences écologiques. Sur la base de la biologie de cette espèce, nous avons donc considéré dans notre mesure de la connectivité le rôle potentiel de barrière de certains éléments paysagers pour le mouvement des papillons ou au contraire de corridor. Nous avons également pris en compte la nature de la matrice agricole entre les taches de ressources.

3.4. Plan de la thèse

Dans la première partie de la thèse, je m'attache à identifier les effets respectifs des activités agricoles, de la qualité des ressources et du paysage sur la structuration et la dynamique des communautés de carabes. Cette partie s'articule autour de trois axes : le premier chapitre vise à évaluer les effets respectifs du type d'habitat à l'échelle locale, des caractéristiques du paysage et des systèmes de production à l'échelle du paysage sur la composition des communautés ; dans un deuxième chapitre, j'aborde la réponse des communautés à différents régimes de pratiques agricoles en fonction du contexte paysager ; le troisième chapitre m'a permis d'étudier à l'échelle locale la réponse à court terme des communautés de carabes à des pratiques ponctuelles.

La deuxième partie a pour objectif de déterminer l'effet des pratiques agricoles sur le mouvement, la distribution et la dynamique du Myrtil, en considérant leurs impacts sur la qualité des ressources localement, mais également sur la dynamique du paysage. Cette partie s'articule autour de trois chapitres. Le premier étudie l'effet de pratiques agricoles ponctuelles sur les mouvements et la distribution des papillons. Le deuxième chapitre aborde l'élaboration d'un modèle prédictif des flux d'individus et de la distribution spatiale des populations en fonction des caractéristiques du paysage. Dans le troisième chapitre, ce modèle est utilisé afin de simuler la dynamique des populations de papillons sous l'influence de pratiques agricoles répétées sur plusieurs années.

PARTIE I.
ACTIVITES AGRICOLES ET DYNAMIQUE DES COMMUNAUTES :
LE CAS DES COLEOPTERES CARABIQUE

INTRODUCTION

Les effets des activités agricoles sur la biodiversité varient fortement en fonction des espèces ou groupes d'espèces considérés comme nous l'avons précisé en introduction. L'étude des relations entre agriculture, paysage et communautés nécessite donc une réflexion préalable quant aux démarches pertinentes à adopter pour décrire les activités agricoles et le paysage pour le groupe d'espèces étudié.

Les coléoptères carabiques constituent un modèle privilégié en écologie. Leur biologie est particulièrement bien connue et ils jouent un rôle potentiel dans le contrôle de ravageurs de cultures (Lang *et al.*, 1999). Après avoir présenté une brève revue bibliographique sur les différents facteurs qui interviennent sur la structuration des communautés de carabes dans les paysages agricoles, nous présenterons la méthodologie adoptée pour prendre en compte l'effet du paysage sur les carabiques dans les paysages bocagers et l'approche adoptée pour décrire la composition des communautés de carabes dans nos différents travaux.

1. Les coléoptères carabiques dans les paysages agricoles

1.1. Les facteurs locaux de distribution des espèces

A l'échelle locale, la présence des espèces est fortement liée aux conditions microclimatiques (température, humidité) (Greenslade, 1965 ; Thiele, 1977) en relation avec la densité du couvert végétal (Hassall *et al.*, 1992 ; Jukes *et al.*, 2001). Les espèces forestières sont hygrophiles et associées à des milieux à végétation dense (Thiele, 1977 ; Burel et Baudry, 1989) ; d'autres espèces sont résistantes à la sécheresse et sont associées à des milieux ouverts, souvent cultivés (Thiele, 1977) ; enfin, certaines espèces sont associées à des conditions de température et d'humidité intermédiaires (Thiele, 1977). Les haies sont caractérisées par la présence simultanée d'espèces forestières et d'espèces de champs (Hooper, 1974 ; Lefeuvre *et al.*, 1976 ; Burel, 1991 ; Petit et Usher, 1998). La distribution locale des espèces de carabiques dépend également de la disponibilité des ressources alimentaires (proies, ressources végétales) (Duffield et Baker, 1990).

1.2. Régulation des populations et distribution des espèces à l'échelle du paysage

Les populations locales de carabes sont caractérisées par des phénomènes successifs d'extinction et de réinstallation, la dispersion des individus étant alors un processus indispensable à la survie des populations (den Boer, 1981 ; 1985). Les populations de carabes sont ainsi définies par den Boer (1981 ; 1985) comme multipartites. La capacité de dispersion des espèces de carabiques est liée à leur mode de locomotion (présence d'ailes ou non). Les espèces de petite taille inféodées aux milieux ouverts ou cultivés sont le plus souvent ailées et ont une bonne capacité de dispersion (den Boer, 1977). Au contraire, les espèces de grande taille associées aux milieux boisés ont perdu leur aptitude à voler et se déplacent en marchant au sol (den Boer, 1977). Plusieurs travaux ont mis en évidence un fonctionnement en métapopulation des carabiques forestiers (Petit, 1994a ; Petit et Burel, 1998b). Dans les paysages bocagers, la distribution et la dynamique des métapopulations de carabiques forestiers est influencée par la présence, la qualité et l'agencement spatial des éléments boisés

dans le paysage (Petit, 1994a), les haies jouant le rôle de corridor pour la dispersion des espèces entre les îlots boisés (Petit, 1994b ; Petit et Burel, 1998a). Les assemblages spécifiques de carabiques des haies sont influencés par la composition et la structure du paysage environnant (Millán Peña, 2001). La réduction des éléments permanents (haies, bois, prairies permanentes) au profit des milieux cultivés se traduit par un remplacement des espèces forestières par des espèces de milieux cultivés (Desender et Turin, 1989 ; Desender *et al.*, 1994 ; Eyre, 1994 ; Burel *et al.*, 1998 ; Millán Peña *et al.*, 2003). La composition des communautés de carabiques est également liée à l'histoire récente du paysage. Petit (1994a) et Burel (1992) montrent que la distribution des carabiques forestiers est plus liée aux structures antérieures du bocage qu'à sa structure présente.

1.3. Agriculture et carabes

La majorité des travaux visant à comprendre l'impact de l'agriculture sur les communautés de carabiques ont le plus souvent été centrés sur l'étude des pratiques agricoles à une échelle locale. Certaines pratiques intensives telles que la fauche, le pâturage, l'utilisation de pesticides et de fertilisants entraînent des modifications importantes des communautés de carabes : diminution des abondances, réduction de certaines espèces, augmentation d'autres. Les effets de ces pratiques sont une mortalité directe dans le cas de la fauche ou du labour (Basedow, 1990 ; Quinn *et al.*, 1991 ; Epstein *et al.*, 2001 ; Langmaack *et al.*, 2001), ou de l'utilisation d'insecticides (Thacker et Hickman, 1990). Ils sont également indirects via les modifications du couvert végétal (Rushton *et al.*, 1989 ; Brust, 1990 ; McAdam *et al.*, 1994 ; Gardner *et al.*, 1997 ; Bhriain *et al.*, 2002) ou de la réduction des ressources alimentaires (Boiteau, 1984 ; Basedow, 1990 ; Varchola et Dunn, 1999). La réponse des communautés de carabiques aux pratiques agricoles varie en fonction des espèces : les espèces forestières sont peu tolérantes aux perturbations des ressources alors que les petites espèces peuvent être favorisées par ces changements (Pollard, 1974a ; Rushton *et al.*, 1989 ; Brust, 1990 ; Blake *et al.*, 1994 ; Epstein *et al.*, 2001). Paradoxalement, ces études ont concerné exclusivement les parcelles cultivées, l'effet des pratiques de gestion des haies et bords de champs étant peu considéré.

Récemment, certains travaux ont abordé la question de l'impact des systèmes de production agricole sur les communautés de carabiques. La plupart des études ont consisté en une comparaison de systèmes dits « biologiques » (fertilisation raisonnée, utilisation réduite de pesticides) à des systèmes « conventionnels » (Booij et Noorlander, 1992 ; Döring et Kromp, 2003 ; Weibull et Östman, 2003 ; Weibull *et al.*, 2003). Les systèmes de production biologiques favorisent la présence et l'abondance de nombreuses espèces, du fait de la réduction des intrants. Seuls Millán Peña *et al.* (2003) ont pris en compte les relations entre la nature et l'intensité des systèmes de production agricole et la structure des paysages bocagers sur les communautés de carabiques. L'intensification des systèmes de production s'accompagne d'une ouverture du paysage qui entraîne un remplacement des espèces forestières par des espèces de champs. Ces modifications sont cependant très spécifiques des systèmes de production considérés (Millán Peña *et al.*, 2003).

1.4. Conclusion

Les processus impliqués dans la structuration et la dynamique des communautés de carabiques dans les paysages agricoles sont donc multiples et doivent être considérés à

différentes échelles. Au regard de la revue bibliographique que nous avons présentée dans les paragraphes précédents, il ressort que les facteurs intervenant sur les communautés de carabiques à l'échelle locale (pratiques agricoles, qualité des ressources) et à l'échelle du paysage (systèmes de production, structure du paysage) sont le plus souvent considérés de façon indépendante.

L'objectif de cette partie est d'évaluer l'importance relative des facteurs intervenant à l'échelle locale et à celle du paysage sur les communautés de carabiques, en considérant les relations entre pratiques agricoles et qualité des ressources à l'échelle locale, mais également les systèmes de production et les caractéristiques du paysage à l'échelle du paysage.

La démarche que nous avons adoptée pour prendre en compte l'impact des activités agricoles sur les communautés de carabiques a été adaptée au paysage particulier dans lequel s'est située cette étude: le bocage. Le bocage est un paysage complexe caractérisé par une grande variété de haies ou bords de champs, en terme de composition floristique, de mode d'entretien de la végétation, et de forme et constitution des talus et fossés (Baudry *et al.*, 2000a). C'est pourquoi nous avons porté un intérêt particulier aux effets, à court et long terme, de diverses pratiques de gestion des bordures de haies ou bords de champs sur les communautés de carabiques car ils ont été peu étudiés jusqu'à présent.

Nous avons ainsi considéré :

- Les effets respectifs du type d'habitat, des systèmes de production agricole et du paysage vu à une échelle spatiale large ; les données ont été recueillies dans trois unités paysagères de 25 km², les deux premières sur le site atelier de Pleine Fougères en Ille et Vilaine, la troisième dans le département des Côtes d'Armor.
- la réponse des communautés des bords de champs à différents régimes pluri-annuels de gestion en fonction du contexte paysager, dans deux sites de 6 km² sur le site atelier de Pleine Fougères,
- l'impact des pratiques ponctuelles de gestion des bords de champs au moyen d'un dispositif expérimental, afin de comprendre les mécanismes mis en œuvre dans la réponse à court terme des communautés aux perturbations.

2. Méthodologie pour l'étude des communautés de carabiques dans les paysages bocagers

2.1. Caractérisation de l'espace et échelles

Plusieurs auteurs ont souligné le fait que la perception des phénomènes écologiques dépend du grain ou de l'étendue que l'on considère pour décrire le paysage (Turner *et al.*, 1989b; Baudry, 1992 ; Forman, 1995). Le grain d'analyse est défini comme le niveau de résolution spatiale le plus fin utilisé pour décrire le paysage, par exemple la taille d'un pixel pour des données rasterisées ; l'étendue réfère plus à la taille d'une zone d'étude (Turner et Gardner, 1991). Cette terminologie peut s'appliquer également aux espèces (Kotliar et Wiens, 1990), le grain d'une espèce étant la plus petite échelle à laquelle elle perçoit le paysage ; en dessous, elle perçoit l'espace comme homogène, et l'étendue la plus grande échelle à laquelle elle perçoit l'espace, définissant son domaine vital. Lima et Zollner (1996) soulignent le manque de considération de la perception du paysage propre à chaque espèce dans la plupart des travaux d'écologie.

Dans ce travail, nous avons utilisé des méthodes pluri-échelles pour décrire le paysage en terme de composition (occupation du sol, haies) et d'organisation spatiale du paysage (mesure d'hétérogénéité spatiale), en utilisant les Systèmes d'Informations Géographiques.

2.2. Description de la composition des communautés de carabiques

Des indices ont été développés pour quantifier la diversité structurale des communautés (richesse spécifique, diversité spécifique de Shannon, équitabilité, etc.). Cependant, ces mesures ne permettent pas toujours de traduire la réponse des communautés aux changements de la qualité ou de la structure des paysages, comme cela a été démontré par Burel *et al.* (1998), notamment quand le gradient de variables environnementales est faible. Les analyses multivariées constituent alors un bon outil puisqu'elles permettent de considérer la composition spécifique des communautés. Plus récemment, certains auteurs ont souligné l'intérêt de regrouper les espèces en groupes fonctionnels selon des caractéristiques biologiques ou traits d'histoire de vie particuliers, tels que la mobilité, la taille, le régime alimentaire, etc. (Lavorel *et al.*, 1997 ; Lavorel *et al.*, 1998 ; Cole *et al.*, 2002). Cette approche permet de tester l'effet de conditions environnementales sur des groupes d'espèces caractérisés par des traits écologiques généraux plutôt que de se centrer sur quelques espèces particulières.

Nous avons ici considéré la composition spécifique des communautés de carabiques au moyen des outils multivariés, mais également la nature des espèces présentes en terme de traits d'histoire de vie (taille, capacité de dispersion) des espèces afin de mettre en relation la composition des communautés et les différentes variables environnementales.

2.3. Les sites de l'étude

Pour pouvoir considérer l'effet du type et de l'intensité des systèmes de production (chapitre 1), nous avons choisi trois sites de 25km² relativement contrastés en terme de production agricole (figure 1).

Deux sites sont localisés dans le site atelier de Pleine Fougères en Ile et Vilaine (Pleine Fougères Sud : FOD et Pleine Fougères Nord : FOO) et caractérisés par de la production laitière. Le site Atelier de Pleine Fougères est caractérisé par **un double gradient d'ouverture du paysage (réduction du bocage, augmentation de la taille des parcelles) et d'intensification de la production laitière (accroissement de la production, de la taille des exploitations) du sud vers le nord**. Le troisième site est situé à Saint Alban dans les Côtes d'Armor (FAL) et se distingue des deux précédents par une production plus orientée vers de l'élevage industriel porcin et de la culture de céréales ; il est caractérisé par des parcelles de grande taille et un réseau de haies peu dense.

Les trois sites présentent des caractéristiques climatiques similaires, les précipitations annuelles moyennes et la durée d'ensoleillement annuelle moyenne étant légèrement plus importantes à Pleine Fougères (Tableau 1).

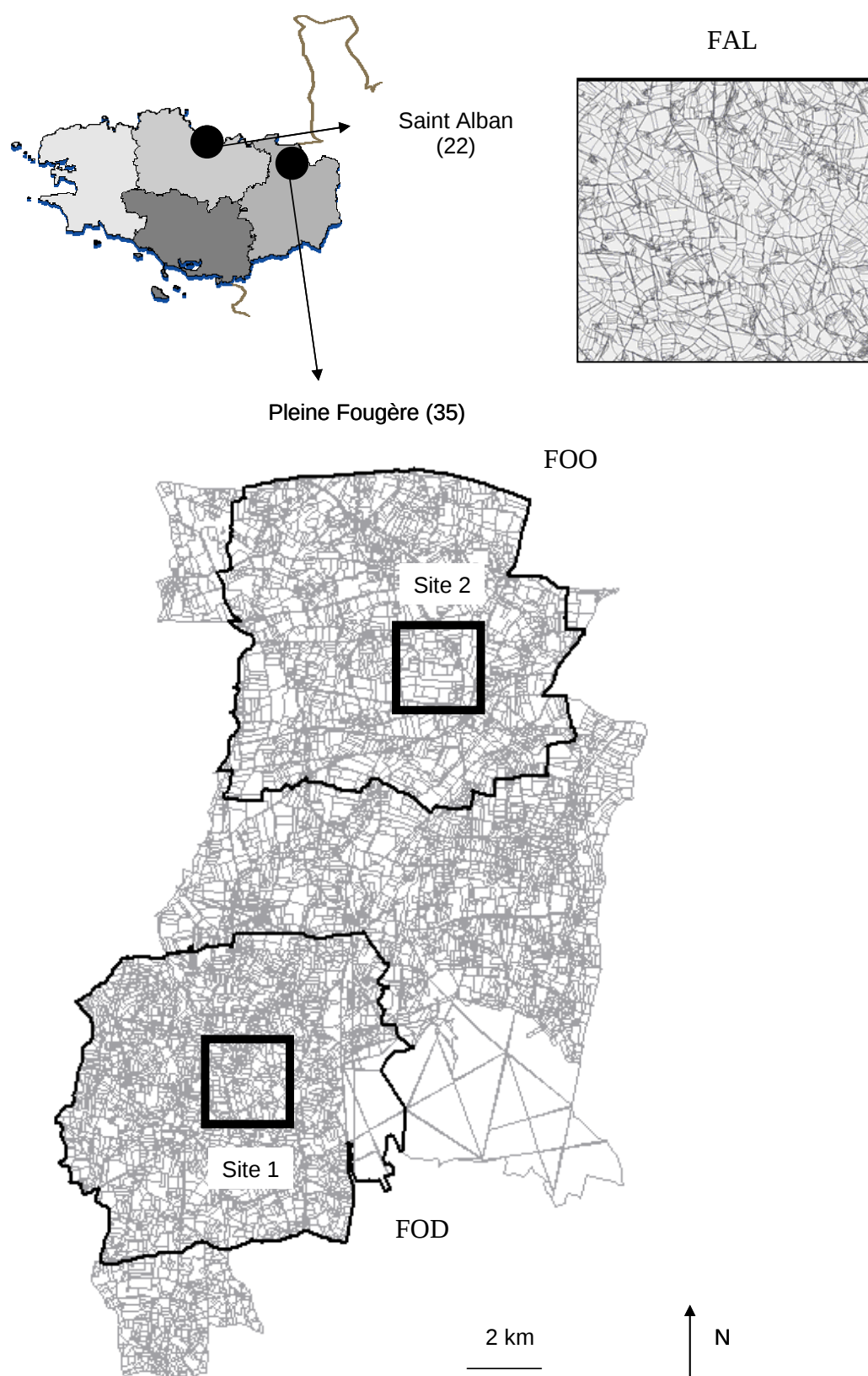


Figure 1. Présentation des sites de l'étude des communautés de carabiques.

Tableau 1. Caractéristiques climatiques (précipitations annuelles moyennes en mm, durée annuelle moyenne d'ensoleillement en heures, températures maximales en juillet en °C) à Pleine Fougères et Saint Alban.

	Précipitations (mm)	Ensoleillement (Heures)	Température (°C)
Pleine Fougères	800	1800	20-22°C
Saint Alban	700	1700	20-22°C

Afin de prendre en compte l'effet des régimes pluri-annuels de gestion des bords de champs (chapitre 2), nous avons choisi deux sites de 6km² dans le site atelier de Pleine Fougères (Pleine Fougères Sud : site 1 ; Pleine Fougères Nord: site 2) (figure 1) où les pratiques de gestion des bords de champs font l'objet d'un suivi régulier depuis plusieurs années par l'unité de recherche INRA SAD Armorique. Ces deux sites sont opposés le long du gradient d'ouverture du paysage ce qui nous a permis de considérer l'effet des régimes de gestion des bords de champs dans des contextes paysagers contrastés.

2.4. Echantillonnage des communautés de carabique dans les sites de l'étude

Le piégeage par pots pièges est la méthode la plus couramment utilisée pour échantillonner les communautés de carabiques. En milieu agricole, elle permet de capturer un grand nombre d'individus et d'espèces, le piégeage pouvant être réalisé de façon simultanée dans un grand nombre de sites (Turin *et al.*, 1991 ; Spence et Niemelä, 1994). Cancela Da Fonseca dans Clavreul (1984) estime qu'au minimum trois pots pièges doivent être mis en place par station d'échantillonnage pour obtenir une estimation fiable de la présence et l'abondance relative des espèces. Concernant la durée d'ouverture des pièges, certains auteurs affirment que seul un échantillonnage conduit sur le long terme, au moins sur une saison de reproduction, permet d'obtenir une estimation fiable de la composition des communautés de carabiques (Sunderland *et al.*, 1995). Cependant, un piégeage plus limité dans le temps peut également conduire à des résultats fiables (Niemelä *et al.*, 1990) quand ils sont interprétés avec précaution. Cette dernière méthode est appropriée lorsque l'objectif est de comparer des assemblages spécifiques entre différents habitats (Maelfait et Desender, 1994). En outre, les comparaisons entre sites sont moins affectées par les effets de pratiques agricoles pendant l'échantillonnage (Jeanneret *et al.*, 2003a). Burel (1991) montre qu'un échantillonnage conduit de mai à juillet permet de capturer 90 à 92% des espèces présentes. L'efficacité des pots pièges varie en fonction de l'activité de la structure de la végétation des stations d'échantillonnage et de caractéristiques spécifiques telles que l'activité des individus ou la taille des espèces (Luff, 1987; Kromp *et al.*, 1995 ; Sunderland *et al.*, 1995 ; Mommertz *et al.*, 1996). Les densités absolues de carabiques obtenues à partir de pots pièges doivent alors être interprétées avec précaution. Cependant, cette méthode permet de donner un ordre de grandeur de la fréquence des espèces et une estimation relative de leurs abondances.

Dans le présent travail, les communautés de carabiques ont été échantillonnées au moyen de pots pièges. Deux principaux facteurs ont contraint la mise en place des protocoles de piégeage (nombre de stations d'échantillonnage, de pièges mis en place par station et durée des sessions de piégeage) : l'effort important que représente le piégeage à l'échelle du paysage, et le protocole de piégeage imposé dans le cadre du programme Européen

GREENVEINS (Chapitre 1), Ainsi, dans le cadre des Chapitres 1 et 2, le nombre de pièges a été restreint à deux par élément permanent échantillonné, pour une durée de piégeage de seize et cinq semaines respectivement. Dans le cadre de l'expérimentation présentée dans le Chapitre 3, le nombre de pièges a été restreint à trois par plot expérimental, et la durée de piégeage à quatre semaines. Le nombre d'espèces capturées dans le cadre du présent travail reste cependant similaire ou supérieur au nombre d'espèces capturées sur les sites de l'étude lors de précédents travaux (Burel *et al.*, 1998 ; Millán Peña *et al.*, 2003), malgré un nombre de pièges ou une durée de piégeage restreints (tableau 2).

Tableau 2. Nombre d'espèces de carabiques capturées dans les sites d'étude lors de précédentes études et dans le cadre de la thèse, et protocoles d'échantillonnage (nombre de pièges, disposition et durée de piégeage).

	Burel <i>et al.</i> (1998)	Millán Peña <i>et al.</i> (2003)	Chapitre 1	Chapitre 2	Chapitre 3
<u>Sites d'étude</u>	Pleine Fougères	Saint Alban	Pleine Fougères, Saint-Alban	Pleine Fougères	Pleine Fougères
<u>Nombre total d'espèces</u>	85	76	89	82	62
<u>Protocole</u>					
Nombre total de pièges	64	30	96	156	45
Disposition des pièges	Transect	3 pièges par haie	2 pièges par élément permanent	2 pièges par haie	3 pièges par plot expérimental
Durée de piégeage	50 semaines	8 semaines	16 semaines	5 semaines	4 semaines

Soumis : Agriculture, Ecosystems and Environment

**CHAPITRE 1 : CARABID ASSEMBLAGES IN AGRICULTURAL
LANDSCAPES – IMPACTS OF HABITAT FEATURES, LANDSCAPE
CONTEXT AT DIFFERENT SPATIAL SCALES AND FARMING
INTENSITY**

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Résumé

Dans les paysages d'agriculture intensive, la dynamique de la biodiversité est liée aux activités agricoles à plusieurs échelles spatio-temporelles. Les pratiques agricoles altèrent la qualité des ressources à l'échelle locale, et les systèmes de production agricole déterminent la composition et l'organisation spatiale des paysages. Les habitats (semi-) permanents jouent alors un rôle essentiel pour le maintien de la biodiversité dans ces paysages. Jusqu'à présent, les effets de ces différents facteurs ont été considérés de façon distincte. Dans cet article, nous testons simultanément les effets de la qualité des habitats, de la structure du paysage et de l'intensité des systèmes de production agricole à l'échelle du paysage. L'objectif de cette étude est de déterminer le rôle des habitats (semi-) permanents pour la biodiversité en fonction des caractéristiques du paysage et de l'intensité de l'agriculture. Nous avons pour cela échantillonné les communautés de carabiques dans les différents types d'habitats permanents présents dans trois unités paysagères contrastées en terme de structure du paysage et d'intensité agricole. La composition des communautés de carabiques est contrainte en premier lieu par le site d'étude dans lequel elles se situent, puis par le type d'habitat et par les caractéristiques du contexte paysager. Les différents habitats permanents sont caractérisés par des assemblages spécifiques différents, en particulier les bois qui s'opposent aux bords de champs en ce qui concerne l'abondance des espèces forestières. L'effet du site d'étude sur les communautés traduit à la fois un effet de la quantité d'habitats boisés (haies et bois) au sein du paysage, mais également de la nature et de l'intensité de la production agricole. La part des grandes espèces, forestières, diminue de façon significative dans le paysage le plus ouvert et caractérisé par des systèmes de production orientés vers de la production porcine et céréalière intensive auxquels sont associées de grandes quantités d'intrants. Les résultats suggèrent donc que l'importance des habitats permanents pour la diversité des carabiques dépend des caractéristiques du paysage et de l'intensité de l'agriculture. En fonction des caractéristiques du paysage, différentes mesures d'aménagement et de gestion devraient être adoptées pour la conservation de la biodiversité.

1. Introduction

Permanent or semi-permanent landscape elements, such as hedgerows, woodlands or permanent grasslands, play a crucial role for biodiversity in cultivated landscapes. They act as habitat (Forman and Baudry, 1984), refuge (Dennis and Fry, 1992) and corridor (Duelli *et al.*, 1990) for many species. In Western France, agricultural landscapes are characterised by the presence of hedgerow networks (Baudry *et al.*, 2000a). Land-use intensification after World War II has led to drastic changes in agricultural landscapes. Hedgerows or woodlots have been removed and permanent grasslands have been reduced (Agger and Brandt, 1988; Meeus, 1990). Land-use intensification also consisted in changes in crops, cultivation practices and farming systems (Canévet, 1992). All these changes were considered as responsible for a major decline of biodiversity (Wilson *et al.*, 1999). Thus, many studies have been developed for understanding the relationships between agricultural intensification and biodiversity. However, few have considered the landscape level (Burel *et al.*, 1998).

Many studies in agro-ecology have focused on beneficial arthropods in agricultural landscapes. Among them, carabid beetles (Coleoptera: Carabidae) have been extensively studied (Kromp, 1999) and they play a potential role in crop pest control (Lang *et al.*, 1999). Hedgerows are important landscape features for carabid beetles. They act as corridor or habitat for forest species (Burel and Baudry, 1989), and temporary refuges for other species (Sotherton, 1984). At the local scale, habitat type, i.e. vegetation and microclimatic conditions, is recognised as a determinant factor of the presence of carabid species (Thiele, 1977; Jeanneret *et al.*, 2003a; Weibull and Östman, 2003). At the landscape scale, carabid assemblages are influenced by the amount and spatial arrangement of permanent landscape elements and by the composition of the arable mosaic (Burel *et al.*, 1998; Millán Peña *et al.*, 2003). As the amount of woodlots and hedgerows decreases mobile field species replace forest species with lower dispersal power. At a finer spatial scale, carabid assemblages are highly sensitive to the landscape context of habitat patches, i.e. to the composition and organisation of the landscape surrounding habitat patches (Millán Peña, 2001). Farming activities influence carabid species assemblages at different spatial scales. At the landscape scale, composition and spatial structure of landscapes are linked to the type and intensity of farming systems (Poudevigne *et al.*, 1997). Millán Peña *et al.* (2003) showed that specialisation toward different farming systems lead to different changes in landscape structure and thus different carabid assemblages in hedgerows. At local scale, farming practices alter resource quality (McAdam *et al.*, 1994; Varchola and Dunn, 1999; Bhriain *et al.*, 2002) or have lethal effect on carabid species (Basedow, 1990; Thacker and Hickman, 1990; Langmaack *et al.*, 2001). Large body-sized species are the most affected by agricultural disturbances (Blake *et al.*, 1994; Ribera *et al.*, 2001). Some studies have suggested that organic farming systems enhance many carabid species compared with conventional farming systems (Dritschilo and Erwin, 1982; Kromp, 1989; Weibull and Östman, 2003; Weibull *et al.*, 2003), as a consequence of lower inputs in organic farms.

Despite the fact that habitat quality, landscape pattern and farming activities are known to explain carabid assemblages, few studies have considered these factors simultaneously (Weibull and Östman, 2003). Thus, their respective effects on carabid assemblages remain unknown. This raises the question of how permanent habitats are important for carabid communities, depending on landscape pattern and agricultural intensity. Another important aspect is the question of scale, as species often respond hierarchically to their environment (Kotliar and Wiens, 1990; Levins, 1992; Fuhlendorf *et al.*, 2002b). Interactions between communities and landscape have to be examined at different spatial

scales, as species respond to landscape structure at their own spatial scale depending on their dispersal ability (Kareiva, 1990). Identifying the appropriate spatial scales for the studied species or group is crucial for biodiversity conservation as it will necessarily determine the appropriate scales for establishing management schemes.

The objective of this study was to determine the relative importance of environmental variables at local (habitat type) and landscape scale (landscape context at different spatial scales, farming intensity at the scale of landscape unit) on carabid communities. Carabid communities were studied in all types of permanent landscape elements in three agricultural landscapes with contrasted landscape pattern and farming intensity. Three hypotheses were tested:

- (i) Intensification of farming systems leads to a decline of forest carabid species, as a consequence of both higher amount of inputs and associated landscape changes,
- (ii) The reduction of permanent landscape elements in the landscape context causes the reduction of species associated to stable habitats, especially the replacement of forest species with low mobility by more mobile species associated to cropped habitats,
- (ii) Habitat type is a better predictor of carabid assemblages than landscape pattern and farming intensification.

2. Study areas and methods

2.1. Study areas

The study was conducted in three 25km² hedgerow network landscapes (bocage) (FOD, FOO, and FAL) in western France (figure 1.1). Interviews of farmers on studied areas revealed contrasted farming systems between the three landscape units (Thenail and Codet, unpublished data).

Figure 1.2 shows the main types of agricultural production in each landscape unit, characterised according to standard gross margin (which depends on the region and type of farm production) and quantitative information about farm production (livestock size, used agricultural area). Table 1.1 summarises the cropping pattern and livestock characteristics in the three landscape units. Farming systems are exclusively oriented toward dairy production in FOD; in this landscape, a high proportion of the UAA (Used Agricultural Area) is covered by grasslands and fodder crops and milk cows predominate in livestock. In FOO, agriculture is mainly oriented toward mixed dairy - cattle and some cash crop production, with half of the UAA covered by grasslands and fodder crops. FAL is characterised by mixed dairy, industrial pig - poultry and cash crop production, cash crops covering the main part of UAA. Stocking rates (number of livestock units per hectare) increase from FOD to FAL.

Considering landscape structure, FOD has still a rather dense network of hedgerows with a high density of trees, many permanent grasslands and small woodlots (table 1.2.). FOO went under a reallocation program in 1992 and has fewer hedgerows with much less trees; permanent grassland and woodland are reduced (table 1.2.). Hedgerow network in FAL is still dense but woodlots and permanent grasslands are reduced (table 1.2.).

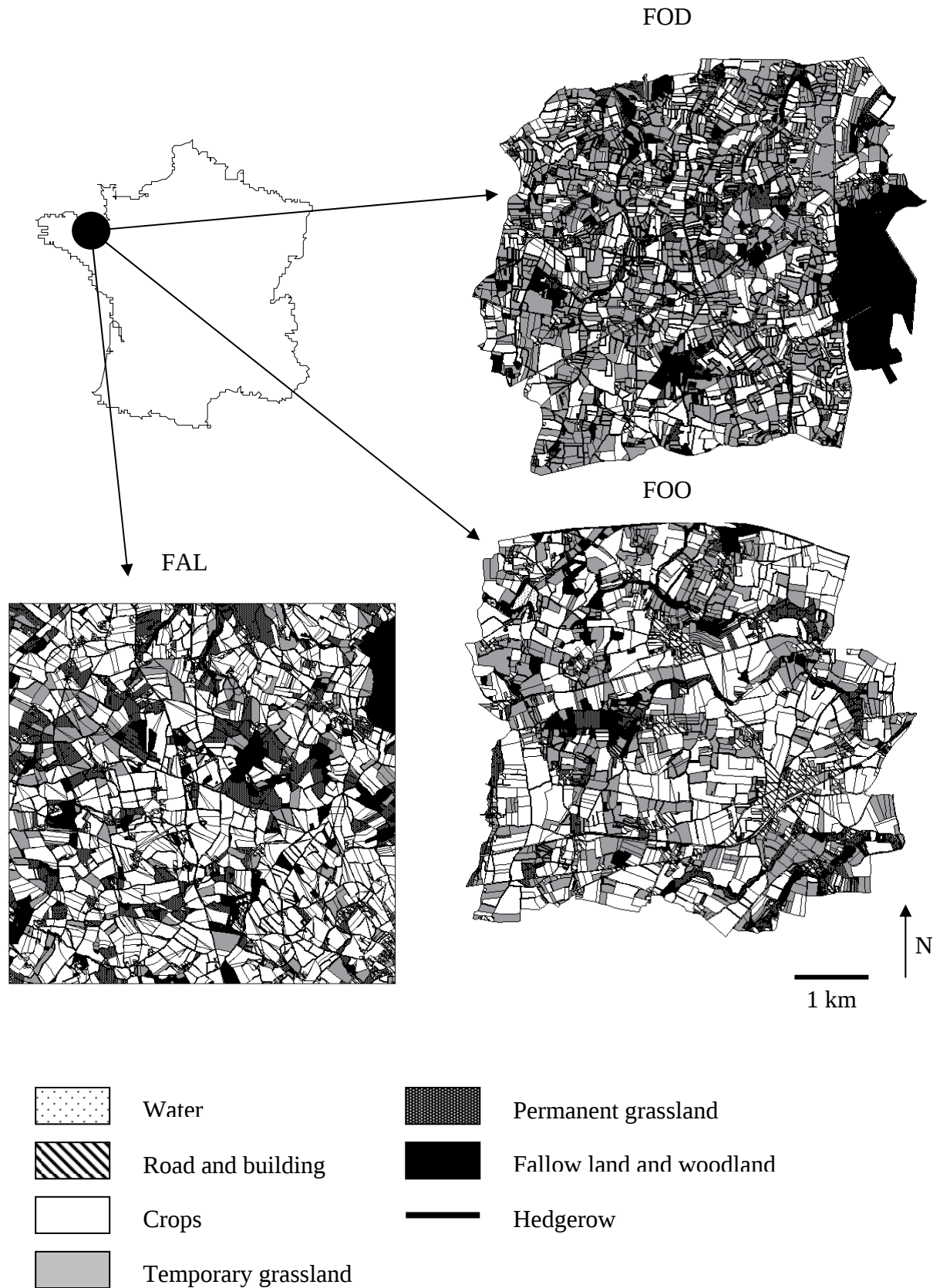


Figure 1.1. Presentation of the three studied landscape units.

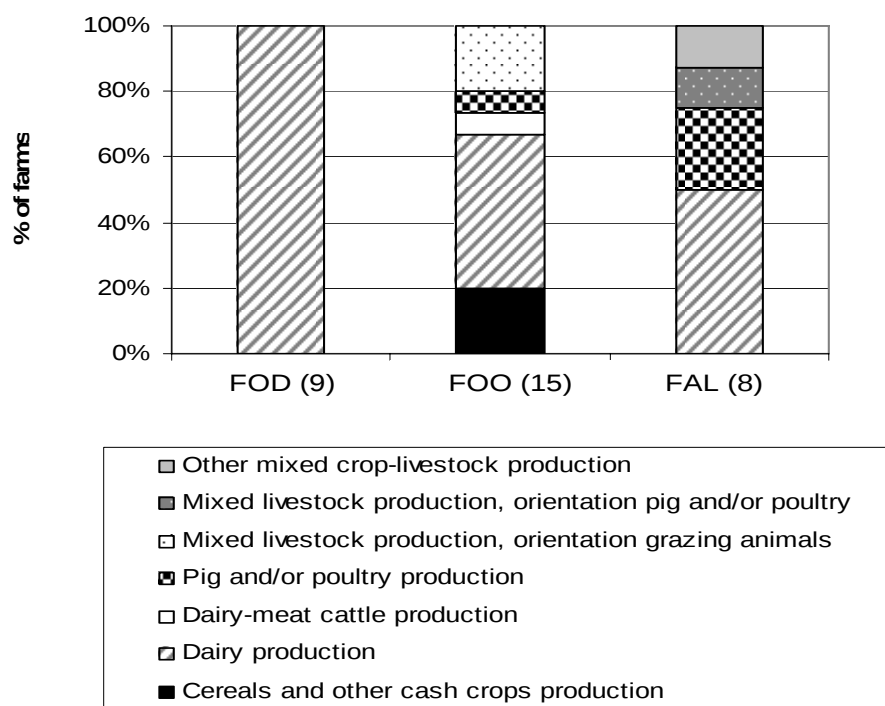


Figure 1.2. Orientation of the agricultural production in the three landscape units. Numbers of interviewed farms in each landscape unit are indicated in parentheses.

Table 1.1. Cropping pattern (proportions of the Used Agricultural Area (UAA) covered by cereals and cash crops, fodder crops, and grasslands) and livestock (number of livestock unit (LU) per hectare of Used Agricultural Land) in the three landscape units. Numbers of interviewed farmers are indicated in parentheses.

	Landscape unit		
	FOD (9)	FOO (15)	FAL (8)
<i>Cropping pattern</i>			
Cereals and other cash crops (%)	31	48	57
Annual fodder crops (%)	19	21	13
Grassland (%)	49	31	29
<i>Livestock</i>			
Milk cow (LU/ha)	0.70	0.59	0.49
Meat cattle (LU/ha)	0.36	0.39	0.24
Pig (LU/ha)	0.00	0.31	2.34
Total stocking rate (LU/ha)	1.06	1.29	3.06

Table 1.2. Composition and structure of the three landscape units (proportion of the land covered by woodlands and permanent grasslands, hedgerow density in meters per hectare).

	Landscape unit		
	FOD	FOO	FAL
Woodland & fallow land (%)	15	7	9
Permanent grassland (%)	30	18	13
Hedgerow density (m/ha)	79	45	68

2.2. Carabid sampling

We sampled carabid assemblages in six types of permanent habitats: hedgerow, grassy field margin, woodland, wet permanent grassland, mesic permanent grassland, and orchard. In each landscape unit, sampling was realized in a core 16 km² area divided in 16 plots of 1km². In each 1km² plot, one habitat was selected as follow: a sampling point was first determined randomly using GIS (Arcview 3.1, 1998 ESRI Inc); habitat being the closest to the random point was then selected for sampling. Type and number of sampled habitats in each landscape unit are indicated in table 1.3.

Table 1.3. Type and number of permanent habitats sampled in each landscape unit.

	Landscape unit		
	FOD	FOO	FAL
Hedgerow	3	4	7
Grassy field margin	2	2	1
Woodland	4	3	3
Orchard	1	2	1
Mesic grassland	4	3	2
Wet grassland	2	2	2

Sampling of carabids was realized using pitfall traps (diameter: 9cm; height: 10cm) containing a formalin solution (5%). Two traps were installed in each sampled habitat. Traps were opened continuously and emptied once a week from June to August 2001 during nine weeks, from April to May 2002 during five weeks, and during two weeks in July 2002, i.e. 16 sampling periods. Species were identified according to Jeannel (1941; 1942) and Trautner and Geigenmuller (1987).

2.3. Characterisation of the landscape context of sampled patches

We used a multiscale approach, where landscapes are viewed as windows of different sizes centred on sampled habitat patches. This approach permits to describe the grain at which species assemblages respond to landscape pattern. Here, we tested three sizes of windows: 50 x 50m (0.25 ha), 250 x 250m (6.25ha) and 500 x 500m (25ha). Maps of landscape units were created in a raster format using IDRISI (Eastman, 1997). Squared windows centred on sampled habitats were created on raster maps using CHLOE software (Baudry and Denis, 1995). Carabid assemblages have been shown to respond to the amount of permanent landscape elements (woodlots, hedgerows, permanent grasslands) in the landscape (Millán Peña *et al.*, 2003). Thus, we calculated three descriptors of the landscape within windows: (1) proportion of pixels of woody permanent elements (woodlots and hedgerows), (2) proportion of pixels of herbaceous permanent elements (permanent grasslands and grassy field margins), and (3) proportion of pixels of crops (maize, other crops and temporary grasslands).

2.4. Analyses

Although indexes such as species richness or diversity are often used to characterise biodiversity, they do not always reflect the response of carabid assemblages to changes in landscape structure as demonstrated by Burel *et al.* (1998). In this study, Canonical Correspondence Analysis (CCA) was used to analyse species-environment relationships

(CANOCO; Ter Braak and Smilauer, 1998). To determine the relative importance of environmental variables on species assemblages, we performed CCA and partial CCA. The aim is to establish a hierarchy of explanatory variables and to eliminate the variables which do not explain significantly variation of species assemblages. This procedure, which is described in Jeanneret *et al.* (1999, 2003b), can be summarised as follows:

- CCA is first performed with each explanatory variable separately to eliminate the variables which do not explain any significant variation (tested with Monte Carlo permutations); modalities of nominal variables are selected with the forward selection module of CANOCO. Then, global CCA is performed on the whole set of environmental variables selected previously and correlations between variables are examined; if collinearity is observed (i.e., here, if correlations ≥ 0.7), variables with the higher correlation value with CCA axes are selected for partial CCA.
- Variance partitioning is then performed through partial CCA; the variance explained by each variable and its significance (Monte Carlo permutations) is obtained after eliminating the variance due to the other variables, which are used as covariables (partial variables).

After variance partitioning, we performed a CCA including the selected explanatory variables after separate and global CCA to illustrate the relationships between the composition of carabid communities and environmental variables. CCA and partial CCA were performed on the carabid assemblages in the 48 sampling locations. Species data were pooled over the 16 sampling periods after having tested equivalencies between the two sampling years. Species abundances were log-transformed before analysis. Species occurring at less than 0.5 % were not included in analysis, so that 57 species were considered in analyses. Environmental variables included in analyses were: habitat type (six categories), landscape context variables at the three spatial scales (nine continuous variables), and landscape unit (three categories).

3. Results

12944 individuals corresponding to 87 species were trapped. This species number was similar or higher than the pool of species observed previously in the same landscapes (Burel *et al.*, 1998; Millán Peña *et al.*, 2003). The full set of trapped species is listed in Appendix 1.

3.1. Relative effects of habitat type, landscape context and landscape unit on carabid assemblages

Separate and global CCA permitted to determine the explanatory variables which significantly explained part of variation. Habitat type explained a significant part (17.9% of variance) of the variation of carabid assemblages (table 1.4). Among the habitat types, hedgerow, woodland and grassy field margin had a significant effect on species assemblages, in contrary to other habitat types. The effect of woodland (5.6% of variance) was higher in comparison with those of hedgerow (4.6% of variance) or grassy field margin (3.8% of variance). Landscape context descriptors explained globally a higher part of variation (31.6% of variance) than habitat type or landscape unit. Among the landscape context descriptors used in analyses, the proportion of grassy elements in landscape context at the three spatial scales of analysis did not explain a significant part of the variation of carabid assemblages. The proportion of crops in 50m windows and of woody elements in 500m windows had the strongest influence on species assemblages (6.1% and 5.9% of variance respectively).

Variation explained by landscape unit was significant (11.9% of variance), landscape unit FAL having a stronger effect on carabid assemblages (7.1% of variance) (table 1.4).

Explanatory variables considered in variance partitioning were: habitat type (hedgerow, woodland, grassy field margin), the proportion of crops in 50m windows and of woody elements in 500m windows, and landscape unit (FOD, FOO, FAL). After elimination of interactions between variables in partial CCA, the greatest part of variance of carabid assemblages was explained by landscape unit (10.3%) and habitat type (9.3%) (table 1.4). The variation of species assemblages explained by landscape context was low; the proportion of woody elements in landscape context (500m windows) explained 3.9% of species variation, whereas the effect of the proportion of crops in 50 windows was not significant after partitioning.

Table 1.4. Percentage of variance explained and p-values (Monte Carlo test) by explanatory variables in separate CCA, explanatory variables eliminated after correlation examination in global CCA, and percentage of variance explained and p-values (Monte Carlo test) by variables in partial CCA.

Variable	Separate CCA		Global CCA	Partial CCA	
	% of variation	p-value	Conserved variables	% of variation	p-value
Habitat type					
Hedgerow	4.6	< 0.05	Yes	9.3	< 0.05
Woodlot	5.7	< 0.05	Yes		
Grassy field margin	3.8	< 0.05	Yes		
Mesic permanent grassland	2.1	NS	-		
Wet permanent grassland	0.0	NS	-		
Orchard	1.7	NS	-		
Total	17.9	< 0.05			
Landscape context					
Woody elements 50m	5.4	< 0.05	No	-	
Grassy elements 50m	2.6	NS	-	-	
Crops 50m	6.1	< 0.05	Yes	1.8	NS
Woody elements 250m	5.6	< 0.05	No	-	
Grassy elements 250m	2.6	NS	-	-	
Crops 250m	4.5	< 0.05	No	-	
Woody elements 500m	5.9	< 0.05	Yes	3.9	< 0.05
Grassy elements 500m	2.6	NS	-	-	
Crops 500m	4.1	< 0.05	No	-	
Total	31.6	< 0.05			
Landscape unit					
FOD	2.4	< 0.05	Yes	10.3	< 0.05
FOO	2.4	< 0.05	Yes		
FAL	7.1	< 0.05	Yes		
Total	11.9	< 0.05			

3.2. Effects of habitat type, landscape context and landscape unit on the composition of carabid assemblages

Figure 1.3 and table 1.5 illustrate the results of the CCA performed on carabid assemblages and explanatory variables selected after separate and global CCA (total explained variation: 30.9%; Monte-Carlo permutations, first axis: $P=0.005$, all axes: $P=0.005$).

Both first and second CCA axes expressed the effects of landscape unit and habitat type on carabid assemblages. The first CCA axis differentiated wooded landscape contexts (500m windows) from cropped ones (50 windows). The important influence of landscape unit on carabid assemblages detected after variance partitioning suggests that the effect of landscape context along the first CCA axis was linked to an effect of landscape pattern of studied landscape units, as illustrated by the opposition between FOD and the two other landscape units along this axis. The first CCA axis also differentiated woodlands from field boundaries. Along this axis, species associated to cropped habitats, e.g. *Pterostichus melanarius* (Illiger) were opposed to the forest species *Abax parallelepipedus* (Piller and Mitterpacher) and to *Pterostichus madidus* (Fabr.) (figure 1.3).

Table 1.5. Correlation coefficients between explanatory variables (selected after separate and global CCA) and the two first axes of the CCA analysis.

Variable	Correlation value	
	Axis 1	Axis 2
Habitat type		
Hedgerow	-0.43	0.35
Woodland	0.61	0.30
Grassy field margin	-0.39	-0.52
Landscape context		
Crops 50m	-0.64	-0.20
Woody elements 500m	0.63	-0.08
Landscape unit		
FOD	0.50	-0.41
FOO	-0.18	-0.45
FAL	-0.31	0.86

The second CCA axis opposed landscape unit FAL, characterized by intensive animal and cash crop production, to FOO and FOD, with dairy or mixed dairy-cattle and some cash crop production. This axis also differentiated grassy field margins from hedgerows. It opposed species like *Pterostichus vernalis* (Panzer) and *Agonum obtusum* (Herbst) to small field species associated to unstable habitats, e.g. *Asaphidion stierlini* (Heyden) and *Bembidion lunulatum* (Fourcroy).

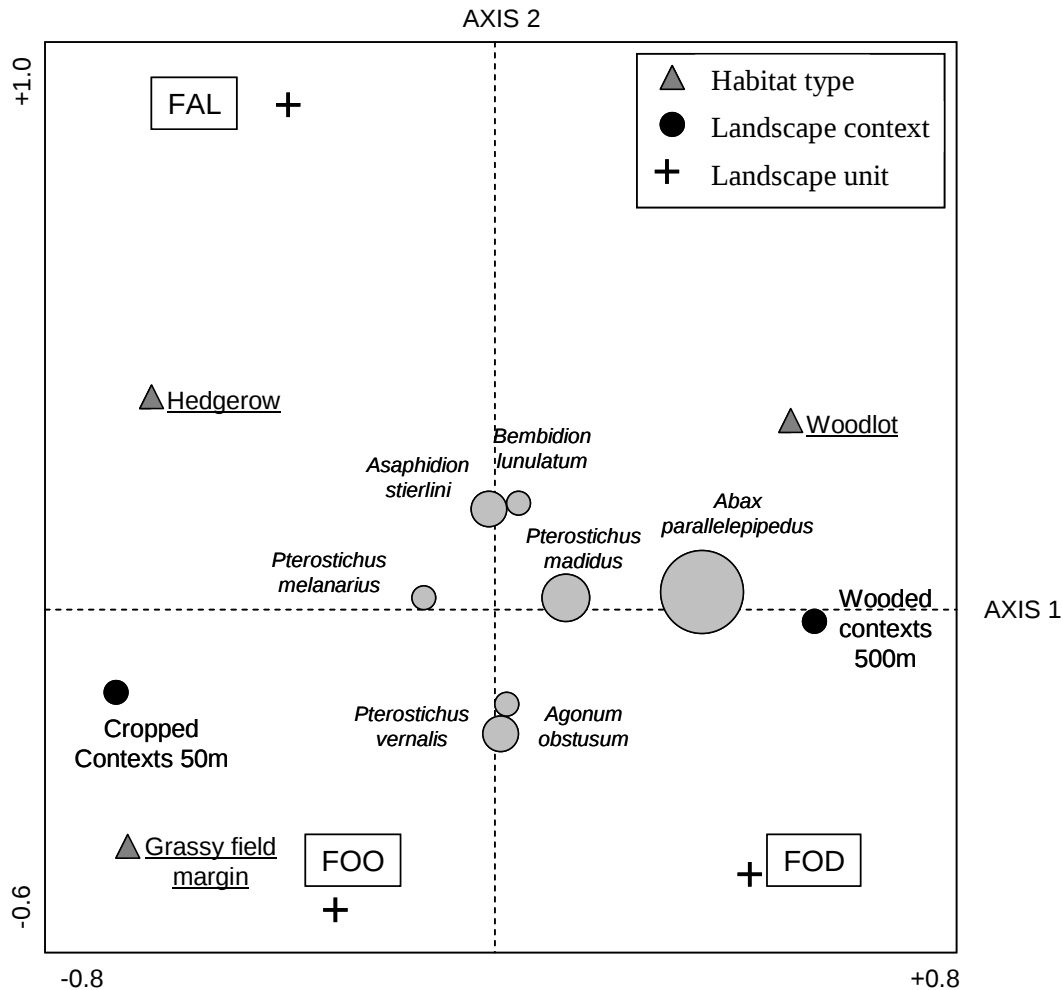


Figure 1.3. Projection of species data and environmental variables on the first factorial plane of CCA analysis. For visibility, only main species are indicated; grey circles indicate position of species in factorial plane; size of circles illustrates fit of species with factorial axes.

3.3. Relationships between scale of analysis, beetle abundance and landscape context

Abundance of large carabid species (body-size>15mm) was compared between the three landscape units (figure 1.4). Body-size of carabid species expresses both their tolerance to disturbance and their dispersal ability. Large-sized species, most often forest species, are intolerant to disturbance and less mobile, whereas small species, mainly field species, are more mobile and tolerant to disturbance (Ribera *et al.*, 2001). The comparison of the abundance of large carabid species between landscape units revealed significant differences between FOD and FAL (Mann Whitney test, $P<0.05$). Large species were especially more abundant in FOD than in FAL (figure 1.4). The abundance of large species in FOO did not differ significantly from those in other landscape units (Mann Whitney test, $P>0.05$).

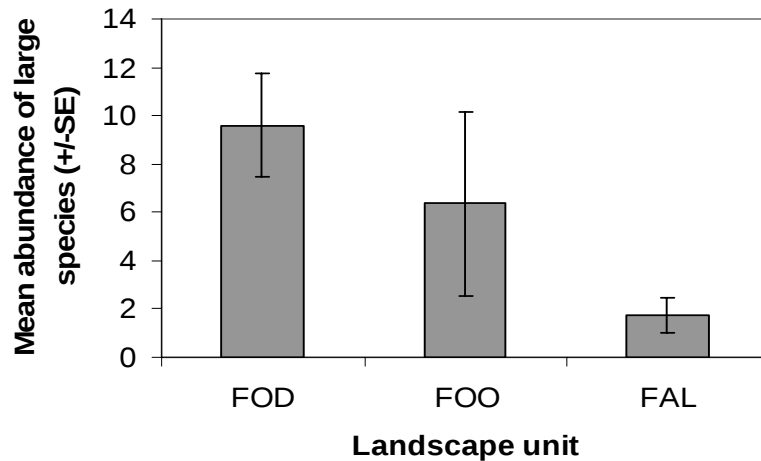


Figure 1.4. Mean abundance of large carabid species (body-length > 15mm) ($\pm$ standard error) in each landscape unit.

3.4. Relationships between spatial scale of analysis, carabid beetle abundance and landscape context

Figure 1.5 represents values of Kendall correlation coefficient between the relative abundance of large (body-size > 15mm), and small carabid species (body-size < 5mm) and the proportion of woody elements or crops in the landscape context at the three scales of analysis.

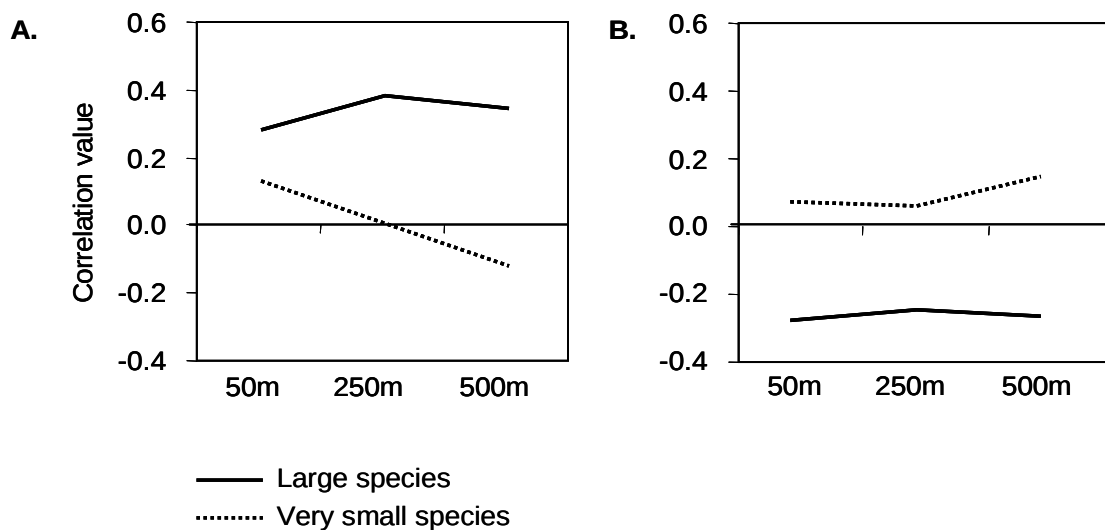


Figure 1.5. Kendall correlation values between abundance of carabid species and landscape context descriptors at the three scales of analysis. A: between abundance of large (body-length > 15mm) and small species (body-length < 5mm) and the proportion of woody elements. B: between abundance of large and small species and the proportion of crops.

Relative abundances of large species were correlated more closely to the proportion of woody elements at the scale of 250m ($r_{250}=0.40$, $P<0.05$), whereas small species were not significantly correlated to the proportion of woody elements at any spatial scale ($P>0.05$).

(figure 1.5 A). Correlation values between abundance of large and small species and proportions of crops were low and non significant for small species (small species: max. $r_{500}=0.16$, $P>0.05$) (figure 1.5 B) but significant for large species (large species: max. $r_{50}=-0.27$, $P<0.05$).

4. Discussion

4.1. Effects of farming systems at the scale of landscape unit

The landscape units were the most important variables constraining carabid species assemblages, followed by habitat type and landscape context characteristics. This main effect of landscape unit expresses the combined influence of the landscape pattern and of the nature and intensity of farming systems at a large spatial scale. Small field species especially dominated carabid assemblages in FAL. This landscape differs from the others by its farming system oriented toward intensive animal and cash crop production; it is also characterised by a reduced network of permanent elements in comparison with FOD. Abundance of forest carabid species decreases with the reduction of permanent elements at the landscape scale (Millán Peña *et al.*, 2003). Intensification of agriculture toward different farming systems leads to different types of landscape in terms of landscape pattern (Poudevigne *et al.*, 1997; Millán Peña *et al.*, 2003). As each landscape has its own history in terms of landscape or agriculture dynamics, the current communities might be the reflect of past changes (den Boer, 1981; Burel, 1992; Petit and Burel, 1998b). The dominance of small field species in FAL might be also the consequence of higher organic fertilisation rates and pesticide use, and more frequent ploughing operations associated to intensive pig breeding and cash crop production. All these practices are known to cause declines of many carabid species over the long term (Basedow, 1990; Epstein *et al.*, 2001; Langmaack *et al.*, 2001; Purvis and Fadl, 2002), large-size species being the most affected (Blake *et al.*, 1994; Ribera *et al.*, 2001).

4.2. Effect of habitat type

Influence of habitat type was particularly important for woodlands, which were characterised by high abundance of forest species (Thiele, 1977). Hedgerows were dominated by field species, though they often display the same forest species than woodlands, especially when characterized by dense vegetation cover (Petit and Usher, 1998). Here, hedgerows had generally dense vegetation, but they were often embedded in cropped areas, that might explain the low abundance of forest species. Habitat type might also reflect an effect of management regimes. Field boundaries in studied landscapes were often managed with herbicides by farmers. The low abundance of forest species in grassy field margins and hedgerows might be the consequence of repeated herbicide treatments over years.

4.3. Response of carabid assemblages to landscape context

Landscape context had a significant effect on carabid species assemblages, but lower than those of habitat or landscape unit variables. Nevertheless, forest species were more associated to landscape contexts with many woody elements, either woodlands or hedgerows, in concordance with results of previous studies (Millán Peña *et al.*, 2003). Spatial effects can be detected only at specific scales depending on the dispersal rates of studied organisms and

their foraging radius (Kareiva, 1990; Roland and Taylor, 1997; Steffan-Dewenter, 2002). We thus used a multiscale approach to describe the grain at which carabid species assemblages perceive the landscape. Our hypothesis was that low mobile species perceive the landscape at fine scales, while more mobile species perceive it at coarser scales (Keitt *et al.*, 1997). Our results show that large species, which are the more often apterous, responded more to the proportion of woody elements in landscape context at intermediate scale of analysis (250m) and to the amount of crops at fine scale (50m). Small species, which are more mobile, did not respond to any landscape descriptors regardless of the scale. However, the low values of correlation coefficients between landscape context variables and carabid abundance raise the question of the appropriateness of variables and scales of analysis used to describe the landscape context. Further analyses should be conducted with consideration of a wider range of spatial scales and other variables to describe the landscape context.

5. Conclusion

Previous studies have found a higher effect of habitat type on carabid communities in comparison with landscape context characteristics (Jeanneret *et al.*, 2003a, Weibull and Östman, 2003). However, our results show that the nature and intensity of farming systems at a large spatial scale might constrain carabid assemblages more than habitat conditions, as already demonstrated for plants in the same landscapes (Le Coeur *et al.*, 1997). The major effect of landscape unit on carabid assemblages is consistent with predictions of hierarchy theory (Allen and Star, 1982; O'Neill *et al.*, 1986; Urban *et al.*, 1987). Hierarchy theory predicts that ecological systems are organized in distinct levels, each operating at its own spatial and temporal scale and that phenomena at the higher levels in the hierarchy constraint phenomena at lower levels (Allen and Star, 1982; O'Neill *et al.*, 1986; Urban *et al.*, 1987). Our study underlines the necessity of considering the relationships between landscape and farming systems at the landscape scale. The role of permanent landscape elements for carabid diversity differs according to the landscape where they are located, in relation to the nature and intensity of farming systems. Some of the measures promoted by agri-environmental schemes to favour species diversity are the introduction of semi-natural elements and the reduction of inputs. Organic farming has been especially shown to enhance carabid diversity (Booij and Noorlander, 1992; Döring and Kromp, 2003; Weibull and Östman, 2003; Weibull *et al.*, 2003). Our results show that the conservation of carabid diversity in intensive agricultural landscape needs to promote a connected network of permanent landscape elements at the landscape scale, e.g., by plantation of new hedgerows but also the conversion of arable land into permanent grasslands. This implies to operate changes in farming systems. In less intensive agricultural landscapes, where permanent landscape elements are numerous, the reduction of inputs, such as the reduction of fertilisers and insecticides in crops but also of herbicides on field boundaries, should be promoted.

Acknowledgements

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Appendix 1. Name and abundance of carabid beetle species collected in the three landscape units.

Name	Total
<i>Pterostichus cupreus</i> (L.)	2858
<i>Pterostichus madidus</i> (Fabr.)	1739
<i>Bembidion properans</i> (Stephens)	1205
<i>Nebria brevicollis</i> (Fabr.)	837
<i>Harpalus rufipes</i> (De Geer)	643
<i>Pterostichus melanarius</i> (Illiger)	465
<i>Agonum dorsale</i> (Pontoppidan)	441
<i>Abax parallelepipedus</i> (Piller & Mitterpacher)	373
<i>Pterostichus strenuus</i> (Panzer)	346
<i>Trechus quadristriatus</i> (Schrank)	303
<i>Notiophilus biguttatus</i> (Fabr.)	269
<i>Agonum lugens</i> (Duftschmid)	262
<i>Pterostichus versicolor</i> (Sturm)	247
<i>Bembidion lunulatum</i> (Fourcroy)	237
<i>Pterostichus anthracinus</i> (Panzer)	211
<i>Bembidion tetracolum</i> (Say)	205
<i>Pterostichus vernalis</i> (Panzer)	203
<i>Asaphidion stierlini</i> (Heyden)	165
<i>Loricera pilicornis</i> (Fabr.)	135
<i>Bembidion iricolor</i> (Bedel)	119
<i>Leistus fulvibarbis</i> (Dejean)	109
<i>Brachynus sclopeta</i> (Fabr.)	107
<i>Bembidion biguttatus</i> (Fabr.)	106
<i>Bembidion quadrimaculatum</i> (L.)	98
<i>Agonum albipes</i> (Fabr.)	89
<i>Carabus purpurascens</i> (Fabr.)	77
<i>Notiophilus quadripunctatus</i> (Dejean)	74
<i>Metabletus obscuroguttatus</i> (Duftschmid)	69
<i>Agonum obscurum</i> (Herbst)	67
<i>Bembidion obtusum</i> (Serville)	65
<i>Stomis pumicatus</i> (Panzer)	58
<i>Anisodactylus binotatus</i> (Fabr.)	53
<i>Agonum muelleri</i> (Herbst)	49
<i>Pterostichus niger</i> (Schaller)	41
<i>Diachromus germanus</i> (L.)	38
<i>Notiophilus palustris</i> (Duftschmid)	36
<i>Synuchus nivalis</i> (Panzer)	34
<i>Badister unipustulatus</i> (Bonelli)	34
<i>Asaphidion flavipes</i> (L.)	34
<i>Carabus problematicus</i> (Herbst)	31
<i>Harpalus rufibarbis</i> (Fabr.)	28
<i>Agonum nigrum</i> (Dejean)	27
<i>Carabus nemoralis</i> (Müller)	21
<i>Acupalpus dubius</i> (Schilsky)	20
<i>Microlestes maurus</i> (Sturm)	19

Appendix 1 (continued).

Name	Total
<i>Metabletus truncatellus</i> (L.)	18
<i>Leistus ferrugineus</i> (L.)	18
<i>Drypta dentata</i> (Rossi)	17
<i>Chlaenius nigricornis</i> (Fabr.)	17
<i>Bembidion harpaloides</i> (Serville)	16
<i>Agonum assimile</i> (Paykull)	16
<i>Microlestes minutulus</i> (Goeze)	15
<i>Acupalpus meridianus</i> (L.)	13
<i>Notiophilus rufipes</i> (Curtis)	12
<i>Metabletus foveatus</i> (Fourcroy)	11
<i>Brachynus explodens</i> (Duftschmid)	11
<i>Harpalus aeneus</i> (Fabr.)	10
<i>Carabus granulatus</i> (L.)	9
<i>Dyschirius globus</i> (Herbst)	8
<i>Clivina collaris</i> (Herbst)	8
<i>Badister sodalis</i>	8
<i>Badister peltatus</i> (Panzer)	8
<i>Badister bipustulatus</i> (Fabr.)	8
<i>Demetrias atricapillus</i> (L.)	7
<i>Eotachys bistriatus</i>	6
<i>Parophonus maculicornis</i> (Duftschmid)	5
<i>Agonum sexpunctatum</i>	5
<i>Acardystus flavescens</i>	5
<i>Clivina fossor</i> (L.)	4
<i>Harpalus rubripes</i> (Duftschmid)	4
<i>Carabus intricatus</i> (L.)	4
<i>Amblystomus niger</i> (Heer)	4
<i>Stenolophus mixtus</i>	4
<i>Carabus auratus</i> (L.)	4
<i>Dromius linearis</i> (Olivier)	3
<i>Agonum viduum</i> (Panzer)	3
<i>Agonum viridicupreum</i>	3
<i>Stenolophus teutonus</i> (Schränk)	2
<i>Calathus piceus</i> (Marsham)	2
<i>Bembidion mannerheimi</i> (Sahlberg)	2
<i>Trechoblemus micros</i>	1
<i>Stenolophus skrimshirani</i> (Stephens)	1
<i>Pristonychus terricola</i>	1
<i>Oodes helopoïdes</i> (Fabr.)	1
<i>Olisthopus rotundatus</i> (Paykull)	1
<i>Harpalus tardus</i> (Panzer)	1
<i>Agonum moestum</i>	1
Total abundance	12944
Total number of species	87

CHAPITRE 2 : FIELD MARGIN CARABID (COLEOPTERA : CARABIDAE) ASSEMBLAGES – THE INFLUENCE OF LANDSCAPE CONTEXT ON THE SENSITIVITY TO FARMING PRACTICES

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Résumé

Dans les paysages d'agriculture intensive, les facteurs de la dynamique de la biodiversité sont principalement liés aux activités agricoles à plusieurs échelles spatio-temporelles. Les pratiques agricoles altèrent la qualité des ressources à l'échelle locale, et les systèmes de production agricole déterminent la composition et l'organisation spatiale des paysages. Jusqu'à présent, les effets de ces différents facteurs ont été considérés de façon distincte. Dans cet article, nous testons simultanément les effets de la structure du paysage et des pratiques agricoles sur les communautés de carabiques de bords de champs dans des paysages agricoles bocagers bretons (France). L'objectif de cette étude est de déterminer si des pratiques agricoles similaires influencent la biodiversité de la même façon dans différents contextes paysagers. Les communautés de carabiques ont été caractérisées par un échantillonnage stratifié selon les régimes de gestion des bords de champs sur les cinq dernières années, dans des contextes paysagers contrastés en terme de composition et d'hétérogénéité spatiale à différentes échelles. La composition des assemblages spécifiques de carabes est fortement influencée par le contexte paysager. Les espèces forestières sont présentes dans les bords de champs situés dans des contextes paysagers boisés, tandis que les espèces de champs prédominent dans les bords de champs situés dans des zones cultivées. Les régimes de gestion des bords de champs affectent la composition actuelle des communautés de carabiques. Les espèces forestières sont plus abondantes dans les bords de champs sans entretien ou pâturés et piétinés par les animaux en comparaison des bordures pulvérisées aux herbicides pendant les cinq dernières années. Ces différences sont dues à une diminution de la qualité du couvert végétal et probablement de la disponibilité des proies pour ces espèces. Les effets des régimes de gestion sur les communautés diffèrent en fonction du contexte paysager, et sont significatifs dans les contextes boisés. La conservation de la biodiversité dans les paysages d'agriculture intensive nécessite d'adopter des régimes de gestion impliquant une succession de pratiques spécifiques. Cependant, ces mesures ne pourraient être efficaces que dans des contextes paysagers favorables aux espèces concernées. Les pratiques agricoles et les caractéristiques du paysage devraient être pris en compte pour mettre en place des plans de gestion pour la conservation de la biodiversité.

1. Introduction

Agricultural landscapes are typically viewed as a mosaic of arable and grassland fields and non productive areas such as hedgerows. Research on biodiversity has emphasised the role of the latter as habitat (Forman and Baudry, 1984), temporary refuge (Dennis and Fry, 1992) and corridor (Duelli *et al.*, 1990) for many species. The spatial arrangement of hedgerows and other permanent areas within agricultural landscapes affects animal or plant diversity depending on the dispersal ability and the ecological requirements of species (Burel *et al.*, 1998; Steffan-Dewenter, 2002; Millán Peña *et al.*, 2003). Although agricultural landscapes have been often considered as composed of habitat patches and corridors imbedded in a neutral matrix of crops (Bennett, 1990; Verboom and van Apeldoorn, 1990), their species composition is influenced by the composition of the arable mosaic (Weibull *et al.*, 2000; Östman *et al.*, 2001). At the local scale, animal or plant species assemblages have been related more to habitat quality and management (Maudsley *et al.*, 2002; Thomas *et al.*, 2002) than to composition and spatial organisation of the surrounding landscape, i.e. of the landscape context of habitat patches. Farming practices, such as herbicide spraying, mowing or grazing, constitute strong disturbances that can alter resource abundance and distribution over the long term by homogenising plant species assemblages and decreasing microhabitat diversity (Maudsley, 2000; Kruess and Tscharntke, 2002). On hedgerow margins, the use of herbicides over years induces homogenisation of the flora, with a shift from perennials to weedy species, while perennials are dominant in grazed margins (Le Coeur *et al.*, 2002).

Species often respond hierarchically to their environment (Kotliar and Wiens, 1990; Levins, 1992; Fuhlendorf *et al.*, 2002b). Interactions between species assemblages and landscape have to be examined at several spatial scales, since species respond to landscape pattern at their own spatial scale (Kareiva, 1990). However, few studies have adopted a hierarchical approach to investigate such relationships (Burel, 1992). In this paper we tested whether species assemblages in similar habitats (vegetation structure) but surrounded by contrasted landscapes respond differently to disturbance (management regimes) according to ecological requirements of species, using carabids as a reference group.

Carabid beetles have been extensively studied (Thiele, 1977; Kromp, 1999) and they play a potential role in crop pest control (Lang *et al.*, 1999). Hedgerows with dense vegetation cover act as corridor for forest species (Burel and Baudry, 1989) and temporary refuges for others (Sotherton, 1984). Carabid assemblages respond to changes in landscape openness and mosaic heterogeneity (Millán Peña *et al.*, 2003). As the amount of woodlots and hedgerows decreases, mobile field species replace forest species with lower dispersal power (Burel *et al.*, 1998; Millán Peña *et al.*, 2003). Few studies have considered the effects of hedgerow margin management on carabid assemblages (Canter and Tamis, 1999), but their impacts in fields have been well documented (Kromp, 1999). Species assemblages are progressively dominated by field species (Gibson *et al.*, 1992; Gardner *et al.*, 1997), according to the decrease in vegetation complexity and the associated decline of available prey species (Varchola and Dunn, 1999). The response of carabid species to management practices depends on species tolerance to disturbance, which is related to dispersal ability and body size, large species being more affected than smaller ones (Blake *et al.*, 1994; Ribera *et al.*, 2001).

This study aimed at comparing contrasting management regimes of field margins, herbicide spraying, grazing and no management, on carabid assemblages in different landscapes. We posed the hypothesis that carabid species composition of field margins was controlled by three sets of variables:

- 1- margin management: field species should dominate in field margins intensively managed over years
- 2- boundary structure: shrubs and tree density may favour forest species
- 3- surrounding landscape patterns: the presence of forest species is linked to the amount of woody elements in the landscape context

According to hierarchy theory (O'Neill *et al.*, 1986) higher levels (landscape) constraint lower ones (margins), Therefore we expected that landscape pattern would be a better predictor of species composition than management, as demonstrated for plants in the same study area (Le Coeur *et al.* 2002).

2. Study area and methods

2.1. Study area

The study was conducted in a hedgerow network landscape (bocage) in Brittany, France. This is a long-term ecological research site (Burel *et al.*, 1998; Baudry *et al.*, 2000b). Farming systems are oriented toward milk production. Permanent and temporary grasslands and cereals (wheat and maize) are the dominant land uses. Data were collected from two 6.25 km² landscape units (figure 2.1). These units correspond respectively to two sites (unit 1: A and unit 2: C) studied by Le Coeur *et al.* (1997), who demonstrated significant differences between landscape pattern. Unit 1 is located in a dense hedgerow network (126 m/ha) and fine grain area with several woodlots, while unit 2 is more open with a reduced and fragmented hedgerow network (67 m/ha). The proportion of crop land differs, in unit 2 there is a high proportion of maize and other cereals while in unit 1 there is a larger proportion of grasslands. Previous surveys of farming systems show that livestock density and production are higher in unit 2 (Thenail, 2002).

2.2. Sampling

Hedgerows, and more generally field boundaries, are defined as the segment between two different fields (Le Coeur *et al.*, 2002). A field boundary is split into two field margins related to the adjacent fields. Each margin has its own management regime linked to the farmer and field use (Baudry *et al.*, 1998; Marshall and Moonen, 2002). Herbaceous vegetation is sprayed with herbicides or mowed to limit weed invasions in adjacent crops and it is sometimes grazed or trampled down by cattles if adjacent to a pasture. We classified field margins according to their past management regimes to select sampling locations (Jacques Baudry & Dominique Volland, unpublished data). From 1995 to 1999, management practices (rolling, herbicide spraying, tilling, mowing, burning, grazing, trampling by animal) were recorded on 188 field margins in unit 1 and on 180 field margins in unit 2. Observations of farming practices were carried out from ten to twelve times per year, from January to November. Using Correspondence and Cluster analyses on management data, we obtained three final classes of management regime: (i) field margins unmanaged for five years, (ii) field margins with continuous herbicide spraying, and (iii) field margins with repeated grazing and trampling. When considering both margins of hedgerows, hedgerows in studied areas were grouped into six combinations of management.



Figure 2.1. Description of landscape units.

We decided to sample, when available, five hedgerows per combination. Finally, 23 and 16 hedgerows corresponding to 46 and 32 field margins were selected in units 1 and 2 respectively (table 2.1). Management practices in 2000 and during the sampling period in 2001 were also recorded twice a year. They were similar to previous years, thus we tested the cumulative effect of seven years of management practices.

Table 2.1. Number of sampled hedgerows per combination of management and corresponding number of sampled field margins per class of management (NM: no management; GT: grazing with trampling; H: herbicide spraying) in the two landscape units.

	Unit 1	Unit 2	Total
<i>Hedgerow</i>			
NM-NM	4	1	5
NM-GT	0	0	0
NM-H	5	5	10
GT-GT	4	1	5
GT-H	5	5	10
H-H	5	4	9
Total	23	16	39
<i>Field margin</i>			
NM	13	7	20
GT	13	7	20
H	20	18	38
Total	46	32	78

Carabid beetle assemblages were sampled in selected field margins by the mean of pitfall traps. Two traps containing a formalin solution (5%) were installed per margin five to ten meters apart depending on the length of hedgerow (figure 2.2). We installed 92 and 64 traps respectively in units 1 and 2. Traps were opened continuously and emptied once a week from 12th June 2001 to 19th July 2001, i.e. five sampling periods. According to these dates, sampling was realised between the main period of activity of spring and autumn breeders. However, our objective was not to describe exhaustively carabid assemblages for the whole breeding period (which was done by Burel *et al.*, 1998), but to compare at a given time species assemblages according to management regimes and landscape characteristics. In this context, short-term sampling of carabid assemblages is an appropriate approach (Maelfait and Desender, 1994). Furthermore, comparison between sampling locations is less affected by the effect of intra-annual farming practices (Jeanneret *et al.*, 2003a).

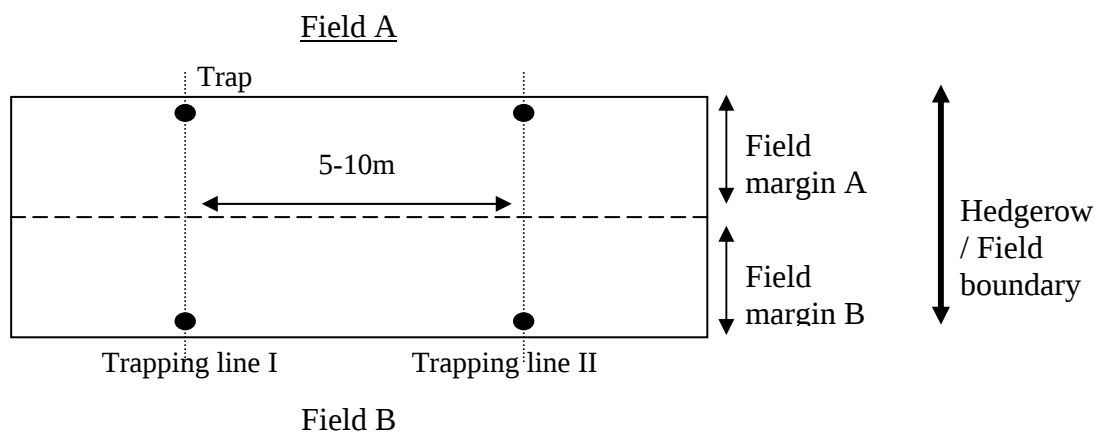


Figure 2.2. Design of carabid beetle sampling in hedgerows.

2.3. Characterisation of landscape context at several spatial scales

We used a multiscale approach combining local conditions (margin management, hedgerow vegetation structure) and landscape conditions. Landscapes are viewed as windows of different size centred on the sampled margins. This permits to describe the grain at which carabid assemblages react to landscape context. According to Keitt *et al.* (1997), the spatial scale at which species perceive the landscape is related to their dispersal ability: low mobile species perceive the landscape at a fine scale in contrary to species with higher dispersal abilities. Here, two sizes of windows, 50 x 50m i.e. 0.25 ha (fine grain) and 450 x 450m i.e. 20.25 ha (coarse grain) were tested. We hypothesised that species assemblages might respond differently to landscape conditions at these two scales according to dispersal ability of species. Maps of landscape units were created in a raster format using IDRISI (Eastman, 1997). Carabid assemblages have been shown to respond to the amount of permanent habitats (woodlots, hedgerows, permanent grasslands) in landscape context (Millán Peña *et al.* 2003). Thus, three descriptors of the landscape were calculated within windows (CHLOE; Baudry and Denis, 1995): the proportion of woody elements (woodlots and hedgerows), the proportion of crops, and the proportion of grasslands (Appendix 2.A).

2.4. Vegetation data

The structure of hedgerows was grouped into three classes corresponding to different density of shrubs and trees: (i) dense vegetation cover, i.e. almost continuous shrubby layer with many trees, (ii) discontinuous vegetation cover, i.e. discontinuous shrubby layer and some trees and (iii) sparse vegetation cover, i.e. no shrubs and no or rare trees (Appendix 2.A).

2.5. Statistics

Species richness, diversity and evenness are often used to characterise biodiversity. However, these synthetic indices do not always reflect the response of carabid beetle assemblages to changes in the composition and organisation of the landscape as demonstrated by Burel *et al.* (1998). Thus we used Canonical Correspondence Analysis (CCA) to relate species data to environmental variables (CANOCO, Ter Braak and Smilauer, 1998). The variables introduced in CCA were: management regime (3 categories: no management, herbicide spraying, grazing), vegetation structure (3 categories: dense, intermediary, sparse), landscape context descriptors in 50m and 450m windows (6 continuous variables). To determine the relative importance of management regime, vegetation structure and landscape context descriptors, CCA and partial CCA were performed. CCA performed with each variable separately followed by global CCA with the whole set of variables permit to eliminate the variables which do not explain significantly variation of species assemblages. To hierarchy the remnant explanatory variables, variance partitioning is then performed through partial CCA; the variance explained by each variable is obtained after eliminating the variance due to the other variables, which are used as covariables (partial variables). Significance of variables in CCA and partial CCA is tested by the mean of Monte Carlo permutations. The detailed procedure is described in Jeanneret *et al.* (1999; 2003b). A CCA including the selected explanatory variables after separate and global CCA was realised to illustrate the relationships between the composition of carabid assemblages and environmental variables. CCA and partial CCA were conducted on the carabid assemblages in

the 79 field margins (the two traps per margin being pooled). Species occurring at less than 0.5 % were considered as rare and not included in analysis.

To determine how species with contrasted ecological requirements responded to management regimes depending on landscape conditions, simple regression analysis was carried out on species abundances per management regime and proportion of woody habitats in the landscape context at the two spatial scales. We focused on two contrasted groups of species, i.e. large (body-length > 15 mm) and very small species (body-length < 5 mm). In fact, body-size expresses both tolerance to disturbance and dispersal ability of species: large species are mainly wingless and intolerant to disturbance, while very small species are more mobile and associated to unstable habitats (Blake *et al.*, 1994; Ribera *et al.*, 2001).

3. Results

3221 individuals corresponding to 82 species were trapped. This species number was similar or higher than the pool of species observed previously in the same landscapes or in nearby landscapes (Burel *et al.*, 1998; Millán Peña *et al.*, 2003). The full set of trapped species is listed in Appendix 2.B.

3.1. Selection of significant environmental variables and variance partitioning

Separate and global CCA permitted to select explanatory variables which significantly explained variance of species assemblages. Local conditions of field margins, i.e; management regime and vegetation structure, explained a significant part of carabid species assemblages (table 2.2).

Table 2.2. Percentages of variance explained and p-values (Monte Carlo test) by explanatory variables in separate CCA, explanatory variables eliminated after correlation examination in global CCA, and percentage of variance explained and p-values (Monte Carlo test) by variables in partial CCA.

Variable	Separate CCA		Global CCA Selected variables	Partial CCA	
	% of variation	p-value		% of variation	p-value
Local conditions					
Management regime	5.9	< 0.05	Yes	3.8	< 0.05
Vegetation structure	4.4	< 0.05	Yes	3.9	< 0.05
Landscape context					
Woody elements 50m	8.0	< 0.05	Yes	3.3	< 0.05
Grasslands 50m	3.1	< 0.05	No	-	
Crops 50m	5.1	< 0.05	Yes	2.6	< 0.05
Woody elements 450m	11.0	< 0.05	Yes	4.8	< 0.05
Grasslands 450m	1.6	NS	-	-	
Crops 450m	5.5	< 0.05	No	-	

Among the types of management regimes, herbicide spraying and no management had the greater effect. Grazing was eliminated as correlated with herbicide spraying (Pearson correlation, $r=-0.73$). Among the classes of vegetation structure, intermediary vegetation did not explain a significant part of variance. Landscape context descriptors explained a significant part of variance, globally higher than local conditions (table 2.2). Among landscape variables, the proportion of grasslands in 450m windows did not influence significantly carabid assemblages. The proportion of woody elements in 50m and 450m windows had a stronger influence on species assemblages. The proportion of grasslands in 50m windows was eliminated as correlated with the proportion of crops in 50m windows (Pearson correlation, $r=-0.73$).

Variance partitioning through partial CCA allowed to rank the significant explanatory variables according to explained variance. The part of variance attributed to landscape context descriptors was higher than variation explained by local conditions (table 2.2). The proportion of crops in 50m windows and of woody elements in 50m and 450m windows explained 10.7% of variance, whereas the influence of the proportion of crops in 450m windows was not significant after variance partitioning. Management regime and vegetation structure explained a similar part of variance (3.8% and 3.9% respectively).

3.2. Analysis of the relationships between carabid species assemblages and significant environmental variables

Figure 2.3 shows the projection of carabid species data and significant explanatory variables (i.e. selected after separate and global CCA) on the first factorial plane of CCA (total explained variance: 25.7 %; Monte-Carlo permutations, first axis: $P=0.005$, all axes: $P=0.005$). Table 2.3 gives correlation values between environmental variables and CCA axes 1 and 2.

The first CCA axis accounted for 12.2% of total variance. It differentiated mainly wooded landscape contexts (50m and 450m windows) from cropped ones (50m windows) (table 2.3, figure 2.3). The first CCA axis was mainly defined by forest species with low dispersal ability such as *Carabus problematicus* (Herbst), in opposition to more mobile species such as *Pterostichus melanarius* (Illiger) (figure 2.3). The second CCA axis accounted for 4.3% of total variance. It differentiated unmanaged field margins located in wooded landscape contexts (50m windows) from sprayed field margins with sparse vegetation (table 2.3, figure 2.3). Along this axis, field species such as *Bembidion quadrimaculatum* (L.) and *Pterostichus cupreus* (L.) were opposed to *Pterostichus strenuus* (Panzer) (figure 2.3).

3.3. Variation of carabid abundance depending on management regime and landscape context

Abundances of carabid species per type of management regime of field margins were plotted over the proportion of woody elements in landscape context (50m and 450m windows). We focused on two contrasted groups of species according to wing morphology, i.e. apterous and macropterous, following Ribera *et al.* (1999a, 1999b) (Appendix 2.B). In fact, wing morphology expresses dispersal ability of species: wingless species, mainly forest species, are few mobile, whereas macropterous species are more mobile and associated to open habitats (Blake *et al.*, 1994; Ribera *et al.*, 2001; Cole *et al.*, 2002).

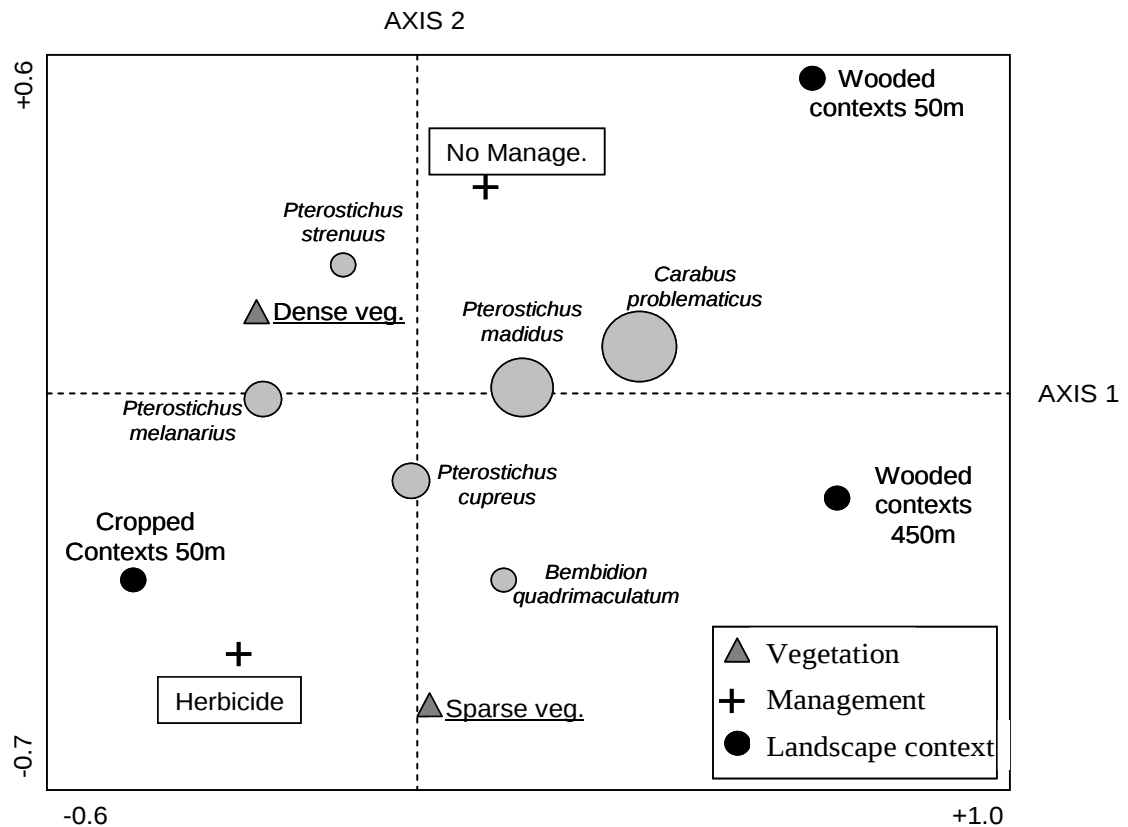


Figure 2.3. Projection of species data and environmental variables on the first factorial plane of CCA analysis. For visibility, only main species are indicated; grey circles indicate position of species in factorial plane; size of circles indicate fit of species with factorial axes.

Table 2.3. Correlation coefficients between explanatory variables (selected after separate and global CCA) and the first axes of the CCA analysis.

Variable	Correlation value	
	Axis 1	Axis 2
Management regime		
No management	0.11	0.34
Herbicide spraying	-0.27	-0.45
Vegetation structure		
Dense vegetation	-0.08	0.09
Sparse vegetation	0.04	-0.55
Landscape context		
Woody elements 50m	0.72	0.56
Crops 50m	-0.49	-0.32
Woody elements 450m	0.93	-0.17

The abundance of apterous species increased significantly in unmanaged (50 m windows: $r^2=0.52$, $P<0.05$; 450 m windows: $r^2=0.51$, $P<0.05$), sprayed (50 m windows: $r^2=0.24$, $P<0.005$; 450 m windows: $r^2=0.35$, $P<0.001$) and grazed field margins (50 m windows: $r^2=0.38$, $P<0.001$; 450 m windows: $r^2=0.28$, $P<0.05$) with increasing amount of woody habitats (figure 2.4). The increase in the abundance of apterous species was less pronounced in sprayed margins (figure 2.4). Abundance of macropterous species was not significantly related with the amount of woody elements, excepted in grazed field margins where species abundance tended to decrease (50 m windows: $r^2=0.39$, $P<0.005$; 450 m windows: $r^2=0.36$, $P<0.05$) (figure 2.4). They were generally more abundant in managed field margins (figure 2.4).

4. Discussion

4.1. Respective effects of local and landscape conditions on species assemblages

Species composition of carabid assemblages was influenced both by local and landscape conditions. Species assemblages were first constrained by landscape context characteristics, followed by management regime and vegetation structure. Among the different descriptors of the landscape context, the amount of woody elements in the landscape context had the greater influence on carabid communities. Forest species were mainly present in field margins embedded in wooded landscapes, whereas field species dominated in cropped areas, as showed by previous studies (Burel *et al.*, 1998; Millán Peña *et al.*, 2003). Our results are consistent with hierarchy theory (Allen and Starr, 1982; O'Neill *et al.*, 1986; Urban *et al.*, 1987), which predicts that phenomena at the highest scales in the hierarchy, here the landscape, constraint those at lower levels, in our case local conditions of field margins. Such effects of the landscape context have already been demonstrated in the same landscapes for plants (Le Coeur *et al.*, 1997) and in other landscapes for birds (Grand and Cushman, 2003).

The type of management regime on field margins and vegetation structure significantly influenced carabid species composition, but had lower influence in comparison with landscape context. Field margins sprayed with herbicides and characterised by sparse vegetation were dominated by field species defined as tolerant to habitat disturbance (Thiele, 1977). Forest species were more found in unmanaged field margins. These species are associated with undisturbed habitats with dense vegetation (Thiele, 1977; Eyre, 1994), as a consequence of the length of their life cycle and their high need of stable resources (Blake *et al.*, 1994). Moreover, continuous herbicide applications lead to the homogenisation of the field margin flora (Le Coeur *et al.*, 2002). Habitats with low plant diversity are associated with poorly diversified invertebrate communities (Dennis and Fry, 1992; Thomas *et al.*, 1992), and thus lower availability of prey for predatory carabid beetles (Varchola and Dunn, 1999).

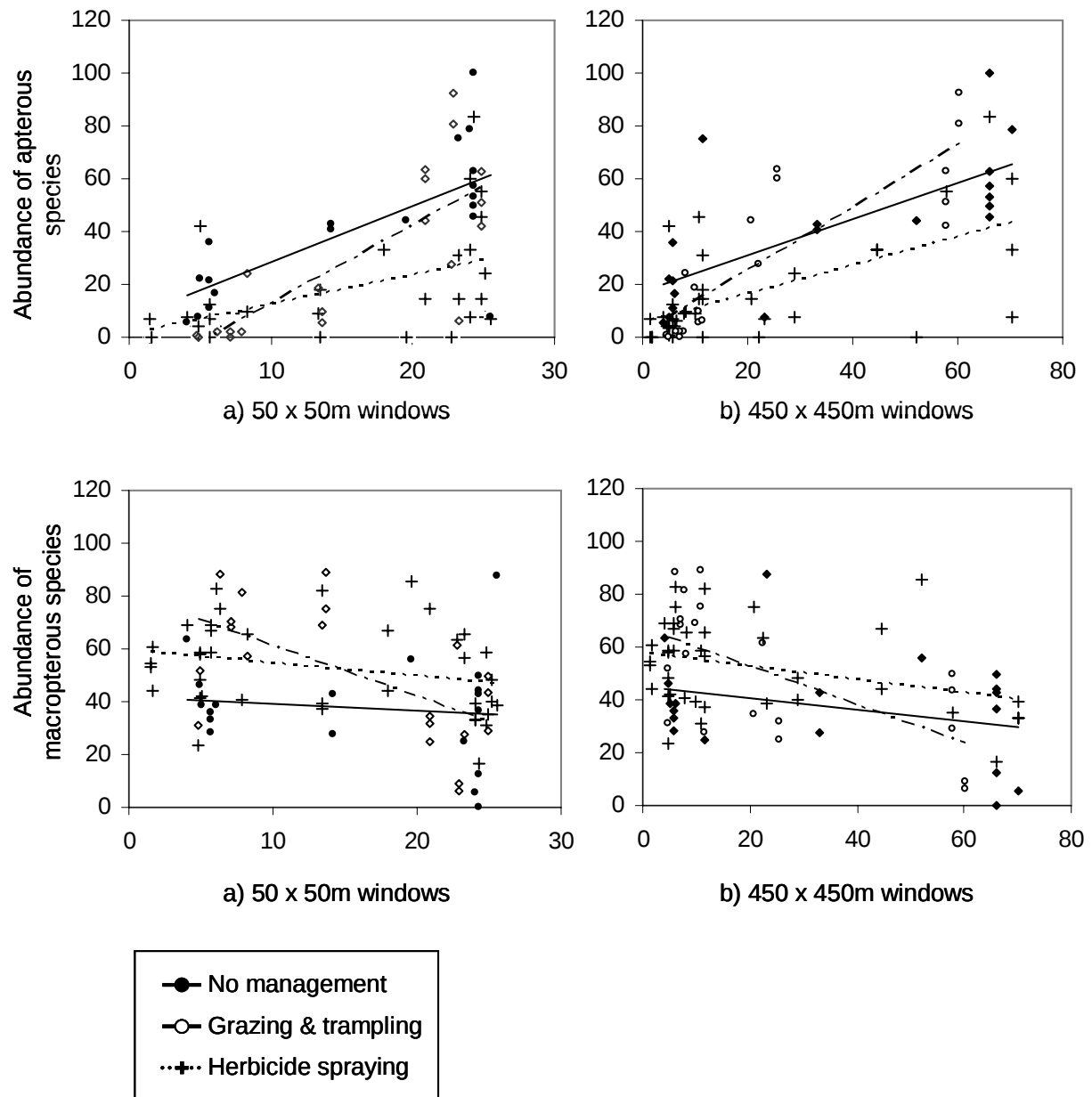


Figure 2.4. Relative abundance of apterous and macropterous species plotted over the proportion of woody elements in landscape context in windows of a) 50 x 50m and b) 450 x 450m. Regression lines are indicated to illustrate the contrasting patterns.

4.2. Sensitivity of carabid communities to management regimes depending on landscape context

Our results revealed that carabid assemblages in similar habitats surrounded by contrasted landscape pattern respond differently to disturbances according to ecological requirements of species. Carabid communities located in wooded landscapes were sensitive to the type of management regime on field margins, since they were composed of many wingless species, which are mainly intolerant forest species. On the contrary, carabid communities located in cropped areas did not respond to management regimes since they were dominated by macropterous species, which are the more often tolerant to repeated disturbances. On the other hand, the persistence of forest, wingless species in managed field margins located in wooded landscapes might be favoured by the presence of proximate hedgerows and woodlots acting as source or refuge for forest species to recolonise disturbed areas (Petit and Burel, 1998a).

There are however strong relationships between management practices and landscape context, at least at a fine scale. Field margin management is linked to the adjacent land-use (Baudry *et al.*, 1998). Land-use allocation is related to physical characteristics of fields (hydromorphy, surface area) and to the structure of the hedgerow network (Thenail and Baudry, in press). In studied landscapes, grasslands are the more often located in areas with small field sizes, dense hedgerow network and woodlots. Consequently, field margins in these areas were the more often unmanaged or grazed. Herbicide spraying was more frequently observed in cropped areas.

4.3. Relationships between species responses to landscape context and spatial scales

How organisms perceive the landscape is a recurrent question in ecology (Wiens and Milne, 1989). Here, we used a multiscale approach to describe the grain at which carabid species assemblages perceive the landscape. The spatial scale at which species perceive the landscape is related to their dispersal ability (Keitt *et al.*, 1997). The main hypothesis is that low mobile organisms perceive the landscape at fine scales, while species capable of long-range dispersal perceive it at coarser scales (Keitt *et al.*, 1997). However, our results did not permit to confirm this hypothesis. Here, field carabid species, the more often highly mobile, were significantly enhanced in cropped landscapes at fine spatial scale (50m) but not at coarse scale. Forest species were related to the amount of woody elements in landscape context at both fine and coarser scales. In our analyses, we consider only two spatial scales for describing the landscape context. Further analyses should be conducted with consideration of a wider range of spatial scales to analyse more accurately the relationships between landscape context characteristics and carabid assemblages.

5. Conclusion

The major changes in carabid fauna following agricultural intensification has been imputed to the removal of permanent elements and the increasing use of pesticides (Desender and Turin, 1989; Desender *et al.*, 1994). The introduction of semi-natural elements and the reduction of inputs have been emphasised to conserve carabid diversity in agricultural landscapes. Our results suggest that depending on the pattern of the current landscape, different measures should be adopted to enhance forest carabid species. In landscapes with

rare permanent elements, action plans should focus on the plantation of new hedgerows and the conversion of arable fields into grasslands, to favour a dense and connected network between existing permanent elements. In landscapes where permanent elements are abundant, conservation priorities should concern not only the maintenance of existing network of permanent elements, but also local farming practices. Field margins have been increasingly managed by herbicide applications. Moderate mowing, emphasised for its potential positive effects on invertebrates (Gardner *et al.*, 1997), may be an alternative to maintain carabid diversity in field margins.

Acknowledgements

We thank warmly Maud Ablain, Violaine Canévet, Delphine Delouvée, Nadine Strabach and Dominique Volland for their field assistance, Philippe Fouillet and Anita Georges for identification work, Yannick Delettre, Didier Le Coeur and Nicolas Schermann for their help in analyses. We are grateful to Pavel Kindlmann and Jana Jersakova for their comments on manuscript. This study was supported by the French Ministry of Environment, DIVA programme.

Appendix 2.A. Type of management regime (NM: no management, GT: grazing with trampling, H: herbicide spraying), vegetation density and landscape context variables of sampled field margins in each landscape unit.

	Hedge #	Management regime		Vegetation	Landscape context 50m			Landscape context 450m		
		Field margin A	Field margin B		Woody	Crops	Grassl.	Woody	Crops	Grassl.
Unit 1	1	H	GT	Sparse	57.9	0.0	42.2	24.9	30.1	41.9
	2	GT	GT	Sparse	57.9	0.0	42.2	24.9	30.1	41.9
	3	GT	GT	Discont.	60.3	0.0	39.7	22.9	32.0	42.4
	4	GT	GT	Discont.	25.6	0.0	74.4	20.8	35.1	42.2
	5	GT	H	Sparse	9.9	0.0	85.1	13.4	28.5	48.8
	6	GT	GT	Sparse	10.7	0.0	89.3	13.7	24.2	52.9
	7	NM	NM	Dense	33.1	51.2	9.1	14.2	42.1	31.5
	8	H	H	Discont.	44.6	0.0	47.9	18.0	31.7	37.1
	9	H	GT	Discont.	20.7	0.0	79.3	20.9	31.7	35.3
	10	H	NM	Discont.	52.1	0.0	47.9	19.6	35.7	37.3
	11	NM	H	Dense	11.6	31.4	57.0	23.3	30.1	34.6
	12	GT	H	Sparse	11.6	31.4	57.0	23.3	30.1	34.6
	13	H	H	Dense	10.7	54.6	34.7	24.8	30.5	34.1
	14	H	H	Dense	28.9	26.5	44.6	25.2	31.4	32.7
	15	NM	H	Dense	23.1	17.4	59.5	25.5	32.4	31.6
	16	GT	H	Discont.	22.3	0.0	77.7	22.7	33.2	31.8
	17	NM	H	Dense	70.3	3.3	26.5	24.0	34.7	35.1
	18	NM	NM	Discont.	66.1	0.0	33.9	24.3	37.5	34.2
	19	H	H	Dense	70.3	3.3	26.5	24.0	34.7	35.1
	20	H	NM	Dense	66.1	0.0	33.9	24.3	37.5	34.2
	21	NM	NM	Dense	66.1	0.0	33.9	24.3	37.5	34.2
	22	NM	NM	Dense	66.1	0.0	33.9	24.3	37.5	34.2
	23	H	H	Dense	11.6	88.4	0.0	13.5	37.9	42.6

Appendix 2.A (continued).

	Hedge #	Management regime		Vegetation	Landscape context 50m			Landscape context 450m		
		Field margin A	Field margin B		Woody	Crops	Grassl.	Woody	Crops	Grassl.
Unit 2	1	NM	H	Discont.	4.1	65.9	28.8	4.1	65.9	28.8
	2	GT	H	Discont.	4.8	66.9	28.3	4.8	66.9	28.3
	3	H	NM	Dense	5.7	31.5	54.1	5.7	31.5	54.1
	4	H	GT	Discont.	7.9	45.1	45.9	7.9	45.1	45.9
	5	GT	GT	Discont.	7.1	47.8	44.6	7.1	47.8	44.6
	6	GT	H	Dense	6.3	45.6	47.4	6.3	45.6	47.4
	7	H	NM	Sparse	4.9	50.4	43.0	4.9	50.4	43.0
	8	H	GT	Dense	8.3	48.4	41.9	8.3	48.4	41.9
	9	NM	H	Dense	6.1	39.4	52.3	6.1	39.4	52.3
	10	NM	H	Discont.	5.0	52.5	40.6	5.0	52.5	40.6
	11	H	H	Sparse	5.7	39.5	47.7	5.7	39.5	47.7
	12	NM	NM	Sparse	5.7	33.5	53.2	5.7	33.5	53.2
	13	GT	H	Sparse	4.9	39.0	45.5	4.9	39.0	45.5
	14	H	H	Dense	4.9	45.0	44.7	4.9	45.0	44.7
	15	H	H	Dense	1.5	89.3	5.7	1.5	89.3	5.7
	16	H	H	Dense	1.6	70.4	24.6	1.6	70.4	24.6

Appendix 2.B. Full names, wing morphology and number of carabid beetle species collected in field margins.

Name	Wing morphology	Total
<i>Pterostichus melanarius</i> (Illiger)	Dimorphic	358
<i>Bembidion properans</i> (Stephens)	Dimorphic	329
<i>Pterostichus madidus</i> (Fabr.)	Apterous	284
<i>Pterostichus cupreus</i> (L.)	Macropterous	229
<i>Nebria brevicollis</i> (Fabr.)	Macropterous	211
<i>Trechus quadristriatus</i> (Schrank)	Macropterous	124
<i>Loricera pilicornis</i> (Fabr.)	Macropterous	108
<i>Agonum dorsale</i> (Pontoppidan)	Macropterous	108
<i>Abax parallelepipedus</i> (Piller & Mitterpacher)	Apterous	105
<i>Harpalus rufipes</i> (De Geer)	Macropterous	99
<i>Amara lunicollis</i> (Schiödt)	Macropterous	92
<i>Bembidion tetracolum</i> (Say)	Dimorphic	78
<i>Carabus problematicus</i> (Herbst)	Apterous	67
<i>Agonum moestum</i> (Duftschmid)	Macropterous	57
<i>Bembidion quadrimaculatum</i> (L.)	Dimorphic	56
<i>Carabus purpurascens</i> (Fabr.)	Apterous	49
<i>Bembidion lunulatum</i> (Fourcroy)	Dimorphic	47
<i>Bembidion obtusum</i> (Serville)	Dimorphic	45
<i>Notiophilus biguttatus</i> (Fabr.)	Dimorphic	38
<i>Anisodactylus binotatus</i> (Fabr.)	Macropterous	38
<i>Calathus piceus</i> (Marsham)	Apterous	31
<i>Pterostichus vernalis</i> (Panzer)	Dimorphic	30
<i>Pterostichus strenuus</i> (Panzer)	Dimorphic	29
<i>Carabus nemoralis</i> (Müller)	Apterous	28
<i>Asaphidion stierlini</i> (Heyden)	Macropterous	25
<i>Stomis pumicatus</i> (Panzer)	Apterous	21
<i>Pterostichus versicolor</i> (Sturm)	Macropterous	20
<i>Bembidion biguttatum</i> (Fabr.)	Dimorphic	20
<i>Agonum obscurum</i> (Herbst)	Macropterous	20
<i>Microlestes maurus</i> (Sturm)	Macropterous	19
<i>Carabus granulatus</i> (L.)	Apterous	16
<i>Asaphidion flavipes</i> (L.)	Macropterous	15
<i>Badister bipustulatus</i> (Fabr.)	Macropterous	14
<i>Amara plebeja</i> (Gyllenhal)	Macropterous	12
<i>Notiophilus quadripunctatus</i> (Dejean)	Dimorphic	12
<i>Agonum muelleri</i> (Herbst)	Macropterous	12
<i>Agonum albipes</i> (Fabr.)	Macropterous	12
<i>Carabus intricatus</i> (L.)	Apterous	10
<i>Notiophilus palustris</i> (Duftschmid)	Dimorphic	9
<i>Calathus fuscipes</i> (Goeze)	-	9
<i>Bembidion mannerheimi</i> (Sahlberg)	Dimorphic	9
<i>Agonum nigrum</i> (Dejean)	Macropterous	8
<i>Panagaeus bipustulatus</i> (Fabr.)	-	7
<i>Nebria salina</i> (Fairmaire & Laboulbene)	Macropterous	7
<i>Amara aenea</i> (De Geer)	Macropterous	6
<i>Amara ovata</i> (Fabricius)	Macropterous	6
<i>Harpalus tardus</i> (Panzer)	Macropterous	6
<i>Harpalus punctatulus</i> (Duftschmid)	Macropterous	6
<i>Diachromus germanus</i> (L.)	Macropterous	6
<i>Agonum assimile</i> (Paykull)	Macropterous	6

Appendix 2.B (continued)

Name	Wing morphology	Total
<i>Stenolophus skrimshiranus</i> (Stephens)	Macropterous	5
<i>Paraphonus maculicornis</i> (Duftschmid)	Macropterous	5
<i>Microlestes minutulus</i> (Goeze)	Macropterous	5
<i>Leistus fulvibarbis</i> (Dejean)	Apterous	5
<i>Leistus ferrugineus</i> (L.)	Apterous	5
<i>Harpalus aeneus</i> (Fabr.)	Macropterous	5
<i>Asaphidion curtum</i> (Heyden)	Macropterous	5
<i>Acupalpus meridianus</i> (L.)	Apterous	5
<i>Pterostichus nigrita</i> (Paykull)	Dimorphic	4
<i>Pterostichus anthracinus</i> (Panzer)	Macropterous	4
<i>Drypta dentata</i> (Rossi)	-	4
<i>Badister unipustulatus</i> (Bonelli)	Macropterous	4
<i>Agonum viduum</i> (Panzer)	Macropterous	4
<i>Pterostichus niger</i> (Schaller)	Dimorphic	3
<i>Amara communis</i> (Panzer)	Macropterous	2
<i>Stenolophus teutonus</i> (Schränk)	Macropterous	2
<i>Oodes helopoïdes</i> (Fabr.)	-	2
<i>Harpalus rubripes</i> (Duftschmid)	Macropterous	2
<i>Dyschirius globosus</i> (Herbst)	Apterous	2
<i>Clivina fossor</i> (L.)	Dimorphic	2
<i>Carabus auratus</i> (L.)	Apterous	2
<i>Badister peltatus</i> (Panzer)	Macropterous	2
<i>Acupalpus dubius</i> (Schilsky)	Apterous	2
<i>Trechus rubens</i> (Fabr.)	Macropterous	1
<i>Trechus obtusus</i> (Erichson)	Macropterous	1
<i>Notiophilus rufipes</i> (Curtis)	Dimorphic	1
<i>Metabletus obscuroguttatus</i> (Duftschmid)	Macropterous	1
<i>Dromius linearis</i> (Olivier)	-	1
<i>Demetrias atricapillus</i> (L.)	-	1
<i>Calathus luctuosus</i> (Latreille)	Apterous	1
<i>Bradycellus harpalinus</i> (Serville)	-	1
<i>Bembidion harpaloides</i> (Serville)	Dimorphic	1
<i>Bembidion dentellum</i> (Thunberg)	Dimorphic	1
<i>Agonum livens</i> (Gyllenhal)	Macropterous	1
Total number of individuals		3045
Total number of species		84

**CHAPITRE 3 : DYNAMICS OF CARABID BEETLE COMMUNITIES
(COLEOPTERA : CARABIDAE) IN RESPONSE TO FIELD MARGIN
MANAGEMENT – AN EXPERIMENTAL ASSESSMENT**

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Résumé

Dans les paysages bocagers, les haies jouent un rôle important pour le maintien de la biodiversité. Les bordures des haies sont gérées par les agriculteurs en fonction de l'utilisation du sol adjacente. Cela se traduit par une grande variabilité spatiale et temporelle des modes de gestion à l'échelle du paysage. Dans cet article, nous avons étudié les effets ponctuels de deux pratiques d'entretien, la pulvérisation d'herbicides et la fauche, sur les communautés de carabiques au moyen d'une approche expérimentale. La réponse des espèces de carabes aux perturbations est liée à certains traits d'histoire de vie : la taille et la capacité de dispersion. Les espèces de champs, de petite taille et mobiles, sont dominantes dans les zones fauchées ou pulvérisées aux herbicides après les traitements. Ces changements sont liés aux modifications du couvert végétal et des conditions microclimatiques. Les traitements entraînent une augmentation immédiate des abondances des petites espèces qui se poursuit jusqu'à la fin de l'expérimentation, du fait de la colonisation des zones traitées par certaines espèces et d'une augmentation de l'activité des individus. Les espèces de carabes qui présentent des traits d'histoire de vie contrastés présentent différentes dynamiques après les traitements. L'abondance des espèces de taille moyenne diminue immédiatement dans les zones fauchées et augmente simultanément dans les zones adjacentes non traitées ou pulvérisées aux herbicides ; au contraire, l'abondance des petites espèces augmente progressivement dans les zones fauchées et pulvérisées aux herbicides. Nous avons posé l'hypothèse que la dynamique à court terme de la communauté est liée aux effets dans le temps des traitements sur la végétation. Cependant, les assemblages spécifiques de carabiques retournent à leur état initial un mois après les traitements, suggérant une forte résilience de la communauté, au moins à l'échelle de la placette expérimentale.

1. Introduction

Agricultural intensification has induced a major decline of biodiversity, as a consequence of habitat loss and fragmentation (Wilcove *et al.*, 1986; Jongman, 2000) and of changes in farming practices (Stoate *et al.*, 2001). Invertebrates, including beneficial arthropods, have been especially reduced under increasing use of pesticides and intensification of other practices such as grazing or fertilisation (Wilson *et al.*, 1999; Morris, 2000). Among them, carabid beetles have been extensively studied (Thiele, 1977; Kromp, 1999) and they play a potential role in crop pest control (Lang *et al.*, 1999). At the local scale, the distribution of carabid species depends on the density of vegetation cover (Hassall *et al.*, 1992; Jukes *et al.*, 2001), forest species being favoured by a dense vegetation cover (Burel and Baudry, 1989).

In agricultural landscapes, hedgerows support a wide diversity of carabid beetles (Thomas and Marshall, 1999). They act as corridor for forest species (Burel and Baudry, 1989), and temporary refuges for other species (Sotherton, 1984). Hedgerow margins are managed according to the adjacent land-use (Baudry and Jouin, 2003). They are currently sprayed with herbicides or mown by farmers to limit weed invasions in adjacent crops, herbicides being increasingly used to allow a gain of time. The consequent reduction of trees and shrubs decreases resources quality (Baudry *et al.*, 1998; Baudry *et al.*, 2000a). Few studies have considered the effects of hedgerow margin management on carabid assemblages (Canters and Tamis, 1999), but their impacts in fields have been well documented (Kromp, 1999). Herbicide spraying and mowing constitute strong disturbances for carabid beetles. At the short term, they alter resources and shelter by suppressing the vegetation cover. At a longer-term scale, they homogenise flora (Miller *et al.*, 1999; Le Coeur *et al.*, 2002) associated to loss of microhabitat diversity and changes in abiotic conditions (Clapperton *et al.*, 2002). The response of carabid communities to environmental stress depends on species tolerance to disturbance, in relation with body size and dispersal ability of species (Blake *et al.*, 1994; Ribera *et al.*, 2001). Large-sized and wingless species are the more affected by disturbances compared to smaller ones, more mobile.

Most of these studies have focused on carabid community dynamics in response to single practices. Hedgerow networks are characterised by high spatial and temporal variability of management regimes of margins, depending of individual decisions of farmers (Baudry *et al.*, 2000a). Thus, it is necessary to investigate the short-term effects of the different management practices of hedgerow margins to understand the driving mechanisms of community dynamics in hedgerow networks over the long term. Several questions arise: does the dynamic of carabid assemblages depend on the temporal effects of farming practices on resources? How do species with contrasted ecological requirements respond on the short term to the different management practices? Does the resilience of communities, defined as the time by which they return to initial or at least equilibrium state after disturbance (Bengtsson, 2002), differ according to species and farming practices?

This study aimed at investigating the short-term effects of herbicide spraying and mowing of hedgerow margins on carabid community with a field experiment. Two hypotheses were tested:

(i) Herbicide spraying and mowing modify carabid assemblages depending on the response of the different species to changes in vegetation cover: large and few mobile species intolerant to disturbance are especially affected.

(ii) Community dynamics after treatment differ between the two practices in relation with their effects on vegetation: mowing induces an immediate response of community due to its immediate effect on vegetation cover, in contrary to herbicide spraying.

2. Materials and Methods

2.1. Study area

The study was conducted in a hedgerow network landscape (bocage) in Brittany, Western France. This area is a long-term research ecological research site (Burel *et al.*, 1998; Baudry *et al.*, 2000b). Agriculture is characterised by dairy production. The landscape is an arable mosaic of small permanent or temporary grasslands and larger cereal fields (wheat and corn), with a dense hedgerow network (265 meters per ha). The experimentation was conducted on a hedgerow margin chosen according to two criteria: it was enough long to perform experiment (192 m) and its vegetation structure was diversified to allow the presence of diverse carabid species. The hedgerow was bordered by wheat at one side and by maize at the other side. Experiment was conducted on the margin adjacent to maize. Both crops were run under conventional management. Hedgerow vegetation was characterised by dense herbaceous (up to 0.5 m) and ligneous layers (up to 1.5 m) with some trees.

2.2. Experimental design

The margin was divided into nine plots, each 1m wide. Four plots (24m each) with treatments were first delimited within the margin. Three untreated plots, i.e. buffer plots (24m each), were then defined between treated plots to limit movements of carabid beetles between treated areas (figure 3.1). Two plots (14m each) were left untreated at the extremities of the margin to avoid border effects. Each of the four treated plots was subdivided in three strips, each 8m long (figure 3.1): the first strip was sprayed with herbicides, the second one was mechanically mown and the third one was left untreated. In each buffer plot, we defined a median strip of 8m long that was considered as reference strip in experiment. Treatments were applied on May 16th 2002 in concordance to the techniques adopted by the farmer in charge of field margin management. Chemical treatments were a mixture of triclopyr (1.3 kg/ha) and 2,4 D (1.2 kg/ha) for ligneous vegetation, and glyphosate (1.8 kg/ha) for herbaceous vegetation. Mowing was realised mechanically, ligneous and herbaceous vegetation being cut at a height of 20 cm. Vegetation residuals were left on the strips after mowing.

2.3. Carabid sampling

Carabid beetles were sampled using pitfall traps containing a formalin solution (5%). In each strip, three traps were installed 2m apart at the bottom of the margin, i.e. 45 traps on the whole field margin (figure 3.1). Traps were opened continuously from April 18th to June 13th 2002. They were emptied once a week during the month before treatments, i.e. four sampling periods. During the ten days following treatments, traps were emptied every two days, i.e. five sampling periods, to follow more precisely the dynamics of carabid beetle community after disturbance. Finally, traps were emptied once a week for the two last weeks, i.e. two sampling period, until June 13th. This led to a total of eleven sampling periods: four

before treatments and seven after treatments. Species were identified according to Jeannel (1941; 1942) and Trautner and Geigenmuller (1987).

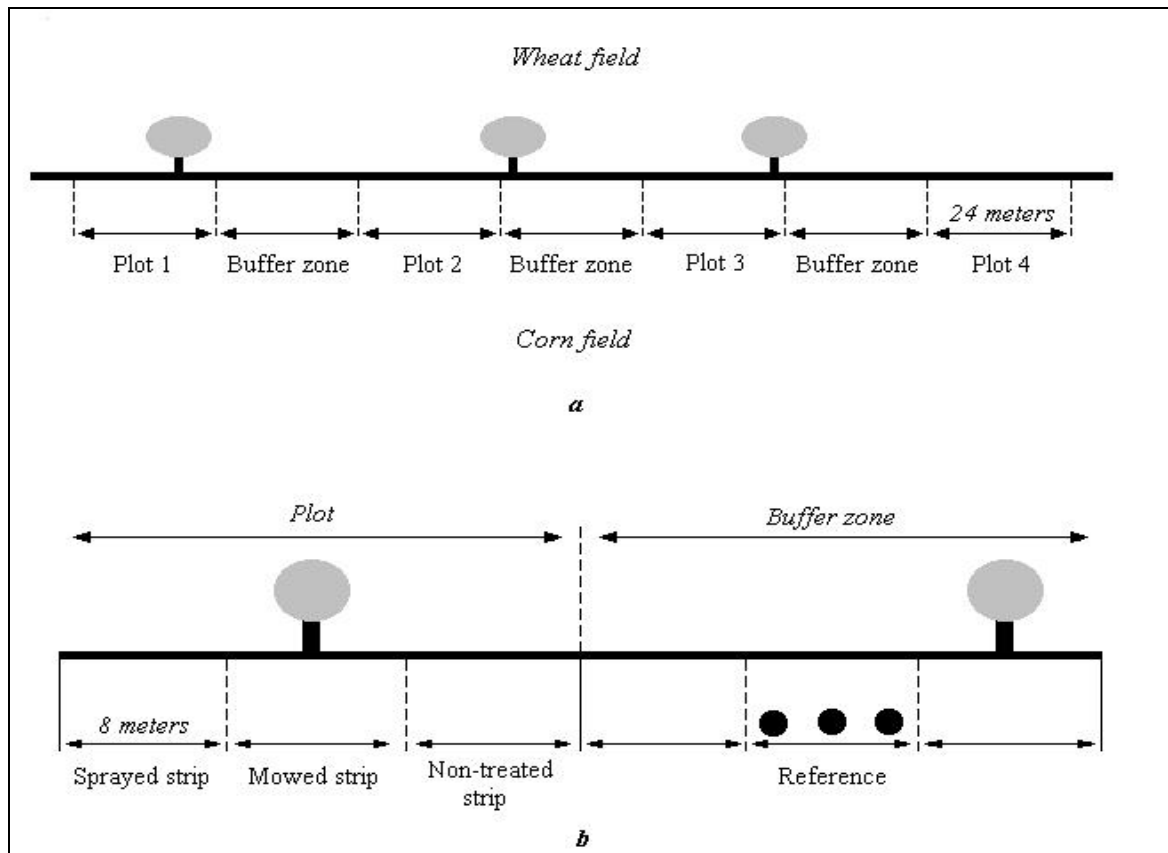


Figure 3.1. Plots delimitation (a) and strip assignment (b) along the hedgerow. Traps, full black circles, are only figured in the reference strip.

2.4. Vegetation and meteorological variables

In each strip, the vegetation structure on field margin was described by the dominant height of herbaceous and ligneous layers (cm). Meteorological conditions (cumulative rainfall (mm), cumulative sunlight time (minutes), and average temperature (Celsius degrees)) were recorded during each sampling period as they influence carabid beetle activity (e.g. for rain see Thomas *et al.*, 1998).

2.5. Statistical analyses

Canonical Correspondence Analysis (CCA) was used to relate species data to environmental variables (CANOCO, Ter Braak and Smilauer, 1998). Relationships between species data and environmental variables are often non-linear. CCA analysis is unimodal and constrained ordination method that is especially appropriate in this context (Ter Braak, 1986). Species data were abundances of species per strip and sampling period (62 species x 15 strips x 11 sampling period). Species occurring at less than 2 % were considered as rare and were not included in analyses. Environmental variables were: plot/replicate identifier before

treatment, time in the experiment (before/after treatment), type of treatment, vegetation structure, rainfall, sunlight intensity and average temperature. Cumulative temperature since the beginning of experiment and the duration of sampling periods were used as covariables in analysis. Variables and covariables used in analysis are listed in table 3.1. Significance of analyses was tested using Monte-Carlo simulations module of CANOCO.

Table 3.1. Description of environmental variables and their use in Canonical Correspondence Analysis.

Variable name	Variable type	Use
Treatment (herbicide, mowing, no treatment, reference)	Qualitative	Variable
Replicate identifier (# 1, 2, 3, 4, buffer zone)	Qualitative	Variable
Before treatments (yes / no)	Qualitative	Variable
Sampling period length (number of days)	Quantitative	Covariable
Height of the shrub layer (cm)	Quantitative	Variable
Height of the herbaceous layer (cm)	Quantitative	Variable
Average temperature (°C)	Quantitative	Variable
Cumulative temperature	Quantitative	Covariable
Sunshine (hours)	Quantitative	Variable
Rainfalls (mm)	Quantitative	Variable

We performed cluster analysis on species coordinates in the first factorial plane of CCA analysis to determinate species groups in term of response to environmental variables. Species composition of each group was then described with specific life traits based on size (body length) and dispersal ability (wing morphology) of species according to Ribera *et al.* (1999a; 1999b). Body size of species was described by four modalities: very small species (<5mm), small species (5-10mm), medium species (10-15mm) and large species (>15mm). Wing morphology of species was characterised by three modalities: apterous or brachypterous species, dimorphic species and macropterous species. When data about species traits was not available, we assumed that species had the same attributes that the most closely related species (Ribera *et al.*, 2001).

Temporal variation in carabid assemblages between before and after treatments was tested by comparing activity-densities of carabid groups according to life-traits before treatments (four weeks pooled) and after treatments (four weeks pooled) by the mean of Mann-Whitney tests. The resilience at the end of the experiment was tested by comparing carabid activity-densities in mowed, sprayed and untreated strips at the fourth sampling and last sampling period with Wilcoxon test.

3. Results

3.1. Impact on community structure

2064 individuals corresponding to 62 species were trapped. The list of trapped species is given in Appendix 3.

The canonical analysis was statistically significant (Monte-Carlo permutations, first axis: $P < 0.05$, all axes: $P = 0.01$). Environmental data explained 10% of the total inertia. Table 3.2 lists correlations of variables with the two first environmental axes as well as their part in explaining total inertia.

On the first CCA axis (F1), undisturbed strips (untreated and reference ones) and strips before treatments (before treatment variable, buffer zones and replicates # 2 to 4) were opposed to disturbed strips, either mowed or sprayed with herbicides, and to replicate # 1 before treatment (figure 3.2). Dominant heights of herbaceous and ligneous layers, as well as rainfall variables were opposed to disturbed strips, while average temperature and sunshine intensity variables were associated with disturbed strips. This suggests that this axis was related with a gradient of disturbance, but also vegetation openness and changes in climatic conditions. The different distribution of experimental plots in factorial plane also suggested some variability in vegetation structure between replicates. Along the second CCA axis (F2), sprayed strips were opposed to mowed ones, suggesting that these practices had different effects on community (figure 3.2).

Table 3.2. Cumulative percentage of explained inertia and correlation of variables with the two first axes of the Canonical Correspondence Analysis.

Variable	% of explained inertia	Correlation with axis F1	Correlation with axis F2
Mowing	1.36	-0.59	0.64
Height of the herbaceous layer	2.61	0.54	0.55
Plot # 1	3.43	-0.39	-0.38
Before treatments	4.28	0.38	-0.09
Herbicide	4.82	-0.16	-0.52
Plot # 4	5.57	0.16	0.56
Height of the shrub layer	6.29	0.35	-0.33
No treatment	6.79	0.54	0.05
Reference	7.43	0.09	-0.14
Buffer zones	7.43	0.03	-0.41
Plot # 2	8.03	0.11	0.22
Plot # 3	8.03	0.13	0.03
Sunshine	8.63	-0.29	-0.05
Average temperature	9.32	-0.18	0.03
Rainfall	9.96	0.29	0.08

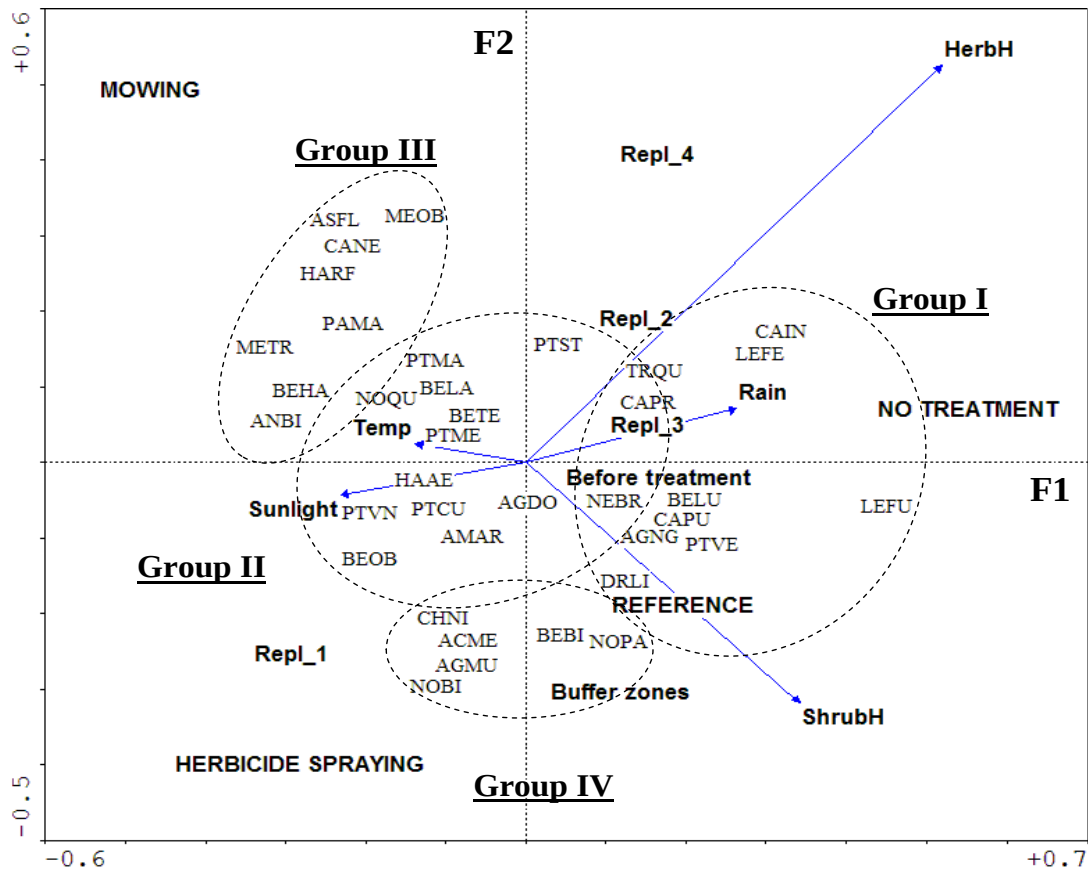


Figure 3.2. Projection on the first canonical plane (F1 x F2) of species data, management and other environmental variables (Repl_1, 2, 3, 4: replicate number; ShrubH and HerbH: height of shrub and herb layers; temp: average temperature; sunlight; rain: rainfalls) of the Canonical Correspondence Analysis. The four sets of species obtained with Cluster Analysis are also represented (species names abbreviated according to Appendix 3).

Cluster analysis performed on species coordinates on the first factorial plane led to four sets of species (figure 3.2). The composition of each group according to body size and wing morphology of species is indicated in table 3.3. The first group (I) was characterised by high proportions of very small and small species, like *Trechus quadristriatus* (Schränk) [TRQU], but also of large, apterous species, e.g. *Carabus intricatus* (L.) [CAIN], and *C. problematicus* (Herbst) [CAPR], which are forest species defined as intolerant to disturbance. This group was associated to undisturbed strips, tall herbaceous and shrubby vegetation, and wet climatic conditions. The second group (II) was dominated by a mixture of very small, dimorphic or macropterous species such as *Bembidion* species and of medium species like *Nebria brevicollis* (Fabr.) [NEBR], associated to open habitats. These species were abundant in all strips regardless of treatment. The other groups were associated to treated strips. The third group (III), associated to mowed strips, was composed of very small and macropterous species (e.g. *Asaphidion flavipes* L. [ASFL]), some medium-sized (*Harpalus rufipes* (De Geer) [HARF]) or large species (*Carabus nemoralis* (Mueller) [CANE]). The last group (IV), dominated by small, very small, dimorphic or macropterous species found to disturbed and open habitats, was associated to strips sprayed with herbicides.

Table 3.3. The four groups of species produced by the CCA analysis showing the number of species in each group (n) and the proportion of species showing species attributes of body size and wing morphology.

Traits	Group 1 (n=10)	Group 2 (n=13)	Group 3 (n=8)	Group 4 (n=6)
<i>Size</i>				
Very small (<5mm)	51	8	34	31
Small (5-10mm)	31	20	31	60
Medium (10-15mm)	5	73	26	10
Large (>15mm)	14	0	8	0
<i>Wing morphology</i>				
Apterous	41	1	8	13
Dimorphic	5	28	23	59
Macropterous	54	72	69	29

3.2. Dynamics and recovery of community

Before grouping data over replicates, between-replicates equivalencies in carabid abundance before and after treatments were tested using Kruskal-Wallis tests. Abundances in reference replicates were equivalent before ($H=1.77$, $P=0.413$) or after treatments ($H=0.904$, $P=0.636$). Abundances in sprayed strips, mowed strips and untreated strips did not differ between replicates before (mowed: $H=5.313$, $P=0.150$; sprayed: $H=7.553$, $P=0.056$; untreated: $H=3.176$, $P=0.365$) and after treatments (mowed: $H=3$, $P=0.392$; sprayed: $H=6.87$, $P=0.076$; untreated: $H=2.35$, $P=0.503$).

Table 3.4 indicates significance (probability values) of Mann-Whitney tests comparing activity-densities of carabid beetles before and after treatments, for the four size groups and the three groups based on wing morphology. Treatments had a significant effect on activity-density of very small species (<5 mm) in mowed and sprayed strips, and on activity-density of medium species (10-15mm) in mowed strips (table 3.4). Activity-density of small (5-10mm) and large carabid species (>15mm) did not vary significantly during the experiment (table 3.4). Activity-densities of macropterous and dimorphic species differed significantly after treatments in mowed and sprayed strips, whereas apterous species were not significantly affected (table 3.4).

Figure 3.3 illustrates the variation in mean activity-density of carabid species between before and after treatment for very small, medium, dimorphic and macropterous species. Figure 3.4 illustrates the variation in time in the activity-density of very small, medium, dimorphic and macropterous species. Activity-densities in mowed, sprayed and untreated strips were subtracted to those in reference strips to overcome variations inherent to species phenology, activity and environmental conditions. Very small and dimorphic species were more abundant in mowed and sprayed strips after treatments; activity-densities of these species increased from the day following treatment to the end of the experiment (figures 3.3 and 3.4). Medium and macropterous species declined in mowed strips immediately after treatment, and increased simultaneously in sprayed and untreated strips; activity-densities of medium and macropterous species increased thereafter in treated strips (figures 3.3 and 3.4).

Table 3.4. Significance or Mann-Whitney test (probability values, *P*) comparing carabid activity-densities (species groups according to body-length and wing morphology) in sprayed, mown, untreated and reference strips between before and after treatments; significant differences in bold.

Traits	Mowing		Herbicide spraying		No treatment		Reference	
	U Stat.	<i>P</i>	U Stat.	<i>P</i>	U Stat.	<i>P</i>	U Stat.	<i>P</i>
<i>Body size</i>								
<5mm	3.5	0.047	2.0	0.023	16.0	0.704	11.0	0.571
5-10mm	13.0	0.850	16.0	0.705	20.0	0.256	16.0	0.705
10-15mm	25.0	0.038	22.0	0.129	14.0	1.000	21.0	0.185
>15mm	13.0	0.843	5.0	0.085	6.5	0.152	6.0	0.080
<i>Wing morphology</i>								
Apterous	20.0	0.252	8.0	0.256	4.0	0.058	8.0	0.246
Dimorphic	2.0	0.023	2.5	0.029	15.0	0.849	9.5	0.393
Macropterous	25.0	0.038	26.0	0.023	23.0	0.089	20.0	0.257

Comparisons of the distribution of species in the different strips between the fourth sampling date (just before treatment) and the last sampling date did not reveal significant differences of activity-densities of very small (Wilcoxon test, $Z=-0.365$; $P=0.715$), small (Wilcoxon test, $Z=0.73$, $P=0.465$), medium (Wilcoxon test, $Z=0$, $P=1.000$) and large species (Wilcoxon test, $Z=0.535$, $P=0.593$). Activity-densities of apterous, dimorphic and macropterous species just before treatment and at the end of the experiment were also similar (Wilcoxon test, $Z=-0.365$, $P=0.715$; $Z=1.826$, $P=0.068$; $Z=-1.826$, $P=0.068$ respectively).

4. Discussion

4.1. Functional response of carabid beetle community to disturbances

Changes in carabid assemblages induced by herbicide spraying and mowing on field margin depended on species tolerance to disturbance, in relation with body-size and dispersal ability of species.

After treatments, disturbed areas were dominated by small and mobile species such as *Bembidion* species, usually found in open and dry habitats (Turin and Heijerman, 1988; Blake *et al.*, 1994; Eyre, 1994). In contrast, canonical analysis showed that large and low mobile species were more found in undisturbed strips. They were mainly *Carabus* species, favoured before disturbance by high vegetation and wet conditions according to their ecological requirements (Thiele, 1977; Eyre, 1994). Thiele (1977) and Greenslade (1965) suggest that microclimate is the main factor determining the distribution of carabid species. Differences in species assemblages between treated and untreated areas might be thus related to changes in microclimatic conditions induced by vegetation opening.

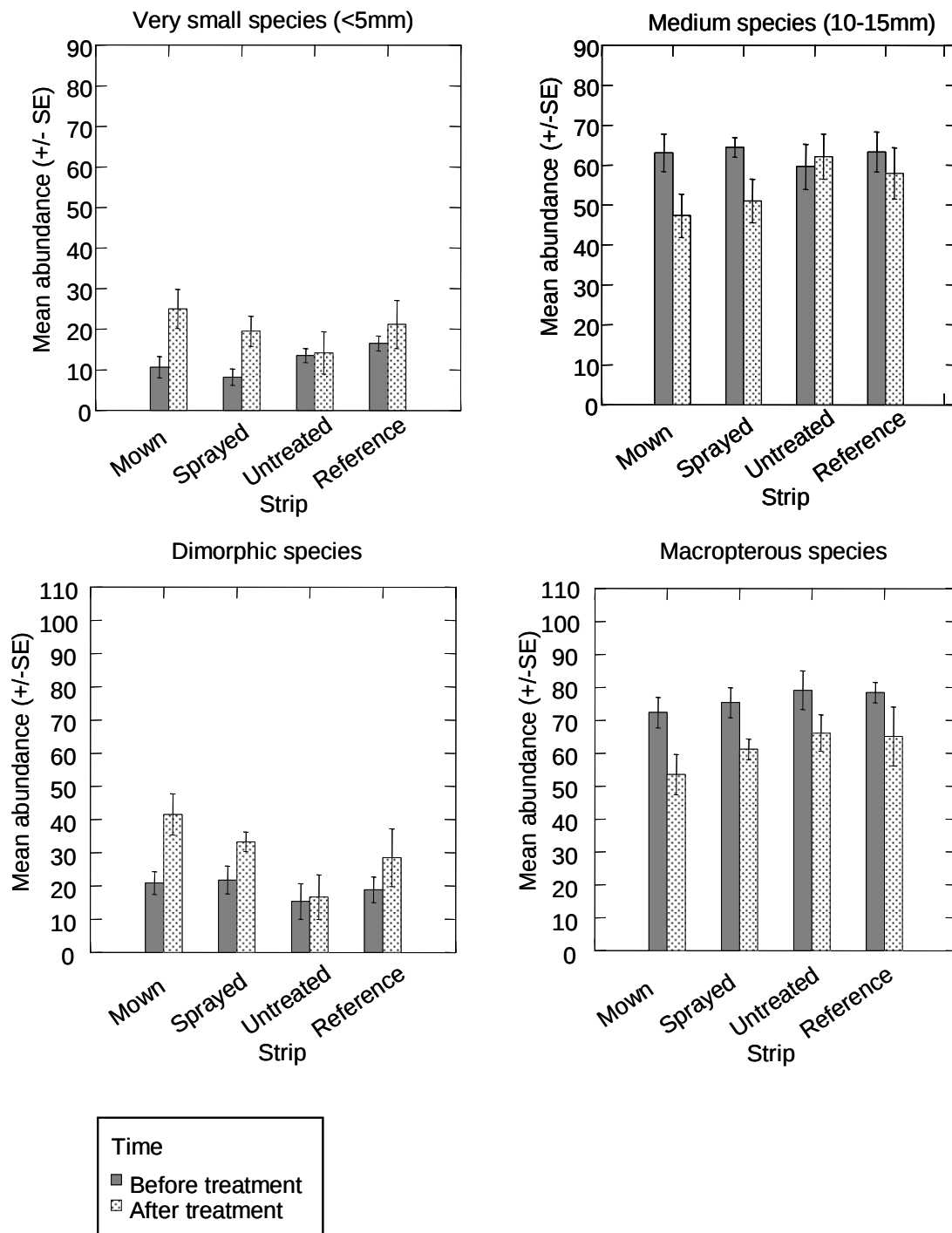


Figure 3.3. Mean activity-density ($\pm$ SE) of very small (<5mm), medium (10-15mm), dimorphic and macropterous species in mown, sprayed, untreated and reference strips before and after treatments.

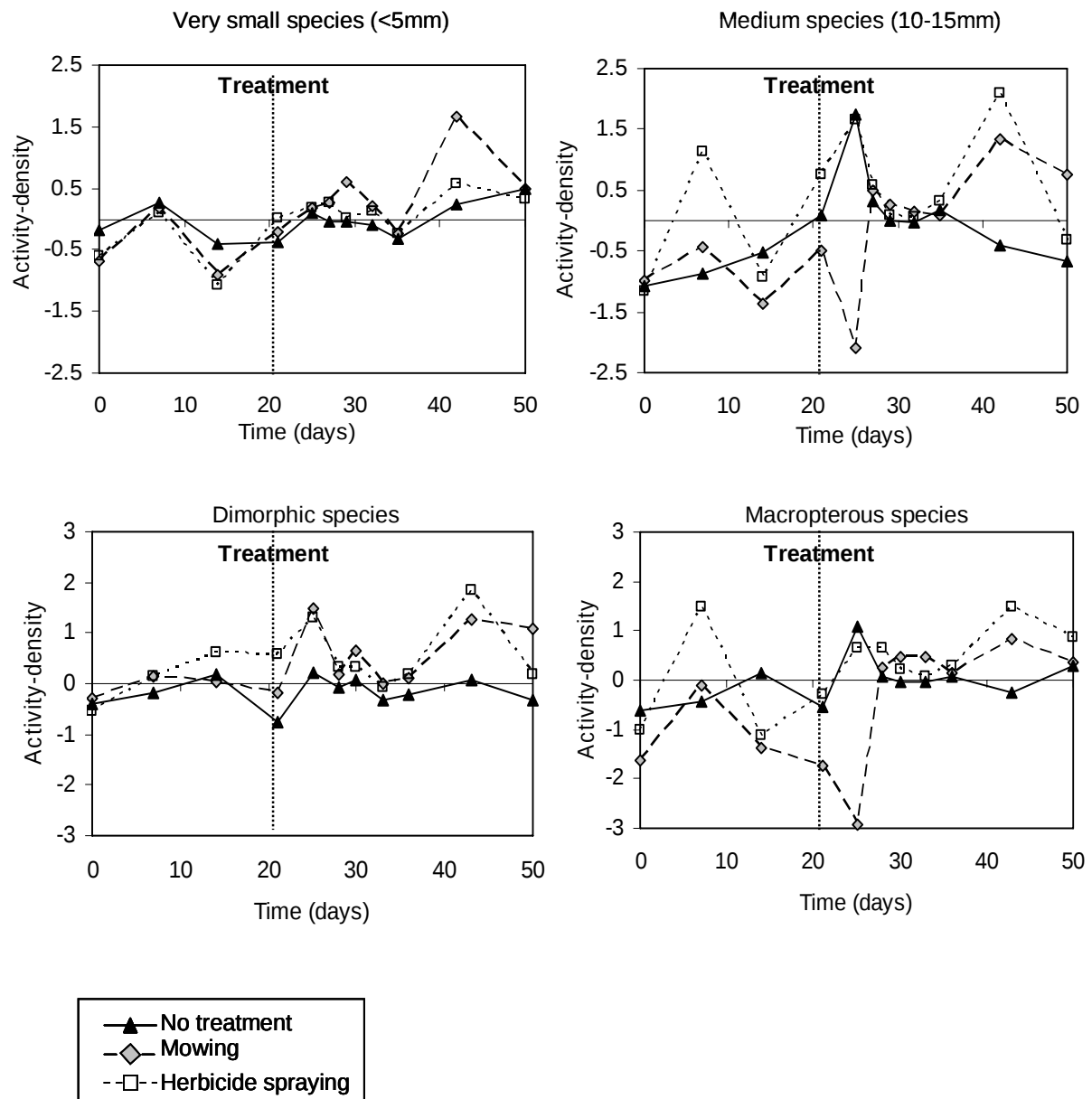


Figure 3.4. Temporal variation in the activity-density of very-small species (<5mm), medium (10-15mm), dimorphic and macropterous species in mown, sprayed, and untreated strips; activity-densities are expressed as the difference compared with reference strips to overcome variation due to species phenology, activity or environmental conditions.

Tolerance to disturbance is related with body-size of individuals and to dispersal ability of species (Ribera *et al.*, 2001; Cole *et al.*, 2002). Unstable habitats are well used by small and mobile species with short life-cycle, whereas large-size, apterous species are the most affected by disturbance as a consequence of their long life cycle and their high need of stable resources (Blake *et al.*, 1994). Our results showed that very small species with high dispersal ability, i.e. with developed wings (macropterous or dimorphic), were dominant in disturbed areas. This predominance of field species has to be related with the history of field margin and adjacent field, in term of management and land-use. During the last years, the adjacent field was used the more often for crops (maize and other cereals), and studied field margin was regularly sprayed with herbicides. This management practice may have selected over years field species.

Though a large set of species was common to sprayed and mowed areas, different species were enhanced depending on the type of treatment. Sprayed strips were especially rich in very small species, while some larger species, such as *Carabus nemoralis*, persisted in mowed areas. This last result is surprising as *Carabus* species are defined as highly affected by disturbances (Rushton *et al.*, 1989; Eyre, 1994; Cole *et al.*, 2002). They might be more tolerant to some kind of disturbance. The absence of *Carabus* species in herbicide spraying might be linked to toxic or repulsive effects of chemical products (Boiteau, 1984; Brust, 1990).

Correlations between functional life-traits of species (size and dispersal ability) and type of response to habitat disturbance allows proposing a classification of species based more on functional traits than taxonomy. Such an approach is valuable as it enables to understand the impacts of agriculture in terms of sensitivity of community rather than of key indicator species (Cole *et al.*, 2002).

4.2. Temporal variability of community

Our results show that species with different ecological/life traits exhibited different dynamics after disturbances. Very small and dimorphic carabid species were enhanced in sprayed and mowed strips after treatments until the end of the experiment. We can hypothesise that these species have colonised disturbed areas from the adjacent field, as a consequence of vegetation opening. Otherwise, disturbance might have induced an increase in the activity of these species, which is related with their satiety state (Wheater, 1991; Fournier and Loreau, 2001). Chiverton and Sotherton (1991) found that individuals in plots with herbicides were hungrier due to low levels of preys, resulting in more activity to find food. The reduction of the vegetation cover would also result in easier movements of individuals and accentuate this pattern (Greenslade, 1964). On the contrary, mowing led to an immediate decline of medium and macropterous species, associated with a simultaneous increase in adjacent sprayed and untreated strips; after a few days, their densities increased in disturbed plots, either mown or sprayed. This can be related with the temporal effects of the two treatments on vegetation: immediate for mowing, delayed for herbicides. Medium species might have responded to the immediate suppression of vegetation by leaving mowed strips toward adjacent untreated or sprayed ones. Previous studies have shown that herbicide spraying cause the departure of large species and the colonization of disturbed areas by field species (Pollard, 1974b; Brust, 1990). Here, activity-densities of large, apterous species did not varied significantly in disturbed strips after treatments, even they were more associated to untreated strips as shown by canonical analysis.

Statistical tests did not reveal any significant differences between before treatment and the last sampling period in activity-densities of carabid species. This suggests that community recovered its initial state one month after treatments, at least at the scale of the experimental plot. This could be determined by the return of resources to their initial state, i.e. by vegetation growth. According to the observed relationship between the community dynamics after disturbance and dispersal ability of carabid species, resilience of species assemblages might depend on the ability of species to quit or colonise disturbed habitats. Bengtsson (2002) noticed that resilience of arthropod forest community after clear-cutting can last several years, showing long oscillations of species abundances and proportions. In the present study, the resilience of carabid community is probably linked to the restricted size of treated areas (Duffield and Aebischer, 1994). This poses the question of how carabid community respond on the short-term to practices conducted on the whole habitat, in terms of abundance or activity fluctuations but also of changes in spatial distribution of species. Further studies should be conducted to determine the role of adjacent structures (crop fields, woodlands, hedgerows) in the recolonisation of disturbed areas.

4.3. Experimental design

The different positions of replicate plots on the factorial plane show that there were evident variations of species assemblage within field margin in relation with heterogeneity of vegetation quality and microclimatic conditions. The results of studies conducted at the local scale might thus be biased depending on where traps are located. The study also reveals how numbers of individuals can fluctuate within field margins and the consequent difficulty to assess the real effects of farming practices at local scale. This is certainly accentuated by the phenology of species and variations in weather conditions. Experiments with replicate plot approach allow overcoming the above problems and are often used for testing impacts of farming practices such as herbicides or insecticide applications (Asteraki *et al.*, 1992; Holland and Reynolds, In Press). However, significant results may be difficult to identify if species are present in low numbers within some of the replicates. This was illustrated in our study, where large species did not indicated significant effect of treatment. Movements of individuals between plots may also confound the interpretation of results. The plot size also biases results of replicate plot approaches, as the duration of the impact of treatments is dependant on the size of the treated area (Duffield and Aebischer, 1994): reinvasion of treated plots by species is faster in smaller plots. However, replicate plot experiments remain reasonable approaches to understand interactions between community dynamics and environmental stress as field scale evaluations of farming practices required important sampling effort.

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Appendix 3. Full names, life-traits (body-length and wing morphology), abbreviation codes and number of carabid beetle species collected in experimental plots.

Species name	Body lenght	Wing morphology	Code	Total
<i>Nebria brevicollis</i> (Fabr.)	10-15mm	Macropterous	NEBR	809
<i>Pterostichus cupreus</i> (L.)	10-15mm	Macropterous	PTCU	259
<i>Bembidion tetracolum</i> (Say)	5-10mm	Dimorphic	BETE	169
<i>Pterostichus melanarius</i> (Illiger)	10-15mm	Dimorphic	PTME	140
<i>Bembidion lampros</i> (Herbst)	<5mm	Dimorphic	BELA	97
<i>Trechus quadristriatus</i> (Schrank)	<5mm	Macropterous	TRQU	79
<i>Agonum dorsale</i> (Pontoppidan)	5-10mm	Macropterous	AGDO	73
<i>Amara</i> spp.	5-10mm	Macropterous	AMAR	58
<i>Leistus ferrugineus</i> (L.)	5-10mm	Apterous	LEFE	44
<i>Bembidion obtusum</i> (Serville)	<5mm	Dimorphic	BEOB	31
<i>Pterostichus vernalis</i> (Panzer)	5-10mm	Dimorphic	PTVN	24
<i>Harpalus aeneus</i> (Fabr.)	5-10mm	Macropterous	HAAE	18
<i>Agonum muelleri</i> (Herbst)	5-10mm	Macropterous	AGMU	16
<i>Notiophilus palustris</i> (Duftschmid)	<5mm	Dimorphic	NOPA	15
<i>Bembidion harpaloides</i> (Serville)	5-10mm	Dimorphic	BEHA	14
<i>Carabus problematicus</i> (Herbst)	>15mm	Apterous	CAPR	14
<i>Dromius linearis</i> (Olivier)	<5mm	Not available	DRLI	13
<i>Agonum nigrum</i> (Dejean)	5-10mm	Macropterous	AGNG	12
<i>Bembidion biguttatus</i> (Fabr.)	<5mm	Dimorphic	BEBI	12
<i>Asaphidion flavipes</i> (L.)	<5mm	Macropterous	ASFL	10
<i>Pterostichus versicolor</i> (Sturm)	10-15mm	Macropterous	PTVE	10
<i>Bembidion lunatulus</i> (Fourcroy)	<5mm	Dimorphic	BELU	9
<i>Harpalus rufipes</i> (De Geer)	10-15mm	Macropterous	HARF	9
<i>Pterostichus madidus</i> (Fabr.)	10-15mm	Apterous	PTMA	9
<i>Carabus purpureus</i> (L.)	>15mm	Apterous	CAPU	8
<i>Notiophilus quadripunctatus</i> (Dejean)	<5mm	Dimorphic	NOQU	8
<i>Acupalpus meridianus</i> (L.)	<5mm	Apterous	ACME	7
<i>Anisodactylus binotatus</i> (Fabr.)	10-15mm	Macropterous	ANBI	7
<i>Pterostichus strenuus</i> (Panzer)	5-10mm	Dimorphic	PTST	7
<i>Chlaenius nigricornis</i> (Fabr.)	10-15mm	Not available	CHNI	6
<i>Metabletus obscuroguttatus</i> (Duftschmid)	<5mm	Macropterous	MEOB	6
<i>Notiophilus biguttatus</i> (Fabr.)	<5mm	Dimorphic	NOBI	6
<i>Carabus intricatus</i> (L.)	>15mm	Apterous	CAIN	5
<i>Carabus nemoralis</i> (Mueller)	>15mm	Apterous	CANE	5
<i>Leistus fulvibarbis</i> (Dejean)	5-10mm	Apterous	LEFU	5
<i>Metabletus truncatellus</i> (L.)	<5mm	Macropterous	METR	5
<i>Paraphonus maculicornis</i> (Duftschmid)	5-10mm	Macropterous	PAMA	5
<i>Bembidion quadrimaculatum</i> (L.)	<5mm	Dimorphic	BEQU	4
<i>Brachynus sclopeta</i> (Fabr.)	5-10mm	Not available	BRSC	3
<i>Stomis pumicatus</i> (Panzer)	5-10mm	Apterous	STPU	3

Appendix 3. (continued)

Species name	Body-length	Wing morphology	Code	Total
<i>Abax parallelepipedus</i> (Piller & Mitterpacher)	>15mm	Apterous	ABPA	2
<i>Acupalpus luteatus</i> (Duftschmid)	<5mm	Apterous	ACLU	2
<i>Agonum lugens</i> (Duftschmid)	5-10mm	Macropterous	AGLU	2
<i>Agonum obscurum</i> (Herbst)	5-10mm	Macropterous	AGOB	2
<i>Badister bipustulatus</i> (Fabr.)	5-10mm	Macropterous	BABI	2
<i>Bembidion iricolor</i> (Bedel)	<5mm	Macropterous	BEIR	2
<i>Carabus auratus</i> (L.)	>15mm	Apterous	CAAU	2
<i>Demetrias atricapillus</i> (L.)	5-10mm	Not available	DEAT	2
<i>Agonum moestum</i> (Duftschmid)	5-10mm	Macropterous	AGMO	1
<i>Amblystomus niger</i> (Heer)	<5mm	Macropterous	AMNI	1
<i>Carabus granulatus</i> (L.)	>15mm	Apterous	CAGR	1
<i>Drypta dentata</i> (Rossi)	5-10mm	Not available	DRDE	1
<i>Eotachys bistriatus</i> (Duftschmid)	<5mm	Not available	EOBI	1
<i>Harpalus punctatulus</i> (Duftschmid)	5-10mm	Macropterous	HAPU	1
<i>Harpalus rufibarbis</i> (Fabr.)	5-10mm	Macropterous	HARU	1
<i>Harpalus tardus</i> (Panzer)	5-10mm	Macropterous	HATA	1
<i>Loricera pilicornis</i> (Fabr.)	5-10mm	Macropterous	LOPI	1
<i>Metabletus foveatus</i> (Fourcroy)	<5mm	Macropterous	MEFO	1
<i>Microlestes minutulus</i> (Goeze)	<5mm	Macropterous	MIMI	1
<i>Stenolophus skimshiranus</i> (Stephen)	5-10mm	Macropterous	STSK	1
<i>Synuchus nivalis</i> (Panzer)	5-10mm	Dimorphic	SYNI	1
<i>Trechus rubens</i> (Fabr.)	<5mm	Macropterous	TRRU	1
Total				2064

PARTIE II.
ACTIVITES AGRICOLES, FLUX D'INDIVIDUS ET DYNAMIQUE DES
POPULATIONS : LE CAS DES PAPILLONS RHOPALOCERES

INTRODUCTION

Les papillons rhopalocères ont été particulièrement touchés par l'intensification agricole. La fragmentation des habitats sous l'influence de l'intensification agricole et les changements des pratiques culturales ont été reconnus comme responsables de ce déclin (Pullin, 1995 ; Feber et Smith, 1995 ; Oates, 1995). De nombreux travaux ont été développés afin d'identifier les facteurs impliqués dans la dynamique des populations de papillons dans les paysages agricoles, en considérant plus particulièrement le rôle de la dispersion des individus dans la survie des populations (Dempster, 1989 ; Thomas, 1991a ; Thomas et Harrison, 1992 ; Wilson et Thomas, 2002). La majorité de ces travaux ont été réalisés sur des paysages dont la composition et la structure spatiale ne varient pas au cours du temps. Pour les espèces de papillons qui sont restreintes aux milieux enherbés tels que les bords de champs ou les prairies, la dynamique des zones enherbées sous l'effet de la fauche, du pâturage ou de la pulvérisation d'herbicides est susceptible d'avoir un effet important sur les mouvements d'individus et la dynamique des populations.

Dans cette partie, notre objectif a été **de tester les effets, à court et long terme, de la dynamique du paysage sous l'influence d'une pratique agricole, la fauche des prairies, sur le mouvement des individus, la distribution et la dynamique des populations de papillons**. Nous avons adopté dans cette partie une approche de modélisation complétée par des observations *in situ* du mouvement des papillons afin de pouvoir caractériser la dynamique des populations de papillons à plus ou moins long terme sous l'effet des pratiques agricoles. Nos objectifs étaient :

- de tester l'effet à court terme de la dynamique du paysage induite par une pratique ponctuelle sur les mouvements et la distribution du Myrtil (chapitre 4), au moyen d'une expérimentation dans deux sites de 1km² situés sur le site atelier de Pleine Fougères
- d'élaborer un modèle prédictif des flux d'individus et de la distribution spatiale des populations en fonction des caractéristiques du paysage (chapitre 5)
- de simuler, au moyen de ce modèle, l'évolution de la dynamique des populations à long terme sous l'effet de la dynamique du paysage induite par les pratiques agricoles (chapitre 6).

Dans les paragraphes suivants, nous définirons le type de mouvement sur lequel a porté notre travail et l'approche adoptée pour décrire la connectivité du paysage pour les papillons. Nous présenterons ensuite le type de modèle choisi pour modéliser les mouvements du Myrtil.

1. Mouvement des individus et connectivité du paysage

Le terme de mouvement prend différents sens selon le niveau auquel on se place et met en jeu différentes fonctions vitales (Ims, 1995) : la migration à l'échelle régionale, la dispersion (sans notion d'aller-retour) des individus au sein des populations fragmentées ou des métapopulations à l'échelle de la mosaïque paysagère, et les mouvements pour l'exploitation des ressources à une échelle plus limitée. Dans ce travail, nous nous sommes intéressés à un papillon diurne, le Myrtil (*Maniola jurtina* L.), qui est une espèce généraliste présente dans des milieux herbacés. Nous avons étudié les mouvements journaliers de ce papillon de recherche de nourriture ou de partenaires pour la reproduction. Le Myrtil est commun en milieu agricole et les données acquises dans l'équipe (Ouin, 2000) nous

permettaient de mettre en place des observations de ses déplacements *in situ* et d'adopter une démarche de modélisation.

La connectivité du paysage⁵ a longtemps été mesurée par la distance euclidienne entre taches (Bennett, 1990 ; Verboom et van Apeldoorn, 1990 ; Moilanen et Hanski, 1998 ; Tischendorf et Fahrig, 2001). Récemment, l'importance de l'hétérogénéité de la matrice a été reconnue (Pain *et al.*, 2000 ; Ricketts, 2001). En tant que mesure de l'interaction entre le paysage et le mouvement des organismes, la connectivité du paysage doit refléter à la fois l'hétérogénéité spatiale du paysage, les exigences écologiques et les capacités de dispersion des espèces (Vos *et al.*, 2001). Pour les papillons, la connectivité du paysage dépend de la quantité et de l'organisation spatiale des taches de ressources, de la présence de corridors entre ces taches, mais également du comportement des individus face à certains éléments du paysage qui peuvent agir comme des filtres ou des barrières aux déplacements des individus (Fry et Robson, 1994 ; Hill *et al.*, 1996 ; Kuussaari *et al.*, 1996 ; Haddad et Baum, 1999 ; Baguette *et al.*, 2000). Dans cette partie, **nous avons donc adopté une approche fonctionnelle pour étudier les interactions entre mouvement des papillons et paysage**, en considérant la quantité et l'organisation spatiale des zones enherbées et la présence de corridors herbeux (bords de champs) entre ces taches ; nous avons également posé l'hypothèse que les bois constituent des barrières aux mouvements du Myrtil.

2. Modélisation du mouvement des individus et de la distribution des populations

Il existe de nombreux modèles visant à prédire le mouvement seul ou comme partie d'une dynamique de population. Dans les modèles spatialement implicites, les paramètres spatiaux pris en compte sont limités à la taille, l'isolement spatial des taches ou leur nombre (Hanski, 1994a ; Hanski et Gilpin, 1997). Les modèles spatialement explicites repèrent tout objet ou tache dans l'espace et considère la nature du paysage entre les taches. Parmi cette dernière catégorie de modèles, nous distinguerons les modèles basés individus des modèles basés populations. Dans les approches basées individus, l'individu est reconnu comme une unité fondamentale à la compréhension des phénomènes généraux (King *et al.*, 1991 ; Sutherland, 1996), ce qui permet d'incorporer les mécanismes locaux qui déterminent les processus dynamiques à l'échelle de la population (Murdoch *et al.*, 1992). La distribution spatiale des populations résulte ainsi de l'agrégation des réponses des individus aux caractéristiques locales du paysage (Turchin, 1989). Les modèles populationnels de mouvement ne prennent pas en compte les interactions locales des individus avec le paysage, et cherchent plus à modéliser les flux d'individus entre taches ou la distribution des individus au sein du paysage, en relation avec diverses variables du paysage (Hill *et al.*, 1996 ; Roland *et al.*, 2000).

Nous avons porté notre choix sur un modèle basé individus spatialement explicite, afin de déterminer à une échelle fine les interactions entre le Myrtil et son environnement. Les données issues d'observation *in situ* du mouvement des papillons ont été utilisées afin de tester la validité des prédictions du modèle.

⁵ "The degree to which landscape facilitates or impedes movements" - Taylor *et al.*, 1993

**CHAPITRE 4 : SHORT-TERM SCALE DYNAMICS OF
AGRICULTURAL LANDSCAPES UNDER FARMING PRACTICES –
THEIR EFFECTS ON BUTTERFLY MOVEMENTS**

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Résumé

Dans les paysages fragmentés, le mouvement est un processus clé de la survie des espèces. Dans les paysages agricoles, les mouvements de papillons sont influencés par les caractéristiques du paysage et par les conditions locales des taches de ressources. La mosaïque des ressources est dynamique sous l'effet des pratiques agricoles. Cependant, on ignore l'effet de cette dynamique sur les mouvements des individus et la distribution des populations. Nous avons testé l'impact de la dynamique du paysage induite par la fauche sur les mouvements et la distribution d'un papillon, le myrtil *Maniola jurtina* L., au moyen d'expériences de capture-marquage-recapture dans deux paysages présentant une composition et une structure contrastées. Dans les deux sites de l'étude, la fauche n'entraîne pas de changements significatifs de la distribution des papillons au sein du paysage. La distribution des papillons dépend de la surface des taches de ressources et de la qualité des ressources nectarifères, le myrtil étant plus abondant dans les prairies. La fauche ne modifie pas le mouvement de *Maniola jurtina* dans le paysage où les éléments herbeux, prairies et bords de champs, sont nombreux et connectés. Au contraire, la fauche entraîne des modifications significatives des mouvements de papillons dans le paysage le plus ouvert. Dans ce paysage, les mouvements de papillons sont contraints par la distance entre taches de ressources et restreints aux prairies voisines après la fauche. Nous avons posé l'hypothèse que la réponse des populations de papillons à la fauche dépend de la connectivité du paysage. Dans les paysages agricoles, la prise en compte explicite des pratiques agricoles est importante pour comprendre les interactions entre la dynamique des populations et la structure du paysage. D'autre part, les pratiques agricoles et les caractéristiques du paysage doivent être considérées pour la conservation des papillons dans les paysages agricoles, du fait que certaines mesures pourraient être inefficaces dans des paysages fragmentés et peu connectés.

1. Introduction

The intensification of agriculture in landscapes of Western Europe has induced a drastic decrease of permanent habitats (Agger and Brandt, 1988). In such fragmented landscapes, movement is a key process of species survival (Wiens *et al.*, 1993b; Wiens *et al.*, 1997; McIntyre and Wiens, 1999), either being dispersal at the metapopulation level, seasonal dispersal or daily movements of individuals for foraging and breeding. Landscape connectivity, defined here as the degrees to which the landscape facilitates or impedes movement (Taylor *et al.*, 1993), expresses interactions between species movement and landscape patterns. Landscape connectivity depends on the distance between resource patches (Bennett, 1990; Verboom and van Apeldoorn, 1990; Moilanen and Hanski, 2001), but also on the presence of corridors or stepping-stones and on the heterogeneity of the surrounding landscape (Pain *et al.*, 2000; Ricketts, 2001; Tischendorf and Fahrig, 2001; Schneider *et al.*, 2003).

Many butterfly species have declined under agricultural intensification (Pullin, 1995; Thomas, 1996). Thus, many studies have focus on the driving factors of butterfly survival in fragmented landscapes, with a special interest on dispersal. Distance between resource patches, heterogeneity of the landscape between resources patches, patch area, and resource quality have been shown to influence butterfly movements (Hill *et al.*, 1996; Kuussaari *et al.*, 1996; Baguette *et al.*, 2000). Dispersal is also influenced by aggregative behavior of individuals, especially for males, in patches with high density of butterflies (Scott, 1974; Brakefield, 1982a; Kuussaari *et al.*, 1996).

In agricultural landscapes, many butterfly species are restricted to grassy areas such as field margins and hedges (Dover *et al.*, 1992; Dover, 1994), grasslands and meadows (Oates, 1995). The farming practices conducted on herbaceous areas, i.e. herbicide spraying, grazing and mowing, modify drastically resource quality, by suppressing nectar and host plants for butterflies and potential refuges supplied by tall vegetation. Farming practices have thus a drastic impact on butterfly survival (Oates, 1995). At the landscape scale, farming practices cause changes in the distribution of resources and in spatial heterogeneity. Even the impacts of long-term changes in landscape heterogeneity on animal movement have been investigated (Baudry *et al.*, 2003), the effects of landscape dynamics on the short-term remain unconsidered. The changes in resource distribution caused by farming practices conducted locally may influence butterfly movements, their abundance, and their distribution.

In this study, the impact of mowing on the movement of a grassland species, the meadow brown *Maniola jurtina* L. (Satyridae), was investigated in two landscapes with contrasted spatial structure. We tested whether mowing of a single resource patch leads to changes in butterfly movements and distribution at the landscape scale and whether these changes are controlled by patch characteristics (resource quality, patch area) and by the connectivity of the landscape between resource patches.

2. Study area and methods

2.1. The species

The meadow brown is one of the most abundant butterfly species in agricultural landscapes, found in a variety of herbaceous habitats, such as meadows, road verges or field margins. *Maniola jurtina* is classified as a sedentary species, with a minimal home range estimated as 0.5 ha (Brakefield, 1982a) although in certain cases it can disperse over several kilometres (Schneider *et al.*, 2003). *Maniola jurtina* is shown to be a generalist species in terms of food plants. Larvae of *M. jurtina* feed on a wide range of grasses, the most used being *Poa* spp. L. (Vane Wright and Ackery, 1981); adults feed on various flowering plants (Porter *et al.*, 1992).

2.2. Study area

The study was conducted in two 1km² landscape units from Western France (Northern Brittany) (figure 4.1). These sites represent fine grain hedgerow network landscapes (“bocage”). Farming systems are oriented toward milk production; maize, wheat and meadows are the main land-covers. The two studied landscapes have contrasted composition and spatial structure. Site 1 is characterised by a large proportion of arable land devoted to meadows, a high density of field margins, and fine grain size (average field size) (table 4.1). Site 2 is dominated by large fields of crops and contains a more reduced and fragmented network of field margins (table 4.1). Figure 4.1 shows that meadows are clearly more spatially isolated in site 2 than in site 1. At each study site, movement sampling was conducted in several herbaceous patches selected according to their nature (meadow, road verge and lane), their quality in term of flower abundance, and their spatial distribution. Ten herbaceous patches were sampled in each site (figure 4.1):

- Six meadows, two road verges and two lanes in site 1,
- Five meadows, three roads verges and two lanes in site 2.

2.3. Disturbance of butterfly resources: mowing

To test the impacts of mowing on butterfly movements, one meadow among the ten studied patches was mown during the experiment at each site (figure 4.1). Mowing was realised mechanically by farmers. Movement sampling was conducted at each site before mowing and from the day following mowing. The experiment was realised during the peak of activity of *Maniola jurtina*, i.e. late June – early July as we observed in previous years in the same study area. Thus, the comparisons of butterfly movements between before and after mowing could not be biased by emergence patterns of butterflies. Moreover, butterfly sex-ratios were similar during the experiment in both study sites. A vegetation survey was carried out before mowing in order to assess the overall quality of vegetation in term of flower density in studied patches: 0: no flower; 1: <10%; 2: 10 to 25%; 3: 25 to 50%; 4: 50 to 75%; 5: >75%. Data on host plant abundance were not collected, as *Poa* spp. and other grasses were abundant in all studied patches. Changes in habitat quality induced by mowing were quantified by recording vegetation height (cm) before and after mowing in all patches and by assigning a null value to flower density after mowing.

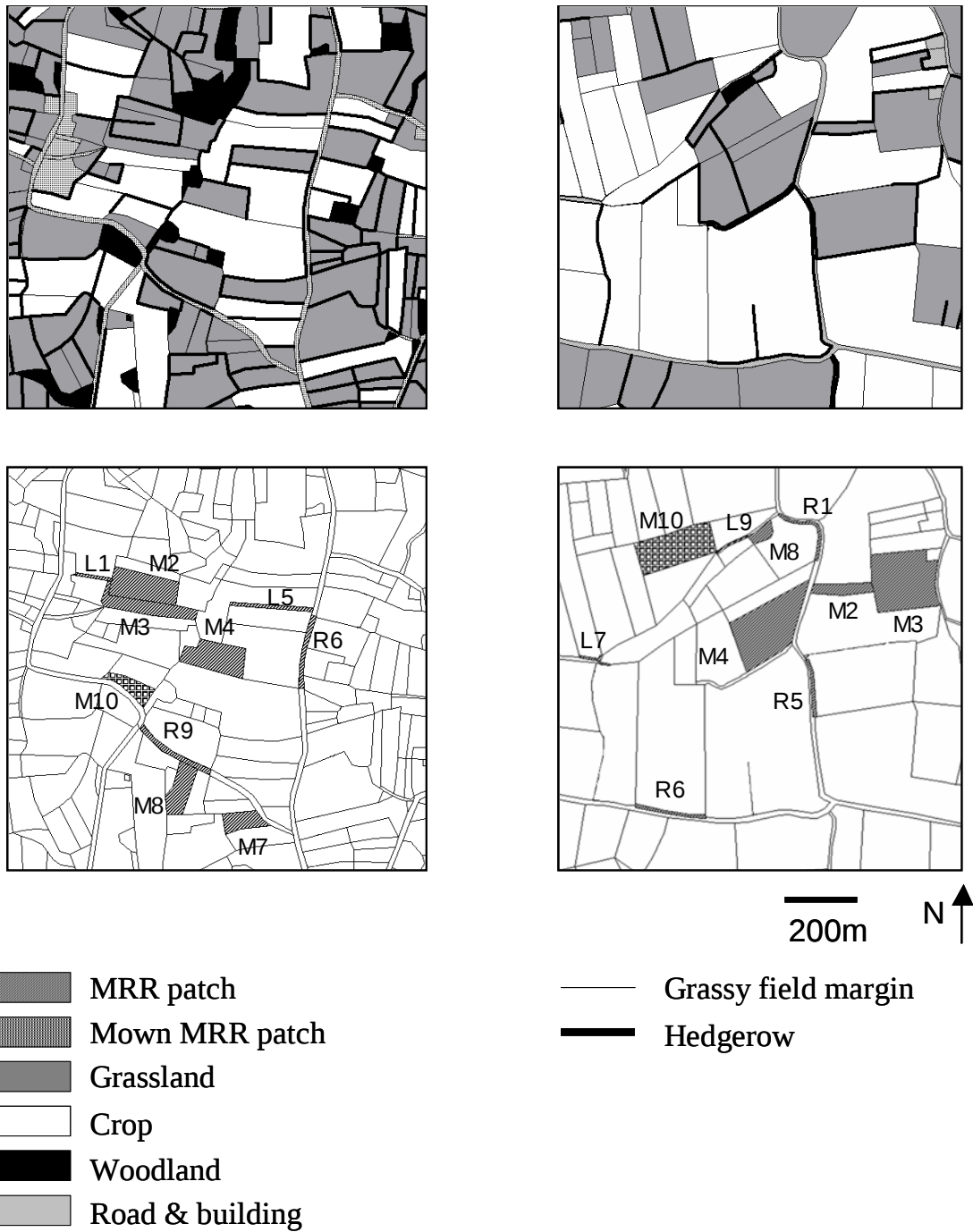


Figure 4.1. Studied sites and MRR patches (site 1: left; site 2: right). M: meadow, L: lane, R: road verge.

Table 4.1. Landscape composition (proportion of the surface area covered by meadows and crops) and structure (density of field margins in meters per hectare, and average field size in ha) in the two study sites.

	Site 1	Site 2
Proportion of meadows	53	37
Proportion of crops	33	62
Density of field margins (m/ha)	322	186
Average field size $\pm$ SE (ha)	0.55 ± 0.53	1.49 ± 1.62

2.4. Butterfly movement sampling

Butterfly movement was recorded during June and July 2000 using mark-release-recapture experiments. 14 sessions of mark-release-recapture experiments (two weeks) were conducted at each site. In each site, seven mark-release-recapture sessions (one week) were conducted before mowing and seven mark-release-recapture sessions (one week) after mowing to test the effect of mowing on butterfly movements. One mark-release-recapture session corresponded to the successive sampling according to a fixed sequence of the ten patches at each site and was performed in one day. During each session, butterflies that were captured for the first time were identified by individual numbers on wing (with no-odour pen), and then after released. At the same time, their capture location, i.e. patch number, was recorded. When recapturing butterflies, individual number and recapture location were recorded. The time spent in each patch was proportional to its surface area and to the number of observers to maintain a constant sampling intensity.

2.5. Landscape description between patches

Landscape composition and structure between patches was described using GIS (ArcView 3.2, 1998; ESRI). Studied areas were characterised with five land-cover categories: (i) crops, (ii) meadows, (iii) field margins, (iv) woodland, and (v) others land-covers (water, roads, and buildings). Between each pair of patches, landscape descriptors were extracted in a buffer area, the size of this area corresponding to the average of departure patch diameter and arrival patch diameter (Martin and Ouin, 1998). Landscape connectivity between pairs of patches was described by the proportion of the land covered by meadows, by the density of field margins (in meters per hectare) and by the minimal distance between centres of patches. Distances between patch centres were considered instead of distances between patch edges to avoid null distances in the case of adjacent patches.

2.6. Analysis

Butterfly fluxes between patches were characterised by the number of butterflies marked in one patch and recaptured in the other patch, movement in both directions being considered. Fractions of residents, emigrants and immigrants were calculated respectively as the percentage of residents, emigrants, and immigrants out of the total number of recaptured butterflies.

The effect of mowing on inter-patch movements and fractions of residents, immigrants and emigrants was tested by the mean of Wilcoxon paired test of the SYSTAT (Systat Software Inc., USA) package. None of variables used to describe butterfly movements fitted assumptions of normality and linearity for regression analysis, even after data transformation. Thus, they were related to landscape descriptors (% of meadows, density of field margins, minimal distance) and patch characteristics (vegetation height, flower abundance, patch area,) by the mean of Pearson correlations.

3. Results

3.1. Influence of mowing on the abundance and distribution of butterflies

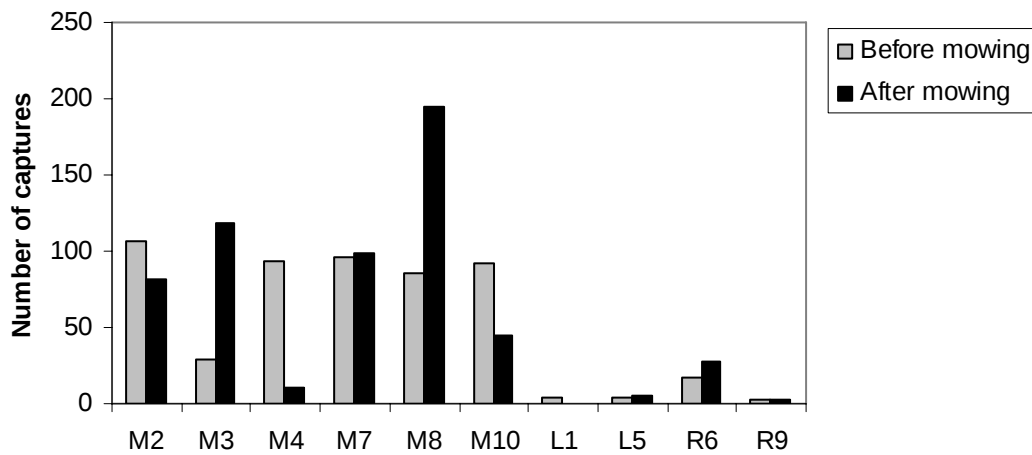
During summer 2000, 2555 butterflies were marked, 1112 individuals in site 1 and 1443 in site 2. Recapture rates consisted in 30% in site 1 and 19% in site 2.

The species shows similar spatial distribution before and after mowing in the two sites (Wilcoxon test; site 1: $Z=0.18$; $P=0.86$; site 2: $Z=-0.61$; $P=0.54$), despite localized decreases in the number of captures in mown patches (figure 4.2). In both sites, patch area was correlated with the number of captures on a patch before and after mowing (table 4.2). Number of captures was correlated with flower density index before and after mowing in site 1, and before mowing in site 2 (table 4.2). In site 1, the meadow brown was more abundant in meadows than in linear features, i.e. lanes or road verges (figure 4.2). In site 2, butterflies were especially more abundant in meadow M3 than in other studied patches (figure 4.2).

Table 4.2. Pearson correlation coefficients between number of captures, fractions of residents, immigrants and emigrants, with vegetation height, flower density index and patch area before and after mowing, in the two sites. In bold: significant, $P < 0.05$.

	before mowing			After mowing		
	Vegetation height (cm)	Flower density	Patch area (ha)	Vegetation height (cm)	Flower density	Patch area (ha)
<i>Site 1</i>						
Nb. captures	0.00	0.39	0.77	-0.32	-0.27	0.53
Residents	-0.05	0.52	0.69	-0.26	-0.28	0.75
Immigrants	-0.14	0.38	0.91	-0.23	-0.30	0.74
Emigrants	0.00	0.49	0.84	-0.31	-0.33	0.63
<i>Site 2</i>						
Nb. captures	-0.31	0.58	0.58	-0.21	0.77	0.59
Residents	-0.28	0.56	0.49	-0.13	0.71	0.52
Immigrants	-0.44	0.18	0.16	-0.21	0.69	0.43
Emigrants	-0.37	0.61	0.61	-0.25	0.54	0.32

a)



b)

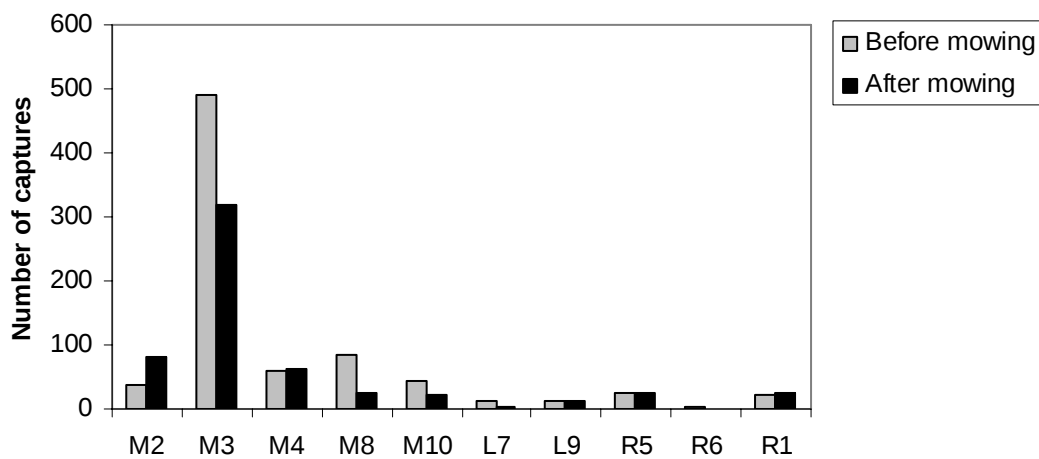


Figure 4.2. Number of captures in each MRR patch before and after mowing in a) site 1, b) site 2. M: meadow, L: lane, R: road verge.

3.2. Influence of mowing on butterfly movements

Butterfly fluxes between resource patches were statistically similar before and after mowing in site 1 (Wilcoxon test, $Z=-0.47$; $P=0.63$). In this site, fluxes were positively correlated with the proportion of meadows before and after mowing, and with the density of field margins between patches before mowing (table 4.3). Fluxes were negatively related to minimal distance between patches (table 4.3). Butterfly movements were more frequent between meadows M2, M3, M4 and mown meadow M10, either before or after mowing (figure 4.3). In site 2, the meadow brown exhibited different inter-patch movements before and after mowing (Wilcoxon test, $Z=-2.36$, $P=0.02$). Before mowing, butterfly fluxes were not correlated with any of the landscape descriptors (table 4.3). Butterflies moved more frequently between meadows M2, M3, M8 and mown meadow M10; a few long-distance flights, such as between M2 and R9, were also observed (figure 4.3). After mowing, fluxes

were negatively correlated with inter-patch distance (table 4.3). Butterfly movements were then almost restricted to closest or adjacent patches (meadows M2 and M3) (figure 4.3). Fluxes between mown meadow M10 and other patches were reduced after mowing.

Table 4.3. Pearson correlation coefficients between inter-patch fluxes with proportion of meadows, density of field margins and distance between patches, before and after mowing, in the two sites. In bold: significant, $P < 0.05$.

	Meadows (%)	Field margin (m/ha)	Distance (km)
<i>Site 1</i>			
Before mowing	0.43	0.26	-0.51
After mowing	0.45	0.41	-0.32
<i>Site 2</i>			
Before mowing	-0.03	-0.24	-0.05
After mowing	0.03	-0.07	0.31

Fraction of residents, emigrants, immigrants in studied patches did not differ significantly before and after mowing in site 1 (Wilcoxon test; residents: $Z=-0.34$, $P=0.74$; immigrants: $Z=0.95$, $P=0.34$; emigrants: $Z=0.36$, $P=0.72$) and in site 2 (Wilcoxon test; residents: $Z=-0.53$, $P=0.59$; immigrants: $Z=0.15$, $P=0.88$; emigrants: $Z=0.77$, $P=0.44$), despite localized changes in a few meadows (figure 4.4). In site 1, the proportions of residents, emigrants and immigrants were correlated with flower density before mowing and with patch area before or after mowing (table 4.2). In site 2, flower density and patch area were related to fractions of residents before and after mowing (table 4.2). Proportion of immigrants was correlated with vegetation height before mowing and with flower density and patch area after mowing (table 4.2). Fraction of emigrants was related to vegetation height, flower density and patch area before mowing, and to flower density after mowing (table 4.2).

4. Discussion

4.1. Effect of mowing on butterfly distribution

Despite of localized decrease of butterfly numbers in mown patches after mowing, the spatial distribution of *Maniola jurtina* before mowing was similar to its distribution after mowing in both studied sites. Butterflies were more abundant in large resource patches, i.e. meadows, than in linear features such as road verges and lanes. Steffan-Dewenter and Tscharntke (2000) outlined such relationships between butterfly abundance and habitat size. Abundance of the meadow brown in herbaceous patches was correlated with nectar resource density or vegetation height, which have been defined as important factors for this species (Wynhoff, 1992; Dover, 1997a; Schneider *et al.*, 2003). Feber and Smith (1995) tested the effects of mowing on field margins on the abundance of the meadow brown. They showed that mowing induces changes in the spatial distribution of butterflies, that is a drop in the abundance of *Maniola jurtina* in cut plots and a simultaneous increase in butterfly abundance in uncut plots. Here, we could not demonstrate such changes in butterfly distribution.

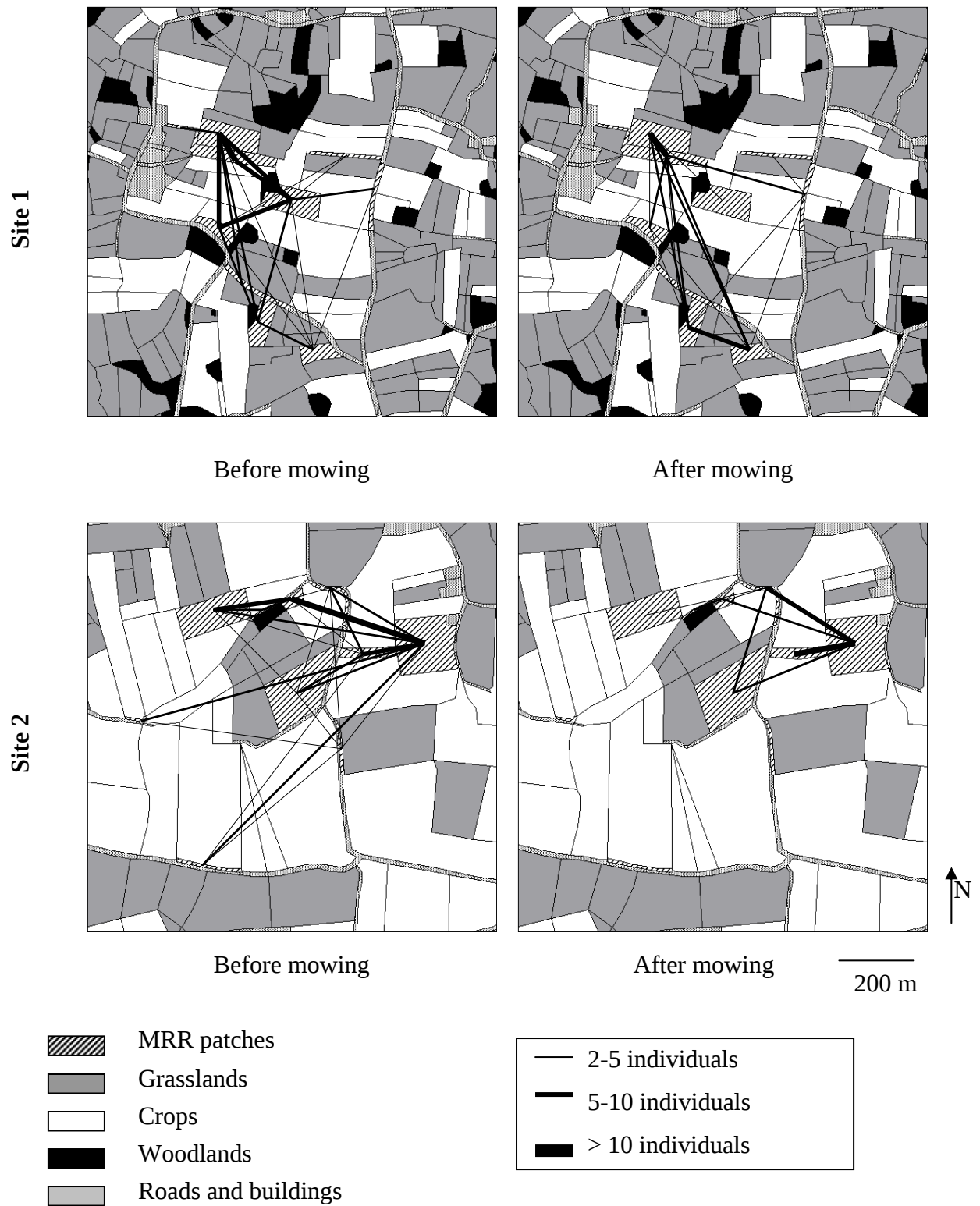
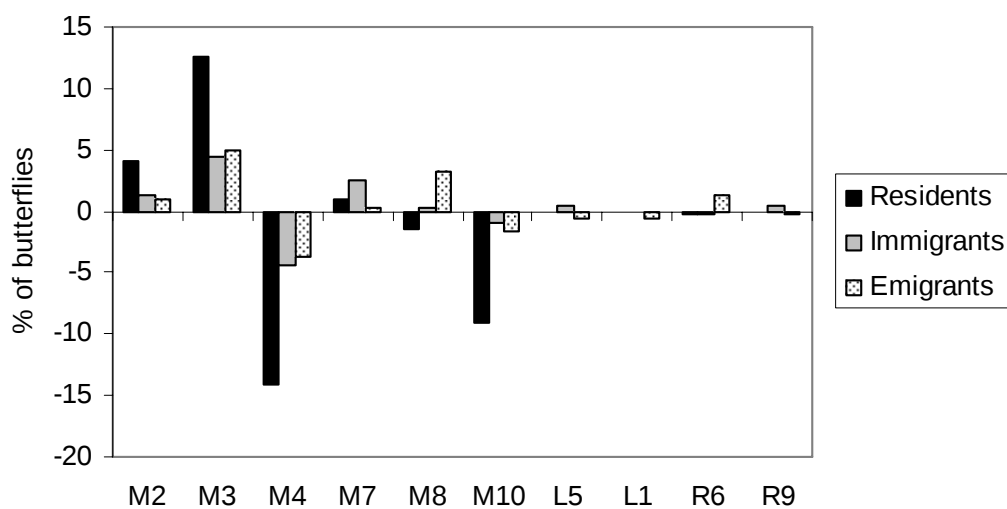


Figure 4.3. Fluxes of butterflies between MRR patches in studies sites before and after mowing. M: meadow, L: lane, R: road verge.

a)



b)

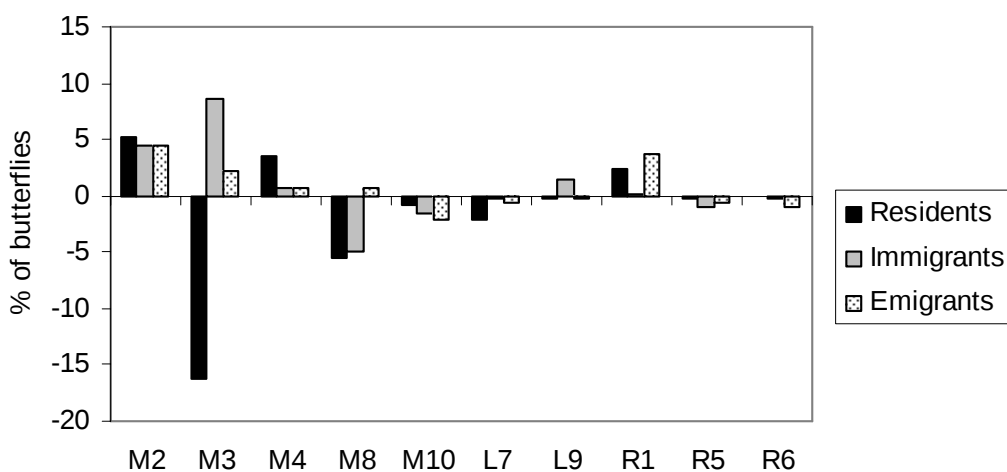


Figure 4.4. Variation between before and after mowing in the fraction of residents, emigrants and immigrants before and after mowing in a) site 1 and b) site 2. M: meadow, L: lane, R: road verge.

4.2. The effect of mowing on butterfly movements

Mowing did not lead to significant changes in residency, emigration or immigration in resources patches in both sites. Butterflies stayed the more often in large patches with high flower density, mainly meadows. Butterflies immigrated preferentially toward large meadows with high flower density. Emigration was also higher out of these patches. The effect of patch size on butterfly movement has been already underlined (Hill *et al.*, 1996). On the other hand, our results conflicts with previous studies where no relationships between patch area and butterfly movements were found (Kuussaari *et al.*, 1996; Schneider *et al.*, 2003). The probability for butterflies to reach resource patches might be higher for larger patches such as meadows compared with linear features such as road verges or lane banks. The influence of nectar supply and vegetation on the distribution and movement of *Maniola jurtina* has already been observed (Wynhoff, 1992; Merckx and Van Dyck, 2002). The observation of an increasing emigration rate with higher flower density has also been made for the meadow brown by Schneider *et al.* (2003), who found that *Maniola jurtina* was more inclined to leave a good patch compared to another meadow species, the scarce copper.

Mowing did not affect butterfly fluxes between resource patches in site 1. Fluxes in this site were more frequent between close patches and were enhanced by the presence of field margins and meadows between resources patches, either before or after mowing. This underlines the role of stepping stone habitats and corridors on butterfly movement (Dover, 1994; Fry and Robson, 1994; Kuussaari *et al.*, 1996; Baguette *et al.*, 2000; Ricketts, 2001; Sutcliffe *et al.*, 2002). In site 2, mowing led to significant changes in inter-patch movements of butterflies, fluxes being almost restricted to two or three close meadows after mowing. In this landscape, butterfly fluxes were mainly constrained by distance between patches, in agreement with the findings of previous studies (Schneider *et al.*, 2003; Hill *et al.*, 1996; Baguette *et al.*, 2000). This contrasted response of butterflies to mowing might be linked to the differences in landscape connectivity between the two study sites. Site 1 is characterized by a large amount of meadows and a dense network of field margins. This connected network of herbaceous patches might have permit the redistribution of butterflies in surrounding undisturbed patches after mowing, as suggested by the positive effect of meadows and field margins on inter-patch fluxes. On the contrary, meadows and field margins are much more reduced in site 2 and distance between herbaceous patches are higher. Thus, butterfly redistribution after mowing might have been limited to close patches as a consequence of the spatial isolation of remnant patches. On the other hand, other factors might contribute to differentiate the response of butterflies to mowing between the two sites. First, the studied landscapes differ by the type and intensity of farming practices and farming systems, farming production being especially more intensive in site 2. More frequent and extended applications of pesticides in this landscape could have accentuated the different pattern between sites. Moreover, the effect of mowing in site 2 might be linked to an effect of the spatial scale of the study. Large areas of meadows located at the south limit of site 2 were not considered in movement sampling. The movements of individuals toward hedges and road verges embedded in crops suggest that butterflies may have moved toward meadows out of the studied area. The influence of spatial scale on quantifying butterfly movement has been pointed out by Schneider (2003). She recommended large-scale studies to get a more accurate picture of butterfly dispersal ability. Further study should be conducted with consideration of coarser spatial scale for studying the response of butterflies to landscape dynamics.

5. Conclusion

Local disturbance of resources induced by mowing was showed to lead to changes in butterfly movements at the landscape scale, at least in open and fragmented landscape. The redistribution of individuals was mainly dependant on patch isolation. In more connected landscape, butterfly movements were enhanced by the presence of meadows and field margins between patches. There is a current debate on how landscape connectivity should be measured. Metapopulation models assume that landscape connectivity can be described only by the degree of patch isolation (Verboom and van Apeldoorn, 1990; Moilanen and Hanski, 2001), whereas several authors outline that landscape connectivity depends not only on the distance between habitat patches, but also on the presence of corridors or stepping-stones and on heterogeneity of the landscape (Pain *et al.*, 2000; Ricketts, 2001). This study confirms that measures of landscape connectivity should not only integrate patch isolation, but also the permeability of the matrix between patches.

Many studies of animal movement in agricultural landscapes consider landscape characteristics without taking into account the potential influence of farming practices conducted locally. This study shows that a punctual and localized farming practice can significantly influence butterfly movement and distribution at the landscape scale, especially in fragmented and low connected landscapes. It seems thus necessary to integrate explicitly farming practices for understanding the relationships between butterfly population dynamics and landscape structure in agricultural landscapes. Moreover, this study suggests that landscape connectivity might play a determinant role in the response of butterflies to farming practices. Promoting some environmentally friendly farming practices might not be sufficient for the conservation of butterflies in fragmented and low connected landscapes. In such landscapes, conservations priorities should be first to convert crops into meadows or meadows to favour a connected network of grassy areas.

Acknowledgements

We thank Maud Ablain, Violaine Canévet, and Gabrielle Sauret for field assistance. This research was supported the Programme Environment Vie et Société (Motive) of the CNRS.

Sous presse : Ecological Entomology

**CHAPITRE 5 : CAN ASSUMPTION OF A NON-RANDOM SEARCH
IMPROVE OUR PREDICTION OF BUTTERFLY FLUXES BETWEEN
RESOURCE PATCHES ?**

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Résumé

La compréhension des processus de dispersion qui permettent le maintien des populations dans les paysages fragmentés est devenu un enjeu majeur en biologie de la conservation et en aménagement. Cependant, pour la plupart des espèces, on ignore si les individus se déplacent selon des stratégies particulières ou, au contraire, de façon aléatoire. Récemment, des travaux ont montré que les mouvements du papillon *Maniola jurtina* au sein du paysage pour la recherche des ressources ne suivent pas un schéma aléatoire. Dans ce cas, cela pourrait être problématique pour les modèles actuels de métapopulation, notamment pour ceux basés sur les taux de dispersion des individus. En outre, la plupart des modèles ne prennent en compte que la taille et l'isolement spatial des taches d'habitat, sans considérer l'influence de la matrice entre les taches. Dans cet article, nous avons posé l'hypothèse que les déplacements de *Maniola jurtina* entre les taches de ressources sont expliqués à la fois par des mouvements non aléatoires des individus et par les caractéristiques du paysage entre les taches. Un modèle de mouvement a été élaboré à partir de la littérature et comparé à des données réelles de mouvements obtenues par capture-marquage-recapture dans deux paysages bocagers sur deux ans. Le modèle prédit de façon satisfaisante les flux de papillons au sein du paysage et conduit à de meilleures prédictions en comparaison d'un modèle basé uniquement sur la taille des taches et la distance entre taches. Notre modèle devrait donc être préféré aux approches simples basées sur des déplacements aléatoires des individus et sur l'isolement spatial des taches, dans la mesure où l'on dispose de données concernant les paysages étudiés. Cependant, les modèles basés sur la taille des taches et leur isolement spatial restent utiles d'un point de vue théorique.

1. Introduction

Habitat loss and its fragmentation are seen as major threats to many species (Wilcove *et al.*, 1986; Jongman, 2000), especially in Western Europe, where expansion of farmland at the expense of uncultivated habitats such as permanent grasslands and hedgerows has led to drastic changes of agricultural landscapes. For species living in fragmented habitats, dispersal is a key process for survival (Wiens *et al.*, 1993a; McIntyre and Wiens, 1999). Understanding dispersal patterns that enable small, spatially isolated populations to survive has therefore become an important issue in conservation biology and landscape management (Fry, 1995; Cooper and Power, 1997). The metapopulation concept provides a general explanation for how species in fragmented landscapes can survive: movements of individuals between spatially isolated populations allow a metapopulation to survive due to colonization or recolonization of existing or vacant habitat patches (Gilpin and Hanski, 1991; Hanski and Gilpin, 1997). However, detailed information about how individual animals disperse is limited because of the difficulty in keeping track of dispersing individuals in the field (Zollner and Lima, 1999). Hence, for most of the species of interest to metapopulation biology it is not known whether dispersing individuals navigate or follow systematic search strategies, as opposed to moving randomly. Most metapopulation models therefore simply assume random movement (Hanski, 1998) and generate colonization patterns for patches depending on variables such as patch size and isolation. This means that these models characterize landscape connectivity (the degree to which landscape facilitates or impedes movements - Taylor *et al.*, 1993) only by the degree of patch isolation (Verboom and van Apeldoorn, 1990; Moilanen and Hanski, 2001). However, several authors have shown that landscape connectivity depends not only on the distance between habitat patches, but also on the presence of corridors or stepping-stones and on heterogeneity of the landscape (Pain *et al.*, 2000; Ricketts, 2001).

Many butterfly species live in fragmented habitats with networks of local populations. Therefore, they are especially threatened by loss and fragmentation of their habitats (Thomas, 1984; Thomas, 1991b; New *et al.*, 1995). Patch area, patch isolation, patch quality, and sex have been identified as factors influencing butterfly dispersal (Dover *et al.*, 1992; Hanski, 1994b; Hill *et al.*, 1996; Kuussaari *et al.*, 1996; Baguette *et al.*, 1998; Baguette *et al.*, 2000; Petit *et al.*, 2001). In the special case of agricultural landscapes, patches can be seen as mosaic of crops and uncultivated land (Ricketts, 2001; Sutcliffe *et al.*, 2002). The meadow brown (*Maniola jurtina* L.) shows dispersal rates that are typical of butterfly metapopulations and has been the subject of several recent studies. Conradt *et al.* (2000) investigated their ability to return to a suitable habitat. They concluded that the meadow brown does not seek habitat by means of random flight. Their experimental butterflies used a non-random, systematic, search strategy in which they flew in loops around the release point and returned periodically to it. Conradt *et al.* (2000) point out that if dispersers actively orientate towards or search systematically for distant habitat, this may be problematic for existing metapopulation models, including models of the evolution of dispersal rates in metapopulations. Recently, Schneider *et al.* (2003) found that the distance decay curve (dependence of the frequency of flights on their distance) of *M. jurtina* fitted a negative exponential function and that the mean flight distance for both males and females was between 60 and 70 m.

In the work reported here, it is being tested to what extent the non-random dispersal patterns described by Conradt *et al.* (2000) and Schneider *et al.* (2003) can explain *Maniola jurtina* fluxes between herbaceous areas in agricultural landscapes. A model is being presented that assumes the non-random search described by Conradt *et al.* (2000) with both

shape and parameters of the distance decay curve following Schneider *et al.* (2003), which assumes that the composition of the landscape between resource patches affects butterfly movements. The predictions of this model are then compared with the two-years capture-recapture data on *Maniola jurtina* fluxes in two contrasting landscapes in terms of connectivity and with predictions of a simple regression model that includes sizes of departure and arrival patches and distances between these two as its variables.

2. Methods

2.1. The species

The meadow brown (*Maniola jurtina*) is one of the most abundant butterfly species in agricultural landscapes, found in a variety of habitats, although many populations have been lost due to agricultural intensification. It is a species of open grassland, heath land, hay meadows, roadside verges, hedgerows, and woodland clearings and rides. This butterfly is active even during dull weather when most other species are inactive. There is one generation per year with adults on the wing between mid June and September. The eggs are laid on a variety of grasses including fescues (*Festuca* spp.), bents (*Agrostis* spp.), and meadow grasses (*Poa* spp.). The young larvae feed during the day relying on their green colouring for camouflage. *Maniola jurtina* is classified as a sedentary species, with a minimal home range estimated as 0.5 ha (Brakefield, 1982a), although in certain cases it can disperse even over several kilometres (Schneider *et al.*, 2003). Landscape elements with tall vegetation such as woodland can act as a barrier of movement for grassland butterfly species, including *Maniola jurtina* (Sutcliffe and Thomas, 1996; Haddad, 1999), leading to changes in flight direction (Fry and Robson, 1994).

2.2. Study area

The study was conducted in two landscape units in Western France (Northern Brittany), each 1 km² in size. These sites represent fine grain hedgerow network landscapes (*bocage*). Agriculture in both sites is oriented toward milk production; maize, wheat, and grasslands for pasture cover the majority of land. Sites 1 and 2 exhibit contrasted spatial structure. Site 1 is located in a dense hedgerow network and fine grain area with several woodlots, while site 2 is more open and contains a more reduced and fragmented hedgerow network. The sites also differ in the intensity of agricultural production. Site 2 is characterised by a high proportion of large cropped areas of maize and other cereals, compared to site 1 with more grassland. The studied landscapes are described using GIS (IDRISI; Eastman, 1997). Crops, woodland, temporary grasslands, permanent grasslands, hedgerows, and grassy field margins were distinguished.

2.3. Butterfly movement

At each study site, movement sampling was conducted in several herbaceous areas selected according to their nature (meadow, grassland, grassy field margin, hedgerow bank, road bank, and lane bank) and their spatial distribution. Sampled areas were distributed in square kilometre restricted areas in order to cover the average range of daily movements of *Maniola jurtina* (Brakefield, 1982a). Eight and ten patches were chosen at sites 1 and 2 in 1998, and 15 patches at each site in 1999.

Butterfly movement was recorded during 1998-1999 using mark-release-recapture experiments. Every day, one mark-release-recapture session was performed, which consisted of successive sampling of all the patches at each site in a fixed sequence and was performed within one day. Ten mark-release-recapture sessions and 21 mark-release-recapture sessions were conducted respectively in 1998 and 1999 at each site. During each session, butterflies that were captured for the first time were identified by individual numbers on wing (with no-odour pen), and released thereafter. At the same time, their capture location, i.e. patch number, was recorded. When recapturing butterflies, individual's number and recapture location were recorded. The time spent in each patch was proportional to its surface area to maintain a constant sampling intensity. The flux from patch i to patch j was calculated as:

$$M'_{ij} = 100 \cdot \frac{M_{ij}}{\sum_{k=1}^n M_{ik}}, i \neq j,$$

where M_{ij} is the number of recaptures in patch j (at any time during the experiment) of individuals, which were captured in patch i ; capture means the *first* capture of an individual – when it was marked – and recapture the subsequent recapture of this individual (no individual was recaptured more than once in our data).

Proportion of residents, M'_{ii} , was estimated for each patch as the proportion of individuals recaptured in the same patch:

$$M'_{ii} = 100 \cdot \frac{M_{ii}}{\sum_{k=1}^n M_{ik}}.$$

Proportion of immigrants, I_i , was defined for each patch as the percentage of individuals entering patch i , out of the total number of recaptured individuals:

$$I_i = 100 \times \frac{\sum_{j=1, j \neq i}^n M_{ji}}{\sum_{k,l=1}^n M_{kl}}$$

Thus the butterfly fluxes, the proportions of residents, and the proportions of immigrants were calculated using the data from the whole study period (ten days in 1998 and 21 days in 1999).

2.4. The spatial model

Each landscape studied was considered as a mosaic of 5×5 m pixels, so that each of the experimental patches consisted of many pixels. Each of the pixels was characterized by the type of its land cover: 1 - water; 2 - woodland and fallow land; 3 - crops; 4 - roads and buildings; 5 - temporary grasslands; 6 - permanent grasslands; 7 - grassy field margin; 8 -

hedgerow. For the model purposes, however, only *good* habitats (grasslands, grassy field margins, and hedgerow margins) and *bad* habitats (water, woodland and fallow land, crops and roads, and buildings) were distinguished (see figures 5.1 and 5.2). Landscape composition was different between the two years of observations in either of the sites due to crop succession, resulting in different spatial distribution of *good* and *bad* habitat for butterflies (see figures 5.1 and 5.2). This enabled us to have different cases of landscape composition in the simulations. It was assumed that woodlands acted as a barrier for butterfly movements, according to the grassland status of the meadow brown. Consistently with Conradt *et al.* (2000), it was assumed that the butterflies are using a non-random, systematic search strategy in which they fly in loops around the starting point and return periodically to it, provided they do not find a *good* habitat. In the model, this was performed as follows:

1. In each step, the direction of flight, *Dir*, and its length, *Length*, were chosen at random.
2. Direction of flight was chosen from a uniform distribution, $Dir \in <0;360^\circ>$.
3. Following Schneider *et al.* (2003), length of flight, *Length*, was chosen from a negative exponential distribution with a constant mean, *Mean*. *Mean* = 70 m was chosen for the main simulation, as it is the commonest mean distance of flight of *Maniola jurtina* (Schneider, 2003; Schneider *et al.*, 2003).
4. The individual was assumed to move linearly in the direction *Dir* for a distance *Length*. If at any time during the flight the individual hit a woodland or fallow land, it was assumed to land. If the individual hit area boundary during the flight, it was allowed to leave the system.
5. If the individual starting from pixel P_s did not hit any woodland or fallow land or area boundary during the flight in the direction *Dir* for a distance *Length*, and if after having completed the whole flight it arrived to a pixel P_a , it was assumed to land in P_a , if either P_a was *good*, or if P_s was *bad* (which might have happened, if it hit woodland during the previous flight). If P_s was *good* and P_a was *bad*, it was assumed to return to P_s and land there.
6. In the next step, the butterfly was assumed to take off from the point, where it had landed in the previous step, as defined in points 4 and 5, and the whole procedure starting from point 1 was repeated.

In both experimental landscapes and in each of the experimental patches within the landscape, an initial position of the butterfly was chosen at random and the procedure described above (points 1 – 6) was performed one thousand times, so simulating 1000 flights of one butterfly, the first one starting in the pixel selected, the second one starting in the pixel, where the butterfly landed after having performed the first flight (as defined in points 4 and 5), etc. This was repeated 1000 times for each landscape and each patch selected. Thus, in biological terms, one thousand of *experimental butterflies* were simulated for each patch and each site, each of which completed 1000 flights. Point 2 above means that the *experimental butterflies* were not assumed to be able to learn from unsuccessful flights, as follows from Conradt *et al.* (2000). Note that different types of behaviour described in points 4 and 5 above reflect two different situations: hitting a woodland *during* the flight is only a signal to changing flight direction and continuing the search, while arrival to a *bad* pixel at the *end* of the flight is a signal to return to the take-off pixel.

N_{ij} was then calculated as the number of times any of the experimental butterflies, the initial position of which was in patch *i*, landed in patch *j* during the simulation. In order to

make this value comparable with the empirical fluxes, M'_{ij} , and with the empirically obtained proportions of residents, M'_{ii} , we used the transformation

$$N'_{ij} = 100 \cdot \frac{N_{ij}}{\sum_{k=1}^n N_{ik}},$$

and compared then N'_{ij} , with M'_{ij} .

The number of flights used in the simulations might have affected the model predictions of the proportion of butterflies, which decide to disperse, and of the proportion of individuals not recaptured. However, no data was available about the actual number of flights of the real butterflies. Therefore, the proportions of resident individuals, N_{ii} , were taken out of all further analyses with the only exception of calculating correlations between the proportions of residents observed and those predicted by the spatial model, and the proportions of residents observed and patch area, which is legal, as the ratios $N'_{11}:N'_{22}:\dots:N'_{nn}$ and $M'_{11}:M'_{22}:\dots:M'_{nn}$ are not likely to be affected by either the sampling effort or the number of flights in the simulation (while their actual values might be), and therefore the correlation coefficients between these, or between these and patch area are not affected, either.

As Schneider (2003) reports, a broad variation in the mean distance of flight of *Maniola jurtina*, model sensitivity to the parameter *Mean* was explored and additional simulation runs were performed in which this parameter was varied by 5 m from 5 m to 100 m.

2.5. The regression model

The empirical data was then fitted by a regression model

$$\overline{M'}_{ij} = \frac{aA_i^b A_j^c}{D_{ij} + d}, i \neq j$$

that includes sizes of departure (A_i) and arrival (A_j) patches and distances between these two (D_{ij}) as its variables, a , b , c , and d model parameters, and $\overline{M'}_{ij}$ as the flux predicted by the regression model by minimising the residual sum of squares, $\sum_{i,j} (M'_{ij} - \overline{M'}_{ij})^2$.

Similarly to usual assumptions of metapopulation models it is assumed here that fluxes are positively associated with sizes of the departure and arrival patches, and negatively associated with the distance between these two. Thus the model parameters a , b , c , and d were not obtained from an independent data set, as it was the case of the spatial model, but by means of fitting the data. In addition, the regression model includes four parameters (a , b , c , and d), while the spatial model only one (*Mean*); the latter was not fitted and its value was obtained from an independent data set: *Mean* = 70 m (Schneider *et al.*, 2003). For all these reasons one would therefore expect a better fit in the regression model, represented, e.g. by lower residual sum of squares.

2.6. Analysis

In order to make the predictions of the spatial and regression models comparable, all fluxes predicted by the spatial model, by the regression model and the empirical data were recalculated to relative (percentage) values as

$$N'_{ij} = 100 \cdot \frac{N_{ij}}{\sum_{j=1}^n N_{ij}}, \quad M'_{ij} = 100 \cdot \frac{M_{ij}}{\sum_{j=1}^n M_{ij}}, \quad \overline{M}'_{ij} = 100 \cdot \frac{\overline{M}_{ij}}{\sum_{j=1}^n \overline{M}_{ij}}.$$

Similarity between the matrices of predicted vs. observed fluxes, i.e. between the matrices $N = (N'_{ij})$, $M = (M'_{ij})$ and $\overline{M} = (\overline{M}'_{ij})$ was then tested by means of Mantel's test (Mantel, 1967). As a formal hypothesis test, Mantel's test can be used to compare an observed data matrix to one posed by a conceptual or numerical model; the test is to summarize the strength of the correspondence between the two matrices (see e.g. Shirley *et al.*, 2003). Significance levels were determined with Monte Carlo permutations (Manly, 1998) by performing 1000 permutations for each test. As the diagonals of the matrices (proportions of residents) were clearly strongly dominant and because of the possible bias mentioned in *The spatial model* section, they were deleted from the permutation tests, which lowered the test significance levels. In other words, if the test including only non-diagonal elements has shown that the two matrices were significantly different at significance level α , then the same test with diagonals included would show that these matrices are even *more* significantly different – at an even lower significance level $\alpha' < \alpha$.

In addition, to compare the goodness of fits of the spatial and regression models, residual sums of squares of non-diagonal terms for the pairs of matrices N and M (measure of fit of the spatial model) and M and $\overline{M}$ (measure of fit of the regression model) were calculated.

Pearson's correlation coefficients in the SYSTAT (Systat Software Inc., USA) package were used to calculate the correlations between the proportions of residents and immigrants predicted by the spatial model and those observed, between the patch surface area and observed proportions of residents and immigrants, between the proportions of immigrants and those predicted by the regression model, between the inter-patch fluxes and those predicted by each of the two models, and between the inter-patch distance and observed fluxes.

3. Results

Figures 5.1 and 5.2 enable comparison of the predictions of the spatial model for *Mean* = 70 m, and of the predictions of the regression model, with the empirical capture-recapture data for sites 1 and 2 respectively, and for two years, 1998 and 1999.

Table 5.1 shows values of Pearson's correlation coefficients between the proportions of residents and immigrants predicted by the spatial model and those observed, between the patch surface area and observed proportions of residents and immigrants, between the

proportions of immigrants and those predicted by the regression model, between the inter-patch fluxes and those predicted by each of the two models, and between the inter-patch distance and observed fluxes. The results of the spatial model for the mean flight distance equal to 70 m were consistently used here.

3.1. Comparison of predictions of the spatial model with observed data

Results of Mantel's tests of the significance of differences between the matrices of observed fluxes vs. those predicted by the spatial model for both sites, two years, and each of the 20 simulation runs (differing in the mean distance of the butterfly flight, *Mean*, which was varied by 5 m from 5 m to 100 m) are shown in table 5.2. Butterfly fluxes as predicted by the spatial model were similar to the observed data ($P < 0.01$), the exception being site 2 in 1998, where the fluxes predicted differed from observed data for each mean flight distance considered in the simulations. A very weak dependence of the significance level on the mean flight distance, *Mean*, is evident.

Figures 5.1 and 5.2 also demonstrate that the spatial distribution of butterfly fluxes, in terms of presence or absence of movements, was relatively well predicted by the spatial model, especially at site 1 in 1998 and at site 2 in 1999. There were some differences between the spatial distributions of predicted and observed fluxes in terms of movement intensity.

Table 5.1 shows that the spatial model predictions of the proportions of residents were significantly positively correlated with the observed data at site 1 in 1999. Spatial model predictions of the proportions of immigrants were always positively correlated with the observed data, but significantly so only in 1999 at both sites. Spatial model predictions of the inter-patch fluxes were always significantly positively correlated with the observed data, with the exception of site 2 in 1998, when the positive correlation was not significant.

Table 5.1. Pearson's correlation coefficients between observed proportion of residents (proportion of individuals that were recaptured in the same patch) and those predicted by the spatial model (S, column 1), between the observed proportion of residents and patch area (A, column 2), between the empirical proportions of immigrants and those predicted by the spatial model (S, column 3) and the regression model (R, column 4), the empirical proportion of immigrants and patch area (A, column 5), the empirical fluxes and those predicted by the spatial model (S, column 6) and regression model (R (R, column 7) and the empirical fluxes and inter-patch distance (D, column 8) for both sites and both years.

Site	Year	Correlation coefficient							
		Residents		Immigrants			Fluxes		
		S	A	S	R	A	S	R	D
1	1998	0.48	0.54	0.65	0.165	0.73	0.563*	0.165	-0.328*
1	1999	0.74*	0.58	0.61*	0.426*	0.31	0.379*	0.426*	-0.311*
2	1998	-0.22	-0.02	0.53	0.242	0.88*	0.155	0.242	0.094
2	1999	0.24	0.26	0.92*	0.534*	0.72*	0.499*	0.534*	-0.275*

*: $P < 0.05$

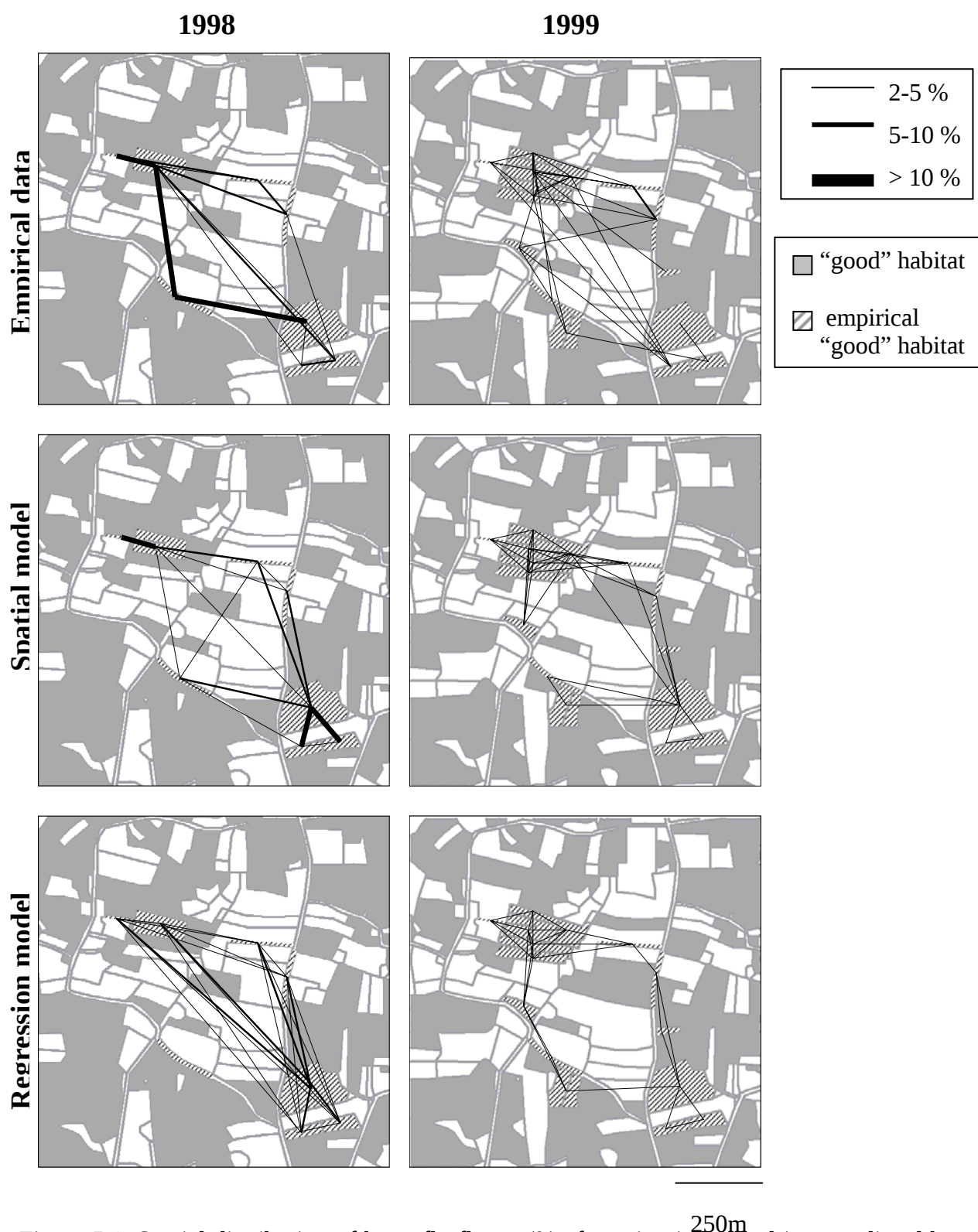


Figure 5.1. Spatial distribution of butterfly fluxes (% of moving individuals) as predicted by the spatial model (middle) and the regression model (bottom) compared with spatial distribution of observed fluxes. Results are presented for two years, 1998-1999 and site 1. Fluxes lower than 2% are not depicted..

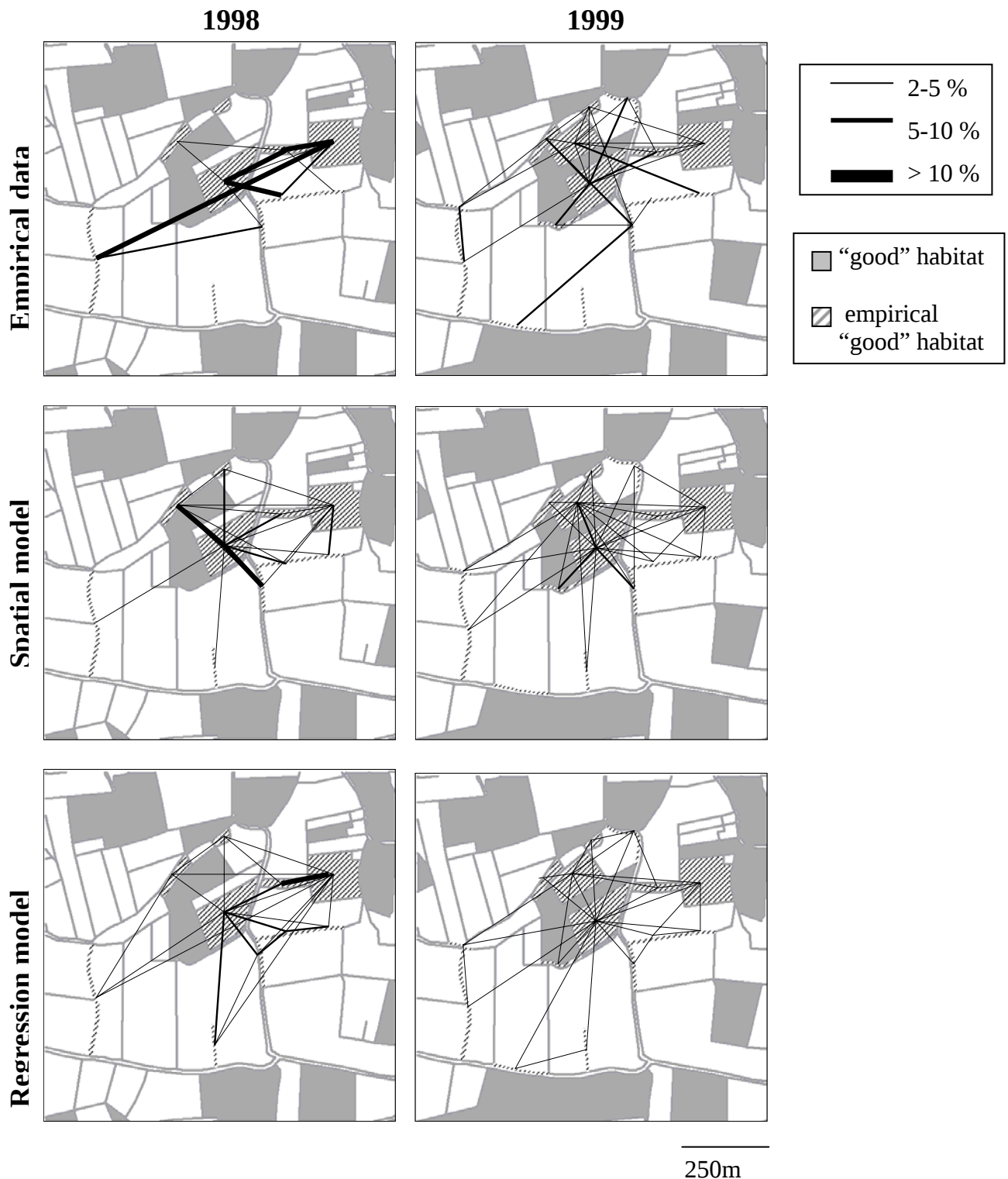


Figure 5.2. Spatial distribution of butterfly fluxes (% of moving individuals) as predicted by the spatial model (middle) and the regression model (bottom) compared with spatial distribution of observed fluxes. Results are presented for two years, 1998-1999 and site 2. Fluxes lower than 2% are not depicted.

Table 5.2. Results of the Mantel's test – probabilities that the matrices of fluxes predicted by the spatial model and observed fluxes are independent of each other. The diagonals of the matrices were not considered.

Mean distance of flight (m)	Site 1		Site 2	
	1998	1999	1998	1999
5	0.001	0.001	0.099	0.001
10	0.002	0.001	0.100	0.001
15	0.001	0.001	0.082	0.001
20	0.003	0.001	0.100	0.001
25	0.002	0.001	0.100	0.001
30	0.002	0.001	0.106	0.001
35	0.002	0.001	0.102	0.001
40	0.003	0.001	0.121	0.001
45	0.001	0.001	0.093	0.001
50	0.001	0.001	0.101	0.001
55	0.002	0.001	0.081	0.001
60	0.003	0.001	0.091	0.001
65	0.003	0.001	0.088	0.001
70	0.002	0.001	0.078	0.001
75	0.003	0.001	0.080	0.001
80	0.001	0.001	0.071	0.001
85	0.005	0.001	0.076	0.001
90	0.002	0.001	0.064	0.001
95	0.003	0.001	0.083	0.001
100	0.005	0.001	0.066	0.001

3.2. Comparison of predictions of the regression model with observed data

Figures 5.1 and 5.2 enable comparison of the predictions of the regression model with the empirical capture-recapture data for sites 1 and 2 respectively, and for two years, 1998 and 1999. Mantel's tests have shown that the differences between the matrices of observed fluxes vs. those predicted by the regression model for both sites in the two years were not statistically significant ($P < 0.01$), which means that even the predictions of the regression model were similar to the observed data.

Table 5.1 shows that the proportions of immigrants and inter-patch fluxes predicted by the regression model were significantly positively correlated with the observed data at both sites in 1999, that the patch area was significantly positively correlated with the proportion of immigrants at site 2 in both years, and that the observed inter-patch fluxes were significantly negatively correlated with inter-patch distance except at site 2 in 1998.

Table 5.3 shows that the proportions of residents and those of immigrants were larger in large patches.

Table 5.3. Observed proportions of residents and immigrants in empirical patches for both sites and both years.

	Site 1			Site 2		
	Patch number	Residents	Immigrants	Patch number	Residents	Immigrants
1998	1	40	2	1	63	13
	2	85	60	2	86	75
	3	79	3	3	100	6
	4	85	18	4	75	4
	5	89	42	5	91	4
	6	75	19	6	0	0
	7	80	13	7	50	9
	8	50	1	8	85	30
				9	100	10
				10	100	0
1999	1	0	0	1	24	39
	2	62	126	2	47	38
	3	13	47	3	50	0
	4	11	34	4	100	19
	5	89	35	5	29	78
	6	53	16	6	0	0
	7	75	35	7	82	55
	8	25	2	8	60	229
	9	37	96	9	57	54
	10	45	79	10	50	34
	11	47	86	11	0	24
	12	58	72	12	0	0
	13	86	3	13	20	1
	14	77	61	14	6	6
	15	70	61	15	62	135

3.3. Comparison of the predictions of the spatial and regression models

Results of Mantel's tests suggest that both models are able to satisfactorily predict the fluxes between the empirical patches at a very high significance level ($P < 0.01$). However, Mantel's test is rather conservative for the purpose of comparison of goodness of fit, as the difference between the pair of matrices tested has to be relatively large for the test to be significant. Thus comparison of residual sums of squares between the observed values and those predicted by the two models seems to be more adequate.

Table 5.4 shows the residual sums of squares of the non-diagonal terms for the pairs of matrices N and M (measure of fit of the spatial model) and M and $\overline{M}$ (measure of fit of the regression model). The regression model consistently gives a worse fit and in three out of the four cases the residual sum of squares for the regression model is 1.3-2.5 times larger than that for the spatial model. In addition: the regression model fits four parameters to the empirical data, while the spatial model makes its completely independent prediction, without fitting any parameters (the parameter *Mean* was not fitted – we are using its value suggested by the literature instead, rather than fitting it to the data, and subsequently we are showing

that the spatial model results are not sensitive to changes of its value). Rules of statistics suggest that such model should be preferred, which either yields a smaller residual sum of squares, or has fewer parameters, or both. Thus in this case, both criteria are in favour of the spatial model.

Table 5.4. Residual sums of squares of non-diagonal terms for the pairs of matrices N and M (measure of fit of the spatial model) and M and $\bar{M}$ (measure of fit of the regression model) for the two empirical sites and years 1998-1999.

	Site 1		Site 2	
	1998	1999	1998	1999
Spatial model	4627	11843	18795	18186
Regression model	11546	17331	24585	19169

This is further supported by the correlation coefficients presented in table 5.1. Predictions of the inter-patch fluxes are better correlated with the empirical data for the spatial model (three statistically significant correlation coefficients for the spatial model, compared with only two for the regression model), while the correlations between the predictions of the proportions of immigrants and empirical data are comparable for both models.

4. Discussion

No previous knowledge derived from this data was incorporated into the spatial model. For spatial model building, literature predictions exclusively on *Maniola jurtina* flight behaviour were used, so that the spatial model predictions are verified by using a completely independent data set. The results of Mantel's test show that the spatial model fits the empirical data well and is not too sensitive to the value of mean flight distance, *Mean*. This is further supported by the correlation coefficients presented in table 5.1 and by the residual sums of squares in table 5.4. Visual inspection of figures 5.1 and 5.2 suggests a reasonable similarity between model's predictions and empirical data.

The spatial model was based on two assumptions. The first hypothesis was that *Maniola jurtina* adopts a non-random, systematic, search strategy in which it flies in loops around the release point and returns periodically to it (Conradt *et al.*, 2000). Second, it was assumed that the landscape composition between habitat patches affects butterfly movements, i.e. that woodlands act as a barrier (Sutcliffe and Thomas, 1996; Haddad, 1999) and resource patches act as stepping-stones or corridors for butterflies. In the spatial model, hitting the barrier was simulated by changing the flight direction (point 4 in the model) and assumption of landing in a *good* patch and performing further flight afterwards (point 5 in the model and assumption of the total of 1000 flights for each butterfly) simulated *good* patches acting as stepping-stones. Despite of some obvious differences between the spatial model predictions and empirical data, our results show that the spatial model gives better predictions of butterfly movements than did the regression model based only on patch area and isolation. This

indicates that the assumptions made in the spatial model might be important for describing, how butterfly movements are affected by landscape composition.

The differences between the spatial model predictions and the observed spatial distribution and intensity of *Maniola jurtina* fluxes between habitat patches can be attributed to simplifications in the assumptions of the spatial model. All hedgerow margins were considered as suitable habitats for the meadow brown and thus as potential corridors used by butterflies for reaching other habitat patches (Dover, 1994). However, banks of some hedgerows consist of high, dense woody and shrubby vegetation, which makes them impermeable for butterflies (Fry and Robson, 1994), depending on the orientation of the hedgerow relative to the direction of butterfly movement. In addition, differences in resource quality between different habitat patches were not taken into account. In agricultural landscapes, local abundance and diversity of flowering plants is related to the farming practices conducted here: different management regimes lead to different plant species assemblages (Le Coeur *et al.*, 2002). Thus, the *good* habitats such as temporary and permanent grasslands may in reality differ in quality – as perceived by butterflies – because of differences in the diversity and abundance of flowering plants here. The management regimes of herbaceous areas might influence *Maniola jurtina*'s behaviour and distribution in resource patches, as demonstrated in previous studies for other butterfly species (Sparks and Parish, 1995; Dover, 1997b). Finally, it was assumed that all non-herbaceous areas other than woodland influenced butterfly movement in a similar way, which is a simplification of reality. As the type of the inter-patch matrix influences butterfly movements (Ricketts, 2001), a potential improvement of the model might be assigning different viscosities to the different land-covers composing the landscape matrix. For this, however, lots of extensive data sets about actual viscosity would be needed. Thus although there are potentials for improvement of the spatial model, the results show that both detailed information about flight behaviour of individuals and landscape connectivity between habitat patches are important factors, worth to be integrated in models of butterfly movements.

The differences between spatial model predictions and observed fluxes can also be explained by certain limitations inherent to butterfly sampling. Studying movement at the landscape scale is problematic because of the difficulty to realise exhaustive and large-scale sampling in the field. The surface area of the studied landscapes was thus limited to 1 km² for practical reasons. The scale of the study area has a major impact on the results of mark-release investigations, and large-scale studies are recommended to get a more accurate view of butterfly dispersal ability (Schneider, 2003). Mark-release-recapture methods can underestimate long-distance dispersers, especially for species that live in patchy habitats in fragmented landscapes (Wilson and Thomas, 2002). Thus, because of the relatively small scale of the sampling caused by limitations in manpower and the bias inherent to mark-release-recapture methods, the study might thus underestimate long-distance movements of butterflies in the landscape.

The question remains, whether the spatial model gives a significant improvement, compared with much simpler approaches, which generate colonization patterns for patches depending on variables such as patch size and isolation (the regression models). Figures 5.1 and 5.2, table 5.1 and especially table 5.4 provide a partial answer. In most cases, the spatial model based on the assumptions of Conradt *et al.* (2000) and Schneider *et al.* (2003) gives either a considerably better, or at least comparable prediction of actual butterfly fluxes than a simple prediction of the regression model based on patch size and distance between patches. Thus if data are available about the actual landscape under consideration, the spatial model

should be preferred to the regression model. However, in general theoretical considerations the regression model based on patch size and the degree of its isolation will retain its value.

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**CHAPITRE 6 : CONSERVATION OF BUTTERFLY POPULATIONS IN
DYNAMIC LANDSCAPES – THE ROLE OF FARMING PRACTICES
AND LANDSCAPE MOSAIC**

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Résumé

Dans ce travail, nous avons étudié les effets de la dynamique du paysage sous l'effet de pratiques agricoles répétées (fauche des prairies) sur les mouvements et la distribution d'un papillon diurne, *Maniola jurtina* L. (Satyridae). Nous avons utilisé un modèle de simulation existant, validé au moyen de données issues d'observations in situ du mouvement des papillons, pour prédire l'évolution des populations de papillons en milieu agricole selon différents scénarios d'intensité de perturbation (proportion de prairies fauchées au sein du paysage) et de régime de gestion (date de fauche dans la saison, i.e. période d'activité des papillons). L'augmentation de la quantité d'habitats perturbés au sein du paysage se traduit par une isolation croissante des taches d'habitats restantes pour les papillons. Cela conduit à une réduction des mouvements de papillons entre les taches et à plus long terme à un déclin marqué des populations dans les taches d'habitat. Ces modifications varient en fonction de la date de fauche dans la saison, la fauche en début de saison étant la plus néfaste pour les papillons. Jusqu'à présent, l'influence de la dynamique des paysages agricoles sur la survie des espèces a été étudiée en considérant les changements durables tels que la réduction des milieux boisés. Nos résultats montrent cependant que l'effet de la dynamique du paysage à plus court terme sous l'influence des régimes de pratiques agricoles ne devrait pas être négligée.

1. Introduction

During the last decades, evaluating consequences of landscape dynamics under human pressure on ecological processes that may lead to species extinctions became a central issue in landscape ecology and conservation biology. In agricultural landscapes, intensification of production and practices led to drastic changes of landscapes in many areas of Western Europe (Agger and Brandt, 1988), which caused a major loss of biodiversity (McLaughlin and Mineau, 1995; Wilson *et al.*, 1999). Understanding impacts of such changes is thus crucial for determination of the driving factors for species survival in agricultural landscapes and for elaboration of conservation plans (Baker, 1989; Meeus, 1995).

Species distribution and survival in heterogeneous landscapes is mainly driven by their movement (Wiens *et al.*, 1993b; Wiens *et al.*, 1997; McIntyre and Wiens, 1999), this being either dispersal at the metapopulation level (Taylor, 1990; Johnson *et al.*, 1992; Hanski *et al.*, 1996; Szacki, 1999) or daily movements of individuals for foraging and breeding (Wiklund, 1977; Dunning *et al.*, 1992; Brommer and Fred, 1999). Interactions between species movement and landscape patterns are expressed by landscape connectivity (“the degree to which the landscape facilitates or impedes movement” - Taylor *et al.*, 1993). There is an ongoing debate on how connectivity should be measured. Metapopulation biologists visualise landscapes as habitats embedded in a neutral matrix (Bennett, 1990; Verboom and van Apeldoorn, 1990; Moilanen and Hanski, 2001). On the contrary, landscape ecologists consider landscape connectivity as depending not only on distance between habitat patches, but also on the presence of stepping-stones and corridors, and on the matrix heterogeneity (Pain *et al.*, 2000; Ricketts, 2001; Tischendorf and Fahrig, 2001). Measures of connectivity in agricultural landscapes should thus integrate the presence and spatial arrangement of permanent structures like hedgerows or woodlots, as well as the heterogeneity of the agricultural mosaic (With *et al.*, 1997).

The effect of farming activities on the dynamics of agricultural landscapes can be seen at different temporal scales. At the long-term scale, changes in farming systems induce strong and durable changes in the landscape (field size, amount of uncultivated or cropped areas). At the short-term scale, land-use successions between years, and crop growth and farming practices within a year also change the landscape mosaic. Thus, considering the dynamics of agricultural landscapes under different farming practices is crucial for understanding, how species move and ultimately survive there. However, only few studies investigating interactions between species movement and landscape structure in agricultural landscapes have considered the effects of farming activities (Baudry *et al.*, 2003). In this paper, we focused on the consequences of landscape dynamics under different farming practices on species movement and distribution, using butterflies as a reference group.

In agricultural landscapes, most butterfly species are restricted to uncultivated herbaceous elements, such as field margins and hedgerows (Dover, 1994), or grasslands and meadows (Oates, 1995). Types and regimes of management of these herbaceous areas, i.e. spraying by herbicides or fertilisers, grazing or mowing are critical for butterfly survival, as they drastically modify habitat quality for butterflies by suppressing the availability of nectar-offering plants providing food for adults, of plants suitable for butterfly oviposition and of tall vegetation that can be used as refuges (Oates, 1995). Impacts of farming practices on butterfly survival are dependent on timing of the disturbance within the period of butterfly activity (Oates, 1995). Badly timed practices can produce inappropriate conditions for adults or larvae, and cause populations to collapse (Feber and Smith, 1995; Oates, 1995). Farming

practices cause changes in the distribution of resource patches, in spatial heterogeneity and in connectivity at the landscape level. Such changes are expected to influence butterfly abundance (Thomas, 1991a) and survival at the long term (Kuussaari *et al.*, 1996).

Here we used a modelling approach to study, how landscape dynamics induced by mowing of meadows can influence the distribution and abundance of the meadow brown (*Maniola jurtina* L., Satyridae) over years. Models of species movements often simply assume random movement of organisms (Hanski, 1998) and generate colonization patterns for patches depending mainly on patch size and isolation. However, a truly realistic model of organism movement should consider both the heterogeneity of the landscape, the requirements of individuals and their dispersal distance (Vos *et al.*, 2001). Therefore we used here a model we had developed previously, which assumes that the meadow brown uses a non-random, systematic, search strategy when dispersing, and that the composition of the landscape between resource patches affects its movements (Kindlmann *et al.*, In press). We simulated the evolution of butterfly distribution and abundance in agricultural landscapes depending on different scenarios of disturbance. Existing field data on the effect of mowing on butterfly movement were used to see, how the model perceives such changes. We studied, whether repeated mowing over years would lead to a decline of butterfly populations, as a consequence of the progressive isolation of remnant resource patches, whether this decline depends on the amount of disturbed habitats and/or on the timing of mowing within the period of butterfly activity.

2. Methods

2.1. Study area

The study was conducted in a 1km² landscape unit in Western France (Northern Brittany) (figure 6.1), representing fine-grained hedgerow network landscape (“bocage”). Agriculture in this landscape is oriented toward milk production; maize, wheat and grasslands for pasture cover the majority of land. It is characterised by a large proportion of arable land devoted to meadows (53% of the land) and only few cropped areas of maize and other cereals (33%). It also has a high density of hedgerows and grassy field margins (322 meters / ha), and fine grain size (average field size: 0.55 ± 0.53 ha). Meadows are either used as pastures or mown for animal forage.

2.2. Butterfly movement sampling

Sampling of *Maniola jurtina* movements was conducted in the year 2000, in ten herbaceous patches, i.e. 6 meadows, two road verges and two lanes, using mark-release-recapture methods (figure 6.1). One meadow among the studied meadows was mown during the experiment; the mark-release-recapture experiments were conducted for seven days before and seven days after mowing. The experiment was realised during the main peak of activity of *Maniola jurtina*, i.e. end june – ealy july, as observed previously in the same study area (Annie Ouin, unpublished data). Thus, the comparisons between before and after mowing of meadow could not be biased by emergence patterns of butterflies. Every day, one mark-release-recapture session was performed, which consisted of successive sampling of all the patches in a fixed sequence and was performed within one day. During each session, butterflies that were captured for the first time were identified by individual numbers on wing

(with no-odour pen), and released thereafter. At the same time, their capture location, i.e. patch number, was recorded.

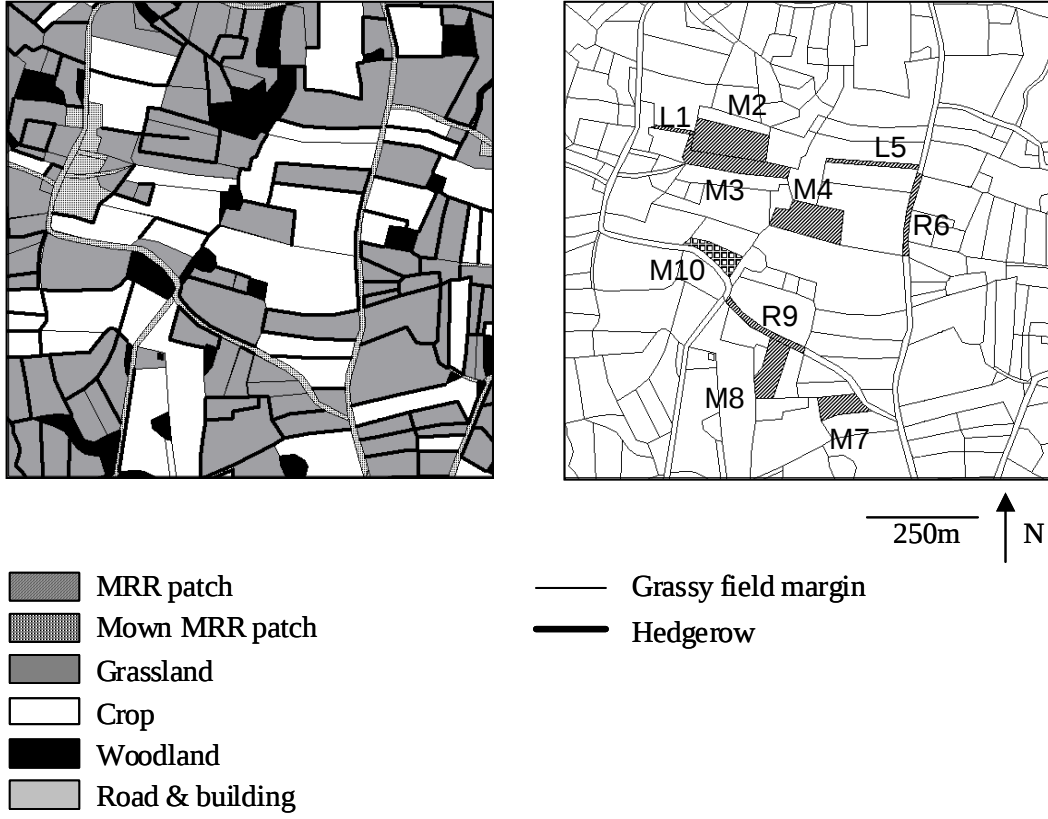


Figure 6.1. Study area and Mark-Release-Recapture experimental patches in 2000. M: meadow, L: lane, R: road verge.

When recapturing butterflies, individual's number and recapture location were recorded. The time spent in each patch was proportional to its surface area to maintain a constant sampling intensity.

The flux from patch i to patch j was calculated as:

$$M'_{ij} = 100 \cdot \frac{M_{ij}}{\sum_{k=1}^n M_{ik}}, i \neq j,$$

where M_{ij} is the number of recaptures in patch j (at any time during the experiment) of individuals, which were captured in patch i ; capture means the *first* capture of an individual – when it was marked – and recapture the subsequent recapture of this individual (no individual was recaptured more than once in our data).

Proportion of residents, M'_{ii} , was estimated for each patch as the proportion of individuals recaptured in the same patch:

$$M'_{ii} = 100 \cdot \frac{M_{ii}}{\sum_{k=1}^n M_{ik}}.$$

Proportion of immigrants, I_i , was defined for each patch as the percentage of individuals entering patch i , out of the total number of recaptured individuals:

$$I_i = 100 \times \frac{\sum_{j=1}^n M_{ji}}{\sum_{k,l=1}^n M_{kl}}$$

Number of butterflies in each patch was finally defined as the sum of immigrants I_i and residents M'_{ii} .

2.3. The within-year model

The studied landscape was considered as a mosaic of 5×5 m pixels, so that each of the experimental patches consisted of many pixels. Each of the pixels was characterized according to the value of its land cover in terms of habitat quality for butterflies: *good* habitat (grassland, grassy field margin, and hedgerow margin) and *bad* habitat (water, woodland and fallow land, crop, and road and building). It was assumed that woodlands acted as a barrier for butterfly movements, according to the grassland status of the meadow brown. Consistently with Conradt *et al.* (2000), it was assumed that the butterflies are using a non-random, systematic search strategy in which they fly in loops around the starting point and return periodically to it, provided they do not find a *good* habitat. In the model, this was performed as follows:

1. In each step, the direction of flight, *Dir*, and its length, *Length*, were chosen at random.
2. Direction of flight was chosen from a uniform distribution, $Dir \in <0;360^\circ>$.
3. Following Schneider *et al.* (2003), length of flight, *Length*, was chosen from a negative exponential distribution with a constant mean, *Mean*. *Mean* = 70 m was chosen for the main simulation, as it is the commonest mean distance of flight of *Maniola jurtina* (Schneider, 2003; Schneider *et al.*, 2003).
4. The individual was assumed to move linearly in the direction *Dir* for a distance *Length*. If at any time during the flight the individual hit a woodland or fallow land, it was assumed to land. If the individual hit area boundary during the flight, it was allowed to leave the system.
5. If the individual starting from pixel P_s did not hit any woodland or fallow land or area boundary during the flight in the direction *Dir* for a distance *Length*, and if after having completed the whole flight it arrived to a pixel P_a , it was assumed to land in P_a , if either P_a was *good*, or if P_s was *bad* (which might have happened, if it hit woodland during the previous flight). If P_s was *good* and P_a was *bad*, it was assumed to return to P_s and land there.
6. In the next step, the butterfly was assumed to take off from the point, where it had landed in the previous step, as defined in points 4 and 5, and the whole procedure starting from point 1 was repeated.

In each of the experimental patches within the landscape, an initial position of the butterfly was chosen at random and the procedure described above (points 1 – 6) was performed 10 times, so simulating 10 flights of one butterfly, the first one starting in the pixel selected, the second one starting in the pixel, where the butterfly landed after having performed the first flight (as defined in points 4 and 5), etc. This was repeated 1000 times for each patch selected.

N_{ij} was then calculated as the number of times any of the experimental butterflies, the initial position of which was in patch i , landed in patch j after having completed 10 flights. In order to make this value comparable with the empirical fluxes, M'_{ij} , and with the empirically obtained proportions of residents, M'_{ii} , we used the transformation

$$N'_{ij} = 100 \cdot \frac{N_{ij}}{\sum_{k=1}^n N_{ik}},$$

and compared then N'_{ij} with M'_{ij} .

To simulate the effect of mowing, unmown meadows were considered as a *good* habitat, while mown meadows were considered as a *bad* habitat. We considered three scenarios: mowing *before* the butterflies begin to activate on wing, in which case the mown meadow was considered as *bad* habitat during all 10 flights, mowing *during* the season, in which case the mown meadow was considered as a *good* habitat during the first 5 flights, and as a *bad* habitat during the last 5 flights, and mowing *after* the season of butterfly activity (equivalent to *absence* of mowing from the point of view of the butterfly), in which case the meadow was considered as *good* habitat during all 10 flights.

2.4. Comparison of the model predictions with empirical data

Similarity between the matrices of predicted vs. observed fluxes, i.e. between the matrices $N = (N'_{ij})$ and $M = (M'_{ij})$ was then tested by means of Mantel's test (Mantel, 1967). Significance levels were determined by performing 1000 permutations for the test (Manly, 1998). Only the similarity of inter-patch fluxes between the observed and predicted values was compared and therefore the diagonals of the matrices (proportions of residents) were deleted from the permutation tests. In addition, to compare the goodness-of-fit of the model, residual sums of squares of non-diagonal terms for the pairs of matrices N and M (measure of fit of the model) were calculated. Pearson's correlation coefficients in the SYSTAT (Systat Software Inc., USA) package were used to calculate the correlations between the proportions of residents and immigrants predicted by the model and those observed, and between the inter-patch fluxes and those predicted by the model.

2.5. Between-years model

To simulate the between-years dynamics of the butterflies, we assumed that the numbers of eggs laid in a patch are proportional to N'_{ij} . This means that we followed only females in the simulation. Provided the sex ratio is constant during the season and close to 1:1, this is a reasonable assumption. The number of eggs laid in one year was then assumed to be proportional to the number of butterflies, which appear in the patch the next year, the

constant of proportionality, K , reflecting the combined effect of the number of eggs laid per one butterfly and of their survival to the adult stage. We iterated each scenario for 10 years, in order to see the long-term effect of different management regimes on the population dynamics of the butterflies. This simulation was repeated for the following scenarios:

- No disturbance: no meadows mown during the 10 years,
- Low disturbance intensity: part of meadows mown each year during the 10 years, representing about 20% of the area covered by all meadows,
- High disturbance intensity: part of meadows mown each year during the 10 years, representing about 80% of the area covered by all meadows.

In each of the last two scenarios, mowing at the beginning, during, and at the end of the season (the last option is equivalent to absence of mowing) was considered.

Figure 6.2 shows the composition of the landscape in terms of good habitats for butterflies for each of the three scenarios after mowing. In the scenario of low disturbance intensity, the landscape still has numerous patches of *good* habitat (meadows), while in the scenario of high disturbance intensity, almost exclusively linear *good* habitats (field margins) remain in the landscape.

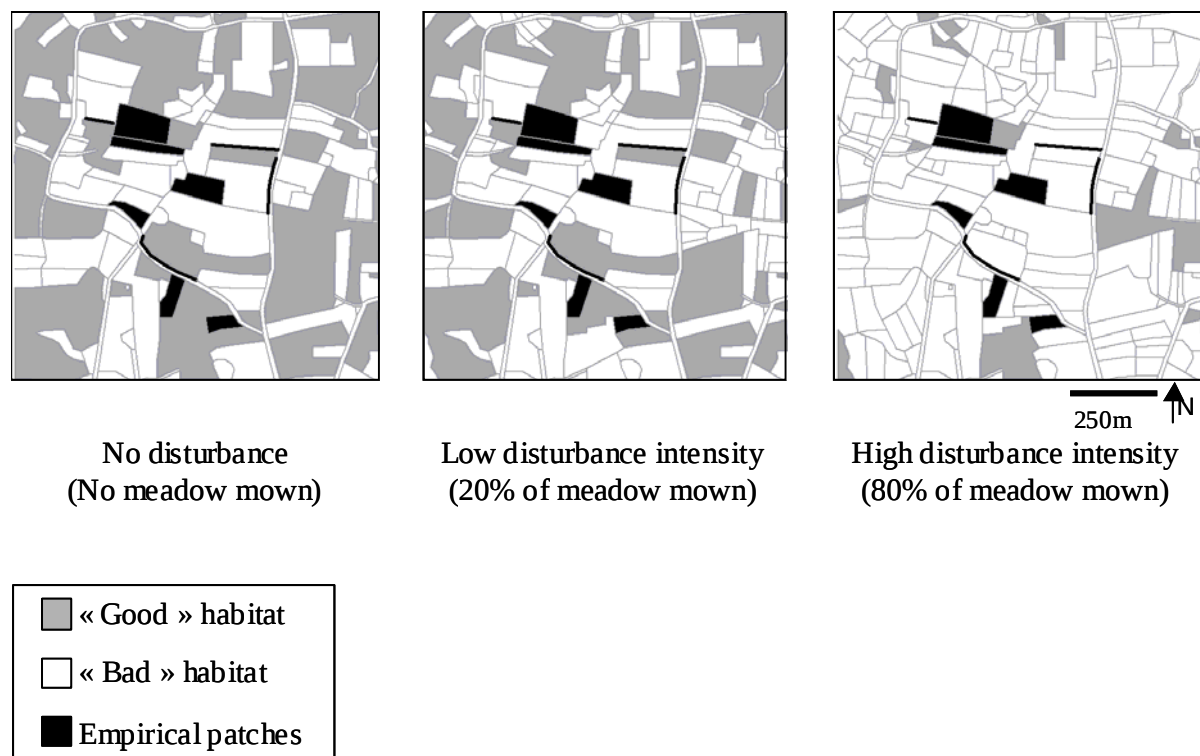


Figure 6.2. Landscape pattern for the three disturbance scenarios (left: scenario 1 = no disturbance i.e. no meadows mown; middle: scenario 2 = low disturbance intensity i.e. 20% of meadows mown; right: scenario 3: high disturbance intensity i.e. 80% of meadows mown).

3. Results

3.1. Comparison of the observed and predicted butterfly numbers within a year

Figure 6.3 shows the comparison of the observed and predicted numbers of butterflies in the patches, measured as $\sum_i N_{ij}$, in the periods before and after mowing. A striking similarity of the model predictions and empirical data is evident. According to the Mantel's tests the probabilities that the matrices of the observed fluxes vs. those predicted by the model differ from each other are $P < 0.001$ for both the before and after mowing situations. Predicted numbers of butterflies in patches were statistically significantly positively correlated with the observed ones, both before and after mowing (Pearson correlations: before mowing: $r=0.72$, $P < 0.05$; after mowing: $r=0.42$, $P < 0.05$).

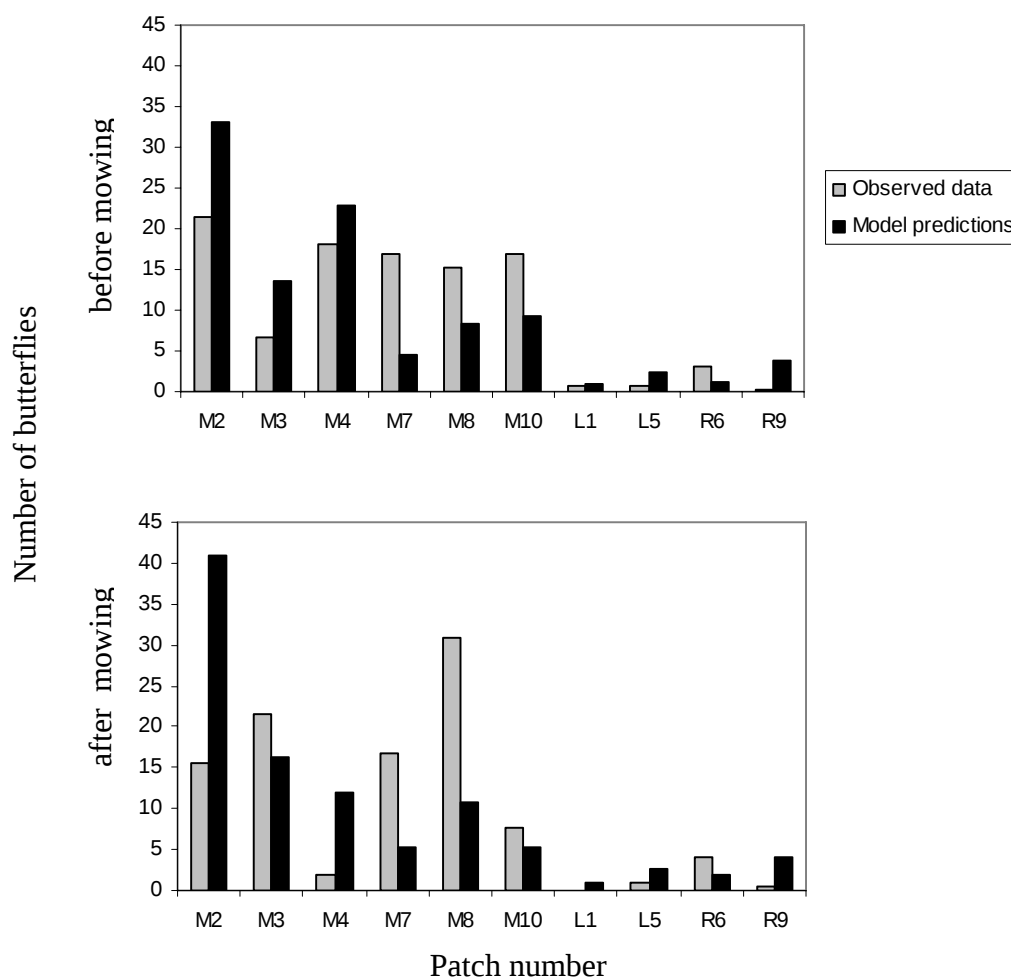


Figure 6.3. Numbers of butterflies in empirical patches observed in 2000 and predicted by the model before (top) and after mowing (bottom). M: meadow; L: lane, R: road verge.

Thus it can be concluded that the model satisfactorily mimics the real situation, similarly to Kindlmann *et al.* (In press). As observed during experiment, the model predicted a high aggregation of butterflies in some meadows; e.g. in meadow # 2, compared with linear features, road verges and lanes. This result suggests that linear features were less accessible

for butterflies, as the distribution of individuals predicted by the model depends on the interaction between butterfly movement and the landscape pattern.

Figure 6.4 shows the comparison of the differences between the numbers of butterflies in individual patches before and after mowing in empirical data and those predicted by the model. Again, predicted differences between the numbers of butterflies in patches before and after mowing were significantly correlated with the empirical ones (Pearson correlation: $r=0.58$, $P<0.05$). It is clearly seen that the butterfly abundances in the mown patches decreased considerably, while those in unmown meadows increased and those in linear habitats (road verges and lane banks) were not significantly affected.

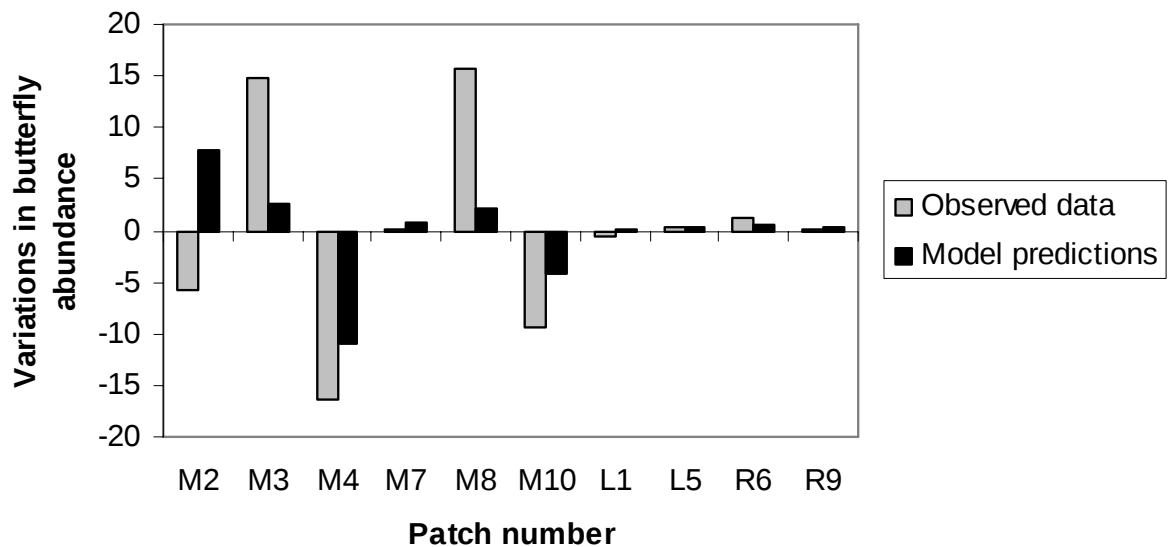


Figure 6.4. Fluctuations in butterfly numbers in empirical patches observed in 2000 and predicted by the model before (top) and after mowing (bottom). M: meadow; L: lane, R: road verge.

3.2. Predicted long-term effect of agricultural practices on butterfly population dynamics

Figure 6.5 shows the development of the butterfly population under the two scenarios of disturbance intensity (20% and 80% of meadows mown respectively) and the differing management regimes: no meadows mown during the 10 years (equivalent to late mowing), meadows mown during the period of butterfly activity each year during the 10 years, and meadows early mown each year during the 10 years. All these simulations were performed for three different values of the constant K ($K=1000$, 800, 600), as we did not have any information about its actual value.

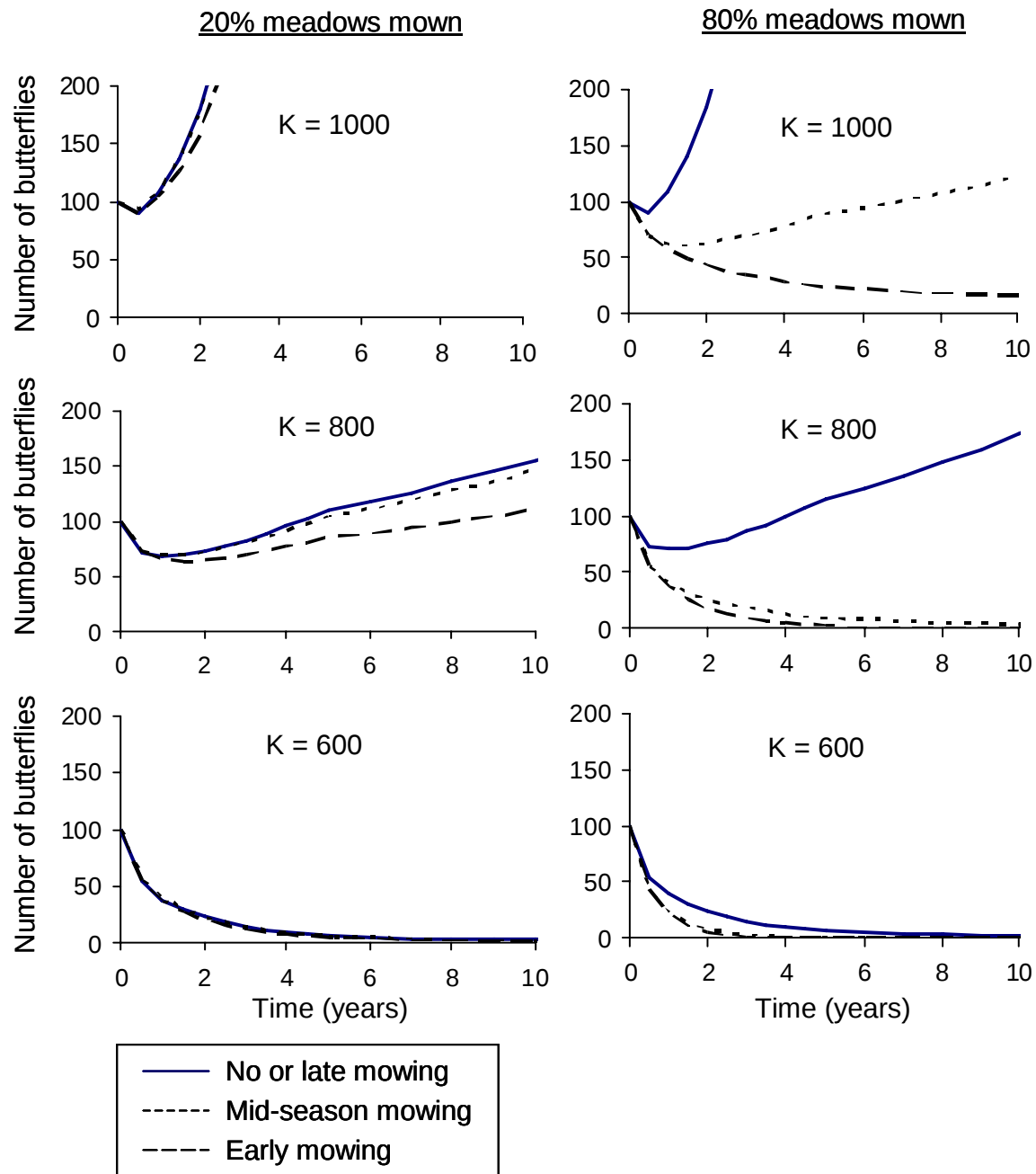


Figure 6.5. Between-years variations in total butterfly numbers for the two scenarios (left: 20% of meadows mown; right: 80% of meadows mown) depending on the different management regimes (no or late mowing, mid-season mowing, early mowing) and the values of the constant K ($K=1000$, 800, 600).

Quite clearly, there are dramatic differences in terms of the fate of the population between different management regimes applied to the patches in question.

Absence of mowing resulted in survival of the butterfly population for values of the constant K equal to 1000 and 800. This was illustrated by an increase in total butterfly numbers, which was especially conspicuous for $K=1000$ and more moderate for $K=800$ (figure 6.5). Absence of mowing during the 10 years led to a decline in butterfly numbers for the smallest value of K ($K=600$) – in biological terms, when butterfly fecundity was very low and/or their juvenile mortality was very large.

Repeated mowing over the years had different effects on the development of butterfly population depending on disturbance intensity. Repeated mowing did not affect the survival of butterfly populations for low disturbance intensity (20% of meadows mown), as illustrated by the increase in butterfly abundance over years for constant $K=1000$ and 800 (figure 6.5). For the smallest value of K ($K=600$), mowing at low intensity led to a drop in butterfly numbers (figure 6.5). On the contrary, intensive mowing (80% of meadows mown), especially early in the season, often had fatal effects on the survival of the butterfly population, as illustrated by the drop in total butterfly numbers (figure 6.5). The model predicted almost complete decline of population after three or five years of repeated disturbance (mowing) for constant $K=600$ and 800 respectively. On the contrary, the model predicted a strong decline of the population in the case of early mowing and a slight increase in butterfly numbers for mid-season mowing for the largest value of K .

3.3. Long-term dynamics of butterfly populations in individual patches

Figure 6.6 illustrates the relative fluctuations of butterfly abundance in individual patches between the first and the tenth year of simulations for low (20% of meadows mown) and high intensity of disturbance (80% of meadows mown) respectively, under the three management regimes (no or late mowing, mid-season mowing and early mowing). Clearly, the variations in butterfly numbers were not similar in the different patches depending on the intensity of disturbance and the type of management regimes, suggesting different degrees of patch isolation for butterflies.

Absence of mowing during the 10 years led to an increase in butterfly numbers in all patches for $K=1000$, which was proportionally more pronounced in some meadows (e.g. meadows # 2, 3 and 4), compared with other meadows (meadows # 7 and 8) and linear features (figure 6.6). This confirms that the latter patches were less accessible for butterflies. The pattern predicted for $K=800$ was similar, the exception being a slight drop of butterfly numbers in linear features and meadows # 7 and 8. For the smallest value of K ($K=600$), absence of mowing induced a decrease in butterfly abundance, proportionally higher in the less isolated patches, according to the overall decline of the butterfly population (figure 6.6).

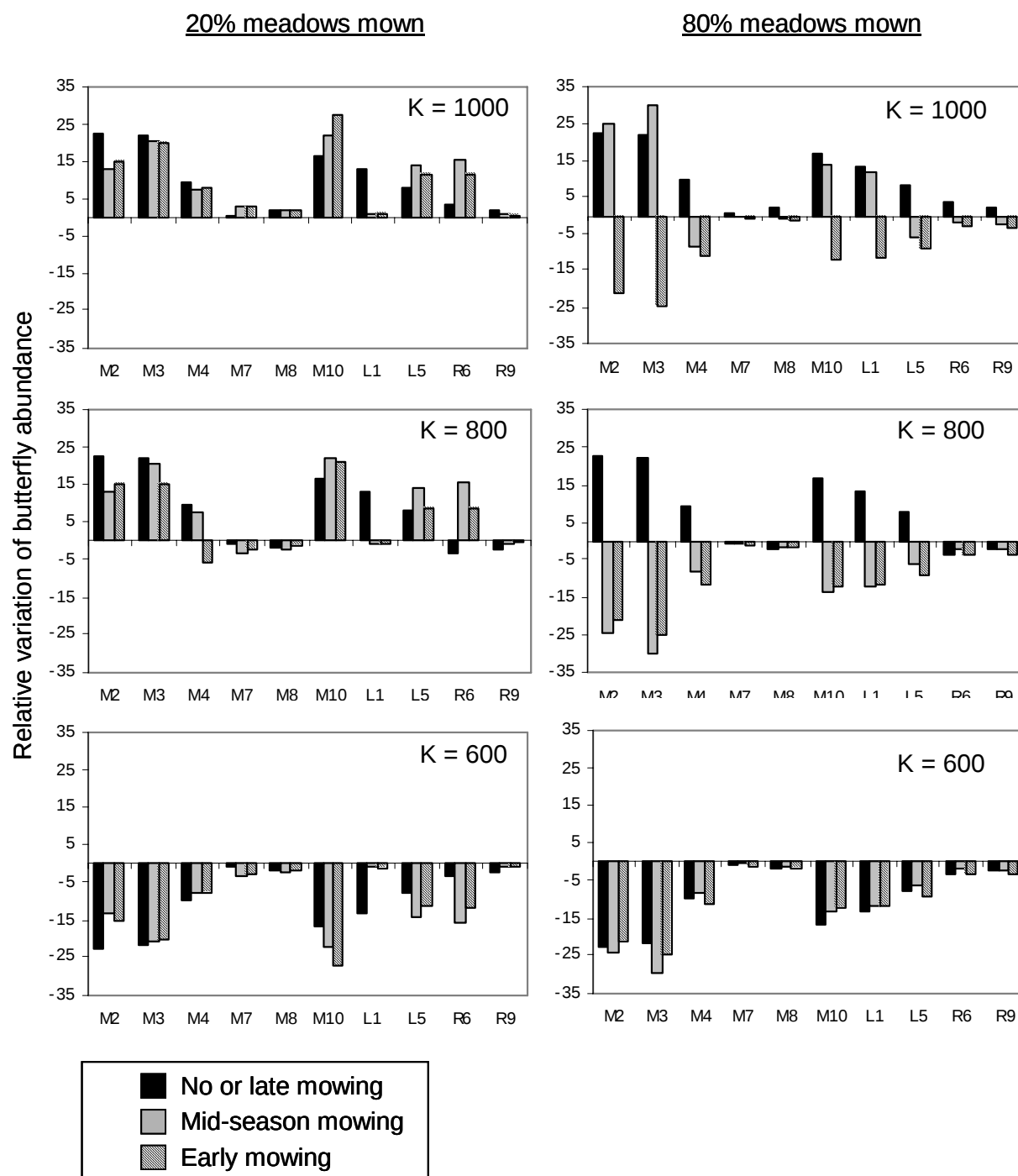


Figure 6.6. Relative variation rate of butterfly numbers in individual patches, between the first and the tenth year of simulation for the two scenarios (left: 20% of meadows mown; right: 80% of meadows mown) depending on the different management regimes (no or late mowing, mid-season mowing, early mowing) and the values of the constant K ($K=1000, 800, 600$). M: meadow, L: lane, R: road verge.

For low intensity of disturbance, mowing over years, either early or during the season, led to an increase in butterfly numbers in all patches especially pronounced in the more accessible ones (e.g. meadows # 2, 3, 10) for the highest value of the constant K ($K=1000$) (figure 6.6). For $K=800$, mowing at low intensity caused a slight drop in butterfly numbers in the more isolated patches (meadows # 7 and 8, road verge # 9) and an increase in butterfly population in other patches (figure 6.6). For the smallest value of the constant K ($K=600$), low intensive mowing led to an overall decline of butterfly populations proportionally more pronounced in the less isolated patches (figure 6.6).

For high intensity of disturbance, mid-season mowing during the 10 years resulted in a drop of butterfly numbers in the isolated patches and an increase of butterfly population proportionally more conspicuous in accessible meadows, for constant $K=1000$ (figure 6.6). For other scenarios of management regimes (mid-season mowing for $K=800$ and 600, and early mowing), mowing at high intensity resulted in a decline of butterfly populations proportionally higher in the less isolated patches, in accord with the predicted population extinction (figure 6.6).

4. Discussion

4.1. Predicted effects of repeated disturbances on the long-term dynamics of butterfly populations

Our model predicted that farming practices such as mowing might lead to significant changes in the abundance of butterfly populations and affect their long-term survival. These changes are dependent on two factors: the amount of meadows in the landscape mown each year, i.e., the intensity of disturbance, and the timing of mowing in the period of butterfly activity.

According to the assumptions made in the model, the predicted distribution of butterflies in the landscape reflects their ability to reach herbaceous habitats, i.e., the connectivity of the landscape: it depends on the presence of stepping-stone habitats (meadows) and of corridors (field margins) between resources patches, but also on the presence of landscape elements that act as barriers for butterfly movements, woodlands in our case (Kindlmann *et al.*, In press). The model predicted that mowing of herbaceous patches results in progressive isolation of butterfly populations in some herbaceous patches over years, leading ultimately to population extinction. Disturbances cause changes in spatial heterogeneity of landscapes and in the distribution of habitat patches at the landscape scale (Denslow, 1985). Here, we can expect that mowing of meadows led to significant changes in landscape connectivity and modified the chance for butterflies to reach suitable resource patches, mown areas impeding butterfly movements between resources patches. The predicted response of butterfly populations to mowing differed depending on the amount of disturbed habitats in the landscape: low disturbance intensity (20% of meadows mown) allowed the persistence or expansion of butterfly populations in contrary to what was observed in the scenario with high disturbance intensity (80% of meadows mown). This can be related to the different landscape patterns that resulted from mowing in the two scenarios. Low disturbance intensity allowed persistence of some large herbaceous patches, whereas in the scenario with high disturbance intensity, the remaining suitable habitats were almost only field margins. We can expect that butterfly populations are sensitive to the degree of change in landscape connectivity according to the amount of disturbed habitats in the landscape. Although field

margins can play an important role for butterflies as corridors or habitats (Dover, 1989; Fry and Robson, 1994; Dover, 1996), they might be not sufficient for the survival of butterfly populations in the long term.

Understanding the effects of landscape pattern on ecological processes and of the causes of changes therein is one of the major challenges in landscape ecology and conservation biology. Until now, most studies have focused on changes in uncultivated habitats, e.g. forest cover, but few have considered the role of farming activities in the landscape dynamics (Baudry *et al.*, 2003). Our study has shown that farming practices should be considered explicitly to understand how the landscape dynamics could affect survival of species associated with agricultural habitats, especially those with low mobility. *Maniola jurtina* does not have exact requirements for oviposition or for larval and adult food (Feber, 1993), but it has a limited mobility in comparison with other farmland butterfly species. The temporal and spatial structure of agricultural land acts against the persistence of populations of less mobile species (Feber and Smith, 1995). Major disruptions caused by farming practices, which characterise agricultural habitats, make the supply of resources unpredictable (MacDonald and Smith, 1991). Because of this temporal and spatial patchiness, the habitat may be underutilised simply because many butterfly species are insufficiently mobile to respond to the changing distribution of resources.

Our model predicted that timing of mowing in the season is crucial for the persistence of butterfly populations, early-season mowing having the strongest negative impact. Our results are consistent with previous knowledge on the effect of timing of farming practices. Mowing in summer can affect species that are on the wing at that time (Feber *et al.*, 1996). Badly timed grazing or mowing will produce inappropriate conditions for butterflies, which will cause butterfly populations to collapse (Oates, 1995). Meadows, which are cut late or in mid-summer, can support vast populations of grassy-feeding species such as *Maniola jurtina* (Oates, 1995). Late cutting has two advantages for butterflies: it provides a continuous supply of nectar resources and undisturbed habitat in which females can oviposit and/or the larvae can feed or complete their development (Feber and Smith, 1995). The effect of timing of mowing on the survival of the butterfly populations can sometimes have quite unexpected effects on the optimal management regimes of certain specific conservation areas, where protection of different species is the aim. E.g., we know of a nature reserve (Milikovice in the Czech Republic) that contains an endangered orchid, *Dactylorhiza majalis*, and an endangered butterfly, *Maculinea telejus*. The larvae of the latter live on *Sanguisorba officinalis*, which flowers in July, while *D. majalis* is in bloom in June. As *D. majalis* requires regular mowing for its proper development and long-term survival, the site has been regularly mown after *D. majalis* fruited, but sometimes before *S. officinalis* has finished flowering. This management resulted in a flourishing population of *D. majalis*, but – because of its host plant was cut – a decline in abundance of *M. telejus* after about 10 years.

4.2. Understanding species dynamics in agricultural landscapes: limitations and contributions of the present modelling approach

Simulations of the between-years dynamics of butterfly populations were based on the parameter K , reflecting the fecundity of females and the larvae survival to the adult stage, i.e. the reproductive success of butterflies. Simulations were performed with three value of this constant ($K = 1000, 800, 600$). We did not have any information about the actual value of this parameter for *Maniola jurtina*, but the values considered in simulations are obviously not

realistic in a quantitative point of view. The model appeared to be highly sensitive to the value of K as demonstrated by the contrasted predicted patterns for the three tested values. This underlines the need for a better calibration of the model to this input parameter, so that more realistic values of the reproductive success of the Meadow Brown can be integrated. Nevertheless, the values of reproductive success of *Maniola jurtina* in the between-years model remains meaningful in a qualitative point of view, as illustrated by our results.

Empirical studies of the dynamics of populations are problematic because of the difficulty to realize long-term sampling and to replicate observations at the landscape scale. In this context, modeling allows to formalize hypotheses about population functioning (Fahrig, 1991) and to replicate experiments on a range of various landscapes (Turner *et al.*, 1995). Here, simulations were restricted to one case study area, especially to a “bocage” landscape exhibiting a dense network of herbaceous patches, and to a fine spatial scale (1km²) to allow comparisons between model predictions and empirical data. Movement patterns, population structure and dynamics may differ according to the scale of the study (Hill *et al.*, 1996; Schneider, 2003) and to the landscape pattern of a particular study area (Stith *et al.*, 1996). Thus, one must keep in mind that the results are specific to the scale of the present study area and that they can not be extrapolated to more fragmented and intensively cultivated landscapes. Further simulations should be conducted on a range of various landscapes with different amount and spatial arrangement of herbaceous habitats and at different spatial scales to determine to what extent the model predictions vary according to these parameters.

Movement and species distribution have often been simulated in neutral landscapes (Gardner *et al.*, 1987; Gardner and O'Neill, 1991; With *et al.*, 1999). In neutral models, landscapes represent regular grids composed of good habitats and a hostile matrix and individuals are expected to move randomly between good habitats. The use of real landscapes in simulations permits to relate environmental processes and societal aspects of the landscapes. Here, results of comparison of the actual and predicted fluxes within a year strongly support the assumption that farming practices such as mowing can simply be modelled for *Maniola jurtina* by assuming that the corresponding habitat character changes from being *good* to being *bad*. Timing of mowing can then be simulated by appropriate timing of this change during the 10 flights simulated. Therefore the modification of the model to incorporate short-term agricultural practices is substantiated. Thus it seems possible to simulate the response of species to agricultural disturbance without integrating highly detailed data such as quality of resource - in the case of butterflies, changes in nectar and host resources. An interesting support for the goodness-of-fit of the model follows from figure 6.3: The most conspicuous discrepancy between the model predictions and empirical data is the prediction that butterfly abundance in meadow M2 should be higher after mowing, compared with its abundance before mowing, while the empirical data show exactly the opposite. Meadow M2 has been grazed at low intensity by sheep towards the end of the experiment. Thus butterflies, which have left the mown patches, if they arrived to this patch, have met sheep, which probably disturbed them to such an extent, that they did not stay here and continued in searching for a more quiet patch.

Our scenarios of farming disturbance were very simple in comparison of what really happens in agricultural landscapes. In hedgerow network landscapes, the agricultural mosaic is characterised by a shifting mosaic of land-uses and associated farming practices. Furthermore, timings of farming practices are highly fluctuating depending on the phenology of the different crops and decisions of farmers. However, our modelling approach permits to consider to some extent how farming practices influence population dynamics via the changes

in the amount and spatial organisation of herbaceous patches in the agricultural mosaic. According to percolation theory, landscape connectivity decreases non-linearly with the decreasing amount of habitats and movements are inexistent under a defined threshold (With *et al.*, 1997; With and King, 1999a; 1999b). Here, we tested two contrasted scenarios of disturbance intensity, but it would be interesting to test different scenarios simulating a large variation of disturbance intensity to determine if such a threshold exists for butterfly persistence.

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CONCLUSION GENERALE

L'objectif de cette thèse est d'étudier les facteurs intervenant dans la dynamique de la biodiversité dans les paysages agricoles, en considérant les processus dans la dynamique des communautés et des populations, et le mouvement des individus. L'originalité de nos travaux a été la prise en compte explicite des activités agricoles à différentes échelles d'espace et de temps, comme déterminant la qualité des ressources, mais également comme facteur d'organisation et de dynamique du paysage.

Ce travail s'est intégré dans deux programmes de recherche pluridisciplinaires, « *Vulnerability of biodiversity in agroecosystems as influenced by land-use intensity and green veining* » et « *Diversité et agriculture : analyse agronomique et écologique des unités spatio-temporelles pertinentes pour la gestion de la biodiversité* ». Leurs objectifs allient recherche et transfert vers les acteurs de la gestion des paysages. Les résultats présentés identifient les facteurs de la structuration et de la dynamique des communautés à plusieurs échelles, et du mouvement des individus et de la dynamique des populations dans les paysages agricoles. Nous avons pu décrire les échelles spatio-temporelles pertinentes en terme de gestion et d'aménagement.

Dans cette discussion, nous dégagerons les points forts innovants au regard de l'état des connaissances sur le thème de la biodiversité dans les paysages agricoles. Nous mettrons tout d'abord l'accent sur les différents facteurs qui interviennent sur la dynamique des communautés et des populations dans les paysages agricoles. Nous soulignerons ensuite l'importance d'adopter une approche fonctionnelle pour décrire la réponse des espèces au paysage. Enfin, nous terminerons en énonçant des propositions en terme d'aménagement, et en décrivant les perspectives de recherches qui se dégagent à l'issue de ce travail.

1. Hiérarchie des facteurs déterminant la dynamique de la biodiversité dans les paysages agricoles bocagers

L'étude des fonctionnements écologiques dans les paysages agricoles relève des compétences de plusieurs disciplines. Notre démarche de travail s'est intégrée dans une réflexion commune mise en place depuis plusieurs années par l'équipe Ecologie du Paysage et l'unité de recherche INRA SAD Armorique de Rennes. Les concepts de l'écologie du paysage nous ont permis de faire le lien entre les activités agricoles et les concepts théoriques en écologie (Burel, 1995), et l'approche agronomique a permis quant à elle d'apporter un regard plus « technique » des paysages agricoles (Deffontaines, 1996). Le choix de se référer à des objets d'étude communs nous a conduit à décrire les activités agricoles à différentes échelles : celle du paysage où nous avons décrit les systèmes de production et celle de l'unité de gestion (parcelle ou bord de champ) par l'agriculteur où nous avons considéré les pratiques.

Nous avons montré que, si les effets des activités agricoles sur la biodiversité sont observés aux différents niveaux pris en compte, les facteurs qui interviennent aux niveaux supérieurs (paysage et systèmes de production agricoles) ont un effet plus important en comparaison de ceux des niveaux inférieurs (qualité des ressources et pratiques agricoles).

1.1. Les niveaux spatiaux

Structure du paysage et systèmes de production

Les résultats nous permettent d'affirmer que l'effet du **paysage est plus important pour expliquer les patrons de biodiversité que les conditions locales**. La composition et l'organisation spatiale du paysage déterminent la composition des communautés, la distribution des populations et le mouvement des individus. Ainsi, la présence et l'abondance des carabiques forestiers dans les milieux permanents dépendent plus de la présence et de la quantité d'éléments boisés alentour que de la qualité des ressources (type et densité du couvert végétal) à l'échelle locale. Les milieux permanents permettent le mouvement des individus entre les îlots boisés et concourent à la survie des populations de ces carabiques forestiers (den Boer, 1981 ; Petit, 1994b ; Petit et Burel, 1998a). De même, les mouvements des papillons et leur distribution entre les éléments herbeux sont plus contraints par la connectivité du paysage (présence et arrangement spatial des prairies) et la taille des taches de ressources que par la qualité de la végétation à l'échelle locale. Des résultats identiques ont été précédemment obtenus pour les plantes (Le Coeur *et al.*, 1997 ; Le Coeur *et al.*, 2002), les oiseaux (Grand et Cushman, 2003) et les papillons (Jeanneret *et al.*, 2003a). Jeanneret *et al.* (2003a) ont observé un effet significatif des caractéristiques du paysage sur la composition des communautés de carabiques, mais moins marqué en comparaison de la qualité des habitats à l'échelle locale.

La composition et la structure du paysage sont fortement liées à la nature et l'intensité des systèmes de production agricole actuels. Nous avons montré dans le chapitre 1 que des paysages caractérisés par des systèmes de production contrastés (orientation laitière versus porcine - céréalière) présentent des réseaux d'éléments permanents (bois, prairies ...) différents. Ces différentes structures des réseaux d'éléments permanents contribuent à différencier les paysages en terme de composition des communautés de carabiques. Les recherches visant à comprendre l'effet de l'intensité de la production agricole sur la biodiversité se sont le plus souvent limitées l'étude de régimes de pratiques culturales associés à des systèmes de production contrastés (biologiques vs. conventionnels) (Dritschilo et Erwin, 1982 ; Weibull et Östman, 2003 ; Weibull *et al.*, 2003). Nos résultats soulignent l'importance de prendre en compte les relations entre la nature et l'intensité des systèmes de production agricoles et les caractéristiques du paysage.

Qualité des ressources et perturbations

Localement, les pratiques agricoles déterminent la capacité d'accueil des habitats pour les espèces, en modifiant la qualité des ressources (nourriture, microclimat, refuges, etc.). Parmi les différentes espèces de carabiques, les espèces forestières sont les plus sensibles aux perturbations des ressources. Ces espèces sont le plus souvent faiblement représentées au sein des communautés de carabiques en milieu agricole. Par conséquent, les descripteurs tels que la richesse spécifique, la diversité spécifique ou l'abondance totale des individus se révèlent inappropriés pour détecter la réponse des communautés de carabiques aux perturbations (Burel *et al.*, 1998). La comparaison des effets de différents régimes de gestion des bords de champs a révélé que la réponse des communautés dépend des effets propres à chaque pratique sur les conditions locales, la pulvérisation d'herbicides étant la plus néfaste par ses effets sur la végétation. Si les impacts des pratiques agricoles considérées individuellement sur la biodiversité sont bien documentés (Freemark et Boutin, 1995 ; McLaughlin et Mineau, 1995 ; Fuhlendorf *et al.*, 2002a ; Kruess et Tschamtkke, 2002), les

études comparant les effets de différentes pratiques restent rares (Wardle *et al.*, 1999 ; Le Coeur *et al.*, 2002). Cependant, ces études comparatives sont nécessaires afin de déterminer si l'on doit privilégier l'utilisation de certaines pratiques agricoles ou au contraire une diversité de pratiques pour le maintien de la biodiversité (Le Coeur *et al.*, 2002).

Les modifications de la qualité des ressources sous l'effet des pratiques agricoles interviennent également sur la distribution des espèces en inhibant les flux d'individus au niveau du paysage. Nous avons constaté que certaines pratiques ou régimes de pratiques peuvent ainsi conduire à un isolement spatial des populations de *Maniola jurtina* dans certaines taches de ressources et influencer la survie de cette espèce à plus ou moins long terme. Des milieux soumis à des perturbations répétées pourront ainsi constituer des obstacles au mouvement des individus vers des taches de ressources. Plusieurs auteurs ont souligné l'effet de la qualité des corridors sur la dispersion des individus, la dynamique des populations fragmentées et la distribution des espèces (Burel, 1989 ; Henein et Merriam, 1990 ; Petit et Burel, 1998a). Dans les paysages agricoles, l'efficacité des éléments du paysage pour la dispersion des individus est liée aux régimes de pratiques agricoles. En outre, la réponse des communautés de carabiques à l'échelle du site d'étude à certaines régimes de pratiques (fertilisants, pesticides) associés aux systèmes de production intensifs (Chapitre 1) laisse supposer qu'il existe une relation entre la distribution des espèces, les pratiques agricoles et la qualité du réseau d'éléments permanents à une échelle large. Dans les paysages bocagers, les bords de champs sont gérés par les agriculteurs en relation avec l'usage des parcelles adjacentes (Baudry *et al.* 1998 ; Baudry et Jouin, 2003). Ces usages et pratiques sont répartis au sein du territoire d'exploitation en fonction de différentes contraintes (pente, nature des sols, distance au siège d'exploitation, etc.), contribuant ainsi à l'organisation de la mosaïque agricole (Thenail et Baudry, Sous presse). La diversité des pratiques au sein d'un même territoire d'exploitation ou entre différents territoires se traduit par une forte diversité du réseau bocager en terme de structures de végétation des bords de champs (Baudry *et al.*, 1998, ; Baudry et Jouin, 2003). Les communautés de carabiques étant sensibles à certains régimes de gestion des bords de champs, cette diversité de pratiques et de structures de végétation peut contribuer à différencier les communautés de carabiques entre des sites caractérisés par des systèmes de production contrastés. Des travaux antérieurs ont mis en évidence un effet de l'intensité de l'agriculture à l'échelle du paysage sur la biodiversité (Le Cœur *et al.*, 1997 ; Burel *et al.*, 1998 ; Millán Peña *et al.*, 2003). Dans le présent travail, la prise en compte explicite des pratiques agricoles, par observations ou enquêtes auprès des agriculteurs, a permis de mettre en relation les pratiques agricoles, les systèmes de production dans lesquelles elles s'inscrivent et la dynamique de la biodiversité.

Sensibilité aux perturbations et paysage

La sensibilité de la biodiversité aux pratiques agricoles conduites localement dépend fortement des caractéristiques du paysage. La réponse des communautés aux pratiques agricoles dépend de la composition et la structure du paysage, qui déterminent la présence des espèces les plus sensibles aux perturbations. Les caractéristiques du paysage déterminent les possibilités pour les espèces à fuir les milieux perturbés, atteindre des zones refuges, et recoloniser les milieux après les perturbations. Ainsi, les carabiques forestiers persistent dans des milieux soumis à des perturbations répétées lorsqu'ils se situent dans des contextes paysagers boisés. Nous pouvons également poser l'hypothèse que la recolonisation des milieux perturbés par ces espèces est contrainte par la qualité du réseau de haies alentour en terme de diversité des structures de végétation sous l'effet des régimes de gestion. L'approche fonctionnelle que nous avons adoptée dans le chapitre 3 pour décrire la réponse

des communautés de carabiques aux perturbations a permis de mettre en évidence une relation entre la réponse des différentes espèces et certains traits d'histoire de vie. La taille et la capacité de déplacement des espèces traduisent les possibilités des espèces à fuir ou (re)coloniser les milieux perturbés et à survivre dans des milieux instables sur le long terme. Pour les carabiques, peu mobiles, nous pouvons supposer que ces déplacements se limitent sur le court terme aux éléments paysagers adjacents. L'étude de l'impact de la fauche sur les mouvements journaliers des papillons, plus mobiles, a permis de montrer que la fauche affecte peu la distribution de *Maniola jurtina* au sein du paysage lorsque les éléments herbeux sont nombreux et connectés, les papillons se redistribuant alors vers les taches de ressources plus ou moins proches.

Jusqu'à présent, les effets des pratiques agricoles sur la biodiversité ont été considérés à l'échelle de la parcelle, de la placette expérimentale voire du microcosme (Kareiva et Andersen, 1988 ; Leigh et Johnson, 1994). Nos résultats soulignent l'importance de ne plus considérer l'élément du paysage comme un objet indépendant en terme de fonctionnement, (Le Coeur, 1996 ; Le Coeur *et al.*, 2002), les caractéristiques du paysage pouvant être des variables plus pertinentes pour expliquer la dynamique de la biodiversité que les pratiques agricoles conduites localement (Duelli *et al.*, 1999).

1.2. Le temps

Nous avons démontré dans le paragraphe précédent comment les niveaux spatiaux supérieurs (paysage) exercent un contrôle sur les processus se déroulant aux niveaux spatiaux inférieurs (tache de ressources). **Au regard de nos résultats, nous pouvons également distinguer les réponses de la biodiversité aux activités agricoles selon différentes échelles temporelles.**

Nous avons vu que l'importance des réseaux d'éléments permanents au sein des paysages agricoles bocagers est liée à la nature et l'intensité des systèmes de production agricole. Nous n'avons pas considéré ici l'histoire des sites étudiés, mais la composition et la structure de ces paysages sont le résultat de processus souvent lents et durables (arasement ou plantation de haies, restructuration du parcellaire). Ces modifications sont spécifiques des systèmes de production agricoles et de leur dynamique (Poudevigne *et al.*, 1997 ; Millán Peña *et al.*, 2003). Il n'y a pas *a priori* de relation synchrone entre la distribution spatiale des espèces et les caractéristiques du paysage ; la distribution des espèces dépend des patrons actuels des paysages mais également de leurs états passés (Blondel, 1986 ; Burel, 1992 ; Petit et Burel, 1998b). **Il nous apparaît donc important de faire référence à l'histoire des paysages en relation avec l'évolution des systèmes de production pour interpréter les relations des espèces avec la structure du paysage.**

A l'échelle locale, nos résultats ont mis en évidence que les pratiques agricoles ont un effet peu marqué sur la biodiversité à court terme. Les communautés de carabiques répondent immédiatement aux perturbations des ressources mais retournent à leur état initial avant perturbation, suggérant une certaine résilience du système (Bengtsson, 2002). Au niveau des populations de papillons, la fauche n'entraîne à court terme que des modifications localisées de la distribution des individus. **Au contraire, les régimes pluri-annuels de gestion ont un impact plus marqué sur la structuration des communautés ou la survie des populations, en relation avec l'instabilité des milieux sous l'effet des perturbations répétées des ressources.**

La reconnaissance des propriétés hiérarchiques des systèmes écologiques a souligné l'importance de considérer plusieurs échelles spatiales et temporelles dans l'étude des processus écologiques (O'Neill *et al.*, 1986 ; Turner *et al.*, 1989a ; Hobbs, sous presse). **Nos résultats nous semblent fondamentaux dans le sens où ils apportent un regard nouveau quant à l'étude des déterminismes de la biodiversité dans les paysages agricoles. Ainsi, la compréhension des effets de l'intensification agricole sur la biodiversité nécessite de considérer les activités agricoles à différentes échelles spatiales et temporelles.** Les études qui se restreignent à une échelle peuvent ne pas détecter les phénomènes se déroulant à des échelles inférieures ou supérieures (Grand et Cushman, 2003 ; Hobbs, sous presse). Les travaux visant à comprendre l'effet de l'intensification agricole sur la biodiversité se sont le plus souvent limités à l'étude locale des pratiques culturales (Dritschilo et Erwin, 1982 ; Weibull et Östman, 2003 ; Weibull *et al.*, 2003) ou ont considéré de façon implicite les relations entre la structure du paysage et l'intensité agricole. Nos résultats soulignent **l'importance de faire le lien entre la nature et l'intensité des systèmes de production agricoles et les caractéristiques du paysage, en terme de structure du réseau d'éléments permanents, mais également en terme de diversité et organisation des régimes de pratiques.** Cela implique de prendre en compte de façon explicite les relations entre agriculture et paysage et de ne pas se limiter à l'étude locale des impacts de certaines pratiques ou régimes de pratiques, considérées individuellement ou comme partie d'un système de production donné.

En outre, l'étude des interactions entre biodiversité et agriculture doit être conduite à différentes échelles temporelles. Si les études conduites sur un pas de temps court (expérimentations) sont nécessaires à la compréhension des mécanismes mis en œuvre dans la réponse de la biodiversité aux perturbations locales des ressources, il apparaît plus pertinent de privilégier les études sur le plus long terme. La prise en compte d'un pas de temps pluri-annuel permet de considérer les effets des régimes de pratiques agricoles en relation avec les successions culturales et le fonctionnement des exploitations. La prise en compte d'un pas de temps plus long (décennie) permet d'appréhender les interactions entre les changements durables des paysages agricoles et l'évolution des systèmes de production. Ces deux dernières approches nécessitent la mise en place d'observations des activités agricoles sur le long terme. Dans le présent travail, le suivi des activités agricoles sur le Site Atelier de Pleine Fougères a permis d'adopter une telle approche.

2. Perception des espèces et paysage

2.1. Hétérogénéité du paysage et communautés

La description de la structure des paysages est fonction de la façon dont le chercheur perçoit les différents éléments du paysage (Allen et Hoekstra, 1992). De nombreux indices ont été développés pour décrire la structure spatiale des paysages (Baudry et Baudry-Burel, 1982 ; Turner et Gardner, 1991). Cependant, ces indices sont fortement dépendants de l'échelle spatiale à laquelle on se place (Turner *et al.*, 1989b ; O'Neill *et al.*, 1996) et ne permettent pas de traduire la perception du paysage propre à chaque espèce. La méthode que nous avons adoptée pour décrire le paysage, basée sur la prise en compte de l'ensemble des éléments du paysage dans des fenêtres de taille variable, nous a permis de souligner **l'importance de tester différents descripteurs du paysage pour traduire la réponse des communautés à la composition et la structure du paysage.**

En premier lieu, il n'y a pas une « échelle du paysage » définie *a priori* : il est nécessaire de réaliser des analyses pluri-échelles pour identifier la réponse des espèces aux caractéristiques du paysage. Chaque espèce perçoit en effet le paysage à une échelle qui lui est propre, en relation avec son domaine vital et ses capacités de dispersion (Kareiva, 1990 ; Keitt *et al.*, 1997). L'approche pluri-échelles adoptée pour caractériser le contexte paysager des milieux échantillonnés s'avère être un outil approprié pour identifier et comparer les échelles de perception de différentes espèces, comme nous l'avons illustré pour les espèces de carabiques. Si les espèces de milieux cultivés, relativement mobiles, répondent aux caractéristiques du paysage sur toute la gamme des échelles spatiales considérées, les espèces forestières y répondent, elles, à des échelles spécifiques. Certaines espèces, telles que *Abax parallelepipedus*, sont en effet favorisées par des contextes paysagers boisés à une échelle fine, tandis que d'autres, e.g. les espèces du genre *Carabus*, sont favorisées par ces conditions à des échelles plus grossières. Ces différentes réponses sont liées aux processus impliqués au niveau du fonctionnement des populations de carabiques forestiers. *Abax parallelepipedus* peut se maintenir dans les paysages agricoles sous la forme de populations fragmentées (Petit, 1994a) : les populations locales sont situées dans les bois et les nœuds ou intersections du réseau de haies (Petit et Burel, 1993), les haies jouant le rôle de corridor pour la dispersion des individus entre les bois (Petit, 1994b). Au contraire, d'autres espèces telles que *Carabus purpurescens* ne survivent pas dans des haies isolées (Burel, 1989) et nécessitent donc des taches boisées étendues.

Nous avons également montré que les différentes espèces de carabiques ne répondent pas aux mêmes variables du paysage : certaines espèces répondent à la quantité d'éléments boisés au sein du paysage, d'autres semblent plus sensibles à la présence d'éléments permanents herbeux, et d'autres encore à celle des cultures. L'hétérogénéité de la mosaïque agricole doit donc être considérée dans son ensemble afin de traduire la perception du paysage propre à chaque espèce (Burel *et al.*, 1998 ; Millán Peña *et al.*, 2003). Cependant, il est difficile de prendre en compte les exigences écologiques de chaque espèce. Certains auteurs se sont ainsi engagés dans une démarche plus fonctionnelle, en proposant une typologie des espèces ou groupes d'espèces sur la base de traits d'histoire de vie (dispersion, taille, etc.) (Lavorel *et al.*, 1997 ; Lavorel *et al.*, 1998 ; Ribera *et al.*, 2001 ; Cole *et al.*, 2002). Nous avons utilisé le critère de la taille des individus pour exprimer les relations entre espèces de carabiques et paysage. Cette approche s'est avérée pertinente pour traduire des différences globales de réponse de groupes d'espèces contrastées (espèces de champs versus forestières), mais nous avons constaté que ce critère ne reflète pas toujours les diverses réponses des espèces au sein d'un groupe (espèces forestières).

2.2. Connectivité structurelle et connectivité biologique

La démarche que nous avons utilisée pour étudier les mouvements de papillons et leur distribution au sein du paysage nous a permis de montrer que **la mesure de la connectivité du paysage ne se résume pas à une caractérisation binaire ou neutre de l'espace** (matrice / taches de ressources) où seules la surface des taches de ressources et leur isolement spatial sont pris en compte. Les mouvements de papillons sont fonction de la présence et de l'organisation spatiale des éléments herbeux, de l'hétérogénéité de la mosaïque, et de l'adaptation du comportement des papillons face à certains éléments du paysage (e.g. effet barrière des bois, effet corridor des bords de champs). L'isolement spatial des taches herbeuses (distance euclidienne) et leur surface ne suffisent pas à eux seuls à expliquer les mouvements du Myrtil au sein du paysage. Nos résultats s'inscrivent dans le débat actuel de

la mesure de la connectivité du paysage (Moilanen et Hanski, 2001 ; Tischendorf et Fahrig, 2001). Les modèles de connectivité basés sur une vision « binaire » du paysage apportent des éléments de réponse quant aux interactions entre mouvement des organismes et paysage. Une telle mesure structurelle de la connectivité peut suffire à traduire la réponse des espèces spécialistes et peu mobiles au paysage (Baudry et Merriam, 1988). **Cependant, pour des espèces plus mobiles et plus généralistes, une approche plus fonctionnelle de la connectivité basée sur la biologie et le comportement des espèces devrait être adoptée.**

Dans ce contexte, les modèles de connectivité basés individus apportent un cadre conceptuel et méthodologique approprié, puisqu'ils permettent de prendre en compte de façon précise les facteurs qui interagissent avec les individus dans la prédiction des flux à des échelles supérieures (Lomnicki, 1992 ; Turchin, 1998). Cette approche de modélisation a été critiquée du fait qu'elle ne conduit pas toujours à des prédictions quantitatives fiables des flux d'individus (Blanché *et al.*, 1996 ; With et Crist, 1996). Cependant, nos résultats montrent que l'intégration de données concernant le comportement des individus en fonction de la viscosité du paysage permet d'obtenir des prédictions satisfaisantes des flux d'individus et de la distribution des populations, comme l'ont souligné Jonsen et Taylor (2000).

3. Applications des travaux de recherche

La mise en oeuvre des programmes agri-environnementaux constitue une étape importante vers la conciliation des objectifs de production et de conservation de la biodiversité dans les paysages agricoles. Les mesures agri-environnementales concernent à la fois les opérations d'aménagement des paysages et les opérations de gestion localement. Elles visent ainsi à favoriser le maintien ou l'introduction d'éléments (semi-)permanents (haies, prairies) au sein des paysages, à privilégier la réduction d'intrants (pesticides, fertilisants) dans les modes de gestion des cultures ou des éléments incultes, etc. Une approche hiérarchique des relations entre biodiversité et agriculture est alors indispensable pour identifier la ou les échelle(s) auxquelles doivent se porter les priorités de gestion (Grand et Cushman, 2003). Notre approche nous a permis d'identifier des échelles spatio-temporelles pertinentes en terme de gestion et d'aménagement.

Nos résultats montrent que la composition et la structure du paysage sont un élément prioritaire à intégrer dans l'élaboration des plans de gestion et d'aménagement pour la conservation de la biodiversité. Ainsi, en fonction des caractéristiques des paysages, différentes mesures peuvent être conseillées. Dans des paysages ouverts où les milieux permanents sont réduits, l'accent devra être mis en priorité sur la restauration de ces milieux au sein du paysage. Ces aménagements doivent concerner non seulement la quantité, mais également l'agencement spatial des milieux permanents au sein du paysage. Dans des paysages caractérisés par un réseau de milieux permanents dense et connecté, il sera plus judicieux d'envisager certains changements au niveau des pratiques mises en oeuvre sur plusieurs années par les agriculteurs.

Les aménagements à mettre en oeuvre au niveau du paysage dépendent cependant des espèces ou groupes d'espèces considérées. Dans le cas des coléoptères carabiques, la conservation des espèces forestières implique de favoriser les milieux boisés (bois, haies). Ces milieux peuvent cependant agir comme une barrière au mouvement de papillons tels que le Myrtil, qui seront plus favorisés par le maintien de milieux prairiaux. **Cela impose alors de faire un choix au niveau des espèces que l'on veut favoriser.**

4. Perspectives de recherche

4.1. Caractérisation de l'espace

La caractérisation de la composition et la structure du paysage est classiquement réalisée en considérant des descripteurs issus d'interprétations cartographiques d'occupation du sol (Forman et Godron, 1986 ; Turner et Gardner, 1991 ; Cullinan et Thomas, 1992). Dans ce travail, nous avons utilisé des mesures traduisant l'importance et la diversité des différents types d'occupation du sol, ou la quantité de haies pour décrire le paysage. Nous avons cependant montré que les modifications de la qualité des ressources sous l'effet des pratiques agricoles peuvent contraindre les flux d'individus au niveau du paysage et intervenir ainsi sur la distribution des espèces. **La question qui se pose désormais est de savoir si les patrons de biodiversité sont plus liés à la connectivité structurelle du réseau d'éléments permanents, ou à l'organisation spatiale des pratiques au sein de ce réseau. Il nous semble important d'adopter une approche plus fonctionnelle des paysages agricoles, en prenant en compte de façon explicite les pratiques agricoles dans la description de la composition et la structure du paysage.** Cela implique de considérer l'unité de gestion par l'agriculteur (haie unité de gestion ou parcelle) comme unité de cartographie. Une telle approche permettrait de traduire le rôle plus ou moins important de milieux soumis à des régimes de gestion différents pour le mouvement des individus et la distribution des espèces.

4.2. Connectivité du paysage et modélisation

La modélisation est un outil qui permet d'étudier les effets de la variabilité temporelle de la connectivité du paysage sous l'influence des activités agricoles (Baudry *et al.* 2003). Dans ce travail, le modèle que nous avons développé nous a permis de simuler l'effet de la dynamique du paysage sous l'influence de régimes interannuels de perturbations sur le mouvement des individus entre taches de ressources et leurs conséquences sur la dynamique des populations. A l'issue de ces résultats, plusieurs perspectives de recherches peuvent être envisagées :

- Notre approche s'est limitée à la prise en compte de scénarios simplifiés de perturbations. Il nous semble intéressant d'adopter une approche plus « réaliste » de la dynamique du paysage **en intégrant dans la mesure du possible la diversité spatiale et temporelle des pratiques ou régimes de pratiques.** Une telle démarche pourrait permettre de définir des zones de moindre perméabilité pour le mouvement des individus basées non plus sur la seule structure du paysage mais sur la dynamique des différents milieux sous l'effet des pratiques agricoles.
- En outre, notre approche s'est limitée à une espèce et à un type de paysage. L'application de notre approche de modélisation à d'autres modèles biologiques et à une gamme de paysages variée pourrait permettre de définir une mesure plus générale de la connectivité du paysage pour les espèces.

4.3. Groupes fonctionnels

La caractérisation des communautés en groupes fonctionnels suscite un intérêt croissant en écologie. Une telle démarche permet d'interpréter la réponse des communautés aux modifications de leur environnement en considérant certains traits d'histoire de vie des espèces plutôt que leur composition spécifique (Blondel, 1995 ; Lavorel *et al.*, 1997 ; Cole *et al.*, 2002). Dans notre travail, nous avons utilisé certains critères spécifiques (taille, capacité de dispersion) pour décrire la réponse des communautés aux perturbations et au paysage. Il nous semble important d'approfondir cette approche en intégrant d'autres traits d'histoire de vie des espèces.

REFERENCES BIBLIOGRAPHIQUES

- Agger, P., et Brandt, J. 1988. Dynamics of small biotopes in Danish agricultural landscapes. *Landscape Ecology* **1**: 227-240.
- Alard, D., et Poudevigne, I. 1999. Factors controlling plant diversity in a rural landscape: a functional approach. *Landscape and Urban Planning* **46**: 29-39.
- Allen, T.F.H., et Star, T.B. 1982. *Hierarchy: perspectives for ecological complexity*. The University of Chicago Press.
- Allen, T.F.H., et Hoekstra, T.W. 1992. *Toward a unified ecology*. The University of Chicago Press.
- Asteraki, E.J., Hanks, C.B., et Clements, R.O. 1992. The impact of the chemical removal of the hedge-base flora on the community structure of carabid beetles (Col., Carabidae) and spiders (Araneae) of the field and hedge bottom. *Journal of Applied Entomology* **113**: 398-406.
- Auger, P., Baudry, J., et Fournier, F. 1992. *Hiérarchies et échelles en écologie*. Naturalia publications.
- Baguette, M., Petit, S., et Quéva, F. 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequence for conservation. *Journal of Applied Ecology* **37**: 100-108.
- Baguette, M., Vansteenwegen, C., Convi, I., et Nève, G. 1998. Sex-biased density-dependent migration in a metapopulation of the butterfly *Procllossiana eunomia*. *Acta Oecologica* **19**: 17-24.
- Baker, W.L. 1989. A review of models of landscape change. *Landscape Ecology* **2**: 111-135.
- Balent, G. 1987. *Structure, fonctionnement et évolution d'un système pastoral. Le pâturage vu comme un facteur écologique piloté, dans les Pyrénées Centrales*, Thèse Université de Rennes I, Rennes.
- Basedow, T. 1990. Effects of insecticides on carabidae and the significance of these effects for agriculture and species number, pp. 115-125, In: *The role of ground beetles in ecological and environmental studies* (N.E. Stork, ed.). Intercept, Andover, Hampshire.
- Basore, N.L., Best, L.B., et Wooley, J.B. 1986. Bird nesting in Iowa not-tillage and tillage cropland. *Journal of Wildlife Management* **50**: 19-28.
- Baudry, J. 1985. *Utilisation des concepts de landscape ecology pour l'analyse de l'espace rural. Utilisation du sol et des bocages*. Thèse d'état, Université de Rennes I, Rennes.
- Baudry, J. 1992. Approche spatiale des phénomènes écologiques : détection des effets d'échelle, pp. 221-283, In: *Hiérarchies et échelles en écologie* (P. Auger, J. Baudry, F. Fournier, eds.). Naturalia Publications, Cahors (France).
- Baudry, J., et Baudry-Burel, F. 1982. La mesure de la diversité spatiale: utilisation dans les évaluations d'impacts. *Acta Oecologica Oecologica Applicata* **3**: 177-190.
- Baudry, J., et Merriam, G. 1988. Connectivity and connectedness: fonctionnal versus structural patterns in landscapes, pp. 23-28 In: *Connectivity in landscape ecology. Proc. 2nd IALE Seminar* (K.F. Schreiber, ed.). Münstersche Geographische Arbeiten.
- Baudry, J., et Denis, D. 1995. *Chloe: a routine for analysing spatial heterogeneity (IDRISI image files)*, INRA, SAD-Armorique, Rennes, France.
- Baudry, J., et Jouin, A. 2003. *De la haie aux bocages: organisation, dynamique et gestion*. INRA, Ministère de l'Aménagement du Territoire et de l'Environnement, Rennes.

- Baudry, J., Jouin, A., et Thenail, C. 1998. La diversité des bordures de champs dans les exploitations agricoles de pays de bocage. *Etudes et Recherches sur les Systèmes agraires* **31**: 117-134.
- Baudry, J., Bunce, R.G.H., et Burel, F. 2000a. Hedgerows: and international perspective on their origin, function and management. *Journal of Environmental Management* **60**: 7-22.
- Baudry, J., Burel, F., Thenail, C., et Le Coeur, D. 2000b. A holistic landscape ecological study of the interactions between farming activities and ecological patterns in Brittany, France. *Landscape and Urban Planning* **50**: 119-128.
- Baudry, J., Burel, F., Aviron, S., Martin, M., Ouin, A., Pain, G., et Thenail, C. 2003. Temporal variability of connectivity in agricultural landscapes: do farming activities help? *Landscape Ecology* **18**: 303-314.
- Bengtsson, J. 2002. Disturbance and resilience in soil animal communities. *European Journal of Soil Biology* **38**: 119-125.
- Bennett, A.F. 1990. Habitat corridors and the conservation of small mammals in a fragmented forest environment. *Landscape Ecology* **4**: 109-122.
- Benton, T.G., Vickery, J.A., et Wilson, J.D. Sous presse. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*.
- Bertrand, G. 1975. Pour une histoire écologique de la France rurale, pp. 34-113, In: *Histoire de la France rurale*. Le Seuil, Paris.
- Bhriain, B.N., Sheehy Skeffington, M., et Gormally, M. 2002. Conservation implications of land use practices on plant and carabid beetle communities of two turloughs in Co. Galway, Ireland. *Biological Conservation* **105**: 81-92.
- Blake, S., Foster, G.N., Eyre, M.D., et Luff, L.M. 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia* **38**: 502-512.
- Blanché, S., Casas, J., Bigl, F., et Janssen-Van bergeijk, K.E. 1996. An individual based model of Trichogramma foraging behavior : parameter estimation for single females. *Journal of Applied Ecology* **33**: 425-434.
- Blondel, J. 1986. *Biogéographie évolutive*. Masson, Paris.
- Blondel, J. 1995. *Biogéographie : approche écologique et évolutive*. Masson, Paris.
- Boiteau, G. 1984. Effects of planting date, plant spacing, and weed cover on populations of insectes, arachnids and entomophthoran fungi in potato fields. *Environmental Entomology* **13**: 751-756.
- Booij, C.J.H., et Noorlander, J. 1992. Farming systems and insect predators. *Agriculture, Ecosystems and Environment* **40**: 125-135.
- Brakefield, P.M. 1982a. Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution and dispersal. *Journal of Animal Ecology* **51**: 713-726.
- Brakefield, P.M. 1982b. Ecological studies on the butterfly *Maniola jurtina* in Britain. II. Population dynamics: the present position. *Journal of Animal Ecology* **51**: 727-738.
- Brakefield, P.M. 1987. Geographical variability in, and temperature effects on, the phenology of *Maniola jurtina* and *Pyroni tithonus* in England and Wales. *Ecological Entomology* **12**: 139-148.

- Brommer, J.E., et Fred, M.S. 1999. Movement of the Apollo butterfly *Parnassius apollo* related to host plant and nectar plant patches. *Ecological Entomology* **24**: 125-131.
- Brookfield, H.C. 1972. Intensification and disintensification in Pacific agriculture. *Pacific Viewpoint* **13**: 30-48.
- Brust, G.E. 1990. Direct and indirect effects of four herbicides on the activity of carabid beetles (Coleoptera : Carabidae). *Pesticid Sciences* **30**: 309 - 320.
- Burel, F. 1989. Landscape structure effects on carabid beetles spatial patterns in western France. *Landscape Ecology* **2**: 215-226.
- Burel, F. 1991. *Dynamique d'un paysage réseaux et flux biologiques*, Thèse Université de Rennes I, Rennes, France.
- Burel, F. 1992. Effect of landscape structure and dynamics on species diversity in hedgerow networks. *Landscape Ecology* **6**: 161-174.
- Burel, F. 1995. Ecological patterns and processes in European agricultural landscapes. *Landscape and Urban Planning* **31**: 412 pp.
- Burel, F. 1996. Hedgerows and their role in agricultural landscapes. *Critical Review in Plant Sciences* **15**: 169-190.
- Burel, F., et Baudry, J. 1989. Hedgerow network patterns and process in France., pp. 99-120, In: *Changing landscapes: an ecological perspective* (R.T.T. Forman, ed.). Springer, New York.
- Burel, F., et Baudry, J. 1999. *Ecologie du paysage : concepts, méthodes et applications*. Tec et Doc, Paris.
- Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., Thenail, C., Brunel, E., et Lefeuvre, J.C. 1998. Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica* **19**: 47-60.
- Canévet, C. 1992. *Le modèle agricole breton : histoire et géographie d'une révolution agro-alimentaire*. Presses Universitaires de Rennes, Rennes.
- Canter, K.J., et Tamis, W.L.M. 1999. Arthropods in grassy field margins in the Wieringermeer: scope, population development and possible consequences for farm practices. *Landscape and Urban Planning* **46**: 63-69.
- Chamberlain, D.E., et Fuller, R.J. 2000. Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agriculture, Ecosystems and Environment* **78**: 1-17.
- Chiverton, P.A., et Sotherton, N.W. 1991. The effects on beneficial arthropods of the exclusion of herbicides from cereal crop edges. *Journal of Applied Ecology* **28**: 1027-1039.
- Clapperton, M.J., Kanashiro, D.A., et Behan-Pelletier, V.M. 2002. Changes in abundance and diversity in microarthropods associated with Fescue Prairie grazing regimes. *Pedobiologia* **46**: 496-511.
- Clavreul, D. 1984. *Contribution à l'étude des interrelations paysage / peuplement faunistiques en région de grande culture*. Thèse Université de Rennes 1, Rennes.
- Cole, L.J., McCracken, D.I., Dennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Murphy, K.J., et Waterhouse, T. 2002. Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland. *Agriculture, Ecosystems and Environment* **93**: 323-336.

- Conradt, L., Bodsworth, E.J., Roper, T.J., et Thomas, C.D. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proceedings of the Royal Society of London B* **267**: 1505-1570.
- Cooper, A., et Power, J. 1997. *Species dispersal and land use processes*. International Association for Landscape Ecology, Preston.
- Cullinan, V.I., et Thomas, J.M. 1992. A comparison of quantitative methods for examining landscape pattern and scale. *Landscape Ecology* **7**: 211-227.
- Deffontaines, J.P. 1996. Du paysage comme moyen de connaissance de l'activité agricole à l'activité agricole comme moyen de production du paysage. Un point de vue d'agronome. *Compte-Rendu de l'Académie d'Agriculture* **82**: 57-69.
- Delettre, Y., et Morvan, N. 2000. Dispersal of adult terrestrial Chironomidae (Diptera) in agricultural landscapes. *Freshwater Biology* **11**: 399-411.
- Delettre, Y., Morvan, N., Tréhen, P., et Grootaert, P. 1998. Local biodiversity and multi-habitat use by Empididae (Diptera). *Biodiversity and Conservation* **7**: 9-25.
- den Boer, P.J. 1977. *Dispersal power and survival of carabids in a cultivated countryside*, Communication of the Biological Station of Wijster.
- den Boer, P.J. 1981. On the survival of populations in a heterogeneous and variable environment. *Oecologia* **50**: 39-53.
- den Boer, P.J. 1985. Fluctuations of density and survival of carabid populations. *Oecologia* **67**: 322-330.
- Dennis, P., et Fry, G. 1992. Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland? *Agriculture, Ecosystems and Environment* **40**: 95-115.
- Denslow, J.S. 1985. Disturbance-mediated coexistence of species, pp. 307-323, In: *The ecology of natural disturbance and patch dynamics* (S.T.A. Pickett, P.S. White, eds.). Academic Press, New York.
- Desender, K., et Turin, H. 1989. Loss of habitats and changes in the composition of the ground beetle and tiger beetles fauna in four west European countries since 1950 (Coleoptera: Carabidae, Cicindelidae). *Biological Conservation* **48**: 277-294.
- Desender, K., Dufrêne, M., et Maelfait, J.-P. 1994. Long-term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land-use by means of database covering more than a century, pp. 247-252, In: *Carabid beetles: ecology and evolution* (K. Desender, M. Dufrêne, M. Loreau, M.L. Luff, J.-P. Maelfait, eds.). Kluwer Academic Publishers, Netherlands.
- Döring, T.F., et Kromp, B. 2003. Which carabid species benefit from organic agriculture? A review of comparative studies in winter cereals from Germany and Switzerland. *Agriculture, Ecosystems and Environment* **98**: 153-161.
- Dover, J.W. 1989. The use of flowers by butterflies foraging in cereal field margins. *Entomologist's Gazette* **40**: 283-294.
- Dover, J.W. 1994. Arable field margins: factors affecting butterfly distribution and abundance, pp. 59-66, In: *Field margins: integrating agriculture and conservation* (N.D. Boatman, ed.). BCPC Publications, Farnham.

- Dover, J.W. 1996. Factors affecting the distribution of satyrid butterflies on arable farmland. *Journal of Applied Ecology* **33**: 723-734.
- Dover, J.W. 1997a. The importance of shelter for butterflies in open landscapes. *Journal of Insect Conservation* **1**: 89-97.
- Dover, J.W. 1997b. Conservation heathlands: effects on butterfly distribution and behaviour. *Agriculture, Ecosystems and Environment* **63**: 31-49.
- Dover, J.W., Clarke, S.A., et Rew, L. 1992. Habitats and movement patterns of Satyrid butterflies (Lepidoptera: Satyridae) on arable farmland. *Entomologist's Gazette* **43**: 29-44.
- Dowdeswell, W.H., Ford, E.B., et McWhirter, K.G. 1957. Further studies on isolation in the butterfly *Maniola jurtina* L. *Heredity* **2**: 51-65.
- Dritschilo, W., et Erwin, T.L. 1982. Responses in abundance and diversity of cornfield carabid communities to differences in farm practices. *Ecology* **63**: 900-904.
- Duelli, D., Studer, M., Marland, I., et Jakob, S. 1990. Population movements of arthropods between natural and cultivated areas. *Biological Conservation* **54**: 193-207.
- Duelli, P., Obrist, M.K., et Schmatz, D.R. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture, Ecosystems and Environment* **74**: 33-64.
- Duffield, S.J., et Baker, S.E. 1990. Spatial and temporal effects of dimethoate use on populations of carabidae and their prey in winter wheat, pp. 95-104, In: *The role of ground beetles in ecological and environmental studies* (N.E. Stork, ed.). Intercept, Andover, Hampshire.
- Duffield, S.J., et Aebischer, N.J. 1994. The effect of spatial scale of treatment with dimethoate on invertebrate population recovery in winter wheat. *Journal of Applied Ecology* **31**: 17-24.
- Dunning, J.B., Danielson, B.J., et Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* **65**: 169-175.
- Eastman, J.R. 1997. *IDRISI for Windows - user's guide*, Clark University.
- Epstein, D.L., Zack, R.S., Brunner, J.F., Gut, L., et Brown, J.J. 2001. Ground beetle activity in apple orchards under reduced pesticide management regimes. *Biological Control* **21**: 97-104.
- Eyre, M.D. 1994. Strategic explanation of carabid species distributions in northern England, pp. 267-275, In: *Carabid beetles: ecology and evolution* (K. Desender, M. Dufrêne, M. Loreau, M.L. Luff, J.-P. Maelfait, eds.). Kluwer Academic Publishers, Netherlands.
- Fahrig, L. 1991. Simulation methods for developing general landscape level hypotheses of single species dynamics, pp. 415-441, In: *Quantitative methods in landscape ecology* (M.G. Turner, R.H. Gardner, eds.). Springer Verlag, New York.
- Fahrig, L., et Merriam, G. 1994. Conservation of fragmented populations. *Conservation Biology* **8**: 50-59.
- Feber, R.E. 1993. *The ecology and conservation of butterflies on lowland arable farmland*. University Press of Oxford.
- Feber, R.E., et Smith, H. 1995. Butterfly conservation on arable farmland, pp. 84-97, In: *Ecology and conservation of butterflies* (A.S. Pullin, ed.). Chapman & Hall, London.

- Feber, R.E., Smith, H., et MacDonald, D.W. 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology* **33**: 1191-1205.
- Fjellstad, W.J., et Dramstad, W.E. 1999. Patterns of change in two contrasting Norwegian agricultural landscapes. *Landscape and Urban Planning* **45**: 177-191.
- Forman, R.T.T. 1995. Some general principles of landscape and regional ecology. *Landscape Ecology* **10**: 133-142.
- Forman, R.T.T., et Baudry, J. 1984. Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* **8**: 449-510.
- Forman, R.T.T., et Godron, M. 1986. *Landscape ecology*. John Wiley & sons, New York.
- Fournier, E., et Loreau, M. 2001. Activity and satiation state in *Pterostichus melanarius*: an experiment in different agricultural habitats. *Ecological Entomology* **26**: 235-244.
- Freemark, K. 1995. Assessing effects of agriculture on terrestrial wildlife: developing a hierarchical approach for the US EPA. *Landscape and Urban Planning* **31**: 99-115.
- Freemark, K., et Boutin, C. 1995. Impacts of agricultural herbicide use on terrestrial wildlife in temperate landscapes: a review with special reference to North America. *Agriculture, Ecosystems and Environment* **52**: 67-91.
- Fry, G. 1995. Landscape ecology and insect movement in arable ecosystems, pp. 177-202, In: *ecology and integrated farming systems* (D.M. Glen, M.P. Greaves, H.M. Anderson, eds.). John Wiley & Sons, Chichester.
- Fry, G., et Robson, W.J. 1994. The effects of field margins on butterfly movement. *BCPC Monograph* **58**: 111-116.
- Fuhlendorf, S.D., Engle, D.M., Arnold, D.C., et Bidwell, T.G. 2002a. Influence of herbicide application on forb and arthropod communities of North American tallgrass prairies. *Agriculture, Ecosystems and Environment* **92**: 252-259.
- Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M., et Shackford, J.S. 2002b. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landscape Ecology* **17**: 617-628.
- Gardner, R.H., et O'Neill, R.V. 1991. Pattern, process and predictability: the use of neutral models for landscape analysis, pp. 289-308, In: *Quantitative methods in landscape ecology* (M.G. Turner, R.H. Gardner, eds.). Springer Verlag, New York.
- Gardner, R.H., Milne, T.B., Turner, M.G., et O'Neill, R.V. 1987. Neutral models for the analysis of broad scale landscape pattern. *Landscape Ecology* **1**: 19-28.
- Gardner, S.M., Hartley, S.E., Davies, A., et Palmer, S.C.F. 1997. Carabid communities on heather moorlands in Northeast Scotland: the consequences of grazing pressure for community diversity. *Biological Conservation* **81**: 275-286.
- Gibson, C.W.D., Brown, V.K., Losito, L., et McGavin, G.C. 1992. The response of invertebrate assemblies to grazing. *Ecography* **15**: 166-176.
- Gibson, D.J., Seastedt, T.R., et Briggs, J.M. 1993. Management practices in tallgrass prairie: large- and small-scale experimental effects on specie composition. *Journal of Applied Ecology* **30**: 247-255.
- Gilpin, M., et Hanski, I. 1991. *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, London.

- Grand, J., et Cushman, S.A. 2003. A multi-scale analysis of species-environment relationships: breeding birds in a pitch pine-scrub oak (*Pinus rigida* - *Quercus ilicifolia*) community. *Biological Conservation* **112**: 307-317.
- Greenslade, P.J.M. 1964. The distribution, dispersal and size of a population of *Nebria brevicollis* (F.) with comparative studies on three other carabidae. *Journal of Animal Ecology* **33**: 311-333.
- Greenslade, P.J.M. 1965. On the ecology of some British Carabid beetles with special reference to life histories. *Trans. Soc. Br. Entomol.* **16**: 151-179.
- Gutzwiller, K.J., et Anderson, S.H. 1992. Interception of moving organisms: influences of patch shape, size, and orientation on community structure. *Landscape Ecology* **6**: 293-303.
- Haddad, N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* **9**: 612 - 622.
- Haddad, N.M., et Baum, K.A. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* **9**: 623-633.
- Hanski, I. 1994a. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**: 151-162.
- Hanski, I. 1994b. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation* **68**: 167-180.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* **396**: 41-49.
- Hanski, I., et Gilpin, M. 1997. *Metapopulation biology, ecology, genetics and evolution*. Academic Press, London.
- Hanski, I., Moilanen, A., Pakkala, T., et Kuussaari, M. 1996. The quantitative incidence function model and persistence of an endangered butterfly. *Conservation Biology* **10**: 578-590.
- Hassall, M., Hawthorne, A., Maudsley, M., White, P., et Cardwell, C. 1992. Effects of headland management on invertebrate communities in cereal fields. *Agriculture, Ecosystems and Environment* **40**: 155-178.
- Henein, K., et Merriam, G. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecology* **4**: 157-170.
- Hietala-Koivu, R. 2002. Landscape and modernizing agriculture: a case study of three areas in Finland in 1954-1998. *Agriculture, Ecosystems and Environment* **91**: 273-281.
- Hill, J.K., Thomas, C.D., et Lewis, O.T. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies - implications for metapopulation structure. *Journal of Animal Ecology* **65**: 725-735.
- Hobbs, N.T. Sous presse. Challenges and opportunities in integrating ecological knowledge across scales. *Forest Ecology and Management*.
- Holland, J.M., et Reynolds, C.J.M. Sous presse. The impact of soil cultivation on arthropod (Coleoptera and Araneae) emergence on arable land. *Pedobiologia*.
- Hooper, M.D. 1974. Hedgerow removal. *Biologist* **21**: 81-86.
- Hushton, M.A. 1995. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press.

- Ims, R.A. 1995. Movement patterns related to spatial structures, pp. 85-109, In: *Mosaic landscapes and ecological processes* (L. Hansson, L. Fahrig, G. Merriam, eds.). Chapman & Hall, London.
- INRA, ENSA, et Université de Rennes. 1976. *Les bocages: histoire, écologie, économie*, C.R. table ronde CNRS: les écosystèmes bocagers.
- Jeannel, R. 1941. *Coléoptères carabiques, Faune de France*.
- Jeannel, R. 1942. *Coléoptères carabiques II, faune de France*.
- Jeanneret, P., Schüpbach, B., et Luka, H. Sous presse. Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. *Agriculture, Ecosystems and Environment*.
- Jeanneret, P., Schüpbach, B., Lips, A., Harding, J., Steiger, J., Waldburger, M., Bigler, F., Fried, P.M., 1999. Biodiversity patterns in cultivated landscapes: modelling and mapping with GIS and multivariate statistics, pp. 85-94, In: *Heterogeneity in Landscape Ecology* (M.J. Maudsley, E.J.P. Marshall, eds.). IALE Publications, UK.
- Jeanneret, P., Schüpbach, B., Pfiffner, L., Walter, T., 2003a. Arthropod reaction to landscape and habitat features in agricultural landscapes. *Landscape Ecology* **18**, 253-263.
- Jeanneret, P., Schüpbach, B., Pfiffner, L., Herzog, F., Walter, T., 2003b. The Swiss agri-environmental programme and its effects on selected biodiversity indicators. *Journal of Nature Conservation* **11**, 213-220.
- Johnson, A.R., Wiens, J.A., Milne, B.T., et Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* **7**: 63-75.
- Jongman, R. 2000. The difficult relationship between biodiversity and landscape diversity, pp. 72-83 In: *Multifunctional landscapes: interdisciplinary approaches to landscape research and management* (J. Brandt, B. Tress, G. Tress, eds.). Centre for Landscape Research, Roskilde, Denmark.
- Jonsen, I., et Taylor, P.D. 2000. *Calopteryx* Damselfly dispersions arising from multiscale responses to landscape structure. *Conservation Ecology* [Online] **4**: <http://www.consecol.org/vol4/iss2/art4>.
- Jukes, M.R., Peace, A.J., et Ferris, R. 2001. Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. *Forest Ecology and Management* **148**: 271-286.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Phil. Trans. R. Soc. Lond.* **330**: 175-190.
- Kareiva, P., et Andersen, M. 1988. Spatial aspects of species interactions: the wedding of models and experiments, pp. 38-54, In: *Community ecology* (A. Hastings, ed.). Springer, New York.
- Keitt, T.H., Urban, D.L., et Milne, B.T. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* [Online] **1**: <http://www.consecol.org/vol1/iss1/art4>.
- Kindlmann, P., Aviron, S., Burel, F., et Ouin, A. Sous presse. Can assumption of a non-random search improve our prediction of butterfly fluxes between resource patches? *Ecological Entomology*.
- King, A.W., Johnson, A.R., et O'Neill, R.V. 1991. Transmutation and functional representation of heterogeneous landscapes. *Landscape Ecology* **5**: 239-253.

- Kotliar, N.B., et Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**: 253-260.
- Kromp, B. 1989. Carabid beetle communities (Carabidae, Coleoptera) in biologically and conventionally farmed agroecosystems. *Agriculture, Ecosystems and Environment* **27**: 241-251.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment* **74**: 187-228.
- Kromp, B., Pflügl, Ch., Hradetzky, R., et Idinger, J. 1995. Estimating beneficial arthropod densities using emergence traps, pitfall traps and the flooding method in organic fields. In: *Arthropod Natural Enemies in Arable Land I. Density, Spatial Heterogeneity and Dispersal* (S. Toft, W. Riedel, eds.), *Acta Jutlandica* **70**: 87-100.
- Kruess, A., et Tschamntke, T. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* **106**: 293-302.
- Kuussaari, M., Nieminen, M., et Hanski, I. 1996. An experimental study of migration in the glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* **65**: 791-801.
- Lambin, E.F., Rounsevell, M.D.A., et Geist, H.J. 2000. Are agricultural land-use models able to predict changes in land-use intensity? *Agriculture, Ecosystems and Environment* **82**: 321-331.
- Lang, A., Filser, J., et Henschel, J.R. 1999. Predation by ground beetles and wolf spiders on herbivorous insects in a maize crop. *Agriculture, Ecosystems and Environment* **72**: 189-199.
- Langmaack, M., Land, S., et Buchs, W. 2001. Effects of different field management systems on the carabid coenosis in oil seed rape with special regard to ecology and nutritional status of predacious *Poecilus cupreus* L. (Col. Carabidae). *Journal of Applied Entomology* **125**: 313-320.
- Lavorel, S., McIntyre, S., Landsberg, J., et Forbes, T.D.A. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* **12**: 474-477.
- Lavorel, S., Touzard, B., Lebreton, J.-D., et Clément, B. 1998. Identifying functional groups for response to disturbance in an abandoned pasture. *Acta Oecologica* **19**: 227-240.
- Le Coeur, D. 1996. *La végétation des éléments linéaires non cultivés des paysages agricoles : identification à plusieurs échelles spatiales, des facteurs de la richesse et de la composition floristiques des peuplements*, Thèse Université de Rennes I, Rennes.
- Le Coeur, D., Baudry, J., et Burel, F. 1997. Field margin plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning* **37**: 57-71.
- Le Coeur, D., Baudry, J., Burel, F., et Thenail, C. 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. *Agriculture, Ecosystems and Environment* **89**: 23-40.
- Lefeuvre, J.-C., Missonnier, J., et Robert, Y. 1976. Caractérisation zoologique - écologie animale : Rapport de synthèse, In: *Les bocages: histoire, écologie, économie* (CNRS, INRA, ENSA, Université de Rennes I, eds.).
- Leigh, R.A., et Johnson, A.E. 1994. *Long-term experiments in agricultural and ecological sciences*. Oxon, CANB International.
- Levins, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**: 1943-1967.

- Lima, S.L., et Zollner, P.A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* **11**: 131-135.
- Lomnicki, A. 1992. Population ecology from the individual perspective, pp. 3-17, In: *Individual-based models and approaches in ecology* (D.L. De Angelis, L.J. Gross, eds.). Chapman & Hall, New York.
- Luff, M.L. 1987. Biology of polyphagous ground beetles in agriculture. *Agricultural and Zoological Review* **2**: 237-278.
- MacDonald, D.W., et Smith, H. 1991. New perspectives on agro-ecology, pp. 413-449, In: *The ecology of temperate cereal fields* (L.G. Firbank, N. Carter, J.F. Darbyshire, G.R. Potts, eds.). Blackwell Scientific Publications, Oxford.
- Maelfait, J.-P., et Desender, K. 1994. Possibilities of short-term carabid sampling for site assessment studies, pp. 217-226, In: *Carabid beetles: ecology and evolution* (K. Desender, M. Dufrêne, M. Loreau, M.L. Luff, J.-P. Maelfait, eds.). Kluwer Academic Publisher, Netherlands.
- Manly, B.F.J. 1998. *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman & Hall, London.
- Mantel, N. 1967. The detection of disease clustering and a generalised regression approach. *Cancer Research* **27**: 209-220.
- Marshall, E.J.P., et Moonen, A.C. 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment* **89**: 5-21.
- Martin, M., et Ouin, A. 1998. Modelling butterfly movements in agricultural landscapes, pp. 341-345 In: *IALE European Congress* (J.W. Dover, R.G.H. Bunce, eds.), Preston.
- Martin, M., Bastardie, F., Richard, D., et Burel, F. 2001. Studying boundary effects on animal movement in heterogeneous landscapes: the case of *Abax ater* (Coleoptera: Carabidae) in hedgerow network landscapes. *Compte Rendu de l'Académie des Sciences de Paris. Sciences de la vie* **324**: 1029-1035.
- Maudsley, M.J. 2000. A review of the ecology and conservation of hedgerow invertebrates in Britain. *Journal of Environmental Management* **60**: 65-76.
- Maudsley, M., Seeley, B., et Lewis, O. 2002. Spatial distribution patterns of predatory arthropods within an English hedgerow in early winter in relation to habitat variables. *Agriculture, Ecosystems and Environment* **89**: 77-89.
- McAdam, J.H., Bell, A.C., et Henry, T. 1994. Field margin flora and fauna changes in response to grassland management practices. *BCPC Monograph* **58**: 153-160.
- McArthur, R.H., et Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton.
- McIntyre, N.E., et Wiens, J.A. 1999. Interactions between landscape structure and animal behavior: the role of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecology* **14**: 437-447.
- McLaughlin, A., et Mineau, P. 1995. The impact of agricultural practices on biodiversity. *Agriculture, Ecosystems and Environment* **55**: 201-212.
- Meeus, J.H.A. 1990. The transformation of agricultural landscapes in western Europe. *Milieu* **6**: 225-236.
- Meeus, J.H.A. 1995. Pan-European landscapes. *Landscape and Urban Planning* **31**: 57-79.

- Merckx, T., et Van Dyck, H. 2002. Interrelations among habitat use, behavior and flight-related morphology in two cooccurring satyrine butterflies, *Maniola jurtina* and *Pyronia tithonus*. *Journal of Insect Behavior* **15**: 542-561.
- Millán Peña, N. 2001. *Effets de l'évolution des paysages agricoles sur les communautés animales (carabes et petits mammifères): approche pluri-échelle*, Thèse Université de Rennes I, Rennes, France.
- Millán Peña, N., Butet, A., Delettre, Y., Morant, P., et Burel, F. 2003. Landscape context and carabid beetles (Coleoptera: Carabidae) communities of hedgerows in western France. *Agriculture, Ecosystems and Environment* **94**: 59-72.
- Miller, J.H., Boyd, R.S., et Edwards, M.B. 1999. Floristic diversity, stand structure and composition 11 years after herbicide site preparation. *Canadian Journal of Forest Research* **29**: 1073-1083.
- Milne, B.T., et Forman, R.T.T. 1986. Peninsulas in Maine: woody plant diversity, distance, and environmental patterns. *Ecology* **67**: 967-974.
- Moilanen, A., et Hanski, I. 1998. Metapopulation dynamics: effect of habitat quality and landscape structure. *Ecology* **79**: 2503-2515.
- Moilanen, A., et Hanski, I. 2001. On the use of connectivity measures in spatial ecology. *Oikos* **95**: 147-151.
- Mommertz, S., Schauer, C., Kösters, N., Lang, A., et Filser, J. 1996. A comparison of D-Vac suction, fenced, and unfenced pitfall trap sampling of epigeal arthropods in agro-ecosystems. *Annals of Zoological Fennici* **33**: 117-124.
- Moonen, A.C., et Marshall, E.J.P. 2001. The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. *Agriculture, Ecosystems and Environment* **86**: 187-202.
- Morant, P. 1999. Contribution de la télédétection pour l'analyse et la cartographie du paysage bocager armoricain. *Mappemonde* **18**: 61-71.
- Morris, M.G. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation* **95**: 129-142.
- Morvan, N., Delettre, Y., Trehen, P., Burel, F., et Baudry, J. 1994. The distribution of Empididae (Diptera) in hedgerow network landscapes., pp. 123-127, In: *Field margin: integrating agriculture and conservation* (N.D. Boatman, ed.). BCPC Publications, Farnham.
- Murdoch, W.W., McCauley, E., Nisbet, R.M., Gurney, S.C., et De Roos, A.M. 1992. Individual-based models: combining testability and generality, pp. 18-35, In: *Individual-based Models and Approaches in Ecology: Population, Communities and Ecosystems* (D.L. De Angelis, L.J. Gross, eds.). Chapman & Hall, New York.
- Naveh, Z., et Lieberman, A.S. 1994. *Landscape ecology: theory and application*. Springer, New York.
- New, T.R., Pyle, R.M., Thomas, J.A., et Hammond, P.C. 1995. Butterfly conservation management. *Annual Review of Entomology* **40**: 57-83.
- Niemelä, J., Halme, E., et Haila, Y. 1990. Balancing sampling effort in pitfall trapping of carabid beetle. *Entomologica Fennica* **1**: 233-238.
- Noss, R. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**: 355-364.

- Oates, M.R. 1995. Butterfly conservation within the management of grassland habitats, pp. 98-112, In: *Ecology and conservation of butterflies* (A.S. Pullin, ed.). Chapman & Hall, London, UK.
- O'Neill, R.V., De Angelis, D.L., Waldle, J.B., et Allen, T.F.H. 1986. *A hierarchical concept of ecosystems*. Princeton University Press.
- O'Neill, R.V., Hunsaker, C.T., Timmins, S.P., Jackson, B.L., Jones, K.B., Riitters, K.H., et Wickham, J.D. 1996. Scale problems in reporting landscape pattern at the regional scale. *Landscape Ecology* **11**: 169-180.
- Östman, Ö., Ekbom, B., et Bengtsson, J. 2001. Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology* **2**: 365-371.
- Ouin, A. 2000. *Hétérogénéité spatiale des paysages et processus écologiques. Cas de Rhopalocères dans le bocage breton*. Thèse Université de Rennes 1, Rennes.
- Ouin, A., Paillat, G., Butet, A., et Burel, F. 2000. Spatial dynamics of wood mouse (*Apodemus sylvaticus*) in an agricultural landscape under intensive use in Mont Saint Michel Bay (France). *Agriculture, Ecosystems and Environment* **78**: 159-165.
- Paillat, G., et Butet, A. 1996. Spatial dynamics of the bank vole (*Clethrionomys glareolus*) in a fragmented landscape. *Acta Ecologica* **17**: 553-559.
- Pain, G., Baudry, J., et Burel, F. 2000. Landpop: un outil d'étude de la structure spatiale des populations animales fragmentées. *Géomatique* **10**: 89-106.
- Petit, S. 1994a. *Métapopulations dans les réseaux bocagers : analyse spatiale et diffusion*, Thèse Université de Rennes I, Rennes.
- Petit, S. 1994b. Diffusion of forest carabid species in hedgerow network landscapes, pp. 337-443, In: *Carabid beetles: ecology and evolution* (K. Desender, M. Dufrêne, M. Loreau, M.L. Luff, J.-P. Maelfait, eds.). Kluwer Academic Publisher, Netherlands.
- Petit, S., et Burel, F. 1993. Movement of *Abax ater* (Col. Carabidae): do forest species survive in hedgerow networks ? *Vie Milieu* **43**: 119-124.
- Petit, S., et Burel, F. 1998a. Connectivity in fragmented populations : *Abax parallelepipedus* in a hedgerow network landscape. *Life Sciences* **321**: 55-61.
- Petit, S., et Burel, F. 1998b. Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. *Agriculture, Ecosystems and Environment* **69**: 243-252.
- Petit, S., et Usher, M.B. 1998. Biodiversity in agricultural landscapes : the ground beetle communities of woody uncultivated habitats. *Biodiversity and Conservation* **7**: 1549-1561.
- Petit, S., Moilanen, A., Hanski, I., et Baguette, M. 2001. Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. *Oikos* **92**: 491-500.
- Pollard, E. 1968. Hedges: III The effect of removal of the bottom flora of hawthorn hedgerow on the Carabidae of the hedge bottom. *Journal of Applied Ecology* **5**: 125-139.
- Pollard, E. 1974a. A comparison between the carabidae of a hedge and field site and those of a woodland glade, In: *Hedges* (E. Pollard, M.D. Hooper, N.W. Moore, eds.). Collins, W. & Sons, London.
- Pollard, E. 1974b. The effect of removal of the bottom flora of a hawthorn hedgerow on the Carabidae of the hedge bottom, pp. 125-139, In: *Hedges* (E. Pollard, M.D. Hooper, N.W. Moore, eds.). Collins, W. & Sons, London.

- Pollard, E., Hooper, M.D., et Moore, N.W. 1974. *Hedges*. Collins & sons, London.
- Porter, K., Steel, C.A., et Thomas, J.A. 1992. Butterflies and communities, pp. 139-177, In: *The ecology of butterflies in Britain* (R.L.H. Dennis, ed.). Oxford University Press, Oxford.
- Poudevigne, I., van Rooij, S., Morin, P., et Alard, D. 1997. Dynamic of rural landscapes and their main driving factors: a case study in the Seine Valley, Normandy, France. *Landscape and Urban Planning* **38**: 93-103.
- Pullin, A.S. 1995. *Ecology and conservation of butterflies*. Chapman & Hall, London.
- Purvis, G., et Fadl, A. 2002. The influence of cropping rotations and soil cultivation practice on the population ecology of carabids (Coleoptera: Carabidae) in arable land. *Pedobiologia* **46**: 452-474.
- Quinn, M.A., Kepner, R.L., Walgenbach, D.D., Nelson Foster, R., Bohls, R.A., Pooler, P.D., Reuter, K.C., et Swain, J.L. 1991. Effects of habitat characteristics and perturbation from insecticides on the community dynamics of ground beetles (Coleoptera, Carabidae) on mixed-grass rangeland. *Environmental Entomology* **20**: 1285-1294.
- Reenberg, A., et Baudry, J. 1999. Land-use and landscape changes - the challenge of comparative analysis of rural areas in Europe, pp. 23-41, In: *Land-use changes and their environmental impact in rural areas in Europe* (R. Krönert, J. Baudry, I.R. Bowler, A. Reenberg, eds.). Parthenon, Lancs.
- Ribera, I., Dolédec, S., Downie, I.S., et Foster, G.N. 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* **82**: 1112-1129.
- Ribera, I., Foster, G.N., Downie, I.S., McCracken, D.I., et Abernethy, V.J. 1999a. A comparative study of the morphology and life traits of scottish ground beetles (Coleoptera, Carabidae). *Ann. Zool. Fennici* **36**: 21-37.
- Ribera, I., McCracken, D.I., Foster, G.N., Downie, I.S., et Abernethy, V.J. 1999b. Morphological diversity of ground beetles (Coleoptera: Carabidae) in Scottish agricultural land. *Journal of the Zoological Society of London* **247**: 1-18.
- Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* **158**: 88-99.
- Robinson, R.A., et Sutherland, W.J. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* **39**: 157-176.
- Roland, J., et Taylor, P.D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**: 710-713.
- Roland, J., Keyghobadi, N., et Fownes, S. 2000. Alpine parnassius butterfly dispersal: effectsof landscape and population size. *Ecology* **81**: 1642-1653.
- Romero-Alcaraz, E., et Avila, J.M. 2000. Landscape heterogeneity in relation to variations in epigaeic beetle diversity of a Mediterranean ecosystem. Implication for conservation. *Biodiversity and Conservation* **9**: 985-1005.
- Rushton, S.P., Luff, M.L., et Eyre, M.D. 1989. Effects of pasture improvement and management on the ground beetle and spider communities of upland grasslands. *Journal of Applied Ecology* **26**: 489-503.
- Schippers, P., Verboom, J., Knaapen, J.P., et van Apeldoorn, R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS based random walk model. *Ecography* **19**: 97-106.

- Schneider, C. 2003. The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. *Ecological Entomology* **28**: 252-256.
- Schneider, C., Dover, J.W., et Fry, G.L.A. 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. *Ecological Entomology* **28**: 219-227.
- Scott, J.A. 1974. Mate-locating behavior of butterflies. *The American Midland Naturalist* **91**: 103-117.
- Shirley, M.D.F., Rushton, S.P., Smith, G.C., South, A.B., et Lurz, P.W.W. 2003. Investigating the spatial dynamics of bovine tuberculosis in badger populations: evaluating an individual-based simulation model. *Ecological Modelling* **167**: 139-157.
- Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P., et Wilson, J.D. 2001. Changes in agricultural land-use and breeding performance of some granivorous farmland passerines in Britain. *Agriculture, Ecosystems and Environment* **84**: 191-206.
- Solbrig, O.T. 1991. *From genes to ecosystems: a research agenda for biodiversity*, IUBS-SCOPE-UNESCO, Paris.
- Sotherton, N.W. 1984. The distribution and abundance of predatory arthropods overwintering on farmland. *Ann. Appl. Biol.* **105**: 423-429.
- Sparks, T.H., et Parish, T. 1995. Factors affecting the abundance of butterflies in field boundaries in Swavesey fens, Cambridgeshire, UK. *Biological Conservation* **73**: 221-227.
- Spence, J.R., et Niemelä, J.K. 1994. Sampling carabid assemblages with pitfall traps: the adness and the method. *Canadian Entomologist* **126**: 881-894.
- Steffan-Dewenter, I. 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology* **27**: 631-637.
- Steffan-Dewenter, I., et Tscharnkte, T. 2000. Butterfly community structure in fragmented habitats. *Ecology Letters* **3**: 449-456.
- Stith, B.S., Fitzpatrick, J.W., Woolfenden, G.E., et Pranty, B. 1996. Classification and conservation of metapopulations: a case study of the Florida scrub jay, pp. 187-216, In: *Metapopulation and Wildlife Conservation* (D.R. McCullough, ed.), Island Press, Washington, DC, USA..
- Stoate, C., Boatman, N.D., Borralho, R.J., Rio Carvalho, C., De Snoo, G.R., et Eden, P. 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* **63**: 337-365.
- Sunderland, K.D., De Snoo, G.R., Dinter, A., Hance, T., Helenius, J., Jepson, P., Kromp, B., Lys, J.-A., Samu, F., Sotherton, N.W., Toft, S., et Ulber, B. 1995. Density estimation for invertebrate predators in agroecosystems, In: *Arthropod Natural Enemies in Arable Land I. Density, Spatial Heterogeneity and Dispersal* (S. Toft, W. Riedel, eds.), *Acta Jutlandica* **70**: 133-162.
- Sutcliffe, O.L., et Thomas, C.D. 1996. Open corridors appear to facilitate dispersal by Ringlet Butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* **10**: 1359-1365.
- Sutcliffe, O.L., Bakkestuen, V., Fry, G., et Stabbetorp, O.E. 2002. Modelling the benefit of farmland restoration: methodology and application to butterfly movement. *Landscape and Urban Planning* **63**: 15-31.

- Sutherland, W.J. 1996. *From individual behavior to population ecology*, Oxford University Press, Oxford.
- Szacki, J. 1999. Spatially structured populations: how much do they match the classic metapopulation concept? *Landscape Ecology* **14**: 369-379.
- Taylor, P.D. 1990. Metapopulations, dispersal, and predator-prey dynamics: an overview. *Ecology* **71**: 429-433.
- Taylor, P.D., Fahrig, L., Henein, K., et Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos* **68**: 571-573.
- Ter Braak, C.J.F. 1986. Canonical correspondance analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.
- Ter Braak, C.J.F., et Smilauer, P. 1998. *CANOCO reference manual and User's guide to Canoco for Windows: Software for Canonical Community Ordination (version 4)*. Microcomputer Power, New York, USA.
- Thacker, J.R.M., et Hickman, J.M. 1990. Techniques for investigating the routes of exposure of carabid beetles to pesticides, pp. 105-113, In: *The role of ground beetles in ecological and environmental studies* (N.E. Stork, ed.). Intercept, Andover.
- Thenail, C. 2002. Relationships between farm characteristics and the variation of the density of hedgerows at the level of a micro-region of bocage landscape. Study case in Brittany, France. *Agricultural Systems* **71**: 207-230.
- Thenail, C., et Baudry, J. Sous presse. Variation of farm spatial land use pattern according to the structure of the hedgerow network (bocage) landscape: a case study in northeast Brittany. *Agriculture, Ecosystems and Environment*.
- Thiele, H.U. 1977. *Carabid beetle in their environments*. Springer-Verlag, Heidelberg, New-York.
- Thomas, C.D. 1991a. Spatial and temporal variability in a butterfly population. *Oecologia* **87**: 577-580.
- Thomas, C.D., et Harrison, S. 1992. Spatial dynamics of a patchily distributed butterflies species. *Journal of Animal Ecology* **61**: 437-446.
- Thomas, C.F.G., et Marshall, E.J.P. 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems and Environment* **72**: 131-144.
- Thomas, C.F.G., Parkinson, L., et Marshall, E.J.P. 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia* **116**: 103-112.
- Thomas, J.A. 1984. The conservation of butterflies in temperate countries: past efforts and lessons for future, pp. 333-353, In: *The biology of butterflies* (R.I. Vane Wright, P.R. Ackery, eds.). Academic Press, London.
- Thomas, J.A. 1991b. Rare species conservation: case studies of European butterflies, pp. 149-197, In: *The Scientific Management of Temperate Communities for Conservation* (I.F. Spellerberg, F.B. Goldsmith, M.G. Morris, eds.). Blackwell Scientific Publications, Oxford.
- Thomas, J.A. 1996. The case for a science-based strategy for conserving threatened butterfly populations in the UK and North Europe, pp. 1-6, In: *Species survival in fragmented landscapes* (J. Settele, C.R. Margules, P. Poschlod, K. Henle, eds.). Kluwer Academic Publisher, Dordrecht.

- Thomas, M.B., Sotherton, N.W., Coombes, D.S., et Wratten, S.D. 1992. Habitat factors influencing the distribution of polyphagous predatory insects between field boundaries. *Annals of Applied Biology* **120**: 197-202.
- Thomas, S.R., Noordhuis, R., Holland, J.M., et Goulson, D. 2002. Botanical diversity of beetle banks: effects of age and comparison with conventional arable field margins in southern UK. *Agriculture, Ecosystems and Environment* **93**: 403-412.
- Tischendorf, L., et Fahrig, L. 2001. On the use of connectivity measures in spatial ecology. A reply. *Oikos* **95**: 152-155.
- Trautner, J., et Geigenmuller, K. 1987. *Tiger beetles, ground beetles. Illustrated key to the Cicindelidae and Carabidae of Europe*. Josef Margraf, Aichtal.
- Turchin, P. 1989. Population consequences of aggregative movement. *Journal of Animal Ecology* **58**: 75-100.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modelling populations redistribution in animals and plants*. Sinauer Publisher, Sunderland.
- Turin, H., et Heijerman, T. 1988. Ecological classification of forest-dwelling carabidae (Coleoptera) in the Netherland. *Tijdschrift voor Entomologie* **131**: 65-71.
- Turin, H., Alders, K., Den Boer, P.J., Van Essen, S., Heijerman, T.H., Laane, W., et Penterman, E. 1991. Ecological characterization of carabid species (Coleoptera, Carabidae) in the Netherlands from 30 years of pitfall sampling. *Tijdschrift voor Entomologie* **134**: 279-304.
- Turner II, B.L., et Meyer, W.B. 1994. Global land-use and land cover change: an overview, pp. 3-10, In: *Changes in land use and land cover: a global perspective* (W.B. Meyer, B.L. Turner II, eds.). Cambridge University Press, Cambridge.
- Turner, M.G., et Gardner, R.H. 1991. *Quantitative methods in landscape ecology*. Springer Verlag, New York.
- Turner, M.G., Dale, V.H., et Gardner, R.H. 1989a. Predicting across scales: theory development and testing. *Landscape Ecology* **3**: 245-252.
- Turner, M.G., O'Neill, R.V., Gardner, R.H., et Milne, B.T. 1989b. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* **3**: 153-162.
- Turner, M.G., Arthaud, G.J., Engstrom, R.T., Hejl, S.J., Liu, J., Loeb, S., et McKelvey, K. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* **5**: 12-16.
- Urban, D.L., O'Neill, R.V., et Shugart, H.H. 1987. Landscape ecology. *Bioscience* **37**: 119-127.
- van Dorp, D., et Opdam, P.F.M. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology* **1**: 59-73.
- Vane Wright, R.I., et Ackery, P.R. 1981. *The biology of butterflies*. Academic Press, British Museum.
- Varchola, J.M., et Dunn, J.P. 1999. Changes in ground beetle (Coleoptera: Carabidae) assemblages in farming systems bordered by complex or simple roadside vegetation. *Agriculture, Ecosystems and Environment* **73**: 41-49.
- Verboom, B., et van Apeldoorn, R. 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. *Landscape Ecology* **4**: 109-122.

- Vos, C.C., Verboom, J., Opdam, P.F.M., et Ter Braak, C.F.J. 2001. Toward ecologically scaled landscape indices. *The American Naturalist* **183**: 24-40.
- Wardle, D.A., Nicholson, K.S., Bonner, K.I., et Yeates, G.W. 1999. Effects of agricultural intensification on soil-arthropod population dynamics, community structure, diversity and temporal variability over a seven year period. *Soil Biology and Biochemistry* **31**: 1691-1706.
- Weibull, A.-C., et Östman, Ö. 2003. Species composition in agroecosystems: the effect of landscape, habitat and farm management. *Basic and Applied Ecology* **4**: 349-361.
- Weibull, A.-C., Bengtsson, J., et Nohlgren, E. 2000. Diversity of butterflies in the agricultural landscape : the role of farming system and landscape heterogeneity. *Ecography* **23**: 743-750.
- Weibull, A.-C., Östman, Ö., et Granqvist, A. 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation* **12**: 1335-1355.
- Wheater, C.P. 1991. Effect of starvation on locomotor activity in some predacious coleoptera (Carabidae, Staphylinidae). *The Coleopterists Bulletin* **45**: 371-378.
- Wiens, J.A., et Milne, B.T. 1989. Scaling of "landscapes" in landscape ecology, or, in landscape ecology from a beetle's perspective. *Landscape Ecology* **3**: 87-96.
- Wiens, J.A., Crist, T.O., et Milne, B.T. 1993a. On quantifying insect movements. *Environmental Entomology* **22**: 709-715.
- Wiens, J.A., Schooley, R.I., et Weeks, R.D. 1997. Patchy landscapes and animal movements : do beetle percolates ? *Oikos* **78**: 257-264.
- Wiens, J.A., Stenseth, N.C., Van Horne, B., et Ims, R.A. 1993b. Ecological mechanisms and landscape ecology. *Oikos* **66**: 369-380.
- Wiklund, C. 1977. Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). *Oikos* **28**: 56-68.
- Wilcove, D.S., McLellan, C.H., et Dobson, A.P. 1986. Habitat fragmentation in the temperate zone, pp. 237-256, In: *Conservation biology* (M.E. Soule, ed.). Sinauer Associates Inc., Sunderland, Massachusetts.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., et Bradbury, R. 1999. A review of abundance and diversity of invertebrates and plant food of granivory birds in Northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment* **75**: 13-30.
- Wilson, R.J., et Thomas, C.D. 2002. Dispersal and the spatial dynamics of butterfly populations, pp. 257-278, In: *Dispersal ecology* (J. Bullock, R. Kenward and R. Hails, eds.). Blackwell Science, Oxford.
- With, K.A., et Crist, T.O. 1996. Translating across scales: simulating species distributions as the aggregate response of individuals to heterogeneity. *Ecological Modelling* **96**: 125-137.
- With, K.A., et King, A.W. 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* **14**: 73-82.
- With, K.A., et King, A.W. 1999b. Extinction thresholds for species in fractal landscapes. *Conservation Biology* **13**: 314-326.
- With, K.A., Gardner, R.H., et Turner, M.G. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* **78**: 151-169.

- With, K.A., Cadaret, S.J., et Davis, C. 1999. Movement responses to patch structure in experimental fractal landscapes. *Ecology* **80**: 1340-1353.
- Wynhoff, I. 1992. Micro-distribution and flower preference of the Meadow Brown (*Maniola jurtina*) and the Ringlet (*Aphantopus hyperantus*), pp. 177-185, In: *Future of butterflies in Europe, strategies for survival* (T. Pavlicek-van Beek, H.A. Ovaa, J.G. van der Made, eds.). Agricultural University Wageningen, Wageningen.
- Zollner, P.A., et Lima, S.L. 1999. Search strategies for landscape-level interpatch movements. *Ecology* **80**: 1019-1030.

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Résumé

Dans cette étude, nous analysons les interactions entre l'intensité de l'agriculture, les habitats permanents et la dynamique de la biodiversité dans des paysages bocagers de l'Ouest de la France, en prenant l'exemple des insectes (Coléoptères Carabiques, Lépidoptères Rhopalocères). L'objectif est d'identifier les effets respectifs des facteurs locaux – qualité des ressources et pratiques agricoles – et des facteurs intervenant à l'échelle du paysage – caractéristiques du paysage et systèmes de production agricole. Deux approches sont adoptées pour examiner ces relations, (i) une approche empirique des facteurs d'organisation des communautés de carabes et (ii) une approche de modélisation des flux d'individus et de la dynamique d'une espèce de papillon (*Maniola jurtina* L.).

Les résultats montrent que la quantité et l'arrangement spatial des haies, bois et autres milieux permanents au sein du paysage sont des facteurs plus importants pour expliquer la dynamique de la biodiversité que les facteurs locaux ; ces caractéristiques du paysage sont liées à la nature et l'intensité des systèmes de production agricole actuels. A l'échelle locale, la capacité d'accueil des habitats pour les espèces est déterminée par les pratiques agricoles qui modifient la qualité des ressources ; ces modifications interviennent sur la distribution des espèces en inhibant les déplacements des individus entre taches de ressources. Cependant, la réponse de la biodiversité aux pratiques agricoles dépend fortement des caractéristiques du paysage environnant, qui déterminent la présence des espèces les plus sensibles aux perturbations.

Ces résultats permettent d'identifier des échelles spatio-temporelles pertinentes en terme de gestion et d'aménagement pour la conservation de la biodiversité dans les paysages agricoles.

Mots clés : écologie du paysage, agriculture, biodiversité, hétérogénéité spatio-temporelle, éléments permanents, invertébrés.

Abstract

We analyze the interactions between farming intensity, permanent habitats and biodiversity dynamics – especially insects (Carabid beetles, Butterflies) – in hedgerow network landscapes in Western France. We aim at identifying the relative effects of local factors – resource quality and farming practices – and landscape factors – landscape pattern and farming systems. Two approaches were adopted: (i) an empirical study of the factors implicated in the organisation of carabid communities and (ii) a modelling approach of the movements and population dynamics of a butterfly species (*Maniola jurtina* L.).

The results show that the amount and spatial organisation of hedgerows, woodlands and other permanent habitats in the landscape are more important factors for explaining biodiversity dynamics than local factors; these landscape characteristics are linked to the type and intensity of actual farming systems. At the local scale, habitat suitability for species is determined by farming practices that modify resource quality; these modifications also influence species distribution by impeding movements of individuals between resource patches. However, the response of biodiversity to farming practices depends strongly on the landscape pattern that determines the presence of species intolerant to disturbances.

These results permit to identify appropriate spatio-temporal scales to design action plans for the conservation of biodiversity in agricultural landscapes.

Keywords : landscape ecology, agriculture, biodiversity, spatio-temporal heterogeneity, permanent landscape elements, invertebrates.