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# Simulation of agricultural landscapes to study population dynamics of pest and auxiliary

Khadija Sabir

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Master thesis

# **Simulation of agricultural landscapes to study population dynamics of pest and auxiliary**

by

**Khadija Sabir**

**Registered school: SupAgro Montpellier**

A thesis submitted in partial fulfillment of the requirement for diploma of Master of Sciences and Technologies, Agriculture sciences and Agrifood sciences under EMJMD “Plant Health in Sustainable Cropping Systems”

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**President: Frédéric Hamelin**

**Members: Elena Kazakou**  
**Guillaume Fried**



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**Khadija Sabir**

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## **Abstract:**

Crop pests remain a constant threat to global food security despite of the intensive measures of crop protection. Loss of habitat heterogeneity because of landscape simplification and excessive use of external fossil and agrochemical inputs has partially eliminated the ecological functions provided by communities of potentially beneficial organisms. So, it is crucial to understand on-farm management and composition of landscapes surrounding agricultural fields, which strongly impact biological control. Up to now, most studies in the literature are limited to particular fields and often they do not consider the spatial and temporal heterogeneity of landscape at a larger scale. In this context, we propose to develop a landscape model that allows us to study ecological characteristics linked to landscape composition and organization at a large spatial scale. This generative stochastic landscape model allows simulating large numbers of landscapes based on various predefined configurations of parameters controlling habitat quality. These simulations are used as an input to run a spatially explicit population dynamics model. We use the combined model to study how the variations in landscape structure lead to fluctuations in pest and auxiliary population densities depending on large-scale habitat heterogeneity, which ultimately affects biological control service. The particular pest-predator system that has motivated this theoretical study is composed of the codling moth pest and its predators in apple orchards, but our model is generic enough to be adaptable to and interpretable for other insect species. Based on an extensive simulation study, we found that spatial heterogeneity and landscape structure have a strong effect on pest-predator population dynamics. Integration of such concepts and knowledge into agricultural land-use management can pave the way to modern, productive and environmentally friendly crop production systems.

## **Key words:**

Agricultural intensification, Codling moth, Conservation biological control, Crop protection, Landscape heterogeneity, Population dynamics, Reaction-diffusion model, Stochastic landscape model.

## Résumé:

Les ravageurs des cultures représentent une préoccupation d'envergure mondiale en raison des pertes en qualité et en quantité qu'ils causent. Ils constituent une menace majeure pour la sécurité alimentaire mondiale en dépit de mesures intensives de protection des cultures. Depuis le milieu du vingtième siècle, une tendance drastique vers une simplification des paysages a entraîné une augmentation de la production agricole par la conversion d'habitats naturels et semi-naturels en champs cultivés. Ainsi, la perte de l'hétérogénéité de l'habitat et l'utilisation excessive des intrants fossiles et agrochimiques externe a partiellement remplacé et supprimé les services écologiques fournis par les communautés d'organismes potentiellement bénéfiques. Cependant, pour réduire ces effets négatifs et pour remplacer l'utilisation d'intrants chimiques nocifs, la lutte biologique offre des solutions respectueuses de l'environnement et importantes pour la lutte durable des ravageurs. Dans les exploitations agricoles, la gestion et la composition des paysages autour des champs agricoles ont un fort impact sur la lutte biologique.

Les paysages complexes augmentent l'abondance des ennemis naturels et de leur diversité avec des conséquences sur la pression de la prédation. En revanche, certaines études montrent que les paysages agricoles complexes non seulement améliorent les services écosystémiques (conservation de lutte biologique), mais peuvent également avoir des effets antagonistes. Dans ces cas, les paysages complexes peuvent impliquer des interactions négatives entre les ennemis naturels (compétition, prédation intra-guilde,...) rendant la lutte biologique inefficace.

La littérature récente suggère que la structure spatio-temporelle de l'habitat dans les paysages agricoles peut éviter des interactions négatives entre les populations de prédateurs. Cependant, à cause des changements concernant l'utilisation des terres et des habitats semi-naturels, les structures (potentiellement) disponibles dans les paysages arables actuels se limitent généralement aux haies en bord de champs, apparaissant sous forme de bandes linéaires dans les paysages. Les haies jouent un rôle important grâce à leur fonction stable dans le temps par rapport aux champs de cultures ; elles fournissent des connexions entre les différentes parcelles isolées et présentent une source alimentaire alternative. Cependant, peu de recherches ont été effectuées sur la dynamique des populations de ravageurs et auxiliaires en tenant compte de différents scénarios de complexité du paysage par rapport au compartiment cultivé, aux habitats semi-naturels et aux structures linéaires (haies).

Par conséquent, pour redessiner les paysages agricoles dans le but d'une lutte plus durable, il est important de comprendre les caractéristiques écologiques liées à la composition et configuration du paysage dans des paysages complexes. Ces caractéristiques soutiennent la biodiversité et peuvent augmenter ou réduire le contrôle biologique. Il est essentiel d'identifier l'importance écologique des éléments paysagers représentant une faible proportion de surface (tels que les haies) dans le paysage agricole, et leur rôle dans le contrôle des ravageurs.

Dans ce contexte, nous proposons de développer un modèle stochastique du paysage, couplé ensuite avec un modèle de dynamique de population spatialement explicite basé sur des équations aux dérivées partielles. L'objectif principal de notre étude théorique, basée sur des simulations *in silico*, est de répondre aux questions de recherche suivantes: Quels sont les facteurs qui influent sur les densités de population de prédateurs et de ravageurs dans un paysage complexe? Comment les traits d'histoire de vie des insectes modifient-ils l'effet de l'hétérogénéité du paysage? Quelle est la relation entre les parasites et la population des

prédateurs dans le paysage complexe? L'hétérogénéité du paysage peut-elle diminuer le nombre de traitements de pesticides en améliorant la lutte biologique par conservation?

Le générateur stochastique de paysages permet de simuler un grand nombre de paysages basés sur différentes configurations de paramètres prédéfinis contrôlant la qualité de l'habitat. Dans notre étude, nous utilisons un paysage agricole de la région Selommes (une région agricole dans le centre de la France), en appliquant quelques prétraitements mineurs à la géométrie observée, nécessaires pour notre modèle. Nous supposons qu'un paysage est composé de champs agricoles (éléments de surface 2D), séparés par des arêtes (éléments linéaires 1D), sur une échelle spatiale relativement importante. Dans le modèle, les champs sont classés, selon une proportion préfixée, en deux types d'habitat potentiel pour les organismes et les auxiliaires: un premier type représentant la culture principale (qui pourrait être une culture pérenne comme les vergers de pommiers), et un second type d'habitat, qui pourrait correspondre à un autre type de culture (annuelle ou pérenne) ou à de l'habitat semi-naturel. Une proportion variable des linéaires séparant les champs est convertie en haies pour augmenter les habitats semi-naturels autour des parcelles cultivées. Un champ aléatoire gaussien multivarié est utilisé pour marquer les éléments du paysage et pour gérer l'agrégation spatiale des différents types, potentiellement corrélés en eux.

Les simulations du paysage selon différentes configurations des paramètres régissant les proportions et l'agrégation spatiale des éléments paysagers sont utilisées en entrée du modèle de dynamique de population. Le système proie/prédateur qui a motivé cette étude théorique se compose du ravageur carpocapse (*Cydia pomonella* L., Lepidoptera: Tortricidae) et de son prédateur spécialiste présumé (des coléoptères au sol, Carabidae) dans les vergers de pommiers. Les principales hypothèses du modèle sont: le ravageur est spécialiste des pommiers, les autres parcelles représentant donc un puits pour lui. Les haies constituent l'habitat principal du prédateur en l'absence de ravageur, et le prédateur est spécialiste de ce ravageur. Dans les champs cultivés, le prédateur trouve une ressource d'alimentation alternative, à savoir le ravageur. Cependant, ce modèle est assez général et pourrait facilement être adapté aux caractéristiques d'autres systèmes prédateurs / parasites. Le modèle intègre aussi de possibles applications phytosanitaires si la densité de proie dépasse un certain seuil dans les parcelles cultivées.

Nous avons mené une étude de simulation extensive. À l'aide d'une analyse de sensibilité et de modèles de régression sur les sorties des modèles simulés, nous avons pu dégager des résultats importants sur les facteurs régissant la dynamique des populations entre prédateurs et ravageurs. En particulier, nos résultats indiquent que la proportion de haies et la migration des prédateurs sont importantes pour augmenter la population des prédateurs. La migration et la diffusion des prédateurs dans les champs sont des traits cruciaux ayant des effets positifs compensatoires sur la population des prédateurs. Notre étude a montré que le réseau de haies en bordure des champs joue un rôle clé pour améliorer la capacité de dispersion intrinsèque des prédateurs. Nous avons constaté que la proportion des cultures représente le principal facteur provoquant une augmentation de la population de ravageurs sur tous les niveaux d'agrégation du paysage; elle conduit donc à une augmentation du nombre de traitements phytosanitaires sur le paysage. Cependant, les effets négatifs de la proportion des cultures peuvent être compensés par l'amélioration de la disponibilité de l'habitat semi-naturel. Il est important de noter que nous avons pris un produit phytosanitaire à spectre étroit ayant aucun effet néfaste sur la population

des prédateurs. En effet, certains résultats pourraient être différents si le pesticide appliqué a un effet substantiel sur le prédateur.

Notre étude confirme que l'hétérogénéité spatiale et la structure du paysage ont un effet important sur la dynamique des populations des prédateurs et ravageurs. Certains résultats restent encore difficiles à expliquer car les variations dans les sorties de modèle ne dépendent pas directement des configurations des paramètres d'entrée, mais sont une conséquence de la stochasticité du modèle. Cependant, nous pouvons conclure que l'habitat naturel augmente la population des prédateurs, mais il ne montre pas de corrélation forte avec la réduction du ravageur. Néanmoins, la densité des prédateurs maintient la densité des parasites en-dessous du niveau du seuil économique, empêchant ainsi des fortes densités très localisées des ravageurs. Cela réduit le nombre d'applications phytosanitaires nécessaire.

La présente étude est une approche descendante, et l'intégration de ces concepts et connaissances dans la gestion de l'utilisation des terres agricoles peuvent ouvrir la voie à des systèmes de production de cultures modernes, productives et respectueuses de l'environnement.

### **Mots clés:**

Contrôle biologique par conservation, Dynamique des populations, Hétérogénéité du paysage, Intensification agricole, Modèle de réaction-diffusion, Modèle stochastique de paysage, Protection des cultures.

Crop yield losses because of the agricultural pests are difficult to quantify accurately at global scale because of availability of patchy data across crops and ecosystems (Oerke, 2006). But the decrease in crop produce quality and quantity may be massive enough to threaten the global food security despite intensive measures of crop protection (Martin *et al.*, 2013). In this era of modern agriculture with increasing pressure to reduce use of harmful chemical inputs, biological control offers one of the major and environmental friendly solutions for sustainable pest management (Van Lenteren, 1992; Bale *et al.*, 2008; Hendrichs *et al.*, 2009). However on-farm management and the composition of landscapes surrounding agricultural fields strongly impact biological control (Hendrickx *et al.*, 2007; Tscharntke *et al.*, 2012). Since the mid of the 20th century, the drastic increase in simplification of the landscapes has resulted in increased agriculture production by converting natural and semi-natural habitats into arable fields but it has also lead to substantial loss of non-crop field margins (Jenkins, 2003; Godfray *et al.*, 2010). Because of this, a negative relationship has arisen between agriculture intensity and biodiversity of agricultural landscapes, accompanying its negative impacts on water and soil, human and ecosystem health (Tscharntke *et al.*, 2005). Loss of habitat heterogeneity and excessive use of external fossil and agrochemical inputs has partially replaced and suppressed the ecological services provided by communities of beneficial organisms (Kremen *et al.*, 2002; Benton *et al.*, 2003; Hooper *et al.*, 2005; Tscharntke *et al.*, 2005).

Complex agricultural landscapes generally alter the natural enemy communities mainly by increasing natural enemy abundance and diversity. Such expected changes in the natural enemy community composition are mediated by the heterogeneity of crop composition and structure. It provides a diversity of habitats and resources to natural enemies resulting from more alternative prey, microclimate heterogeneity and refuges from their own predators and for overwintering (Landis *et al.*, 2000; Sunderland and Samu, 2000; Altieri and Nicholls, 2005; Rusch *et al.*, 2010; Ratnadass *et al.*, 2012). However, increases in the predation pressure are more related to the probability of presence of a key voracious predator species and the functional complementarity of species, hence buffering the link between landscape complexity and biocontrol services (Loreau *et al.*, 2001; Schmidt *et al.*, 2005; Bianchi *et al.*, 2006; Kremen and Chaplin-Kramer, 2007; Drapela *et al.*, 2008; Schmidt *et al.*, 2008). Despite that, a positive relationship has been documented between landscape complexity and rates of parasitism/predation in many crop production systems (Bianchi *et al.*, 2006; Thies *et al.*, 2008; Boccaccio and Petacchi, 2009; Gardiner *et al.*, 2009).

In some cases, however, it has also been observed that complex landscapes can imply negative antagonistic interactions between natural enemies (flying insects, ground dwellers) and birds, resulting in ineffective biological control (Martin *et al.*, 2013; Perez-Alvarez *et al.*, 2018). Predators may prey less on the crop pest because they are diverted from it by alternative prey in the hedges (i.e. dilution effect) (Koss *et al.*, 2004), or because of increased intra-guild predation, or both (Halaj and Wise, 2002). Moreover, in complex landscapes availability of overwintering habitats with alternative resources may also increase pest populations in addition to natural enemies (Tscharntke *et al.*, 2005). This shows that landscape composition not only mediates ecosystem services (conservation biological control) but may also represent a disservice. Therefore, to redesign agricultural landscapes, it is important to understand the ecological

characteristics linked to landscape composition and configuration in complex landscapes, which support biodiversity and may enhance or reduce biological control.

Because of current land-use changes, semi-natural habitat is typically confined to hedgerows which are in form of linear strips within arable landscapes. These play an important role with their stable landscape feature in time as compared to crop fields. Hedges may also promote exchange of species by establishing connections between different isolated patches, therefore acting as line corridors. This supports natural enemy dispersal and movement to escape from disturbances and to find food resources scattered in time and space (Roques and Bonnefon, 2016; Tschardtke *et al.*, 2016; Cohen and Crowder, 2017). Therefore, it is crucial to identify the ecological importance of small proportion elements (i.e. hedges) in spatial and temporal dynamic agricultural landscape, and study how these connections should organize such that they provide a habitat niche to build natural enemy communities and then aid in their dispersal over large-scale heterogeneous habitat for effective pest suppression.

Only little research has been done on population dynamics of pest and auxiliary in combination with diverse landscape complexity (cultivated and semi-natural habitats) and its linear structures (hedges). It has reported that presence of windbreaks and spontaneous hedgerows around the orchards favours the biocontrol by natural enemies (Maalouly *et al.*, 2013). In another study they found higher population of pest in abandoned orchards as compared to commercially managed orchards (Joshi *et al.*, 2016). Moreover, these studies were mainly limited to a particular field and did often not consider the spatial and temporal heterogeneity of landscape at a larger scale at the same time.

Therefore, to fill those research gaps, we have here developed a stochastic landscape model coupled with a spatially explicit population dynamic model driven by a system of partial differential equations. The main research questions of the study are as follows: What are the factors that influence the pest-predator population densities in complex landscape? How do life history traits modify the effect of landscape heterogeneity? What is the relationship between pest and predator population in complex landscape? Can landscape heterogeneity reduce the number of pesticide treatments by enhancing the conservation biological control? Our research findings ultimately established concepts about ecological characteristics that can enhance or reduce the conservation biological control.

For this study, the model system that we assumed is apple crop pest (e.g. Codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) with its assumed specialist predator (Ground beetle; Carabidae). We choose this system because of availability of research data of this system in the south of France (Ricci *et al.*, 2009; de Roince *et al.*, 2012; Dainese *et al.*, 2017). Notice however that there is no loss of generality since our model system could easily be adapted to the characteristics of other predator/pest systems.

### 1- Biological control:

#### i) History and types of biological control:

The use of a population of an organism to control the population of another organism such as an insect pest, weed or other microbial organisms, is simply known as biological control. This method has been used in agriculture for centuries, but the big wave of activity in modern era started at the end of the nineteenth century when parasitic flies (*Cryptochaetum iceryae*) (Diptera: Cryptochaetidae), and the vedalia beetles (*Rodolia cardinalis*) (Coleoptera: Coccinellidae) were successfully introduced in California citrus orchards to control cottony-cushion scale (*Icerya purchasi*) (Hemiptera: Monophlebidae) in the late (De Bach, 1964; Caltagirone, 1981; Van Lenteren and Godfray, 2005). However, later in the mid-1940s' this method was replaced by synthetic pesticide industry until a research named 'Silent Spring' was published (Carson, 1962). The main emphasis of the book was on how rigorous use of pesticides contaminated almost every part of the environment and lead to toxicological effects to non-target organisms (insects, plants, fish, and birds). This caused augmented global awareness and interest to develop alternatives to synthetic pesticides. This opened an opportunity for biological control methods to be used in safe management of agricultural pests and resulted in a greater application in agriculture worldwide (Aktar *et al.*, 2009; Gay, 2012; Azmathullah *et al.*, 2013; Barratt *et al.*, 2018). Since 2009, European Union (EU) has been advocating the use of biological control in its Sustainable Use of Pesticides Directive (Parliament, 2009).

There are four known types of biological control: natural, conservation, classical, and augmentative biological control (Eilenberg *et al.*, 2001; Cock *et al.*, 2010). Natural biological control is one of many ecosystem services which reduces the pest organisms by naturally occurring beneficial organisms of the system (Costanza *et al.*, 1997; MEA, 2005). Without any human intervention, this natural phenomenon can be found in all ecosystems of the world, and economically this type of biological control provides the greatest contribution to agriculture (Waage and Greathead, 1988). Conservation biological control is based on the manipulation of agroecosystems to protect and stimulate the performance of naturally occurring pest enemies of an ecosystem (Bottrell *et al.*, 1998; Weller *et al.*, 2002; Rodriguez-Saona *et al.*, 2012). This method is more appropriate as compared to certain other types of biological control because natural enemies do not need time to adapt to new environments, and some major environmental concerns can be avoided (Barbosa, 1998). In classical biological control, natural enemies of particular pests are usually collected from their area of origin and then released in problematic areas to reduce pest population (Cock *et al.*, 2010). This is the first widely practiced type of biological control (De Bach, 1964). Finally, in augmentative biological control, natural enemies such as parasitoids, predators or micro-organisms are mass-reared commercially and released in large numbers. The periodic release can be labeled as inundative, i.e. targeting immediate control of pests in crops during short production cycle, or seasonally innoculative, i.e. aiming at the control of pests during several generations in crops with a long production cycle (Cock *et al.*, 2010; Lorito *et al.*, 2010; Van Lenteren, 2012; Parnell *et al.*, 2016).

## **ii) Importance of conservation biological control:**

Biological control service can provide a crucial contribution to manage agriculture pests because the estimated annual loss in crop produce is estimated about 470 billion dollars (Culliney, 2014). These economic losses, coupled with food security issues of the Earth's growing population, result in a huge demand to address the increase of food availability in coming decades (Tilman *et al.*, 2011; Godfray and Garnett, 2014). Intensive use of insecticides with their negative impacts on soil, water and environment also causes resistance in pest populations, making insecticides ineffective. This declined the availability of products to control crop pests respecting the stringent regulatory demands for human and environmental safety. In this context, biological control offers a sustainable and environmentally sound alternative to pesticides for regulating pest populations (Pimentel, 2005; Jonsson *et al.*, 2008). The estimated value of biological control service is \$4.5 billion to \$17 billion in the United States only (Pimentel *et al.*, 1997; Losey and Vaughan, 2006).

## **iii) Main factors affecting conservation biological control:**

During the last century, crop production has increased through agriculture intensification coming with high input management practices and landscape changes widely identified as unsustainable (Matson *et al.*, 1997; Robinson and Sutherland, 2002; Benton *et al.*, 2003; Potts *et al.*, 2010). Landscape simplification through rapid anthropogenic disappearance of natural ecosystems resulted in loss of biodiversity and threatened the ecosystem services (biological control and pollination services) (Landis *et al.*, 2008; Geiger *et al.*, 2010; Bommarco *et al.*, 2013). Recurrent use of broad spectrum insecticide applications cause death of natural enemies of pests and ultimately lead to pest outbreaks through reduced biological control (Pimentel, 2005; Geiger *et al.*, 2010). Landscape changes include enlargement of fields, reduced diversity of crops and cropping patterns and loss of landscape elements (hedges, grassy margins) which tends to render landscapes more homogeneous with large-scale monocultures. Such landscapes do not provide diversity of habitats to sustain a variety of natural enemy species (Tschardt *et al.*, 2008; Médiène *et al.*, 2011).

## **2- Sustainable agricultural intensification:**

Agroecosystems are often manipulated through diversification of vegetation patterns and revised farming practices that enhance the conservation biological control (CBC) service. Thus, it is believed that biodiversity conservation can enhance CBC by increasing the predator population, but it can also have a direct impact on pest (positive or negative), independent of natural enemies (Poveda *et al.*, 2008; Trujillo, 2011; Lu *et al.*, 2014).

Mostly, conservation biological control tends to focus on specific crop fields, and vegetative manipulation is usually done within the fields, along its borders or in few adjacent fields within that particular farming unit. At this small scale, activity of natural enemies may be enhanced by enhancing plant diversity through mixed cropping, strip cropping and intercropping within fields, and semi-natural habitat near field margins. This establishes a favourable microclimate with key ecological resources for natural enemies, i.e. alternative prey/hosts, shelters, oviposition sites and alternative plant food (pollen and nectar) (Begg *et al.*, 2017). Generally agriculture fields situated in mosaics of habitat types are managed and organized



specifically for suppression of agriculture pests by natural enemies (Müller and Brodeur, 2002; Straub *et al.*, 2008).

It is often assumed that farms with complex habitats and less intensive management practices are more suitable for biodiversity conservation and functionality. This reduces the need for human intervention with external inputs and supports a greater number of natural enemy diversity, which can enhance the provision of the ecosystem service of biological pest control. In contrast, if we take a broader prospective at the landscape level, agroecosystems range from areas dominated by a single cropping system (structurally simple) to diverse cropping systems embedded in a natural habitat matrix (structurally complex). A high number of contrary studies can be found where increases in natural enemy diversity do not always lead to effective biological control (Straub *et al.*, 2008; Letourneau *et al.*, 2009; Macfadyen *et al.*, 2011). In some situations, identification of key species for the control of a target pest is more crucial than species diversity (Ives *et al.*, 2005; Straub *et al.*, 2008). Additionally, this habitat diversity can also represent a suitable environment for a large number of pest species at several key stages of their life-cycle (Blitzer *et al.*, 2012; Parry *et al.*, 2015).

In complex landscapes, pest control by natural enemies usually varies with respect to their interactions among individuals. Interactions with spatio-temporal environment changes (habitat, resources) can lead to negative effects through intraguild predation or apparent competition, neutral effects and no gain in functionality when sharing similar niches (Ives *et al.*, 2005; Straub and Snyder, 2006). These interactions can also lead to additive effects with complementarity resource use (Macfadyen *et al.*, 2011).

### **i) Role of spatio-temporal variability:**

Semi-natural habitats in spatially and temporally heterogeneous agricultural landscapes play an important role owing to their stable yet heterogeneous landscape features (due to the metapopulation dynamics and environmental fluctuations) in time and space. In contrast to this, crop mosaics only undergo regular compositional changes due to crop rotation, which alters spatial and temporal heterogeneity (Vasseur *et al.*, 2013). Because of current land-use changes, semi-natural habitat is usually limited to hedgerows, which are in form of (quasi-) linear strips within arable landscapes. They induce many important biotic (e.g., habitats, refuges for small mammals, birds and invertebrates) and abiotic properties (e.g., windbreak). They also promote exchange of species between isolated patches, therefore acting as line corridors (Forman, 1983; Sustek, 1992). In a landscape, insects often have limited dispersal and movement; specifically for natural enemies, it is very critical to escape from disturbances and to find resources scattered in space and time. So, hedges offering semi-natural habitats adjacent to crop fields have a major impact on insect communities by making corridors and establishing connections between different isolated patches of the landscape (Roques and Bonnefon, 2016; Tschardtke *et al.*, 2016; Cohen and Crowder, 2017).

Utilization of hedges as an alternative food source can drive evolutionary changes in insects because various chemical components of their novel diets confront their physiological systems. So, new selection pressures can be imposed because of dietary shifts, which leads to evolutionary changes (Vogel *et al.*, 2014; Hoang *et al.*, 2015). This can result in an expansion of target prey or host range consumption among biological control agents through an adaptation

process (Wright and Bennett, 2018). Moreover, specific habitat structures within dynamic agriculture landscape can prevent negative interactions among natural enemies populations (Janssen *et al.*, 2007).

The spatial heterogeneity of the crops is described by crop diversity, their spatial arrangement (field size) and their temporal heterogeneity owing to changes in crop patterns/rotations. It has been reported that this variability may affect biodiversity and associated ecosystem services (Vasseur *et al.*, 2013; Šálek *et al.*, 2018), but the effects of landscape composition and configuration are difficult to disentangle because they are typically highly correlated in agricultural landscapes (Fahrig *et al.*, 2011).

There are few examples studying their effects separately; they concluded that crop diversity and configuration have positive effects on predatory arthropods and biological control (Palmu *et al.*, 2014; Fahrig *et al.*, 2015; Bertrand *et al.*, 2016). However, these positive effects may not always directly translate into negative effects on pest abundance (Chaplin-Kramer *et al.*, 2011). A possible reason is that most studies do not take into account the vegetation patterns at the landscape level that shape resource availability for pests and that strongly influence the local scale impact of natural enemies (Perović *et al.*, 2010; Veres *et al.*, 2013; Paredes *et al.*, 2015).

To meet future food security demands, sustainable agriculture systems based on intensification of ecological principles, which may enhance the ecosystem services provided by biodiversity (i.e. biological control), rather than greater reliance on non-renewable resources (i.e. chemical inputs), should be designed (Doré *et al.*, 2011; Bommarco *et al.*, 2013). This requires good understanding of the biotic processes (ecological and agronomic) that govern ecosystem service delivery, and it further requires better comprehension of interactions among herbivore arthropods, natural enemies and crop management strategies at a broader scale. Most of the research on biological control represents a bottom-up process with focuses on a single crop species or a very specific pest. Instead, we should rather focus on a holistic and top-down approach to develop a well-functioning biosphere allowing us to overcome food security issues.

## **ii) Use of landscape modelling:**

Landscapes are considered as an assemblage of mosaic elements. On many spatial and temporal scales, these elements evolve and interact (Forman and Godron, 1981; Burel, 2003), modifying the landscape spatial organization expressed through its composition and configuration (patch shape and sizes) (Li and Reynolds, 1994). It is far from being trivial to design sustainable agricultural landscapes. The reasons lie in complex interactions between natural and human processes, resulting in synergies or antagonisms among services, indirect effects or emerging patterns (Bennett *et al.*, 2009). Thus, it has always been difficult to conduct landscape-scale experiments. In this context, modelling can provide a key contribution to the design of sustainable agricultural landscapes (Poggi *et al.*, 2018). In particular, landscape models, which may be defined as “any mathematical model designed to represent at least one landscape pattern-process relationship of interest” (Jones, 2002), have been used to understand the landscape dynamics and the ecological processes they support (Baker, 1989; Sklar and Costanza, 1991). In particular, the simulation of land cover and land use distributions and changes is useful because it provides a realistic and dynamic aid to spatial studies (Lambin *et al.*, 2000; Veldkamp and Verburg, 2004). Landscape models are also used to forecast and build scenarios of visualization of a system (Shoute *et al.*, 1994), but they are less frequent in land-use

planning and agriculture. Nevertheless, simulations have been performed to allocate crops on a farm or landscape and to organize the agricultural landscape for specific environmental problems (e.g. water pollution) (Le Ber and Benoît, 1998; Carsjens and Van Der Knaap, 2002; Aviron *et al.*, 2007). Generally, however, landscape elements occupying only a small proportion of area (i.e hedges) are not considered despite their high ecological importance (as explained in above section). Therefore, multi-disciplinary research integrating landscape modelling offer a promising approach to understand the landscape dynamics, and to assess how they affect various phenomena such as biological control.

## 3<sup>rd</sup> Chapter

## Models and methods

### 1- A stochastic landscape generator with a focus on habitat quality:

In this study, we assume that a landscape consists of agricultural fields (2D surface elements) separated by edges (1D linear elements) over a relatively large spatial scale. Fields were allocated with two types of potential habitat for pests and auxiliaries: crops representing the principal culture (which could be a perennial crop such as apple orchards), and a second type of habitat, which could correspond to either another type of culture (annual or perennial) or to seminatural habitat. A certain proportion of edges separating fields are converted to hedges to provide seminatural habitats surrounding field crops. For the sake of simplicity, we will speak of “crop type” when referring to the distinction between the principal crop (“crop”) and the alternative habitat type (“non-crop”), the latter typically being of semi-natural type. Crop allocation therefore refers to choosing the crop fields.

A general landscape simulator could proceed in two steps by decomposing the landscape into its surface geometry (i.e., the fields separated by hurdles) and its habitat quality (i.e., crop type and hedgerows). Even if the geometry of the landscape may be an important characteristic (e.g., the size and shape of fields can impact the dynamics through fragmentation), we here do not focus on that part of the simulator but rather on the allocation of the crop and hedgerows for a given fixed landscape geometry extracted from a real landscape. The real landscape is preprocessed to transform it to a so-called T-tessellation, a mathematical representation that can now be routinely used for simulating varied landscape geometries (Kiêu *et al.*, 2013; Papaïx *et al.*, 2014).

Working on stochastically simulated rather than real landscapes is particularly useful (i) to control for particular properties of the environment through the choice of model parameters (here, allocation and aggregation of crops and hedges); (ii) to consider landscape variability around a given configuration of environmental parameters (iii) to model interactions between landscape elements (1D and 2D), which allows generating varied landscape organization patterns: mixed, mosaic and grouped; (iv) owing to the random nature of the model, to generate many different realizations of landscapes obeying the same geometric parameters and featuring the same patterns. This approach allows us to decompose the impact of landscape organization on agro-ecological processes into A) what is explained by the landscape characteristics that we control and B) uncertainty: the variation in the results that we can attribute to the differences in

landscapes that are not directly controlled by the parameters that we fix. We also give a particular importance on the realistic visual appearance of the simulated landscapes, which makes them more accessible to interpretation and to comparisons with existing landscapes. Moreover, communicating methods and results to a non-expert public may also become easier. If uncertainty is high in B), we may explore which additional landscape descriptors could explain this variability.

### i) Representing landscape geometry as a T- tessellation:

Tessellation methods partition the space into non overlapping geometrical figures leaving no holes, such as polygons representing agricultural fields in our case. Among different available tessellation types, we here choose the T-tessellation, which partitions the space into polygon shapes with the additional constraint of T-shaped vertices. A *T-vertex* always lies at the intersection of three edges with two of its incident segments aligned (see Fig.3.1c) (Kiêu *et al.*, 2013; Papaïx *et al.*, 2014). Software tools such as GenExp-LandSiTes (Le Ber *et al.*, 2009) or LiTe<sup>1</sup> could be used to simulate a T-tessellation representation of real landscape with specific geometric patterns, such as evenly sized and near-rectangular fields.

T-tessellation models are useful for modeling and generating field patterns since they allow controlling certain geometric characteristics of real landscapes such as the number, shape and size of polygons in a relatively simple and intuitive way (Gaucherel, 2008; Le Ber *et al.*, 2009; Kiêu *et al.*, 2013; Papaïx *et al.*, 2014).

In our study, we use an agricultural landscape of the Selommès region (a farming region in central France, see Fig.3.1a), whose observed geometry has been preprocessed to satisfy the requirements of a T-tessellation (Fig.3.1b). We here have not generated any new landscape patterns, which could present an interesting extension to our simulation experiment in future work.

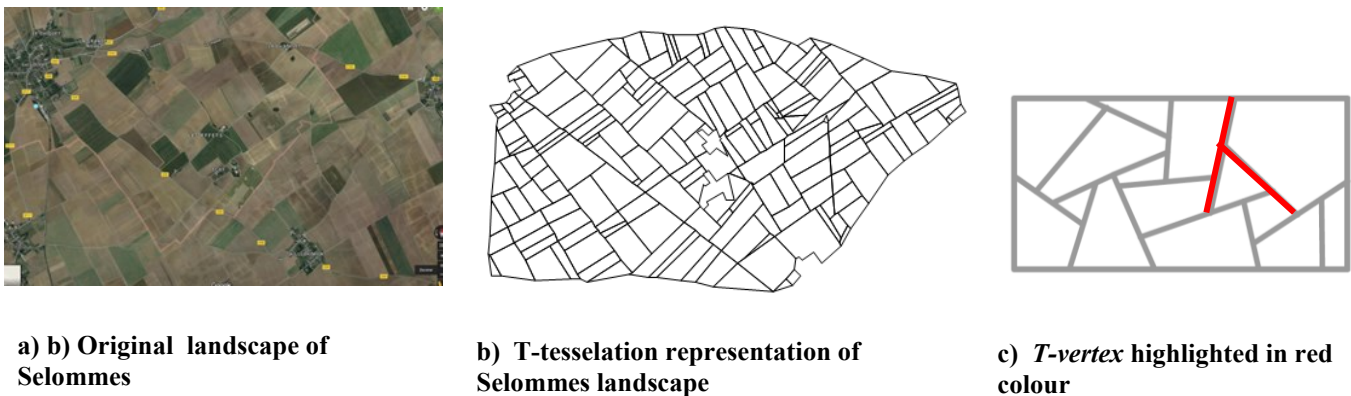


Figure 3.1. Representation of landscape geometry of Selommès region (a) using T-tessellation method (b,c).

<sup>1</sup> <http://kien-kieu.github.io/lite/>

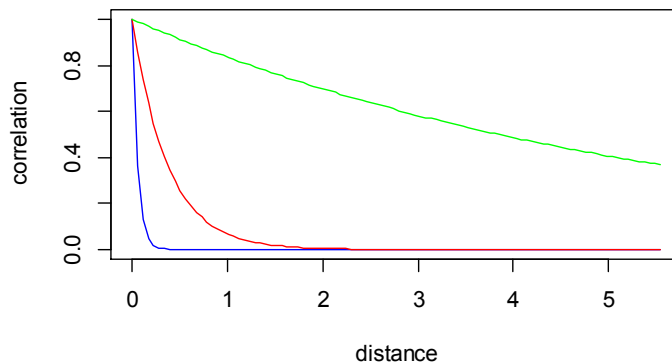
## ii) Use of Gaussian random fields for controlling spatial aggregation of landscape elements:

For simulating the spatial allocation of crops (vs. non-crop) to polygons and of hedges to edges in the T-tessellation, we work with simulations of Gaussian random fields (*GRFs*). By thresholding a GRF for determining the allocation of different categories (e.g., crop vs non-crop), we can use the trend and correlation structure in a latent GRF to control how and where certain allocation types spatially aggregate in the landscape. More formally, a *GRF*  $W$  is a random surface over 2D space, for which the multivariate distribution of the values  $(W(x_1), W(x_2), \dots, W(x_n))$  observed at points  $x_1, x_2, \dots, x_n$  in the landscape always corresponds to a multivariate normal distribution, characterized by its mean vector and its covariance matrix  $\Sigma$ . To avoid confusion with the threshold value (see section iii for more details), we fix the mean of the GRF to 0 in the following, and we consider covariance matrices that are correlation matrices, with the diagonal values of  $\Sigma$  fixed to 1 such that the variance of  $W(x)$  is always 1. The strength of spatial dependence in the *GRF* will govern the strength of clustering of landscape elements. We here opt for the classical exponential correlation function, such that the degree of aggregation is stationary and isotropic over space and will be characterized by its range parameter  $\varphi >= 0$ . The limiting case of  $\varphi = 0$  corresponds to “no spatial dependence” between landscape elements of the same category. Stationarity and isotropy imply that the behavior at two locations is determined only by the distance  $|x_j - x_i|$  between any two points  $x_j$  and  $x_i$ .

In mathematical notation, we can write

$$(W(x_1), W(x_2), \dots, W(x_n)) \sim N((0, 0, \dots, 0), \Sigma), \text{ with } \Sigma_{ij} = \exp(-|x_i - x_j|/\varphi)$$

for any collection of points  $x_1, x_2, \dots, x_n$ , where  $|x_i - x_j|$  refers to the Euclidean distance between the two locations  $x_i$  and  $x_j$ . The exponential correlation function is illustrated in Fig. 3.2 showing the values of the range parameter used in our simulation study.



**Figure 3.2. Correlation functions used in simulation study:** Here we fixed the following values for the range parameters ( $\varphi$ ) that is defined as “diameter of the Selommes region divided by 100,15,1”. The graph shows that by increasing the  $\varphi$  value, the correlation decreases more slowly, which yields scenarios from spatially very weakly dependent (blue line) to very highly dependent (high aggregation, green line) of landscape organization structures.

### iii) Marking landscape elements using multivariate Gaussian random fields:

#### a) Non-interacting elements: uncorrelated latent Gaussian random fields:

For each type of elements of the landscape geometry (i.e., points, lines, polygons...), a separate Gaussian random field (*GRF*) can be used to assign a category (e.g. crop / no crop, hedge / no hedge) by thresholding the *GRF*. For that purpose, a *GRF* is simulated on specific locations chosen to represent the elements under consideration (e.g., midpoints for linear segments, center points for polygons). Here we considered only two categories for each landscape element (hedge: yes/no, crop: type1/type2). Categories are then defined by fixing a threshold for the values of the *GRF* and then attributing category 1 if the value is above the threshold, and the alternative category 0 otherwise. Given a simulation of a *GRF*, the proportion of each category can then be simply controlled by varying the threshold value until the desired proportion is obtained. Thus, proportion and spatial aggregation can be controlled in the latent *GRF* framework. We here choose thresholds that are constant over space, leading to landscape patterns that are “stationary” over space. Notice that it would be possible to include trends in the threshold, for instance if we always want to have a higher proportion of one category in a specific subregion.

Different *GRF* can be simulated for 1D and 2D elements of the landscape. Hedge and crop will be assigned respectively to the value in the corresponding *GRFs* and thresholds, where we fix two thresholds, one for each of the marks (hedges and crop types). We use the two proportions of hedge proportion and crop proportion as input parameters and then fix the threshold accordingly. A relatively high proportion of the category hedge or crop respectively corresponds to a relatively low threshold for the respective *GRF*, i.e. more 1D elements would convert to hedges, or more 2D elements would convert to crop. Notice, however, that we can also combine a high proportion for one element category (e.g., crop) with a low proportion for another element category (e.g., hedges). In the calculation of proportions, we attribute different “weights” to individual elements: a hedgerow contributes through its length to the overall length of hedges in a landscape, and a field contributes with its surface area to the overall area of the landscape.

In the following, we write  $A_j$  for the “volume fraction” of the  $j^{\text{th}}$  individual element. For instance, the value of  $A_{h,j}$  for an edge  $j$  is given as the length of edge  $j$ , divided by the sum of lengths of all edges in the landscape. Similarly, for the  $j^{\text{th}}$  field, the value of  $A_{c,j}$  is given as the surface area of field  $j$ , divided by the overall surface area of the landscape. Formally, given a proportion value  $p \in [0,1]$  and the *GRF*  $W(x)$  simulated for controlling one of the landscape elements with representative points  $x_1, \dots, x_n$ , then we assign its two categories  $C=1$  or  $C=0$  as follows. We denote by  $(j)$  the index of the  $j^{\text{th}}$  largest value in  $W(x_1), \dots, W(x_n)$ . For instance, in the sequence 1,4,3,2, we get (1)=2, (2)=3, (3)=4 and (4)=1. A threshold index  $j_0$  is now fixed such that

$$\sum_{j=1}^{j_0} A_{(j)} \geq p \text{ and } \sum_{j=1}^{j_0-1} A_{(j)} < p$$

Therefore,  $W(x_{(j_0)})$  will act as threshold value in the *GRF*, and we assign

$C=1$  if  $W(x_j) \geq W(x_{j_0})$  and  $C=0$  otherwise.

The *GRF* will therefore assign category  $C=1$  to  $j_0$  elements. The procedure of simulating a *GRF* and calculating a threshold value for assigning the category is here done separately for crop and hedgerow allocation.

### **b) Interacting elements: correlated latent gaussian random fields:**

If we simply simulate the *GRFs* independently for each landscape element collection (edges/polygons), then the categories of each element are assigned independently (“non-interacting elements”). This is not always realistic in practice; for example, if crop fields are not surrounded by hedges, then we cannot observe their influence on pest-predator population dynamics and their role in biological control service. To remedy this issue for simulation, we later build a system of two correlated *GRFs*, with an additional parameter governing the strength of correlation

For handling interactions between the aggregation patterns of crop allocation and hedgerow allocation, we used bivariate *GRFs*, i.e. two *GRFs* which may be correlated positively or negatively. Each of the two *GRFs* determines the values for one element, and the correlation between the fields determines interaction of different elements. The type of correlation (positive or negative) leads to the behavior that crop allocation to a field will favor or disadvantage respectively the allocation of hedgerows to the surrounding edges. Here, we handle such interaction through the idea of co-regionalization of Gaussian random fields: the *GRF* values used for hedges and crops are defined as weighted sums of the values from the two initially independent *GRFs*.

Two independent *GRFs*  $W_1(s)$ ,  $W_2(s)$  with exponential correlation functions depending on range parameters  $\varphi_1$  ( $cor(x_{hi}, x_{hj}) = \exp(-|x_{hi} - x_{hj}|/\varphi_1)$ ) and  $\varphi_2$  ( $cor(x_{ci}, x_{cj}) = \exp(-|x_{ci} - x_{cj}|/\varphi_2)$ ) for hedges and crops respectively were used to calculate correlated fields (Fig.3.3c) according to the following general formula, with weight parameters  $\varrho_h, \varrho_c \in [-1,1]$ :

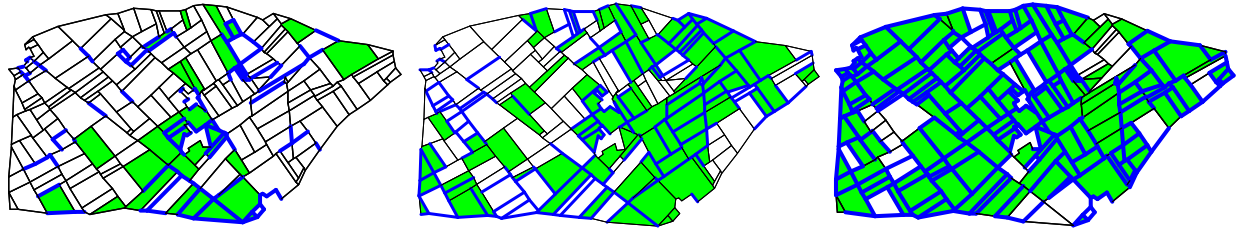
$$a) W_h(s) = \varrho_h W_1(s) + \sqrt{1 - \varrho_h^2} W_2(s) \text{ (Correlated field for hedges)}$$

$$b) W_c(s) = \varrho_c W_1(s) + \sqrt{1 - \varrho_c^2} W_2(s) \text{ (Correlated field for crops)}$$

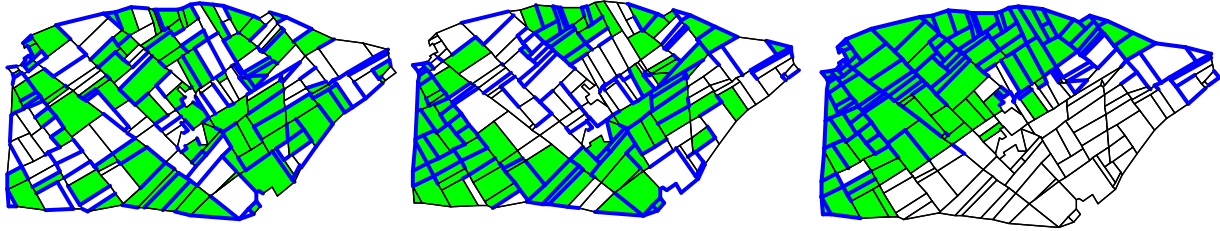
For a simpler and more parsimonious formulation, we fix  $\varrho_h = 1$  such that  $W_1$  defines the *GRF* used for hedges, and we allow for  $\varrho_c \in [-1, 1]$  to control the correlation between  $W_h$  and  $W_c$ . Choosing only one parameter simplifies the control of correlation between hedges and crops. Then, the cross-correlation function between the *GRFs* for hedges and crops is as follows:

$$Corr(W_h(s_1), W_c(s_2)) = \varrho_c \exp(-dist(s_1, s_2)/\varphi_1).$$

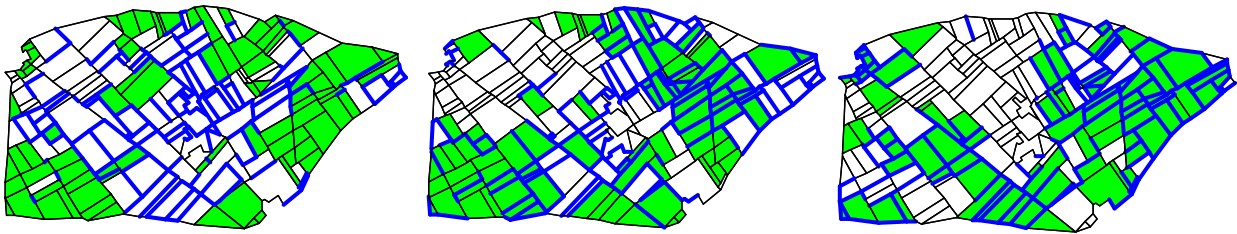
Specifically, if we look at the correlation of hedges and crops at the same location  $x$ , we obtain  $Corr(W_h(x), W_c(x)) = \varrho_c$ . Moreover, for simplicity of notation can drop the subscript  $c$  and simply write  $\varrho$  for the correlation parameter between hedges and crops.



a) Increasing proportion of hedges and crop fields.



b) Increasing spatial aggregation.



c) Increasing correlation.

Figure 3.3. Examples of simulated landscape structures with interacting elements: Two types of fields (i) crop (green) (ii) non-crop (white), and edges with hedges (blue) dispatched around 604 fields. The top line shows an increasing proportion of crop and hedges (low (0.2), medium (0.5) and high (0.8)) from left to right with fixed parameter configuration for aggregation (landscape diameter divided by 15) and correlation (0.7) between hedge and crop *GRFs* (a). The 2<sup>nd</sup> line shows an increasing crop and hedges aggregation level (mixed (landscape diameter divided by 100), mosaic (landscape diameter divided by 15) and grouped (landscape diameter divided by 1)) from left to right with fixed proportion of crop and hedges (0.5) and correlation (0.7) between them (b). The bottom line shows an increase in correlation (negative correlated (-0.9), low positive correlation (0.4), high positive correlation (0.9)) between hedges and crop *GRFs* from left to right with fix proportion of hedges and crop (0.5) and aggregation (landscape diameter divided by 10) (c).



## 2- Population dynamics model:

We developed a spatially explicit predator-pest model based on a system of partial differential equations. Our model was built on an already developed approach that considers both 2D diffusion on surface elements and 1D diffusion on linear elements (Roques & Bonnefon, 2016). Specifically, we here assumed that the pest can be encountered only in fields and is absent from the edges. However, it is assumed that the pest is a specialist of apple orchard and thus has positive growth (in the absence of dispersal) only in those fields. Hedges form the main habitat of the predator in the absence of pest. The predator forages on fields for alternative resource, i.e. the pest in our simulation setup.

### (i) Predator:

#### a) Population dynamics of the predator along 1D landscape elements:

Linear 1D elements of landscape matrix are denoted by  $h_i$ . We assumed the following 1-dimensional reaction-diffusion model on linear elements for the predator:

$$\begin{cases} \partial_t v_{h_i} = \partial_{xx} D_1^v v_{h_i} + r_v v_{h_i} \left(1 - \frac{v_{h_i}}{K_{h_i}}\right) & \text{if the edge } h_i \text{ has a hedge} \\ v_{h_i} = 0 & \text{otherwise} \end{cases} \quad (1)$$

In equation (1),  $D_1^v$  is the diffusion parameter of the predator along hedges,  $r_v$  is the intrinsic growth rate of the predator and  $K_{h_i}$  is the carrying capacity of the hedge  $i$ .

#### b) Population dynamics of the predator along 2D landscape elements:

Polygon-shaped 2D fields are denoted by  $\Omega_i$ . The population density of predators in each field is modelled by a reaction-diffusion equation with mobility parameter within field  $D_2^v$ , predation rate  $\beta$ , and mortality  $m_v$ :

$$\partial_t v_{\Omega_i} = \Delta D_2^v v_{\Omega_i} - m_v v_{\Omega_i} + \beta u_{\Omega_i} v_{\Omega_i}. \quad (2)$$

### (ii) Pest:

#### a) Population dynamics of the pest along 1D landscape elements:

We consider that edges do not host the pest, and that they do not modify directly its population dynamics. We thus have:

$$u_{h_i} = 0 \quad \forall i. \quad (3)$$

#### b) Population dynamics of the pest along 2D landscape elements:

The pest is assumed to live only in fields. In addition, the crop fields represent a source of pest whereas the non-crop fields are a sink for the pest. Therefore, in the absence of dispersal from fields hosting the crop, the pest population vanishes in fields hosting the non-crop type. A

chemical treatment is applied to a given crop field when the pest population in that field reach a given threshold which was fixed to 0.2. The bidimensional reaction-diffusion model is as follows:

$$\begin{cases} \partial_t u_{\Omega_i} = \Delta D^u u_{\Omega_i} + r_u u_{\Omega_i} \left(1 - \frac{u_{\Omega_i}}{C_{it}}\right) - \beta u_{\Omega_i} v_{\Omega_i} & \text{for } \Omega_i \text{ with crop type 1} \\ \partial_t u_{\Omega_i} = \Delta D^u u_{\Omega_i} - m_u u_{\Omega_i} - \beta u_{\Omega_i} v_{\Omega_i} & \text{for } \Omega_i \text{ with crop type 2} \end{cases} \quad (4)$$

The carrying capacity  $C_{it}$  of the field  $i$  changes in time due to possible chemical treatments:

$$\begin{cases} C_{it} = K_{\Omega_i} & \text{if no chemical treatment is applied} \\ C_{it} = \frac{K_{\Omega_i}}{200} & \text{during the period } e_t \text{ for which the treatment is efficient} \end{cases}$$

An additional mortality term could be added to model the effects of chemical treatments but it would have implied the modification of both growth and carrying capacity. For that reason and to keep the model parsimonious, possible effects of chemical treatments were assumed to change only the carrying capacity. In equation (4),  $D^u$  represents the mobility of the pest,  $r_u$  is its intrinsic growth rate on crop type 1 fields,  $\beta$  is the predation rate and  $m_u$  is the mortality rate of the pest on crop type 2 fields.

### (iii) Coupling the dynamics over the entire landscape:

Using the framework described in Roques & Bonnefon (2016), the dynamics described by equations (1) to (4) were coupled to define predator-pest dynamics over landscapes such as those described in part 1. To that purpose, the fluxes of individuals between 1D and 2D elements of the landscape were defined as follow:

- Edges (with or without a hedge) do not affect the pest population dynamics, i.e., the pest perceives the landscape as a heterogeneous 2D environment without 1D effects of linear elements.
- Edges without a hedge do not affect the predator population dynamics, i.e., two fields separated by an edge without a hedge will be perceived as a unique (potentially heterogeneous) 2D element by the predator.
- The predator is attracted by hedges, thus migration from fields to hedges is very high.
- The predator could potentially have an aversion to go outside its natural habitat; therefore, migration from hedges to fields is always lower than migration from fields to hedges.

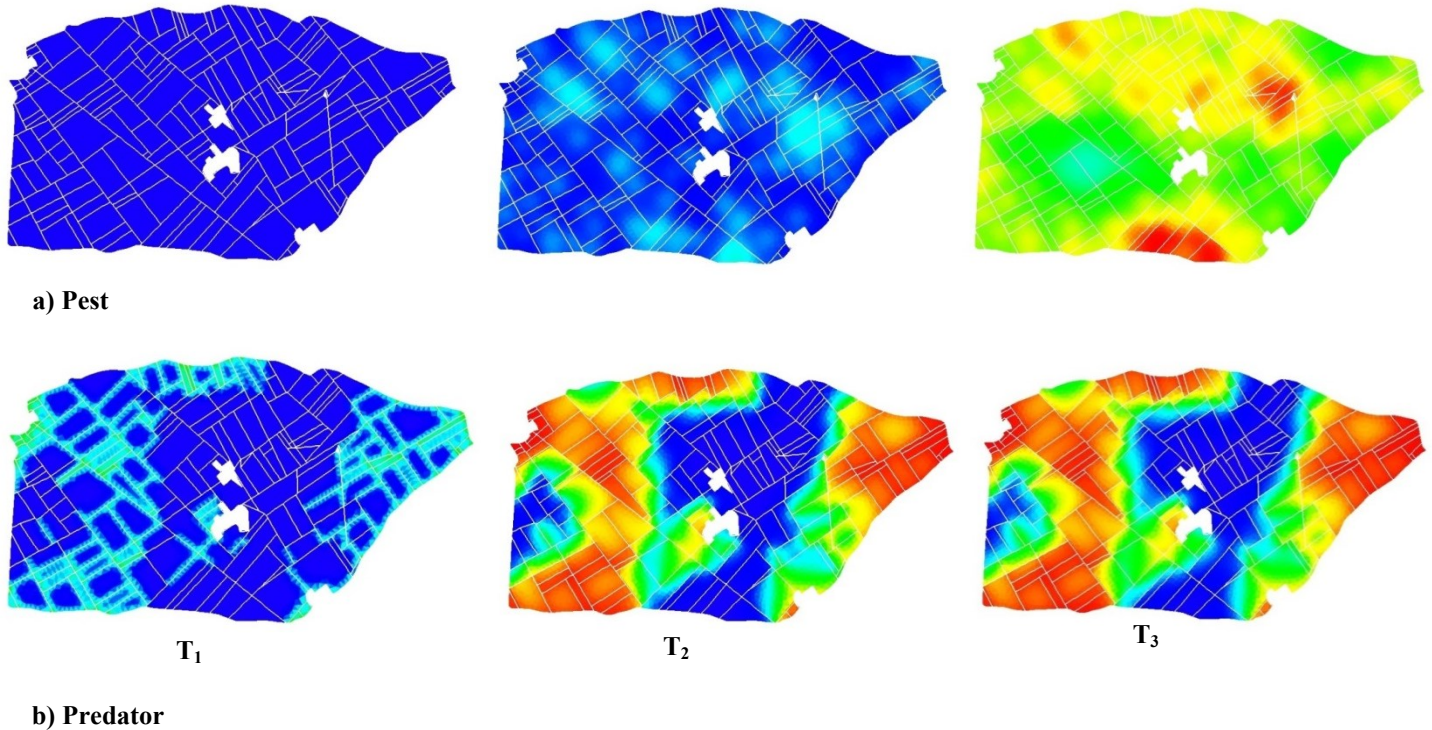
Finally, we considered reflecting conditions on the boundaries of the landscape, meaning that in- and out-fluxes between the landscape and its surrounding environment are equal.

### (iv) Inoculation and spatio-temporal design:

Initially (at time 0), the predator is present in all hedges at carrying capacity. The pest is then introduced randomly in time and space. For one simulation, the average number of pest inoculations is proportional to the proportion of crop field area in the landscape, by considering that in a landscape with 100% of crop an average of 25 pest inoculations are observed. Then, the total number of inoculations is drawn from a Poisson distribution, and inoculated fields are

picked at random with probability depending on their relative surface. A small disk situated at the centroid of the field is then inoculated with a given density of the pest.

The spatial unit is 1 kilometer, and the “diameter” of the landscape is 5.55 km. Simulations are performed over a  $[0,1]$  time interval representing a cropping season of several months. Time step is 0.01 meaning that the time unit can be considered as the day. The simulations were performed using the Freefem++ finite-element framework (Hecht, 2012). Figure (3.4) shows an example of a simulation.



**Figure 3.4. Simulation of pest-predator population dynamics in absence of pesticide application at different time intervals: At the initial stage, the pest density is zero (dark blue colour), followed by random introduction of pest (areas with light blue colour)(a). As the time proceeds, pest density increases (from left to right) according to the carrying capacity of fields (top right; very high density shown in red colour). However, in the case of the predator (b), light blue colour shows the presence of predator in hedges at initial time. As time proceeds, predator density increases and diffuses to surrounding fields (large patches in red colour), and pest population reduces. At  $T_3$ , high pest density can only be seen in areas where the predator population is absent.**

### 3- Simulation study: parameter values and experimental design:

The focus of this study is on the role of landscape structure on pest and natural enemy dynamics. Because the effect of landscape structure is intimately linked to the dispersal capacities of species, we decided also to add the parameters governing dispersal to the analysis. In addition, we assumed that spatial aggregation of the crop and the hedges are the same. Finally, for each of the parameter combinations studied, we considered a certain number of landscape replicates to study the effect of uncontrolled landscape features.

We have decided to perform the numerical simulations for two types of experimental design:

(i) Complete factorial design to explore the 6 parameters of interest (spatial aggregation ( $\varphi$ ), crop proportion, hedges proportion, pest dispersion, predator dispersion and predator migration) for 3 different levels of each parameter, all the others being fixed (Table. 1). For each combination of these six parameters, 20 landscape replicates were simulated. This makes a total of  $3^6 \times 20 = 14580$  simulations. This allows analyzing all cross combinations of any order to estimate the interactions.

(ii) This experimental design includes a larger number of levels (1000) for 6 input parameters but only a subset of all possible combinations of levels of different parameters. It is designed specifically to reveal the range of variation in the response variable due to parameter values and low-order interactions between different parameters. It is called as Sobol design. To take landscape stochasticity into account, each combination was replicated 15 times, resulting in a total of 97500 simulations.

#### **4- Statistical methods for analysing simulation output:**

Generalized linear models (GLMs) with the Gamma distribution for the response variable and a log link function (R package lme4, R3.2.3) were used to analyze the variations in the response variables given by the pest and predator densities and by the number of pesticide treatments averaged over all crop fields and integrated over time, using the complete factorial design (i) from above. All the input variables (spatial aggregation, crop proportion, hedges proportion, pest dispersion, predator dispersion and predator migration) were treated as continuous covariables except for spatial aggregation level, which was considered as a factor with three levels. We constructed a GLM model formula containing interactions up to 2<sup>nd</sup> order. Moreover, we analysed the simulations of the Sobol design (ii) by fitting a “regression tree” for all three response variables (pest population, predator population and number of pesticide treatments). Regression trees show the threshold values of explanatory variables that explain the most important variations in response variables along iterated binary splits of the values of the explanatory variables. Moreover, we have run a Sobol sensitivity analysis for the experimental design (ii). As the stochasticity was accounted for by replicating simulations for each parameter combination, we performed sensitivity analyses on the mean and standard deviation of the response variable values averaged over landscape replicates and crop fields. Within the R software v. 3.0.3 (Team, 2003), Sobol’s sequences and indices were obtained using the packages fOptions (v. 3010.83) and sensitivity (v. 1.11), respectively. First-order indices were estimated with Sobol–Saltelli’s method (Tarantola *et al.*, 2007; Saltelli *et al.*, 2010), whereas total indices were estimated with Sobol–Jansen’s method (Jansen, 1999; Saltelli *et al.*, 2010). The 95% confidence intervals (CI95) of the sensitivity indices were estimated using 10 000 bootstrap replicates (Archer *et al.*, 1997). In each sensitivity analysis, key interactions were identified using polynomial regression. A third degree polynomial including interactions restricted to polynomial terms of degree two was fitted to the means and standard deviations of the model output (Schwarz, 1978).

**Table 3.1: Description of parameter values used in our simulations.**

Parameters	Description	Values		units
		Min	max	
<b>For landscape model</b>				
$\varphi$	Aggregation of hedges and crops	5.55/100	5.55	-
$P_c$	Proportion of crop	0	1	-
$P_h$	Proportion of hedges	0	1	-
$\varrho$	Correlation between crops and hedges $GRF_S$	0.5		-
<b>Parameters for population dynamic mode</b>				
$D_2^v$	2D diffusion rate of the predator	0.0625	12	$km^2d^{-1}$
$m_v$	Mortality rate of the predator	10		$d^{-1}$
$\beta$	Predation rate	4		$d^{-1}$
$\rho_{21}$	Migration rate of the predator from field to hedge	5		-
$D_1^v$	1D diffusion rate of the predator	12		$km^2d^{-1}$
$r_v$	Intrinsic growth rate of the predator on hedges	14		$d^{-1}$
$K_{h_i}$	Carrying capacity of hedges for the predator	1		
$\rho_{12}$	Migration rate of the predator from hedge to field	0	5	
$D^u$	2D diffusion rate of the pest	0.0625	12	$km^2d^{-1}$
$r_u$	Intrinsic growth rate of the pest	14		$d^{-1}$
$C_{it}$	Carrying capacity of 2D system for the pest	20 (when no treatment is applied) 0.1 (after the treatment)		
$m_u$	Mortality rate	10		$d^{-1}$

**1- Results:****i) Sensitivity of predator, pest density and pesticide treatments to model parameters**

We start by reporting results of Sobol sensitivity analysis in terms of first-order effects and total effects of parameters. The sensitivity analysis of the mean of model outputs across landscape replicates shows that variations in predator population density, averaged over the crop fields and landscape replicates, are mainly explained by predator migration (49%) and by the proportion of hedges (36%). Both variables have a positive effect on the predator (see Fig.4.2a,b and Section 2 for further details). In addition, the total and first order sensitivity indices have similar values (14% and 13% respectively), showing that interactions have little impact on this output (Fig.4.1a). For the pest population density and the average number of pesticide applications, crop proportion is the most important parameter contributing respectively to 85% and 89% of the model output variability, again with only little interaction between model parameters (Fig.4.1b, c). Both response variables react positively to crop proportion (see Fig.4.2c,d and Sections 2 for further details).

Interestingly, the sensitivity analysis of standard deviation of model outputs across landscape replicates gives different importance to the input variables as compared to the mean values. For the predator, crop proportion is found to have the most important role (Fig.4.1d). Indeed, in this case, crop proportion, predator migration, hedge proportion and spatial aggregation explain respectively 22%, 18%, 13% and 3% of the variance of model outputs. The situation remains almost unchanged for the pest density and pesticide treatments, but with a lower influence of crop proportion than for the mean response over landscape replicates; other parameters play only a minor role (Fig.4.1e,f). In addition, interactions between model parameters are also important to explain variations of predator and pest density as well as of pesticide treatments among landscape replicates. This reflects the fact that particular landscape structures characterized by a combination of several descriptors have to be considered to understand the drivers of predator-pest dynamics (see Section 2 and discussion).

Finally, we point out that these results are in accordance with results based on regression trees (see appendix Fig 1 for further details).

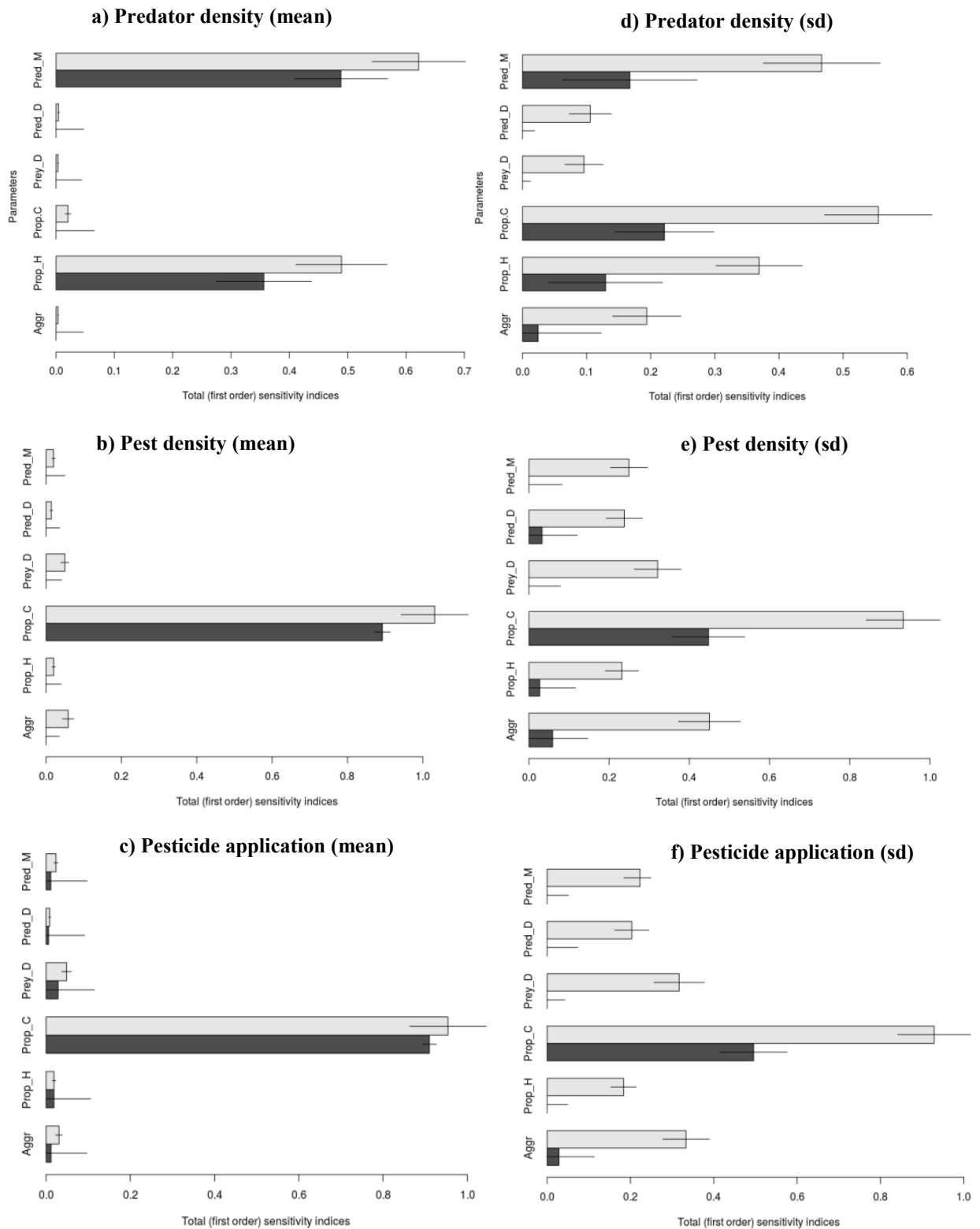
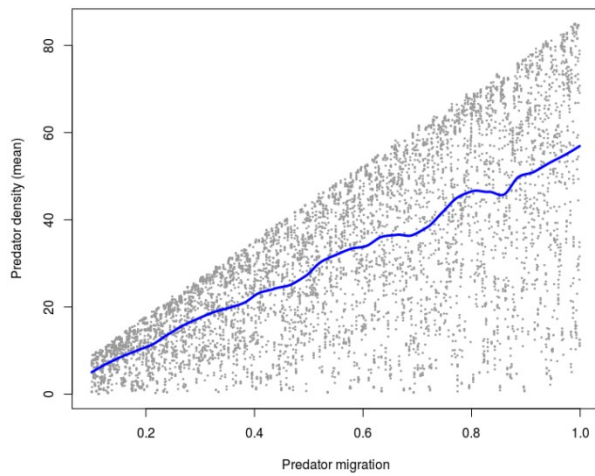
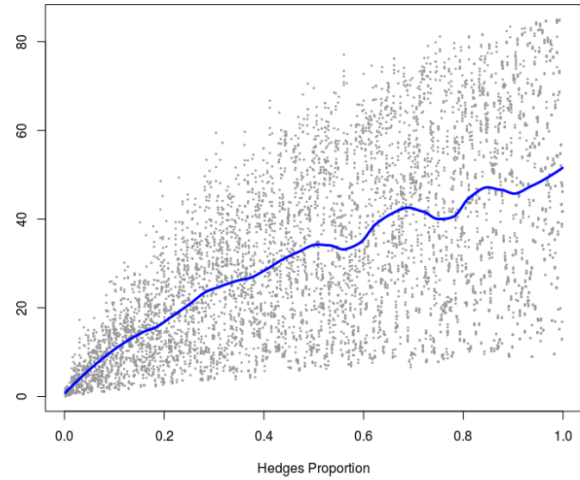


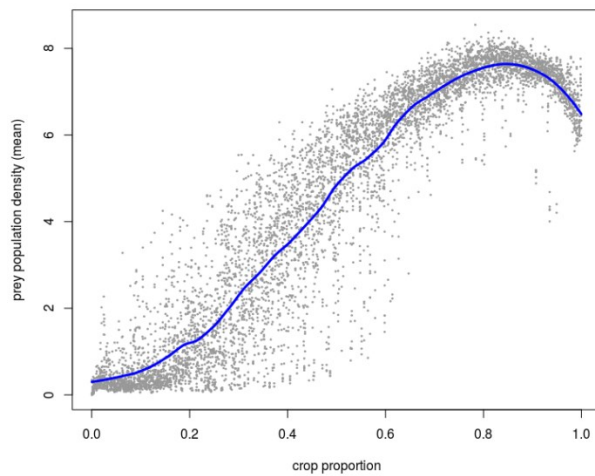
Figure 4.3. Sobol sensitivity analysis: Total sensitivity indices (grey bar) and first-order sensitivity indices (black bar) of aggregation (Aggr ( $\varphi$ )), hedge proportion (Prop\_H ( $P_h$ )), crop proportion (Prop\_C ( $P_c$ )), pest diffusion rate (Pest\_D ( $D^u$ )), predator diffusion rate (Pred\_D ( $D_2^v$ )) and predator migration rate (Pred\_M ( $\rho_{12}$ )) for the mean of predator density (a), pest density (b) and pesticide application (c) and the standard deviation of predator density (d), pest density (e) and pesticide application (f). The length of the bar indicates the mean of the sensitivity index, and the solid line indicates its 95% confidence interval.



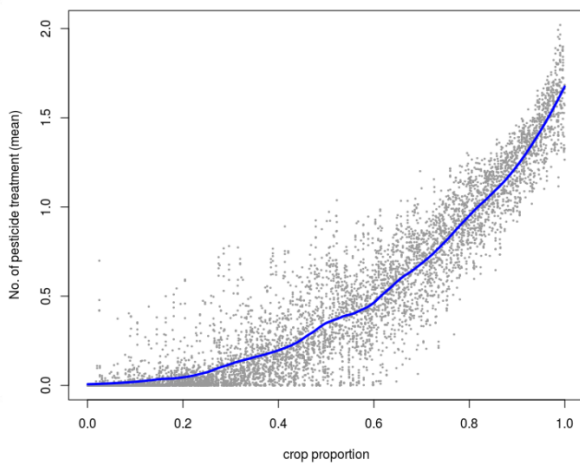
**a) Predator migration-predator density relationship**



**b) Hedges proportion-predator density relationship**



**c) Crop proportion-pest density relationship**



**d) Crop proportion-pesticide application relationship**

**Figure 4.2.** Effect of selected target parameter on model output: Model outputs (grey dots, mean over the 15 landscape replicates) for all parameter combinations, and smoothed curves based on a third order polynomial regression (blue line). Predator density averaged over the crop fields vs. predator migration (a) and hedges proportion (b). Pest population density (c) and number of pesticides treatments (d) averaged over crop fields vs. crop proportion.

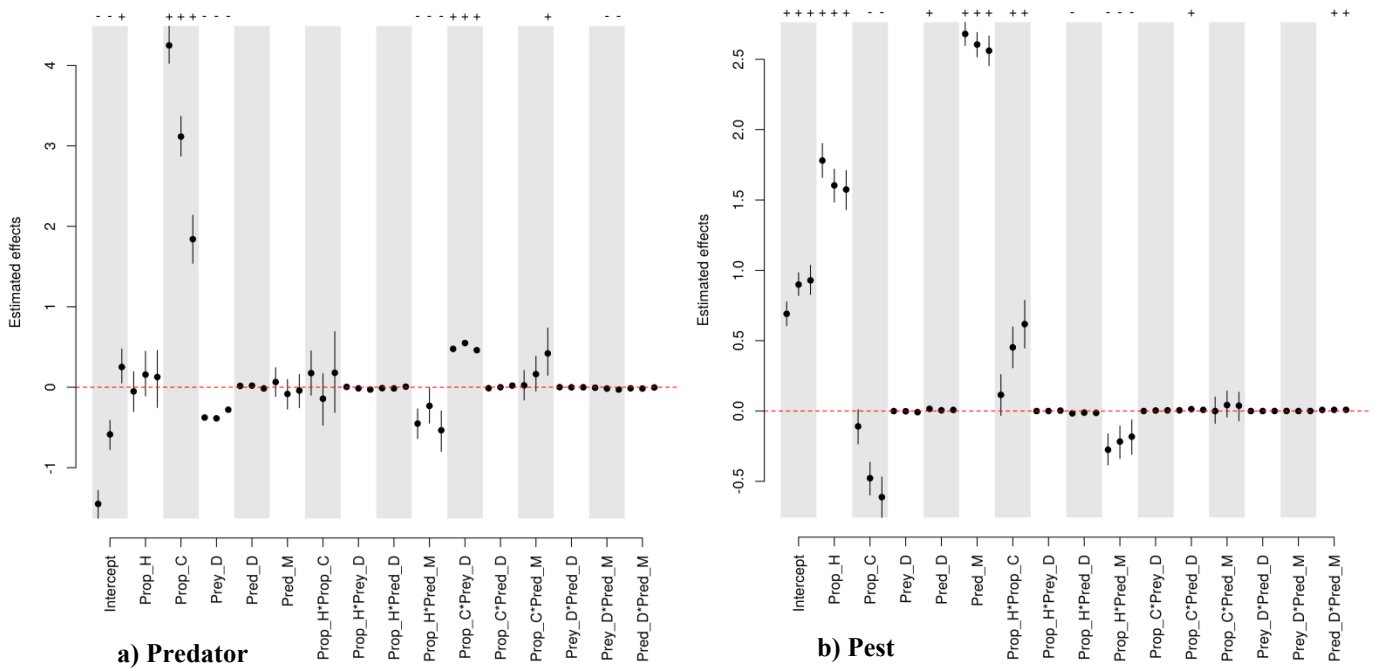
## ii) Effects of the landscape structure on predator-pest dynamics:

Spatial aggregation has a small but positive effect on predator population density (Fig.4.3b, first column). As expected, increases in the proportion of hedges increase the predator density with a trend towards a lower effect in highly aggregated landscapes (Fig.4.3b, second column). Crop proportion negatively influences the predator population, and this effect was reinforced as the spatial aggregation increases (Fig.4.3b, third column). However, crop



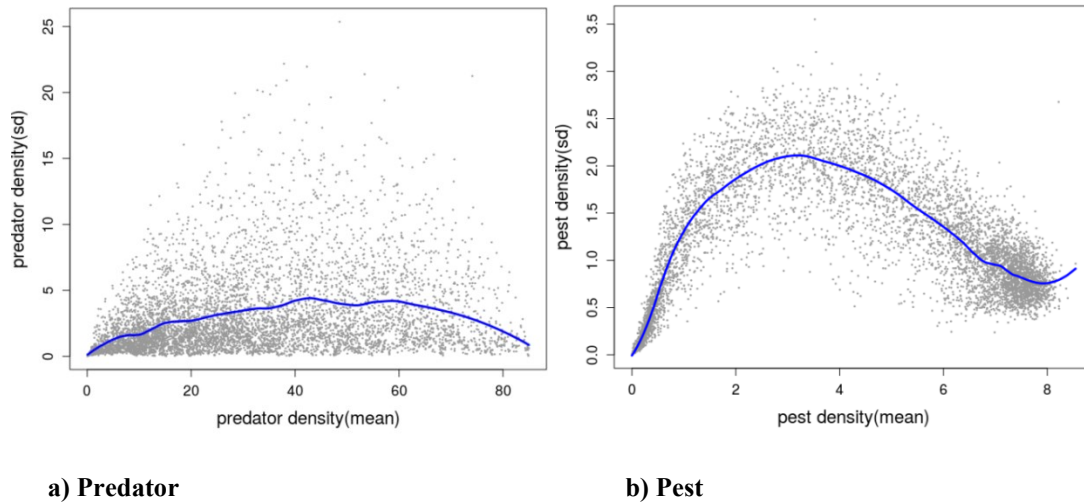
proportion positively interacts with hedge proportion, indicating that hedges can buffer the negative effect of increases in crop proportion especially in highly aggregated landscapes (Fig.4.3b, seventh column). Finally, predator migration has a positive effect (Fig.4.3b, sixth column) on the density of the predator, reflecting the greater accessibility of the pest in the landscape. Hedge proportion and predator migration interact negatively, showing that increases in one of these parameters lower the effect of the other (Fig.4.3b, tenth column).

Spatial aggregation of the crop has a strong positive effect on pest density (Fig.4.3a, first column), showing that less fragmented landscapes support a bigger pest population. As found in the sensitivity analyses, crop proportion has the highest positive effect on pest population (Fig.4.3a, third column). However, increases in spatial aggregation decrease the effect of crop proportion (Fig.4.3a, third column), as fragmentation and availability of favorable habitats often interact. Faster pest diffusion has a negative effect on pest population density (Fig.4.3a, fourth column), certainly due to spill-over from crop to non-crop fields. This effect is, however, lowered when crop proportion increases (Fig.4.3a, eleventh column) due to a greater probability of reaching crop fields. The proportions of hedges and predator migration have no isolated effect respectively, but they interact to reduce the pest population density (Fig.4.3a, tenth column). Finally, when spatial aggregation is high, predator migration increases the positive effect of crop proportion (Fig.4.3a, thirteenth column).

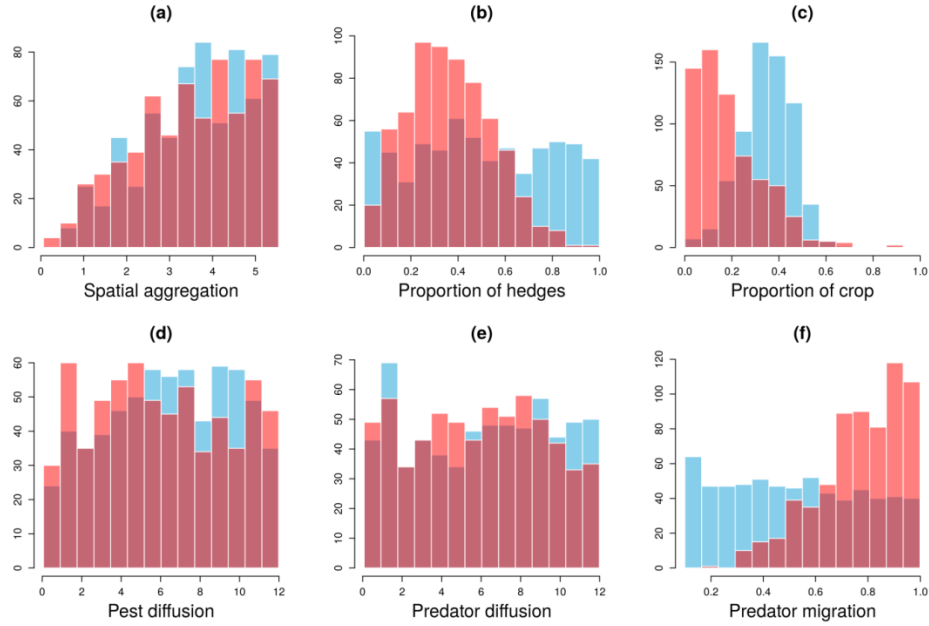


**Figure 4.3** Effect of input parameters (aggregation (Intercept ( $\varphi$ )), hedge proportion (Prop\_H ( $P_h$ )), crop proportion (Prop\_C ( $P_c$ )), pest diffusion rate (Pest\_D ( $D^u$ )), predator diffusion rate (Pred\_D ( $D_2^p$ )) and predator migration rate (Pred\_M ( $\rho_{12}$ ))) and interaction among them on pest and predator population dynamics: Coefficient estimates (dots) along with the 95% bootstrap confidence intervals (solid lines) of each parameter of the GLM for the pest (a) and the predator (b) population density. The three estimated values of each effect correspond to different spatial aggregation in increasing order from the left to the right. Positive and negative signs on top of the display show the significance of the effect at a 5% threshold.

Figure 4.4 shows the relationship between the mean and standard deviation over the 15 landscape replicates simulated for each parameter configuration. For both the predator and pest population density, the standard deviation is low at low and high mean values, which depicts that landscapes highly favourable or highly unfavourable to the predator and the pest always give very similar outputs with only very small stochastic variations around the mean pattern. Interestingly, in between the two extremes, the standard deviation increases, leading to a bell-shape of the relationship (Fig.4.4). Consequently, those landscapes leading to intermediate pest and predator densities on average represent also the cases where pest and predator dynamics are the least predictable through model parameters, meaning that particular spatial structures not explicitly accounted for by the model structure are of importance in determining population dynamics. To identify the situations leading to highly variable outputs, we selected the parameter combinations leading to a standard deviation above the 90% quantile of the distribution of standard deviations. For the predator population density, we find that spatial aggregation, proportion of hedges and crops and predator migration are responsible for this variability. Indeed, landscapes characterized by a medium to high aggregation, around 30-40% of hedges and low crop proportion, and in combination with a high predator migration, lead to highly variable predator density (Fig.4.5). For the pest, medium to high spatial aggregation and a crop proportion around 40% lead to the higher variability in population density (Fig.4.5). These results are consistent with the sensitivity analysis (Fig.4.1d,e).



**Figure 4.4. Relationship between mean and variance of predator (a) and pest (b) population density. For each parameter configuration, a grey dot represents the empirical mean and standard deviation values of model output over the 15 landscape replicates, and the blue line shows a smoothed prediction of a third order polynomial regression**



**Figure 4.5. Identification of input parameters configuration leading to highly variable outputs: Histograms (blue: pest; red: predator) of the six model parameters for the situations leading to a standard deviation upper than the 90% quantile of the distribution of standard deviations. a) spatial aggregation ( $\phi$ ), b) proportion of hedges ( $P_h$ ), c) proportion of crop ( $P_c$ ), d) pest diffusion ( $D^u$ ), e) predator diffusion ( $D^v$ ) and f) predator migration ( $\rho_{12}$ ).**

### iii) Effects of landscape and resulting predator-pest dynamics on pesticide applications:

As expected, the number of pesticide applications responds almost to the same variables as the pest population density (Fig.4.6). Increases in spatial aggregation increase the number of pesticide applications (Fig.4.6, first column). Crop proportion has the highest and positive effect on the number of pesticide applications with a decreasing effect according to spatial aggregation (Fig.4.6, third column). Pest diffusion reduces the number of pesticide applications with a reduced effect as the spatial aggregation increases (Fig.4.6, fourth column) and as the proportion of crop increases (Fig.4.6, eleventh column). Finally, interaction between the proportions of hedges and predator migration reduces the number of pesticide applications (Fig.4.6, tenth column).

In addition to the GLM, and to study the relationship between pest population density, predator population density and the number of pesticide applications, we investigated the possible links between these variables. Obviously, a clear relationship between the pest density and the number of pesticide applications is found (Fig.4.7a). In addition, there is a slightly decreasing trend in the number of pesticide applications as the predator population density increases (Fig.4.7b). However, we find that the relationship between pest and predator is difficult to predict in this system, as increases in predator population density do not directly translate into a decrease in pest population density (Fig.4.7c). These contrasting results could be explained by the fact that the predator maintains the pest population density below the treatment threshold, facilitating its spread across the landscape.

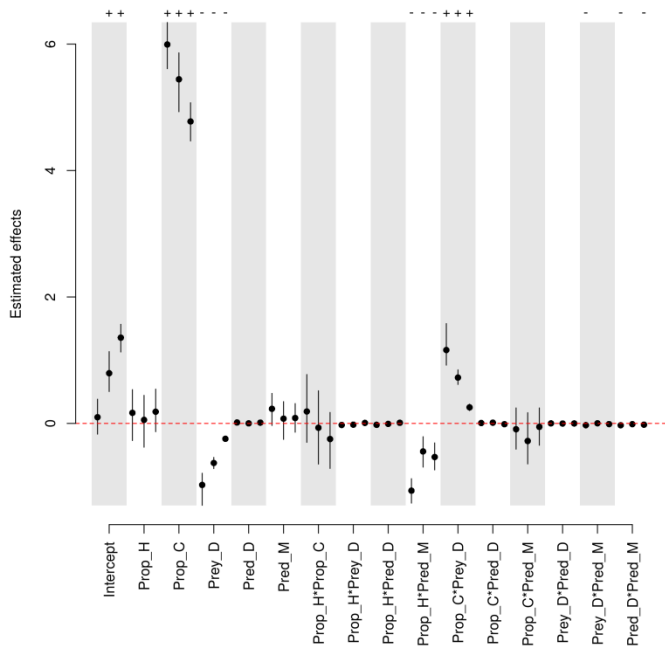


Figure 4.6. Coefficient estimates (dots) along with the 95% bootstrap confidence intervals (solid lines) of each parameter (aggregation (Intercept ( $\varphi$ )), hedge proportion (Prop\_H ( $P_h$ )), crop proportion (Prop\_C ( $P_c$ )), pest diffusion rate (Pest\_D ( $D^u$ )), predator diffusion rate (Pred\_D ( $D^v$ )) and predator migration rate (Pred\_M ( $\rho_{12}$ ))) of the GLM for the number of pesticide applications. The three estimated values of each effect correspond to different spatial aggregation in increasing order from the left to the right. Positive and negative sign shows the significance of the effect at a 5% threshold.

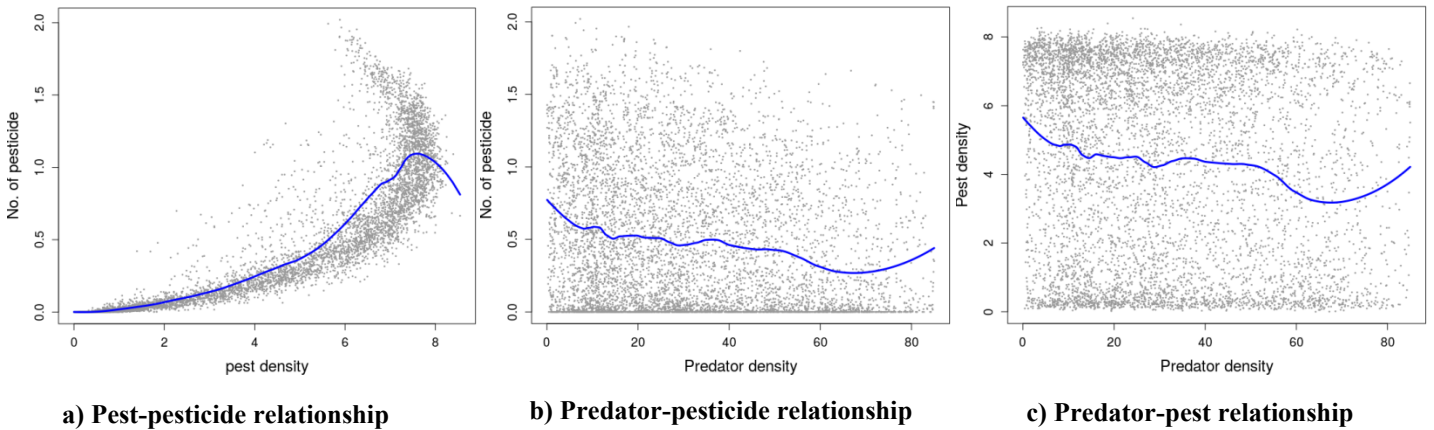


Figure 4.7. Relationship between pest-predator population density and pesticide application: Number of pesticide applications as a function of pest (a) and predator (b) population density and pest population density as a function of predator population density (c). Grey dots represent the mean values of model output over the 15 landscape replicates and prediction of a third order polynomial regression (blue line).

## 2- Discussion:

To foster and preserve a well-functioning biosphere allowing us to overcome food production sustainability issues, sustainable management of crop areas with respect to pests and diseases requires a better understanding of landscape dynamics in natural ecosystems. The present study is a top-down approach to characterize the influence of different landscape elements and their organization on biological control service. This study is based on a stochastic landscape model, coupled with a deterministic and spatially explicit pest-predator model. Main findings of research are that landscape characteristics affected the pest and predator population dynamics. The proportion of hedges and predator migration were found important to enhance the predator population and reduce the number of pesticide applications. However this did not translate into a lower density of pest across the landscape. Predator migration and diffusion within fields are important traits that have compensatory positive effect on predator population.

We found that crop proportion was the major determinant to increase the pest population over all levels of landscape aggregation; it thus leads to an increase in the number of pesticide treatments over the whole landscape. This is in accordance with Zhao *et al.* (2015); they report that landscape simplification or very homogenous landscape structure facilitates the population growth of insect pests owing to the weak presence of natural enemies. This results in reduced predation and increased number of pesticide treatments (Lohaus *et al.*, 2013; Zhao *et al.*, 2013; Zhao *et al.*, 2015; Rusch *et al.*, 2016). However, increases in aggregation reduce the positive effect of crop proportion. This behaviour might be explained by the fact that increasing crop proportion in fragmented landscape ensures food availability to pest all over the landscape. Instead, in highly aggregated landscape, patch size is already big enough to sustain a huge pest population, lowering the effect of an increase in habitat proportion.

Additionally, crop proportion was found to reduce the predator population. However we found that the negative effects of crop proportion on predator population can be compensated by enhancing the availability of seminatural habitat. Indeed, when the predator population has access to resources in both crop and non-crop patches, this derives their mobility between the two habitats (Tscharntke *et al.*, 2005). Our study confirms that increase predator migration increases the predator population. Therefore, a high number of seminatural habitats are necessary in homogenous landscapes to sustain a high population density of natural enemies (Tylianakis *et al.*, 2007; Thies *et al.*, 2011; Fabian *et al.*, 2013). These can buffer the negative impacts of crop proportion and can reduce the number of pesticide treatments. It is important to note that we assumed a narrow sense pesticide having no adverse effects on the predator population. Indeed, certain results might be different if a broad sense pesticide were applied.

We found strong effects of landscape aggregation and organization on pest-predator population dispersal capacity. It is reported that crop monocultures over large area provide a concentrated resource on which pests may accumulate in high densities (Root, 1973). However rearrangement of habitat patches in complex landscapes might drive pest mobility (Baggio *et al.*, 2011). This is confirmed from our results that pest diffusion reduces pest population, possibly because pest diffusion makes them accessible to predators with less mobility. Another possible reason for this is that dispersion of pest individuals owing to resource alteration might cause their spillover to non-crop fields. When the non-crop fields act as sink, then this spillover at the crop/non-crop interface decreases the pest population (Tscharntke *et al.*, 2005; Moxley *et al.*,

2017), resulting in low local density of pest. When the crop proportion increases, dilution effects are reduced implying a lower effect of pest diffusion on pest density.

A fairly common claim is that the increase in seminatural habitat in a landscape is generally beneficial for natural enemies; it was confirmed by our model system for a single pest species and its predator (see also Rusch *et al.*, 2010; Tschardtke *et al.*, 2016). Additionally we found that connectivity and configuration of natural habitat is equally significant since aggregation supports higher predator population. This shows that connectivity between different patches reduces the chance of food chain truncation for predator population and the degradation of trophic structure, which usually results from habitat fragmentation (Hunter, 2002). In addition to that, small patches in weakly aggregated landscapes may form a suitable habitat niche for natural enemies, and connectivity between patches enhances the predator spillover to surrounding crop fields and increases the predation pressure. On the other hand, the insufficient amount and proximity of natural habitats in highly aggregated structures where hedges are in contact with few fields leads to competition among species for available food resources and survival, which may impede a substantial increase in predator population abundance (Segoli and Rosenheim, 2012; Dreyer and Gratton, 2014). Therefore, landscape connectivity provided by hedges offering seminatural habitat is critical for predators due to their dependency on movement through different ecological areas for their survival (Coppolillo *et al.*, 2004; Michalski and Peres, 2005). In our approach, connectivity was not directly controlled, instead different level of connectivity resulted from different combination of habitat proportion and aggregation. As we found that variability between model outputs due to landscape stochasticity corresponded to particular combinations of habitat proportion and aggregation, it would be interesting to develop a landscape generator controlling for more functional features.

## 5<sup>th</sup> Chapter

## Conclusion and future perspectives

We can conclude that simulation-based approaches provide important insights into the drivers of pest-predator population dynamics that are relevant for conservation planning. Our study corroborates that spatial heterogeneity and landscape structure (size and physical arrangement of patches ) have a huge effect on pest-predator population dynamics.

We found that natural habitat enhances the predator population, but it does not show a very clear correlation with the decrease of the pest density. However, predator density often maintains the pest density below the economic threshold level, and weak aggregation facilitates their diffusion over large landscapes, thus preventing highly localized pest densities. This significantly reduced the number of pesticide treatment.

Vegetation composition (species richness and evenness) and structure remains equally important to ensure a diversity of alternative food source and habitat in seminatural elements . Because it can be a suitable environment for pest species and connectivity between landscape patches can result in outbreaks of insect herbivore (Wisler and Norris, 2005; Blitzler *et al.*, 2012; Midega *et al.*, 2014; Maguire *et al.*, 2015; Parry *et al.*, 2015). Extending our model system with

respect to such aspects could help us to even better understand the variable value of seminatural habitat for conservation biological control.

In this first analysis, we considered non-spatial outputs by averaging pest and predator densities over crop fields. However, it is obvious that populations are structured in space and time with possible important implications for the management of pest outbreaks. Indeed it could be more simple and easy to control a localized population than a diffused population. Even if we build the model structure on a real system, no parameter estimation was performed, this should be developed in order to give better advices. Finally, the model could include a larger number of pest and predator species, inter/intra-species interactions and different trophic network structures to understand the role of pest and predator diversity on the efficacy of biological control.

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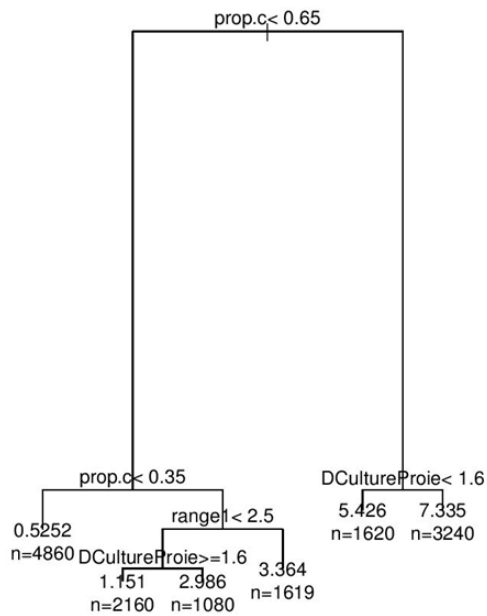
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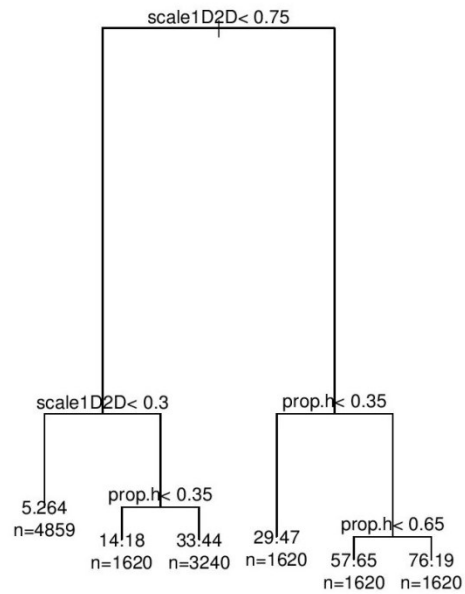
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# Appendix

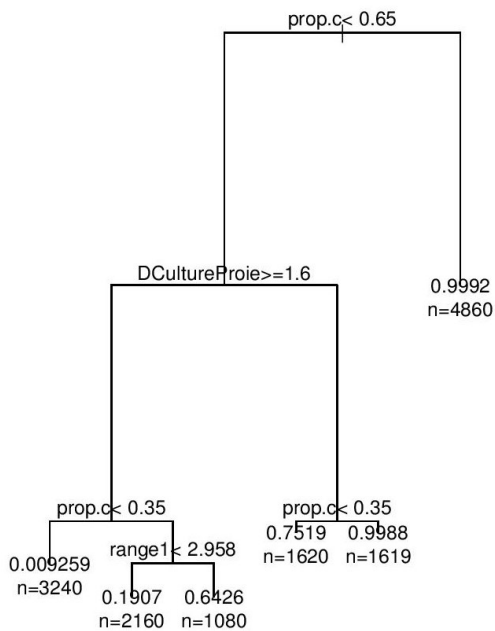
**Annex 1:** Regression tree analysis which characterize the relationship between pest-predator (a,b) population dynamics and pesticide application (c) as response variable against set of 6 covariates as explanatory parameters.



a) Predator



b) Pest



b) Pesticide application

## Annex 2. GLM analysis (Summary)

### a) Predator density

Deviance Residuals:

Min	1Q	Median	3Q	Max
-3.9307	-0.4954	-0.1185	0.1999	5.4819

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
range10.05546123	-1.4493199	0.0914635	-15.846	< 2e-16 ***
range10.3697415333333333	-0.5864882	0.0914635	-6.412	1.48e-10 ***
range15.546123	0.2507690	0.0914785	2.741	0.006127 **
range10.05546123:prop.h	-0.0546230	0.1327339	-0.412	0.680696
range10.3697415333333333:prop.h	0.1593664	0.1327339	1.201	0.229908
range15.546123:prop.h	0.1287212	0.1327339	0.970	0.332178
range10.05546123:prop.c	4.2431486	0.1327339	31.967	< 2e-16 ***
range10.3697415333333333:prop.c	3.1158139	0.1327339	23.474	< 2e-16 ***
range15.546123:prop.c	1.8362886	0.1327339	13.834	< 2e-16 ***
range10.05546123:DCultureProie	-0.3770290	0.0114210	-33.012	< 2e-16 ***
range10.3697415333333333:DCultureProie	-0.3862465	0.0114210	-33.819	< 2e-16 ***
range15.546123:DCultureProie	-0.2776993	0.0114227	-24.311	< 2e-16 ***
range10.05546123:DCulturePredator	0.0164094	0.0114210	1.437	0.150802
range10.3697415333333333:DCulturePredator	0.0187474	0.0114210	1.641	0.100717
range15.546123:DCulturePredator	-0.0154233	0.0114227	-1.350	0.176964
range10.05546123:scale1D2D	0.0672857	0.0970588	0.693	0.488166
range10.3697415333333333:scale1D2D	-0.0893730	0.0970588	-0.921	0.357164
range15.546123:scale1D2D	-0.0474286	0.0970732	-0.489	0.625142
range10.05546123:prop.h:prop.c	0.1812803	0.1718485	1.055	0.291496
range10.3697415333333333:prop.h:prop.c	-0.1477232	0.1718485	-0.860	0.390017
range15.546123:prop.h:prop.c	0.1727840	0.1718485	1.005	0.314700
range10.05546123:prop.h:DCultureProie	0.0042340	0.0130473	0.325	0.745557
range10.3697415333333333:prop.h:DCultureProie	-0.0136454	0.0130473	-1.046	0.295651
range15.546123:prop.h:DCultureProie	-0.0288379	0.0130473	-2.210	0.027102 *
range10.05546123:prop.h:DCulturePredator	-0.0116814	0.0130473	-0.895	0.370635
range10.3697415333333333:prop.h:DCulturePredator	-0.0149970	0.0130473	-1.149	0.250395
range15.546123:prop.h:DCulturePredator	0.0068875	0.0130473	0.528	0.597583
range10.05546123:prop.h:scale1D2D	-0.4497905	0.1143307	-3.934	8.39e-05 ***
range10.3697415333333333:prop.h:scale1D2D	-0.2279244	0.1143307	-1.994	0.046219 *
range15.546123:prop.h:scale1D2D	-0.5373247	0.1143307	-4.700	2.63e-06 ***
range10.05546123:prop.c:DCultureProie	0.4767904	0.0130473	36.543	< 2e-16 ***
range10.3697415333333333:prop.c:DCultureProie	0.5489154	0.0130473	42.071	< 2e-16 ***
range15.546123:prop.c:DCultureProie	0.4586236	0.0130473	35.151	< 2e-16 ***
range10.05546123:prop.c:DCulturePredator	-0.0117289	0.0130473	-0.899	0.368691
range10.3697415333333333:prop.c:DCulturePredator	-0.0004915	0.0130473	-0.038	0.969954
range15.546123:prop.c:DCulturePredator	0.0201279	0.0130473	1.543	0.122927
range10.05546123:prop.c:scale1D2D	0.0201982	0.1143307	0.177	0.859774
range10.3697415333333333:prop.c:scale1D2D	0.1686953	0.1143307	1.476	0.140099
range15.546123:prop.c:scale1D2D	0.4266747	0.1143307	3.732	0.000191 ***
range10.05546123:DCultureProie:DCulturePredator	0.0005757	0.0009906	0.581	0.561153
range10.3697415333333333:DCultureProie:DCultPredator	-0.0012745	0.0009906	-1.287	0.198248
range15.546123:DCultureProie:DCulturePredator	-0.0007185	0.0009907	-0.725	0.468324
range10.05546123:DCultureProie:scale1D2D	-0.0065453	0.0086803	-0.754	0.450839
range10.3697415333333333:DCultureProie:scale1D2D	-0.0165679	0.0086803	-1.909	0.056325 .
range15.546123:DCultureProie:scale1D2D	-0.0295498	0.0086818	-3.404	0.000667 ***
range10.05546123:DCulturePredator:scale1D2D	-0.0130793	0.0086803	-1.507	0.131889



range10.3697415333333333:DCulturePredator:scale1D2	-0.0160257	0.0086803	-1.846	0.064882
range15.546123:DCulturePredator:scale1D2D	-0.0034732	0.0086818	-0.400	0.689125

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.5166904)

Null deviance: 56403.3 on 14579 degrees of freedom  
Residual deviance: 7208.3 on 14531 degrees of freedom  
AIC: 39366

## b) Pest density

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.9892	-0.2921	-0.1405	0.2777	1.2335

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
range10.05546123	6.893e-01	4.340e-02	15.882	< 2e-16 ***
range10.3697415333333333	8.977e-01	4.340e-02	20.685	< 2e-16 ***
range15.546123	9.305e-01	4.341e-02	21.436	< 2e-16 ***
range10.05546123:prop.h	1.786e+00	6.298e-02	28.359	< 2e-16 ***
range10.3697415333333333:prop.h	1.604e+00	6.298e-02	25.473	< 2e-16 ***
range15.546123:prop.h	1.574e+00	6.298e-02	24.985	< 2e-16 ***
range10.05546123:prop.c	-1.071e-01	6.298e-02	-1.700	0.089065 .
range10.3697415333333333:prop.c	-4.731e-01	6.298e-02	-7.512	6.18e-14 ***
range15.546123:prop.c	-6.108e-01	6.298e-02	-9.698	< 2e-16 ***
range10.05546123:DCultureProie	-4.599e-04	5.419e-03	-0.085	0.932366
range10.3697415333333333:DCultureProie	-1.150e-03	5.419e-03	-0.212	0.831926
range15.546123:DCultureProie	-8.429e-03	5.420e-03	-1.555	0.119926
range10.05546123:DCulturePredator	1.591e-02	5.419e-03	2.936	0.003326 **
range10.3697415333333333:DCulturePredator	5.494e-03	5.419e-03	1.014	0.310731
range15.546123:DCulturePredator	7.404e-03	5.420e-03	1.366	0.171995
range10.05546123:scale1D2D	2.682e+00	4.606e-02	58.234	< 2e-16 ***
range10.3697415333333333:scale1D2D	2.603e+00	4.606e-02	56.522	< 2e-16 ***
range15.546123:scale1D2D	2.560e+00	4.606e-02	55.586	< 2e-16 ***
range10.05546123:prop.h:prop.c	1.116e-01	8.155e-02	1.369	0.171102
range10.3697415333333333:prop.h:prop.c	4.478e-01	8.155e-02	5.491	4.07e-08 ***
range15.546123:prop.h:prop.c	6.126e-01	8.155e-02	7.513	6.13e-14 ***
range10.05546123:prop.h:DCultureProie	-9.223e-05	6.191e-03	-0.015	0.988114
range10.3697415333333333:prop.h:DCultureProie	-1.099e-04	6.191e-03	-0.018	0.985843
range15.546123:prop.h:DCultureProie	3.718e-03	6.191e-03	0.601	0.548124
range10.05546123:prop.h:DCulturePredator	-1.716e-02	6.191e-03	-2.772	0.005575 **
range10.3697415333333333:prop.h:DCulturePredator	-1.136e-02	6.191e-03	-1.836	0.066445 .
range15.546123:prop.h:DCulturePredator	-1.334e-02	6.191e-03	-2.154	0.031253 *
range10.05546123:prop.h:scale1D2D	-2.733e-01	5.425e-02	-5.038	4.76e-07 ***
range10.3697415333333333:prop.h:scale1D2D	-2.166e-01	5.425e-02	-3.993	6.56e-05 ***
range15.546123:prop.h:scale1D2D	-1.840e-01	5.425e-02	-3.392	0.000695 ***
range10.05546123:prop.c:DCultureProie	-1.602e-04	6.191e-03	-0.026	0.979353
range10.3697415333333333:prop.c:DCultureProie	2.631e-03	6.191e-03	0.425	0.670926
range15.546123:prop.c:DCultureProie	5.160e-03	6.191e-03	0.834	0.404573
range10.05546123:prop.c:DCulturePredator	4.870e-03	6.191e-03	0.787	0.431533
range10.3697415333333333:prop.c:DCulturePredator	1.282e-02	6.191e-03	2.070	0.038427 *
range15.546123:prop.c:DCulturePredator	8.267e-03	6.191e-03	1.335	0.181799

range10.05546123:prop.c:scale1D2D	2.760e-04	5.425e-02	0.005	0.995940
range10.3697415333333333:prop.c:scale1D2D	4.351e-02	5.425e-02	0.802	0.422562
range15.546123:prop.c:scale1D2D	3.751e-02	5.425e-02	0.691	0.489292
range10.05546123:DCultureProie:DCulturePredator	-1.016e-06	4.701e-04	-0.002	0.998275
range10.3697415333333333:DCultureProie:DCultPredator	-1.022e-04	4.701e-04	-0.217	0.827920
range15.546123:DCultureProie:DCulturePredator	4.420e-04	4.701e-04	0.940	0.347164
range10.05546123:DCultureProie:scale1D2D	8.782e-04	4.119e-03	0.213	0.831175
range10.3697415333333333:DCultureProie:scale1D2D	-4.107e-04	4.119e-03	-0.100	0.920567
range15.546123:DCultureProie:scale1D2D	2.434e-04	4.120e-03	0.059	0.952879
range10.05546123:DCulturePredator:scale1D2D	7.415e-03	4.119e-03	1.800	0.071835 .
range10.3697415333333333:DCulturePredator:scale1D2D	8.443e-03	4.119e-03	2.050	0.040405 *
range15.546123:DCulturePredator:scale1D2D	9.136e-03	4.120e-03	2.218	0.026588 *

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.1163418)

Null deviance: 729356.0 on 14579 degrees of freedom  
Residual deviance: 1572.2 on 14531 degrees of freedom  
AIC: 93619

### c) Pesticide application

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.2595	-0.3576	-0.0461	0.2104	3.9688

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
range10.05546123	0.0882469	0.1136018	0.777	0.437292
range10.3697415333333333	0.8059067	0.0993160	8.115	5.53e-16 ***
range15.546123	1.3633343	0.0925763	14.727	< 2e-16 ***
range10.05546123:prop.h	0.1816249	0.1648826	1.102	0.270692
range10.3697415333333333:prop.h	0.0513318	0.1434937	0.358	0.720555
range15.546123:prop.h	0.1819905	0.1324734	1.374	0.169542
range10.05546123:prop.c	6.0049925	0.1726232	34.787	< 2e-16 ***
range10.3697415333333333:prop.c	5.4375920	0.1542419	35.254	< 2e-16 ***
range15.546123:prop.c	4.7657740	0.1421019	33.538	< 2e-16 ***
range10.05546123:DCultureProie	-0.9583213	0.0484530	-19.778	< 2e-16 ***
range10.3697415333333333:DCultureProie	-0.6137248	0.0212642	-28.862	< 2e-16 ***
range15.546123:DCultureProie	-0.2412094	0.0146344	-16.482	< 2e-16 ***
range10.05546123:DCulturePredator	0.0143349	0.0136344	1.051	0.293113
range10.3697415333333333:DCulturePredator	-0.0003932	0.0120738	-0.033	0.974024
range15.546123:DCulturePredator	0.0122163	0.0111529	1.095	0.273398
range10.05546123:scale1D2D	0.2158246	0.1190454	1.813	0.069872 .
range10.3697415333333333:scale1D2D	0.0631225	0.1059964	0.596	0.551514
range15.546123:scale1D2D	0.0888081	0.0967997	0.917	0.358936
range10.05546123:prop.h:prop.c	0.1559954	0.2388174	0.653	0.513645
range10.3697415333333333:prop.h:prop.c	-0.0803773	0.2091595	-0.384	0.700775
range15.546123:prop.h:prop.c	-0.2408281	0.1908610	-1.262	0.207055
range10.05546123:prop.h:DCultureProie	-0.0229004	0.0164860	-1.389	0.164842
range10.3697415333333333:prop.h:DCultureProie	-0.0196760	0.0152727	-1.288	0.197672
range15.546123:prop.h:DCultureProie	0.0072535	0.0133138	0.545	0.585900
range10.05546123:prop.h:DCulturePredator	-0.0225512	0.0137264	-1.643	0.100439
range10.3697415333333333:prop.h:DCulturePredator	-0.0077129	0.0127913	-0.603	0.546539
range15.546123:prop.h:DCulturePredator	0.0106728	0.0119762	0.891	0.372864

range10.05546123:prop.h:scale1D2D	-1.0571840	0.1211540	-8.726	< 2e-16 ***
range10.3697415333333333:prop.h:scale1D2D	-0.4277380	0.1126182	-3.798	0.000147 ***
range15.546123:prop.h:scale1D2D	-0.5294681	0.1060693	-4.992	6.10e-07 ***
range10.05546123:prop.c:DCultureProie	1.1427737	0.0601864	18.987	< 2e-16 ***
range10.3697415333333333:prop.c:DCultureProie	0.7121060	0.0266300	26.741	< 2e-16 ***
range15.546123:prop.c:DCultureProie	0.2518371	0.0180022	13.989	< 2e-16 ***
range10.05546123:prop.c:DCulturePredator	0.0068079	0.0180646	0.377	0.706284
range10.3697415333333333:prop.c:DCulturePredator	0.0138696	0.0160018	0.867	0.386101
range15.546123:prop.c:DCulturePredator	-0.0123994	0.0144856	-0.856	0.392031
range10.05546123:prop.c:scale1D2D	-0.0777688	0.1592451	-0.488	0.625308
range10.3697415333333333:prop.c:scale1D2D	-0.2736013	0.1425230	-1.920	0.054928 .
range15.546123:prop.c:scale1D2D	-0.0528780	0.1288339	-0.410	0.681496
range10.05546123:DCultureProie:DCulturePredator	0.0003353	0.0012502	0.268	0.788571
range10.3697415333333333:DCultureProie:DCulPredator	-0.0021649	0.0011603	-1.866	0.062104 .
range15.546123:DCultureProie:DCulturePredator	-0.0005456	0.0010101	-0.540	0.589130
range10.05546123:DCultureProie:scale1D2D	-0.0281840	0.0109851	-2.566	0.010315 *
range10.3697415333333333:DCultureProie:scale1D2D	0.0022087	0.0103063	0.214	0.830313
range15.546123:DCultureProie:scale1D2D	-0.0107528	0.0090086	-1.194	0.232665
range10.05546123:DCulturePredator:scale1D2D	-0.0284092	0.0091307	-3.111	0.001868 **
range10.3697415333333333:DCulturePredator:scale1D2D	-0.0113828	0.0086327	-1.319	0.187350
range15.546123:DCulturePredator:scale1D2D	-0.0202810	0.0080499	-2.519	0.011772 *

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.3003416)

Null deviance: 1183419.9 on 8827 degrees of freedom

Residual deviance: 2820.8 on 8779 degrees of freedom

AIC: 79699