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Best organic farming expansion scenarios for pest control: a modeling approach

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Abstract

Organic Farming (OF) has been expanding recently in response to growing consumer demand and as a response to environmental concerns. The area under OF is expected to further increase in the future. The effect of OF expansion on pest densities in organic and conventional crops remains difficult to predict because OF expansion impacts Conservation Biological Control (CBC), which depends on the surrounding landscape (i.e. both the crop mosaic and semi-natural habitats). In order to understand and forecast how pests and their biological control may vary during OF expansion, we modeled the effect of spatial changes in farming practices on population dynamics of a pest and its natural enemy. We investigated the impact on pest density and on predator to pest ratio of three contrasted scenarios aiming at 50% organic fields through the progressive conversion of conventional fields. Scenarios were 1) conversion of Isolated conventional fields first (IP), 2) conversion of conventional fields within Groups of conventional fields first (GP), and 3) Random conversion of conventional field (RD). We coupled a neutral spatially explicit landscape model to a predator-prey model to simulate pest dynamics in interaction with natural enemy predators. The three OF expansion scenarios were applied to nine landscape contexts differing in their proportion and fragmentation of semi-natural habitat. We further investigated if the ranking of scenarios was robust to pest control methods in OF fields and pest and predator dispersal abilities. We found that organic farming expansion affected more predator densities than pest densities for most combinations of landscape contexts and OF expansion scenarios. The impact of OF expansion on final pest and predator densities was also stronger in organic than conventional fields and in landscapes with large proportions of highly fragmented semi-natural habitats. Based on pest densities and the predator to pest ratio, our results suggest that a progressive organic conversion with a focus on isolated conventional fields (scenario IP) could help promote CBC. Careful landscape planning of OF expansion appeared most necessary when pest management was substantially less efficient in organic than in conventional crops, and in landscapes with low proportion of semi-natural habitats.

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Introduction

The intensification of agricultural systems in recent decades has relied on both an increase in field area and a larger dependency on chemical pesticides (Duru et al., 2015; Knapp & van der Heijden, 2018). This process led to profound changes in landscapes with a reduction and fragmentation of semi-natural habitats (Sirami et al., 2019; Tschardt et al., 2016) and a reduced diversity of the crop mosaic (Tschardt et al., 2016). This process had demonstrated negative impacts on biodiversity (Perez-Alvarez et al., 2019; Sánchez-Bayo & Wyckhuys, 2019) including on species of interest for agriculture such as pollinators (Goulson Dave et al., 2015; Muth & Leonard, 2019) and pest natural enemies (Sánchez-Bayo & Wyckhuys, 2019; Sirami et al., 2019; Tsutsui et al., 2018). Further, the intensive use of chemical pesticides had negative impacts on human health, and biodiversity (Móznér et al., 2012; Pärn et al., 2012; Sánchez-Bayo & Wyckhuys, 2019). Hence, there is an urgent need to identify alternative farming systems that reduce the negative impacts of intensive agriculture while maintaining yields as much as possible (Colbach et al., 2020; Smith et al., 2020). Organic Farming (OF) is one of these possible alternative systems. The multi-performance of OF recently received much attention, in terms of yield (Knapp & van der Heijden, 2018), of effects on biodiversity (Caprio et al., 2015; Lourenço et al., 2021; Smith et al., 2020), of nutritional value and of global positive impact on human health (Gomiero, 2018; Salomé et al., 2021).

Pest management in OF relies on specific cultural practices and a restricted number of non-synthetic pesticides. Conservation Biological Control (CBC) methods that enhance natural enemy abundance and activity to reduce pest populations (Heimpel & Mills, 2017; Holland et al., 2016) are of particular interest for OF. A wealth of literature, however, demonstrates that the potential and efficiency of CBC within a field do not only depend on local agricultural practices but also on the structure of the surrounding landscape (Begg et al., 2017; Muneret, Auriol, Thiéry, et al., 2019), including its amount of semi-natural habitat (Le Gal et al., 2020; Zamberletti et al., 2021) and the characteristics of the crop mosaic (Hillaert et al., 2018, 2020; Le Gal et al., 2020; Smith et al., 2020).

Organic farming has been expanding recently around the world in response to growing consumer demand and environmental concerns, and the area under OF is expected to increase in the future (Paull & Hennig, 2016). A majority of the literature on OF expansion points toward new organic farmers and fields clustering around existing ones (Gabriel et al., 2009; Marton & Storm, 2021; Sánchez Herrera & Dimitri, 2019; Zollet & Maharjan, 2021). Clustering happens for socio-economic and agronomic reasons, because OF conversion happens primarily “in agriculturally less-favored areas where economic incentives for conversion to organic farming do not need to be high and the loss of production due to conversion will be comparatively small” (Gabriel et al. 2009) such as isolated, hard to access, or less productive areas (Ilbery et al., 1999), but also because OF is often driven by newcomers, who could settle down more easily in the proximity of existing clusters, in less-favored areas, and in places where a “prevalence of small-scale, part-time, and self-sufficiency-oriented farming” is observed (Zollet & Maharjan, 2021).

The effect of OF expansion on pests and their natural enemies can be approximated, in a space for time approach (Blois et al 2013), by investigating how pests and natural enemies are affected by the proportion of OF in the landscape. Studies that investigated pest abundance in crops as a function of OF area in the landscape found that pests were either less (Gosme et al., 2012) or similarly (Muneret et al., 2018; Ricci et al., 2009) abundant when OF area increased. Moreover, predators of pests were either more or similarly abundant (Diekötter et al., 2010, 2016; Djoudi et al., 2018, 2019; Inclán et al., 2015; Lefebvre et al., 2016; Muneret, Auriol, Thiéry, et al., 2019; Puech et al., 2015), reviewed in (Petit et al., 2020), suggesting that earlier studies showing increases in crop damage associated with OF may have been influenced by the low amount of OF in the landscape in its early beginnings and that OF expansion scenarios may be of maximum importance (Muneret, Auriol, Bonnard, et al., 2019).

The effect of OF expansion on pest abundance and CBC in organic and conventional fields is difficult to predict. It will depend on the abilities of the pests and predators to develop in organic and conventional fields, on the interplay between pest and predator and landscape structure that conditions the ability of pests and predators to move among crops and semi-natural habitats (Kremen et al., 2007; Le Gal et al., 2020). More complex landscapes, i.e. landscapes with more, and more fragmented, semi-natural habitats and a more heterogeneous crop mosaic, may sustain more biodiversity (Batáry et al., 2011; Petit et al., 2020; Smith et al., 2020; Tschardt et al., 2021; Tuck et al., 2014) and may support higher spill-over of

predators from semi-natural habitats into crops (Concepción et al., 2008; Tschardt et al., 2012). Such landscapes may also exhibit more movements of pests from semi-natural habitats to crops if pests find resources in semi-natural habitats at some point of their life cycle (Juhel et al., 2017). As a result, an increasing amount of semi-natural habitat in the landscape generally increases the abundance and diversity of natural enemies as well as pest predation and parasitism but its effect on pest abundance or damage is case dependent (Chaplin-Kramer et al., 2011; Karp et al., 2018; Veres et al., 2013). Similarly, pest and predator movements between organic and conventional crops are expected to increase with the edge length between these two crop types. Organic expansion should thus affect more pest abundance in conventional crops when the two crop types are interspersed. The response of pest abundance to OF expansion may moreover differ in organic and conventional fields: local management is expected to have large effects on biodiversity or ecological functions when landscapes are of intermediate intensity but to have little effect when landscapes are either very or very little intensive (the intermediate landscape hypothesis (Perez-Alvarez et al., 2019; Tschardt et al., 2005, 2012)) and, reciprocally, landscape effects are supposed to depend on local practice intensity (Petit et al., 2020). Such interactions have, however, seldom been observed in the field (Petit et al. 2020, but see e.g. Perez-Alvarez, Nault, et Poveda 2019; Ricci et al. 2019).

Given the inherent complexity of conservation biological control (Begg et al., 2017) and the lack of CBC data in the context of OF expansion, modeling appears as a useful tool to understand and forecast how pests and their control may vary during OF expansion in a diversity of landscape contexts. The only published modeling study to our knowledge considered a pest-parasitoid system in a landscape exclusively composed of conventional and organic fields (Bianchi et al., 2013). This study interestingly showed that clustering organic and conventional fields decreased the proportion of OF necessary for maintaining the parasitoid population and decreased pest load. It also showed that intermediate levels of OF may lead to transitory peaks in pest load due to the delay of the parasitoid population response to pest abundance (Bianchi et al., 2013). It is therefore interesting and necessary to study, through modeling approaches, how spatial scenarios of organic farming expansion impact conservation biological control (Adl et al., 2011; Bianchi et al., 2013). As stated by Petit et al. (2020), such modeling approaches “can offer *in silico* tests of the consequences of much larger proportions of agroecological practices in the landscape” and could be combined with empirical studies to “provide key insights about how natural enemies and pests will behave in future landscapes.”

In the following, we pair a grid-based landscape model and a spatially explicit Lotka-Volterra type predator-prey model (Ciss et al., 2016; Roques, 2015) to investigate how contrasted scenarios of OF expansion, defined by their spatial arrangements, impact pest abundance in organic and conventional crops. The scenarios are applied to a diversity of landscapes differing in their amount of semi-natural habitat and its fragmentation. We further investigate if the ranking of scenarios is robust to pest control methods in OF fields and pest and predator dispersal abilities.

Methods

1. Overview

The modeling procedure comprises three main elements. The first is a stochastic landscape model to initiate the structure of the landscape, i.e. the total area and fragmentation of semi-natural habitat and the initial area of organic and conventional crops. The second is a population dynamics model to represent the dynamics of interacting pests and their predators on the changing landscapes. The third is a set of spatial scenarios of OF expansion that govern landscape change over time (Figure 1).

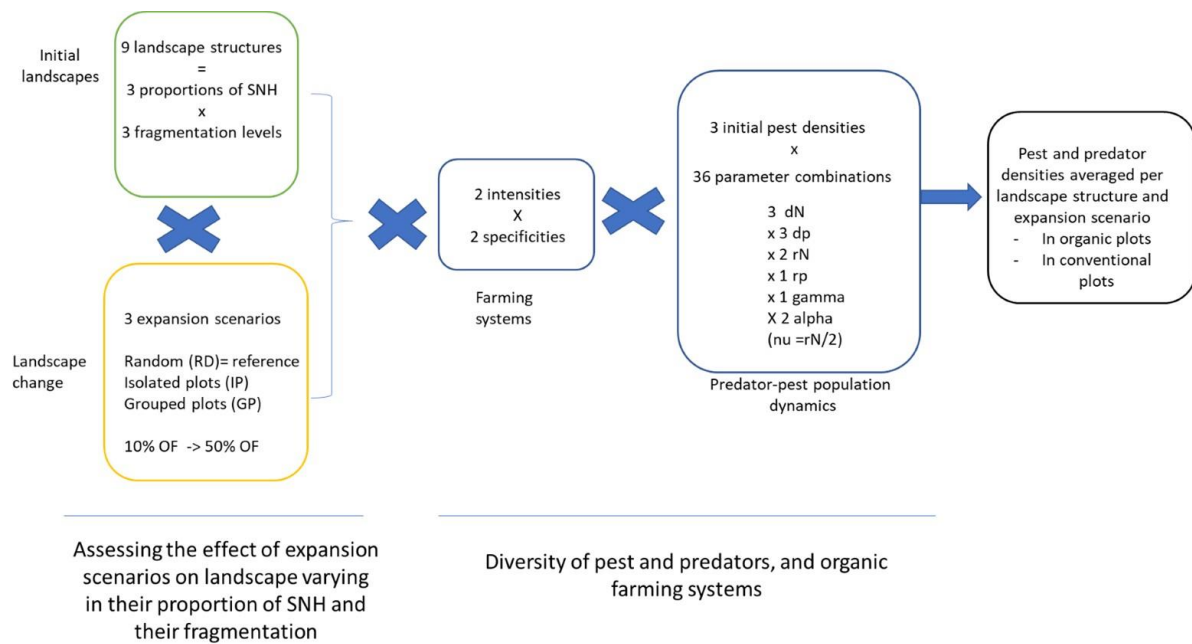


Figure 1 - The simulation design combines three spatial scenarios of organic farming expansion (Random versus IP or GP) in nine landscape contexts (3 proportions of seminatural habitats (SNH) x 3 fragmentation levels) for various predator-pest population dynamics (36 pest biology parameter combinations and 4 pest management types in the organic farming system). The green box corresponds to the landscape model, the blue box to the population dynamic model and the orange box to the land change scenarios.

2. Landscape and population dynamics models

2.1. Stochastic landscape model to set the initial landscape context

To set the landscape context in which to initiate the joint simulation of OF expansion and pest and predator population dynamics, we used a landscape model initially developed by Roques and Stoica (2007), then improved by Roques (2015). This landscape model generates stochastic landscapes with several types of land uses over a square grid ($n \times n$ matrix). Land use allocations were parametrized by the proportion of each type of land use and the fragmentation level of one target land use (Roques 2015; Ciss et al. 2016). This fragmentation is controlled by the fr parameter, which is an index of fragmentation *per se* (Fahrig, 2003). fr measures the landscape-level average proportion of neighbors among the 4 closest neighbors of each cell of that land use that are not of the same land use type. fr is in the range [0,1], and increases with fragmentation. To reach the desired fragmentation level, grid cells are first randomly allocated to one of the land uses, controlling for the proportion of cells associated to each land use. Then a Metropolis-Hastings algorithm is run to optimize the spatial distribution of the cells associated with the target land use. The algorithm stops when the distance between the observed and the desired fragmentation index is below a tolerance threshold.

Here, we set up initial landscapes composed of three land uses: (i) semi-natural habitats (SNH), (ii) Organic Farming crops (OF), and (iii) Conventional Farming crops (CF). We controlled the proportions of these land uses and the fragmentation level fr of SNH. (Table 1). fr is thus an index of fragmentation *per se*. High values of fr resulted in landscapes with more numerous and smaller SNH patches and increased edge length between SNH and crop patches (Fig. 1, S1.1, S1.2, S1.3).

2.2. Population dynamic model

2.2.1. General description

We modeled the spatio-temporal dynamics of a pest and a generalist predator species interacting over the lattice generated by the landscape model according to (Martinet & Roques, 2022). The model describes the density of the predator population $P_t(x)$ and of the pest population $N_t(x)$ at each position $x = (i, j)$ over the grid and at each time step t (equations 1). The variation over time (indicated with sign ') of pest

($N'_t(x)$) and predator ($P'_t(x)$) densities at each position depends on their dispersal in and out of this position, their intrinsic growth (i.e. population growth in absence of pesticides and of interactions between pests and predators), mortality due to pesticides, and mortality (for the pest) or growth (for the predator) due to predation.

$$\begin{cases} N'_t(x) = \underbrace{d_N D[N_t(x)]}_{\text{Dispersal}} + \underbrace{f_N(t, x, N_t(x))}_{\text{Growth}} - \underbrace{\rho n(t, x)N_t(x)}_{\text{Mortality}} - \underbrace{\alpha_1 N_t(x)P_t(x)}_{\text{Predation}} \\ P'_t(x) = \underbrace{d_P D[P_t(x)]}_{\text{Dispersal}} + \underbrace{f_P(t, x, P_t(x))}_{\text{Growth}} - \underbrace{\rho p(t, x)P_t(x)}_{\text{Mortality}} + \underbrace{\alpha_2 N_t(x)P_t(x)}_{\text{Predation}} \end{cases} \quad (1)$$

Dispersal: $D[.]$ defined as $D[U(x)] = D[U_{ij}] = (U|i + 1j + U_{i-1j} + U_{ij+1} + U_{ij-1} - 4U_{ij})/\delta_x^2$ is the discrete Laplace operator modeling the movements of the individuals to adjacent cells, $\delta_x = 1/n$ being the length of a unit cell in the landscape. From each position $x = (i, j)$, and during a time interval $\delta_t \ll 1$, a proportion $\frac{4d_N\delta_t}{\delta_x^2}$ of the pest population (resp. $\frac{4d_P\delta_t}{\delta_x^2}$ of the predator population) moves to its 4 adjacent cells. Thus d_N and d_P directly control the mobility of the pest and predator populations. We assume periodic conditions at the boundaries of the lattice.

Growth: The terms $f_N(t, x, N_t(x))$ and $f_P(t, x, P_t(x))$ stand for the pest and predator intrinsic growth functions. They are controlled by parameters r_N and r_P respectively (Table 1). The predator being a generalist, it can grow in absence of pests.

Table 1 - List of model parameters.

Parameter	Description	Unit	Values
Landscape model:			
n	Size of the lattice		24
fr	Fragmentation index	dimensionless	{0.1,0.5,0.9}
pSNH	Percentage semi-natural habitat	%	{10, 25, 50}
T	Time horizon	year	50
Model of population dynamics:			
d_N	Pest dispersal coefficient	unit area.year ⁻¹	$\frac{1}{n^2}\{0.1,0.5,1\}$
d_P	Predator dispersal coefficient	unit area.year ⁻¹	$\frac{1}{n^2}\{0.1,0.5,1\}$
r_N	Pest intrinsic growth rate	year ⁻¹	$2\{\ln(50), \ln(100)\}$
r_P	Predator intrinsic growth rate	year ⁻¹	$\ln(2)$
γ	Predator life expectancy in crops	year	1/2
α	Predation index	indiv ⁻¹ year ⁻¹	$\frac{1}{\gamma}\{4/3, 4\}$
v	Pest management effect	year ⁻¹	$r_N/2=\{\ln(50), \ln(100)\}$

Mortality: $\rho_N(t, x)N_t(x)$ and $\rho_P(t, x)P_t(x)$ account for the pest and predator death rates caused by pest management. Mortality is controlled by parameter v (Table 1).

Predation: The interaction terms $-\alpha_1 N_t(x)P_t(x)$ and $\alpha_2 N(x)P_t(x)$ describe the effects of predation on the pest and predator growth rates, respectively. We assume standard Lotka–Volterra interactions

between the pest population and its predator, which means that the pest death rate increases linearly with the density of the predator, and conversely the growth rate of the predator increases linearly with the pest population density. We also assume that $\alpha_1 = \alpha_2 = \alpha$ (Table 1)

The system is scaled so that the carrying capacities of P and N are both equal to 1 thus the population densities are expressed in units of their respective carrying capacities.

2.2.2. Timing of ecological processes

The year is divided into equal intervals δ_t each corresponding to a dispersal event of pests and predators. The number of intra-annual time steps is thus calculated as $1 + (1/\delta_t)$. Each year is divided into two periods $[0, \frac{1}{2}[$ and $[\frac{1}{2}, 1]$ during which ecological processes differ (Table 2). Pests are specialized on the crop and their phenology matches that of the crop. The first half of the year schematically represents the season where the crop is absent, pests do not reproduce and there are no pest management practices. Pest densities only depend on their dispersal and predation by predators. During the second half of the year, when the crop is present, pests furthermore reproduce and are affected by pest management practices in the crop. The predators, in contrast, reproduce all year long in semi-natural habitats (loosely mimicking taxa that include both spring and autumn reproduction) and suffer from intrinsic mortality in crops. Their density increases further in both semi-natural habitats and crops when the pest is present. Predators thus behave as generalist predators that feed on the pest prey, and on alternative prey in semi-natural habitats. Like pests, they are affected by pest management practices in crops during the second half of the year.

Table 2 - Values of the growth functions $f_N(t, x, N_t(x))$ and $f_P(t, x, P_t(x))$. r_N is the pest intrinsic growth rate in the crops in the absence of pest management, γ the natural enemy life expectancy in the absence of resources and r_P the natural enemy birth rate in semi-natural habitats.

Time span	$f_N(t, x, N)$		$f_P(t, x, P)$	
	$[0, \frac{1}{2}[$	$[\frac{1}{2}, 1]$	$[0, \frac{1}{2}[$	$[\frac{1}{2}, 1]$
Land use				
Conventional	0	$r_N N(1 - N)$	$-P/\gamma$	$-P/\gamma$
Organic	0	$r_N N(1 - N)$	$-P/\gamma$	$-P/\gamma$
Semi-natural habitats	0	0	$r_P P(1 - P)$	$r_P P(1 - P)$

2.2.3. Organic farming systems

There exists a diversity of organic farming systems with more or less intensive pest management strategies (Marliac et al., 2015). To represent this diversity, we considered four theoretical types of organic farming (Table 3). In the most intensive OF systems (*Int-Gen* and *Int-Spe*), pest management is as efficient in organic fields as in conventional ones so that the mortality of pests due to pest management practices is the same. These two OF systems differ by the specificity of these control measures that either do not (*Int-Spe*) or do (*Int-Gen*) affect predators, but less than in conventional fields. Examples of efficient and specific pesticides are microorganisms targeting pests such as viruses (Graillot et al., 2016) or other microorganisms (Deshayes et al., 2017). Other pest management measures such as pesticides (e.g. spinosad) or nets are efficient on pests but also affect some predators (Dib et al., 2010). In the extensive OF systems (*Ext-Gen* and *Ext-Spe*) pest management is less efficient in OF fields and pest mortality rates are half those in conventional fields. As before, these two OF systems differ by the specificity of their pest management practices that either do (*Ext-Gen*) or do not (*Ext-Spe*) affect predators (Table 3).

Table 3 - Effects of pest management practices on the pest and the natural enemies in conventional (CF) and organic farming. Four organic farming systems were considered. Int-Spe and Int-Gen correspond to intensive pest management (high pest mortality) while Ext-Spe and Ext-Gen are less intensive. In Int-Spe and Ext-Spe systems, pest management practices are specific to the pest and do not affect predators while in Int-Gen and Ext-Gen systems, management is less specific.

	$\rho_N(t, x)$	$\rho_P(t, x)$
CF	2ν	2ν
Int-Spe	2ν	0
Int-Gen	2ν	ν
Ext-Gen	ν	$\nu/2$
Ext-Spe	ν	0

2.2.4. Parameter values

Intrinsic growth rates: The pest reproduces only during the second half of the year. During one year, the population would increase by a factor of $\exp(rN)/2$ in the absence of any limiting factor. We thus assumed that, under these conditions, the population would increase by a factor of 50 or 100 over the season. We assumed a lesser yearly increase for the predator of $\exp(rp)=2$, i.e. a population doubling in the absence of pests or any limiting factor. To compensate for this increase, we assumed a life expectancy of the predator on the crops of $\gamma=1/2$ year, in the absence of pests.

Mortality due to pest management practices: We assumed that the mortality rate induced by pest management practices is comparable to pest growth rates ($2 \nu \in \{ \ln 50, \ln 100 \}$). The mortality due to pest management practices reaches its maximum value for both pests and predators in the conventional fields and for pests only in the most intensive OF systems (Int-Spe and Int-Gen). In these situations, mortality compensates for the pest population's local increase and drastically reduces predator populations. Mortality caused by pest management practices is reduced by half or set to 0 for predators depending on the OF systems (Table 3).

Dispersal: The values for d_N and d_P were chosen so that approximately between 0.1% (d_N or $d_P=0.1/n^2$) and 1% (d_N or $d_P=1/n^2$) of individuals in a given cell move to neighboring cells every day.

3. Initial Conditions

3.1. Landscapes

Simulations were run on 9 landscape contexts differing in their proportion of semi-natural habitats (SNH) (either 10, 25, or 50% of total area) and in the fragmentation of these habitats (*fr* values: 0.1, 0.5 and 0.9). Initially, 10% of crops were organic (OF) and 90% conventional (CF) based on the current national proportions in France (ORAB PACA, 2020) and on the proportion of worldwide cropped and pasture land that is practicing some forms of organic farming (Pretty et al, 2018). Based on that, we generated initial landscapes with three proportions of each land-use, named respectively *Qin1* (10% SNH; 9% OF; 81% CF), *Qin2* (25% SNH; 7.5% OF; 67.5% CF), and *Qin3* (50% SNH; 5% OF; 45% CF). In the remainder of this paper, we refer to these three initial conditions in terms of their SNH proportions (SNH 10%, 25% and 50%). Initial OF crops were allocated randomly among crop cells. Each simulation of the model was run on a different initial landscape.

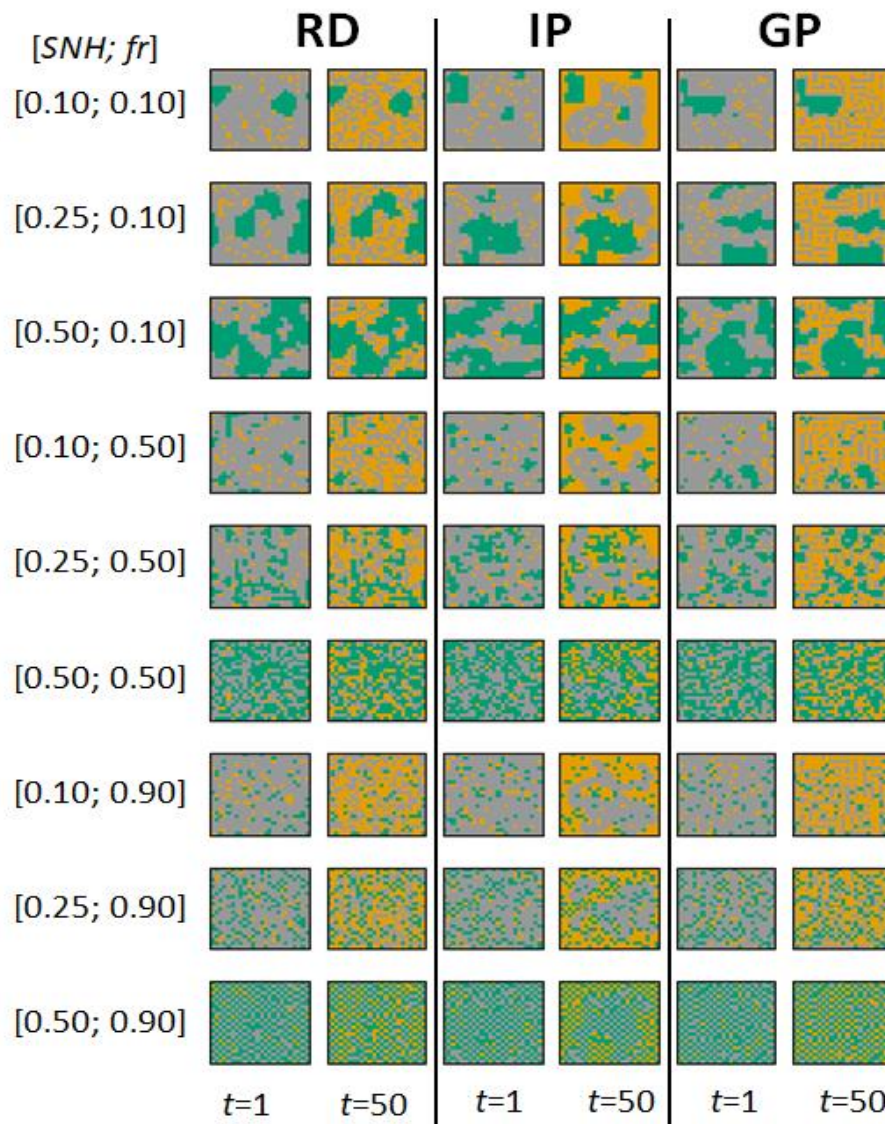


Figure 2- Examples of landscape structures at the beginning ($t=1$) and the end ($t=50$) of the organic expansion. The figure provides one example landscape for each combination of landscape context and OF expansion scenarios. SNH= proportion of semi-natural habitat; fr : fragmentation of semi-natural habitat; RD, IP and GP refer to the three scenarios of selection of CF fields to convert to OF: selection of random, isolated or grouped fields; Grey: conventional (CF), orange: organic (OF), green: semi-natural habitat (SNH).

3.2 Population dynamics

At $t=1$ predators are introduced in all semi-natural habitats with initial density $P1_{SNH}$. The predators are allowed to reproduce and disperse until $t=3$. At $t=3$ pests are introduced in the crops with initial density $N1_{crop} = P1_{SNH}$. To assess the impact of initial conditions on our conclusions, we set three extreme values for $P1_{SNH}$: 0.1, 0.5 and 1. We then performed simulations during a 15-years burn-in period in order to allow the stabilization of pest and predator dynamics before organic farming expansion.

4. Spatial scenarios of organic farming expansion

From each initial landscape, we simulated OF expansion from $t=15$ to $t=50$ years in order to sequentially convert 50% of the initial conventional crop area to OF. For each simulation, OF expansion was progressive, i.e. approximately 6.25% of the initial conventional crop area was converted to OF every 5 years. The total number of conventional fields to be converted depended on the initial cultivated area and the target proportion of OF. The final compositions of landscapes corresponding to the three initial proportion of

semi-natural habitats were respectively Qen1(10% SNH; 49.5% OF; 40.5% CF), Qen2(25% SNH; 41.25% OF; 33.75% CF), Qen3(50% SNH; 27.5.5% OF; 22.5% CF). Only conventional fields were converted to organic. The area of semi-natural habitat remained constant.

Three spatial conversion scenarios were simulated based on the 4-neighborhood of conventional fields:

- the RD scenario in which we performed a random choice of conventional fields to be converted,
- the IP scenario, in which isolated conventional fields, i.e. fields with as few as possible conventional 4-neighbors, were converted first,
- the GP scenario in which, in contrast to IP, conventional fields with as many as possible conventional 4-neighbors were converted first.

The IP and GP scenarios are two possibly planned scenarios that we compared to the baseline RD scenario in terms of resulting pest densities and predator to pest ratio.

5. Simulation outputs

5.1. Landscape structure

Landscapes can be described in terms of composition, i.e. proportion of the land uses, and configuration, i.e. the spatial arrangement of these land uses (Fahrig & Paloheimo, 1988). Landscape composition was controlled during the simulation. We monitored landscape configuration using three landscape metrics for each land use: the mean patch area, the number of patches, and the edge length (R package *landscape metrics*, Hesselbarth et al, 2019). For a given land use, patches were made of fields of that given land use that were 4-neighbors to at least one field of the same land use. Together, these three metrics indicate whether, for a given proportion of landscape area, one land use is represented by a few large patches or many small patches.

5.2. Pest and predator densities

For each simulation, the densities of pests and predators were monitored at the end of each year and averaged over each land use (SNH, OF and CF). From these, a median predator to pest ratio was calculated per land use as a proxy of the intensity of pest control by predators.

6. Simulation study

Simulations for the three spatial organic farming expansion scenarios mentioned above were performed for each of the nine types of landscapes (3 proportions of SNH x 3 levels of *fr*) aiming at 50% OF fields for each of the four types of OF (Table 3). These simulations were performed for all combinations of the values of the 6 parameters (pest and predator dispersal coefficients, pest and predator intrinsic growth rates, predator life expectancy in crops, interaction term,) and the four farming systems governing pest and predator population dynamics (Table 1, Fig. 1) and the three initial densities of pests and predators. This resulted in a total of 11664 Simulations, each run on a different landscape. We performed 11664 more simulations without any action on the landscapes. These simulations are referred to as Reference (REF).

Comparisons of pest and predator densities and predator to pest ratios among conversion scenarios were performed at the end of the simulations ($t=50$) for each landscape context. As pest density was the main variable of concern regarding OF expansion, we further checked whether the ranking of scenarios was robust with regards to the intensity of OF and the dispersal rate of the pest.

All simulations were performed with (*MATLAB*, 2018a) and all statistical analyses were performed with R software (*R Software*, 2017).

Results

1. Pest and predator dynamics

1.1. Pest and predator dynamics in absence of organic farming expansion

The model behavior was first studied in the absence of organic farming expansion, i.e. at the initial proportions of organic farming. This step first shows that in the absence of organic farming expansion, the average landscape scale densities of pest and predator remained stable over time after approximately 15 years (Figure 3, scenario: REF). These equilibrium densities were independent of the initial pest density

(not shown). Consistent with parameter values, both pest and predator densities were higher in organic fields than conventional fields. Moreover, the density of pests was always larger than that of predators, in both conventional and organic fields (Fig. 3, scenario: REF).

Pest and predator densities did not show a clear response to the increase of proportion of semi-natural habitat and they increased with its fragmentation, probably because cultivated fields were more likely to be close to a semi-natural habitat, increasing spill-over of individuals into cultivated fields. These effects were stronger on predators than pests in organic fields, consistent with the higher dependency of predator reproduction and survival on semi-natural habitats. The predator density, in contrast, remained very low in conventional fields due to pesticides.

These differential effects of landscape characteristics on pests and predators had two consequences. First, pest densities were 2.6 times larger in organic fields than in conventional fields in landscapes with little semi-natural habitat and little fragmentation (SNH=10%, $fr=0.1$) while they were only 1.3 times larger in landscapes with large proportions of fragmented semi-natural habitats (SNH=50%, $fr=0.9$). Second, the predator to pest ratio increased in organic fields but decreased in conventional fields when semi-natural habitat proportion and fragmentation increased.

1.2. Pest and predator dynamics during organic farming expansion

The cultivated landscape changed during organic farming expansion. Compared to their initial area, at the end of organic farming expansion, conventional patches were generally smaller and organic patches larger. Constraints were furthermore imposed by the spatial distribution of semi-natural areas so that patch area varied more in little fragmented landscapes or when there was little semi-natural area. Because they set different priorities regarding field conversion, the different scenarios led to different cultivated patch area dynamics, with some dramatic changes due to conventional patch splitting. The IP scenario notably always resulted in conventional patches that were larger than the other scenarios while the GP scenario generally resulted in larger organic patches (Supplementary material S1.3).

The organic farming expansion affected more predator densities than pest densities for most combinations of landscape contexts and expansion scenarios (Fig. 3). Its impact was also generally stronger in organic than conventional fields and in landscapes with large proportions of fragmented semi-natural habitats. As expected, predator densities in organic fields generally increased. Changes in pest and predator densities and their dynamics, however, depended on expansion scenarios and landscape contexts. Pest dynamics

1.2.1 Pest dynamics

Pest densities in organic fields showed similar changes for the three expansion scenarios (Fig. 3). They tended to slightly increase or remain stable over time in landscapes with little or intermediate proportions of semi-natural habitat and to decrease in landscapes with large proportions of semi-natural habitat. In conventional fields, pest densities showed this same pattern with the RD and GP scenarios but not with the IP scenario. With the IP scenario, pest densities in conventional fields tended to decrease slightly over time whatever the landscape context. As a result, at $t=50$, pest densities were generally smaller with the IP than with the RD and the GP scenario in conventional fields and similar for the three expansion scenarios in organic fields.

1.2.2 Predator dynamics

In organic fields, the effect of organic farming expansion on predator densities was very large compared to its effect on pest densities (Fig. 3). Predator densities increased for the three expansion scenarios. The increase was larger for the IP scenario than for other scenarios, particularly in little fragmented landscapes with intermediate or large proportion of semi-natural habitats. For example, when SNH=25% and $fr=0.1$, with the IP scenario the predator density at $t=50$ was 5.38 times larger than the initial density and was 2.44 times higher than the predator density at $t=50$ with the GP scenario. In contrast, the three scenarios performed similarly in landscapes with the highest proportion and fragmentation of semi-natural habitat (SNH=50%, $fr=0.9$). In these landscapes, the predator density increased by a factor of 1.34 between $t=0$ and $t=50$ with the IP scenario and was only 1.20 times higher than with the GP scenario at $t=50$. The increase in predator density was moderate for the RD and GP scenarios and reached similar values at $t=50$. Their dynamics were, however, qualitatively different. While predator densities increased steadily for the

RD scenario, for the GP scenario, most predator densities showed a transient decrease in the first years following the beginning of organic farming expansion.

Note that in landscapes with 50% SNH predator densities were sometimes larger than pest densities in organic fields (Fig. 3). This was most prominent when fragmentation was high, an indication that it resulted from spillover of predators from semi-natural habitats.

The pattern was very different in conventional fields. Predator densities remained stable at very low values for most landscapes and expansion scenarios. They only increased in the GP scenario in landscapes with high proportion of semi-natural habitats but still remained at low values.

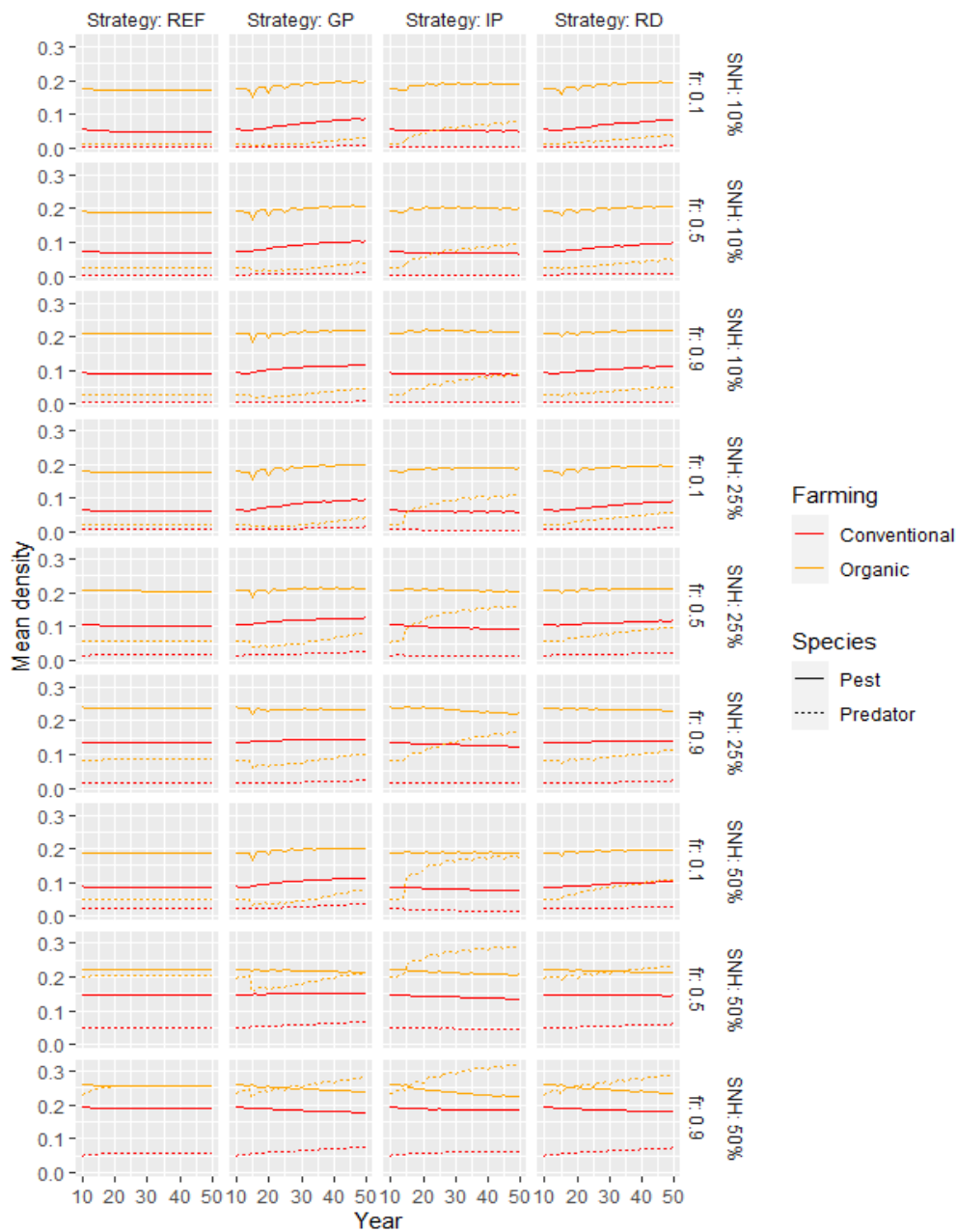


Figure 3 - Effect of organic expansion scenarios on the temporal evolution of the mean density of pests and predators in organic (OF) and conventional farming (CF), as a function of fragmentation (*fr*) and initial proportion of semi-natural habitat (SNH). Reference (REF) represents the absence of organic expansion.

2. Effect of spatial scenarios of organic farming expansion and landscape contexts on resulting pest densities and conservation biological control

2.1. Pest densities

In organic fields, differences in final pest density were limited among expansion scenarios. Pest density in organic fields responded overall little to landscape characteristics and, in particular, less to the different scenarios of OF expansion, despite differences in organic or conventional patch areas (Fig. S1.3), than to the fragmentation of semi-natural habitats (Fig. 4, upper panel). The highest levels of pest densities were obtained for the highest fragmentation levels. For a given level of fragmentation, pest densities in organic fields tended to be lower for the IP scenario but the amplitude of effect was smaller than for fragmentation. In contrast, final pest density in conventional fields (Fig. 4, lower panel) responded both to the OF expansion scenario and to fragmentation, indicating a dependence on conventional and organic patch area (Fig S1.3). As in organic fields, pest density increased with the level of semi-natural habitat fragmentation. In conventional fields, low levels of pest densities could thus be attained for different fragmentation levels given that conventional patch areas were large, a situation provided by the IP scenario in landscapes with small proportion of semi-natural habitats (SNH=10%). Furthermore, the range of variation of pest densities was larger in conventional than organic fields.

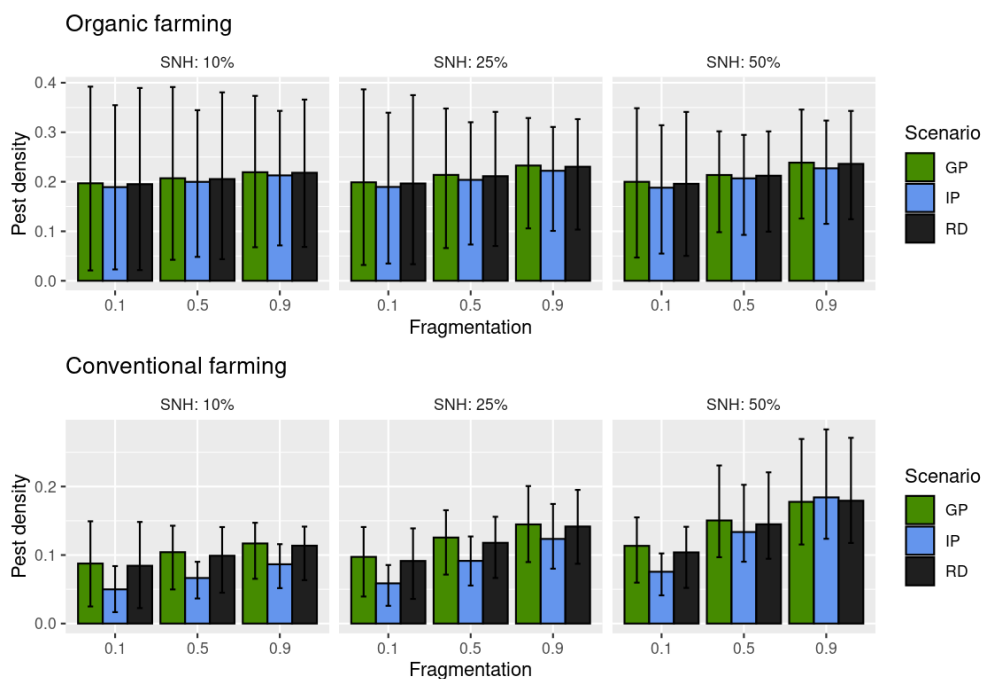


Figure 4. Mean final ($t=50$) density of pests in organic (upper panel) and conventional (lower panel) fields as a function of the landscape context (fragmentation and percentage of semi-natural habitat). Results are presented for each OF spatial expansion scenario: GP (grouped plots), IP (isolated plots), RD (random).

2.2. Conservation biological control

The predator to pest ratio is an indicator of the potential for conservation biological control: a higher ratio indicates that pests are more likely to come across a predator. As a result of the pest and predator dynamics described above, the predator to pest ratio at the end of the simulation was three to four times larger in organic fields than in conventional fields (Fig. 5). It increased with the proportion of semi-natural habitat, in similar relative proportions in organic and conventional fields, from an average of approx 0.2 to 1.25 in organic fields and 0.05 to 0.35 in conventional fields, when the proportion of SNH increased from 10% to 50%. It also increased, but to a much lesser extent with SNH fragmentation. The only significant increase with fragmentation was for landscapes with large proportion of SNH (Fig. 5).

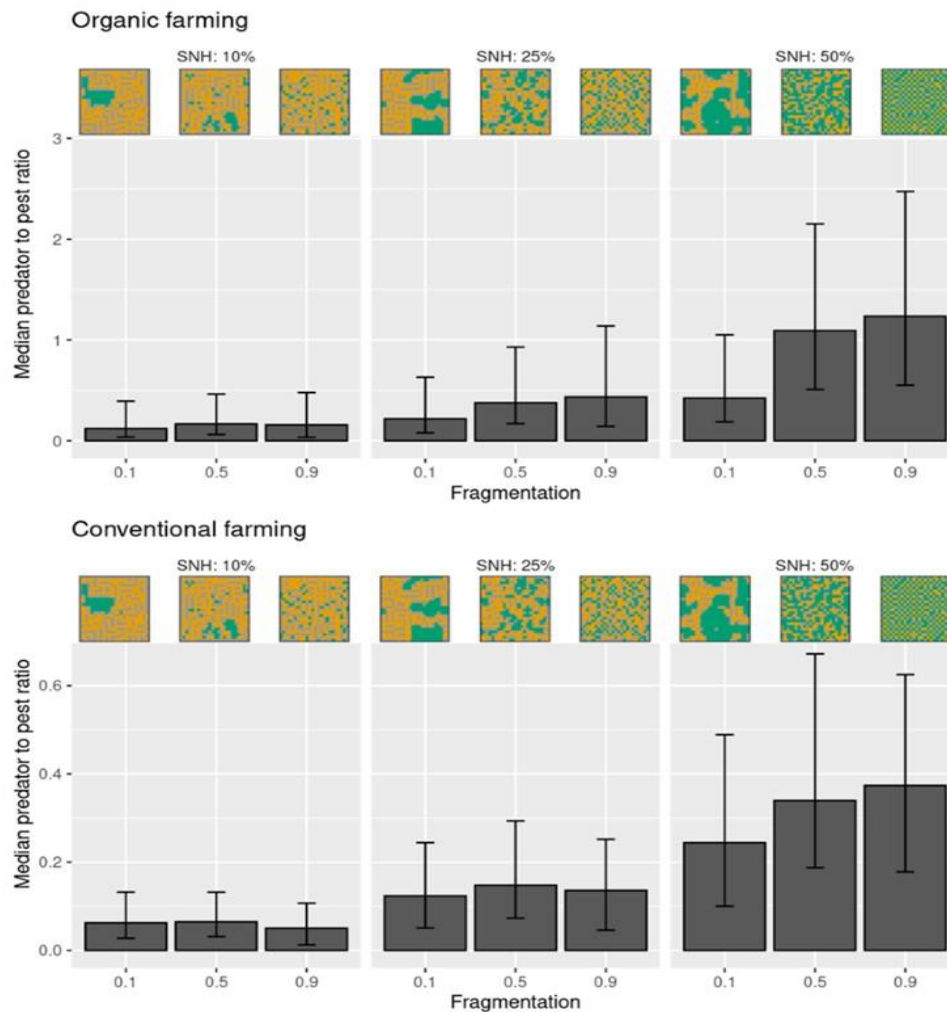


Figure 5 - Median Predator to pest ratio at $t=50$ for the nine types of initial landscapes, in organic fields (upper) and conventional fields (lower). Error bars represent the first and third quartiles over all scenarios and parameter values. Examples of landscape contexts (combinations of fragmentation and percentage of SNH) are provided for illustration. Note that y-axes are on different scales.

More interestingly, we observed a clear ranking of spatial expansion scenarios with $IP > RD > GP$ for the predator to pest ratio in organic fields (Fig. 6). This ranking might be due to the larger increase of predator densities during OF expansion with the IP scenario and the somewhat larger pest densities with the GP scenario (Fig. 3). Relatively to the RD scenario, the predator to pest ratio was from 1.83 times higher (SNH=10%, $fr=0.1$) to 1.1 (SNH=50%, $fr=0.9$) times higher for the IP scenario. In contrast, these ratios for the GP scenario ranged from 0.55 (SNH=10%, $fr=0.1$) to ~ 1 (SNH=50%, $fr=0.9$) times those for the RD scenario.

In conventional fields, predator to pest ratios showed the opposite $GP > RD > IP$ ranking. The difference here was mainly between the IP and the two other scenarios. Ratios were a little larger for the GP scenario than for the RD scenario whatever the landscape context, with values ranging from 1.2 (SNH=10%, $fr=0.1$) to ~ 1 (SNH=50%, $fr=0.9$) times those for the RD scenario. They were the smallest for the IP scenario, particularly in fragmented landscapes with low proportions of semi-natural habitats (from 0.55 (SNH=10%, $fr=0.1$) to 0.8 (SNH=50%, $fr=0.9$) times higher than with the RD scenario, Fig. 6). Consistent with the larger differences in crop patch area in landscapes with few and little fragmented semi-natural habitat, differences between the GP and IP scenarios were largest in such landscapes and very small in landscapes with a large proportion of highly fragmented semi-natural habitats.

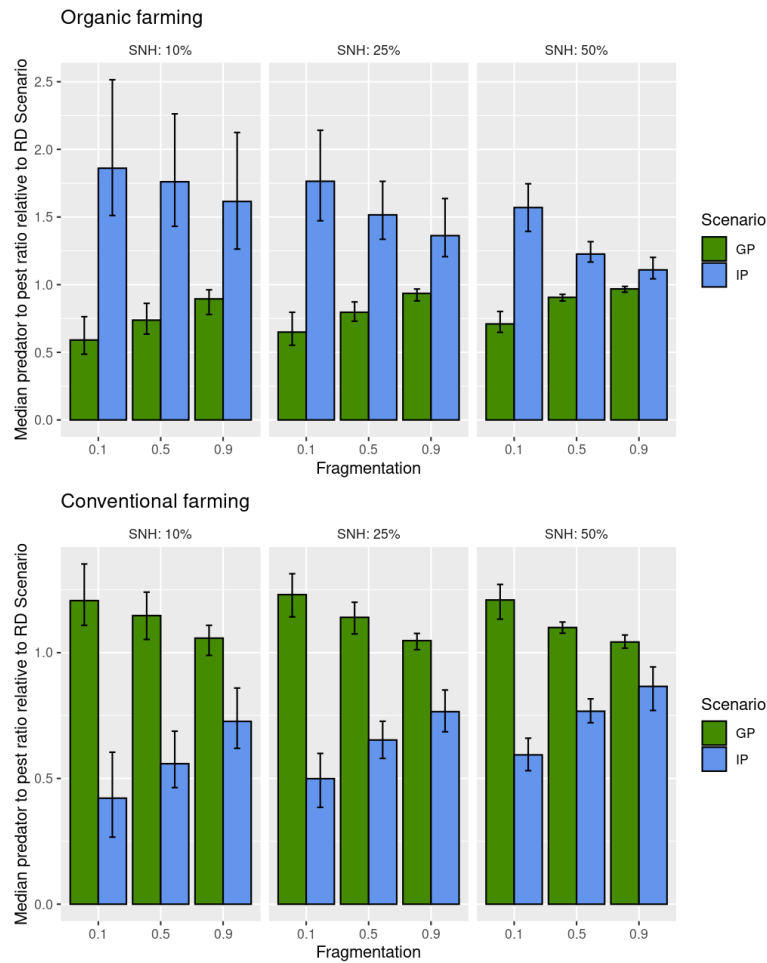


Figure 6. Median predator to pest ratio at $t=50$ in organic and conventional crops for the IP and GP scenarios relative to the ratio obtained for the RD scenario with the same parameter values. Error bars represent first and third quartiles over all combinations of population dynamic parameters.

Discussion

Existing evidence of the positive impacts of OF (Organic Farming) on agrobiodiversity and pest control (eg. Muneret et al. 2019) and its growing adoption by customers and farmers (Paull & Hennig, 2016) highlight the importance of considering how OF expansion may impact the dynamics of agricultural pests (e.g. Petit et al., 2020). Modeling approaches are useful tools to understand and forecast how pest densities and pest control may vary according to crop management and semi-natural habitats at the landscape scale (Begg et al. 2017). In this study, we modeled pest and predator abundances dynamics for contrasted scenarios of OF expansion in different landscapes. Our results indicate that, at the landscape scale, the IP (Isolated Plots converted first) scenario would provide the most benefits for conservation biological control (i.e. predator to pest ratio) in organic fields with little impact on pest densities in conventional fields.

1. Landscape context and OF expansion affect pest and predator densities.

Populations responded to organic farming expansion in the landscape with up to a 437% increase and a 46% decrease in pest and predator densities, indicating that organic farming expansion could indeed lead to significant changes in biological control of pests in both organic and conventional fields depending on the landscape context. Predator densities generally increased or remained stable while pest densities either increased or decreased along OF expansion. When both pest and predator densities increased, predator densities increased more strongly than pest densities. The predator to pest ratio was about three to four times larger in organic than in conventional fields. Changes in pest and predator densities and their dynamics strongly depended on expansion scenarios in interaction with landscape contexts, i.e. the

amount and fragmentation of SNH. Although most scenarios led to overall improvements in predator to pest ratios (seen here as a proxy of conservation biological control, CBC), some led to increases in pest densities, particularly in conventional fields which indicates that in some specific landscapes, carefully planning the spatial expansion of organic farming would be useful to avoid undesirable side effects.

From an ecological point of view, the predator to pest ratio dynamics observed in this study appeared driven by the dynamics of predators which was mostly dependent on the amount of semi-natural habitat (SNH). It was striking that only in landscapes with large proportion of SNH (SNH=50%), did predator densities increase very largely in organic fields and even increase slightly in conventional fields, leading to a decrease of pests in both types of fields. CBC also increased with landscape fragmentation in both OF and CF fields but mostly when the proportion of SNH was high. Since SNH fragmentation increased its edge length with cultivated habitats, this synergy between SNH amount and fragmentation on the level of CBC indicates the importance of predators' spillover from semi-natural habitats on biological control. This interaction is also in line with the frequent observation that complex landscapes with more and more fragmented semi-natural habitats sustain more biodiversity within fields (Muneret, Auriol, Bonnard, et al., 2019; Smith et al., 2020; Tscharrntke et al., 2021) and that reduced distance between SNH and crops favor spillover of predators (Holland et al., 2016; Jonsson et al., 2014; Lavandero et al., 2006; Tylianakis et al., 2006). Incidentally, it may indicate that landscape structures favoring the movement of predators into conventional fields may act as an ecological trap also luring non-target species to fields where mortality is high and long-term persistence impossible (Robertson & Hutto, 2006; Shelton & Badenes-Perez, 2006).

Whatever the expansion scenario, we observed smooth changes in pest and predator densities. This was unexpected given the dramatic changes in the size of patches of OF and CF fields that underwent peculiar processes of progressive percolation/agglomeration (for OF) and its opposite disintegration (for CF) through the conversion of single central fields, leading to non-linear changes and even dramatic thresholds of mean OF and CF patch areas (especially in the IP scenario). This may indicate that the spatial smoothness of a conversion scenario over time is not necessary to maintain generally stable dynamics of biological control at landscape scale, neither in organic nor in conventional farms. This result is an indication that carefully curated temporal plans for OF expansion may not be necessary, and that mean pest infestation risks may remain low for CF farms at the landscape scale. It contrasts with findings on the consequences of OF expansion in a pest - parasitoid model that indicated peaks of pest density for intermediate proportions of OF in the landscape (Bianchi et al. 2013). One main difference is that generalist predators, such as modeled here, may increase in density even in the absence of pests, thus limiting pest population peaks (Symondson et al., 2002).

2. One better scenario of organic farming expansion for CBC?

2.1. A general pattern

The similar pest densities with all spatial expansion scenarios indicates that the choice of one scenario over another bears low risks, while potential benefits were more obvious with noticeable effects on predators. Both the level of conservation biological control (CBC) and pest densities have been used to evaluate the efficiency of pest control in spatial pest-predator models (Bianchi et al., 2013; Zamberletti et al., 2021). Yield or income have also been used (e.g. Le Gal et al., 2020; Milne et al., 2016). Here, because conventional fields relied on pesticides for pest control, and pest densities varied little in organic fields, CBC was a target mostly in organic fields while the main target for conventional fields was the density of pests.

Using these criteria, the IP scenario performed better, by improving CBC in organic fields and doing so at the expense of lower CBC, but not higher pest densities, in conventional fields. Regarding CBC, the IP scenario performed overall better for organic fields because of its clear positive effect on the predator to pest ratio. Patterns were more nuanced for conventional fields. While some scenario x landscape context combinations caused a small improvement in CBC, others caused strong decreases. Interestingly, the effect of expansion scenarios was weaker when they caused increases in CBC than when they caused decreases in CBC. Additionally, the ranking of scenarios was opposite in conventional vs organic fields (IP>RD>GP in organic fields vs GP>RD>IP in conventional fields). From the conventional farming point of view, the absence of planning (RD scenario) may thus constitute a reasonable scenario. However, pest densities in conventional fields were lower with IP than with the other scenarios. The best ranking of the IP scenario

with higher CBC in organic fields and lower pest densities in conventional fields was observed in all landscape configurations, while some landscapes limited the decrease of CBC in conventional fields without canceling it.

The best performance of the IP scenario resulted from two distinct mechanisms: a predator spillover improving CBC in organic fields, and a combination of ‘chemical umbrella’ and lesser pest spillover in conventional fields. The IP scenario prioritized the conversion of fields neighboring organic fields or semi-natural areas. This meant that new organic fields benefitted from the spillover of predators from SNH, albeit with weak effects on pest density. Indeed, the predator to pest ratio improved mainly by an increase in predator numbers. Such trophic network top-heaviness can be caused by exogenous pathways that transfer energy into communities from across spatial and temporal boundaries: here, transfers from SNH (McCauley et al., 2018). With the IP scenario, CBC in organic fields may also have benefitted from a greater distance to conventional fields and from clustering of organic fields and SNH, as chemical pesticide use in conventional fields was modeled to kill most of the pests with strong side-effect on predators, drying both pest and predator populations in their surroundings through a sink effect. Clusters of conventional fields were more preserved from pests by the IP scenario, meaning that conventional fields benefitted from the protection of pesticides used in neighbor fields (the “chemical umbrella” effect) and that organic fields, a potential source of pests, were farther away from the conventional fields. A similar benefit of aggregating fields was found by Edwards et al. (2018) who simulated pest and predator dynamics in annual crops. Grouping annual crops could limit the abundance of dispersal limited pests because pests had to move over longer distances to reach new crop patches and reach central fields and could not build-up populations in the central fields. This best IP scenario is in accordance with the current trend of OF extension mostly happening in areas already rich in OF fields (Gabriel et al., 2009; Marton & Storm, 2021; Sánchez Herrera & Dimitri, 2019; Zollet & Maharjan, 2021).

2.2. Effect of the landscape context on differences between scenarios

In our simulations, landscape configuration had a strong effect with differences in pest density up to two times for a given scenario. The proportion and fragmentation of SNH were generally of similar importance to the difference in the level of CBC between scenarios, although there was a clear decrease associated with the interaction between the two parameters, i.e. the difference between the IP and GP scenarios decreased with higher proportions and fragmentation of SNH. In conventional fields, this amounted mainly to the IP scenario that benefitted slightly from SNH, while SNH did not affect pest density with the GP scenario. In organic fields, IP and GP converged at highest proportion and fragmentation levels, with pest densities of the GP scenario being favored while those of the IP scenario decreased. Interestingly, the IP scenario could bring higher benefits in organic fields in degraded landscapes, while both scenarios brought similar but lower benefits in preserved landscapes. This is consistent with the IP scenario breaking up large clusters of conventional fields, which were less present in landscapes with high proportions and fragmentation of SNH. Consequently, it may be less important to manage the OF expansion scenario in preserved landscapes, while the IP scenario should be favored in degraded landscapes.

2.3. Robustness of the ranking of expansion scenarios

The ranking of OF expansion scenarios appeared robust to both the intensity and specificity of OF systems and the dispersal ability of pests and predators (Supplementary material S2). Varying these parameters did not affect the ranking of spatial expansion scenarios, only their relative differences. For example, intensive OF systems corresponding to intensive pest management (high pest mortality) were characterized by strong control of pest densities, therefore they showed little differences between scenarios. The only clear interaction between OF pest management and expansion scenario was in conventional fields: under extensive OF farming systems, the tendency of the IP scenario towards lower pest densities in conventional fields was reinforced (Supplementary material S2). This is because pest densities were overall higher for extensive OF systems but this did not strongly affect conventional fields, because, by limiting the decrease in CF patch size, the IP scenario resulted in less pest spill-over from organic to conventional fields. Further, dispersal ability had a marginal effect on pest densities (Supplementary material S3). Increasing dispersal tended to increase pest density’s response to landscape configuration (in particular to its fragmentation) in conventional fields, thus increasing differences in pest densities among expansion scenarios.

3. Limits and benefits of the modelling approach

Most mechanistic models of pest control by natural enemies are specific to a biological system and few address landscape scale crop management (reviewed in Alexandridis et al. (2021)). Such models generally comprise numerous parameters and allow deriving conclusions for specific landscape arrangements. Vinatier et al. (2012) for example showed that longer crop rotations reduced the parasitism of oilseed rape pollen beetle by decreasing the spatial and temporal connectivity of the resource for the parasitoid.

In the present study, we chose a mechanistic theoretical model that was based on few ecological processes and a very simplified representation of crop protection practices. Our focus was on comparing spatial scenarios and understanding how these interacted with the landscape patterns. It is recognized that the complexity of processes underlying conservation biological control in landscapes limits the ability of models to represent actual situations. For example, in reality many organisms show complex movement behavior (Gurarie et al., 2016) and interact within complex trophic networks, even in agricultural fields (Macfadyen et al., 2009). Further, while we assumed similar dispersal abilities for the pest and the predator, real species may have different dispersal abilities and thus perceive the landscape at a different grain (Jackson & Fahrig, 2012). Differences among scenarios would, for example, obviously be reduced for long-distance dispersers that would be less affected by landscape structure. We also made strong assumptions about the role of semi-natural habitats for pests and predators, assuming a generalist predator and a crop specialist pest that may survive in semi-natural habitats. Differences among spatial expansion scenarios would, for example, probably have been less if the pest had been able to reproduce in semi-natural habitats and would thus have been less sensitive to the spatial distribution of organic or conventional fields. Interestingly, despite these limitations, our conclusions about the best spatial scenario are consistent with those of the only pest-natural enemy spatially explicit model that, to our knowledge, addressed OF expansion (Bianchi, Ives and Schellhorn, 2013). Using a spatially explicit pest-parasitoid model these authors found that the spatial clustering of organic fields allowed a higher level of biocontrol in organic fields by protecting parasitoids from the detrimental effects of insecticides sprayed in conventional fields. In contrast to our results, however, they reported peaks of pests along OF expansion, possibly because, contrary to our assumptions, the parasitoid was specialized on the pest.

A last limitation of our approach is that results were averaged for organic and conventional fields at the landscape level. This simplification was driven by the large number of simulations to analyze. Aggregating outputs over space, however, may have masked local patterns and possible local peaks in pest densities. In a recent modelling study of a specialist pest and a generalist predator interacting in an heterogeneous agricultural landscape, Zamberletti et al. (2021, 2022) showed for example that semi-natural habitats increased the average landscape scale pest density (by reducing the number of necessary pesticide treatments) but locally reduced peaks of pest populations (Zamberletti et al., 2021, 2022). Further analyses of pest density dynamics at the field level would, thus, be necessary to confirm the better ranking of the IP scenario regarding local CBC and pest densities.

Despite these limitations, our approach set in light processes such as increased spill-over of predators in isolated fields, increased pest management efficiency in large patches of conventional fields and the importance of distance between organic and conventional fields, that help understand consequences of diverse organic farming expansion scenarios. They further highlight that landscape planning appeared most necessary when organic pest management had a low efficiency on pests and in landscapes with low quantities of semi-natural habitats.

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Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Data and code availability

The model used in this study is based on a model developed by Martinet and Roques (2022) that is available on the following public repository: <https://doi.org/10.17605/OSF.IO/Z2QCX>.

The model outputs of the present study, as well as the R scripts used to build graphs and analyse data are available on the Zenodo public repository (Memah et al. 2022): <https://doi.org/10.5281/zenodo.6597282>.

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Supplementary materials

SM1 - Effects of semi-natural habitat fragmentation and OF expansion scenarios on landscape structure

Landscape structure

Increasing semi-natural habitat (SNH) fragmentation (parameter *fr*) resulted in an increase in the number of patches of each habitat type (SNH but also organic farming (OF) and conventional farming (CF)) (Figure S1.1) as well as an increase in edge length among habitat type (Figure S1.2). Patch area and edge length were calculated with R package *landscapemetrics* (Hesselbarth et al. 2019, *Ecography* 42:1648-1657)

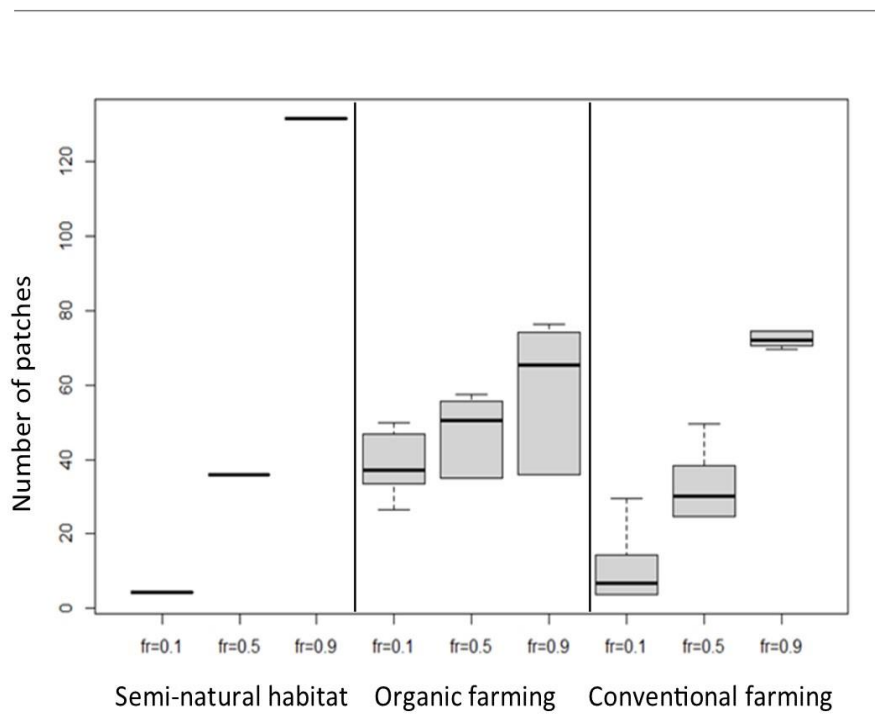


Figure S1.1: Number of patches per landscape and habitat type for the three levels of semi-natural habitat fragmentation *fr*. The graph presents box plots of all values pooled over the 11664 landscapes at the end of simulations of OF expansion (*t*=50) The dark line is the median, whiskers represent the first and third quartiles.

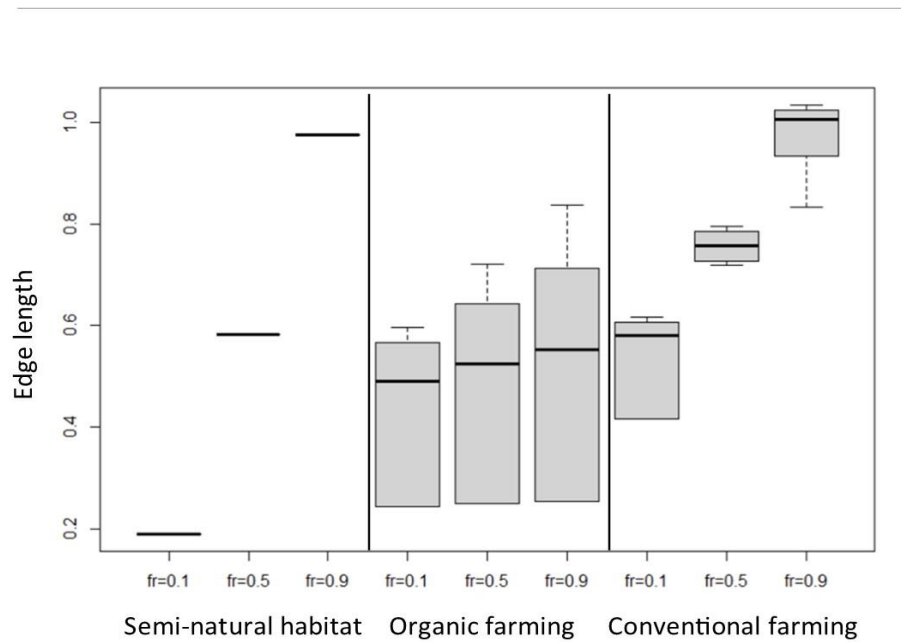


Figure S1.2: Edge length (in pixel side length per pixel) per landscape by habitat type for the three levels of semi-natural habitat fragmentation fr . The graph presents box plots of all values pooled over the 11664 landscapes at the end of simulations of OF expansion ($t=50$). The dark line is the median, whiskers represent the first and third quartiles.

Dynamics of the number and area of organic and conventional patches

As expected, changes in the areas and numbers of organic and conventional patches along organic farming expansion depended on the landscape characteristics (amount of semi-natural habitat and its fragmentation) and on the organic farming expansion scenario. Organic and conventional patches were overall larger and less numerous in landscapes where the amount of semi-natural habitat was small and little fragmented (upper left Fig. S1.3) indicating in particular that the level of semi-natural habitat fragmentation translated to overall landscape fragmentation.

Overall the dynamics of the patch area were driven by two processes. Indeed, the conversion of individual fields from conventional to organic may lead to progressive changes in conventional patch area, either increasing it when converted fields were isolated and/or decreasing it when converted fields were part of a larger patch. In this second situation, the conversion of a single conventional field may occasionally lead to the splitting of a large conventional patch. Such splitting led to large drops in the mean conventional patch area (eg. Fig.S1.3, at 35 years for the GP scenario with $fr=0.1$ and $SNH=10\%$). The symmetrical process of merging organic patches following the conversion of individual fields may create a sudden large increase in mean organic patch area. This last process occurred when the organic share was high enough over the landscape.

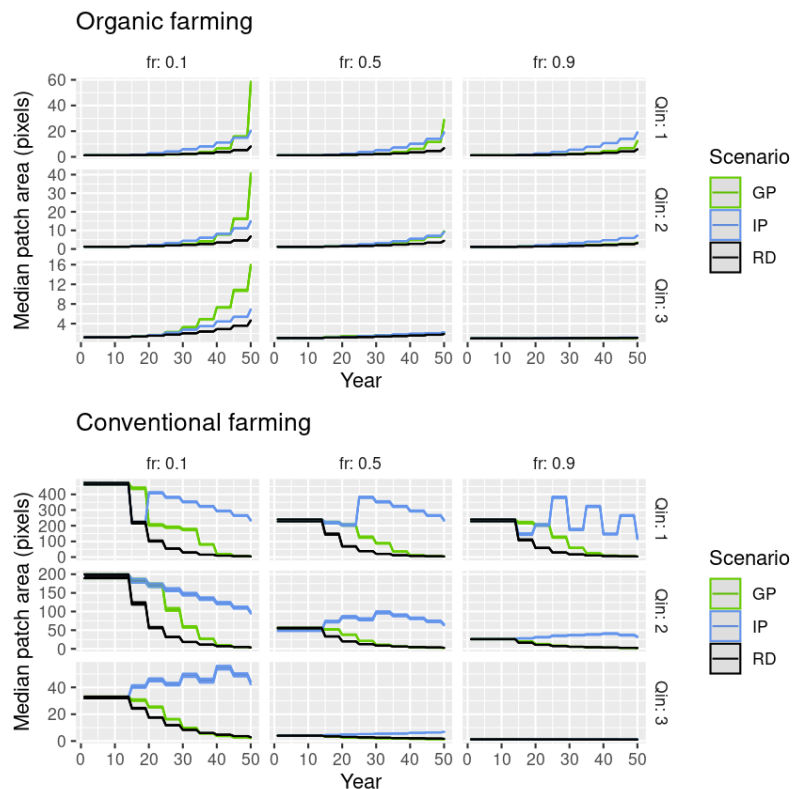


Figure S1.3. Effects of OF expansion scenarios on the area of organic and conventional patches. Landscape change (median patch area in pixels) during the simulations. The envelope around each curve represents the standard error.

Because they set different priorities regarding field conversion, the different scenarios led to different mean patch area dynamics. Constraints were furthermore imposed by the spatial distribution of semi-natural areas. The IP scenario always resulted in conventional patches that were larger than the other scenarios. This is because, when available, conventional fields in the smallest conventional patches were converted to organic which resulted in an initial disappearance of small conventional patches and thus an increase in average conventional patch area. When these small patches were all converted, larger ones started being partially converted to organic, leading to a secondary decrease in conventional patch area (Fig S1.3, after ca. 25 years). These two trends (increase then decrease) were observed in landscapes with both small and large conventional patches initially, i.e. moderately fragmented landscapes with a small to moderate proportion of semi-natural habitat. In little fragmented landscapes with few semi-natural habitats (upper left panel, Fig. S1.3) all conventional patches were large initially so that patch size decreased slowly from the beginning of organic farming expansion. In contrast, in highly fragmented landscapes with a high proportion of semi-natural habitat (lower right panel, Fig. S1.3), there were mostly isolated conventional fields initially so that patch size remained almost constant. The GP scenario, by eroding small parts of large conventional patches at first, slowly and moderately reduced the average conventional patch area. This decrease accelerated in a second step when the erosion incidentally led to the splitting of the still rather large conventional patches into smaller ones. This process was strongest in landscapes with large conventional patches initially, i.e. little fragmented or with a small proportion of semi-natural habitats (left column and upper row panels, Fig. S1.3). Lastly, the RD scenario led to a progressive reduction of conventional patch area by both converting fields located in small patches and reducing the area of large conventional patches.

The effect of organic expansion on the area and number of organic patches was consistent with the above changes to conventional patches. Whatever the expansion scenario, when the landscape was very fragmented and with a large proportion of semi-natural habitat, conversion of conventional fields increased the number of organic fields but not their average area, conventional patches being mostly

composed of single fields (lower right panel, Fig.S1.3). Mean organic patch area increased in all other situations.

Mean organic patch area increased most at first with the IP scenario, particularly when the landscape was a little fragmented (left column, Fig. S1.3) because conventional fields that were converted tended to be neighboring already organic fields. In contrast, with the GP scenario, organic fields first tended to be isolated from other organic fields so that the average patch area increased slowly. However, when the landscape was little fragmented (left column, Fig. S1.3), these small organic patches merged when the proportion of organic farming increased and the average organic patch area increased sharply while the number of patches decreased.

SM2 - Effect of the type of organic farming on pest densities and interaction with expansion scenario

Pests were on average more abundant in both types of fields when organic farming was less intensive, i.e. pest management affected pest population growth less (Table 3) and, to a lesser extent, when it was less specific, i.e. there was a small differential in pest management-induced mortality between predators and pests (Table 3). In organic fields, the intensity of organic farming affected pest abundance far more than specificity, regardless of the amount of semi-natural habitat and its level of fragmentation.

As expected, the effect of organic farming intensity and specificity was much less pronounced in conventional fields. The effect of specificity was very weak. The effect of OF intensity was observable mainly in landscapes that were characterized by a low fragmentation (figure S2) Interestingly, the response of pest density to expansion scenario showed the same pattern whatever the OF type. It was very similar whatever the expansion scenario in organic fields and pest densities were generally lower for the IP scenario in conventional fields.

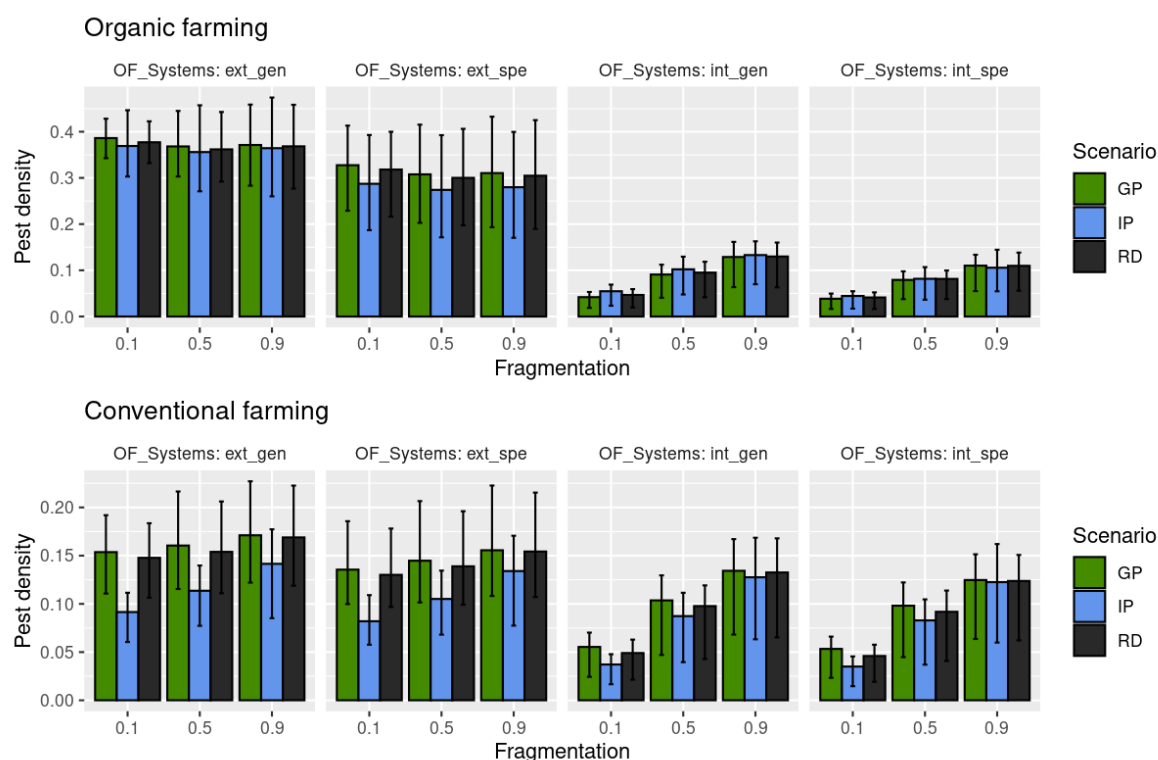


Figure S2. Effects of organic farming expansion scenario, organic farming type and landscape structure on the density of pests in organic and conventional fields. “ext” and “int”: low vs high pest management intensity, respectively. “spe” vs “gen”: specific vs generalist pest management practices, respectively (see Table. 3). Error bars represent standard deviations over landscapes.

The fact that pest management specificity generally had little effect except for the extensive OF systems, confirmed the low effect of predators on pest densities in conventional fields, and the high impact

of pest management compared to CBC in our simulations. For extensive organic systems, organic fields were possibly a source of pests for surrounding fields. Indeed, we observed more pests in conventional fields when organic farming systems were extensive, possibly indicating pest spillover from OF fields with higher pest populations. The latter is supported by the fact that the effect of OF farming system on pest density in CF was reduced in some landscape configurations. Specifically, conventional fields in landscapes with high proportion of SNH were less sensitive to OF farming system intensity, possibly because of lesser proximity to OF sources, and because of higher predator's spillover from SNH.

SM3 - Effect of pests dispersal and SNH fragmentation on pest densities and interaction with OF expansion scenario

Pest dispersal had a lower effect than the other parameters with a maximum delta of ± 0.05 in pest densities (Fig.S3). Pest densities in organic and conventional fields were overall higher when pest dispersal was high but this effect was weak, and mainly observable in conventional fields. In both types of fields, the positive effect of dispersal increased with the level of fragmentation of semi-natural habitats (for example, in conventional fields, for the GP scenario, pest density increased by 0.01 when $fr=0.1$, and by 0.04 when $fr=0.9$ – Fig. S3). There was one exception to this trend with a small decrease in pest density with dispersal. It was observed with the IP scenario in organic fields (from 0.19 to 0.18 for $fr=0.1$, Fig. S3).

The increase in densities with dispersal, fragmentation and their interaction was probably due to a higher ability of pests to avoid CBC-heavy areas (near SNH, which are sources of predators) and to reach resource-rich areas. Globally speaking, dispersal ability amplified the effect of every landscape parameter (fragmentation, expansion scenario).

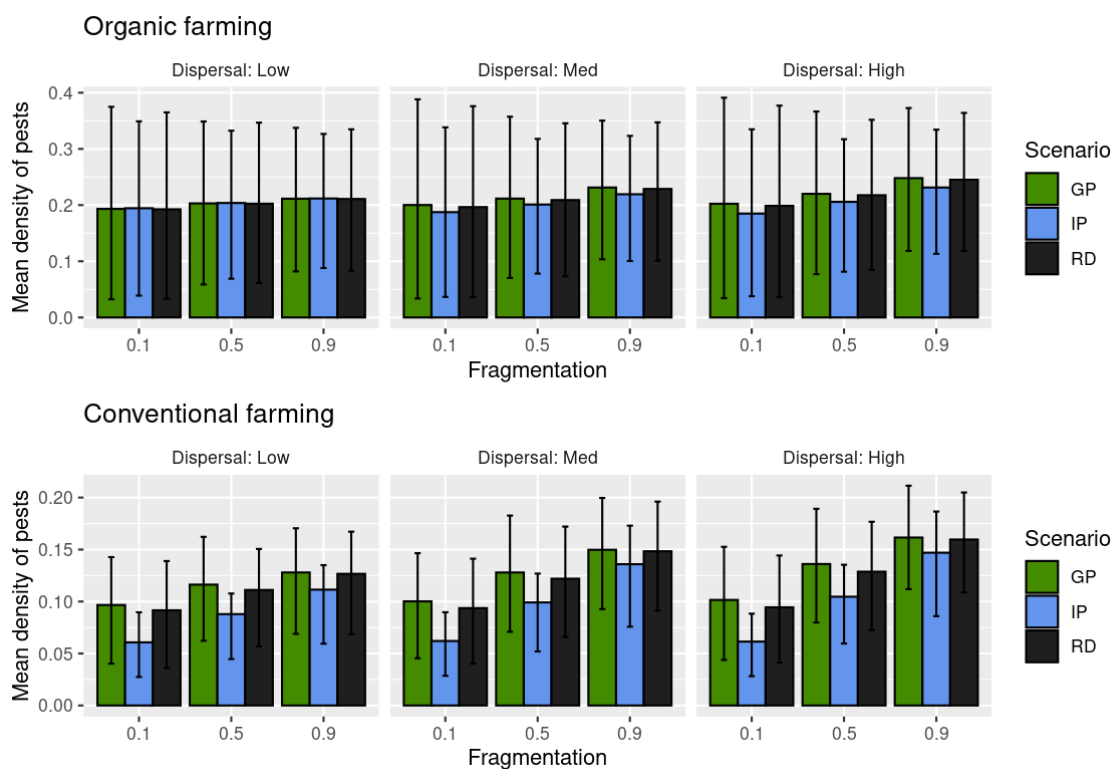


Figure S3. Mean density of pests as a function of pest dispersal, semi-natural habitat fragmentation and organic farming expansion scenario