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An ecological-economic model of land-use decisions, agricultural production, and biocontrol

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Abstract

The regulation of agricultural pests by their natural enemies is a key step in the agroecological transition. The level of biocontrol seems, however, to highly depend on the agronomic and ecological context. It is thus important to identify the conditions under which this ecosystem service is efficient as well as the magnitude of its effects. An actual reduction of pesticide use depends on a change in farmers decisions, calling for the consideration of economic dimensions. We develop a dynamic agroecological-economic model representing land-use and agricultural intensity decisions as well as the dynamics of a crop pest and a natural enemy. Biocontrol is assessed considering both private benefits (increase in farmers' profit) and public benefits (reduction of pesticide use) with respect to a situation without a natural enemy. We provide a theoretical assessment of the magnitude of biocontrol over a wide range of agronomic contexts (spatially explicit maps of agricultural production potential, with heterogeneous distribution and a control of spatial fragmentation) and ecological contexts, described through various parameter values of a reaction-diffusion model. The contexts in which biocontrol plays a significant role are identified, and the role of key parameters discussed. Our open-access model offers a tool to investigate alternative specifications.

Keywords: Biocontrol; Agroecology; Spatial diffusion model; Feedback loop; Pest; Natural enemy

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The intensification of agricultural practices and the simplification of agricultural landscapes have resulted in biodiversity loss in agroecosystems (Benton et al., 2002, 2003) and the reduction of the ecosystem service of natural pest control (Bianchi et al., 2006). In the meanwhile, pest populations have been managed through the use of pesticides, resulting in increased pollution and a social demand to reduce their use. Agroecological approaches, such as a reduction of intensity in croplands and an increased diversity of agricultural landscapes with inclusion of non-crop habitats are presented as a way to foster conservation biocontrol to protect crops (Bianchi et al., 2006). The response of natural enemy populations to landscape diversity is not consistent, however, and does not necessarily result in pest control or reduced damage to crops (Begg et al., 2017; Karp et al., 2018; Shields et al., 2019), limiting the adoption of conservation biocontrol as a pest control strategy.

Is conservation biocontrol an efficient strategy to manage pest? How to assess its potential to protect crops and achieve an actual reduction of pesticide use in different contexts? A larger population of natural enemy may not result in the effective biocontrol of a pest, as the actual ecosystem service will depend on the population of predators, but also on their ability to colonise cropland and to regulate the pest population (Bianchi et al., 2006; Begg et al., 2017). Private and social benefits of biocontrol will also depend on the changes in crop-protection behaviour and the associated reduction in pesticide use, meaning that the issue is not only agroecologic but also economic, with a need to account for farmers' decisions. Management strategies based on conservation biocontrol are more likely to be adopted if they result in effective crop protection and are profitable. Whereas the literature has focused on the identification of the ecological drivers of biocontrol (Perović et al., 2018), few studies consider the actual economic benefit of biocontrol (Shields et al., 2019).

In this paper, we aim at estimating the magnitude of the effect of biocontrol as well as determining some elements of the contexts in which biocontrol could contribute significantly to the management of crop pests. For this purpose, we develop a dynamic agroecological-economic model representing land-use and agricultural intensity decisions as well as the ecological dynamics of a crop pest and a natural enemy. Annual farmers' decisions are driven by profit maximization, accounting for local pest pressure, resulting in a dynamic landscape. Comparing a situation with and without a natural enemy, the biocontrol ecosystem service is assessed at the landscape level through (time-average) profit variation to account for private benefits, and pesticide use reduction to account for social benefits.

One aspect common to most models of interacting species is that the results strongly depend on the parameters, whether these parameters are related to the landscape (Bolker et al., 2003; Roques and Chekroun, 2010) or to biotic interactions (Roques and Chekroun, 2011). As a result, the question of the efficiency of biocontrol requires testing a large number of sets of admissible parameters, and the answer will not be unique but rather give ranges of variation and trends. We thus consider a range of agronomic contexts, described as spatially explicit maps of agricultural production potential, with heterogeneous distribution and spatial configuration, as well as a range of ecological contexts, described through various parameter values of a reaction-diffusion model.

Several research articles studied the drivers of biocontrol, either in terms of landscape composition and the spatial distribution of non-crop habitats (Bianchi et al., 2006), or by considering crop-protection practices (e.g., interactions between pest management in organic and conventional farming systems within a landscape-scale model of parasitoïd-host interactions Bianchi et al. (2013)). These landscape drivers interact with ecological drivers such as dispersal abilities or the degree of specialisation of the natural enemy (Bianchi et al., 2006), creating environmental filters that can influence natural enemy communities and the level of biocontrol through the selection of traits (Perović et al., 2018). These interactions can occur at the local (field and field-edges) and global (landscape) scales (Begg et al., 2017). Few studies, however, address the trade-off with production or the economic valuation of the biocontrol ecosystem service (Karp et al., 2018), suggesting that research should focus on the link between landscape composition and reduced damage, increased yield, and improved profit. The economic value of biocontrol can be assessed at the individual level, estimating the private costs and benefits for a farmer, at a landscape level, accounting for the costs and benefits of a group of farmers whose outcome depends on the interactions among individual decisions influencing (mobile) pest and natural enemy, or at the global level, accounting for the social costs and benefits of crop protection (Naranjo et al., 2015).

Our modelling approach makes it possible to provide an economic value of the biocontrol service at all these scales. Modelling farmers' decisions and their economic and ecological drivers, we can analyse the complex interactions within agroecological-economic systems, accounting for ecological feedback on farmers land use and agricultural intensity decisions. Our model is relatively simple, still, and focuses on stylised patterns, mainly representing ecological traits (Perović et al., 2018), allowing us to illuminate core dynamic interactions and identify key drivers (Müller et al., 2014; Sun et al., 2016). It offers results that complete approaches based on data and statistical analysis to assess pest and natural enemy abundance, predating rates and crop damages as a function of landscape composition (Karp et al., 2018). Other spatially explicit mechanistic simulation models have been designed to study biocontrol in agricultural landscapes but, following the landscape ecology approach (Wiens et al., 1993), the landscape was generally a given of the agroecological models, thereby neglecting endogenous landscape dynamics based on individual farmers decisions accounting for economic aspects and ecological feedback loops (Bianchi et al., 2013). As emphasised by Poggi et al. (2018), an important challenge is to develop feedback models that incorporate spatio-temporal interactions between landscape, ecological processes and stakeholder decisions. Despite their importance, such models, which have proved useful for studying conservation policies (Malawska and Topping, 2018), the evolution of resistance to pesticides (Stratonovitch et al., 2014) and ecosystem services provision (Drechsler, 2020), are still rare.

1. Materials and Methods

1.1. Model overview

We propose a global spatio-temporal model including the simulation of the soil quality map, the integrated simulation of pest and natural enemy dynamics and of agricultural land-use decisions. It accounts for feedback loops between ecological and economic compartments. The stochastic soil quality map model allows the generation of a large number of scenarios, with precise control of average quality and spatial auto-correlation (or, on the contrary, of fragmentation). The ecological part of the model describes the dynamics of a population of crop pest and of their natural enemy, which depend on land uses and pesticide application. The economic part of the model describes farmers' land use and production decisions, i.e., (i) how they allocate land to crop production, or leave it as a non-crop habitat (NCH), e.g., grassland, meadow, or set aside; (ii) how they optimise the use of fertilisers on crops; and (iii) how they define the degree of pest control through pesticide use. These decisions depend on agronomic conditions (encompassed in a local soil quality index), economic conditions (including production price for agricultural outputs, as well as inputs and production costs), and ecological conditions resulting from the presence of pest and their natural enemy. The model computes various indicators to assess the local (at the field level) and regional (at the landscape level) agronomic, economic and environmental performances, at each time. In particular, it makes it possible to provide a theoretical assessment of the magnitude of biocontrol.

1.2. Agronomic context: a stochastic soil quality map model

The model represents an agricultural landscape composed of different plots that each can be used either as a cropland or as a NCH. This landscape is represented on a lattice Ω of dimension $n \times n$, which makes it possible to apply the model to raster data. Each cell $\mathbf{x} = (i, j) \in [1 : n]^2$ represents one hectare, and is characterised by a single quality parameter

$Q(\mathbf{x})$, which represents the potential yield of the plot if used as a cropland, i.e., the maximal yield that could be reached when there is no limiting factor (e.g., with maximal fertilisation) and in the absence of pest damages. This quality parameter takes value in a range that may depend on the studied region and related crop type. We consider the values $Q_{\min} = 0$ an $Q_{\max} = 12$ (tons per hectare), which correspond to realistic minimal and maximal yields for cereal crops in temperate regions (Martinet, 2013). Soil quality can be more or less correlated across space. A given agronomic context can thus be described by a distribution of soil quality within the range $[Q_{\min}; Q_{\max}]$ along with a parameter describing the spatial auto-correlation.

To analyse contrasted cases, we generate random virtual maps based on random soil quality distributions (truncated normal distributions characterised by different mean and variance values) and spatial auto-correlation levels. Each generated map corresponds to a virtual agricultural region of more or less good quality, more or less heterogeneous, and with more of less spatial auto-correlation. This allows us to study a diversity of agronomic contexts, and the effect of landscape configuration on the performance of agroecological systems. More precisely, to build a quality map $Q(\mathbf{x})$ defined on the lattice Ω, we proceed in two steps.

Step 1: Generation of the values in Q. We begin by drawing n^2 values in a truncated normal distribution, within $[Q_{\min}; Q_{\max}]$. This distribution has two parameters. The first parameter is the mode of the distribution (the mean value of the Gaussian before truncation) $\overline{q}$. Higher values correspond here to regions with a higher agricultural potential. The second parameter is the standard deviation s_q. Higher values of this parameter mean more variable soil qualities. This generates a vector Q^* of n^2 values in $[Q_{\min}; Q_{\max}]$ with no a priori on the spatial distribution of these values.

Step 2: Spatial arrangement of the quality map $Q(\mathbf{x})$. In a second step, we use a stochastic model to build spatial arrangements of these quality distributions. Our approach is an extension of the neutral landscape generator MULTILAND (Roques, 2015) intended to theoretical studies on the effect of landscape structure in applied sciences (see also Gaucherel et al., 2014, for a review on landscape modelling approaches). We consider that the lattice Ω is equipped with a 4-neighbourhood system with periodic conditions. In other terms, the domain is considered wrapped on a torus. We denote by $V_{\mathbf{x}}$ the set containing the four neighbours $(i+1, j)$, $(i-1, j)$, $(i, j+1)$ and $(i, j-1)$ of $\mathbf{x} = (i, j)$. Given any spatial arrangement Q of the n^2 values in Q^*, we define the statistic

$$S(Q) = \frac{C}{4} \sum_{\mathbf{x}\in\Omega,\ \mathbf{y}\in V_{\mathbf{x}}} |Q(\mathbf{x}) - Q(\mathbf{y})|, \tag{1}$$

for a given positive constant C ($C = 10$ in our simulations). The statistic $S(Q)$ is directly linked to the soil quality fragmentation. Large values of $S(Q)$ indicate that neighbours tend to be different (higher fragmentation), while low values indicate that neighbours tend to resemble each other (low fragmentation). The landscape model is based on the Gibbs measure P, defined over all the possible arrangements of the values in Q^*:

$$P(X = Q) = \frac{1}{Z} e^{f\,S(Q)} \text{ with the partition function } Z = \sum_{\tilde{Q} \text{ with values in } Q^*} e^{f\,S(\tilde{Q})}. \tag{2}$$

When f increases, the proposed landscape model favours higher values of $S(Q)$, i.e., higher fragmentation: given two arrangements Q_1 and Q_2 of the values in Q^*, with $S(Q_1) > S(Q_2)$,

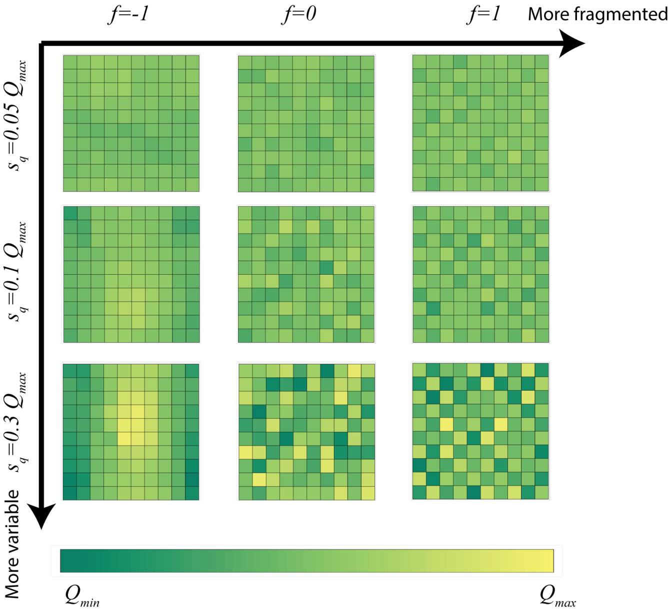


Figure 1: **Soil quality maps simulated with varying values of the fragmentation and variability parameters.**

the relative probability $P(X = Q_1)/P(X = Q_2) = \exp[f(S(Q_1) - S(Q_2))]$ becomes larger as the parameter f is increased. Hence, $f \in \mathbb{R}$ directly controls the topology of the landscape patterns. We refer to it as the *fragmentation parameter*. Typically, negative values of f lead to aggregated maps and positive values lead to fragmented quality maps. We give several examples of quality maps generated with this model in Fig. 1.

1.3. Ecological compartment: a lattice dynamical system with spatial diffusion

We use a lattice dynamical system to describe the intra-annual spatio-temporal dynamics of a pest together with their natural enemy over the landscape Ω, i.e., the finite grid of dimension $n \times n$. Lattice dynamical systems are the discrete-space counterparts of reaction-diffusion models, which are themselves among the most popular models to describe the spatio-temporal dynamics of interacting species in heterogeneous environments (e.g. Shigesada and Kawasaki, 1997; Turchin, 1998; Murray, 2002; Cantrell and Cosner, 2003; Roques, 2013, for reference textbooks). Here, we do not need to describe the spatial dynamics of the species *within* each cell of the map which would be unnecessarily time-consuming for our purpose, hence the use of a discrete-space model adapted to the lattice Ω.

We denote by τ the time since the beginning of the simulation. The (continous) time τ is expressed in years. We also define a discrete year index $t \in \mathbb{N}$ by $t = \lfloor \tau \rfloor$ ($\lfloor \cdot \rfloor$ being the floor function).

We denote by $P_\tau(\mathbf{x})$ the pest density at time τ and in the cell $\mathbf{x}$ and by $N_\tau(\mathbf{x})$ the density of natural enemy. The lattice dynamical system governing the species dynamics and their interactions is

$$\begin{cases} P'_\tau(\mathbf{x}) = & D_P \mathcal{D}[P_\tau(\mathbf{x})] & +g_P(\tau,\mathbf{x},P_\tau(\mathbf{x})) & -\alpha\, P_\tau(\mathbf{x}) N_\tau(\mathbf{x}) & -\varphi_\tau(\mathbf{x}) P_\tau(\mathbf{x}), \\ N'_\tau(\mathbf{x}) = & \underbrace{D_N \mathcal{D}[N_\tau(\mathbf{x})]}_{dispersal} & +\underbrace{g_N(\mathbf{x},N_\tau(\mathbf{x}))}_{growth} & +\underbrace{\alpha\, P_\tau(\mathbf{x}) N_\tau(\mathbf{x})}_{interactions} & -\underbrace{\varphi_\tau(\mathbf{x}) N_\tau(\mathbf{x})}_{pesticide}. \end{cases} \tag{3}$$

Here, the sign ($'$) denotes the derivative with respect to time. We now detail the components of these equations.

Dispersal. We describe the movements of the individuals with a discrete Laplace operator (discrete-space counterpart of the standard Laplace diffusion), corresponding to uncorrelated random walk movements of the individuals over the lattice Ω. For $\mathbf{x} = (i, j)$ and any function $U(\mathbf{x}) = U(i, j)$ defined over the lattice Ω,

$$\mathcal{D}[U(i,j)] = \frac{U(i+1,j) + U(i-1,j) + U(i,j+1) + U(i,j-1) - 4\,U(i,j)}{\delta_x^2}, \tag{4}$$

with $\delta_x = L/n$, L the width of the study site fixed here at $L = 1$ (without loss of generality, up to a scaling in the space variable). The diffusion coefficients D_P and D_N respectively measure the mobility of the pest and of its natural enemy. We assume periodic conditions at the boundary of the lattice, meaning that the study site is embedded in a larger periodic landscape with the same species dynamics over each period cell.

Growth. The functions g_P and g_N describe the growth (or decline) of the pest and natural enemy populations, in the absence of interactions between these two species and of pesticide treatments. Regarding the pest dynamics, we assume that the growth is zero during the first half of the year, corresponding to the months following the harvest, which occurs at each discrete time $t \in \mathbb{N}$.

During the second half of the year, we assume a standard logistic growth, with parameters which depend on the land use and on the quality parameter at the current position $\mathbf{x}$:

$$g_P(\tau,\mathbf{x},P_\tau(\mathbf{x})) = \begin{cases} 0 & \text{if } \tau \in [t, t+1/2) \\ R_{P,\tau}(\mathbf{x}) P_\tau(\mathbf{x}) \left(1 - \frac{P_\tau(\mathbf{x})}{Q(\mathbf{x})}\right) & \text{if } \tau \in [t+1/2, t+1) \end{cases} \tag{5}$$

The intrinsic growth rate $R_{P,\tau}(\mathbf{x})$ takes a positive value ($R_{P,\tau}(\mathbf{x}) = r_P > 0$) over cultivated cells and is nil ($R_{P,\tau}(\mathbf{x}) = 0$) over NCH. It therefore depends on the current land use in the cell $\mathbf{x}$ at time τ. On cultivated cells, and during the second half of the year, we make the assumption that the maximum number of pests that can be reached in a cell $\mathbf{x}$ before saturation is proportional to the potential yield $Q(\mathbf{x})$. This makes sense as the potential yield $Q(\mathbf{x})$ was precisely defined as the maximal yield that could be reached in the absence of pest (and without other limiting factors). Up to a scaling factor, meaning here that we change the unit in which the pest population is measured, the carrying capacity for the pest is simply $Q(\mathbf{x})$.

Regarding the natural enemy dynamics, we assume that the natural enemy do not reproduce on crops. Their dynamics are thus driven by death only, with a rate $1/\gamma$, γ being the natural enemy life expectancy. On NCH, we assume a logistic growth with intrinsic growth rate $r_N > 0$. Up to a renormalization (the population of natural enemy is expressed in proportion of the carrying capacity), the carrying capacity is fixed at 1. Overall, we thus assume the following form for the function g_N:

$$g_N(\mathbf{x}, N_\tau(\mathbf{x})) = \begin{cases} -N_\tau(\mathbf{x})/\gamma \text{ on crops,} \\ r_N N_\tau(\mathbf{x})\,(1 - N_\tau(\mathbf{x})) \text{ on NCH.} \end{cases} \tag{6}$$

Interactions. We assume standard Lotka-Volterra interactions between the pest population and its natural enemy, which means that the pest death rate increases linearly with the density of natural enemy, and conversely the growth rate of the natural enemy increases linearly with the pest population density. For simplicity, we assume a 'one-to-one' relationship i.e., the population of natural enemy is increased by one unit when one unit of pest population is consumed, with a same interaction factor α summarising predation efficiency.

Pesticide effects. We assume that pesticide treatments increase the death rate of both species in the same way. Again, this is a simplifying assumption: it is known that the natural enemies are often sensitive to pesticides (Potter and Held, 2002), but the impact on the death rate may not be identical for the two species. The term $\varphi_\tau(\mathbf{x})$ takes the value 0 in the absence of treatment (NCH and non-treated crops). On treated crops, we assume a baseline mortality rate $\varphi_\tau(\mathbf{x}) = \rho > 0$ on slightly treated crops, which is doubled in highly treated crops: $\varphi_\tau(\mathbf{x}) = 2\,\rho$.

A fundamental issue is to determine as realistic as possible values for the parameters D_P, D_N, r_P, r_N, γ, ρ and α. Of course, they depend on the considered species and pesticide. In Supplementary Material SI 1, we determine reasonable orders of magnitude, with simplified models where each mechanism is considered independently. The corresponding values are summarised in Table 1.

1.4. Economic decision model

The economic part of the model is a dynamic Multi-Agent Model (cellular automaton) in discrete time. It determines, for each time period $[t, t+1)$, local land use and agricultural practices according to an optimisation pattern.

Each cell of the lattice can be allocated either to a representative crop or to NCH. These two uses generate different returns, reduced by set up costs when applicable. We consider asymmetric land-use change costs $\mathcal{C}$, with a higher cost to set up a NCH with ecological benefits (sewing and management costs) than to overturn it (tillage and herbicide use), i.e., $\mathcal{C}_{C\to NCH} > \mathcal{C}_{NCH\to C} > 0$.

All economic values are expressed per hectare (ha), to avoid scale effects. We thus implicitly assume constant return to scale on all fixed production factors (labor, capital, etc.) other than land. There are decreasing returns to scale on land, due to the heterogeneous soil quality (Martinet, 2013)

Farmers rationality, anticipations, and decisions. We assume that the decisions in each cell mimics a rational farmer maximising profit. To represent the fact that crop protection through the use of pesticide is more a discrete decision regarding the frequency of treatments than a decision on a treatment quantity over a continuous range, we consider three possible levels of treatment: no treatment at all, an average-treatment level, and a high-treatment level. In terms of calibration, we inspire our parameter values from the Treatment Frequency Index

(TFI) for main field crops en France (AGRESTE, 2019), considering a moderate level of treatment at 3 unit-dose per ha and per year, and a high level at 6 unit-dose per ha and per year. As a consequence of this modelling choice, at the beginning of the period (representing a cultivation year), the farmer has four options corresponding to land-use and crop protection combinations, i.e., NCH, untreated cropland, moderately-treated cropland, and highly-treated cropland. For each of these options, optimal fertiliser application can be determined and an anticipated profit computed (see the details below). Then, the farmer selects the optimal use of the plot by choosing the profit-maximising option. The model thus determines the land use and pesticide application for all plots (or equivalently, cells), offering a starting point for the modelling of the ecological annual dynamics.

Such a local decision pattern relies on an anticipation of local pest population and associated damages under the four potential land-use and pest-control options. This anticipated local pest population is denoted by $\tilde{P}_{t+1}(\mathbf{x})$. This is the population accounted for in profit maximisation and land-use decisions. The local population will depend on the ecological dynamics of pest and natural enemy populations in the landscape, and thus not only on local decisions. Anticipating this population in practice would be a very difficult task for two reasons. First, it would require to know in advance the exact composition and structure of the landscape, which would result from the separate choices of all farmers. Second, it would require to have perfect knowledge of ecological populations' size across the whole landscape and of ecological spatial dynamics. To avoid heroic assumptions on farmers' ability to foresee these dynamics, we assume that the farmer accounts only for local pest growth given initial pest population in the field, without accounting for future predation and diffusion. This means that biocontrol has an ex post effect, through past predation and a lower pest population, but is not accounted for ex ante. This assumption also implies that the anticipation does not depend on other farmers' decisions, allowing us to abstract from game-strategic considerations arising from simultaneous decisions among interacting agents (Costello et al., 2017). Overall, this means that $\tilde{P}_{t+1}(\mathbf{x})$ is the solution at time $t+1$ of the simplified model:

$$\tilde{P}'_\tau(\mathbf{x}) = g_P(\tau, \mathbf{x}, \tilde{P}_\tau(\mathbf{x})) \text{ with initial condition } \tilde{P}_t(\mathbf{x}) = P_t(\mathbf{x}).$$

Return on cropland. The return on cropland depends on local yield $Y_t(\mathbf{x})$, crop price p, input costs for fertilisers (λ_ϕ) and pesticides (λ_φ), fixed costs ν and potential conversion costs $\mathcal{C}_{NCH \to C}$ if the plot was used as a NCH at the previous time period. We assume that the representative crop price is constant across time, but global market effects could be included, for example by modelling price fluctuation with a dynamic system of auto-correlated prices with exogenous random shocks, and assuming that farmers have rational anticipations, as in (Barraquand and Martinet, 2011).

Cropland profit thus reads

$$\pi_t^C(\mathbf{x}) = p\, Y_t(\mathbf{x}) - \lambda_\phi \phi_t(\mathbf{x}) - \lambda_\varphi \varphi_t(\mathbf{x}) - \nu - \mathbf{1}_{NCH \to C} \mathcal{C}_{NCH \to C} \tag{7}$$

Crop yield and pest damages. Croplands have a yield $Y_t(\mathbf{x})$ which is heterogeneous across space, depending on the local soil quality $Q(\mathbf{x})$, but also on the use of fertilisers $\phi_t(\mathbf{x})$ and on damages L from pests (yield loss) depending on local pest population $P_{t+1}(\mathbf{x})$ at the harvest time $t+1$ (end of the economic year $[t, t+1)$). As the pest population is mobile, these damages depend both on local decisions (pesticide use) but also on land uses and pesticide use across the whole landscape, as well as on the presence of a natural enemy.

To model agricultural production, we consider a yield function of the 'Mitscherlich-Baule' type (Llewelyn and Featherstone, 1997; Kastens et al., 2003; Frank et al., 1990) augmented of pest damages:

$$Y_t(\mathbf{x}) = Q(\mathbf{x}) \left(1 - c_1 e^{-c_2 \phi_t(\mathbf{x})}\right) \left(1 - L\left(\mathbf{x}, P_{t+1}(\mathbf{x})\right)\right). \tag{8}$$

The parameter c_1 represents the share of potential yield linked to fertilisation, and the parameter c_2 determines the marginal effect of fertilisation on yield. These two parameters are exogenous and depend on the crop-type. Farmers determine the optimal level of fertiliser to be applied in any treatment option by maximising profit with respect to the decision variable ϕ given anticipated pest populations $\tilde{P}_{t+1}(\mathbf{x})$. Given the equations for yield and profit, standard conditions leads to the optimal value

$$\phi_t(\mathbf{x}) = \frac{-1}{c_2} ln \left(\frac{\lambda_\phi}{p c_1 c_2 Q(\mathbf{x}) \left(1 - L(\mathbf{x}, \tilde{P}_{t+1}(\mathbf{x}))\right)} \right). \tag{9}$$

The term $L(\mathbf{x}, P_{t+1}(\mathbf{x}))$ corresponds to the production loss due to pest damage, which we assume to depend on the local pest population at the end of the period, i.e., at the harvest time. Other assumptions could have been considered as well, depending on the type of pest, for instance the production loss may depend on the cumulated number of pests during the cultivation period. Several damage functions have been proposed in the literature. For example, Mitchell (2001) uses the functional form $\frac{aP}{1+bP}$, in which the parameters a and b are related to the virulence of the pest. The limit of this type of damage function is that it does take the link between the production level and the carrying capacity of the pest in the plot into account, and how this link affects the damage level. Assuming that the carrying capacity of the pest is proportional to the production level, and that this carrying capacity is reached when damages are maximal (full crop destruction), we assume here that damages are proportional to the density of the pest, i.e.,

$$L(\mathbf{x}, P_{t+1}(\mathbf{x})) = P_{t+1}(\mathbf{x})/Q(\mathbf{x}),$$

where we recall that the carrying capacity of the pest is proportional to the production level, and that this carrying capacity is reached when damages are maximal (full crop destruction), leading to $L(\mathbf{x}, P_{t+1}(\mathbf{x})) = 1$ when $P_{t+1}(\mathbf{x}) = Q(\mathbf{x})$. With this representation of damages, pest virulence is directly linked to the pest growth rate over the cultural period. Note that the level of pesticide use does not appear explicitly in the expression, but affects yield indirectly through the local pest density reduction, and thus reduces losses.

Return on NCH. NCH generate a return s_{NCH} (e.g., an agroenvironmental subsidy), so that the profit for this land use is

$$\pi_t^{NCH}(\mathbf{x}) = s_{NCH} - \mathbf{1}_{C \to NCH} \mathcal{C}_{C \to NCH} \tag{10}$$

where $\mathbf{1}_{C \to NCH}$ is equal to 1 if the plot was a cropland at time $t-1$, and 0 otherwise. This return does not depend on soil quality, nor on the pest population.

1.5. Parameter values and simulation plan

Our simulations aim at assessing the performance of different agricultural landscapes, and the way it is influenced by biocontrol. For this purpose, we consider different contexts. The agronomic context is described by three parameters: the mean soil quality, its variation, and the fragmentation index. The ecological context is described by six parameters: the pest diffusion coefficient, the natural enemy diffusion coefficient, the pest growth rate, the natural enemy growth rate, the natural enemy life expectancy in a crop, and the predation rate. The economic context only varies with respect to the efficiency of pesticide, i.e., the induced mortality rate. We explain how the model can be used with varying economic contexts in the discussion.

We detail in Table 1 the full list of parameters of the whole agronomic-ecological-economic model.

We considered a relatively large number of reasonable contexts: 27 agronomic contexts × 48 ecological contexts × 3 levels of pesticide-induced mortality rate. This led to 3 888 contexts.

Though the ecological and economic compartments are deterministic, the overall model is stochastic due to the soil quality map part. For each set of parameter values $(\overline{q}, s_q, f)$ we generated 8 quality maps Q. For each map, we simulate the economically-driven landscape in the absence of pest, and what happens when the pest is introduced. The idea is to assess the resilience of the landscape to the pest invasion, given the population of natural enemy in the landscape. For each simulation, we initialised the ecological model by assuming that the density of natural enemy was 1 (i.e., equal to the carrying capacity) in the NCH. In an attempt to reduce the effect of this initial choice, we let the system evolve without pest during 3 years. Then, the pest was introduced at the end of the third year, at a density $0.2\,Q(\mathbf{x})$ (20% of the carrying capacity) and the model was simulated over $T = 10$ additional years.

Altogether, as we generated 8 repetitions for each of the 27 agronomic contexts and simulated the ecological-economic model for each set of parameters, we ran 31 104 simulations, a quarter of which corresponds to the absence of natural enemy (when the predation rate is zero).

1.6. Performance indicators

To assess the performance of the agricultural landscape in the different scenarios, we define the mean profit (denoted by π) and the mean TFI (denoted by TFI) for pesticide use, both expressed per ha and per year. These two quantities represent two important outcomes for society, the value of agricultural production and the level of chemical pollution by pesticides. They are defined as mean values over space and time. Spatial average makes it possible to account for the dual effect of NCH, that reduce the cultivated area but contribute to crop protection by supporting biocontrol. Temporal average smooths temporal fluctuations. The indicators are computed from the introduction of the pest in the landscape to the simulation horizon, corresponding to T years ($T = 10$ in our simulations).

$$\pi = \frac{1}{T}\sum_{t=1}^{T}\frac{1}{n^2}\sum_{\mathbf{x}\in\Omega}\pi_t(\mathbf{x}) \text{ and } \mathrm{TFI} = \frac{1}{T}\sum_{t=1}^{T}\frac{1}{n^2}\sum_{\mathbf{x}\in\Omega}\mathrm{TFI}_t(\mathbf{x}), \tag{11}$$

where $\pi_t(\mathbf{x})$ and $\mathrm{TFI}_t(\mathbf{x})$ depend on the land use. In particular $\mathrm{TFI}_t(\mathbf{x}) = 0$ in NCH and non-treated crops, $\mathrm{TFI}_t(\mathbf{x}) = 3$ units in moderately-treated crops, and $\mathrm{TFI}_t(\mathbf{x}) = 6$ units in highly-treated crops.

Notation	Description	Values	Unit	Source
$\overline{q}$	Mode of the soil quality distrib.	$Q_{\max} \times \{0.3, 0.5, 0.7\}$	$\text{ton} \cdot \text{ha}^{-1}$	
s_q	Std. dev. of the soil quality distrib.	$Q_{\max} \times \{0.05, 0.1, 0.3\}$	$\text{ton} \cdot \text{ha}^{-1}$	
f	Fragmentation parameter	$\{-1, 0, 1\}$	dimensionless	
D_P	Pest diffusion coeff.	$\frac{1}{n^2} \times \{0.1, 1\}$	$\text{km}^2 \cdot \text{year}^{-1}$	Supplementary Material SI 1
D_N	Natural enemy diffusion coeff.	$\frac{1}{n^2} \times \{0.1, 1\}$	$\text{km}^2 \cdot \text{year}^{-1}$	Supplementary Material SI 1
r_P	Pest growth rate	$\{\ln(4), \ln(10^2), \ln(10^4)\}$	year^{-1}	Supplementary Material SI 1
r_N	Natural enemy growth rate	$\ln(2)$	year^{-1}	Supplementary Material SI 1
γ	Life expectancy of N in a crop	1/2	year	Supplementary Material SI 1 and Lövei and Sunderland (1996)
α	$P - N$ interaction term	$\{0, 1/3, 5/6, 4/3\}$	$N^{-1} \cdot \text{year}^{-1}$ or $P^{-1} \cdot \text{year}^{-1}$	Supplementary Material SI 1
ρ	baseline pesticide-induced mortality rate	$\{\ln(4), \ln(10^2), \ln(10^4)\}$	year^{-1}	Supplementary Material SI 1
$\mathcal{C}_{C \to NCH}$	NCH set up cost	219.4	$\text{Euros} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$	Miao et al. (2013)
$\mathcal{C}_{NCH \to C}$	Cropland set up cost	27.4	$\text{Euros} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$	Miao et al. (2013)
s_{NCH}	return on NCH	300	$\text{Euros.ha}^{-1} \cdot \text{year}^{-1}$	value inspired from MAEC subsidies
c_1	share of potential yield depending on fertilisation	0.38	none	Monod et al. (2002)
c_2	marginal effect of fertilisation on yield	0.015	$\text{ha} \cdot \text{kg}^{-1}$	Monod et al. (2002)
p	agricultural output price	150	$\text{Euros} \cdot \text{ton}^{-1}$	value inspired from Agreste data for main field crops
λ_ϕ	fertiliser cost	1.62	$\text{Euros} \cdot \text{kg}^{-1}$	computed from AGRESTE data for a mix (N,K,P)=(3,1,1)
λ_φ	pesticide cost	33	$\text{Euros} \cdot \text{IFT}^{-1}$	Butault et al. (2010)
ν	cropland fix costs	110	$\text{Euros} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$	computed from AGRESTE data (seeds, insurances, fuel).

Table 1: Summary of the main notations and parameter values

For scenarios with no predation ($\alpha = 0$, or equivalently $N = 0$), which correspond to an absence of biocontrol, we denote these quantities by π^0 and TFI^0. They are used as a benchmark to assess the effect of biocontrol.

Given these mean profit and TFI, for each simulation scenario, we are able to compute two indicators related to biocontrol. Our first indicator measures the profit gain in the presence of biocontrol compared to the absence of biocontrol:

$$\Delta\pi = \pi - \pi^0. \tag{12}$$

Our second indicator measures the reduction in TFI in the presence of biocontrol compared to the absence of biocontrol:

$$\Delta\mathrm{TFI} = \mathrm{TFI}^0 - \mathrm{TFI}. \tag{13}$$

These two indicators represent the social benefits of the biological ecosystem services, composed of an economic gain on agricultural production and a reduced pollution due to pesticide savings. Note that they are defined such that positive values correspond to a benefit.

2. Results

Global effects of biocontrol. We depict in Fig. 2 the distributions of the profit gain $\Delta\pi$ and of the reduction in TFI, $\Delta\mathrm{TFI}$, compared to the absence of biocontrol. The mean profit gain is 5.7 euros/ha (corresponding to 1.3% of mean profit) and the 95% interquantile range $(-0.1, 43.6)$. The mean reduction in TFI is $1.2 \cdot 10^{-2}$ units (corresponding to 0.7% of mean TFI) and the 95% interquantile range for reduction in TFI $(-0.4, 0.3)$. The average effect of biocontrol is thus relatively low when parameters are chosen at random within the ranges we explored.

These distributions are computed over the whole simulated dataset. Of course, they can change if we consider a subset of parameters, or if we assume that some parameter values occur with a higher probability. Nevertheless, they give a first global picture of the potential effect of biocontrol. It is then important to identify the ranges of parameters for which biocontrol has an important effect, i.e., the agroecological contexts in which biocontrol would be significant.

Trade-off analysis. We present in Fig. 3 the bivariate distribution of the profit gain and reduction in TFI, again computed over the whole set of parameters.

First, in 6% of the simulations, biocontrol has a significant effect on profit gain (in the following sense: $|\Delta\pi|$ is larger than 5% of the mean profit) and in 25% of the simulations, it has a significant effect on TFI reduction ($|\Delta\mathrm{TFI}|$ is larger than 5% of the mean TFI). Altogether it has a significant effect on at least one of the two dimensions in 26% of the simulations. On the other hand, in 74% of the simulations, biocontrol has no significant effect, neither on profit nor pesticide use reduction.

For simulations in which the effect is significant, we observe two main trends, with a part of the distribution (upper diagonal) corresponding to a simultaneous positive effect of biocontrol on the profit gain and on the reduction in TFI. In this part of the distribution, we note a strong positive correlation between $\Delta\pi$ and $\Delta\mathrm{TFI}$ (Pearson linear correlation coefficient 0.83). Another part of the distribution (lower diagonal, Pearson correlation coefficient -0.45) corresponds to a positive effect of biocontrol on profit gain, but a negative effect on the reduction of TFI (pesticide use is increased with respect to the scenario without biocontrol in this case). Still, among the simulations where we observed a significant effect, two-third of the distribution (66%) lies in the positive quadrant with a positive effect of biocontrol on both dimensions.

We looked for typical parameters that lead to

1. a significant win-win biocontrol, with both large private gains (profits) and large public gains (pesticide use reduction). In that respect, we computed the modal parameter values (most frequent parameter value) corresponding to the top-right region in Fig. 3, corresponding to the 10% highest profit gain ($\Delta\pi > 15$) and 10% highest reduction in TFI ($100 \times \Delta\mathrm{TFI} > 15$). In this window, we obtained the following modal values, for respectively $(\overline{q}, s_q, f, D_P, D_N, r_P, \alpha, \rho)$:

   $$(0.3Q_{\max}, 0.3Q_{\max}, 1, 1/n^2, 0.1/n^2, \ln(4), 4/3, \ln(4)).$$

   This corresponds to areas of relatively low agricultural potential, a highly fragmented and variable landscape, and a poorly efficient pesticide. From an ecological point of view, biocontrol seems to be favoured by a pest that grows relatively slowly and is highly mobile, but a predator relatively less mobile with a high predation rate.
2. a negative or not significant effect of biocontrol. The modal parameter values that lead to these situations (lower 10%): ($\Delta\pi < 0$ and $100 \times \Delta\mathrm{TFI} < -3$) are

   $$(0.3Q_{\max}, 0.1Q_{\max}, -1, 0.1/n^2, 0.1/n^2, \ln(10^2), 5/6, \ln(4)).$$

   This corresponds to a context with species that do not move a lot in a non-fragmented landscape.
3. a paradoxical effect of biocontrol, with private gains (increased profit) but public costs (increased pesticide use). Here, we looked for the modal parameter values that lead to a significant increase of profit gain (10% highest profit gain, i.e., $\Delta\pi > 15$) but a negative decrease in TFI (lower 10%, i.e., $100 \times \Delta\mathrm{TFI} < -3$). We obtained the modal values: $(\overline{q}, s_q, f, D_P, D_N, r_P, \alpha, \rho) = (0.5Q_{\max}, 0.3Q_{\max}, 0, 1/n^2, 1/n^2, \ln(10^2), 4/3, \ln(4))$. This corresponds to highly variable agricultural landscapes, with mobile pest and predators, a high predation rate and a poorly efficient pesticide.

Some trends can be inferred from these parameter values: the win-win situations are characterised by different ecological parameters (higher pest diffusion, lower pest growth rate and higher effect of predation) and a higher fragmentation compared to the case where the effect of biocontrol is not significant. The lower diagonal (case 3.) is rather characterised by the agronomic variables: a paradoxical effect of biocontrol tends to arise with a highly variable soil quality contexts. To get a better understanding of the interplay between these parameters, we conduct some statistical analysis.

Effect of agronomic, ecological and economic parameters on the efficiency of biocontrol. We denote by Θ the vector of parameters $(\overline{q}, s_q, f, D_P, D_N, r_P, \alpha, \rho)$. For each ecological, agronomic and economic parameter θ_i, we define the marginal means associated with the value $\theta_i = y$:

$$\overline{\Delta\pi}_i(y) = \mathrm{mean}_{\Theta\, s.t.\, \theta_i = y}(\Delta\pi(\theta)) \text{ and } \overline{\Delta\mathrm{TFI}}_i(y) = \mathrm{mean}_{\Theta\, s.t.\, \theta_i = y}(\Delta\mathrm{TFI}(\theta)). \qquad (14)$$

We plotted in Fig. 4 the variations of these quantities when y is increased: the lines connect the points $(\overline{\Delta\pi}_i(y) - \overline{\Delta\pi}_i(y_{min}), \overline{\Delta\mathrm{TFI}}_i(y) - \overline{\Delta\mathrm{TFI}}_i(y_{min}))$ when y varies within the range associated with the parameter θ_i. The arrow points toward the direction of variation when y is increased. We thus get a simple summary of the marginal effect of each parameter on biocontrol. Note that a higher effect of biocontrol on a given outcome does not necessarily mean that this outcome will take on higher values when the parameter is increased. For instance, increasing a parameter may decrease the profit gain independently of biocontrol, but it can in parallel increase the effect of biocontrol.

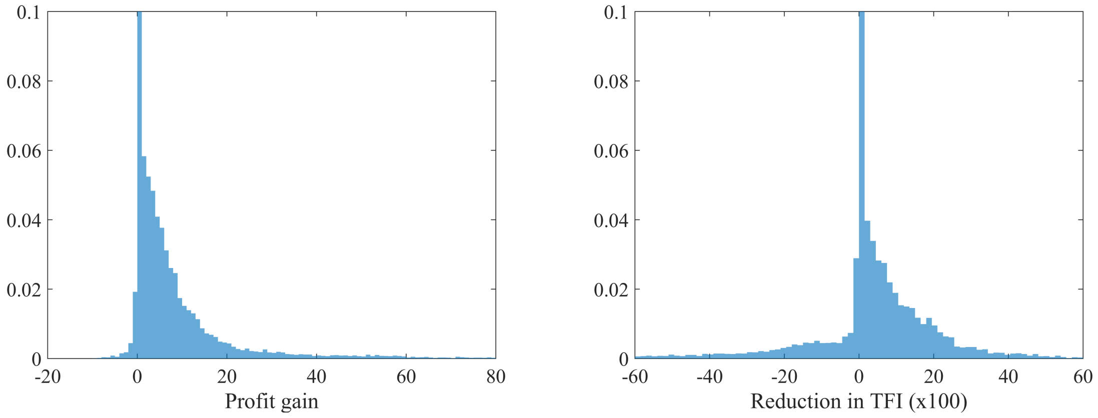
Based on this Fig. 4, we deduce the following impact of the variables on the expected effect of biocontrol:

- Regarding the agronomic variables: increasing the soil quality reduces $\Delta\pi$ and ΔTFI; more variable quality maps lead to increased $\Delta\pi$ but lower ΔTFI; more fragmented quality maps lead to higher values of $\Delta\pi$ and ΔTFI.
- Regarding the ecological variables: larger pest diffusion leads to increased $\Delta\pi$ and ΔTFI; larger natural enemy diffusion leads to decreased $\Delta\pi$ and ΔTFI; larger pest growth leads to lower ΔTFI but the effect on $\Delta\pi$ is not clear. A larger interaction factor α (higher predation efficiency) leads to increased $\Delta\pi$, but the effect on ΔTFI is less clear.
- Regarding the effect of the pesticide: increasing the pesticide-induced mortality rate leads to decreased $\Delta\pi$ and increased ΔTFI.

The effect of biological control is stronger in landscapes with a lower agronomic potential. The reason may be that in these landscapes NCH are more frequent as crop profit is lower. There are thus more natural enemy in the landscape when soil quality is low, everything else being equal. The interpretation of the effect of the soil quality variability (which was already observed in the trade-off analysis above) can be due to the fact that in more heterogeneous landscapes, there are more plots of lower agronomic quality, which are likely to be used as NCH, favouring the natural enemy. In more fragmented landscapes, the pest tends to spend more times in NCH, which increases the effect of predation. This effect is even increased when the pest diffusion is high. Conversely, when the diffusion of the natural enemy is higher, though it may have an easier access to the pest, it is also subject to detrimental effects due to the absence of resource during a part of the year and to the effect the pesticide.

When the pest growth rate is increased, even if the initial population is lower in the presence of the natural enemy, the farmer will often anticipated large pest pressure at the end of the period and use pesticide anyway, limiting the effect of biological control on the reduction of TFI. The effect of predation efficiency on biocontrol is less obvious than might have been expected. Although it leads to higher profits, thanks to reduced damages to crops, it has a limited effect on ΔTFI, meaning that it does not lead to a change in crop protection behaviour.

The effect of the parameter ρ (pesticide-induced mortality) on profit gain can be explained as follows. The more effective the pesticide is, the more farmers would favour its use, resulting in situations with low pest pressure and a high profit. The effect of biocontrol on profit is thus lower than in a situation with a less effective pesticide, in which it is used less and biocontrol has a more important role in pest regulation and crop protection. There is more room, however, to reduce pesticide use in a situation of a widely used efficient pesticide, predation being a substitute to the pesticide at the margin.



(a) $\Delta\pi$ (b) $100 \times \Delta$TFI

Figure 2: **Marginal distributions of the profit gain and the reduction in TFI, compared to an absence of biocontrol.**

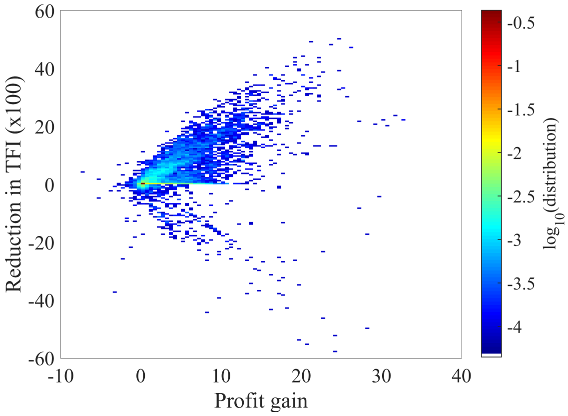


Figure 3: **Bivariate distribution profit gain vs reduction in TFI, compared to an absence of biocontrol.**

In general, when the effect of biocontrol on profit gain or reduction in TFI increases, this may either be due to a direct effect of the variable considered on the effectiveness of predation or to indirect effects caused by interactions with other variables and farmer's decisions.

Linear regression model with interactions. The trends in Fig. 4 correspond to the mean effect of each parameter, averaged over all other parameters. Due to interactions between parameters, these trends may not always reflect the real effect of the parameter, depending on the current context (i.e. the other parameter values). We checked the robustness of the above analysis with a linear regression model with two-way interactions (*stepwiselm* Matlab® function, Statistics and Machine Learning toolbox; uses the p-value for an F-test of the change in the sum of squared error to add or remove terms in the model):

$$\Delta\pi = \beta_0 + \sum_{i=1,\ldots,8} \beta_i\,\theta_i + \sum_{i,j=1,\ldots,8} \beta_{i,j}\,\theta_i\,\theta_j + \varepsilon, \tag{15}$$

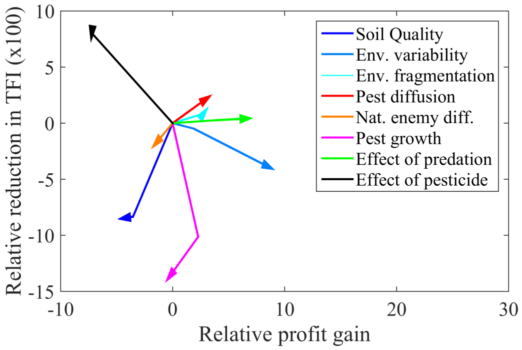


Figure 4: **Marginal effects of the parameters.** The arrows depict the variation in the biocontrol-induced profit gain and reduction in TFI, when a given parameter is increased, compared to when this parameter takes its lowest value. When an arrow points in the positive (resp. negative) direction, it means that the effect of biocontrol is stronger (resp. lower) when the parameter is increased.

and similarly

$$100\,\Delta\mathrm{TFI} = \gamma_0 + \sum_{i=1,\ldots,8} \gamma_i\,\theta_i + \sum_{i,j=1,\ldots,8} \gamma_{i,j}\,\theta_i\,\theta_j + \varepsilon. \tag{16}$$

Once fitted, the model (15) explains about one half of the variations in $\Delta\pi$, i.e., of the variations in the effect of biocontrol on profit ($R^2 = 0.48$). Regarding the TFI, the model (16) explains one third of the variations in ΔTFI ($R^2 = 0.34$). The parameter values β_i, β_{ij}, γ_i, γ_{ij} are available as in Supplementary Material SI 2, Tables S2.1 and S2.2. The signs of β_i and γ_i inform us about the role of each parameter on the effect of biocontrol. These signs are mostly consistent with the findings in Fig. 4, with some exceptions. In particular, this approach shows that the effect of the pesticide-induced mortality is complex and results from multiple interactions with other parameters. Its direct effect seems to increase the profit gain due to biocontrol, but it has negative interactions with all the other parameters (last line in Table S2.1, Supplementary Material SI 2), which results in the overall negative effect observed in Fig. 4. It means that having an efficient pesticide tends to hampers the beneficial effect of the other parameters on profit, which may be caused by a lower pest pressure and a higher mortality of the natural enemy. Among these interactions, we observe a strong negative interaction coefficient between pesticide-induced mortality rate and predation efficiency (α): increasing α decreases the effect of ρ on profit gain and vice versa. Regarding ΔTFI, conversely, the interaction coefficients are mostly positive, resulting in an overall positive effect of pesticide-induced mortality on ΔTFI, although the intrinsic effect is negative ($\gamma_i < 0$, see the last line in Table S2.2, Supplementary Material SI 2). The antagonistic effect of soil quality variability that was observed above (positive effect on profit gain and negative effect on ΔTFI) is not observed through the linear coefficients β_i, γ_i which are both positive. This global paradoxical trend seems to be caused by a highly negative interaction coefficient with the pest growth rate parameter: the decrease in predation effect observed when the pest has a high growth rate is reinforced in a landscape with strong variability, which leads to greater use of pesticides.

3. Discussion

In this paper, we developed a model that represents agricultural land-use and crop protection decisions, as well as the ecological dynamics of pests and their natural enemy. Our modelling approach provides a tool to assess biocontrol in a controlled framework, which offers several features.

First, by modelling the economic decisions of land use and pest control, we are able to assess effective biocontrol, i.e., the extra profit farmers derive from biocontrol and the social benefits corresponding to the reduction of pesticide-use thanks to biocontrol. The ecosystem service of biocontrol is not only dependent on ecological conditions, but also of the economic behaviour of farmers who will turn a potential service into actual benefits, by reducing pesticide use. On the contrary, there may be no service of biocontrol in spite of an ecological function of pest predation if farmers use a lot of pesticide anyway, without accounting for the current pest pressure. As advocated in Poggi et al. (2018), obtaining such results is of course only possible with feedback models with spatio-temporal interactions between landscape, ecological processes and stakeholder decisions, as we developed in this study.

Second, there has been many attempts to quantify biocontrol from field data, but the results are often context dependent and difficult to explain and generalise. A modelling approach can study biocontrol on a large range of contexts, providing insights on the agronomic and ecological conditions that are more likely to lead to efficient biocontrol. Our modelling exercise suggests that there are very few situations where biocontrol induces a profit loss and a majority of win-win situations (in two thirds of our simulations with a significant effect), with often a positive correlation between profit gain and reduction in TFI. The use of biocontrol is therefore low risk for profit loss, and the situations that increase the efficiency of biocontrol over one dimension also tend to increase its effect on the other dimension. Nevertheless, we observed a very limited effect in many of the agroecological conditions we studied. For some conditions, however, biocontrol has a significant positive effect on private profit and/or reduction of pesticide use. Some rare situations can also lead to greater use of pesticides, particularly in environments with high soil quality and significant variability.

Some parameters seem to have a stronger effect on the magnitude of biocontrol. The effect of biocontrol seems to be more limited in areas with higher agricultural potential, or when the pest has a high growth rate. Other parameters seem to favour biocontrol. First, landscape fragmentation, which was already known in landscape ecology to increase the efficiency of predation (Roques and Chekroun, 2010; Ryall and Fahrig, 2006), or a more mobile pest. In both cases, the pest will more likely encounter natural enemies in non-crop habitats. Interestingly, there are many examples of species for which dispersal capacity is traded off against reproduction (‘D-R’ trade-off) (Hanski et al., 2006; Bonte and Bafort, 2018). Our study indicates that biocontrol is more efficient for pest species with a ‘D’ strategy. Scarab beetles are an example of pests with a relatively low reproduction rate, whose predators include ants, staphylinids and carabids (Jackson and Klein, 2006).

These results offer prospects for empirical research. They emphasise the need for the joint analysis of parameters driving biocontrol in empirical studies. In particular, our simulations reveal some cross-effects that could be assessed in the field. For example, there seems to be a negative cross-effect between the efficiency of pesticide to regulate the pest and the efficiency of predation (increasing α decreases the effect of ρ on profit gain and vice versa). This effect comes in particular from the hypothesis of a non-specific pesticide, increasing the mortality rate of the two species in the same way. Although the mortality rate may of course be different for the two species, the predators involved in biocontrol are often very sensitive to pesticides (Potter and Held, 2002). More subtle interactions may also emerge, e.g. between soil quality variability and pest growth rate, with a negative cross-effect on pesticide reduction. Variability in itself (conversely to fragmentation, see Fig. 1 to observe the difference between these two descriptors of the soil quality map) is known to be beneficial to pest population growth in the absence of predation (Berestycki et al., 2005), which may explain this effect.

Of course, the determination of the 'true' effect of biocontrol should rely on an array of approaches, not just one. In this respect, bringing our approach in the game appears very useful. We point out that, beyond the results discussed above, we have developed a generic tool which can be exploited under other conditions which are not necessarily those of this study. The Matlab codes used to generate the analyses conducted here are available and fully commented `https://doi.org/10.17605/OSF.IO/Z2QCX`.

These results, related to the effect of the agronomic context (land-use variability and fragmentation) on biocontrol, provide an indication on the changes that could be made in agrocosystem to increase biocontrol. In terms of future work, we see two interesting extensions for the economic part of the model. First, the model can be used to study how to influence land-use and pest control decisions through public policies. Incentives (pesticide taxation, non-crop habitat subsidies, or a price-bonus for pesticide-free production) can be used to modify the economic context and lead to dynamic landscapes with a higher level of biocontrol and less pesticide use. Second, the model could be used to study the role of farmers' agroecological knowledge on biocontrol. In the present version, farmers take their decisions according to the local pest density only. One could examine if accounting for the predator density (at local or at the landscape level), i.e., relying on agroecological knowledge, would improve the benefits from biocontrol.

Data availability.. All of the Matlab codes that led to the results in this paper are available in the Open Science Framework repository: `https://doi.org/10.17605/OSF.IO/Z2QCX`.

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