

Title: More pests but less treatments: ambivalent effect of landscape complexity on Conservation Biological Control

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1 **Abstract:**

2 In agricultural landscapes, the amount and organization of crops and semi-natural habitats (SNH)
3 have the potential to promote a bundle of ecosystem services due to their influence on ecological
4 community at multiple spatio-temporal scales. SNH are relatively undisturbed and are often source of
5 complementary resources and refuges, supporting more diverse and abundant natural pest enemies.
6 However, the nexus of SNH proportion and organization with pest suppression is not trivial. It is thus
7 crucial to understand how the behavior of pest and auxiliary species, the underlying landscape
8 structure, and their interaction may influence conservation biological control (CBC). Here, we develop
9 a generative stochastic landscape model to simulate realistic agricultural landscape compositions and
10 configurations of fields and linear elements. Generated landscapes are used as spatial support over
11 which we simulate a spatially explicit predator-prey dynamic model. We find that SNH boost predator
12 population, but predator movement from hedges to fields is fundamental for an efficient pest regulation
13 by auxiliaries and to decrease pesticide treatments. Moreover landscape elements may lead to different
14 effects on pest reduction depending on the considered scale. Integration of species behaviors and traits
15 with landscape structure at multiple scales are needed to provide useful insights for CBC.

16 **Introduction**

17 Agricultural landscape simplification results in substantial loss of semi-natural mosaics and of non-
18 crop field margins. It is often associated with high pest abundance, which in turn requires a higher
19 pesticide input (1,2). Consequently, a negative relationship emerges between intensity of agriculture
20 and agricultural landscape biodiversity (3) because of a partial replacement and suppression of the
21 ecological services provided by communities of beneficial organisms (4,5). Habitat heterogeneity is
22 key to allow cross-system fluxes of organisms across agro-ecological interfaces by influencing
23 ecological dynamics within those habitats (6,7) and potentially increasing natural enemy abundance
24 and diversity in agricultural systems (8,9). In addition, complex landscape favours habitat and resource

25 diversity for natural enemies with increased availability of alternative preys, higher microclimate
26 heterogeneity, the presence of refuges from their own predators and for overwintering (10). In arable
27 land, semi-natural habitat (SNH) is typically restricted to hedgerows. These linear structures play an
28 important role as relatively perennial line corridors because of their temporal stability with respect to
29 crop fields. Their presence supports natural enemy dispersal and movement to escape from
30 disturbances and to find food resources scattered in time and space (11,12).

31 While SNH favours the presence or abundance of functional groups of organisms in landscapes, it
32 can also results in ineffective conservation biological control (CBC) (12,13) with no, or even negative
33 effects on pest control (12–14). A meta-analysis revealed that pest pressure in complex landscapes is
34 reduced in 45% of cases, not affected in 40% of cases and increased in 15% of cases (9). For example,
35 the effect of landscape structure on pests themselves remains inconclusive, as many crop pests also
36 benefit from nearby non-crop habitat (12–14). In particular, SNH can offer more complementary
37 resources to pests rather than to natural enemies to complete their life cycle (6). Predator abundance is
38 not always enough to guarantee a consistent reduction of pest species (15) in case of the presence of
39 alternative prey (known as *dilution effect*) (16), or increased intra-guild predation (17). Life history
40 traits, in particular those traits related to mating systems, competitive skills, movement abilities and
41 habitat use, are also of major importance by affecting species responses to landscape heterogeneity and
42 being readily linked with ecological processes (18). Thus, effect direction and magnitude jointly
43 depend on organisms and landscapes under study (19,20).

44 The impacts of landscape structure on pest population dynamics are generally investigated through
45 empirical correlative approaches with global descriptors at landscape level, due to the difficulty of
46 manipulating large landscapes for local analyses and for the lack of the spatio-temporal dimension. The
47 main drawback of these approaches is the difficulty of linking correlation levels to population dynamic
48 processes such as local population growth or migration behaviour (21). A complementary approach

49 consists in coupling generative landscape models with population dynamics models to explore how
50 different landscape configurations, including the hedge network structure, affect CBC (22) .

51 In this work, we develop a stochastic model to generate realistic landscapes, where we simulate a
52 spatially explicit population dynamic model of a predator-pest system integrating dispersal both on
53 agricultural fields and on hedge network. A major goal is to implement a general simulation-based
54 approach to obtain theoretical insights on CBC by incorporating landscape effects and species traits,
55 which can serve as basis to formulate practical recommendations. Specifically, following questions are
56 investigated: (i) What are the main factors that influence the predator-pest population densities in
57 complex landscape? (ii) How do life history traits modify the effect of landscape heterogeneity? (iii)
58 Can landscape heterogeneity reduce number of pesticide applications by enhancing CBC?

59 **2 Models and methods**

60

61 **2.1 Stochastic landscape model**

62 The landscape is represented through a vectorial approach, which is appropriate for representing the
63 highly regular geometrical patterns of agricultural landscapes (23,24). It is composed of polygons
64 representing fields, separated by edges. Landscape elements are characterized by their geometry (e.g.,
65 vertex coordinates, size and shape), and by categorical information defining the land-cover (e.g., crop
66 or natural habitat). The landscape geometrical structure is fixed and based on a real landscape with an
67 extent of 5.55 km. The landscape is transformed into a T-tessellation (25,26) composed of 188
68 polygons with a total of 577 edges.

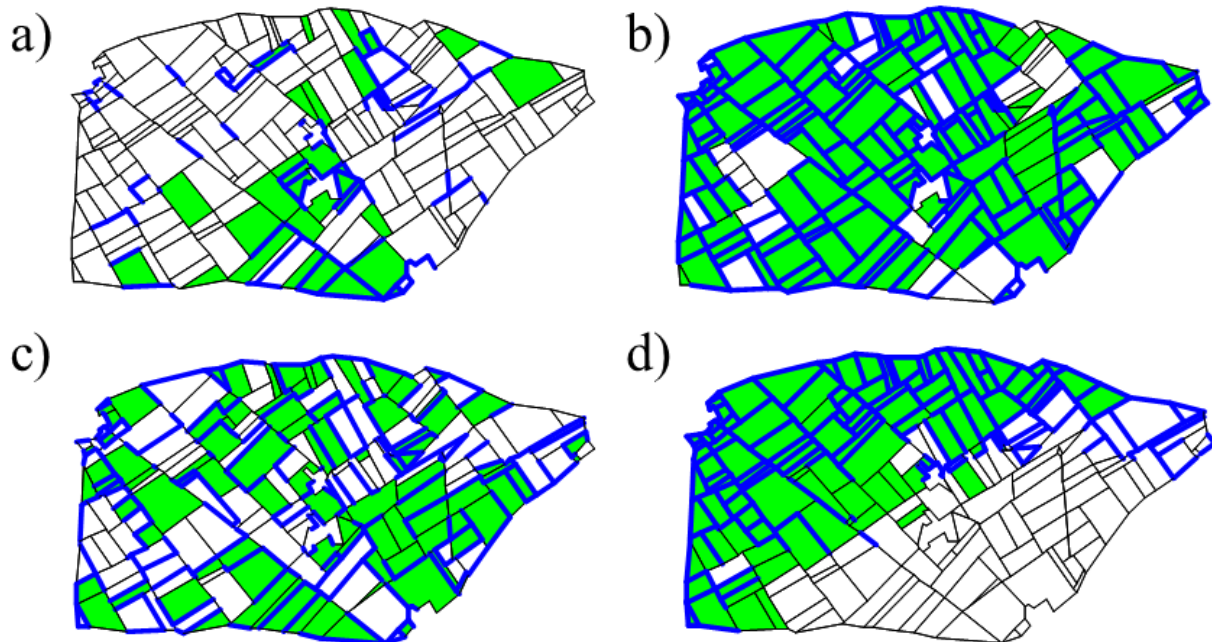
69 We use Gaussian random fields (GRFs) to allocate a proportion of polygons and edges as crops
70 representing the principal culture and hedges to provide SNHs, respectively. A threshold on the
71 simulated GRF values is set to attribute specific landscape elements depending on the value being
72 below or above the threshold. By definition, a GRF denoted by W is a random surface over continuous
73 2D space, for which the multivariate distribution of the values $(W(x_1), W(x_2), \dots, W(x_n))$ observed at

74 a finite number of locations x_1, x_2, \dots, x_n in the landscape corresponds to a multivariate normal
75 distribution, characterized by its mean vector and its covariance matrix Σ . The mean is fixed to 0 and
76 the exponential correlation function is used for Σ , such as $\Sigma_{ij} = e^{-\left(\frac{|x_i - x_j|}{\varphi}\right)}$, where $|x_j - x_i|$ is the
77 Euclidean distance between any two points x_j and x_i . The range parameter $\varphi \geq 0$ governs the strength
78 of clustering of category allocation to landscape elements. To handle the interactions between the
79 allocation of hedge and crop, we simulated two correlated GRFs for crop ($W_c(s)$) and hedge ($W_h(s)$):

$$W_c(s) = \rho W_h(s) + \sqrt{1 - \rho^2} \tilde{W}(s),$$

80 where $\rho \in [-1, 1]$ controls the correlation between W_h and \tilde{W} , which is a GRF independent from W_h .
81 The parameter used for the landscape models with their range of values can be found in Table 1. Figure
82 1 shows an example of four landscapes simulated according to different proportions and aggregation
83 levels of hedges and crop fields.

84



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86 Figure 1: Examples of simulated landscape structures with interacting elements using the following
 87 allocation categories: for fields, (i) crop (green) and (ii) non-crop (white); for edges, (i) hedge (blue)
 88 and (ii) no-hedge (black). First row: low (a) and high (b) proportions of crop and hedges (0.2 and 0.8,
 89 respectively), with fixed parameter configuration for aggregation and fixed correlation between crop
 90 and hedges (0.5). Second row: low (c) and high (d) crop and hedge aggregation level from left to right,
 91 with fixed proportion of crop and hedges (0.5) and fixed correlation between crop and hedges (0.5).

92 2.2 Predator-pest model

93 We developed a spatially explicit predator-pest model based on a system of partial differential
 94 equations. The model is built on a previously developed model that considers both 2D diffusion on
 95 polygons and 1D diffusion on edges (11). Simulations are performed over a [0,1]-time interval
 96 representing a cropping season of several months with a time step of 0.01, such that the time unit
 97 corresponds to one day. The model parameters and their range of simulated values are reported in
 98 Table 1. Numerical simulations of the spatio-temporal partial differential equation system of pest-
 99 predator dynamics are performed using the Freefem++ finite-element framework (27).

100

101 Table 1: Description of parameter values.

| Parameters | Description | Values | | units |
|---|--|----------|------|---------------|
| | | Min | max | |
| For landscape model | | | | |
| φ | Aggregation of hedges and crops | 5.55/100 | 5.55 | km |
| P_c | Proportion of crop | 0 | 1 | - |
| P_h | Proportion of hedges | 0 | 1 | - |
| ρ | Correlation between crops and hedges GRF_S | 0.5 | | - |
| Parameters for population dynamic mode | | | | |
| D_2^p | 2D diffusion rate of the predator | 0.0625 | 12 | $km^2 d^{-1}$ |
| m_p | Mortality rate of the predator | 5 | 15 | d^{-1} |
| β | Predation rate | 1 | 10 | d^{-1} |

| | | | | |
|-------------|--|---------------------------|----|--------------|
| ρ_{21} | Migration rate of the predator from field to hedge | 5 | - | |
| D_1^v | 1D diffusion rate of the predator | 12 | | km^2d^{-1} |
| r_v | Intrinsic growth rate of the predator on hedges | 10 | 20 | d^{-1} |
| K_{h_i} | Carrying capacity of hedges for the predator | 1 | | |
| ρ_{12} | Migration rate of the predator from hedge to field | 0 | 5 | |
| D^u | 2D diffusion rate of the pest | 0.0625 | 12 | km^2d^{-1} |
| r_u | Intrinsic growth rate of the pest | 10 | 20 | d^{-1} |
| C_{it} | Carrying capacity of 2D system for the pest | 20 (without treatment) | | |
| | | 0.1 (after the treatment) | | |
| m_u | Mortality rate of the pest | 5 | 15 | d^{-1} |

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2.2.1 Predator dynamics:

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Hedges are the main habitat of the predator. Using notations t for time and x for a spatial location,

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we thus assume the following 1-dimensional reaction-diffusion model for the predator density v_{h_i} on

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the edge h_i :

$$\begin{cases} \partial_t v_{h_i} = \partial_{xx} D_1^v v_{h_i} + r_v v_{h_i} \left(1 - \frac{v_{h_i}}{K_{h_i}}\right) & \text{if the edge } h_i \text{ has a hedge,} \\ v_{h_i} = 0 & \text{otherwise,} \end{cases} \quad (7)$$

107

Where D_1^v is the diffusion parameter of the predator along hedges, r_v is the intrinsic growth rate of the

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predator, and K_{h_i} is the carrying capacity of the hedge i . If two hedges are linked together at one of

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their endpoints, then the dynamics in Equation (7) apply continuously across the junction.

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In addition, the predator forages on fields where it feeds on the pest. The population density v_{Ω_i} of

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predators in a field Ω_i is modelled by a reaction-diffusion equation with mobility parameter within field

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D_2^v , predation rate β , and mortality m_v :

$$\partial_t v_{\Omega_i} = \Delta D_2^v v_{\Omega_i} - m_v v_{\Omega_i} + \beta u_{\Omega_i} v_{\Omega_i}. \quad (8)$$

113 2.2.2 Pest dynamics

114 We consider that edges do not modify directly pest population dynamics. Writing u_{h_i} for the pest
115 density in an edge h_i :

$$u_{h_i} = 0 \quad \text{for all } i. \quad (9)$$

116 The pest is a specialist of the principal culture and, without dispersal, it shows positive growth only
117 in crop fields. The bidimensional reaction-diffusion model for the pest density u_{Ω_i} in field Ω_i is

$$\begin{cases} \partial_t u_{\Omega_i} = \Delta D_2^u u_{\Omega_i} + r_u u_{\Omega_i} \left(1 - \frac{u_{\Omega_i}}{C_{it}}\right) - \beta u_{\Omega_i} v_{\Omega_i} & \text{for } \Omega_i \text{ with crop,} \\ \partial_t u_{\Omega_i} = \Delta D_2^u u_{\Omega_i} - m_u u_{\Omega_i} - \beta u_{\Omega_i} v_{\Omega_i} & \text{for } \Omega_i \text{ with non-crop,} \end{cases} \quad (10)$$

118 where D_2^u is the diffusion parameter of the pest in fields, r_u is its intrinsic growth rate on crop category,
119 β is the predation rate, and m_u is the mortality rate of the pest on non-crop fields.

120 In a crop field, a pesticide treatment is applied when the average pest population density in that field
121 exceeds a given threshold, which we here fix to 0.2 individuals/m² per small unit of space and time.
122 Pesticide treatments reduce the carrying capacity C_{it} of the field i (equation (10)):

$$\begin{cases} C_{it} = K_{\Omega_i} & \text{if no pesticide treatment is applied,} \\ C_{it} = \frac{K_{\Omega_i}}{200} & \text{during the period } e_t \text{ for which the treatment is efficient.} \end{cases} \quad (11)$$

124 An additional mortality term could be added to account for the effects of pesticide treatments, but it
125 would have implied the modification of both growth and carrying capacity. For that reason and to keep
126 the model parsimonious, possible effects of pesticide treatments are assumed to change only the
127 carrying capacity (Eq.11). Similarly, mortality other than for predation or pesticide treatments could
128 have occurred in crop fields, but we have opted against this option for the sake of parsimony.

129 2.2.3 Coupling predator-pest dynamics over the entire landscape

130 Using the framework described in (11), the dynamics described by equations (7) to (10) are coupled
131 over the full landscape using the following assumptions (see the Supplementary Information (SI) for

132 more details): (i) edges (with or without a hedge) do not represent a barrier for the pest, (ii) edges
133 without a hedge do not represent a barrier for the predator, (iii) the predator is attracted by hedges, thus
134 migration from fields to hedges (ρ_{21}) is relatively high, (iv) the predator shows aversion to move
135 outside its natural habitat, thus migration from hedges to fields (ρ_{12}) is lower than migration from
136 fields to hedges. We consider reflecting conditions on landscape boundaries, meaning that in- and out-
137 fluxes between the landscape and its surrounding environment are equal.

138 **2.2.4 Inoculation and spatio-temporal design**

139 Initially, the predator is present in all hedges at carrying capacity. The pest is introduced randomly
140 in space and time. The average number of pest inoculations in a single simulation is proportional to the
141 proportion of crop field area in the landscape, and we draw the actual number of inoculations from a
142 Poisson distribution. The maximal average number of pest inoculations was fixed to 25 when the crop
143 is grown in all fields. Inoculated crop fields are picked at random with probability depending on their
144 relative surface.

145 **2.3 Statistical methods for analysing simulation outputs**

146 We define an experimental design based on Sobol's sequences leading to 11,500 distinct parameter
147 configurations. For each parameter combination, we consider 15 landscape replicates, leading to a total
148 of 172,500 simulations.

149 We first conduct a Sobol sensitivity analysis on the mean and standard deviation of predator density,
150 pest density and number of treatments by averaging the outputs over landscape replicates and crop
151 fields. First-order indices were estimated with Sobol-Saltelli's method (28,29), whereas total indices
152 are estimated with Sobol-Jansen's method (28,30). These analysis are performed within the R software
153 v. 3.0.3 (R Team, 2003), using the packages fOptions (v. 3010.83) and sensitivity (v. 1.11).

154 Then, to further explore direction and magnitude of variations in response variables with respect to
155 landscape parameters, we applied Generalized linear models (GLMs). Pest and predator densities, and

156 pesticide treatment numbers (if different from 0), are analysed as response variable by using the
157 Gamma distribution with log-link function. Additionally, pesticide treatment presence/absence during a
158 simulation is analysed using a GLM with binomial distribution. We develop GLM formulas containing
159 covariable interactions (see Table 1) up to 2nd order, and we use a step-wise variable selection
160 algorithm based on the Bayesian information criterion (BIC) in order to select the “best subset” of
161 variables for each model.

162 Finally, we use Generalized Linear Mixed-Effect models to analyse treatment occurrences by taking
163 into account their spatial position in the landscape. We use the log-transformed area (*Area*) and
164 perimeter (*Perimeter*) to take into account the geometrical properties of the fields, and we use the
165 number of adjacent crop fields (Adj_C), the number of adjacent hedges (Adj_H), and the number of
166 treatments applied in the adjacent crop fields (Adj_{Tr}) to take into account the composition and
167 dynamics in local neighbourhoods. In addition, we include the estimated linear effects from the global
168 models as offsets. The random effect is structured by the landscape simulation to account for its
169 specific dynamics. By analogy with the global GLMs, the presence/absence of treatments is analysed
170 using the binomial response distribution, and pesticide treatment numbers are analysed with the
171 Gamma distribution for the response variable with a log-link function. We consider predictor
172 interactions up to 2nd order. These analyses are performed using the R package lme4 with R version
173 3.2.3 (31).

174 **3 Results**

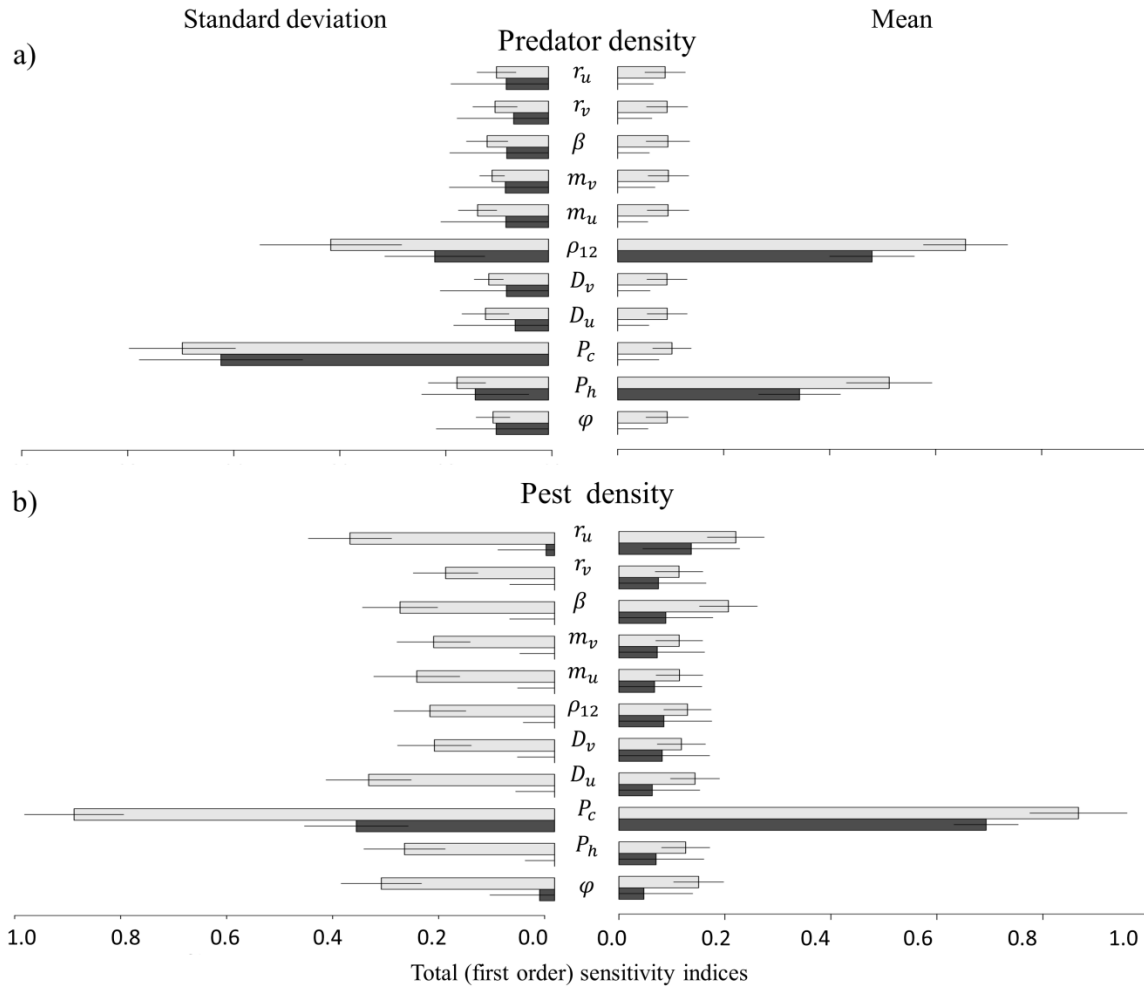
175 **3.1 Sensitivity of predator density, pest density and pesticide treatments to model** 176 **parameters**

177 The sensitivity analysis of the mean of model outputs across landscape replicates (Figure 2a right)
178 shows that variations in predator population density are mainly explained by predator migration
179 ($I_{\rho_{12}} = 50\%$) and by the proportion of hedges ($I_{P_h} = 41\%$), whereas interactions among parameters
180 have little impact on the outputs. For the pest population density and the average number of pesticide

181 treatments, crop proportion ($I_{P_c} = 78\%$ and $I_{P_c} = 83\%$, respectively) and pest growth rate ($I_{r_u} = 17\%$
182 and $I_{r_u} = 15\%$, respectively) are the most important parameters to explain model output variability,
183 again with only little interaction between model parameters (Figure 2b right). Complete results of
184 pesticide treatments are in the SI.

185 The sensitivity analysis of standard deviation of model outputs across landscape replicates gives
186 different importance to the input variables as compared to the mean values. For the predator, crop
187 proportion (P_c), predator migration (ρ_{12}), hedge proportion (P_h) and spatial aggregation (φ) explain
188 respectively 55%, 19%, 9% and 9% of the variability of model outputs (Figure 2a left). For the pest and
189 pesticide treatments, results are consistent with the analysis on the mean. However, interactions
190 between model parameters are important to explain variations of predator and pest density, as well as
191 of pesticide treatments among landscape replicates. This implies that particular landscape structures
192 characterized by a combination of several descriptors have to be considered to fully understand the
193 drivers of predator-pest dynamics.

194



195

196 Figure 2: Sobol sensitivity analysis: Total sensitivity indices (light grey bar) and first-order
 197 sensitivity indices (black bar) of space-time averaged values for predator density (a) and pest density
 198 (b), based on the mean (right) or on the standard deviation (left) over replicated simulations. The length
 199 of the bar indicates the mean of the sensitivity index, and the solid line indicates its 95% confidence
 200 interval.

201 3.2 Landscape structure effects on the predator-pest dynamics

202 Effects of landscape variables (denoted $E_{variable}$ in the following) on predator density highlight a
 203 positive effect of hedge proportion ($E_{P_h} = 0.40 \pm 0.05$), a negative effect of crop proportion ($E_{P_c} =$
 204 -0.20 ± 0.04) and a positive interaction among both variables ($E_{P_h:P_c} = 0.08 \pm 0.02$), which
 205 implies that hedges can buffer the negative effect of increased crop proportion. Migration from hedges

206 to fields ($E_{\rho_{12}} = 0.56 \pm 0.01$) has the highest positive effect on predator density with again a positive
207 interaction with crop proportion.

208 As expected, crop proportion ($E_{P_c} = 1.50 \pm 0.16$), as well as spatial aggregation ($E_{\varphi} = 0.55 \pm$
209 0.02), have a strong positive effect on pest density. Both variables interact negatively ($E_{\varphi:P_c} =$
210 -0.11 ± 0.01), as high aggregation results in an increase of the size of contiguous crop fields, which
211 lowers the effect of increased crop proportion. The positive effect of crop proportion is lowered by its
212 interaction with hedge proportion ($E_{P_h:P_c} = 0.03 \pm 0.06$) and also with predator migration from hedge
213 to fields ($E_{P_c:\rho_{12}} = 0.06 \pm 0.06$). Counterintuitively at first sight, an increase in hedge proportion
214 ($E_{P_h} = 0.09 \pm 0.11$) has a positive effect on pest population. Indeed, predator presence over all the
215 landscape helps to stabilize the pest population by keeping it under the thresholds triggering a pesticide
216 treatment. This is further confirmed by the fact that hedge proportion ($E_{P_h} = 0.32 \pm 0.57$), predator
217 spillover ($E_{\rho_{12}} = 0.61 \pm 0.34$) and concurrence of high crop proportion and aggregation ($E_{\varphi:P_c} =$
218 0.24 ± 0.09) have a positive effect on the presence of pesticide treatments, but a negative effect on
219 treatment numbers ($E_{P_h} = -0.11 \pm 0.07$, $E_{\rho_{12}} = -0.19 \pm 0.08$, $E_{\varphi:P_c} = -0.07 \pm 0.01$).

220 Among species traits, predator migration from hedges to fields ($E_{\rho_{12}} = -0.13 \pm 0.12$) has the
221 highest negative impact on pest density. Pest diffusion ($E_{D_u} = -1.03 \pm 0.01$), due to a dilution effect,
222 and the predating rate ($E_{\beta} = -0.24 \pm 0.01$), have also a negative impact on the pest, while the growth
223 rate ($E_{r_u} = 0.41 \pm 0.01$) contributes positively to pest density. Figure S3 shows all estimated effects
224 and confidence intervals for predator and pest density and treatment presence/absence and number, see
225 also Table 2 for a sum up.

226 **3.4 Effect of local landscape on pesticide treatment**

227 Presence of pesticide treatments is negatively influenced by field area and perimeter ($E_{Area} =$
228 -0.32 ± 0.01 , $E_{Perimeter} = -0.10 \pm 0.03$). These effects reflect both a slower pest diffusion in large

229 fields and a higher spillover of predators in fields with long perimeter. Conversely, when treatments
 230 occurred in a field, their total number increases with field perimeter due to spillover from the
 231 neighbourhoods. An increase in the number of adjacent crop fields produces a positive effect on the
 232 presence ($E_{Adj_C} = 0.74 \pm 0.01$) and number ($E_{Adj_C} = 0.20 \pm 0.002$) of treatments while an increase
 233 in the number of adjacent hedges leads to a negative effect on the presence ($E_{Adj_H} = -0.07 \pm 0.01$)
 234 and number ($E_{Adj_H} = -0.05 \pm 0.001$) of treatments. Whereas in the global model the increase of
 235 hedge proportion is associated with a positive effect on the presence of treatments, we attribute the
 236 negative effect at local level to the fact that the predator tends to locally maintain the pest density under
 237 the application threshold, especially after a first treatment. The number of treatments in adjacent fields
 238 is positively correlated to the local presence ($E_{Adj_{Tr}} = 2.99 \pm 0.01$) and number ($E_{Adj_{Tr}} = 0.13 \pm$
 239 0.001) of treatments, indicating local pullulation of the pest. Figure S4 shows all estimated local effects
 240 and confidence intervals for treatment presence/absence and number, see also Table 2 for a sum up.

241

242

243 Table 2: Summary of the presented estimated effects for predator and pest density (left) and for the
 244 presence/absence (P/A) and number (No.) of treatment (right) at landscape and field scale. + means positive
 245 effect, - means negative effect, NS means non significant effect.

246

| Density | | | | Treatment | | | |
|------------------|---------------------|------|---|------------------|-------------------|-----|---|
| Effect | Predator | Pest | | Effect | P/A | No. | |
| <i>Landscape</i> | E_{P_h} | + | + | <i>Landscape</i> | E_{P_h} | + | - |
| | E_{P_c} | - | + | | $E_{\rho_{12}}$ | + | - |
| | $E_{P_h:P_c}$ | + | + | | $E_{\varphi:P_c}$ | + | - |
| | $E_{\rho_{12}}$ | + | - | <i>Patch</i> | E_{area} | - | - |
| | $E_{\varphi:P_c}$ | NS | - | | E_{perim} | - | + |
| | $E_{P_c:\rho_{12}}$ | + | + | | E_{Adj_C} | + | + |

| | | | | | |
|-------------|---|---|----------------|---|---|
| E_{D_u} | + | - | E_{Adj_H} | - | - |
| E_{β} | + | - | $E_{Adj_{Tr}}$ | + | + |
| E_{r_u} | + | + | | | |

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248 **4 Discussion**

249 Sustainable management of pests and diseases in agro-ecosystems requires a better understanding of
250 how landscape structure drives and alters population dynamics. By simulating different landscape
251 configurations including linear corridors, and the predator-pest dynamics, the present research aims at
252 characterizing the joint influence of landscape structure and species traits on CBC service. Our study
253 corroborates that spatial heterogeneity, landscape structure (i.e., the size and physical arrangement of
254 patches), species traits and their interactions play a key role for CBC.

255 Crop proportion is the major determinant of increasing pest population and resulting in an increased
256 number of pesticide treatments over the whole landscape. Indeed, increasing crop proportion in
257 fragmented landscapes ensures food availability to the pest all over the landscape (1,2,12). In highly
258 aggregated landscapes, the size of contiguous crop patches is already large enough to sustain a
259 relatively large pest population, thus lowering the effect of an increase in crop proportion (14). The
260 effects of crop proportion and spatial aggregation are intimately linked to pest growth rate and dispersal
261 capability. Indeed, unfavourable landscape properties for the pest (i.e., low proportion and high
262 fragmentation) can be compensated by a higher growth rate. However, the effect of dispersal is a
263 double-edged sword since high dispersal helps spreading on fragmented landscapes but comes with a
264 larger amount of propagules lost in unsuitable habitats, potentially leading to a dilution effect (3,33,34).

265 As expected, hedge proportion (i.e., SNHs) positively affects predator presence in agricultural
266 landscapes. In addition, the predator's ability to move between SNHs and crop habitats is the parameter
267 that increases most strongly the predator density, since it enables predators to reach complementary

268 resources in crop fields more easily. Spillover from adjacent habitat is reported to have a major impact
269 on pest populations in crop fields (3,12,34). Spillover not only depends on predator propensity to
270 forage outside their natural habitat, but also on semi-natural patch connectivity and on crops and
271 natural enemy reservoir interface (35). Thus, different combinations of SNH proportion and
272 aggregation influence landscape structural connectivity and are also important determinants of predator
273 efficiency in regulating crop pests (35).

274 In our representation, hedges are modeled as source of predators where they have a logistic growth.
275 This is a simplification for predator dynamics in their natural habitat, as we do not consider potential
276 prey presence in hedges and predator foraging behaviour in crop fields. For example, the growth rate,
277 instead of being constant, could depend on the time spent in the fields and on the number of consumed
278 preys. In addition, predating rate and consumption rate are crucial in determining the efficiency of CBC
279 (36). Here, these parameters are not identified as influent in the dynamics, perhaps because they are
280 assumed identical (parameter β in our model). Finally, another strong assumption may be that pesticide
281 treatments do not affect predator mortality. However, in crop fields a positive predator growth rate
282 relies only on pest, such that a strong pest reduction due to treatments is automatically translated into a
283 strong impact on predator density when such treatments occur. Thus, adding extra-mortality in crop
284 fields should not modify the results that much. To account for major pesticide treatment effects, an
285 impact on predator mortality in its natural habitat should be considered.

286 In our analysis, we found that predator ability to disperse from hedges to crop fields has a major
287 influence on pest density and related treatments. High crop proportion enhances pest density, but this
288 effect is counter-balanced by the joint effect of hedge proportion and predator spillover, which favours
289 predator pressure and reduces pesticide treatment application. Indeed, hedges ensure an increased
290 landscape functional connectivity, which enables predators to successfully disperse and feed on
291 complementary resources in the fields. Interestingly, however, we found that if SNHs can sustain a

292 high population of natural enemies (37), this is not sufficient to achieve a decrease in pest density.
293 Indeed, by keeping the pest population density under the treatment threshold, the predator population
294 can favour its spread across the landscape, thus increasing pest density at the landscape scale, even if
295 fewer treatments are applied. Most of the studies consider the amount of SNH as a proxy for predator
296 presence and focus on how landscape structure directly influences CBC. However, as highlighted by
297 our results (see also 37), the extent to which species are influenced by landscape heterogeneity depends
298 on their traits. For example, (39) argue that natural enemies with an oriented movement are better able
299 to deliver pest control services. They discuss the interplay among predator mobility, proportion of crop
300 and SNHs. More generally, SNH predator spillover is expected to be particularly strong when (i)
301 predator attack rates on prey are high, (ii) predator movement abilities are substantial, and (iii) predator
302 mortality rates in the recipient habitat are low (40).

303 The amount of predator spillover, and the distance over which pest and predator can spread, both
304 depend on local configurational variables such as field size, shape, amount of shared edge, and
305 connectivity (19). Large fields can support high pest volumes, but it has been demonstrated that the
306 relationship between field size and pest density can take several forms depending on assumptions,
307 conditions and species considered (41). Our results show a negative effect of large field area on the
308 need to use pesticides and on the number of required applications, which, accordingly to (41), may
309 come from the elevated growth rate of the prey combined with its good dispersal ability. By contrast,
310 the perimeter shows a positive relationship with pest density by increasing treatment numbers due to
311 the spillover from surrounding fields. However, when long perimeters are coupled with hedge presence
312 on them, predator spillover into fields reduces pesticide treatment numbers (9). Interestingly, we show
313 a contrasted effect of hedge depending on the scale considered. At global scale, the proportion of
314 hedges shows a positive effect on pest density and has a negative effect only on treatment application

315 presence. At local scale, the number of edges adjacent to a crop field shows an even more important
316 impact on CBC by negatively affecting both the local presence and number of treatments (37).

317 Landscape simplification is a major driver of pest abundance and consequently has strong impacts
318 on the necessity of pesticide treatments and their frequency. We find that natural habitat enhances
319 predator population, but it does not systematically translate into a strong correlation with pest density
320 decrease. However, a relatively high predator density often helps maintaining pest density below the
321 economic threshold level above which pesticides are applied, thus preventing highly localized pest
322 densities. By contrast, predator spillover from hedges to fields is fundamental for CBC; it reduces pest
323 density and guarantees high predator fluxes and different habitat connectivity. At field scale, landscape
324 geometrical features, hedge presence and habitat connectivity are able to influence predator-pest
325 dynamics, and therefore they affect the number of pesticide treatments. This highlights the importance
326 of conducting a multi-scale analysis to consider the differences in outcomes at landscape and patch
327 scale for pest CBC (14). In most of our analyses, we considered global outputs by averaging pest and
328 predator densities over crop fields. However, populations are obviously structured in space and time.
329 Thus, a complementary analysis studying how landscape structure impacts predator-pest spatio-
330 temporal dynamics would bring more insights on pest outbreak determinants. Moreover, a larger
331 number of pest and predator species, inter/intra-species interactions and also different trophic network
332 structures, could be considered in future work to better understand the role of pest and predator
333 diversity on CBC efficacy.

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