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Habitat fragmentation and food security in crop pollination systems

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Abstract

1. Ensuring stable food supplies is a major challenge for the 21st century. There is consensus that increased food production is necessary, but not sufficient, to achieve food security, and that agriculture should also aim at stabilizing crop production over time. In this context, biodiversity-based approaches to food security are increasingly being supported based on the fact that biodiversity can increase and stabilize crop production. However, agricultural systems are often highly fragmented and our current understanding of how such fragmentation affects biodiversity and food production remains incomplete, thus limiting our capacity to manage agricultural landscapes for food security.
2. We developed a spatially explicit model of crop dynamics to investigate how the fragmentation of natural habitats for agricultural conversion impacts food production and food security, with a focus on animal-dependent crop production.
3. Fragmentation produces a variety of spatial and biodiversity-mediated effects that affect both the mean and stability (temporal invariability) of animal-dependent crop production.
4. Fragmentation has a dual effect on animal-dependent production. On the one hand, spatial aggregation of natural land decreases animal-dependent production by reducing the *Landscape Pollination Potential*, a metric that captures fragmentation and pollinator spillover effects within the agricultural landscape. But aggregation increases animal-dependent production by maintaining a higher pollinator diversity in larger fragments of natural habitat. The net effects of fragmentation on animal-dependent crop production depend on the land-use change pattern, the strength of the pollinator spillover to crop land and the animal pollination dependence of crops.
5. *Synthesis*. Our study sheds new light in the food security debate by showing that high and stable crop production depends on biodiversity and the spatial fragmentation of agricultural landscapes, and by revealing the ecological mechanisms of food security in crop pollination systems. Management for food security should consider factors such as pollinators' spillover, the amount and spatial aggregation of semi-natural habitat and the animal pollination dependence of crops. This information would be useful to design agricultural landscapes for high *Landscape*

Pollination Potential. These results are highly relevant in the global change context, and given the worldwide trends in agriculture, which shifts towards more animal-dependent crop production.

KEYWORDS

biodiversity, ecosystem services, food security, global change, habitat fragmentation, pollination, stability

1 | INTRODUCTION

Ensuring stable food supplies for a growing population is one of the United Nations Sustainable Development Goals (2017). Biodiversity-based approaches to food security suggest that safeguarding species diversity is fundamental to increase yields and guarantee stable yields. This is supported by theory and data reporting positive effects of biodiversity on the mean values of various ecosystem functions and services, such as biomass production, nutrient cycling and crop pollination (Lefcheck et al., 2015; Woodcock, 2019). Additionally, biodiversity can stabilize ecosystem service supply by providing an insurance against environmental fluctuations (Loreau et al., 2003), which are predicted to intensify under global change (Fischer et al., 2013; Giorgi et al., 2001; Saltz et al., 2006). Biodiversity insurance effects have been observed in agriculture, where a greater diversity of crops is associated with increased year-to-year temporal stability of total production (Renard & Tilman, 2019; Winfree & Kremen, 2009). However, most biodiversity in intensively managed agricultural landscapes is found in the remaining fragments of (semi) natural habitat not converted into crop land, and the effects of such non-crop biodiversity on the provision and stability of crop production are not clearly understood. This has led to a growing concern over the large-scale conversion of natural habitats into crop land and their effects on biodiversity and food production (Godfray & Garnett, 2014; Réchauchère et al., 2018; United Nations Sustainable Development Goals, 2017).

Agricultural systems are often highly fragmented with areas of intensive cultivation interspersed among remnant patches of semi-natural habitat. This loss and fragmentation negatively affect biodiversity and many ecosystem functions and services (Haddad et al., 2015; Rybicki et al., 2020). Despite this, fragments of natural habitat continue to supply important services. The spatial coexistence of crops and natural land creates an opportunity for spillover effects (Rand et al., 2006), a situation where ecological interactions extend across habitats boundaries and propagate ecological functions. In some cases, fragmentation can increase ecosystem service supply (Haan et al., 2020; Martin et al., 2019), for example, if fragmentation of natural habitat for pollinators optimizes interspersion with crop land to maximize crop pollination (Brosi et al., 2008). But fragmentation can also reduce ecosystem service supply if biodiversity decreases significantly in the remnant fragments of natural habitat (Haddad et al., 2015). For most services, however, we do not know how fragmentation affects their provision in fragmented landscapes, and this limits our capacity to manage biodiversity-based ecosystem service provision, for example, crop pollination and food security in human-dominated landscapes.

Recent research has revealed strong, nonlinear effects of land-use change on crop production at multiple spatial scales. For example, theoretical studies agree on the hump-shaped relationship between animal pollination-dependent crop production and the fraction of remnant natural land within intensive farming systems (Braat & ten Brink 2008; Mitchell et al., 2015; Montoya et al., 2019). Empirical research on the stability of animal-pollination-dependent crop production shows that stability decreases with agricultural intensification and the degree to which crops depend on animal pollination (Deguines et al., 2014; Garibaldi, Aizen, et al., 2011; Garibaldi, Steffan-Dewenter, et al., 2011; Garibaldi et al., 2014). Changes in crop production stability of animal-pollinated crops also depend on the spatial composition and structure of agricultural landscapes, such as the amount of natural land cover (Montoya et al., 2019) and the isolation of crops from natural land (Garibaldi, Steffan-Dewenter, et al., 2011). Overall, both theoretical and empirical studies suggest that improved management of agricultural landscapes should increase the amount and stability of animal-pollination-dependent crop production, and that an understanding of how the spatial pattern of land-use change—fragmentation—impacts ecosystem services is key to achieve this goal. However, none of these studies have simultaneously combined crop dynamics at different scales and spatially explicit landscapes to investigate the effects of land-use change on biodiversity and crop production services. Furthermore, while multiple factors can influence crop production in fragmented agroecosystems, our current understanding of how they interact and determine crop production stability, and thus food security, remains incomplete.

There is general consensus that increased food production is necessary, but not sufficient, to achieve food security (Godfray & Garnett, 2014), and that agriculture, especially in the global change context, should also aim at stabilizing crop production over time (Montoya et al., 2020; Schmidhuber & Tubiello, 2007). Bearing this in mind, we here extend a model of crop dynamics into a spatially explicit landscape to investigate how habitat loss and fragmentation, that is, the amount and spatial configuration of semi-natural habitat, influence the mean provision and stability of crop production in agricultural landscapes. We focus on animal-dependent crop production because (a) animal crop pollination is a key agricultural service that depends on biodiversity (pollinator animals) and (b) worldwide agriculture is shifting towards more animal pollination-dependent food production systems (Aizen et al., 2009; Breeze et al., 2014). Because the way food is produced worldwide threatens the existence of much of the world's biodiversity that contributes to crop pollination and food security, we explore how changes in biodiversity following land-use change affect animal-dependent crop production in fragmented agroecosystems. Thus, our model accounts for a variety of potential drivers of crop production mean and stability, such as loss and fragmentation of natural habitat and biodiversity, that are difficult to address collectively in empirical studies. Specifically, we address two questions: (a) How does the spatial pattern of land-use change influence the provision and stability of animal-dependent crop production in agroecosystems? (b) How does biodiversity in fragmented landscapes influence animal-dependent crop production and food security?

2 | MATERIALS AND METHODS

To study the effects of habitat fragmentation on biodiversity and crop production, we extended a non-spatial model of crop dynamics (Montoya et al., 2019) to a spatially explicit landscape. Our model has two types of patches: crop land and semi-natural habitat. Crop land is used to grow annual crops with varying degrees of dependence on animal pollination, whereas semi-natural habitat shelters biodiversity, including 'wild' plants and pollinators. The model does not consider managed honeybees as they do not depend on semi-natural habitat for nesting, and generally pollinate less efficiently than non-managed pollinators (Garibaldi et al., 2013). Naturalized *Apis* species are implicitly considered in the model as they nest in semi-natural habitat and forage across the landscape. This model represents intensively managed agricultural systems, where crop land does not host significant levels of biodiversity, and spatial heterogeneity is broadly defined by two patch types.

The model investigates the expected biodiversity (i.e. species richness) and crop production, with a special focus on animal-dependent crop production, at the farm level (i.e. crop yield per area) and landscape level (i.e. the magnitude and stability of crop production). We distinguish between two additive ecosystem services associated with crop production: the production that results from wild animal pollination (hereafter animal-dependent production), and the production that is independent from animal pollination (animal-independent production), but can be wind- or self-pollinated. Pollinators are assumed to be generalist central-place foragers that nest in semi-natural habitat (Gill et al., 2016), yet move across the landscape to forage on flowering crops, 'wild' plants or both. Crop land and semi-natural habitat are therefore linked by the pollinators' foraging movement. For simplicity, the model assumes similar foraging movements across pollinators. The main difference between the non-spatial and spatial models lies on the way pollinators link these two patch types: whereas in the non-spatial model pollinators move globally and reach all crop land, the spatial model imposes restrictions to pollinator's movement based on the spatial structure of the agricultural landscape (i.e. distribution of crop land and semi-natural habitat) and the foraging range of pollinators (i.e. spillover). A conceptual representation of the model, including non-spatial and spatial components, as well as key model assumptions, is provided in Figure 1. In what follows, we first describe the spatial agroecosystem model and then present a simpler, mean-field approximation of the model that we use to produce the results.

2.1 | Spatial agroecosystem model

The addition of space allows (a) to explore a continuous gradient of land-use change patterns, from completely random to highly aggregated, that encompasses a wide range of fragmentation scenarios, (b) to investigate the effects of fragmentation on pollinator diversity and crop production services and (c) to study how variations in the strength of spillover from semi-natural habitat to crop land—that is, the distance decay of pollination flow—affects animal-dependent crop production. To do this, we simulated a continuous gradient of land-use change patterns, and therefore fragmentation, based on the aggregation degree of semi-natural habitat. A complete description of the model parameters is found in Table 1. Information on model parameterization is in Appendix S1.

2.1.1 | Landscape pattern generation

The landscape consisted of a two-dimensional lattice (25 × 25 cells) where individual cells can have either of two states: crop land or semi-natural habitat. We generated land-use change patterns by iteratively creating crop land cells in a landscape that consisted initially only of semi-natural land. In a single step of the algorithm, only one semi-natural habitat cell is selected and converted. The pattern generation is controlled by a parameter w that determines the clustering degree of the land-use change pattern (see Appendix S1). Hence, for $w = 0$, all semi-natural land cells had the same relative probability to be chosen, leading to a fully random, unclustered pattern. Larger values of w resulted in more aggregated patterns. Therefore, variation in the value of w allowed us to produce a continuous gradient of land-use change patterns, and therefore fragmentation, based on the aggregation degree. For each land-use change pattern, we characterized fragmentation of the remaining semi-natural habitat by quantifying mean fragment size, number of fragments, mean fragment perimeter and perimeter:area ratio. Fragmentation directly affects pollinator diversity (through the estimation of the metapopulation capacity) and the *Landscape Pollination Potential* (LPP), which, in turn, influence crop production services (see below).

2.1.2 | General model dynamics

Pollinators, 'wild' plants and crop production are represented by Equations 1–3. In these equations, the first term defines growth and

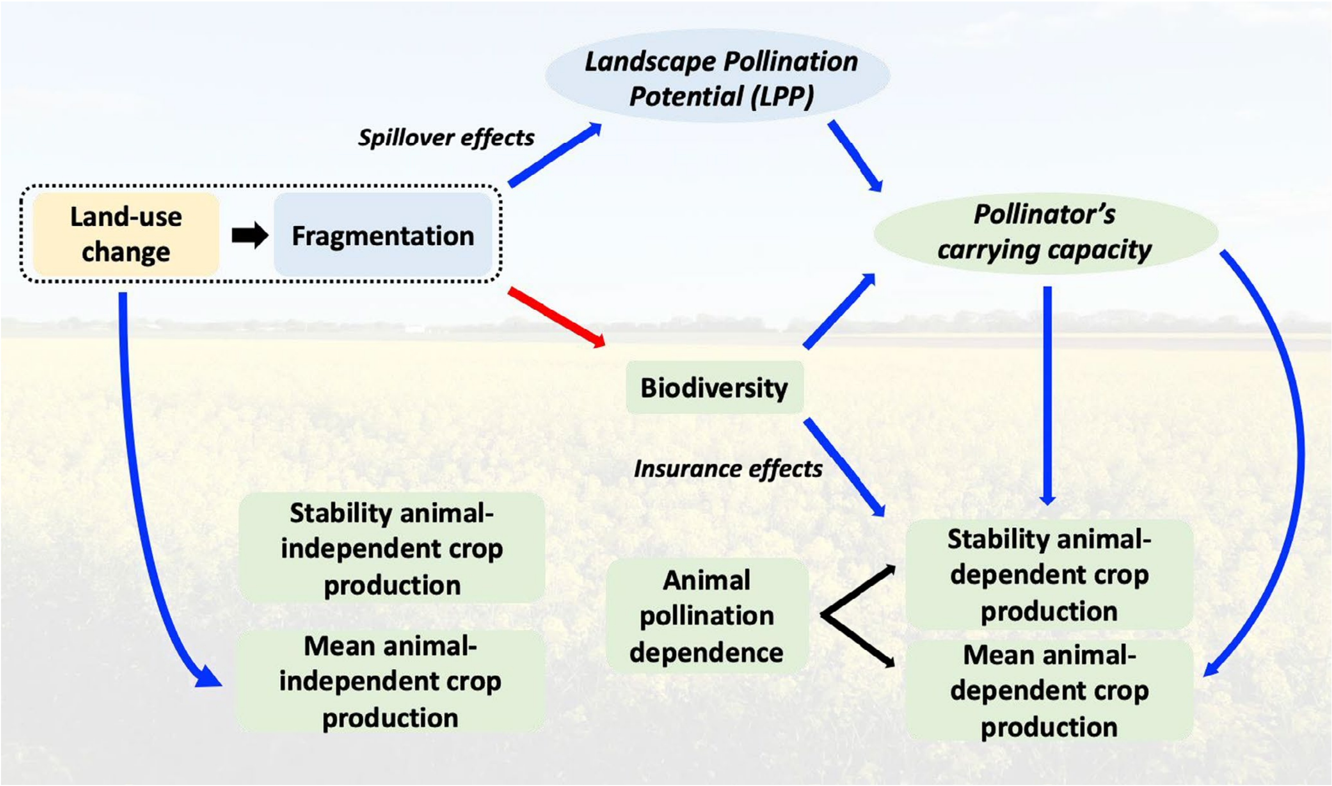

FIGURE 1 Conceptual diagram of our modelling framework. Green boxes represent non-spatial components of the model, whereas blue boxes are the additions that space brings to the model. Adding space allows (i) to explore a continuous gradient of land-use change patterns, from completely random to highly aggregated, that encompasses a wide range of fragmentation scenarios, (ii) to investigate the effects of fragmentation on pollinator diversity and animal-dependent crop production and (iii) to study how variations in the strength of spillover from semi-natural habitat to crop land—that is, the distance decay of pollination flow—affects animal-dependent production. Following a mean-field approximation, the Landscape Pollinator Potential (LPP) of the agricultural landscape captures the full complexity of fragmentation effects on ecosystem service supply that are not mediated by biodiversity. The model has some key assumptions: (i) agricultural system is intensively managed, defined by two patch types (crop land, semi-natural habitat), where crops are harvested yearly; (ii) pollinators are generalist central-place foragers, similar in movement patterns; (iii) pollinator spillover follows a logistic distance-decay function and (iv) positive relationships between pollinator diversity and animal-dependent production (mean and stability). Different effects are represented by different arrow colours: blue for positive, red for negative, black for neutral or context-dependent. Land-use change does not affect stability of animal-independent crop production (see main text), and no arrow is drawn. For further information on model assumption, see Methods and Appendix S1

is modelled using the discrete Ricker equation, whereas the second and third terms add environmental and demographic stochasticity to the model:

$$P_k(t+1) = P_k(t)\exp\left(r_{P,k}(t)\left(1-\frac{P_k(t)}{k_P A_1}\right)\right) + \sigma_P^e u_P^e(t)\,P_k(t) + \frac{\sigma_P^d u_P^d(t)}{\sqrt{P_k(t)}}P_k(t), \tag{1}$$

$$W_k(t+1) = W_k(t)\exp\left(r_{W,k}(t)\left(1-\frac{W_k(t)}{k_W A_1}\right)\right) + \sigma_W^e u_W^e(t)\,W_k(t) + \frac{\sigma_W^d u_W^d(t)}{\sqrt{W_k(t)}}W_k(t), \tag{2}$$

$$C_k(t) = A_1\left[Z_C + r_{C,k}(t)\right]\left(1+\sigma_C^e u_C^e(t)\right), \tag{3}$$

P_k represents the pollinators, W_k 'wild' plants and C_k crop production in cell k, with $P_k(t) = W_k(t) = 0$ if k is a crop land cell, and $C_k(t) = 0$ if k is semi-natural habitat. One unit of time t corresponds to one growing season, $P(t)$ and $W(t)$ can be interpreted as total biomass of pollinators and 'wild' plants over growth season t, respectively, whereas $C(t)$ is the total crop production at the end of the growing season t. $r_{P,k}(t)$, $r_{W,k}(t)$ and $r_{C,k}(t)$ are the pollinators', 'wild' plants' and crop's per capita growth rates, respectively. Z_C is the crop production independent of animal pollination, which allows varying degrees of animal dependence production. C_k is thus the sum of animal-dependent and -independent parts of crop production. k_P and k_W are the carrying capacities of pollinators and 'wild' plants, respectively, per unit area. A_1 is the area of a single cell; A is total landscape area; $A[1 - \omega_{sn}]$ is the total crop land area and $A\omega_{sn}$ is total semi-natural area. In the non-spatial model, k and A_1 were not defined. Stochasticity is included in the form of $\sigma\, u(t)$, where σ^2 is the variance (^{e}environmental or ^{d}demographic) and $u(t)$ are independent Gaussian random variables with zero mean and unit variance, of pollinators ($\sigma_P u_P$), 'wild' plants ($\sigma_W u_W$) or crops ($\sigma_C u_C$) (see model stochasticity section below).

TABLE 1 Parameters and variables of the model

Parameters & variables	Definition	Dimensions	Units
Parameters			
α_P	Maximum growth rate of pollinators	dimensionless	0.9
α_W	Maximum growth rate of semi-natural plants	dimensionless	0.9
α_C	Maximum crop production derived from pollinator interactions	mass·area^{-1}	1,000
β_P	Half-saturation constant of pollinators	mass	0.6
β_W	Half-saturation constant of 'wild' plants	mass·area^{-1}	0.6
β_C	Half-saturation constant of crop plants to pollinators	mass·area^{-1}	0.01
k_P	Carrying capacity of pollinators per unit area	mass·area^{-1}	*
k_W	Carrying capacity of semi-natural plants per unit area	mass·area^{-1}	5,000
A	Total landscape area	area	10
n^2	Number of cells in the simulated landscape	dimensionless	625
A_1	Area of a single cell	area	1
ω_{sn}	Proportion of semi-natural habitat	dimensionless	{0–1}
w	Aggregation parameter of the fragmentation pattern generation algorithm	dimensionless	{0, 5}
Z_C	Crop production independent of animal pollinators	mass·area^{-1}	{0, 1,000, 4,000}
d_m	Distance over which the pollination flow equals one half of its initial value	distance	{0.1–10}
Δd	Distance over which the pollination flow decreases from 90% to 10% of its initial value	distance	{0.1–10}
c_s	Pre-factor of the SAR function	dimensionless	*
z_s	Exponent of the SAR function	dimensionless	0.25
c_P	Parameters of the power law (k_P dependence on S)	mass·area^{-1}	1
z_P	Parameters of the power law (k_P dependence on S)	dimensionless	{0, 0.26, 0.5}
$\sigma^e{}_P$	Environmental standard deviation of pollinators	dimensionless	0.8
$\sigma^e{}_W$	Environmental standard deviation of 'wild' plants	dimensionless	0.02
$\sigma^e{}_C$	Environmental standard deviation of crop production	dimensionless	0.03
$\sigma^d{}_P$	Demographic standard deviation of pollinators	mass$^{-1/2}$	0.1
$\sigma^d{}_W$	Demographic standard deviation of semi-natural plants	mass$^{-1/2}$	0.5
$u^e{}_P$, $u^d{}_P$, $u^e{}_W$, $u^d{}_W$, $u^e{}_C$	Gaussian random variables with zero mean and unit variance. u^e = environmental, u^d = demographic P = pollinators; W = 'wild' plants; C = crop plants	dimensionless	Gaussian random variables with zero mean and unit variance
S	Number of pollinator species	dimensionless	*
b	Parameter modulating the effect of the meta-population capacity (SFAR)	dimensionless	{10, 20, 50}
$1/\delta$	Dispersal distance to calculate meta-population capacity (SFAR)	dimensionless	{1–10}
λ_M	Meta-population capacity (SFAR)	dimensionless	*
Variables			
$C_k\,(t)$	Biomass of crop plants (crop production) in cell k	mass	*
$W_k\,(t)$	Biomass of semi-natural or 'wild' plants in cell k	mass	*
$P_k\,(t)$	Biomass of pollinators in cell k	mass	*
$r_{P,k}\,(t)$	Intrinsic growth rate of pollinators in cell k	dimensionless	*
$r_{W,k}\,(t)$	Intrinsic growth rate of 'wild' plants in cell k	dimensionless	*
$r_{C,k}\,(t)$	Crop production derived from pollinator interactions	mass·area^{-1}	*

(Continues)

TABLE 1 (Continued)

Parameters & variables	Definition	Dimensions	Units
Other			
d_{kl}	Distance between cells *k* and *l*	distance	*
ε_{kl}	Distance-decay function of ecosystem service flow	dimensionless	*

Note: An asterisk in the unit column indicates that the value of that parameter depends on fragmentation.

2.1.3 | Growth rate of pollinators and plants

Since pollinators are assumed to be generalist central-place foragers, pollinator's growth rate depends on the availability of resources ('wild' plants and crops) in the neighbourhood. Plant and pollinator uptake of resources, as well as the animal-dependent crop production, follow a saturating, type II functional response, widely supported and consistent with real biological examples (Holland, 2015; Holland et al., 2013; Thébault & Fontaine, 2010). Growth rates are thus defined by the following Monod/Michaelis–Menten equations:

$$r_{P,k}(t) = \frac{\alpha_P \left[\frac{\sum_{l \notin L} \varepsilon_{kl} W_l(t) + \sum_{l \in L} \varepsilon_{kl} C_l(t)}{A} \right]}{\beta_P + \frac{\sum_{l \notin L} \varepsilon_{kl} W_l(t) + \sum_{l \in L} \varepsilon_{kl} C_l(t)}{A}}, \tag{4}$$

$$r_{W,k}(t) = \frac{\alpha_W \left(\frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A} \right)}{\beta_W + \frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A}}, \tag{5}$$

$$r_{C,k}(t) = \frac{\alpha_C \left[\frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A} \right]}{\beta_C + \frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A}}, \tag{6}$$

where ε_{kl} is the distance-decay function representing the decrease in ecosystem service flow from semi-natural habitat to crop land (i.e. spillover effects, see below); *L* is the set of crop land cells; α_P and α_W are the maximum growth rates of pollinators and 'wild' plants, respectively; β_P and β_W are half-saturation constants of pollinators and 'wild' plants, respectively; α_C is the maximum crop production derived from pollination, and β_C is the half-saturation constant of crops.

Because crops vary in their dependency on animal pollination, different crop types can respond differently to landscape fragmentation. In our model, the degree to which crops depend on animal pollination is measured by $\alpha_C/(Z_C + \alpha_C)$, and reflects the part of total crop production dependent on animal pollination—that is, animal-dependent production. Landscape crop production is estimated by summing up the individual contribution of each cell *k*. Thus, for total crop production, we obtained $C(t) = \sum_{k \in L} C_k(t)$. We assume that crops are harvested yearly; hence, mean crop production represents the temporal mean of the yearly averaged crop production across the agricultural landscape. Crop yield per unit of agricultural area is calculated by dividing total crop production by crop land area.

2.1.4 | Model stochasticity

To investigate the effects of fragmentation on crop production stability, the model includes environmental and demographic stochasticity (second and third terms, Equations 1–3). Stochasticity is included in the form of $\sigma\, u(t)$, where σ^2 is the variance and $u(t)$ are independent Gaussian random variables with zero mean and unit variance, of pollinators ($\sigma_P u_P$), 'wild' plants ($\sigma_W u_W$) or crops ($\sigma_C u_C$). Environmental stochasticity ($\sigma^e u^e(t)$) reflects variation in weather variables, for example, temperature and rainfall, whereas demographic stochasticity ($\sigma^d u^d(t)$) emerges from stochastic variation in individuals' births and deaths, commonly observed in nature and important in small populations. Crops are sown at high densities, and thus we assume demographic stochasticity is prevented in crops. These two sources of stochasticity add biological realism to the model, as they allow variation in the biomass of pollinators, 'wild' plants and crops, useful to assess stability. We used $1/\mathrm{CV}^2$ as a metric of stability (invariability), where CV is the temporal coefficient of variation of crop production. This measure of stability is commonly used in ecological studies (Loreau & De Mazancourt, 2013).

2.1.5 | Distance decay of pollinators (spillover effects)

The spatially explicit nature of the model allows to study how variations in the strength of spillover effects influences crop pollination. Ecosystem service distance decay (ε_{kl}) affects the flow of pollination to crop land: the further crops are from semi-natural habitat, the more difficult it is for pollinators to reach the crops, and thus the smaller the effect of pollinators on crop production. To model spillover effects, we used a logistic distance-decay function adapted from Mitchell et al. (2015) (Appendix S1). This function is consistent with both theoretical predictions (Rand et al., 2006; Ricketts et al., 2008; Ries et al., 2004) and empirical observations (Farwig et al., 2009; Martins et al., 2015; Mitchell et al., 2014) of the effects of habitat edges and distance-to-habitat fragment gradients on ecosystem service provision. The logistic distance-decay function has two parameters: (a) the distance from semi-natural cell edge at which the pollination flow equals one half of its initial value—50% decay distance—(d_m) and (b) the distance over which the pollination flow decreases from 90% to 10% of its initial value—90% to 10% decay distance (Δd).

2.1.6 | Fragmentation, biodiversity and crop pollination

To consider the effects of fragmentation on biodiversity and crop production, we included two relationships in our model: (a) the dependence of pollinator diversity on the amount and distribution of semi-natural habitat and (b) the dependence of crop production on pollinator diversity. In the first case, we used the *Species-Fragmented Area Relationship* (SFAR; Hanski et al., 2013), which extends one of the oldest known and most documented patterns in ecology—the species–area relationship (SAR)—to fragmented landscapes. Despite recent debate has ensued on the relative importance of habitat loss versus fragmentation on species diversity (Fahrig et al., 2018; Fletcher et al., 2018; Rybicki et al., 2020), empirical evidence shows that larger and more connected fragments of natural habitat in general host more biodiversity than smaller, more isolated fragments (Haddad et al., 2015). In agricultural landscapes, this means that different fragmentation patterns will affect biodiversity and crop production in different ways. In an agricultural landscape, the SFAR can be modelled as a power law: $S = c_s \left(A\omega_{sn}\right)^{z_s}$, where S is pollinator diversity, $A\omega_{sn}$ is the total area of semi-natural habitat and z_s is the power-law exponent. The pre-factor c_S is not a constant as in the standard SAR; rather, it decreases in more fragmented landscapes (see Appendix S1 for more details).

For the second relationship—the dependency between crop production and pollinator diversity—we created a dependence of pollinator's carrying capacity (k_P) on biodiversity following a power law: $k_P = c_P S^{z_P}$, where S is the number of pollinator species estimated by the SFAR, and c_P, z_P are parameters of the power law (Liang et al., 2016; O'Connor et al., 2017). Although pollinators can differ in their pollination efficiency (Kleijn et al., 2015; Matsuki et al., 2008; Willcox et al., 2017), such differences do not dilute the positive relationship between pollinator diversity and crop production and yield, as reported in meta-analytical studies (Woodcock et al., 2019). Additionally, we considered the ability of pollinator diversity to provide an insurance against environmental fluctuations. Following the biodiversity insurance hypothesis (Loreau et al., 2003), pollinator diversity insures crop production because many pollinators better maintain crop production if pollinators differ in their responses to environmental variation. We followed the ecological literature and made pollinators' environmental stochasticity inversely related to their diversity ($\sigma_P^e = e_P/S^q$; Tilman, 1999). Demographic stochasticity acts at the individual level, and in the same manner for conspecifics and heterospecifics; thus, there is no insurance effect for demographic stochasticity.

2.2 | Non-spatial model results: Summary

The relationship between mean crop production and the proportion of semi-natural habitat is hump-shaped, and the height and position of the hump depends on crop pollination dependence ($\alpha_C/(Z_C + \alpha_C)$) and the crop relative requirement for pollinator densities (β_C/k_P) (Figure S1; Montoya et al., 2019). Higher and lower values of these factors, respectively, shift maximum production to higher fractions of semi-natural habitat. On the other hand, the stability of animal-dependent crop production is generally an increasing function of proportion of semi-natural habitat and is also determined by the same factors: higher crop pollination dependence and crop relative requirement for pollinators decrease stability.

2.3 | Mean-field approximation of the spatial model

Given the computational demands of the model, we developed a mean-field approximation which replaces the detailed spatial flows between semi-natural habitat and crop land cells by their values spatially averaged over the landscape. More precisely, we substituted the pollination flow decay coefficients (Equations 4–6) by the average $\overset{!!}{\varepsilon}$ (i.e. the average value of ε_{kl} when taking a random cell $k \in L$ and a random cell $l \notin L$):

$$\overset{!!}{\varepsilon} = \frac{1}{\left(1-\omega_{sn}\right)n^2}\frac{1}{\omega_{sn}n^2}\sum_{k \in L, l \notin L}\varepsilon_{kl}. \tag{7}$$

This quantity has two complementary interpretations (see Appendix S2 for the derivation). First, it is the fraction of semi-natural habitat from which a crop land cell can be pollinated, averaged over all crop land cells. Second, it is the fraction of crop land that is reachable by pollinators from a semi-natural habitat cell, averaged over all semi-natural cells. Taken together, these two interpretations can be summarized by the term *Landscape Pollination Potential* or LPP (LPP replaces $\overset{!!}{\varepsilon}$ hereafter; $0 \le \text{LPP} \le 1$).

The mean-field approximation is a very accurate description of the ecosystem service dynamics in agricultural landscapes (Figure 2; Appendix S2) and shows that the spatial effects of fragmentation on animal-dependent crop production are determined by LPP. Thus, LPP is a metric that captures fragmentation and pollinator spillover effects within agricultural landscapes. To consider the spatial structure of land-use change, the term β_C/k_P of the non-spatial model must be replaced by.

$$\frac{1}{\text{LPP}}\frac{\beta_C}{k_P}, \tag{8}$$

where β_C/k_P is the crop relative requirement for pollinators (described above).

3 | RESULTS

The results here presented correspond to the mean-field approximation, as it provides a very accurate description of the model dynamics (Figure 2). We present three groups of results: (a and b) the effects of LPP and biodiversity on crop production and (c) the net effects of fragmentation on animal-dependent production.

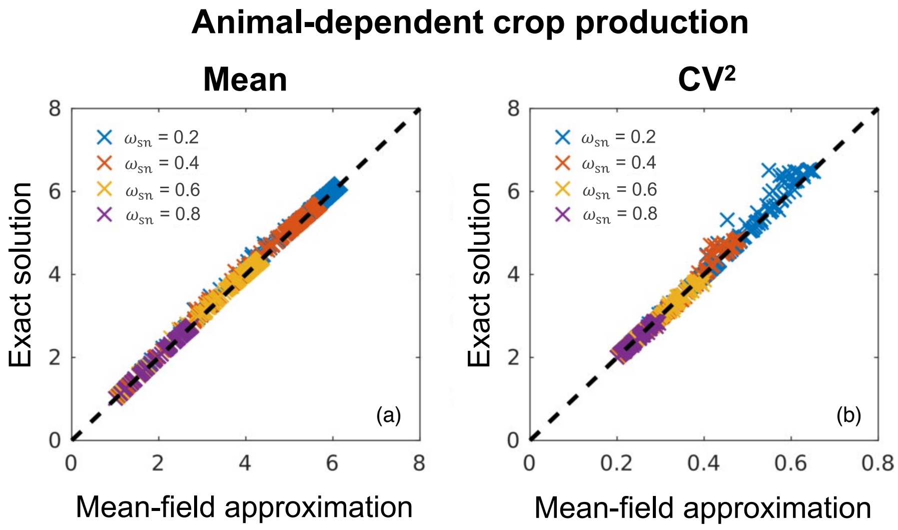

FIGURE 2 Mean-field approximation versus Exact solution. (a) Mean animal-dependent crop production. (b) Variability of animal-dependent crop production (measured as coefficient of variation [CV], the inverse of stability). A range of fragmentation patterns with different levels of spatial aggregation were generated for different fractions of semi-natural habitat. For different fractions of semi-natural habitat ω_{sn}, we generated 200 fragmentation patterns using the algorithm described in the methods section, with aggregation parameter w drawn uniformly from the interval [0, 5], and pollinator spillover distance d_m drawn uniformly from the interval [0.1, 4]. For each fragmentation pattern, we computed the mean and stability of animal-dependent crop production in two different ways: first by solving exactly the spatially explicit model (Appendix S2, Equations S8 and S17) and second by using the mean-field approximation (Appendix S2, Equations S35 and S36). ω_{sn} is the proportion of semi-natural habitat. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $\beta_C = 0.01$, $A = 10$, $Z_C = 1{,}000$, $\alpha_C = 1{,}000$, $k_W = 5{,}000$, $k_P = 0.1$, $\sigma_P^e = 0.8$, $\sigma_P^d = 0.1$, $\sigma_C^e = 0.03$, $\alpha_C = 1{,}000$, $z_P = 0.26$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$, $b = 10$, $q = ½$, pollination dependence = 50%

3.1 | Effects of LPP on crop production

When LPP = 1, fragmentation effects are negligible and crop dynamics are identical to those of the non-spatial model (Figure 3a–c, dark-blue lines). In this case, we retrieve the same mechanisms of the non-spatial model (Montoya et al., 2019). The effects of fragmentation kick off when LPP < 1. Lower LPP reduces the carrying capacity of pollinators *effectively*; that is, the effects of LPP on the mean and stability of crop production can be fully taken into account by changing the value of the pollinators' carrying capacity from k_P to LPP*k_P (Equation 8). LPP-driven reduction in pollinators' carrying capacity decreases the mean provision of animal-dependent production (Figure 3a) and crop yield per area (crop yield per area increases with semi-natural habitat, but larger LPP saturates this relationship earlier; Figure 3c). The same is true for the stability of animal-dependent production, except at small fractions of semi-natural habitat and/or small values of LPP (Figure 3b). LPP has no effect on animal-independent crop production as it does not depend on animal pollination and, therefore, on semi-natural habitat; its mean value decreases linearly with semi-natural habitat, whereas its stability is solely determined by environmental stochasticity (Figure 3d,e). Because of this, animal-independent crop production is not further considered in subsequent results. Whereas the full complexity of the spatial fragmentation effects (i.e. those not mediated by biodiversity) on animal-dependent production is captured by LPP (Figure S2), we did not find any clear, consistent effect of specific fragmentation metrics (Figure S3), except for '*Number of crop land cells > distance threshold*'. This is because the latter variable uses distance-decay parameter d_m as the reference threshold, and it is thus correlated with LPP. However, the dependence of both metrics on d_m does not really explain their correlation: LPP measures the fraction of crop land within a distance d_m of semi-natural habitat and quantifies the interspersion of semi-natural habitat and crop land at the scale of the pollination spillover distance d_m, thus capturing an important dimension of fragmentation (i.e. interspersion) that is not or poorly considered by the standard fragmentation metrics. Finally, the effect of LPP on animal-dependent production increases with the degree to which crops depend on animal pollination: higher pollination dependence shifts maximum production to higher fractions of semi-natural habitat at landscape and local scales, and the stability of animal-dependent production increases faster (Figure S4), consistent with Montoya et al. (2019).

Landscape pollination potential depends on two factors: fragmentation and spillover, or the distance decay of ecosystem service flow. High aggregation (low fragmentation) and fast distance decay result in lower LPP (LPP < 1), which, in turn, reduces animal-dependent crop production. These two factors interact: only when the flow of pollinators to crop land is limited (fast distance decay) aggregation patterns influence animal-dependent production. When no restrictions exist in the flow of pollinators to crop land, LPP is maximum and fragmentation does not affect animal-dependent production (LPP ≈ 1).

3.2 | Effects of biodiversity on crop production

In parallel to LPP, pollinator diversity also impacts animal-dependent crop production. As expected, biodiversity enhances

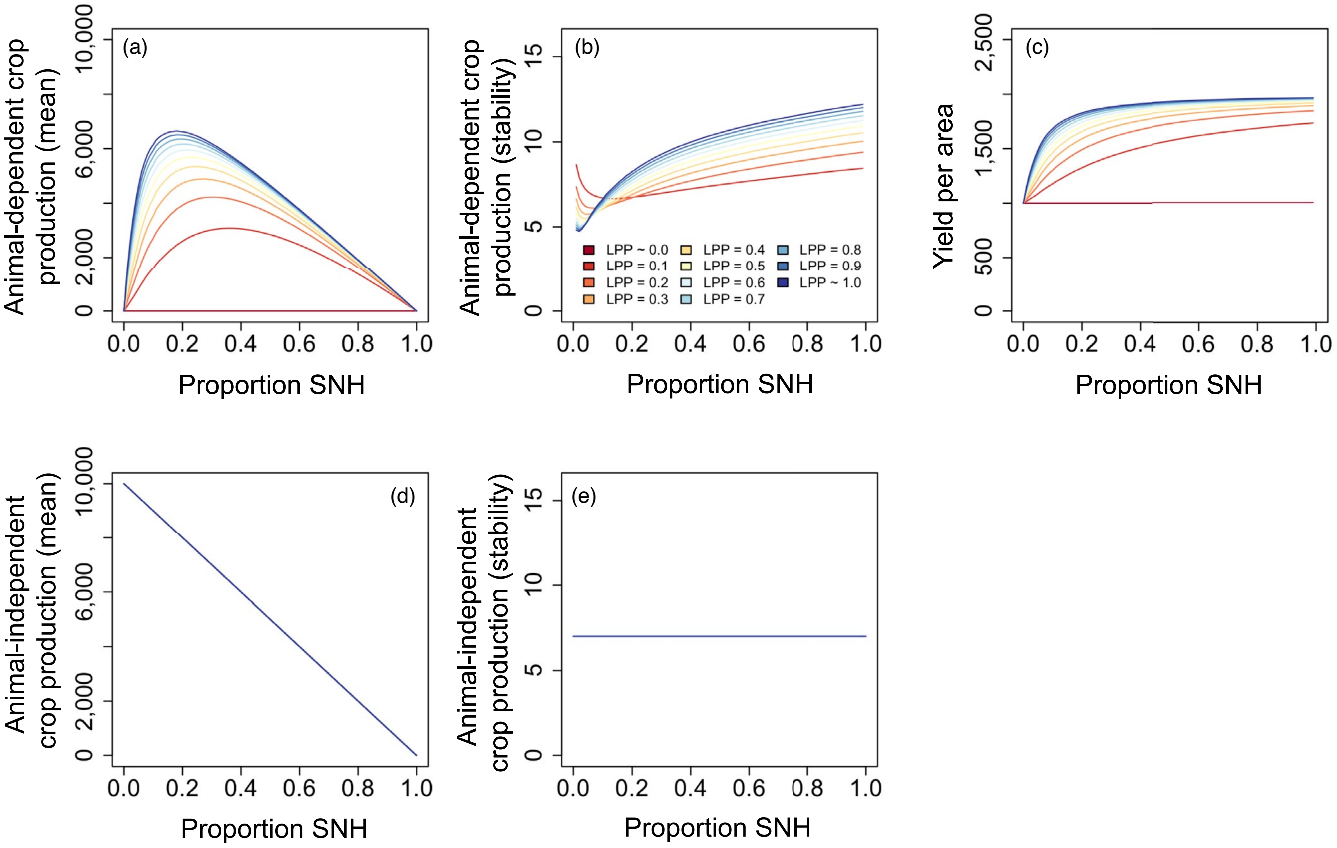

FIGURE 3 Effects of landscape composition and landscape pollination potential (LPP) on crop production. (a) Mean animal-dependent production, (b) stability of animal-dependent production stability, (c) total yield per area, (d) mean animal-independent production and (e) stability of animal-independent production. Ecosystem services are represented as a function of the proportion of semi-natural habitat, for different LPP. LPP includes the effects of fragmentation—more specifically, the aggregation pattern of land-use change—and the distance decay of ecosystem service flow. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $\beta_C = 0.01$, $A = 10$, $Z_C = 1{,}000$, $\alpha_C = 1{,}000$, $k_W = 5{,}000$, $\sigma_P^e = 0.8$, $\sigma_P^d = 0.1$, $\sigma_C^e = 0.03$, $\alpha_C = 1{,}000$, $z_P = 0.26$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$, $b = 10$, $q = ½$, pollination dependence = 50%

animal-dependent production at local (i.e. yield per area) and landscape scales (Figure 4a,c), and stabilizes animal-dependent production (Figure 4b) by increasing the pollinators' carrying capacity, and by reducing the response of animal-dependent production to environmental fluctuations. A higher biodiversity effect (larger z_P) increases both mean animal-dependent production and its stability, as well as yield per area.

3.3 | Net effects of fragmentation on crop production

Fragmentation has a dual effect on animal-dependent crop production. On the one hand, aggregation of semi-natural fragments decreases pollination by lowering LPP, which, in turn, reduces the pollinators' carrying capacity. On the other hand, aggregation benefits biodiversity (Figure S5), which, in turn, increases pollinators' biomass and animal pollination. The net effect of fragmentation on animal-dependent production depends on the distance decay of ecosystem service flow (d_m) and the proportion of semi-natural habitat remaining. When the decay distance is low (Figure 5, first row), fragmentation effects tend to be positive for mean animal-dependent production and yield per area because the fraction of crop land within reach from non-crop land areas is higher. Yet, the stability of animal-dependent production decreases due to the lower biodiversity in fragmented landscapes, except at high fractions of semi-natural habitat where the impact of fragmentation is minimum. Conversely, when the decay distance is high, semi-natural fragments are perceived as more connected and animal-dependent production is not limited by space. In this case, fragmentation becomes irrelevant, or even negative, due to the lower biodiversity in fragmented landscapes (Figure 5, last row).

4 | DISCUSSION

Our analysis reveals a variety of effects of land-use change on biodiversity and crop production. Using a mean-field approximation, our model suggests that (a) the full complexity of the fragmentation-induced spatial effects on animal-dependent crop production is captured by one factor—the Landscape Pollination Potential of the remaining semi-natural land (LPP)—which determines the mean and

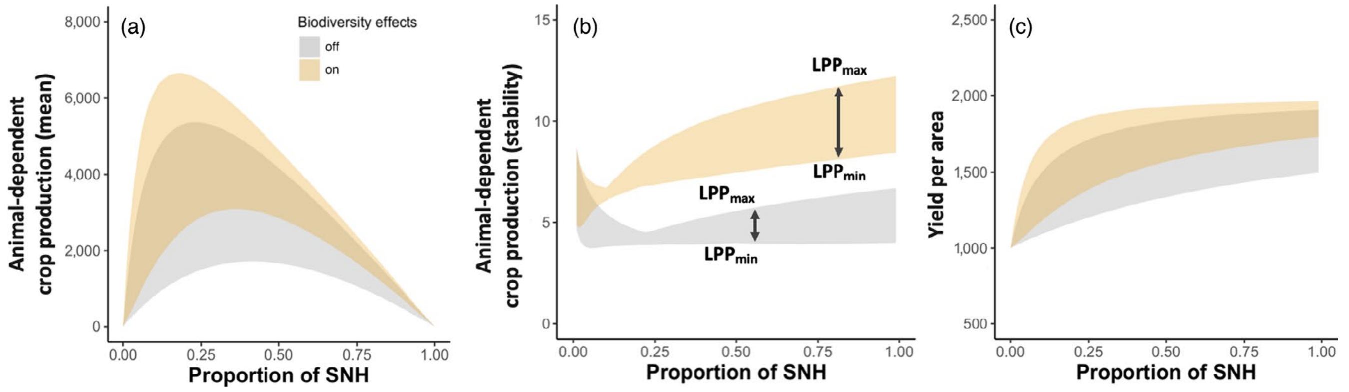

FIGURE 4 Effects of biodiversity on animal-dependent crop production. Plots show the response of animal-dependent production mean and stability (panels a and b), and yield per area (panel c)—as a function of the proportion of semi-natural habitat (SNH). All landscape pollination potential (LPP) values are contained within the shadows, whose limits are determined by the minimum and maximum values across the range of LPP (illustrated by the arrows joining $\mathrm{LPP}_{\min}$ and $\mathrm{LPP}_{\max}$ values in panel b). Biodiversity can affect crop production in a two-way manner. On the one hand, biodiversity influences mean animal-dependent production and yield per area by increasing the carrying capacity of pollinators ($k_p = c_P S^{z_P}$). On the other hand, biodiversity impacts the stability of animal-dependent crop production both indirectly—increasing the carrying capacity of pollinators—and directly—reducing the response of animal-dependent production to environmental fluctuations ($\sigma_P^e = e_P/S^q$). For each ecosystem service, the plots compare two scenarios: (i) a scenario where biodiversity has no effect on animal-dependent production ($z_P = 0$, $q = 0$), represented by the grey shadows, versus (ii) a scenario where biodiversity has an effect on animal-dependent production ($z_P = 0.26$, $q = ½$) (Liang et al., 2016; O'Connor et al., 2017; Tilman, 1999), represented by the light orange shadows. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $\beta_C = 0.01$, $A = 10$, $Z_C = 1{,}000$, $\alpha_C = 1{,}000$, $k_W = 5{,}000$, $\sigma_P^e = 0.8$, $\sigma_P^d = 0.1$, $\sigma_C^e = 0.03$, $\alpha_C = 1{,}000$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$, $b = 10$, pollination dependence = 50%

stability of animal-dependent production; (b) fragmentation reduces biodiversity and increases LPP, thus impacting animal-dependent production in opposite directions and (c) the net effects of fragmentation on animal-dependent production depend on the strength of pollinators' spillover to crop land, the proportion of semi-natural habitat remaining and the degree to which crops depend on animal pollination.

The loss of semi-natural land has contrasting effects on agricultural landscapes: biodiversity decreases, animal-independent crop production increases while animal-dependent crop production is maximized at intermediate fractions of semi-natural habitat. But fragmentation can modify these relationships in two ways. First, land-use change can produce multiple patterns of aggregation of semi-natural habitat fragments. These patterns, combined with the strength of the spillover of pollinators to crop land, determine the Landscape Pollination Potential of semi-natural land, which is one main driver of food production in animal-dependent agriculture. The second type of effects are mediated by biodiversity, as the level of aggregation of semi-natural habitat affects the pollinator richness. Such purely spatial and biodiversity-mediated effects modify the carrying capacities of pollinators, which ultimately determine animal-dependent crop production. The mean-field approximation shows that the effects of space on animal-dependent production can be interpreted in the same terms as varying the pollinator's carrying capacity in the non-spatial model, that is, a lower LPP reduces the pollinator's carrying capacity and the provision of animal-dependent production.

Our results suggest that understanding the factors that affect Landscape Pollinator Potential is a fundamental step towards food security in animal-dependent agriculture. If no restrictions exist in the flow of pollinators to crop land, LPP is maximum and the spatial structure of land-use change does not affect crop dynamics. In this situation, semi-natural fragments are perceived as more connected and the provision and stability of animal-dependent production is not conditioned by the spatial configuration, that is, spatial and non-spatial models converge. However, agricultural landscapes are fragmented to some extent and the foraging ranges of most organisms are local (Darvill et al., 2004; Geib et al., 2015; Zurbuchen et al., 2010), which produces higher aggregation and weaker spillover effects, thus reducing LPP. Such reductions in LPP affect crop production by (a) decreasing mean animal-dependent production and total yield per area and (b) decreasing the stability of animal-dependent production along the semi-natural habitat gradient. Because LPP can have important implications for crop production, it would be interesting to operationalize this metric in empirical studies and landscape management. The estimation of LPP in real farming systems would require data on the aggregation of semi-natural habitat, and on the spillover of pollinators to adjacent crops. The former can be obtained with GIS processing of aerial pictures or satellite images. For the latter, information on foraging distances of existing pollinator species (this comes from ecological censuses) combined with experimental studies could be used to reveal species' foraging patterns and how the flow of pollinators to adjacent crop land decays with distance (examples of this type of studies are Rand et al., 2006; Ricketts et al., 2008; Ries et al., 2004). This information will be useful to design agricultural landscapes for high LPP. Although measuring LPP in empirical studies demands more data than simple, traditional fragmentation

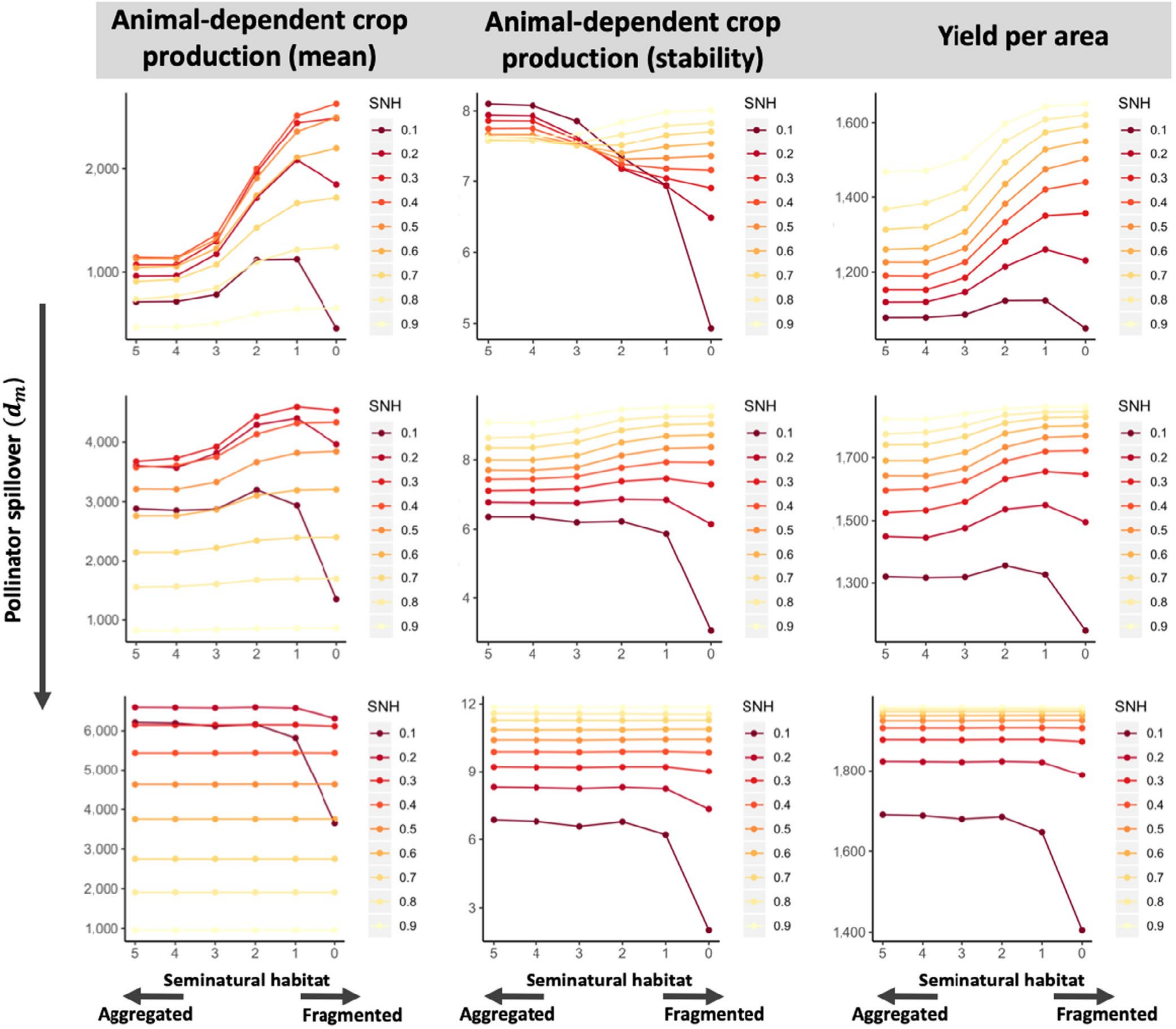

FIGURE 5 Net effects of aggregation on animal-dependent crop production. Columns represent, from left to right, mean and stability of animal-dependent production, and yield per area. Ecosystem services are plotted as a function of fragmentation for different proportion of semi-natural habitat or SNH (as opposed to Figures 3 and 4). In each plot, fragmentation increases in the *x*-axis from left to right. Darker lines correspond to lower fractions of semi-natural habitat, which are more typical of intensive farming systems. Rows represent increasing values of pollinator spillover or decay distance d_m (0.5, 1, 5). Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $\beta_C = 0.01$, $A = 10$, $Z_C = 1{,}000$, $\alpha_C = 1{,}000$, $k_W = 5{,}000$, $\sigma_P^e = 0.8$, $\sigma_P^d = 0.1$, $\sigma_C^e = 0.03$, $\alpha_C = 1{,}000$, $z_P = 0.26$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$, $b = 10$, $q = ½$, pollination dependence = 50%

metrics, this investment is worthy as LPP can be a better predictor of crop production.

Producing food requires land, and increasing the land devoted to farming reduces the land devoted to biodiversity conservation. This and other recent empirical studies show that pollinator diversity can increase food production (Catarino et al., 2019; Dainese et al., 2019; Woodcock et al., 2019), and lead to lower variability in agricultural productivity. This is relevant in the global change context, as biodiversity can stabilize animal-dependent crop production by providing an insurance against environmental fluctuations, which are predicted to intensify under global change (Fischer et al., 2013; Giorgi et al., 2001; Saltz et al., 2006). The response of biodiversity to land-use change depends on the amount and the spatial structure of semi-natural habitat. For example, although the effects of fragmentation on biodiversity are stronger at low-intermediate fractions of semi-natural habitat—typical of intensive farming systems—aggregation favours biodiversity within semi-natural habitat fragments. The stabilizing effect of biodiversity and its role in food security is increasingly supported, even at crop levels (Renard & Tilman, 2019). Our results add to this view and point to biodiversity conservation as one key policy to achieve food security.

Our findings are consistent with previous studies that found nonlinear effects of fragmentation on ecosystem services (Keitt, 2009; Mitchell et al., 2015), and provide a theoretical basis of the effects of fragmentation on the stability of animal-dependent crop production. Fragmentation has a dual effect on animal-dependent production. On the one hand, aggregation decreases animal-dependent production by reducing the Landscape Pollination Potential. On the other hand, aggregation increases animal-dependent production by maintaining higher biodiversity, especially when the proportion of semi-natural habitat within the agricultural landscape is medium or low. The net effects of aggregation on animal-dependent crop production depend on the strength of spillover effects. These results have management implications (e.g. land sharing–sparing debate; Fischer et al., 2014; Grass et al., 2019), as the goals of different landscape managers can be conditioned by the way that natural land is converted into crops. For example, maintaining a large number of semi-natural fragments may be a better strategy at multiple spatial scales than maintaining a few large fragments when pollinator flow to crop land is low. Yet, this strategy may increase the temporal variability of animal-dependent production at low-intermediate proportions of semi-natural habitat, reflecting a trade-off between ecosystem service mean and stability. Conversely, larger fragments of semi-natural habitat have higher pollinator diversity when the fraction of semi-natural habitat is low or intermediate, and higher biodiversity can stabilize animal-dependent production. These results agree with recent claims that the land sharing–sparing dichotomy lends itself to overly simplistic policy prescriptions (Kremen, 2015), and suggest that management decisions for food security should consider factors such as pollinators' spillover, the amount and spatial aggregation of semi-natural habitat and the animal pollination dependence of crops. Our results also provide recommendations for landscapes with both animal-independent and -dependent crops. In such cases, for a given proportion of semi-natural habitat, management should maximize the Landscape Pollination Potential while preserving pollination diversity, favouring mean crop production and its stability. This could be achieved by increasing fragmentation of semi-natural habitat in the vicinity of animal-dependent crops, but without making semi-natural habitat patches too small so that biodiversity is not negatively affected. Animal-independent production only depends on how much semi-natural habitat there is, and is not affected by fragmentation because it does not depend on animal pollinators and semi-natural habitat.

Aside from Landscape Pollination Potential (see above), what type of empirical data could be used to calibrate key parameters of the model? Carrying capacities of pollinators and wild plants can be approximated from species biomass and ecological censuses of species numbers (Appendix S1), yet this assumes that communities are saturated. On the other hand, animal pollination dependencies of the large majority of crops are available from pollinator exclusion experiments (e.g. Klein et al., 2007). Pollinator spillover depends on the distance-decay function, and its parameters values require data on pollinator movement patterns (distance, range), which can be obtained via experiments and observational studies (e.g. tracking of 'marked' pollinator individuals with remote devices; e.g. Ratnakaye et al., 2021). Finally, experimental studies provide information to calibrate biodiversity estimates in fragmented landscapes (SFAR function; Appendix S1), as well as the effect of pollinator diversity on animal-dependent crop production (Liang et al., 2016; O'Connor et al., 2017).

Our model has several limitations. First, our model focuses on intensive farming systems, where crop land does not host important biodiversity levels; other types of agriculture—for example, organic farming—allow moderate levels biodiversity to thrive within crop land, and can modify the results reported here (Clough et al., 2011). The model does not consider fine-scale semi-natural patches (e.g. wildflower strips, hedgerows) that might support high pollinator diversity by providing complementary resources within a short range from crops, nor it considers habitat quality differences within semi-natural fragments; although the latter can affect the abundance and composition of pollinators, it would not qualitatively affect the positive effect of pollinator diversity on animal-dependent production. Also, the observation that biodiversity loss has either none (stability) or positive (mean) effects on animal-independent crop production may change if organisms responsible for other services, for example, pest control, are included. Besides, although semi-natural habitat had no effect on the stability of animal-independent production, this may change if environmental stochasticity of crops increases with decreasing amounts of semi-natural habitat, as suggested by studies linking semi-natural habitat to climate regulation, natural hazard regulation and water flow regulation services (Harrison et al., 2010). In addition, negative perturbations larger than the ones considered in our model may be possible; although the so-called black-swan events are rare (e.g. they affect ~3% of insect populations; Anderson et al., 2017), they could heavily decrease pollinator diversity, with negative impacts on animal-dependent crop production. Differences in pollination efficiency may affect LPP and could be captured using functional group analysis (Mayfield et al., 2010); yet, the positive diversity-function relationship still holds even considering such differences (Woodcock et al., 2019). Also, differences in flight ability and range across pollinators influence pollinator diversity within agricultural landscapes (e.g. InVEST Crop pollination model, Lonsdorf et al., 2009), and this may, in turn, affect LPP, through its effects on pollinator spillover, and the provision of animal-dependent production. Therefore, differences in movement/flight patterns of pollinators should be considered in future extensions of the model, for example, large bees such as *Bombus* species are powerful long-distance pollinators, whereas smaller bees forage locally (e.g. *Lasioglossum*, *Halictus*). Finally, our model focuses on wild central-place pollinators (i.e. all types of wild bees, including bumble bees and solitary bees), whose presence and abundance directly depend on semi-natural habitat. Non-bee pollinators are excluded as they have diverse nesting habits (e.g. many flies lack central nest locations, and others depend on floral resources only during adult life). However, non-bee pollinators respond less negatively to land-use changes (Rader et al., 2016), and their role in stabilizing animal-dependent production is important in the event of bee declines. Honey bee colonies are used to substitute wild pollinators, yet, with a few exceptions (e.g. honeybees complement and sometimes efficiently pollinate crops of the family *Cucurbitaceae* o *Solanacea*; Macias-Macias et al., 2009), the pollination services of wild pollinators cannot be compensated by managed bees because (a) pollinator-dependent crop land grows more rapidly than the stock of honey bee colonies (Lindström et al., 2016), (b) wild insects generally pollinate crops more efficiently than honeybees (Garibaldi et al., 2013) and (c) honeybees may depress wild pollinator densities (Winfree et al., 2007). Wild central-place foragers thus remain a fundamental group of crop pollinators in agriculturally dominated landscapes (Potts, 2016).

Ensuring stable food supplies is a challenge that may require multiple solutions. Policies to increase production, changing diets, irrigation, crop diversity and tolerance of crops to drought are proposed as stability-enhancing solutions (Bailey et al., 2015; Godfray & Garnett, 2014; Lobell et al., 2008; Renard & Tilman, 2019; Rosenzweig & Parry, 1994). By addressing multiple drivers of crop production in spatially explicit agroecosystems, our study provides a theoretical basis of the effects of fragmentation on the mean and stability of animal-dependent crop production, with strong consequences for food production and food security. These results are highly relevant in the global change context, and given the worldwide trends in agriculture, which shifts towards more pollinator-dependent crops.

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AUTHORS' CONTRIBUTIONS

D.M., B.H. and M.L. conceived the original idea and designed the research; D.M. and B.H. designed the model, with help from M.L. and C.D.M.; D.M. and B.H. performed the analysis; D.M. wrote the first draft of the manuscript; D.M., B.H., S.G., C.D.M. and M.L. contributed to revisions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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