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5 **Habitat fragmentation and food security**
6 **in crop pollination systems**
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32 ***Abstract***

- 33 1. Ensuring stable food supplies is a major challenge for the 21st century. There is
34 consensus that increased food production is necessary, but not sufficient, to achieve
35 food security, and that agriculture should also aim at stabilizing crop production over
36 time. In this context, biodiversity-based approaches to food security are increasingly
37 being supported based on the fact that biodiversity can increase and stabilize crop
38 production. However, agricultural systems are often highly fragmented and our current
39 understanding of how such fragmentation affects biodiversity and food production
40 remains incomplete, thus limiting our capacity to manage agricultural landscapes for
41 food security.
- 42 2. We developed a spatially-explicit model of crop dynamics to investigate how the
43 fragmentation of natural habitats for agricultural conversion impacts food production
44 and food security, with a focus on animal-dependent crop production.
- 45 3. Fragmentation produces a variety of spatial and biodiversity-mediated effects that
46 affect both the mean and stability (temporal invariability) of animal-dependent crop
47 production.
- 48 4. Fragmentation has a dual effect on animal-dependent production. On one hand, spatial
49 aggregation of natural land decreases animal-dependent production by reducing the
50 *Landscape Pollination Potential*, a metric that captures fragmentation and pollinator
51 spillover effects within the agricultural landscape. But aggregation increases animal-
52 dependent production by maintaining a higher pollinator diversity in larger fragments
53 of natural habitat. The net effects of fragmentation on animal-dependent crop
54 production depend on the land-use change pattern, the strength of the pollinator
55 spillover to crop land and the animal pollination-dependence of crops.
- 56 5. *Synthesis*. Our study sheds new light in the food security debate by showing that high

57 and stable crop production depends on biodiversity and the spatial fragmentation of
58 agricultural landscapes, and by revealing the ecological mechanisms of food security
59 in crop pollination systems. Management for food security should consider factors
60 such as pollinators' spillover, the amount and spatial aggregation of seminatural habitat
61 and the animal pollination-dependence of crops. This information would be useful to
62 design agricultural landscapes for high *Landscape Pollination Potential*. These results
63 are highly relevant in the global change context, and given the worldwide trends in
64 agriculture, which shifts towards more animal-dependent crop production.

65

66 **Keywords:** Habitat fragmentation, pollination, biodiversity, food security, stability,
67 ecosystem services, global change

68 **Introduction**

69

70 Ensuring stable food supplies for a growing population is one of the UN Sustainable
71 Development Goals (UN2017). Biodiversity-based approaches to food security suggest
72 that safeguarding species diversity is fundamental to increase yields and guarantee stable
73 yields. This is supported by theory and data reporting positive effects of biodiversity on
74 the mean values of various ecosystem functions and services, such as biomass production,
75 nutrient cycling and crop pollination (Lefcheck et al. 2015; Woodcock 2019).
76 Additionally, biodiversity can stabilize ecosystem service supply by providing an
77 insurance against environmental fluctuations (Loreau et al. 2003), which are predicted to
78 intensify under global change (Giorgi et al. 2001; Saltz et al. 2006; Fischer et al. 2013).
79 Biodiversity insurance effects have been observed in agriculture, where a greater
80 diversity of crops is associated with increased year-to-year temporal stability of total
81 production (Winfree & Kremen 2009; Renard & Tilman 2019). However, most
82 biodiversity in intensively-managed agricultural landscapes is found in the remaining
83 fragments of (semi)natural habitat not converted into crop land, and the effects of such
84 non-crop biodiversity on the provision and stability of crop production are not clearly
85 understood. This has led to a growing concern over the large-scale conversion of natural
86 habitats into crop land and their effects on biodiversity and food production (Godfray &
87 Garnett 2014; UN2017; Réchauchère et al. 2018).

88

89 Agricultural systems are often highly fragmented with areas of intensive cultivation
90 interspersed among remnant patches of seminatural habitat. This loss and fragmentation
91 negatively affect biodiversity and many ecosystem functions and services (Haddad et al.
92 2015; Rybicki et al. 2020). Despite this, fragments of natural habitat continue to supply

93 important services. The spatial coexistence of crops and natural land creates an
94 opportunity for spillover effects (Rand et al. 2006), a situation where ecological
95 interactions extend across habitats boundaries and propagate ecological functions. In
96 some cases, fragmentation can increase ecosystem service supply (Martin et al. 2019;
97 Haan et al. 2020), e.g. if fragmentation of natural habitat for pollinators optimizes
98 interspersions with crop land to maximize crop pollination (Brosi et al. 2008). But
99 fragmentation can also reduce ecosystem service supply if biodiversity decreases
100 significantly in the remnant fragments of natural habitat (Haddad et al. 2015). For most
101 services, however, we do not know how fragmentation affects their provision in
102 fragmented landscapes, and this limits our capacity to manage biodiversity-based
103 ecosystem service provision, e.g. crop pollination, and food security in human-dominated
104 landscapes.

105

106 Recent research has revealed strong, non-linear effects of land-use change on crop
107 production at multiple spatial scales. For example, theoretical studies agree on the hump-
108 shaped relationship between animal pollination-dependent crop production and the
109 fraction of remnant natural land within intensive farming systems (Braat & ten Brink
110 2008; Mitchell et al. 2015; Montoya et al. 2019). Empirical research on the stability of
111 animal pollination dependent crop production shows that stability decreases with
112 agricultural intensification and the degree to which crops depend on animal pollination
113 (Garibaldi et al. 2011a, b, 2014; Deguines et al. 2014). Changes in crop production
114 stability of animal-pollinated crops also depend on the spatial composition and structure
115 of agricultural landscapes, such as the amount of natural land cover (Montoya et al. 2019)
116 and the isolation of crops from natural land (Garibaldi et al. 2011b). Overall, both
117 theoretical and empirical studies suggest that improved management of agricultural

118 landscapes should increase the amount and stability of animal pollination-dependent crop
119 production, and that an understanding of how the spatial pattern of land-use change –
120 fragmentation – impacts ecosystem services is key to achieve this goal. However, none
121 of these studies have simultaneously combined crop dynamics at different scales and
122 spatially-explicit landscapes to investigate the effects of land-use change on biodiversity
123 and crop production services. Further, while multiple factors can influence crop
124 production in fragmented agroecosystems, our current understanding of how they interact
125 and determine crop production stability, and thus food security, remains incomplete.

126

127 There is general consensus that increased food production is necessary, but not sufficient,
128 to achieve food security (Godfray & Garnett 2014), and that agriculture, especially in the
129 global change context, should also aim at stabilizing crop production over time
130 (Schmidhuber & Tubiello 2007; Montoya et al. 2020). Bearing this in mind, we here
131 extend a model of crop dynamics into a spatially-explicit landscape to investigate how
132 habitat loss and fragmentation, i.e. the amount and spatial configuration of seminatural
133 habitat, influence the mean provision and stability of crop production in agricultural
134 landscapes. We focus on animal-dependent crop production because (i) animal crop
135 pollination is a key agricultural service that depends on biodiversity (pollinator animals),
136 and (ii) worldwide agriculture is shifting towards more animal pollination-dependent
137 food production systems (Aizen et al. 2009; Breeze et al. 2014). Because the way food is
138 produced worldwide threatens the existence of much of the world's biodiversity that
139 contributes to crop pollination and food security, we explore how changes in biodiversity
140 following land-use change affect animal-dependent crop production in fragmented
141 agroecosystems. Thus, our model accounts for a variety of potential drivers of crop
142 production mean and stability, such as loss and fragmentation of natural habitat and

143 biodiversity, that are difficult to address collectively in empirical studies. Specifically,
144 we address two questions: (i) How does the spatial pattern of land-use change influence
145 the provision and stability of animal -dependent crop production in agroecosystems? (ii)
146 How does biodiversity in fragmented landscapes influence animal-dependent crop
147 production and food security?

148

149

150 **Materials and Methods**

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

163

164 The model investigates the expected biodiversity (i.e. species richness) and crop
165 production, with a special focus on animal-dependent crop production, at the farm- (i.e.
166 crop yield per area) and landscape-levels (i.e. the magnitude and stability of crop
167 production). We distinguish between two additive ecosystem services associated with

168 crop production: the production that results from wild animal pollination (hereafter
169 animal-dependent production), and the production that is independent from animal
170 pollination (animal-independent production), but can be wind- or self-pollinated.
171 Pollinators are assumed to be generalist central-place foragers that nest in seminatural
172 habitat (Gill et al. 2016), yet move across the landscape to forage on either flowering
173 crops or ‘wild’ plants, or both. Crop land and seminatural habitat are therefore linked by
174 the pollinators’ foraging movement. For simplicity, the model assumes similar foraging
175 movements across pollinators. The main difference between the non-spatial and spatial
176 models lies on the way pollinators link these two patch types: whereas in the non-spatial
177 model pollinators move globally and reach all crop land, the spatial model imposes
178 restrictions to pollinator’s movement based on the spatial structure of the agricultural
179 landscape (i.e. distribution of crop land and seminatural habitat) and the foraging range
180 of pollinators (i.e. spillover). A conceptual representation of the model, including non-
181 spatial and spatial components, as well as key model assumptions, is provided in Fig. 1.
182 In what follows, we first describe the spatial agroecosystem model and then present a
183 simpler, mean-field approximation of the model that we use to produce the results.

184

185 **Spatial agroecosystem model**

186 The addition of space allows: (i) to explore a continuous gradient of land-use change
187 patterns, from completely random to highly aggregated, that encompasses a wide range
188 of fragmentation scenarios, (ii) to investigate the effects of fragmentation on pollinator
189 diversity and crop production services, and (iii) to study how variations in the strength of
190 spillover from seminatural habitat to crop land – i.e. the distance-decay of pollination
191 flow – affects animal-dependent crop production. To do this, we simulated a continuous
192 gradient of land-use change patterns, and therefore fragmentation, based on the

193 aggregation degree of seminatural habitat. A complete description of the model
194 parameters can be found in Table 1. Information on model parameterization is in
195 Appendix S1.

196

197 Landscape pattern generation. The landscape consisted of a two-dimensional lattice
198 (25×25 cells) where individual cells can have either of two states: crop land or seminatural
199 habitat. We generated land-use change patterns by iteratively creating crop land cells in a
200 landscape that consisted initially only of seminatural land. In a single step of the algorithm
201 only one semi-natural habitat cell is selected and converted. The pattern generation is
202 controlled by a parameter w that determines the clustering degree of the land-use change
203 pattern (see Appendix S1). Hence, for $w = 0$ all seminatural land cells had the same
204 relative probability to be chosen, leading to a fully random, unclustered pattern. Larger
205 values of w resulted in more aggregated patterns. Therefore, variation in the value of w
206 allowed us to produce a continuous gradient of land-use change patterns, and therefore
207 fragmentation, based on the aggregation degree. For each land-use change pattern, we
208 characterised fragmentation of the remaining seminatural habitat by quantifying mean
209 fragment size, number of fragments, mean fragment perimeter, and perimeter: area ratio.
210 Fragmentation directly affects pollinator diversity (through the estimation of the
211 metapopulation capacity) and the *Landscape Pollination Potential (LPP)*, which in turn
212 influence crop production services (see below).

213

214 General model dynamics. Pollinators, ‘wild’ plants and crop production are represented
215 by Equations 1-3. In these equations, the first term defines growth and is modelled using
216 the discrete Ricker equation, whereas the second and third terms add environmental and
217 demographic stochasticity to the model:

218

$$219 \quad P_k(t + 1) = P_k(t) \exp(r_{P,k}(t) \left(1 - \frac{P_k(t)}{k_P A_1}\right)) + \sigma_P^e u_P^e(t) P_k(t) + \frac{\sigma_P^d u_P^d(t)}{\sqrt{P_k(t)}} P_k(t) \quad (1)$$

$$220 \quad W_k(t + 1) = W_k(t) \exp(r_{W,k}(t) \left(1 - \frac{W_k(t)}{k_W A_1}\right)) + \sigma_W^e u_W^e(t) W_k(t) + \frac{\sigma_W^d u_W^d(t)}{\sqrt{W_k(t)}} W_k(t) \quad (2)$$

$$221 \quad C_k(t) = A_1 [Z_C + r_{C,k}(t)] (1 + \sigma_C^e u_C^e(t)) \quad (3)$$

222

223 P_k represents pollinators, W_k ‘wild’ plants and C_k crop production in cell k , with $P_k(t) =$
224 $W_k(t) = 0$ if k is a crop land cell, and $C_k(t) = 0$ if k is seminatural habitat. One unit of
225 time t corresponds to one growing season, $P(t)$ and $W(t)$ can be interpreted as total
226 biomass of pollinators and ‘wild’ plants over growth season t , respectively, whereas $C(t)$
227 is the total crop production at the end of the growing season t . $r_{P,k}(t)$, $r_{W,k}(t)$, $r_{C,k}(t)$ are
228 the pollinators’, ‘wild’ plants’ and crop’s per capita growth rates. Z_C is the crop production
229 independent of animal pollination, which allows varying degrees of animal-dependence
230 production. C_k is thus the sum of animal-dependent and -independent parts of crop
231 production. k_P and k_W are the carrying capacities of pollinators and ‘wild’ plants,
232 respectively, per unit area. A_1 is the area of a single cell; A is total landscape area; $A[1 -$
233 $\omega_{sn}]$ is the total crop land area, and $A\omega_{sn}$ is total seminatural area. In the non-spatial model,
234 k and A_1 were not defined. Stochasticity is included in the form of $\sigma u(t)$, where σ^2 is the
235 variance (‘environmental or ‘demographic) and $u(t)$ are independent Gaussian random
236 variables with zero mean and unit variance, of either pollinators (σ_{PUP}), ‘wild’ plants
237 (σ_{WUW}) or crops (σ_{CUC}) (see model stochasticity section below).

238

239 Growth rate of pollinators and plants. Since pollinators are assumed to be generalist
240 central-place foragers, pollinator’s growth rate depends on the availability of resources
241 (‘wild’ plants and crops) in the neighborhood. Plant and pollinator uptake of resources,

242 as well as the animal-dependent crop production, follow a saturating, type II functional
 243 response, widely supported and consistent with real biological examples (Thebault &
 244 Fontaine 2010; Holland et al. 2013; Holland 2015). Growth rates are thus defined by the
 245 following Monod/Michaelis-Menten equations:

246

$$247 \quad r_{P,k}(t) = \frac{\alpha_P \left[\frac{\sum_{l \notin L} \varepsilon_{kl} W_l(t) + \sum_{l \in L} \varepsilon_{kl} C_l(t)}{A} \right]}{\beta_P + \frac{\sum_{l \notin L} \varepsilon_{kl} W_l(t) + \sum_{l \in L} \varepsilon_{kl} C_l(t)}{A}} \quad (4)$$

$$248 \quad r_{W,k}(t) = \frac{\alpha_W \left(\frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A} \right)}{\beta_W + \frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A}} \quad (5)$$

$$249 \quad r_{C,k}(t) = \frac{\alpha_C \left[\frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A} \right]}{\beta_C + \frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A}} \quad (6)$$

250

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

257

258 Because crops vary in their dependency on animal pollination, different crop types can
 259 respond differently to landscape fragmentation. In our model, the degree to which crops
 260 depend on animal pollination is measured by $\alpha_C/(Z_C + \alpha_C)$, and reflects the part of total
 261 crop production dependent on animal pollination – i.e. animal-dependent production.
 262 Landscape crop production is estimated by summing up the individual contribution of
 263 each cell k . Thus, for total crop production we obtained $C(t) = \sum_{k \in L} C_k(t)$. We assume
 264 that crops are harvested yearly; hence, mean crop production represents the temporal

265 mean of the yearly averaged crop production across the agricultural landscape. Crop yield
266 per unit of agricultural area is calculated by dividing total crop production by crop land
267 area.

268

269 Model stochasticity. To investigate the effects of fragmentation on crop production
270 stability, the model includes environmental and demographic stochasticity (second and
271 third terms, Eqs. 1-3). Stochasticity is included in the form of $\sigma u(t)$, where σ^2 is the
272 variance and $u(t)$ are independent Gaussian random variables with zero mean and unit
273 variance, of either pollinators (σ_{PU}), ‘wild’ plants (σ_{WU}) or crops (σ_{CU}). Environmental
274 stochasticity ($\sigma^e u^e(t)$) reflects variation in weather variables, e.g. temperature and rainfall,
275 whereas demographic stochasticity ($\sigma^d u^d(t)$) emerges from stochastic variation in
276 individuals’ births and deaths, commonly observed in nature and important in small
277 populations. Crops are sown at high densities, and thus we assume demographic
278 stochasticity is prevented in crops. These two sources of stochasticity add biological
279 realism to the model, as they allow variation in the biomass of pollinators, ‘wild’ plants
280 and crops, useful to assess stability. We used $1/CV^2$ as a metric of stability (invariability),
281 where CV is the temporal coefficient of variation of crop production. This measure of
282 stability is commonly used in ecological studies (Loreau & De Mazancourt 2013).

283

284 Distance-decay of pollinators (spillover effects). The spatially-explicit nature of the
285 model allows to study how variations in the strength of spillover effects influences crop
286 pollination. Ecosystem service distance-decay (ε_{kl}) affects the flow of pollination to crop
287 land: the further crops are from seminatural habitat, the more difficult it is for pollinators
288 to reach the crops, and thus the smaller the effect of pollinators on crop production. To
289 model spillover effects, we used a logistic distance-decay function adapted from Mitchell

290 et al. (2015) (Appendix S1). This function is consistent with both theoretical predictions
291 (Ries et al. 2004; Rand et al. 2006; Ricketts et al. 2008) and empirical observations
292 (Farwig et al. 2009; Mitchell et al. 2014; Martins et al. 2015) of the effects of habitat
293 edges and distance-to-habitat fragment gradients on ecosystem service provision. The
294 logistic distance-decay function has two parameters: (i) the distance from seminatural cell
295 edge at which the pollination flow equals one half of its initial value – 50% decay distance
296 – (d_m), and (ii) the distance over which the pollination flow decreases from 90% to 10%
297 of its initial value – 90% to 10% decay distance (Δd).

298

299 Fragmentation, biodiversity and crop pollination. To consider the effects of
300 fragmentation on biodiversity and crop production, we included two relationships in our
301 model: (i) the dependence of pollinator diversity on the amount and distribution of
302 seminatural habitat, and (ii) the dependence of crop production on pollinator diversity. In
303 the first case, we used the *Species-Fragmented Area Relationship* (SFAR; Hanski et al.
304 2013), which extends one of the oldest known and most documented patterns in ecology
305 – the species-area relationship (SAR) – to fragmented landscapes. Despite recent debate
306 has ensued on the relative importance of habitat loss *versus* fragmentation on species
307 diversity (Rybicki et al. 2020; Fletcher et al. 2018; Fahrig et al. 2018), empirical evidence
308 shows that larger and more connected fragments of natural habitat in general host more
309 biodiversity than smaller, more isolated fragments (Haddad et al. 2015). In agricultural
310 landscapes, this means that different fragmentation patterns will affect biodiversity and
311 crop production in different ways. In an agricultural landscape, the SFAR can be modeled
312 as a power law: $S = c_s (A\omega_{sn})^{z_s}$, where S is pollinator diversity, $A\omega_{sn}$ is the total area of
313 seminatural habitat, and z_s is the power-law exponent. The prefactor c_s is not a constant

314 as in the standard SAR; rather, it decreases in more fragmented landscapes (see Appendix
315 S1 for more details).

316

317 For the second relationship – the dependency between crop production and pollinator
318 diversity –, we created a dependence of pollinator’s carrying capacity (k_P) on biodiversity
319 following a power law: $k_P = c_P S^{z_P}$, where S is the number of pollinator species estimated
320 by the SFAR, and c_P , z_P are parameters of the power law (Liang et al. 2016; O’Connor
321 et al. 2017). Although pollinators can differ in their pollination efficiency (Matsuki et al.
322 2008; Kleijn et al. 2015; Willcox et al. 2017), such differences do not dilute the positive
323 relationship between pollinator diversity and crop production and yield, as reported in
324 meta-analytical studies (Woodcock et al. 2019). Additionally, we considered the ability
325 of pollinator diversity to provide an insurance against environmental fluctuations.
326 Following the biodiversity insurance hypothesis (Loreau et al. 2003), pollinator diversity
327 insures crop production because many pollinators better maintain crop production if
328 pollinators differ in their responses to environmental variation. We followed the
329 ecological literature and made pollinators’ environmental stochasticity inversely related
330 to their diversity ($\sigma_P^e = e_P / S^q$; Tilman 1999). Demographic stochasticity acts at the
331 individual level, and in the same manner for conspecifics and heterospecifics; thus, there
332 is no insurance effect for demographic stochasticity.

333

334 **Non-spatial model results: summary**

335 The relationship between mean crop production and the proportion of seminatural habitat
336 is hump-shaped, and the height and position of the hump depends on crop pollination
337 dependence ($\alpha_C / (Z_C + \alpha_C)$) and the crop relative requirement for pollinator densities (β_C / k_P)
338 (Fig. S1; Montoya et al. 2019). Higher and lower values of these factors, respectively,

339 shift maximum production to higher fractions of seminatural habitat. On the other hand,
340 the stability of animal-dependent crop production is generally an increasing function of
341 proportion of seminatural habitat and is also determined by the same factors: higher crop
342 pollination dependence and crop relative requirement for pollinators decreases stability.

343

344 **Mean-field approximation of the spatial model**

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

350

$$351 \quad \bar{\varepsilon} = \frac{1}{(1-\omega_{sn})n^2} \frac{1}{\omega_{sn}n^2} \sum_{k \in L, l \notin L} \varepsilon_{kl} \quad (7)$$

352

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

359

360 The mean-field approximation is a very accurate description of the ecosystem service
361 dynamics in agricultural landscapes (Fig. 2; Appendix S2), and shows that the spatial
362 effects of fragmentation on animal-dependent crop production are determined by LPP.

363 Thus, LPP is a metric that captures fragmentation and pollinator spillover effects within

364 agricultural landscapes. To consider the spatial structure of land-use change, the term
365 β_C/k_P of the non-spatial model must be replaced by

$$366 \frac{1}{LPP} \frac{\beta_C}{k_P} \tag{8}$$

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

368

369

370 **Results**

371 The results here presented correspond to the mean-field approximation, as it provides a
372 very accurate description of the model dynamics (Fig. 2). We present three groups of
373 results: (i-ii) the effects of LPP and biodiversity on crop production, and (iii) the net
374 effects of fragmentation on animal-dependent production.

375

376 **Effects of LPP on crop production**

377 When $LPP = 1$, fragmentation effects are negligible and crop dynamics are identical to
378 those of the non-spatial model (Fig. 3A-C, dark-blue lines). In this case, we retrieve the
379 same mechanisms of the non-spatial model (Montoya et al. 2019). The effects of
380 fragmentation kick off when $LPP < 1$. Lower LPP reduces the carrying capacity of
381 pollinators *effectively*; that is, the effects of LPP on the mean and stability of crop
382 production can be fully taken into account by changing the value of the pollinators'
383 carrying capacity from k_P to $LPP*k_P$ (Eq. 8). LPP-driven reduction in pollinators'
384 carrying capacity decreases the mean provision of animal-dependent production (Fig. 3A)
385 and crop yield per area (crop yield per area increases with seminatural habitat, but larger
386 LPP saturates this relationship earlier; Fig. 3C). The same is true for the stability of
387 animal-dependent production, except at small fractions of seminatural habitat and/or
388 small values of LPP (Fig. 3B). LPP has no effect on animal-independent crop production

389 as it does not depend on animal pollination and, therefore, on seminatural habitat; its
390 mean value decreases linearly with seminatural habitat, whereas its stability is solely
391 determined by environmental stochasticity (Fig. 3D-E). Because of this, animal-
392 independent crop production is not further considered in subsequent results. Whereas the
393 full complexity of the spatial fragmentation effects (i.e. those not mediated by
394 biodiversity) on animal-dependent production are captured by LPP (Fig. S2), we did not
395 find any clear, consistent effect of specific fragmentation metrics (Fig. S3), except for
396 ‘*Number of crop land cells > distance threshold*’. This is because the latter variable uses
397 distance-decay parameter d_m as the reference threshold, and it is thus correlated with LPP.
398 However, the dependence of both metrics on d_m does not really explain their correlation:
399 LPP measures the fraction of crop land within a distance d_m of seminatural habitat and
400 quantifies the interspersion of seminatural habitat and crop land at the scale of the
401 pollination spillover distance d_m , thus capturing an important dimension of fragmentation
402 (i.e. interspersion) that is not or poorly considered by the standard fragmentation metrics.
403 Finally, the effect of LPP on animal-dependent production increases with the degree to
404 which crops depend on animal pollination: higher pollination dependence shifts
405 maximum production to higher fractions of seminatural habitat at landscape and local
406 scales, and the stability of animal-dependent production increases faster (Fig. S4),
407 consistent with Montoya et al. (2019).

408

409 LPP depends on two factors: fragmentation and spillover, or the distance-decay of
410 ecosystem service flow. High aggregation (low fragmentation) and fast distance-decay
411 result in lower LPP ($LPP < 1$), which in turn reduces animal-dependent crop production.
412 These two factors interact: only when the flow of pollinators to crop land is limited (fast
413 distance-decay) aggregation patterns influence animal-dependent production. When no

414 restrictions exist in the flow of pollinators to crop land, LPP is maximum and
415 fragmentation does not affect animal-dependent production ($LPP \approx 1$).

416

417 **Effects of biodiversity on crop production**

418 In parallel to LPP, pollinator diversity also impacts animal-dependent crop production.
419 As expected, biodiversity enhances animal-dependent production at local (i.e. yield per
420 area) and landscape scales (Fig. 4A, C), and stabilizes animal-dependent production (Fig.
421 4B) by increasing the pollinators' carrying capacity, and by reducing the response of
422 animal-dependent production to environmental fluctuations. A higher biodiversity effect
423 (larger z_P) increases both mean animal-dependent production and its stability, as well as
424 yield per area.

425

426 **Net effects of fragmentation on crop production**

427 Fragmentation has a dual effect on animal-dependent crop production. On one hand,
428 aggregation of seminatural fragments decreases pollination by lowering LPP, which in
429 turn reduces the pollinators' carrying capacity. On the other hand, aggregation benefits
430 biodiversity (Fig. S5), which in turn increases pollinators' biomass and animal
431 pollination. The net effect of fragmentation on animal-dependent production depends on
432 the distance-decay of ecosystem service flow (d_m) and the proportion of seminatural
433 habitat remaining. When the decay distance is low (Fig. 5, first row), fragmentation
434 effects tend to be positive for mean animal-dependent production and yield per area
435 because the fraction of crop land within reach from non-crop land areas is higher. Yet,
436 the stability of animal-dependent production decreases due to the lower biodiversity in
437 fragmented landscapes, except at high fractions of seminatural habitat where the impact
438 of fragmentation is minimum. Conversely, when the decay distance is high, seminatural

439 fragments are perceived as more connected and animal-dependent production is not
440 limited by space. In this case, fragmentation becomes irrelevant, or even negative, due to
441 the lower biodiversity in fragmented landscapes (Fig. 5, last row).

442

443

444 **Discussion**

445 Our analysis reveals a variety of effects of land-use change on biodiversity and crop
446 production. Using a mean-field approximation, our model suggests that (i) the full
447 complexity of the fragmentation-induced spatial effects on animal-dependent crop
448 production is captured by one factor – the Landscape Pollination Potential of the
449 remaining seminatural land (LPP) – which determines the mean and stability of animal-
450 dependent production; (ii) fragmentation reduces biodiversity and increases LPP, thus
451 impacting animal-dependent production in opposite directions; and (iii) the net effects of
452 fragmentation on animal-dependent production depend on the strength of pollinators’
453 spillover to crop land, the proportion of seminatural habitat remaining, and the degree to
454 which crops depend on animal pollination.

455

456 The loss of seminatural land has contrasting effects on agricultural landscapes:
457 biodiversity decreases, animal-independent crop production increases, while animal-
458 dependent crop production is maximized at intermediate fractions of seminatural habitat.
459 But fragmentation can modify these relationships in two ways. First, land-use change can
460 produce multiple patterns of aggregation of seminatural habitat fragments. These
461 patterns, combined with the strength of the spillover of pollinators to crop land, determine
462 the Landscape Pollination Potential of seminatural land, which is one main driver of food
463 production in animal-dependent agriculture. The second type of effects are mediated by

464 biodiversity, as the level of aggregation of seminatural habitat affects the pollinator
465 richness. Such purely spatial and biodiversity-mediated effects modify the carrying
466 capacities of pollinators, which ultimately determine animal-dependent crop production.
467 The mean-field approximation shows that the effects of space on animal-dependent
468 production can be interpreted in the same terms as varying the pollinator's carrying
469 capacity in the non-spatial model, i.e. a lower LPP reduces the pollinator's carrying
470 capacity and the provision of animal-dependent production.

471

472 Our results suggest that understanding the factors that affect Landscape Pollinator
473 Potential is a fundamental step towards food security in animal-dependent agriculture. If
474 no restrictions exist in the flow of pollinators to crop land, LPP is maximum and the
475 spatial structure of land-use change does not affect crop dynamics. In this situation,
476 seminatural fragments are perceived as more connected and the provision and stability of
477 animal-dependent production is not conditioned by the spatial configuration, i.e. spatial
478 and non-spatial models converge. However, agricultural landscapes are fragmented to
479 some extent and the foraging ranges of most organisms are local (Darvill et al. 2004;
480 Zurbuchen et al. 2010; Geib et al. 2015), which produces higher aggregation and weaker
481 spillover effects, thus reducing LPP. Such reductions in LPP affect crop production by (i)
482 decreasing mean animal-dependent production and total yield per area, and (ii) decreasing
483 the stability of animal-dependent production along the seminatural habitat gradient.
484 Because LPP can have important implications for crop production, it would be interesting
485 to operationalize this metric in empirical studies and landscape management. The
486 estimation of LPP in real farming systems would require data on the aggregation of
487 seminatural habitat, and on the spillover of pollinators to adjacent crops. The former can
488 be obtained with GIS processing of aerial pictures or satellite images. For the latter,

489 information on foraging distances of existing pollinator species (this comes from
490 ecological censuses) combined with experimental studies could be used to reveal species'
491 foraging patterns and how the flow of pollinators to adjacent crop land decays with
492 distance (examples of this type of studies are Ries et al. 2004; Rand et al. 2006; Ricketts
493 et al. 2008). This information will be useful to design agricultural landscapes for high
494 LPP. Although measuring LPP in empirical studies demands more data than simple,
495 traditional fragmentation metrics, this investment is worthy as LPP can be a better
496 predictor of crop production.

497

498 Producing food requires land, and increasing the land devoted to farming reduces the land
499 devoted to biodiversity conservation. This and other recent empirical studies show that
500 pollinator diversity can increase food production (Catarino et al. 2019; Dainese et al.
501 2019; Woodcock et al. 2019), and lead to lower variability in agricultural productivity.
502 This is relevant in the global change context, as biodiversity can stabilize animal-
503 dependent crop production by providing an insurance against environmental fluctuations,
504 which are predicted to intensify under global change (Giorgi et al. 2001; Saltz et al. 2006;
505 Fischer et al. 2013). The response of biodiversity to land-use change depends on the
506 amount and the spatial structure of seminatural habitat. For example, although the effects
507 of fragmentation on biodiversity are stronger at low-intermediate fractions of seminatural
508 habitat – typical of intensive farming systems –, aggregation favours biodiversity within
509 seminatural habitat fragments. The stabilizing effect of biodiversity and its role in food
510 security is increasingly supported, even at crop levels (Renard & Tilman 2019). Our
511 results add to this view and point to biodiversity conservation as one key policy to achieve
512 food security.

513

514 Our findings are consistent with previous studies that found non-linear effects of
515 fragmentation on ecosystem services (Keitt 2009; Mitchell et al. 2015), and provide a
516 theoretical basis of the effects of fragmentation on the stability of animal-dependent crop
517 production. Fragmentation has a dual effect on animal-dependent production. On one
518 hand, aggregation decreases animal-dependent production by reducing the Landscape
519 Pollination Potential. On the other hand, aggregation increases animal-dependent
520 production by maintaining higher biodiversity, especially when the proportion of
521 seminatural habitat within the agricultural landscape is medium or low. The net effects of
522 aggregation on animal-dependent crop production depend on the strength of spillover
523 effects. These results have management implications (e.g. land sharing–sparing debate;
524 Fischer et al. 2014; Grass et al. 2019), as the goals of different landscape managers can
525 be conditioned by the way that natural land is converted into crops. For example,
526 maintaining a large number of seminatural fragments may be a better strategy at multiple
527 spatial scales than maintaining a few large fragments when pollinator flow to crop land
528 is low. Yet, this strategy may increase the temporal variability of animal-dependent
529 production at low-intermediate proportions of seminatural habitat, reflecting a trade-off
530 between ecosystem service mean and stability. Conversely, larger fragments of
531 seminatural habitat have higher pollinator diversity when the fraction of seminatural
532 habitat is low or intermediate, and higher biodiversity can stabilize animal-dependent
533 production. These results agree with recent claims that the land sharing–sparing
534 dichotomy lends itself to overly simplistic policy prescriptions (Kremen 2015), and
535 suggest that management decisions for food security should consider factors such as
536 pollinators’ spillover, the amount and spatial aggregation of seminatural habitat and the
537 animal pollination-dependence of crops. Our results also provide recommendations for
538 landscapes with both animal-independent and -dependent crops. In such cases, for a given

539 proportion of seminatural habitat, management should maximize the Landscape
540 Pollination Potential while preserving pollination diversity, favouring mean crop
541 production and its stability. This could be achieved by increasing fragmentation of semi-
542 natural habitat in the vicinity of animal-dependent crops, but without making semi-natural
543 habitat patches too small so that biodiversity is not negatively affected. Animal-
544 independent production only depends on how much seminatural habitat there is, and is
545 not affected by fragmentation because it does not depend on animal pollinators and
546 seminatural habitat.

547

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

561

562 Our model has several limitations. First, our model focuses on intensive farming systems,
563 where crop land does not host important biodiversity levels; other types of agriculture –

564 e.g. organic farming – allow moderate levels biodiversity to thrive within crop land, and
565 can modify the results reported here (Clough et al. 2011). The model does not consider
566 fine-scale seminatural patches (e.g. wildflower strips, hedgerows) that might support high
567 pollinator diversity by providing complementary resources within a short range from
568 crops, nor it considers habitat quality differences within seminatural fragments; although
569 the latter can affect the abundance and composition of pollinators, it would not
570 qualitatively affect the positive effect of pollinator diversity on animal-dependent
571 production. Also, the observation that biodiversity loss has either none (stability) or
572 positive (mean) effects on animal-independent crop production may change if organisms
573 responsible for other services, e.g. pest control, are included. Besides, although
574 seminatural habitat had no effect on the stability of animal-independent production, this
575 may change if environmental stochasticity of crops increases with decreasing amounts of
576 seminatural habitat, as suggested by studies linking seminatural habitat to climate
577 regulation, natural hazard regulation and water flow regulation services (Harrison et al.
578 2010). In addition, negative perturbations larger than the ones considered in our model
579 may be possible; although these so-called black-swan events are rare (e.g. they affect ~3%
580 of insect populations; Anderson et al. 2017), they could heavily decrease pollinator
581 diversity, with negative impacts on animal-dependent crop production. Differences in
582 pollination efficiency may affect LPP and could be captured using functional group
583 analysis (Mayfield et al. 2019); yet, the positive diversity-function relationship still holds
584 even considering such differences (Woodcock et al. 2019). Also, differences in flight
585 ability and range across pollinators influence pollinator diversity within agricultural
586 landscapes (e.g. InVEST Crop pollination model, Lonsdorf et al. 2009), and this may in
587 turn affect LPP, through its effects on pollinator spillover, and the provision of animal-
588 dependent production. Therefore, differences in movement/flight patterns of pollinators

589 should be considered in future extensions of the model, e.g. large bees such as *Bombus*
590 species are powerful long-distance pollinators, whereas smaller bees forage locally (e.g.
591 *Lasioglossum*, *Halictus*). Finally, our model focuses on wild central-place pollinators (i.e.
592 all types of wild bees, including bumble bees and solitary bees), whose presence and
593 abundance directly depend on seminatural habitat. Non-bee pollinators are excluded as
594 they have diverse nesting habits (e.g. many flies lack central nest locations, and others
595 depend on floral resources only during adult life). However, non-bee pollinators respond
596 less negatively to land-use changes (Rader et al. 2016), and their role in stabilizing
597 animal-dependent production is important in the event of bee declines. Honey bee
598 colonies are used to substitute wild pollinators, yet, with a few exceptions (e.g. honeybees
599 complement and sometimes efficiently pollinate crops of the family *Cucurbitaceae* o
600 *Solanacea*; Macias-Macias et al. 2009), the pollination services of wild pollinators cannot
601 be compensated by managed bees because (1) pollinator-dependent crop land grows more
602 rapidly than the stock of honey bee colonies (Lindström et al. 2016), (2) wild insects
603 generally pollinate crops more efficiently than honeybees (Garibaldi et al. 2013), and (3)
604 honeybees may depress wild pollinator densities (Winfree et al. 2007). Wild central-place
605 foragers thus remain a fundamental group of crop pollinators in agriculturally-dominated
606 landscapes (Potts 2016).

607

608 Ensuring stable food supplies is a challenge that may require multiple solutions. Policies
609 to increase production, changing diets, irrigation, crop diversity, and tolerance of crops
610 to drought, are proposed as stability-enhancing solutions (Rosenzweig & Parry 1994;
611 Lobell et al. 2008; Godfray & Garnett 2014; Bailey et al. 2015; Renard & Tilman 2019).
612 By addressing multiple drivers of crop production in spatially-explicit agroecosystems,
613 our study provides a theoretical basis of the effects of fragmentation on the mean and

614 stability of animal-dependent crop production, with strong consequences for food
615 production and food security. These results are highly relevant in the global change
616 context, and given the worldwide trends in agriculture, which shifts towards more
617 pollinator-dependent crops.

618

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630

631 **Author contributions**

632 D.M., B.H. and M.L. conceived the original idea and designed the research. D.M. and
633 B.H. designed the model, with help from M.L. and C.M. D.M. and B.H. performed the
634 analysis. D.M. wrote the first draft of the manuscript, all authors contributed to revisions.

635

636 **Data availability statement**

637 Data available from the Dryad Digital

638 Repository: <https://doi.org/10.5061/dryad.8sf7m0cn8> (Montoya et al., 2021).

639

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957 **Figures and Tables**

958

959 **Table 1 | Parameters and variables of the model.** An asterisk in the unit column
960 indicates that the value of that parameter depends on fragmentation.

961

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

982

983 **Figure 2 | Mean-field approximation vs Exact solution.** (a) Mean animal-dependent
984 crop production. (b) Variability of animal-dependent crop production (measured as
985 Coefficient of Variation – CV –, the inverse of stability). A range of fragmentation
986 patterns with different levels of spatial aggregation were generated for different fractions
987 of seminatural habitat. For different fractions of seminatural habitat ω_{sn} , we generated
988 200 fragmentation patterns using the algorithm described in the methods section, with
989 aggregation parameter w drawn uniformly from the interval $[0,5]$, and pollinator spillover
990 distance d_m drawn uniformly from the interval $[0.1,4]$. For each fragmentation pattern we
991 computed the mean and stability of animal-dependent crop production in two different
992 ways: first by solving exactly the spatially explicit model (Appendix S2, Eqs. S8 and
993 S17) and second by using the mean-field approximation (Appendix S2, Eqs. S35 and
994 S36). ω_{sn} is the proportion of seminatural habitat. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P =$
995 $\beta_W = 0.6$, $\beta_C = 0.01$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $k_P = 0.1$, $\sigma^e_P = 0.8$, $\sigma^d_P =$
996 0.1 , $\sigma^e_C = 0.03$, $\alpha_C = 1000$, $z_P = 0.26$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$, $b = 10$, $q = \frac{1}{2}$, Pollination
997 dependence = 50%.

998

999 **Figure 3 | Effects of landscape composition and LPP on crop production.** (A) Mean
1000 animal-dependent production, (B) Stability of animal-dependent production stability, (C)
1001 Total yield per area, (D) Mean animal-independent production, (E) Stability of animal-
1002 independent production. Ecosystem services are represented as a function of the
1003 proportion of seminatural habitat, for different LPP. LPP includes the effects of
1004 fragmentation – more specifically, the aggregation pattern of land-use change – and the
1005 distance-decay of ecosystem service flow. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W =$
1006 0.6 , $\beta_C = 0.01$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $\sigma^e_P = 0.8$, $\sigma^d_P = 0.1$, $\sigma^e_C = 0.03$,

1007 $\alpha_C = 1000$, $z_P = 0.26$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$, $b = 10$, $q = 1/2$, Pollination dependence =
1008 50%.

1009

1010 **Figure 4 | Effects of biodiversity on animal-dependent crop production.** Plots show

1011 the response of animal-dependent production mean and stability (panels **A** and **B**), and

1012 yield per area (panel **C**) – as a function of the proportion of seminatural habitat (SNH).

1013 All LPP values are contained within the shadows, whose limits are determined by the

1014 minimum and maximum values across the range of LPP (illustrated by the arrows joining

1015 LPP_{\min} and LPP_{\max} values in panel **B**). Biodiversity can affect crop production in a two-

1016 way manner. On one hand, biodiversity influences mean animal-dependent production

1017 and yield per area by increasing the carrying capacity of pollinators ($k_P = c_P S^{z_P}$). On the

1018 other hand, biodiversity impacts the stability of animal-dependent crop production both

1019 indirectly – increasing the carrying capacity of pollinators – and directly – reducing the

1020 response of animal-dependent production to environmental fluctuations ($\sigma_P^e = e_P / S^q$).

1021 For each ecosystem service, the plots compare two scenarios: (i) a scenario where

1022 biodiversity has no effect on animal-dependent production ($z_P = 0$, $q = 0$), represented by

1023 the grey shadows, *versus* (ii) a scenario where biodiversity has an effect on animal-

1024 dependent production ($z_P = 0.26$, $q = 1/2$) (Tilman 1999; Liang et al. 2016; O'Connor et al.

1025 2016), represented by the light orange shadows. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W$

1026 $= 0.6$, $\beta_C = 0.01$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $\sigma_P^e = 0.8$, $\sigma_P^d = 0.1$, $\sigma_C^e = 0.03$,

1027 $\alpha_C = 1000$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$, $b = 10$, Pollination dependence = 50%.

1028

1029 **Figure 5 | Net effects of aggregation on animal-dependent crop production.** Columns

1030 represent, from left to right, mean and stability of animal-dependent production, and yield

1031 per area. Ecosystem services are plotted as a function of fragmentation for different

1032 proportion of seminatural habitat or SNH (as opposed to Figs. 3-4). In each plot,
1033 fragmentation increases in the x-axis from left to right. Darker lines correspond to lower
1034 fractions of seminatural habitat, which are more typical of intensive farming systems.
1035 Rows represent increasing values of pollinator spillover or decay distance d_m (0.5, 1, 5).
1036 Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $\beta_C = 0.01$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$,
1037 $k_W = 5000$, $\sigma^e_P = 0.8$, $\sigma^d_P = 0.1$, $\sigma^e_C = 0.03$, $\alpha_C = 1000$, $z_P = 0.26$, $c_P = 1$, $z_S = 0.25$, $c_S = 10$,
1038 $b = 10$, $q = \frac{1}{2}$, Pollination dependence = 50%.

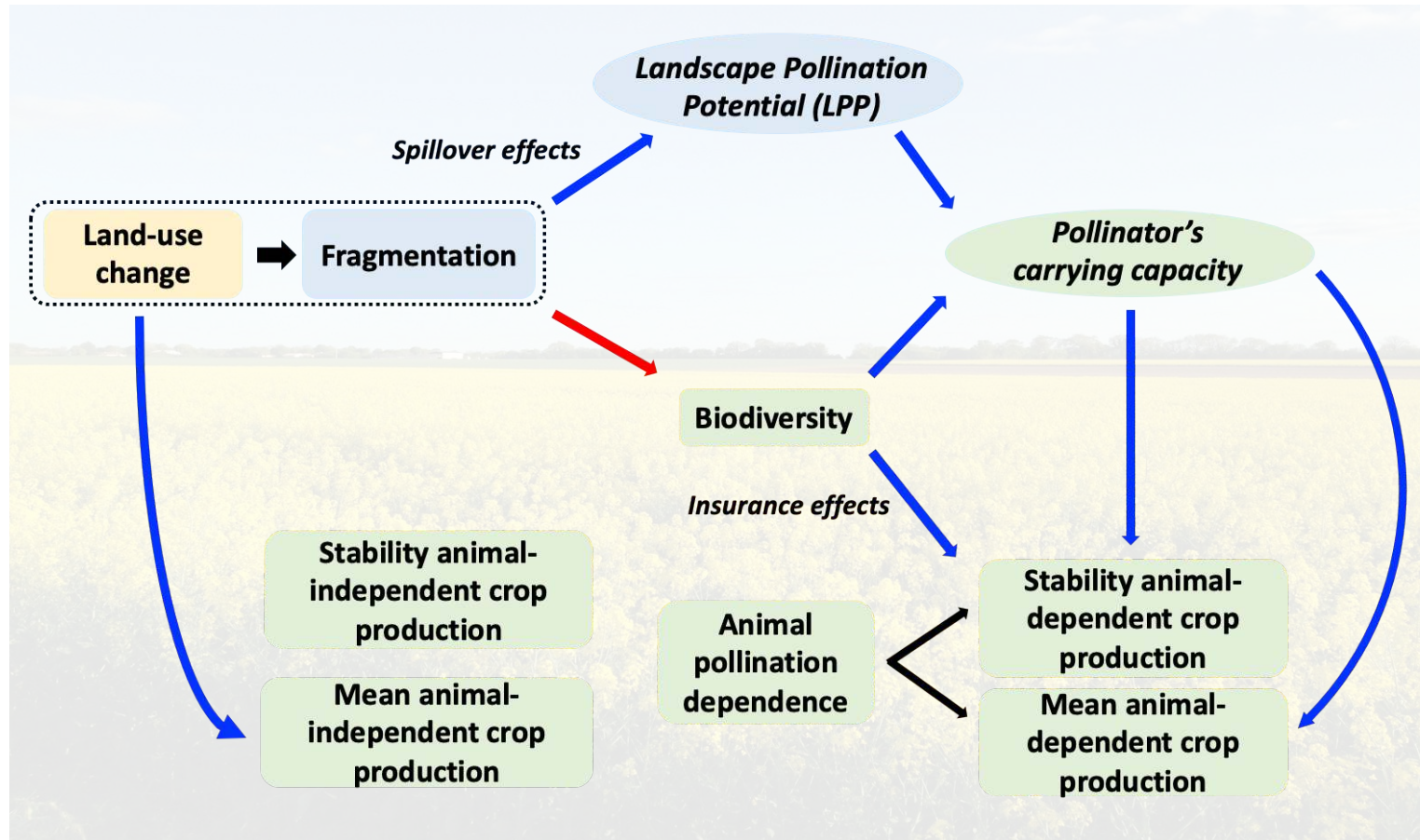
1039 **Table 1 | Parameters and variables of the model.**

1040

Parameters & Variables	Definition	Dimensions	Units
Parameters			
a_P	Maximum growth rate of pollinators	dimensionless	0.9
a_W	Maximum growth rate of semi-natural plants	dimensionless	0.9
a_C	Maximum crop production derived from pollinator interactions	mass·area ⁻¹	1000
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	5000
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, 1000, 4000}
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	Prefactor of the SAR function	dimensionless	*
z_s	Exponent of the SAR function	dimensionless	0.25

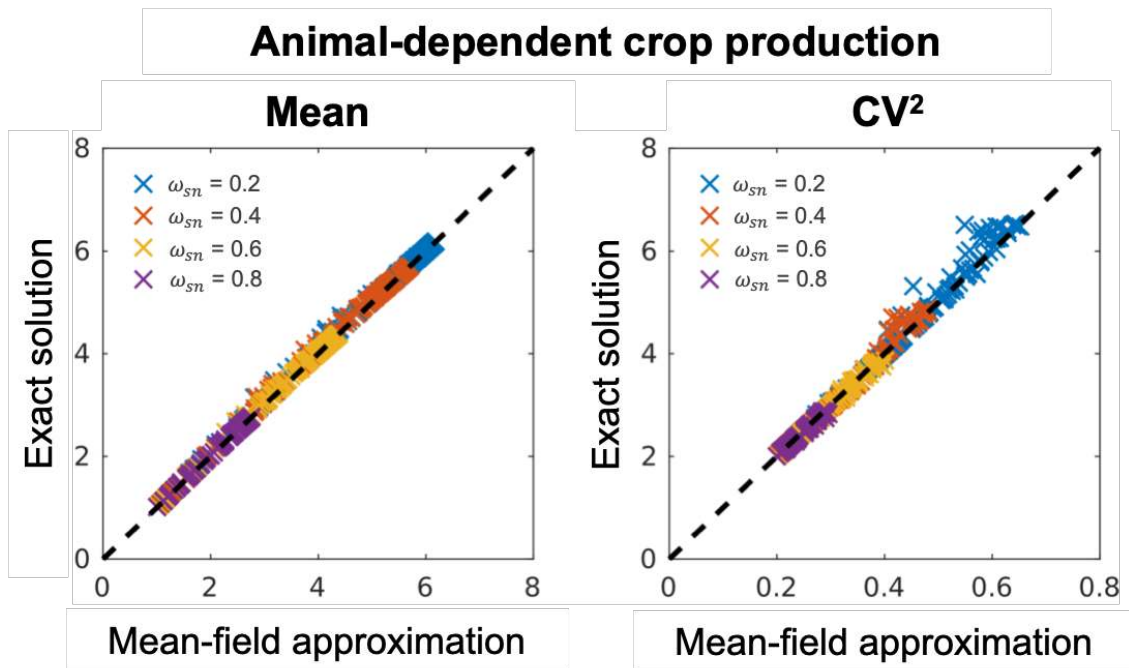
c_P	Parameters of the power law (k_P dependence on S)	mass·area ⁻¹	1
z_P	Parameters of the power law (k_P dependence on S)	dimensionless	{0, 0.26, 0.5}
σ^e_P	Environmental standard deviation of pollinators	dimensionless	0.8
σ^e_W	Environmental standard deviation of ‘wild’ plants	dimensionless	0.02
σ^e_C	Environmental standard deviation of crop production	dimensionless	0.03
σ^d_P	Demographic standard deviation of pollinators	mass ^{-1/2}	0.1
σ^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 metapopulation capacity (SFAR)	dimensionless	{10,20,50}
$1/\delta$	Dispersal distance to calculate metapopulation capacity (SFAR)	dimensionless	{1-10}
λ_M	Metapopulation 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	*
Other			
d_{kl}	Distance between cells k and l	distance	*
ε_{kl}	Distance decay function of ecosystem service flow	dimensionless	*

1042 Figure 1



1043

1044 **Figure 2**

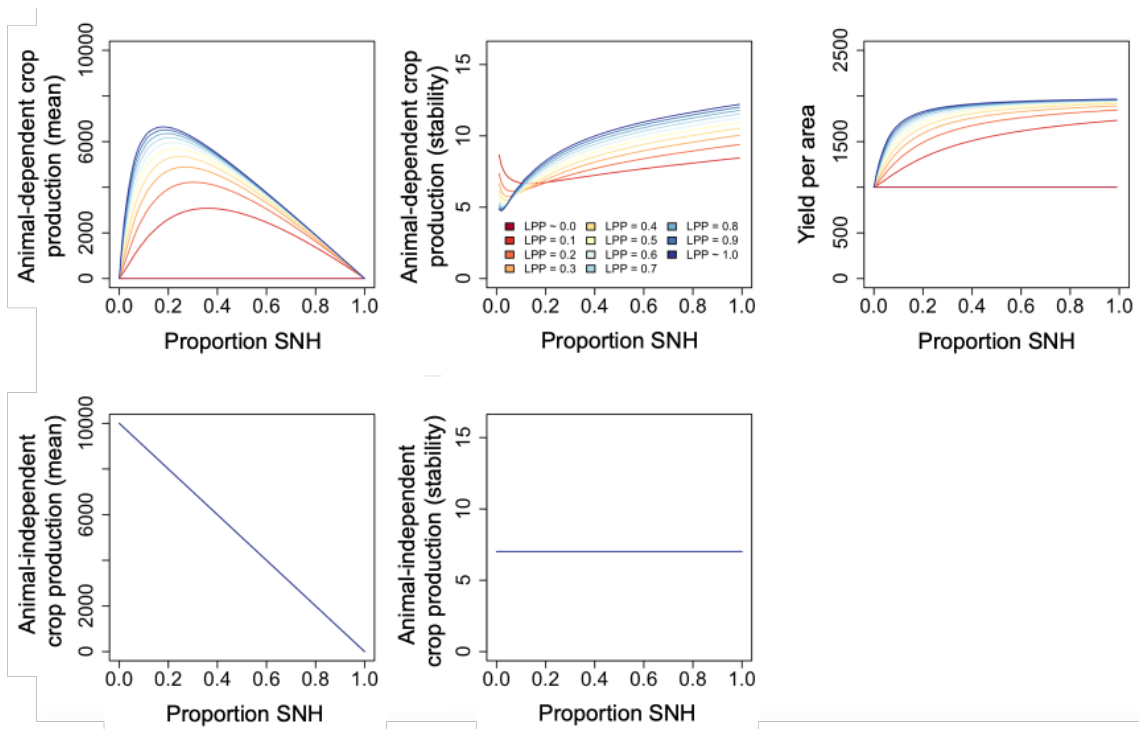


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1047 **Figure 3**

1048



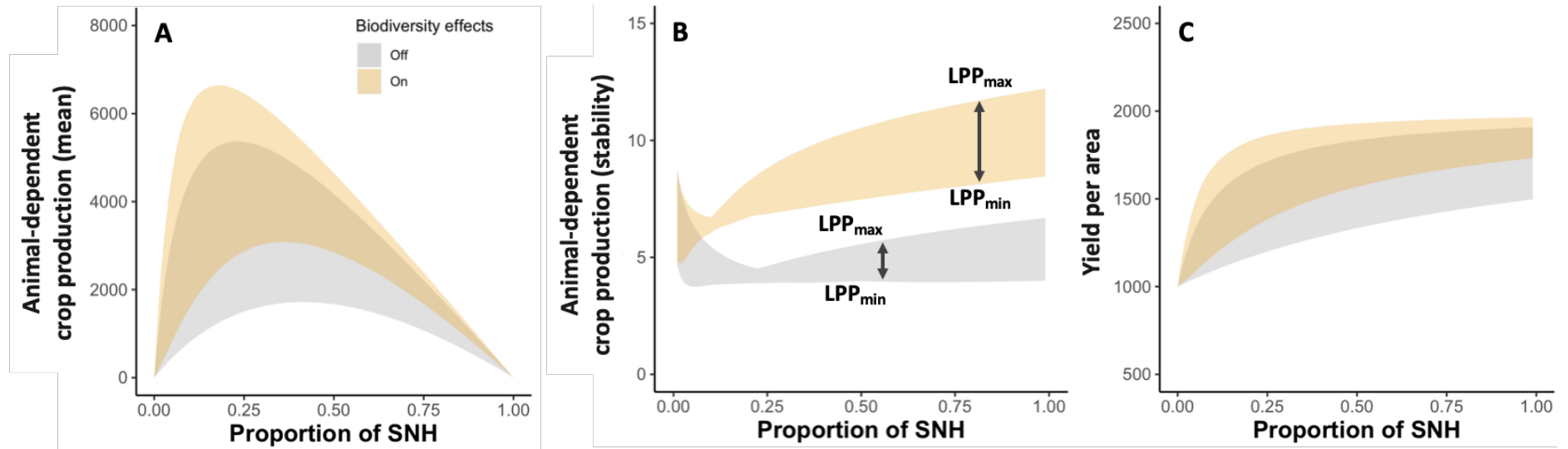
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1051 **Figure 4**

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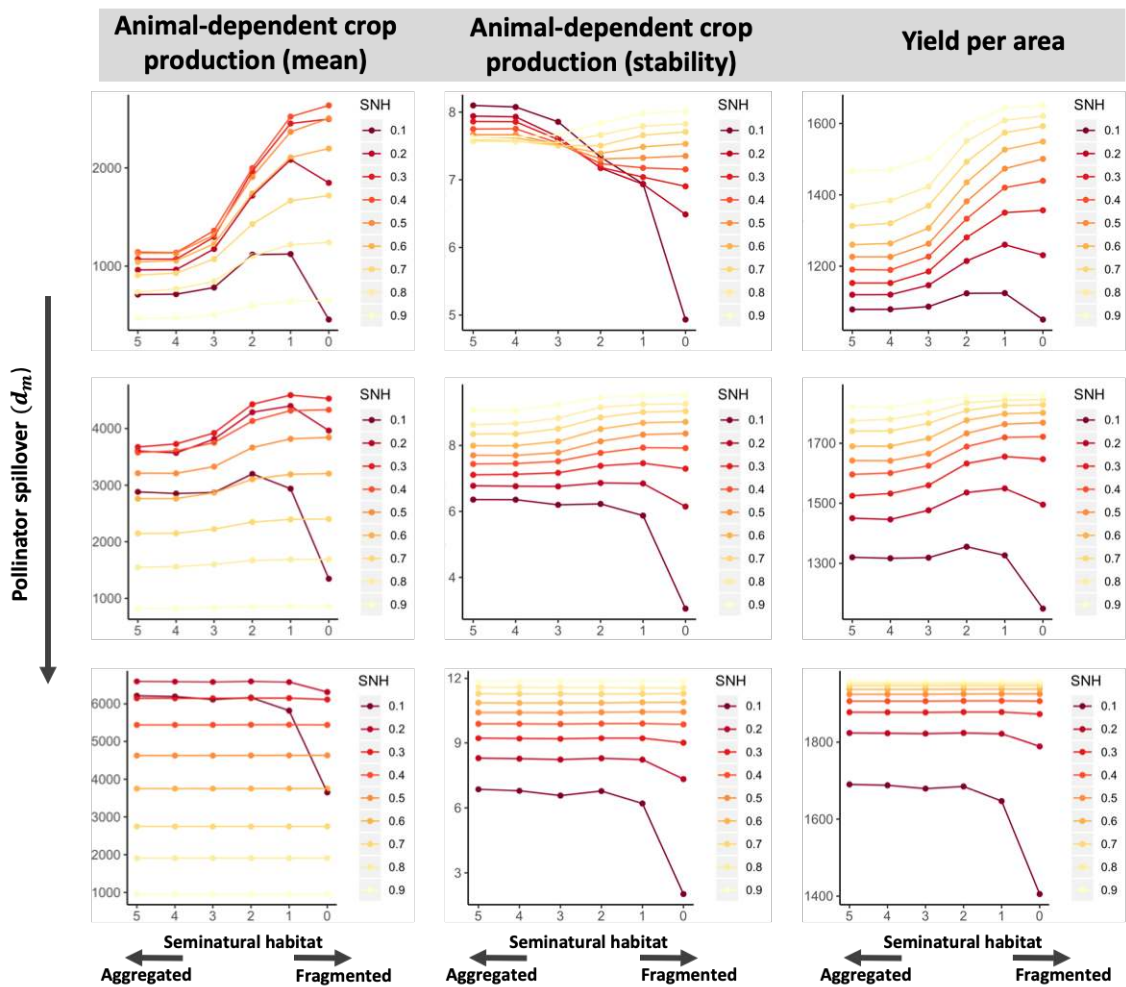
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1057 **Figure 5**

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