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5 **Habitat fragmentation and food security**
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7 **in crop pollination systems**
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30 ***Abstract***
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32 Ensuring stable food supplies is recognized as a major challenge for the 21st century, and
33 one of the UN Sustainable Development Goals. Biodiversity-based approaches to food
34 security are increasingly being supported based on the fact that biodiversity can increase
35 and stabilize crop yields. But agricultural systems are often highly fragmented and it is
36 unclear how such fragmentation affects biodiversity and food production, limiting our
37 capacity to manage agricultural landscapes for food security. Here, we develop a model
38 of crop yield dynamics to investigate how fragmentation of natural habitats for
39 agricultural conversion impacts food production, with a focus on crop pollination. Our
40 results show that fragmentation produces spatial and biodiversity-mediated effects that
41 affect the mean and stability of pollination-dependent crops, with strong consequences
42 for food security. The net effects of fragmentation depend on the strength of the spillover
43 of pollinators to crop land and the degree to which crops depend on animal pollination.
44 Our study sheds new light in the food security debate by showing that high and stable
45 yields depend on biodiversity and the spatial structure of agricultural landscapes, and by
46 revealing the ecological mechanisms of food security in crop pollination systems.
47

48 INTRODUCTION

49 Ensuring stable food supplies for a growing population is one of the UN Sustainable
50 Development Goals¹, and is a challenge that may require multiple solutions. Biodiversity-
51 based approaches to food security suggest that safeguarding certain levels of species
52 diversity is fundamental to increase yields and guarantee stable yields. This is supported
53 by theory and data reporting positive effects of biodiversity on the mean values of various
54 ecosystem functions and services²⁻⁶. Additionally, biodiversity can have a stabilizing
55 effect on ecosystem service supply by providing an insurance against environmental
56 fluctuations⁷, which are predicted to intensify under global change⁸⁻¹¹. Biodiversity
57 insurance effects have been observed in agriculture, where a greater diversity of crops in
58 arable land is associated with increased year-to-year temporal stability of total yields¹².
59 However, most biodiversity in intensively-managed agricultural landscapes is found in
60 the remaining fragments of (semi)natural habitat not converted into crop land, and the
61 effects of such non-crop biodiversity on both the mean provision and stability of crop
62 production are not clearly understood. This has led to a growing concern over the large-
63 scale conversion of natural habitats into crop land and their effects on biodiversity and
64 food production.

65 Agricultural systems are often highly fragmented with areas of intensive cultivation
66 interspersed among remnant patches of seminatural habitat. This loss and fragmentation
67 negatively affect biodiversity and many ecosystem functions and services¹³⁻¹⁵. Despite
68 this, fragments of natural habitat continue to supply important services. The spatial
69 coexistence of crops and natural land creates an opportunity for spillover effects¹⁶, a
70 situation where ecological interactions extend across habitats boundaries and propagate
71 ecological functions. In some cases, fragmentation can increase ecosystem service
72 supply, e.g. if fragmentation of natural habitat for pollinators optimizes interspersions with
73 crop land to maximize crop pollination¹⁷. But fragmentation can also reduce the provision
74 of ecosystem services if biodiversity decreases significantly in the remnant fragments of
75 natural habitat¹³⁻¹⁴. For most services, however, we do not know how fragmentation
76 affects their provision in fragmented landscapes, and this limits our capacity to manage
77 ecosystem service provision and food security in human-dominated landscapes.

78 Recent research has revealed strong and non-linear effects of land conversion on
79 agricultural pollination services at multiple spatial scales¹⁸⁻²⁰. For example, there is
80 consensus on the hump-shaped relationship between the pollinator-dependent component
81 of crop production and the fraction of remnant natural land within intensive farming
82 systems^{20,21}. Research on the stability of crop production shows that yield stability
83 decreases with agricultural intensification and the degree to which crops depend on
84 animal pollination²²⁻²⁵. Changes in crop yield stability of animal-pollinated crops are also
85 dependent on the spatial composition and structure of agricultural landscapes, such as the
86 amount of remnant natural land cover^{20,26} and the isolation of crops from natural land²³.
87 Overall, these studies suggest that improved management of agricultural landscape
88 should increase the amount and stability of production for pollination-dependent crops,
89 and that an understanding of how the spatial pattern of land conversion – i.e.
90 fragmentation – impacts ecosystem services is key to achieve this goal. However, none
91 of these studies have simultaneously combined several ecosystem services, crop yield
92 dynamics at different scales and spatially-explicit landscapes to investigate the effects of
93 land conversion on biodiversity and the provision and stability of ecosystem services in
94 agricultural landscapes.

95

96 There is general consensus that increased food production is necessary, but not sufficient,
97 to achieve food security²⁷, and that agriculture, especially in the global change context,
98 should also aim at stabilizing crop yields over time^{26,28}. Bearing this in mind, we here
99 extend a model of crop yield dynamics into a spatially-explicit landscape to investigate
100 how habitat loss and fragmentation, i.e. the amount and spatial configuration of
101 seminatural habitat, influence the mean provision and stability of several ecosystem
102 services in agricultural landscapes. We focus on crop pollination systems because (i) crop
103 pollination is a key agricultural service that depends on biodiversity, and (ii) worldwide
104 agriculture is shifting towards more pollinator-dependent food production systems^{29,30}.
105 Because the way food is produced worldwide threatens the existence of much of the
106 world's biodiversity that contributes to crop pollination and food security, we explore
107 how changes in biodiversity following land conversion affect the supply of various
108 ecosystem services in fragmented agroecosystems. Specifically, we address two
109 questions: (i) How does the spatial pattern of land conversion, i.e. loss and fragmentation
110 of natural habitat, influence the provision and stability of crop pollination services in
111 agroecosystems? (ii) How does biodiversity in fragmented landscapes influence crop
112 pollination and food security?

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114

115 **METHODS**

116

117 *a. Spatial agroecosystem model*

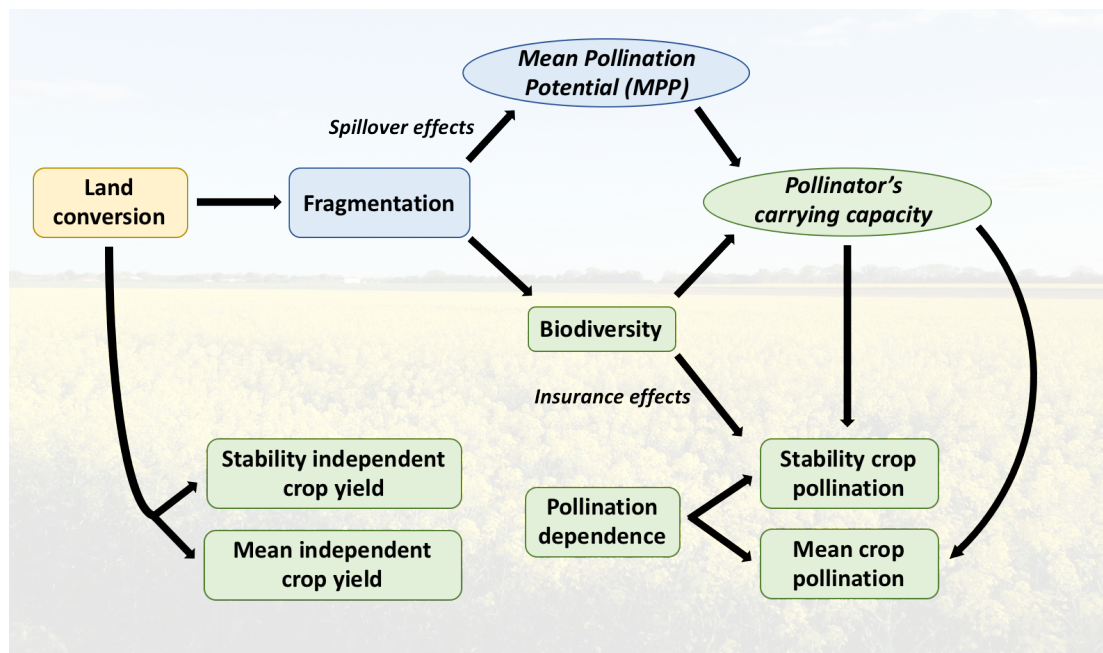
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119 We developed a model to investigate the expected biodiversity (i.e. species richness), crop
120 production at the farm level (i.e. crop yield per area) and landscape crop production (i.e.
121 the magnitude and stability of crop pollination and independent crop yield) in agricultural
122 landscapes with varying degrees of fragmentation and for different crop types (i.e.
123 different levels of animal pollination dependence), yielding a total of six ecosystem
124 service components. In what follows, we describe the model dynamics and the land
125 conversion pattern generation. A conceptual representation of our model is provided in
126 Figure 1.

127

128

129 **Figure 1.** Conceptual diagram of our modelling framework. Green boxes represent non-
130 spatial components of the model, whereas blue boxes are the additions that space brings
131 to the model. Considering space allows: (i) to explore a continuous gradient of land
132 conversion patterns, from completely random to highly aggregated, that encompasses a
133 wide range of fragmentation scenarios, and (ii) to vary the strength of the spillover effect
134 from seminatural habitat to crop land – i.e. the distance-decay of ecosystem service flows.
135 Following a mean-field approximation, the *Mean Pollinator Potential* (MPP) of the
136 agricultural landscape captures the full complexity of fragmentation effects of land
137 conversion on ecosystem service supply that are not mediated by biodiversity (see
138 results).
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144 *Crop dynamics.* We used a model of biodiversity and crop biomass production in
 145 agricultural systems²⁰, and extend it to a spatially-explicit landscape to investigate the
 146 response of ecosystem services to land conversion. The model represents intensively-
 147 managed agricultural landscapes, where crop land does not harbor significant levels of
 148 biodiversity. Spatial heterogeneity is defined by two types of patches: crop land and
 149 seminatural habitat. Crop land is used to grow annual crops with varying degrees of
 150 dependence on wild animal pollination, whereas seminatural habitat shelters biodiversity,
 151 including wild plants and pollinators. The model does not take managed honey bees into
 152 account as they do not depend on the availability of seminatural habitat, and they pollinate
 153 less efficiently compared to non-managed pollinators³¹. Crop land and seminatural habitat
 154 are linked by pollinators' foraging movement. The three components of Montoya et al²⁰
 155 (pollinators, wild plants, and crop yield) are represented by the following equations (they
 156 have been transformed into their spatially-explicit, discrete-time versions):
 157

$$158 \quad P_k(t+1) = P_k(t) \exp(r_{P,k}(t) \left(1 - \frac{P_k(t)}{k_P A_1}\right)) + \sigma_P^e u_P^e(t) P_k(t) + \frac{\sigma_P^d u_P^d(t)}{\sqrt{P_k(t)}} P_k(t) \quad (1)$$

$$159 \quad W_k(t+1) = W_k(t) \exp(r_{W,k}(t) \left(1 - \frac{W_k(t)}{k_W A_1}\right)) + \sigma_W^e u_W^e(t) W_k(t) + \frac{\sigma_W^d u_W^d(t)}{\sqrt{W_k(t)}} W_k(t) \quad (2)$$

$$160 \quad C_k(t) = A_1 [Z_C + r_{C,k}(t)] (1 + \sigma_C^e u_C^e(t)) \quad (3)$$

161 where P_k represents pollinators, W_k wild plants and C_k crop yield in cell k , with $P_k(t) =$
 162 $W_k(t) = 0$ if k is a crop land cell, and $C_k(t) = 0$ if k is seminatural habitat. One unit of
 163 time t corresponds to one growing season, $P(t)$ and $W(t)$ can be interpreted as total
 164 biomass of pollinators and wild plants over growth season t , respectively, whereas $C(t)$ is
 165 the total crop yield at the end of the growing season t . L is the set of crop land cells; k_P
 166 and k_W are the carrying capacities of pollinators and 'wild' plants, respectively, per unit
 167 area. A_l is the area of a single cell; A is total landscape area; $A[1-\omega_{sn}]$ is the total crop land
 168 area, and $A\omega_{sn}$ is total seminatural area. σ_P^e, σ_P^d are the environmental and demographic
 169 stochasticity of pollinators, and σ_C^e is the environmental stochasticity of crops. Equation
 170 (3), is the sum of pollination-dependent and independent parts of crop yield:
 171
 172
 173
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$$175 \quad \text{Independent crop yield: } C_{i_k}(t) = A_1 Z_C (1 + \sigma_C^e u_C^e(t)) \quad (4)$$

$$176 \quad \text{Crop pollination: } C_{d_k}(t) = A_1 r_{C,k}(t) (1 + \sigma_C^e u_C^e(t)) \quad (5)$$

177
 178 In the equations (1-3), $r_{P,k}(t)$, $r_{W,k}(t)$, $r_{C,k}(t)$ are the pollinators', 'wild' plants' and crop's
 179 per capita growth rates, and are defined as:
 180
 181

$$182 \quad r_{P,k}(t) = \frac{\alpha_P \left[\frac{\sum_{l \notin L} \varepsilon_{kl} W_l(t) + \sum_{l \in L} \varepsilon_{kl} C_l(t)}{A} \right]}{\beta_P + \frac{\sum_{l \notin L} \varepsilon_{kl} W_l(t) + \sum_{l \in L} \varepsilon_{kl} C_l(t)}{A}} \quad (6)$$

$$183 \quad r_{W,k}(t) = \frac{\alpha_W \left(\frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A} \right)}{\beta_W + \frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A}} \quad (7)$$

$$184 \quad r_{C,k}(t) = \frac{\alpha_C \left[\frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A} \right]}{\beta_C + \frac{\sum_{l \notin L} \varepsilon_{kl} P_l(t)}{A}} \quad (8)$$

187

188 , where ε_{kl} the distance-decay function representing the decrease of ecosystem service
189 flow from seminatural habitat to crop land (see below). Pollinators are assumed to be
190 generalist central-place foragers that feed on both wild plants and crops³², and pollinator's
191 growth rate thus depends on the availability of resources (wild plants and crops) in the
192 neighborhood. The growth rate of wild plants does not depend on crops. Plant and
193 pollinator uptake of resources follows a saturating, type II functional response, where α_P
194 and α_W are the maximum growth rates; β_P and β_W are half-saturation constants. The
195 pollination-dependent part of crop yield is also assumed to follow a type II functional
196 response (Eq. 5 and 8), where α_C is the maximum crop yield derived from pollination,
197 and β_C is the half-saturation constant of crops. The use of saturating functional responses
198 is widely supported and consistent with real biological examples³³⁻³⁵. A complete
199 description of the model parameters can be found in Table S1.

200

201 Ecosystem service provision at the landscape scale is estimated by summing up the
202 individual contribution of each cell k . Thus, for total crop yield we obtained $C(t) =$
203 $\sum_{k \in L} C_k(t)$. Crop yield per unit of agricultural area is calculated by dividing total crop
204 yield by crop land area.

205

206 *Distance-decay of ecosystem service flow.* One main feature of space, as opposed to
207 spatially-implicit or non-spatial systems, lies in the distance-decay of service flows from
208 one habitat to another. For ecosystem service flow, we used a logistic distance-decay
209 function adapted from Mitchell et al¹⁹. This function is consistent with both theoretical
210 predictions^{16,36-39} and empirical observations⁴⁰⁻⁴² of the effects of habitat edges and
211 distance-to-habitat fragment gradients on ecosystem service provision. Other functions
212 are possible and biologically meaningful (e.g. exponential decay), but they yield similar
213 results (Mitchell et al¹⁹; Figure S1).

214

215 In our model, ecosystem service distance-decay mainly affects the flow of pollination to
216 crop land. ε_{kl} is the distance-decay function of the effect pollinators on crops: the further
217 a crop land cell is from seminatural habitat, the more difficult it is for pollinators to reach
218 that cell, and thus the smaller the effect of P_k on crop biomass. To calculate ε_{kl} , we adapt
219 Mitchell et al¹⁹ distance-decay function as follows (see also Appendix S1):

220

$$221 \quad \varepsilon_{kl} = \frac{1+\beta}{1+\beta \exp(\alpha d_{kl})}, \text{ with} \quad (9)$$

222

$$223 \quad d_m = \frac{1}{\alpha} \ln \frac{0.5+\beta}{0.5\beta} \quad \text{and} \quad \Delta d = \frac{1}{\alpha} \ln \frac{8.1+9\beta}{0.1+\beta}$$

224

225 , where d_{kl} is the distance between cells k and l , and parameters α and β are auxiliary
226 parameters determined by

227

$$228 \quad d_m = \frac{1}{\alpha} \ln \frac{0.5+\beta}{0.5\beta} \quad \text{and} \quad \Delta d = \frac{1}{\alpha} \ln \frac{8.1+9\beta}{0.1+\beta}$$

229

230 , where d_m is the distance from seminatural cell edge at which the pollination flow equals
231 one half of its initial value – 50% decay distance –, and Δd is the distance over which the
232 pollination flow decreases from 90% to 10% of its initial value – 90% to 10% decay
233 distance. The total contribution of animal pollination to crop yield in a given cell k is
234 made up from the summed contributions of individual seminatural habitat cells in the

235 surrounding landscape. We explored a range of d_m values to investigate how variations in
236 distance-from-fragment where service flow decreases influence ecosystem service
237 supply. Variation in Δd had little effect on model results (Figure S2; see also Mitchell et
238 al¹⁹).

239
240 Stochasticity. To investigate the effects of land conversion pattern on yield stability, our
241 model includes environmental and demographic stochasticity. Environmental
242 stochasticity (e.g. variation in temperature, rainfall variability) is included through the
243 terms $\sigma^e u^e(t)$, where $(\sigma^e)^2$ is the environmental variance of either pollinators $((\sigma_P^e)^2)$,
244 ‘wild’ plants $((\sigma_W^e)^2)$ or crops $((\sigma_C^e)^2)$, and $u^e(t)$ are random functions with zero mean and
245 standardized variance; we assume that perturbations have no temporal correlation.
246 Demographic stochasticity $(\sigma^d u^d(t))$ emerges from stochastic variation in individuals’
247 births and deaths. Crops are sown at high densities, and thus we assume demographic
248 stochasticity is prevented in crops, and only affects pollinators and ‘wild’ plants.
249 Demographic stochasticity is included in the form of the first-order normal approximation
250 commonly used in stochastic population dynamics⁴³, where $(\sigma^d)^2$ is the demographic
251 variance of either pollinators $((\sigma_P^d)^2)$ or ‘wild’ plants $((\sigma_W^d)^2)$, and $u^d(t)$ are independent
252 random functions with zero mean and standardized variance. For environmental
253 stochasticity, we take the same perturbation for all cells and for all variables (because
254 weather variations will be more or less the same over the entire landscape). For
255 demographic stochasticity, we take independent perturbations between cells and
256 variables.

257
258 Biodiversity and fragmentation. Despite recent debate has ensued on the relative
259 importance of habitat loss *versus* fragmentation on species diversity^{15,44-46}, empirical
260 evidence shows that larger and more connected fragments of natural habitat in general
261 host more biodiversity than smaller and more isolated fragments¹⁴. In agricultural
262 landscapes, this means that different land conversion patterns (e.g. random, aggregated)
263 will result in different biodiversity levels which will in turn influence ecosystem service
264 supply in many ways. Hanski et al⁴⁷ proposed a way to capture the relationship between
265 biodiversity and habitat fragmentation, namely the *Species-Fragmented Area*
266 *Relationship* (SFAR), which extends the conventional species-area relationship (SAR) to
267 landscapes where fragmentation pervades. The SFAR has the following form:

$$268 \quad S = c_s (A \omega_{sn})^{z_s} e^{-b/\lambda_M} \quad (10)$$

270
271 , where S is pollinator diversity – species richness –, and $A \omega_{sn}$ is the total area of
272 seminatural habitat; b is a parameter modulating the effect of the metapopulation capacity
273 and reflects the ability of species to live in fragmented landscapes (e.g. low b
274 characterized species evolved or well adapted to live in fragmented landscapes). The
275 degree of fragmentation is captured by λ_M , which represents the metapopulation capacity
276 of the fragmented landscape. The metapopulation capacity λ_M is obtained from the leading
277 eigenvalue of a $n \times n$ matrix with elements $m_{ii} = 0$ and $m_{ij} = A_i^x A_j^y f(d_{ij})$, where A_i and A_j
278 are the areas of fragments i and j , x and y are scaling factors (we use $x = 2$, $y = 1$ as in
279 Hanski et al⁴⁷), d_{ij} is the Euclidean distance between the centroids of fragments i and j ,
280 and $f(d_{ij})$ is the dispersal kernel. Following Hanski et al (2013), we assume the exponential
281 dispersal kernel with a cutoff at 0.01, $f(d_{ij}) = \max\{\exp(-\delta d_{ij}), 0.01\}$, where $1/\delta$ gives the
282 average dispersal distance, and estimated λ_M from information on fragment size and
283 distance among fragments (all referred to seminatural habitat). We used the accepted
284 value of $z_s = 0.25$ for a wide range of plants and animals⁴⁸, and allowed dispersal distance

285 and b to vary.

286

287 Changes in landscape structure can affect biodiversity and the ecosystem functions that
288 underlie ecosystem service provision. To consider the effects of fragmentation on
289 biodiversity and crop pollination, we made crop pollination dependent on pollinator
290 diversity. This was done by creating a dependence of pollinator's carrying capacity (k_P)
291 on biodiversity following a power law: $k_P = c_{k_P} S^{z_{k_P}}$, where S is the number of pollinator
292 species estimated by the SFAR, and c_{k_P} , z_{k_P} are the parameters of the power law. We use
293 the values of $c_{k_P}=1$ and $z_{k_P}=0.26$ based on recent literature⁴⁹⁻⁵¹, but also considered two
294 extreme values of h (0.0, 0.5) to more clearly explore the effect of pollinator diversity.
295 Finally, we considered the ability of pollinator diversity to provide an insurance against
296 environmental fluctuations, i.e. insurance effect of biodiversity. To do this, we made $\sigma_P^e =$
297 e_P/S^q , and compared a scenario where environmental stochasticity depends on
298 biodiversity ($q = 1/2$)⁵² with another scenario where biodiversity does not affect
299 environmental stochasticity ($q = 0$). Demographic stochasticity acts at the individual
300 level, and in the same manner for conspecifics and heterospecifics; thus, there is no
301 insurance effect for demographic stochasticity.

302

303 ***b. Land conversion pattern generation***

304

305 The landscape consisted of two-dimensional lattice (25×25 cells) where individual cells
306 can have either of two states: crop land or seminatural habitat. We generated land
307 conversion patterns by iteratively creating crop land cells in a landscape that consisted
308 initially only of seminatural land. In a single step of the algorithm only one semi-natural
309 habitat cell is selected and converted. At each iteration, we determined for each
310 seminatural land cell the number of neighboring crop land cells, a number we denote by
311 m (m is equal to 0, 1, 2, 3 or 4). We then chose randomly one of the seminatural land cells,
312 with a probability that depended on the number of neighboring crop land cells. More
313 precisely, the probabilities were proportional to $p = 0.1^w$ if $m = 0$ and $p = m^w$ if $m \geq$
314 1. These values are actually relative probabilities; that is, they have to be normalized to
315 get the probability of selecting a given cell. Hence, for $w = 0$ all seminatural land cells
316 had the same relative probability to be chosen, leading to a fully random, unclustered
317 pattern. For $w > 0$, seminatural land cells with more neighboring crop land cells had a
318 higher relative probability to be converted, leading to a clustered or aggregated pattern.
319 Larger values of w resulted in more aggregated patterns. Therefore, variation in the value
320 of w allowed us to produce a continuous gradient of land conversion patterns, and
321 therefore fragmentation, based on the aggregation degree (Figure S3). For each land
322 conversion pattern, we characterised fragmentation of the remaining seminatural habitat
323 by quantifying mean fragment size, number of fragments, mean fragment perimeter, and
324 perimeter: area ratio.

325

326

327 **RESULTS**

328

329 *Mean-field approximation*

330 Because the spatially explicit model demands much computational time, we analysed
331 how the spatially-explicit model is linked to the spatially-implicit one. To do so, we
332 developed a mean-field approximation of the spatial agroecosystem model (Eqs. 1-3),
333 which replaces the detailed spatial structure of the landscape by a much simpler, spatially

334 averaged one (see Appendices S2 and S3 for further details on the solution of the full
 335 model and the derivation of the mean-field approximation). To do this, consider the sums
 336 $\sum_{l \notin L} \varepsilon_{kl}$ (Eq. 8): there are $\omega_{sn} n^2$ terms (possible values of l ; n^2 is the number of cells in
 337 the agricultural landscape), and $(1 - \omega_{sn}) n^2$ such sums (possible values of k). It turns out
 338 that the main effects of the spatial structure can be accounted for by a new parameter, $\bar{\varepsilon}$,
 339 defined as

$$340 \quad \bar{\varepsilon} = \frac{1}{(1 - \omega_{sn}) n^2} \frac{1}{\omega_{sn} n^2} \sum_{k \in L, l \notin L} \varepsilon_{kl} \quad (11)$$

342 $\bar{\varepsilon}$ is the average value of ε_{kl} when taking a random cell $k \in L$ and a random cell $l \notin L$. $\bar{\varepsilon}$
 343 has two complementary interpretations. Firstly, it is a measure of the amount of
 344 seminatural habitat supplying pollinators to crop land: if we multiply $\bar{\varepsilon}$ by the area of
 345 seminatural habitat ($R_{SNH} = \omega_{sn} A \bar{\varepsilon} = \omega_{sn} n^2 A_1 \bar{\varepsilon}$), then R_{SNH} is the area from which a
 346 crop land cell can be pollinated averaged over all crop land cells. Secondly, $\bar{\varepsilon}$ quantifies
 347 the amount of crop land that is reachable by pollinators from seminatural habitat: if we
 348 multiply $\bar{\varepsilon}$ by the crop land area ($R_C = (1 - \omega_{sn}) n^2 A_1 \bar{\varepsilon}$), R_C is the crop land
 349 area that a pollinator can reach averaged over all seminatural cells. Taken together, these
 350 two interpretations can be summarized by the term *Mean Pollination Potential* (MPP; 0
 351 $\leq \text{MPP} \leq 1$). Under the mean-field approximation the mean crop yield is (see Appendix
 352 S3):

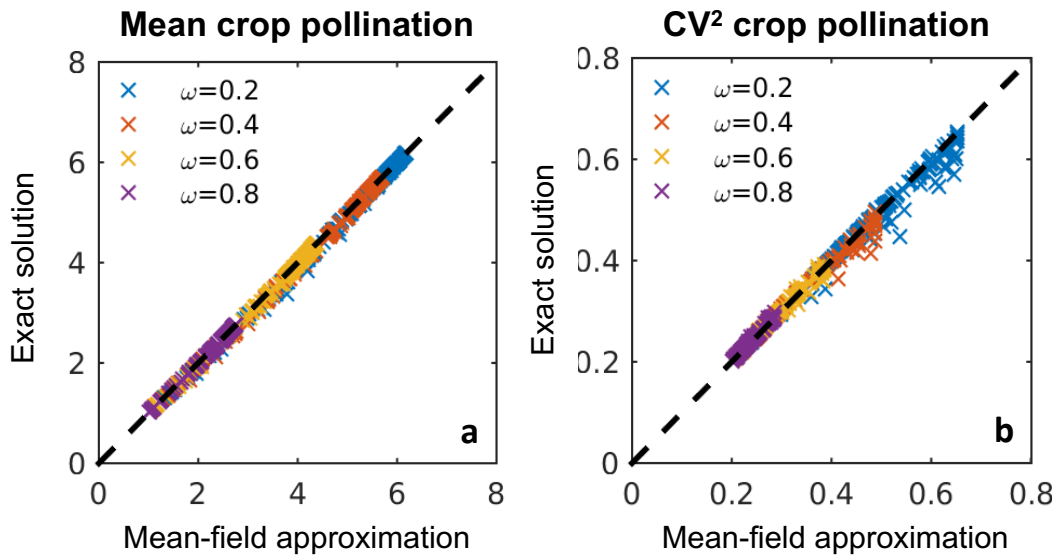
$$353 \quad C^* \approx (1 - \omega_{sn}) A \left(Z_C + \frac{\alpha_C \bar{\varepsilon} k_P \omega_{sn}}{\beta_C + \bar{\varepsilon} k_P \omega_{sn}} \right) \quad (12)$$

354
 355
 356 The variance of crop yield is:

$$357 \quad \text{Var}(C) \approx \frac{((1 - \omega_{sn}) \alpha_C \beta_C)^2}{(\beta_C + \bar{\varepsilon} k_P \omega_{sn})^4 \alpha_C (1 - \alpha_C)} \left((\sigma_P^e \bar{\varepsilon} k_P \omega_{sn} A)^2 + ((\sigma_P^d \bar{\varepsilon})^2 k_P \omega_{sn} A) \right) + (\sigma_C^e C^*)^2 \quad (13)$$

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 359
 360 , with $k_p = a S^h$ (see methods). We found that the mean-field approximation is a very
 361 accurate description of the dynamics of various ecosystem services in agricultural
 362 landscapes, both for mean and stability values (Figure 2).
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 366

367 **Figure 2.** Mean-field approximation vs Exact solution. **(a)** Mean crop pollination. **(b)**
368 Variability of crop pollination (measured as Coefficient of Variation – CV –, the inverse
369 of stability). Exact solution equations can be found in Appendix 2 (Eqs. 8 and 17 for crop
370 pollination mean and variability, respectively). Mean-field results are derived from Eqs.
371 12 and 13 in the main text, for mean and variability of crop pollination, respectively. ω_{sn}
372 is the proportion of seminatural habitat (drawn randomly in $[0,5]$, Figure S3). d_m = drawn
373 randomly in $[1,25]$, expressed in linear dimension of a landscape cell, $z_{kp} = 0.26$.
374 Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$,
375 $k_P = 0.1$, $e_P = 0.8$, $\sigma^d_P = 0.1$, $\sigma^e_C = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%.
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380 The mean-field approximation shows that the fragmentation effects of land conversion
381 on crop pollination services are determined by MPP. To consider the spatial structure of
382 land conversion, the term β_C/k_P of the non-spatial model²⁰ has to be replaced by

$$384 \frac{1}{\bar{\epsilon}} \frac{\beta_C}{k_P} = \frac{\omega_{sn} A}{R_{SNH}} \frac{\beta_C}{k_P} = \frac{(1-\omega_{sn}) A}{R_C} \frac{\beta_C}{k_P} \quad (14)$$

385
386 β_C/k_P is the ratio of crop half-saturation constant relative to pollinators' carrying capacity,
387 and is an *effective* parameter combination that strongly influences crop dynamics, as it
388 quantifies the pollinator requirement of crops relative to the availability of pollinators,
389 i.e. crop relative requirement for pollinators. When β_C/k_P is small, crop yield saturates at
390 lower pollinator biomass than their carrying capacity; when β_C/k_P is large, crop yield
391 saturates at pollinator biomasses much higher than their carrying capacities. β_C/k_P
392 influences both the mean and stability of crop pollination. On one hand, greater values of
393 β_C/k_P increase the effect of pollinator biomass on crop pollination, reducing mean yield
394 and shifting maximum yield to larger amounts of seminatural habitat. On the other hand,
395 β_C/k_P controls how fast the saturation of crop pollination to pollinator biomass sets in and,
396 consequently, how fast the response of crops to pollinator stochasticity drops down; thus,
397 the smaller β_C/k_P the faster the saturation sets in, and so the faster crop yield variability
398 drops when increasing seminatural habitat (Figure S4A). Without distance-decay (or
399 when $MPP \approx 1$), the spatial model collapses into the non-spatial model (Figure 3A-C,
400 dark blue lines; Figure S4B). Fragmentation effects on ecosystem services become
401 stronger when $MPP < 1$, which increases β_C/k_P .

402 403 Spatial constraints/ fragmentation effects on MPP

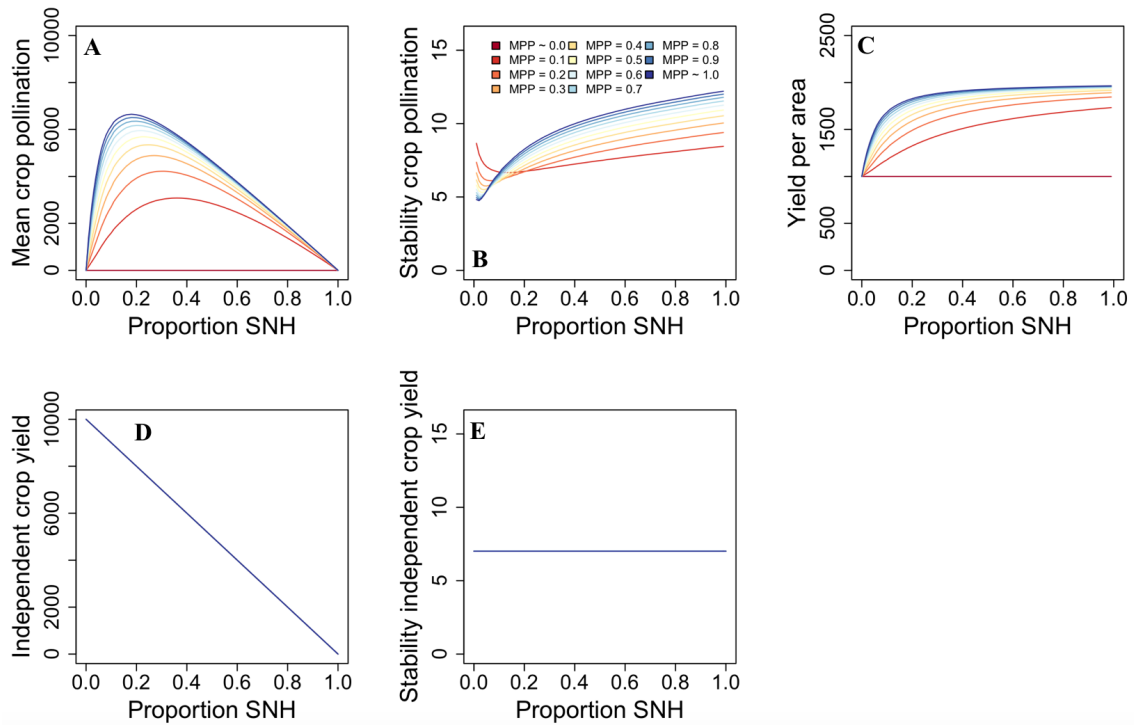
404 MPP depends on two factors: fragmentation – more specifically, the aggregation pattern
405 of land conversion – and the distance-decay of ecosystem service flow. High aggregation
406 (low fragmentation) and fast distance-decay result in lower MPP (Figures S5 and S6),
407 which in turn reduce crop pollination services. These two factors interact: only when the
408 flow of pollinators to crop land is limited (fast distance-decay) aggregation patterns are
409 relevant for crop production (Figure S5A-D). In this case, higher aggregation, through its
410 effects on MPP, not only reduces mean crop pollination and shifts maximum yield to
411 higher fractions of seminatural habitat, but also decreases yield stability along the
412 gradient of seminatural habitat (Figure 3A, B). When no restrictions exist in the flow of
413 pollinators to crop land, MPP is maximum ($MPP \approx 1$; Figure 3) and fragmentation does
414 not affect pollination services (Figure S5E-F).

415 416 MPP effects on ecosystem services

417 We did not find any clear, consistent effect of specific fragmentation metrics on
418 ecosystem services (Figure S7). However, the full complexity of the purely spatial
419 fragmentation effects (i.e. those not mediated by biodiversity) on ecosystem service
420 supply, irrespective of the specific pattern of land conversion, were captured by MPP
421 (Figure S8). When $MPP = 1$, fragmentation effects are negligible and crop dynamics are
422 identical to those of the non-spatial model (Figure 3A-C, dark blue lines). In this case, no
423 additional mechanisms need to be invoked: crop yield dynamics are driven by the crop's
424 relative requirement for pollinators (β_C/k_P , Figure S4) and the degree to which crops
425 depend on animal pollination. The effects of fragmentation kick off when $MPP < 1$.
426 Lower MPP – i.e. more aggregated patterns of land conversion (Figure S5) – reduces the
427 carrying capacity of pollinators (Eq. 14), which decreases the provision of pollinator-
428 dependent ecosystem services (Figure 3A-C). The same is true for crop pollination
429 stability, except at small fractions of seminatural habitat and/or small values of MPP. A

430 higher biodiversity effect (larger z_{kp}) increases both mean crop pollination and its
431 stability, as well as yield per area (Figure S9). MPP has no effect on independent crop
432 yield as it does not depend on animal pollination and, therefore, on seminatural habitat
433 (Figure 3D-E).
434
435
436

437 **Figure 3.** Effects of landscape composition and MPP on ecosystem services. Ecosystem
438 services are represented as a function of the proportion of seminatural habitat, for
439 different MPP. MPP includes the effects of fragmentation – more specifically, the
440 aggregation pattern of land conversion – and the distance-decay of ecosystem service
441 flow. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W =$
442 5000 , $e_P = 0.8$, $\sigma_P^d = 0.1$, $\sigma_C^e = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%, $z_{k_P} =$
443 0.26 .
444
445



446
447

448 The effect of MPP on crop pollination services increases with the degree to which crops
449 depend on animal pollination. Higher pollination dependence of crops shifts maximum
450 yields to higher fractions of seminatural habitat at landscape and local scales, and the
451 stability of crop pollination increases faster (Figure S10).

452

453 *Biodiversity effects on crop pollination*

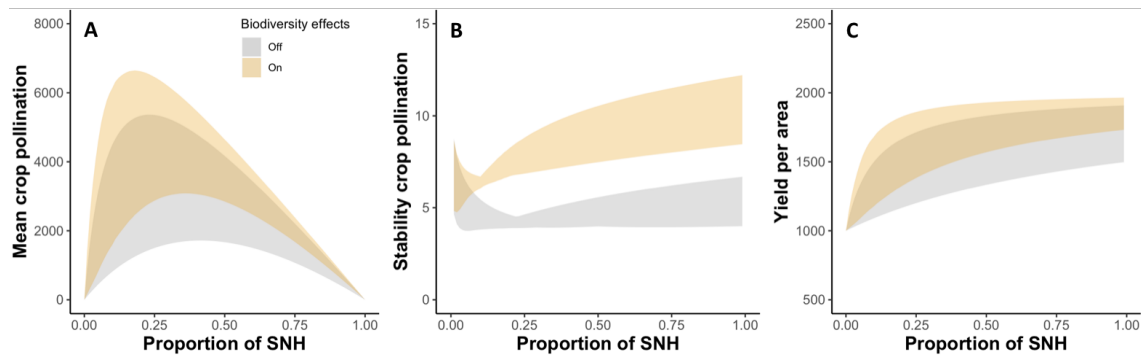
454 Biodiversity decreases with land conversion, but higher aggregation of seminatural
455 fragments alleviates that loss to some extent (Figure S11). The effects of fragmentation
456 on biodiversity are stronger at low-intermediate fractions of seminatural habitat, and are
457 directly influenced by the dispersal distance of organisms and by their ability to live in
458 fragmented landscapes (Figure S12). Biodiversity stabilizes crop pollination by
459 increasing the pollinators' carrying capacity (which affects the variance of crop
460 production, Eq. 13; Fig. 4B), and by reducing the response of crop pollination to
461 environmental fluctuations (Fig. 4C). The former effects are stronger when biodiversity
462 is higher, whereas the latter effects reduce variability of crop pollination especially at
463 increasing biodiversity levels. A higher biodiversity effect (larger z_{kp}) increases both
464 mean crop pollination and its stability, as well as yield per area (Figure S13).

465

466

467 **Figure 4.** Effects of biodiversity on crop pollination. Plots show the response of crop
 468 pollination services – mean and stability of crop pollination (panels **A** and **B**), and yield
 469 per area (panel **C**) – as a function of the proportion of seminatural habitat (SNH). All
 470 MPP values are contained within the shadows, whose limits are determined by the
 471 minimum and maximum values across the range of MPP. Biodiversity can affect crop
 472 pollination in a two-way manner. On one hand, biodiversity influences mean crop
 473 pollination and yield per area by increasing the carrying capacity of pollinators ($k_p =$
 474 $c_{k_p} S^{z_{k_p}}$). On the other hand, biodiversity impacts the stability of crop production both
 475 indirectly – increasing the carrying capacity of pollinators – and directly – reducing the
 476 response of crop production to environmental fluctuations ($\sigma_p^e = e_p / S^q$). For each
 477 ecosystem service, the plots compare two scenarios: (i) a scenario where biodiversity has
 478 no effect on crop pollination ($z_{k_p} = 0, q = 0$), represented by the grey shadows, *versus* (ii)
 479 a scenario where biodiversity has an effect on crop pollination ($z_{k_p} = 0.26, q = 1/2$; Tilman
 480 1999, Liang et al 2016, O’Connor et al 2017, Cardinale et al 2011), represented by the
 481 light orange shadows. Parameter values: $\alpha_p = \alpha_w = 0.9, \beta_p = \beta_w = 0.6, A = 10, Z_C = 1000,$
 482 $\alpha_C = 1000, k_W = 5000, e_p = 0.8, \sigma_p^d = 0.1, \sigma_C^e = 0.03, \alpha_C = 1000,$ Pollination dependence
 483 = 50%.

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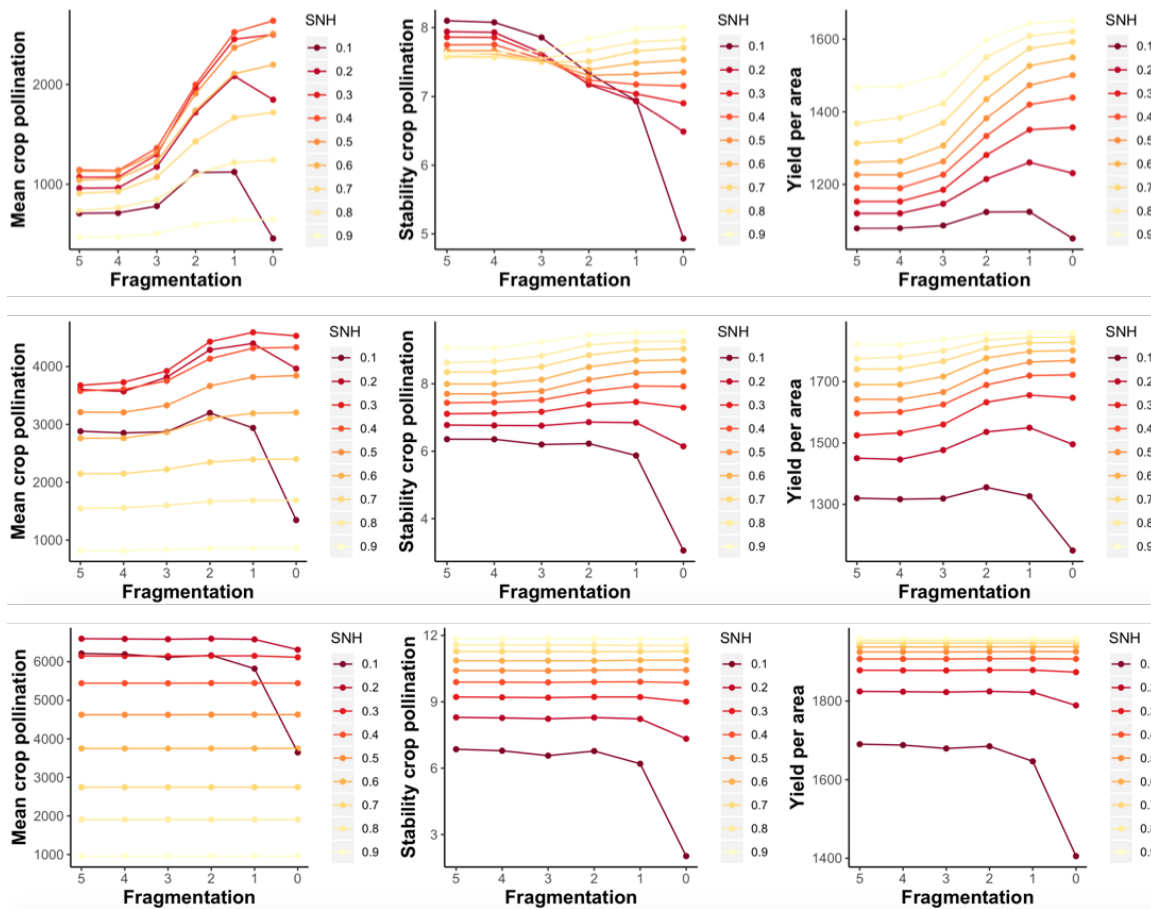
489 *Net effects of fragmentation on ecosystem services*

490 The fragmentation pattern of seminatural habitat has a dual effect on crop pollination
491 services. On one hand, aggregation of seminatural fragments decreases pollination by
492 lowering MPP (Figures S5 and S14), which in turn reduces the carrying capacity of
493 pollinators (Eq. 14). On the other hand, aggregation increases biodiversity (especially at
494 low-intermediate fractions of seminatural habitat; Figure S11), which in turn increases
495 pollinators' biomass (through its positive effects on pollinators' carrying capacity) and
496 the service of pollination (Figure S14). The net effect of fragmentation on ecosystem
497 service supply depends on the distance-decay of ecosystem service flow (d_m) and the
498 proportion of seminatural habitat remaining. When the decay distance d_m is low (Figure
499 5, first row), fragmentation effects tend to be positive for mean crop pollination and yield
500 per area because the fraction of crop land within reach from non-crop land areas is higher
501 (this fraction is lower at very low fractions of seminatural land). Yet, crop pollination
502 stability decreases due to the lower biodiversity levels in fragmented landscapes, except
503 at high fractions of seminatural habitat where the impact of fragmentation is minimum.
504 Conversely, when the decay distance d_m is high, seminatural fragments are perceived as
505 more connected and ecosystem service supply is not limited by space. In this case,
506 fragmentation becomes irrelevant, or even negative, due to the lower biodiversity levels
507 in fragmented landscapes (Figure 5).

508

509

510 **Figure 5.** Net effects of aggregation on crop pollination services. Columns represent,
 511 from left to right, mean and stability of crop pollination, and yield per area. Ecosystem
 512 services are plotted as a function of fragmentation for different proportion of seminatural
 513 habitat or SNH (as opposed to figures 3-4). Fragmentation increases in the x-axis from
 514 left to right (we set $w = m$ for simplicity; higher w, m means more aggregation). Darker
 515 lines correspond to lower fractions of seminatural habitat, which are more typical of
 516 intensive farming systems. Rows represent increasing values of the decay distance d_m
 517 (0.5, 1, 5). Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$,
 518 $k_W = 5000$, $e_P = 0.8$, $\sigma_P^d = 0.1$, $\sigma_C^e = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%, $z_{k_P} =$
 519 0.26.
 520
 521



522
 523

524 DISCUSSION

525

526 Our analysis reveals a variety of effects of land conversion on biodiversity and crop
527 production in intensive crop pollination systems. Using a mean-field approximation of
528 various ecosystem services in spatially-explicit agricultural landscapes, our model
529 suggests that (1) fragmentation impacts food production through spatial and biodiversity-
530 mediated effects; (2) the full complexity of the fragmentation-induced spatial effects on
531 ecosystem service supply, irrespective of the specific pattern of land conversion, is
532 captured by one factor – the mean pollination potential of the remaining seminatural land
533 (MPP) – which determines the mean and stability of pollination services; (3) biodiversity
534 can have a stabilizing effect on crop pollination in fragmented agricultural landscapes;
535 and (4) the net effects of fragmentation on food production depend on the strength of the
536 spillover of pollinators to crop land and the degree to which crops depend on animal
537 pollination.

538

539 The loss of seminatural land has contrasting effects on the ecosystem services considered:
540 biodiversity decreases, independent crop production increases, while crop pollination is
541 maximized at intermediate fractions of seminatural habitat. But fragmentation can modify
542 these relationships in two ways. On one hand, land conversion can produce multiple
543 patterns of aggregation of the remaining fragments of seminatural habitat. These patterns
544 combined with the strength of the spillover of pollinators to crop land determine the mean
545 pollination potential of seminatural land (MPP), which is the main responsible of food
546 production in pollination-dependent agriculture. The second type of effects are mediated
547 by biodiversity, as the level of aggregation of the remaining fragments of seminatural
548 habitat affects the pollinator richness. Such purely spatial and biodiversity-mediated
549 effects modify the carrying capacities of pollinators, which ultimately determine crop
550 pollination services. The mean-field approximation shows that the effects of space on
551 crop production can be interpreted in the same terms as varying the pollinator's carrying
552 capacity in the non-spatial model²⁰.

553

554 Our results suggest that understanding the factors that affect MPP is a fundamental step
555 towards food security. If no restrictions exist in the flow of pollinators to crop land, MPP
556 is maximum and the spatial structure of land conversion does not affect crop yield
557 dynamics. In this situation, seminatural fragments are perceived as more connected and
558 the provision and stability of crop pollination is not conditioned by space, i.e. spatial and
559 non-spatial models converge. However, agricultural landscapes are fragmented to some
560 extent and the foraging ranges of most organisms are local (200 m for small bee species,
561 25–110 m for bumble bees, >200 m for certain bee species⁵³⁻⁵⁶), which produces higher
562 aggregation and weaker spillover effects, thus reducing MPP. Such reductions in MPP
563 affect crop yields by (i) decreasing mean crop pollination and total yield per area, and (ii)
564 decreasing yield stability along the gradient of seminatural habitat. The estimation of
565 MPP in real farming systems would require data on the aggregation level of seminatural
566 habitat fragments within the agricultural landscape, and on the spillover of pollinators to
567 adjacent crops. The former can be obtained with GIS processing of aerial pictures or
568 satellite images of agricultural landscapes. For the latter, information on foraging
569 distances of pollinator species combined with experimental studies could be used to
570 reveal species' foraging patterns and how the flow of pollinators to adjacent crop land
571 decays with distance (e.g.^{16,36,37-39}). This information will be useful to design agricultural
572 landscapes for high MPP.

573

574 Producing food requires land, and increasing the land devoted to farming reduces the land
575 devoted to biodiversity conservation. Our results agree with recent empirical studies
576 showing that higher pollinator diversity increases food production⁶, and further suggest
577 that it can lead to lower variability in agricultural productivity. The response of
578 biodiversity to land conversion depends on the amount and the spatial structure of
579 seminatural habitat loss. For example, although the effects of fragmentation on
580 biodiversity are stronger at low-intermediate fractions of seminatural habitat – typical of
581 intensive farming systems –, aggregation increases the biodiversity levels within
582 seminatural habitat fragments. The stabilizing effect of biodiversity and its role in food
583 security is increasingly supported, even at crop levels¹². Our results add to this view and
584 point to biodiversity conservation as one key policy to achieve food security.

585
586 Our findings are consistent with previous studies that found non-linear effects of
587 fragmentation on ecosystem service provision (e.g.^{18,19}), and provide a theoretical basis
588 of the effects of fragmentation on the stability patterns of crop pollination. Fragmentation
589 has a dual effect on crop production services. On one hand, aggregation decreases crop
590 pollination by reducing MPP. On the other hand, aggregation increases crop pollination
591 by maintaining higher biodiversity, especially at low-intermediate fractions of
592 seminatural habitat. The net effects of aggregation on crop pollination depend on the
593 strength of spillover effects. These results have management implications (e.g. land
594 sharing–sparing debate^{57,58}), as the goals of different landscape managers can be
595 conditioned by the way that natural land is converted into crops. For example,
596 maintaining a large number of seminatural fragments may be a better strategy at multiple
597 spatial scales than maintaining a few large fragments when pollinator flow to crop land
598 is low. Yet, this strategy may increase the temporal variability of crop pollination at low-
599 intermediate proportions of seminatural habitat, reflecting a trade-off between ecosystem
600 service mean and stability. Conversely, larger fragments of seminatural habitat have
601 higher pollinator diversity when the fraction of seminatural habitat is low or intermediate,
602 and higher biodiversity can stabilize crop pollination. These results agree with recent
603 claims that the land sharing–sparing dichotomy lends itself to overly simplistic policy
604 prescriptions⁵⁹, and suggest that management decisions for food security should consider
605 factors such as the distance-decay of pollinator flow, the amount and spatial aggregation
606 of seminatural habitat and the degree to which crops depend on animal pollination.

607
608 Our model has several limitations. For example, our model focuses on intensive farming
609 systems, where crop land does not host important biodiversity levels; other types of
610 agriculture – e.g. organic farming, wildlife-friendly practices – allow moderate levels
611 biodiversity to thrive within crop land, and can modify the results reported here⁶⁰. Second,
612 the observation that biodiversity loss has either none (stability) or positive (mean) effects
613 on independent crop yield may change if organisms responsible for other services, i.e.
614 pest control, are included. Besides, although we do not find any effect of seminatural
615 habitat on the stability of independent crop yield, this may change if environmental
616 stochasticity of crops increases with decreasing amounts of seminatural habitat, as
617 suggested by studies linking seminatural habitat to climate regulation, natural hazard
618 regulation and water flow regulation services⁶¹. Finally, our model focuses on wild
619 central-place pollinators (i.e. all types of wild bees, including bumble bees and solitary
620 bees), whose presence and abundance directly depend on the amount of seminatural
621 habitat³², which provides shelter and habitat for these insects. Honey bee colonies are
622 used to substitute wild pollinator communities, yet the pollination services of wild
623 pollinators cannot be compensated by managed bees because (1) pollinator-dependent

624 crop land grows more rapidly than the stock of, e.g., honey bee colonies⁶², (2) wild insects
625 usually pollinate crops more efficiently than honey bees³¹, and (3) honey bees may
626 depress wild pollinator densities⁶³. Despite other groups of pollinators exist, wild central-
627 place foragers remain a very important group of crop pollinators in agriculturally
628 dominated landscapes^{64,65}.

629

630 Ensuring stable food supplies is one of the 2017 UN Sustainable Development Goals, and
631 is a challenge that may require multiple solutions. Policies to increase yields, changing
632 diets, irrigation, crop diversity, tolerance of crops to drought, among others, have been
633 proposed as stability-enhancing solutions^{12,27,66-68}. Our study sheds new light in this
634 debate by showing that high and stable yields in crop pollination systems depend on
635 biodiversity and the spatial structure of the agricultural landscape, i.e. fragmentation.
636 Fragmentation can produce spatial and biodiversity-mediated effects with the potential to
637 modify the mean and stability of pollination-dependent crop production, which has strong
638 consequences for food production and food security. These results are highly relevant
639 given the worldwide trends in agriculture, which shifts towards more pollinator-
640 dependent crops^{29,30}.

641

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786 **Acknowledgements**

787

788 DM was funded by the EU and INRA in the framework of the Marie-Curie FP7 COFUND
789 People Program, through the award of an AgreeSkills/AgreeSkills+ fellowship, and by
790 and the FRAGCLIM Consolidator Grant, funded by the European Research Council
791 under the European Union's Horizon 2020 research and innovation programme (grant
792 agreement number 726176). This work was supported by the TULIP Laboratory of
793 Excellence (ANR-10-LABX-41) and by the BIOTASES Advanced Grant funded by the
794 European Research Council under the European Union's Horizon 2020 research and
795 innovation program (grant agreement no. 666971).

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798 **Author contributions**

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

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805 **Additional information**

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807 Supplementary Methods (3)

808 Supplementary Tables (1)

809 Supplementary Figures (15)

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812 **Competing interests**

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814 The authors declare no competing financial interests.

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