Habitat fragmentation and food security

in crop pollination systems

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Abstract

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

INTRODUCTION

Ensuring stable food supplies for a growing population is one of the UN Sustainable Development Goals[1], and is a challenge that may require multiple solutions. Biodiversity-based approaches to food security suggest that safeguarding certain levels of species diversity is fundamental to increase yields and guarantee stable yields. This is supported by theory and data reporting positive effects of biodiversity on the mean values of various ecosystem functions and services[2-6]. Additionally, biodiversity can have a stabilizing effect on ecosystem service supply by providing an insurance against environmental fluctuations[7], which are predicted to intensify under global change[8-11]. Biodiversity insurance effects have been observed in agriculture, where a greater diversity of crops in arable land is associated with increased year-to-year temporal stability of total yields[12]. However, most biodiversity in intensively-managed agricultural landscapes is found in the remaining fragments of (semi)natural habitat not converted into crop land, and the effects of such non-crop biodiversity on both the mean provision and stability of crop production are not clearly understood. This has led to a growing concern over the large-scale conversion of natural habitats into crop land and their effects on biodiversity and food production.

Agricultural systems are often highly fragmented with areas of intensive cultivation interspersed among remnant patches of seminatural habitat. This loss and fragmentation negatively affect biodiversity and many ecosystem functions and services[13-15]. Despite this, fragments of natural habitat continue to supply important services. The spatial coexistence of crops and natural land creates an opportunity for spillover effects[16], a situation where ecological interactions extend across habitats boundaries and propagate ecological functions. In some cases, fragmentation can increase ecosystem service supply, e.g. if fragmentation of natural habitat for pollinators optimizes interspersion with crop land to maximize crop pollination[17]. But fragmentation can also reduce the provision of ecosystem services if biodiversity decreases significantly in the remnant fragments of natural habitat[13-14]. For most services, however, we do not know how fragmentation affects their provision in fragmented landscapes, and this limits our capacity to manage ecosystem service provision and food security in human-dominated landscapes.

Recent research has revealed strong and non-linear effects of land conversion on agricultural pollination services at multiple spatial scales[18-20]. For example, there is consensus on the hump-shaped relationship between the pollinator-dependent component of crop production and the fraction of remnant natural land within intensive farming systems[20,21]. Research on the stability of crop production shows that yield stability decreases with agricultural intensification and the degree to which crops depend on animal pollination[22-25]. Changes in crop yield stability of animal-pollinated crops are also dependent on the spatial composition and structure of agricultural landscapes, such as the amount of remnant natural land cover[20,26] and the isolation of crops from natural land[23]. Overall, these studies suggest that improved management of agricultural landscape should increase the amount and stability of production for pollination-dependent crops, and that an understanding of how the spatial pattern of land conversion – i.e. fragmentation – impacts ecosystem services is key to achieve this goal. However, none of these studies have simultaneously combined several ecosystem services, crop yield dynamics at different scales and spatially-explicit landscapes to investigate the effects of land conversion on biodiversity and the provision and stability of ecosystem services in agricultural landscapes.

95
96   There is general consensus that increased food production is necessary, but not sufficient,
97   to achieve food security[27], 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?
113
114
115   **METHODS**
116
117   *a. Spatial agroecosystem model*
118
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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4
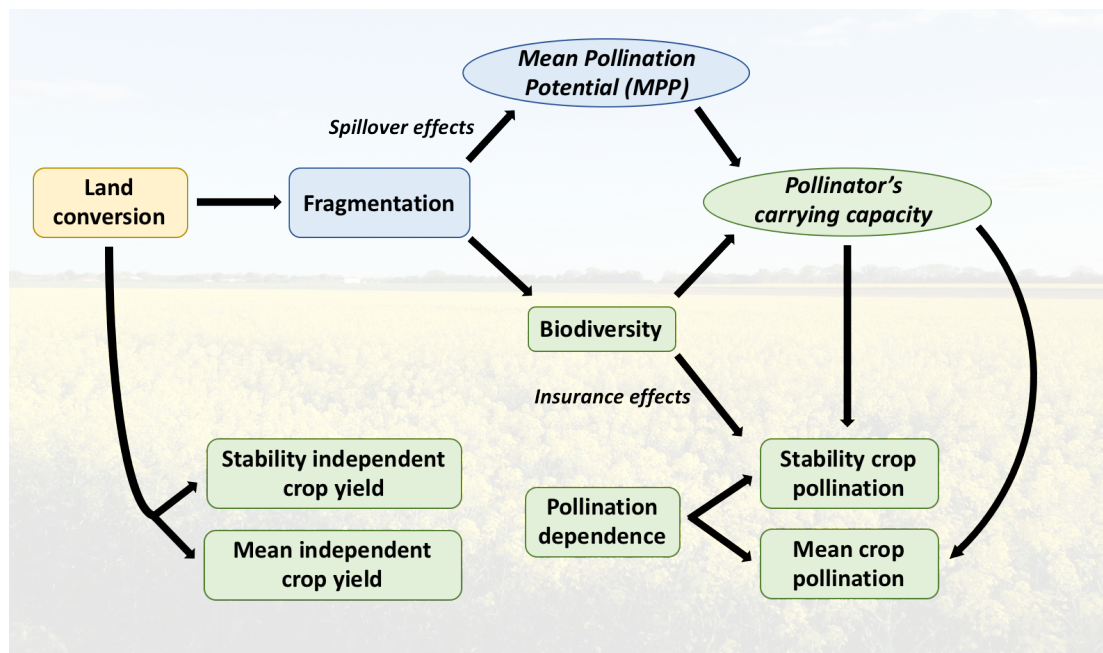
144   _Crop dynamics_. We used a model of biodiversity and crop biomass production in
145   agricultural systems[20], and extend it to a spatially-explicit landscape to investigate the
146   response of ecosystem services to land conversion. The model represents intensively-
147   managed agricultural 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 pollinators[31]. Crop land and seminatural habitat
154   are linked by pollinators' foraging movement. The three components of Montoya et al[20]
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 $$P_k(t+1) = P_k(t)\exp\left(r_{P,k}(t)\left(1 - \frac{P_k(t)}{k_P A_1}\right)\right) + \sigma_P^e u_P^e(t)P_k(t) + \frac{\sigma_P^d u_P^d(t)}{\sqrt{P_k(t)}}P_k(t) \qquad (1)$$

159

160 $$W_k(t+1) = W_k(t)\exp\left(r_{W,k}(t)\left(1 - \frac{W_k(t)}{k_W A_1}\right)\right) + \sigma_W^e u_W^e(t)W_k(t) + \frac{\sigma_W^d u_W^d(t)}{\sqrt{W_k(t)}}W_k(t) \quad (2)$$

161

162 $$C_k(t) = A_1\big[Z_C + r_{C,k}(t)\big](1 + \sigma_C^e u_C^e(t)) \qquad (3)$$

163

164   where P_k represents pollinators, W_k wild plants and C_k crop yield in cell k, with $P_k(t) =$
165     $W_k(t) = 0$ if k is a crop land cell, and $C_k(t) = 0$ if k is seminatural habitat. One unit of
166   time t corresponds to one growing season, $P(t)$ and $W(t)$ can be interpreted as total
167   biomass of pollinators and wild plants over growth season t, respectively, whereas $C(t)$ is
168   the total crop yield at the end of the growing season t. L is the set of crop land cells; k_P
169   and k_W are the carrying capacities of pollinators and 'wild' plants, respectively, per unit
170   area. A_1 is the area of a single cell; A is total landscape area; $A[1-\omega_{sn}]$ is the total crop land
171   area, and $A\omega_{sn}$ is total seminatural area. σ_P^e, σ_P^d are the environmental and demographic
172   stochasticity of pollinators, and σ_C^e is the environmental stochasticity of crops. Equation
173   (3), is the sum of pollination-dependent and independent parts of crop yield:
174

175   _Independent crop yield_: $Ci_k(t) = A_1 Z_C(1 + \sigma_C^e u_C^e(t))$ (4)
176

177   _Crop pollination_: $Cd_k(t) = A_1 r_{C,k}(t)(1 + \sigma_C^e u_C^e(t))$ (5)
178

179   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
180   per capita growth rates, and are defined as:
181

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

183

184 $$r_{W,k}(t) = \frac{\alpha_W\left(\frac{\sum_{l\notin L}\varepsilon_{kl}P_l(t)}{A}\right)}{\beta_W + \frac{\sum_{l\notin L}\varepsilon_{kl}P_l(t)}{A}} \qquad (7)$$

185

186 $$r_{C,k}(t) = \frac{\alpha_C\left[\frac{\sum_{l\notin L}\varepsilon_{kl}P_l(t)}{A}\right]}{\beta_C + \frac{\sum_{l\notin L}\varepsilon_{kl}P_l(t)}{A}} \qquad (8)$$

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 crops[32], 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 examples[33-35]. 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 al[19]. This function is consistent with both theoretical
210   predictions[16,36-39] and empirical observations[40-42] 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 al[19]; 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 al[19] distance-decay function as follows (see also Appendix S1):
220
221     $\varepsilon_{kl} = \frac{1+\beta}{1+\beta \exp(\alpha d_{kl})}$, with   (9)
222
223     $d_m = \frac{1}{\alpha} ln \frac{0.5+\beta}{0.5\beta}$ and $\Delta d = \frac{1}{\alpha} ln \frac{8.1+9\beta}{0.1+\beta}$
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     $d_m = \frac{1}{\alpha} ln \frac{0.5+\beta}{0.5\beta}$ and $\Delta d = \frac{1}{\alpha} ln \frac{8.1+9\beta}{0.1+\beta}$
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 al[19]).
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 dynamics[43], 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 fragments[14]. 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 al[47] 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
269 $$S = c_s (A\omega_{sn})^{z_s} e^{-b/\lambda_M} \qquad\qquad (10)$$
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 x 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 al[47]), 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 animals[48], and allowed dispersal distance

7

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 literature[49-51], 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, $\overline{\varepsilon}$,
339 defined as
340
341 $$\overline{\varepsilon} = \frac{1}{(1-\omega_{sn})n^2}\frac{1}{\omega_{sn}n^2}\sum_{k \in L, l \notin L}\varepsilon_{kl} \qquad (11)$$
342
343 $\overline{\varepsilon}$ is the average value of ε_{kl} when taking a random cell $k \in L$ and a random cell $l \notin L$. $\overline{\varepsilon}$
344 has two complementary interpretations. Firstly, it is a measure of the amount of
345 seminatural habitat supplying pollinators to crop land: if we multiply $\overline{\varepsilon}$ by the area of
346 seminatural habitat ($R_{SNH} = \omega_{sn}A\overline{\varepsilon} = \omega_{sn}n^2A_1\overline{\varepsilon}$), then R_{SNH} is the area from which a
347 crop land cell can be pollinated averaged over all crop land cells. Secondly, $\overline{\varepsilon}$ quantifies
348 the amount of crop land that is reachable by pollinators from seminatural habitat: if we
349 multiply $\overline{\varepsilon}$ by the crop land area ($R_C = \omega_{sn}A\overline{\varepsilon} = (1 - \omega_{sn})n^2A_1\overline{\varepsilon}$), R_C is the crop land
350 area that a pollinator can reach averaged over all seminatural cells. Taken together, these
351 two interpretations can be summarized by the term *Mean Pollination Potential* (MPP; 0
352 $\leq$ MPP $\leq$ 1). Under the mean-field approximation the mean crop yield is (see Appendix
353 S3):
354
355 $$C^* \approx (1 - \omega_{sn})A\left(Z_C + \frac{\alpha_C\overline{\varepsilon}k_P\omega_{sn}}{\beta_C + \overline{\varepsilon}k_P\omega_{sn}}\right) \qquad (12)$$
356
357 The variance of crop yield is:
358
359 $$Var(C) \approx \frac{((1-\omega_{sn})\alpha_C\beta_C)^2}{(\beta_C + \overline{\varepsilon}k_P\omega_{sn})^4\alpha_C(1-\alpha_C)}\left((\sigma_P^e\overline{\varepsilon}k_P\omega_{sn}A)^2 + \left((\sigma_P^d\overline{\varepsilon})^2 k_P\omega_{sn}A\right)\right) + (\sigma_C^e C^*)^2 \qquad (13)$$
360
361 , with $k_p = aS^h$ (see methods). We found that the mean-field approximation is a very
362 accurate description of the dynamics of various ecosystem services in agricultural
363 landscapes, both for mean and stability values (Figure 2).
364
365
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_{k_P} = 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%.
376
377
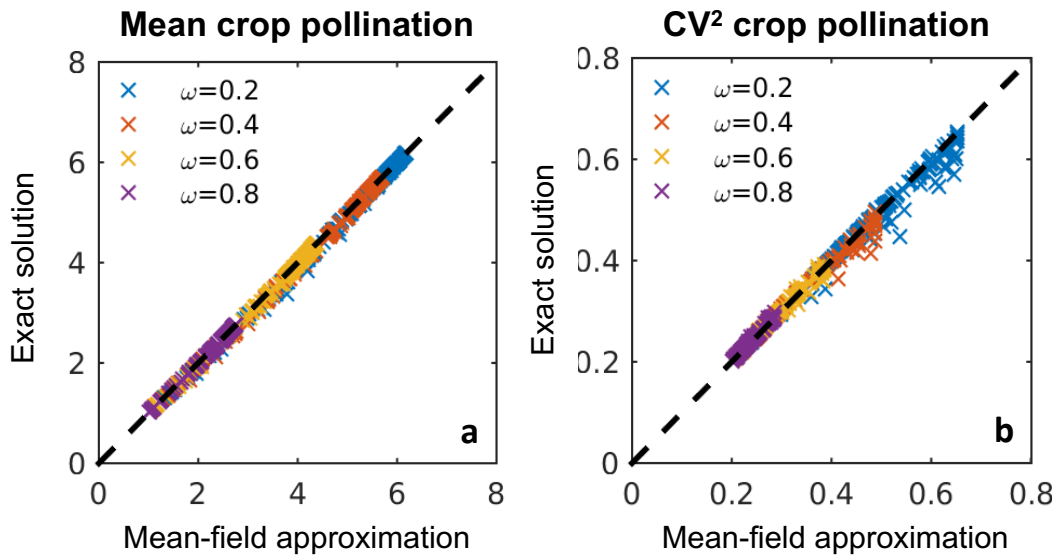
378
379

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 model[20] has to be replaced by
383
384 $$\frac{1}{\varepsilon}\frac{\beta_C}{k_P} = \frac{\omega_{sn}A}{R_{SNH}}\frac{\beta_C}{k_P} = \frac{(1-\omega_{sn})A}{R_C}\frac{\beta_C}{k_P} \qquad (14)$$
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 ≈ 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 ≈ 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

11

430   higher biodiversity effect (larger z_{k_P}) 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

Figure 3. Effects of landscape composition and MPP on ecosystem services. Ecosystem services are represented as a function of the proportion of seminatural habitat, for different MPP. MPP includes the effects of fragmentation – more specifically, the aggregation pattern of land conversion – and the distance-decay of ecosystem service flow. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $e_P = 0.8$, $\sigma^d_P = 0.1$, $\sigma^e_C = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%, $z_{k_P} = 0.26$.
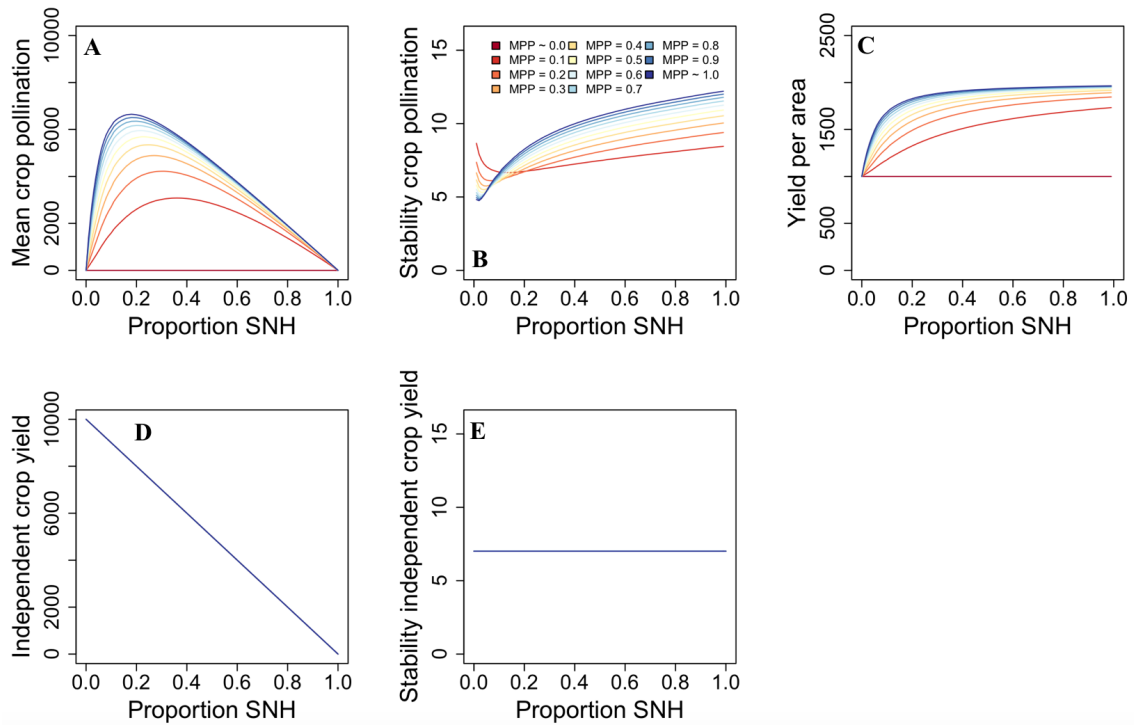
448 The effect of MPP on crop pollination services increases with the degree to which crops
449 depend on animal pollination. Higher pollination dependence of crops shifts maximum
450 yields to higher fractions of seminatural habitat at landscape and local scales, and the
451 stability of crop pollination 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_{k_P}) increases both
464 mean crop pollination and its stability, as well as yield per area (Figure S13).
465
466

Figure 4. Effects of biodiversity on crop pollination. Plots show the response of crop pollination services – mean and stability of crop pollination (panels **A** and **B**), and yield per area (panel **C**) – as a function of the proportion of seminatural habitat (SNH). All MPP values are contained within the shadows, whose limits are determined by the minimum and maximum values across the range of MPP. Biodiversity can affect crop pollination in a two-way manner. On one hand, biodiversity influences mean crop pollination and yield per area by increasing the carrying capacity of pollinators ($k_p = c_{k_P} S^{z_{k_P}}$). On the other hand, biodiversity impacts the stability of crop production both indirectly – increasing the carrying capacity of pollinators – and directly – reducing the response of crop production to environmental fluctuations ($\sigma_P^e = e_P / S^q$). For each ecosystem service, the plots compare two scenarios: (i) a scenario where biodiversity has no effect on crop pollination ($z_{k_P} = 0$, $q = 0$), represented by the grey shadows, *versus* (ii) a scenario where biodiversity has an effect on crop pollination ($z_{k_P} = 0.26$, $q = ½$; Tilman 1999, Liang et al 2016, O'Connor et al 2017, Cardinale et al 2011), represented by the light orange shadows. Parameter values: $\alpha_P = \alpha_W = 0.9$, $\beta_P = \beta_W = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $e_P = 0.8$, $\sigma^d_P = 0.1$, $\sigma^e_C = 0.03$, $\alpha_C = 1000$, Pollination dependence $= 50\%$.
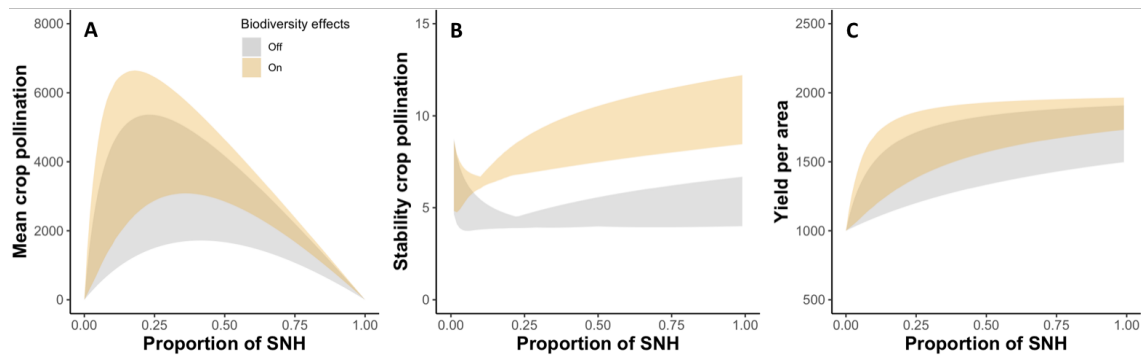
489 *Net effects of fragmentation on ecosystem services*

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

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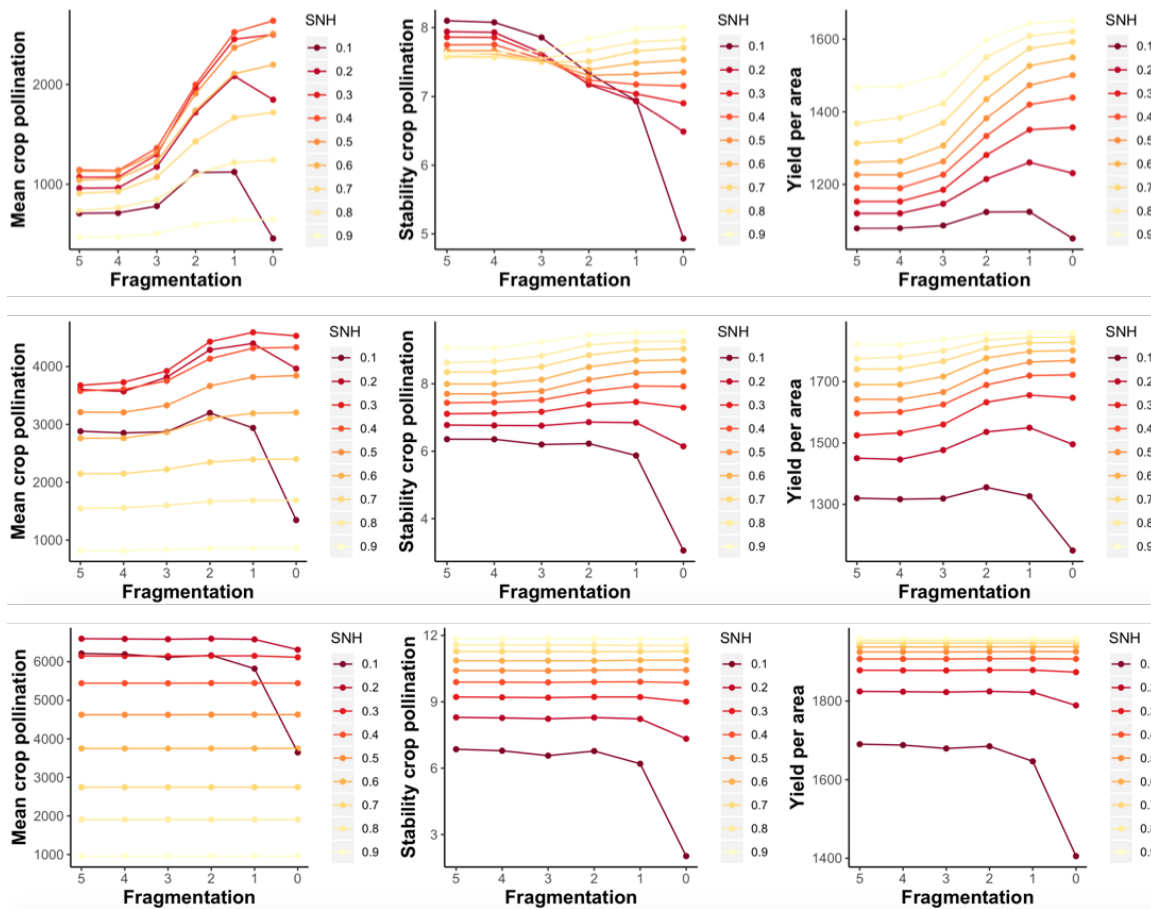
DISCUSSION

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

The loss of seminatural land has contrasting effects on the ecosystem services considered: biodiversity decreases, independent crop production increases, while crop pollination is maximized at intermediate fractions of seminatural habitat. But fragmentation can modify these relationships in two ways. On one hand, land conversion can produce multiple patterns of aggregation of the remaining fragments of seminatural habitat. These patterns combined with the strength of the spillover of pollinators to crop land determine the mean pollination potential of seminatural land (MPP), which is the main responsible of food production in pollination-dependent agriculture. The second type of effects are mediated by biodiversity, as the level of aggregation of the remaining fragments of seminatural habitat affects the pollinator richness. Such purely spatial and biodiversity-mediated effects modify the carrying capacities of pollinators, which ultimately determine crop pollination services. The mean-field approximation shows that the effects of space on crop production can be interpreted in the same terms as varying the pollinator's carrying capacity in the non-spatial model[20].

Our results suggest that understanding the factors that affect MPP is a fundamental step towards food security. If no restrictions exist in the flow of pollinators to crop land, MPP is maximum and the spatial structure of land conversion does not affect crop yield dynamics. In this situation, seminatural fragments are perceived as more connected and the provision and stability of crop pollination is not conditioned by space, i.e. spatial and non-spatial models converge. However, agricultural landscapes are fragmented to some extent and the foraging ranges of most organisms are local (200 m for small bee species, 25–110 m for bumble bees, >200 m for certain bee species[53-56]), which produces higher aggregation and weaker spillover effects, thus reducing MPP. Such reductions in MPP affect crop yields by (i) decreasing mean crop pollination and total yield per area, and (ii) decreasing yield stability along the gradient of seminatural habitat. The estimation of MPP in real farming systems would require data on the aggregation level of seminatural habitat fragments within the agricultural landscape, and on the spillover of pollinators to adjacent crops. The former can be obtained with GIS processing of aerial pictures or satellite images of agricultural landscapes. For the latter, information on foraging distances of pollinator species combined with experimental studies could be used to reveal species' foraging patterns and how the flow of pollinators to adjacent crop land decays with distance (e.g.[16,36,37-39]). This information will be useful to design agricultural landscapes for high MPP.

18

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 production[6], 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 levels[12]. 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   prescriptions[59], 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 here[60]. 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 services[61]. 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   habitat[32], 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 colonies[62], (2) wild insects
625   usually pollinate crops more efficiently than honey bees[31], and (3) honey bees may
626   depress wild pollinator densities[63]. 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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Acknowledgements

Author contributions

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

Additional information

Supplementary Methods (3)
Supplementary Tables (1)
Supplementary Figures (15)

Competing interests

The authors declare no competing financial interests.