

1 *For Ecological Applications: Research article*

2 *Running head: Ecosystem services in agroecosystems*

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4 **Trade-offs in provisioning and stability of multiple ecosystem**
5 **services in agroecosystems**

6

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25 production, trade-offs, stability

26 ***Abstract***

27 Changes in land use generate trade-offs in the delivery of ecosystem services in
28 agricultural landscapes. However, we know little about how the stability of ecosystem
29 services responds to landscape composition, and what ecological mechanisms underlie
30 these trade-offs. Here, we develop a model to investigate the dynamics of three
31 ecosystem services in intensively-managed agroecosystems, i.e. pollination-independent
32 crop yield, crop pollination, and biodiversity. Our model reveals trade-offs and
33 synergies imposed by landscape composition that affect not only the magnitude but also
34 the stability of ecosystem service delivery. Trade-offs involving crop pollination are
35 strongly affected by the degree to which crops depend on pollination and by their
36 relative requirement for pollinator densities. We show conditions for crop production to
37 increase with biodiversity and decreasing crop area, reconciling farmers' profitability
38 and biodiversity conservation. Our results further suggest that, for pollination-dependent
39 crops, management strategies that focus on maximising yield will often overlook its
40 stability. Given that agriculture has become more pollination-dependent over time, it is
41 essential to understand the mechanisms driving these trade-offs to ensure food security.

42 **Introduction**

43 Human population growth and changes in diet preferences worldwide are generating a
44 huge demand for food (Godfray et al 2010). To fulfil this increasing demand,
45 agricultural intensification targets high crop yields. The merits of this approach are
46 clear: the world annual production of cereals, grains, roots, tubers, pulses and oil crops
47 has more than doubled, and the proportion of undernourished people in the world has
48 decreased from 26% to 14% over the past 50 years (FAO 2009, 2011). But yields are no
49 longer increasing in many major crops (Ray et al 2012) and show saturating responses
50 to pesticide levels (Gaba et al 2016, Lechenet et al 2017), which suggests that the
51 benefits of agricultural intensification have plateaued. Furthermore, these benefits have
52 come at a considerable cost to biodiversity. This is particularly worrying for crops
53 whose yield depends on ecosystem functions and services, such as pollination, whose
54 provision has not traditionally been part of management policies (Pywell et al 2015,
55 Tamburini et al 2016).

56

57 Global agriculture largely depends on animal pollination. It is estimated that 70% of
58 1,330 tropical crops (Roubik 2015) and 85% of crops in Europe (Williams 1994) benefit
59 from animal pollination, and that pollinators can increase the production of 75% of the
60 115 most important crops worldwide (Aizen et al 2009). Although the three major crops
61 in terms of biomass are independent of animal pollination (wheat, rice, corn), the
62 cultivated area of pollination-dependent crops is expanding faster than the area of
63 pollinator-independent crops (Breeze et al 2014, Aizen and Harder 2009). In contrast to
64 the global increase in pollination-dependent agriculture, abundance and diversity of
65 wild pollinators are declining worldwide (Goulson et al 2015). Honeybee (and

66 sometimes bumblebee) colonies are used to substitute wild pollinator communities, yet
67 the pollination services of wild pollinators cannot be compensated by managed bees
68 because (i) pollinator-dependent crop land grows more rapidly than the stock of, e.g.,
69 honeybee colonies (Aizen et al 2009), (ii) wild insects usually pollinate crops more
70 efficiently than honeybees (Garibaldi et al 2013), and (iii) honeybees may depress wild
71 pollinator densities (Lindström et al 2016). Wild pollinators thus remain fundamental
72 for agricultural pollination. In agricultural landscapes, the loss of semi-natural habitat is
73 considered to be the first cause of wild pollinator declines (Kennedy et al 2013,
74 Bretagnolle & Gaba 2015), as semi-natural elements (e.g. hedgerows, low-managed
75 grasslands, forest patches) provide foraging, nesting and refuge habitats for pollinator
76 communities (Kremen et al 2004). This land use change therefore leads to a continuous
77 decrease of wild pollinator communities (Garibaldi et al 2014).

78

79 Recent studies have reported ecosystem service trade-offs in agroecosystems (Nelson et
80 al 2009, Allan et al 2015, Sutter & Albrecht 2016). For example, intensive land use
81 favors provisioning services (e.g. crop production) at the cost of other services (e.g.
82 pollination). More specifically, increasing crop land at the expense of semi-natural
83 habitat can largely reduce biodiversity in intensive agricultural landscapes (Allan et al
84 2014), and this may drive ecosystem service trade-offs through negative effects on
85 ecosystem services that depend on biodiversity (Cardinale et al 2012). Thus, it may be
86 impossible to maximize all ecosystem services simultaneously (Bateman et al 2013).
87 These trade-offs underpin the European Commission's Cost of Policy Inaction project
88 (Braat and ten Brink 2008) and the land sharing vs land sparing debate (Green et al
89 2005), a framework that distinguishes between the spatial integration (land sharing) or

90 separation (land sparing) of biodiversity conservation and crop production. A better
91 understanding of the effects of landscape composition on crop production requires
92 moving from the traditional single-service approach, whereby crop yield is studied
93 individually, to a multiple-service framework (Bennett et al 2009), where crop yield and
94 other services, such as biodiversity and pollination, are investigated simultaneously.

95

96 There is a general consensus that decreasing levels of biodiversity can reduce the
97 magnitude and stability of ecosystem processes (Cardinale et al 2012, Tilman et al
98 2006). In intensively-managed agroecosystems, the decline in the diversity of
99 pollinators associated with the loss of semi-natural habitat can alter not only the
100 magnitude but also the temporal stability of animal pollination-dependent crop yield,
101 especially when biodiversity is reduced to the low levels typical of many intensive
102 agricultural areas (Garibaldi et al 2011a). This means that food security will not be
103 achieved by high crop yields alone; agricultural practices should also target a stable
104 provision of crop yield over time, as low crop yield stability can cause unpredictable
105 negative impacts on food supply and farmer income (Schmidhuber and Tubiello 2007).
106 Despite the importance of yield stability and the empirical evidence that the magnitude
107 and stability of ecosystem services do not necessarily co-vary positively (Macfadyen et
108 al 2011, Gagic et al 2012), there have been few studies on the stability of crop yield.
109 These studies have generally found that yield stability decreases with agricultural
110 intensification and crop pollination dependence (Garibaldi et al 2014, 2011a, 2011b;
111 Deguines et al 2014), but the ecological mechanisms that drive these effects have
112 received little attention.

113

114 In this study, we develop a model to predict changes in crop yield and biodiversity
115 along a gradient of landscape composition (i.e. increasing proportions of semi-natural
116 habitat) in agricultural systems. We focus on three ecosystem services, i.e. pollinator-
117 independent crop yield (a provisioning service), crop pollination (a regulating or
118 supporting service), and biodiversity *per se*. We assess the ecosystem service of
119 pollination by measuring crop production resulting from animal pollination. Whether or
120 not biodiversity is an ecosystem service in itself is a matter of debate; here, we consider
121 biodiversity as such because it is directly associated with and drives supporting (e.g.
122 nutrient cycling, primary production) as well as cultural services. We distinguish
123 between two additive ecosystem services associated with total crop yield: the yield that
124 results from wild animal pollination (hereafter crop pollination), and the yield that is
125 independent from animal pollination (hereafter independent crop yield). This separation
126 allows us to quantitatively vary the degree of pollination dependence of crops, in
127 contrast to studies that only make a qualitative distinction between pollination-
128 dependent and pollinator-independent crops (Ghazoul and Koh 2010). We analyse the
129 expected biodiversity (i.e. species richness) and the magnitude and stability of crop
130 pollination and independent crop yield, yielding a total of five ecosystem service
131 components. We focus on how the relative proportion of semi-natural habitat and crop
132 land in the agricultural landscape, and crop pollination dependence influence these five
133 ecosystem service components. Specifically, we address two main questions: (i) What
134 are the trade-offs between biodiversity and the magnitude and stability of crop
135 pollination and independent crop yield in agricultural landscapes? and (ii) How do
136 landscape composition (the relative proportion of semi-natural habitat and crop area in
137 the agricultural landscape), and crop pollination dependence influence these trade-offs?

138

139 **Methods**

140 **Agroecosystem model.** We derive a model for crop biomass production in a spatially
141 heterogeneous agricultural landscape that incorporates environmental and demographic
142 stochasticity. Our model has two types of patches: crop land and semi-natural habitat.
143 Crop land is used to grow annual crops with varying degrees of dependence on wild
144 animal pollination, whereas semi-natural habitat shelters ‘wild’ plants and pollinators.
145 This model represents intensively-managed agricultural systems, where crop land does
146 not host significant levels of biodiversity, allowing spatial heterogeneity to be broadly
147 defined by two patch types. Pollinators live and nest in semi-natural habitats, yet they
148 move across the landscape to forage on either crops or ‘wild’ plants, or both. Crop land
149 and semi-natural habitat are therefore linked by pollinators’ foraging movement. The
150 three components of our model (pollinators, ‘wild’ plants, and crop yield) are
151 represented by the following equations:

152

$$153 \quad \frac{dP}{dt} = r_P(t)P(t)\left(1 - \frac{P(t)}{k_P \omega_{sn} A}\right) + \sigma_P^e u_P^e(t)P(t) + \frac{\sigma_P^d u_P^d(t)}{\sqrt{P(t)}}P(t) \quad (1)$$

154

$$155 \quad \frac{dW}{dt} = r_W(t)W(t)\left(1 - \frac{W(t)}{k_W \omega_{sn} A}\right) + \sigma_W^e u_W^e(t)W(t) + \frac{\sigma_W^d u_W^d(t)}{\sqrt{W(t)}}W(t) \quad (2)$$

156

$$157 \quad C(t) = (1 - \omega_{sn})A \left[Z_C + \frac{\alpha_C [P(t)/A]}{\beta_C + [P(t)/A]} \right] (1 + \sigma_C^e u_C^e(t)) \quad (3)$$

158

159 where P and W represent the maximum yearly biomass of pollinators and ‘wild’ plants,
160 respectively. P does not take managed honeybees into account as they do not depend on

161 the availability of semi-natural habitat, and they pollinate less efficiently compared to
162 non-managed pollinators (Garibaldi et al 2013). The model does not consider within-
163 year dynamics. $C(t)$ is the amount of crop biomass produced in year t , i.e. annual crop
164 yield. $C(t)$ is not represented by a differential equation because crops are harvested and
165 their dynamics do not depend on the previous state. Conversely, pollinators and wild
166 plants are not managed and their actual values depend on previous states. k_P and k_W are
167 the carrying capacities of pollinators and ‘wild’ plants, respectively, per unit area; A is
168 the total landscape area (crop land and semi-natural habitat); ω_{sn} is the proportion of
169 semi-natural habitat within the agricultural landscape ($[1-\omega_{sn}] * A$ is total crop or
170 agricultural area). The model is spatially implicit, which means that pollinators can
171 potentially feed on all crops and ‘wild’ plants present in the agricultural landscape,
172 irrespective of the spatial configuration of the landscape. Hence, this model describes
173 what happens in agricultural landscapes at the scale determined by the pollinator’s
174 foraging range (200 meters for small bee species, 25-110 meters for bumble bees, >200
175 meters for certain bee species (Zurbuchen et al 2010, Geib et al 2015)), which
176 corresponds roughly to the scale of a typical arable field in Europe.

177

178 In the first two equations, $r_P(t)$ and $r_W(t)$ are the pollinators’ and ‘wild’ plants’ per
179 capita growth rates, and are defined as:

$$r_P(t) = c_P \frac{\alpha_P (\phi_W W(t) + \phi_C C(t))}{\beta_P + \phi_W W(t) + \phi_C C(t)} \quad (4)$$

$$r_W(t) = c_W \frac{\alpha_W (P(t)/A)}{\beta_W + (P(t)/A)} \quad (5)$$

183

184 Pollinators are assumed to be generalist central-place foragers that feed on both ‘wild’
185 plants and crops (Kleijn et al 2015). We assume that plant and pollinator uptake of
186 resources follows a saturating, type II functional response, where α_P and α_W are the
187 maximum growth rates; β_P and β_W are half-saturation constants; and c_P and c_W are the
188 conversion rates of pollinators and ‘wild’ plants, respectively, that translate the
189 functional responses into numerical ones. For simplicity, we set conversion rates equal
190 to unity. The pollination-dependent part of crop yield is also assumed to follow a type II
191 functional response, where α_C is the maximum crop yield derived from pollination, β_C is
192 the half-saturation constant of crops, and Φ_W and Φ_C are constants that convert fluxes of
193 ‘wild’ plants and crops, respectively, to pollinator biomass. We use $\Phi_W = \Phi_C = 1$ for
194 simplicity; to allow differences in resource quality of different crop types, we also made
195 Φ_C dependent on crop pollination dependence (see below). The use of saturating
196 functional responses is widely supported and it is consistent with several biological
197 examples (Thebault & Fontaine 2010, Holland et al 2013, Holland 2015). A complete
198 description of the model parameters can be found in Table 1.

199
200 Environmental stochasticity is included through the terms $\sigma^e u^e(t)$, where $(\sigma^e)^2$ is the
201 environmental variance of either pollinators $((\sigma_P^e)^2)$, ‘wild’ plants $((\sigma_W^e)^2)$ or crops
202 $((\sigma_C^e)^2)$, and $u^e(t)$ are random functions with zero mean and standardized variance, that
203 can be correlated through time (a good year for plants might also be good for crops).
204 Demographic stochasticity $(\sigma^d u^d(t))$ arises from stochastic variation in individuals’
205 births and deaths. Because crops are sown at high densities, we assume demographic
206 stochasticity is prevented in crops, and only affects pollinators and ‘wild’ plants.
207 Demographic stochasticity is included in the form of the first-order normal
208 approximation commonly used in stochastic population dynamics (Lande et al 2003),

209 where $(\sigma^d)^2$ is the demographic variance of either pollinators ($(\sigma_P^d)^2$) or ‘wild’ plants
210 ($(\sigma_W^d)^2$), and $u^d(t)$ are independent random functions with zero mean and standardized
211 variance.

212

213 Crops differ greatly in the degree to which animal pollination contributes to yield, from
214 pollinator-independent crops, such as obligate wind- or self-pollinated species (e.g.
215 cereals), to fully animal-pollinated species (e.g. fruit trees, oilseed rape). Within animal-
216 pollinated species, crops differ in their level of dependence on pollination (Klein et al
217 2007). In our model, Z_C represents the part of crop yield that is independent of animal
218 pollination and α_C is the crop yield derived from pollination, and therefore we can
219 estimate crop pollination dependence (%) as $\alpha_C / (\alpha_C + Z_C)$. If $Z_C = 0$ ($\alpha_C > 0$), crop yield
220 depends entirely on animal pollination; conversely, animal pollination-independent
221 crops are defined by $\alpha_C = 0$ ($Z_C > 0$). Most fruit and seed crops lie between these two
222 extremes ($Z_C > 0$, $\alpha_C > 0$). We assume there is no interaction between α_C and Z_C
223 (Bartomeus et al 2015, Gils et al 2016).

224

225 **Mean and stability of ecosystem services.** We use our model to quantify biodiversity
226 and both the mean and the stability of independent crop yield and crop pollination,
227 which make five ecosystem service components, in intensively-managed agricultural
228 landscapes with varying proportions of semi-natural habitat. We assume that, at the end
229 of each cropping season, the amount of animal pollinators, wild plants and crops reach
230 roughly constant values in the absence of environmental and demographic stochasticity
231 at the landscape scale, despite local year-to-year changes in those variables. This year-
232 to-year equilibrium assumption is a reasonable first approximation to a more complex
233 and dynamical system. We use the species-area relationship (SAR) to estimate changes

234 in biodiversity as a function of semi-natural area. We decided to use SAR for estimating
235 biodiversity instead of wild plant biomass or pollinator biomass, because species-
236 biomass relationships are more variable at local/landscape scales such as the one
237 considered here, and negative relationships have been reported (e.g. diversity-
238 productivity) (Cardinale et al 2012). Moreover, when biodiversity is considered a
239 cultural service, it is usually estimated as the number of species. Despite the fact that
240 SAR is usually stronger at spatial scales larger than that of arable fields, where we
241 might observe more variation around the average biodiversity values, it captures the
242 expected mean biodiversity at the scale of an arable field in Europe. We estimated SAR
243 using the conventional power law function ($S=c [\omega_{sn} A]^z$, where S = number of species,
244 c is a constant of proportionality). Theoretical models and field data from a wide range
245 of plant and animal taxa show that the slope, z , of the logarithm of species richness
246 against the logarithm of area is roughly constant, with $z \approx 0.25$ (Crawley and Harral
247 2001). Given that the equilibrium plant and pollinator biomasses are proportional to the
248 area of semi-natural area (Appendix S5: Fig. S1), considering either species richness or
249 biomass would yield the same qualitative results ($R^2 = 0.90$; at the scale of this study, z
250 can be higher (0.4 or 0.5) (Crawley and Harral 2001), yielding an even stronger
251 correlation between the number of species and biomass). We assume that crops are
252 harvested yearly; hence, average crop yield represents the temporal mean of the yearly
253 averaged crop yield across the agricultural landscape. To account for the stability of
254 independent crop yield and crop pollination, we use the inverse of temporal variability,
255 i.e. invariability. Temporal variability is measured as the square of the temporal
256 coefficient of variation (CV^2) of total biomass, i.e. the ratio of the variance to the square
257 of the mean, and is calculated in the stationary regime around the equilibrium. We use
258 $1/CV^2$ as a metric of stability (i.e. invariability) of independent crop yield and crop

259 pollination. This measure of ecosystem stability has been used in recent empirical and
260 experimental studies (Tilman et al 2006, Loreau and De Mazancourt 2013).
261
262 The analytical expressions for the equilibrium and variability of pollinator biomass,
263 wild plant biomass, and crop yield are presented in Appendix S1. A summary of the
264 equations for the five ecosystem service components can be found in Appendix S2 (Eqs.
265 S5-S9). Whenever possible, we estimated parameter values with empirical
266 information. In other cases, we informed parameters with commonly-assigned values
267 found in the literature (McCann et al 2005, Thompson et al 2006, Leroux and Loreau
268 2008, Holland and DeAngelis 20010, Thebault and Fontaine 2010, Morales 2011,
269 Holland et al 2013, Encinas-Viso 2014, Gounand et al 2014). For example, to determine
270 the carrying capacity of pollinators (k_P), we used empirical data on average numbers of
271 individuals and body mass of wild pollinators (Bommarco et al 2012, Rollin et al 2013,
272 Holzschuh et al 2016). For wild plants, we used empirical observations to inform their
273 carrying capacities (k_W) (Craven et al 2016). Also, there is information on independent
274 crop yield that was used to determine Z_C (e.g. <http://data.worldbank.org/>). We allowed
275 variation in α_C and β_C in order to investigate changes in the five ecosystem services
276 components across the amount of semi-natural habitat (ω_{sn}), the degree of crop
277 pollination dependence (Z_C/α_C), and the crop relative requirement for pollinator
278 densities (β_C/k_P). A sensitivity analysis was performed for parameter whose values
279 could not be determined precisely or for which there was variation in their values
280 assigned in the literature, e.g. α_C , α_P , Z_C , β_C , β_P , k_P (Appendix S3). The choice of these
281 parameters for the sensitivity analyses is also justified because they are most relevant
282 for the estimation of equilibrium biomasses. Sensitivity analysis shows that variations in

283 these parameter values did not change the results qualitatively. Analyses were
284 performed in R software (R version 3.2.4, R Core Team 2016).

285

286

287 **Results**

288 *Overall effects of landscape composition on ecosystem service components*

289 Increases in the relative proportion of crop land has contrasting effects on the various
290 ecosystem services. As expected, biodiversity increases with the proportion of semi-
291 natural habitat, as the latter provides area for many taxonomic groups, such as wild
292 plants and pollinators (Figure 1a). Changes in the biomasses of wild plants and
293 pollinators with semi-natural habitat are positively correlated with changes in
294 biodiversity ($R^2 = 0.90$; Appendix S5: Fig. S1). The responses of the pollination-
295 independent and pollination-dependent (i.e. crop pollination) components of crop yield
296 differ strongly. Independent crop yield decreases linearly with the amount of semi-
297 natural habitat because crop land decreases and it does not depend on pollinators
298 (Figure 1c). In contrast, the relationship between crop pollination and the proportion of
299 semi-natural habitat is hump-shaped (Figure 1b), as a result of the contrasting effects of
300 semi-natural habitat on pollinators and crop land. That is, a larger amount of semi-
301 natural habitat increases wild pollinator biomass (Appendix S5: Fig. S1b) but reduces
302 crop land, which results in a hump-shaped relationship that is robust to changes in
303 parameter values (Appendix S3). Total crop yield, i.e. pollination-independent plus
304 pollination-dependent crop yields, displays a similar hump-shaped relationship,
305 especially when crop pollination dependence is moderate to high (Appendix S5: Fig.
306 S2). Interestingly, when measured per unit of crop land, crop yield increases with the

307 proportion of semi-natural habitat, because of the beneficial effect of pollination
308 (Appendix S5: Fig. S3).
309
310 The stability of independent crop yield does not change with semi-natural habitat
311 (Figure 1e) because it does not rely on animal pollination. On the other hand,
312 pollination-dependent yield does depend on animal pollinators, thus crop pollination
313 stability strongly depends on the amount of semi-natural habitat (Figure 1d). Crop
314 stability shows similar trends when measured at landscape scale or per unit of
315 agricultural area.

316

317 ***Role of pollination dependence and crop relative requirement for pollinators***

318 The dependence of crop yield mean and stability on the proportion of semi-natural
319 habitat is controlled by two *effective* parameter combinations, Z_C/α_C and β_C/k_P
320 (Appendix S1). Z_C is the pollinator-independent component of crop yield and α_C is the
321 maximum crop yield derived from pollinator interactions, so Z_C/α_C is inversely related
322 to crop pollination dependence:

$$323 \text{ Pollination dependence} = \frac{1}{1 + Z_C/\alpha_C}$$

324 β_C/k_P is the ratio of crop half-saturation constant relative to pollinators' carrying
325 capacity, and it quantifies the pollinator requirement of crops relative to the availability
326 of pollinators, i.e. crop relative requirement for pollinators. For small values of β_C/k_P
327 (<1) crop yield saturates at lower pollinator biomass than their carrying capacity, but for
328 large values of β_C/k_P (>1) crop yield saturates at pollinator biomasses much higher than
329 their carrying capacities.

330

331 Biodiversity is negatively correlated with mean independent crop yield, and is unrelated
332 to its stability (Figure 1a, c). For increasing levels of pollination dependence, both the
333 mean and stability of total crop yield are increasingly affected by pollination and hence
334 by the amount of semi-natural habitat (Figure 2). The position of the maximum yield
335 along the semi-natural gradient changes with crop pollination dependence and crop
336 relative requirement for pollinators. On one hand, for higher levels of pollination
337 dependence crops require more pollinators and thus maximum crop yield is achieved at
338 larger proportions of semi-natural habitat. On the other hand, high crop relative
339 requirement for pollinators (high β_C / k_P) has the dual effect of reducing mean yield and
340 shifting maximum yield to larger amounts of semi-natural habitat. In general, high crop
341 relative requirement for pollinators is less responsive to the amount of semi-natural
342 habitat, because pollinator densities that will be achieved in the agricultural landscape
343 are unlikely to fulfill crop relative requirement for pollinators (Appendix S4). Mean
344 crop yield per unit of agricultural area increases with the proportion of semi-natural
345 habitat (Appendix S5: Fig. S3), although it starts to show some saturation when crop
346 relative requirement for pollinators is low. Finally we explored the effect of resource
347 quality of different crop types and showed that these results are robust to differences in
348 resource quality of different crop types (e.g. $\Phi_C \sim \alpha_C / (\alpha_C + Z_C)$) (Appendix S4).

349

350 In pollination-dependent crops, the stability of pollination also changes with the fraction
351 of semi-natural habitat: it first decreases (due to the demographic and environmental
352 stochasticity of pollinators), and then increases after a minimum fraction of semi-natural
353 habitat has been reached (due to a drop in the response of crops to pollinator
354 stochasticity), although this response is heavily conditioned by the crop relative
355 requirement for pollinators (Figure 2e-h; Appendix S4). Whereas a higher pollination

356 dependence of crops reduces pollination stability and broadens the range of stability
357 values, crops with a lower pollination dependence are little affected by pollinator
358 stochasticity, and yield stability is mostly determined by the environmental stochasticity
359 of crops. Within each level of crop pollination dependence (Figure 2) the response of
360 yield stability to semi-natural habitat is conditioned by crop relative requirement for
361 pollinators: a low crop relative requirement for pollinators (low β_C/k_P) shifts the
362 stability valley to lower fractions of semi-natural habitat, and stability increases faster.
363 Increasing β_C/k_P expands the region of low stability, and stability requires larger areas
364 of semi-natural habitat to increase. When crop relative requirement for pollinators is
365 very high (high β_C/k_P), crop yield stability decreases monotonically along the full
366 gradient of semi-natural habitat.

367

368 In sum, the contrasting effects of increasing crop land on the various ecosystem services
369 reveal trade-offs (negatively correlated responses) and synergies (positively correlated
370 responses) in the response of biodiversity and the mean and stability of independent
371 crop yield and crop pollination (Figure 3). The exact shape of the ecosystem service
372 trade-offs across the gradient of semi-natural habitat is controlled by the degree to
373 which crops depend on pollination (Z_C/α_C) and by their relative requirement for
374 pollinator densities (β_C/k_P). Variations in parameter values did not change results
375 qualitatively.

376

377 **Discussion**

378 In intensively-managed agricultural systems, increases in the amount of crop land
379 relative to that of semi-natural habitat have major consequences for the provision of
380 multiple ecosystem services. Our model suggests that: (1) changes in landscape

381 composition generate a variety of synergies and trade-offs between biodiversity
382 conservation, crop pollination and independent crop yield, (2) these trade-offs affect not
383 only the magnitude but also the stability of these ecosystem services, and (3) the trade-
384 offs involving crop pollination are strongly affected by the degree to which crops
385 depend on pollination and by their relative requirement for pollinator biomass.

386

387 The loss of semi-natural habitat has contrasting effects on the three ecosystem services
388 considered: biodiversity decreases, independent crop production increases, while
389 pollination-dependent crop production is maximized at an intermediate proportion of
390 semi-natural habitat. These results provide rigorous theoretical foundations for
391 previously hypothesized functional relationships between the magnitude of ecosystem
392 services and landscape composition (Braat and ten Brink 2008). The results further
393 suggest that the exact shape of the hump-shaped relationship between provisioning
394 services and semi-natural habitat is determined by the pollination dependence and the
395 relative requirement of crops for pollinator densities (Figure 2, 3). Greater values of
396 these two factors increase the effect of pollinator biomass on total crop yield, and thus
397 the maximum yield is achieved at higher fractions of semi-natural habitat.

398

399 Importantly, our results suggest that landscape composition also imposes trade-offs on
400 the stability of crop yield. These trade-offs are driven by mechanisms associated with
401 the stochasticity of pollinators and the response of crops to that stochasticity. On the
402 one hand, the stability of crop pollination decreases with the amount of semi-natural
403 habitat when the latter is small because pollinator stochasticity increases. For larger
404 proportions of semi-natural habitat, however, the response of crop yield to pollinator
405 stochasticity drops, with varying effects on pollination stability. The decay in crop

406 response to pollinator stochasticity is caused by the saturation of pollination-dependent
407 crop yield to pollinator biomass (Appendix S4). Crop relative requirement for
408 pollinators controls how fast saturation sets in and, consequently, how fast the response
409 of crops to pollinator stochasticity drops down.

410

411 Taken together, the responses of the mean and stability of ecosystem services to
412 landscape composition produce different patterns across the gradient of semi-natural
413 habitat, from trade-offs (negatively correlated responses) to synergies (positively
414 correlated responses) (Figure 3). At the landscape scale, we found a trade-off between
415 independent mean crop yield and biodiversity, and between crop pollination and
416 independent crop yield when semi-natural habitat is low. Conversely, at low fractions of
417 semi-natural habitat, we observed a synergy between crop pollination and biodiversity.
418 Such synergy between crop production and biodiversity also became apparent when
419 considering crop production per unit of agricultural area, revealing the possibility to
420 reconcile farmers' profitability (at field scale) and biodiversity conservation (at
421 landscape scale). Trade-offs and synergies can also occur within ecosystem services,
422 e.g. crop pollination mean and its stability co-vary negatively except at low-to-
423 intermediate amounts of semi-natural habitat. These patterns give moderate support to
424 the intermediate landscape-complexity hypothesis (Tscharrntke et al 2012), which states
425 that the effectiveness of agro-environmental management strategies is higher in simple
426 (1-20% non-crop area) than in either cleared (<1% non-crop area) or complex (>20%
427 non-crop area) landscapes. For moderate-to-high levels of crop pollination dependence
428 and high crop relative requirement for pollinators, increases in the amount of semi-
429 natural habitat benefit biodiversity and crop pollination both in terms of average
430 provision and stability in simple landscapes. Despite simple agricultural landscapes are

431 often areas where cultivated crops have a low degree pollination dependency (except
432 from species like oilseed rape and sunflower), these benefits are also larger in simple
433 landscapes when crop yield per unit of agricultural land is considered. Surprisingly
434 though, with a few exceptions (e.g. Dufлот et al 2015), most intensively-managed
435 agricultural landscapes show very low proportions of semi-natural habitat (<5%;
436 Öckinger and Smith 2007, Henckel et al 2015). Additionally, increasing in the amount
437 of semi-natural habitat benefits other services such as pest control (Sutter and Albrecht
438 2016). In sum, consistent with empirical observations (Pywell et al 2015, Tamburini et
439 al 2016), the existing trade-offs and synergies suggest that moderate increases in the
440 amount of semi-natural habitat in simple agricultural landscapes (1-20% non-crop area)
441 allow ecosystem services essential for crop production to be maintained, which in turn
442 increases the magnitude and stability of crop yield.

443

444 Our findings are also consistent with recent studies suggesting that the interaction
445 between agricultural intensification and the level of pollination dependence of crops
446 determines the stability of crop production at large spatial scales. For instance, using an
447 intensification index that includes the amount of semi-natural habitat in agroecosystems,
448 a recent study found that the stability of the yield of the 54 major crops in France
449 decreases in more intensive agriculture, and that this reduction is more pronounced for
450 higher crop pollination dependence (Deguines et al 2014). Similarly, long-term data
451 from FAO suggest that a greater pollination dependence of crops leads to lower and less
452 stable crop yields (Garibaldi et al 2011a). By considering multiple inter-related
453 ecosystem services simultaneously, our results add a mechanistic understanding of these
454 ecosystem service trade-offs in intensively-managed agroecosystems.

455

456 The trade-offs in ecosystem service provision revealed by our model have two major
457 implications for the management of intensive agricultural systems. First, the effects of
458 biodiversity loss on crop production that result from agricultural intensification depend
459 on the level of pollination dependence of crops. Whereas in pollinator-independent
460 agriculture reductions in biodiversity and crop pollination have no effect on
461 provisioning services (crop production), for pollination-dependent agriculture crop
462 production relies on biodiversity (e.g. wild plants provide foraging, nesting and refuge
463 for pollinators), and the trade-off between biodiversity conservation and crop
464 production is mediated by biodiversity loss. Such reduction in biodiversity reduces the
465 delivery of regulating services, and this has a direct negative effect not only on mean
466 yield but also on its stability. Secondly, our results suggest that simultaneously
467 maximizing crop yield mean and stability is often impossible for pollination-dependent
468 crops, and therefore, management strategies that focus on maximising mean yield will
469 overlook its stability. Specifically, enhancing crop yield by increasing crop land would
470 be counterproductive for pollination-dependent crops, at least below a threshold of
471 semi-natural habitat. There is, however, a notable exception to this: maximization of
472 crop yield mean (both at the landscape scale and per unit of agricultural area) and crop
473 yield stability can be achieved at 20-40% of semi-natural habitat when crops show
474 intermediate-to-high degrees of animal pollination dependence and crop relative
475 requirement for pollinators is low.

476

477 The yield mean and stability of crops with greater pollinator dependence has
478 continuously decreased from 1961 to 2008 (Garibaldi et al 2011a). This suggests that
479 the relative requirement for pollinators of many world crops is high, as pesticide use has
480 diminished the carrying capacity of pollinators in semi-natural habitat during the same

481 period of time (Goulson et al 2015). To compensate for low crop yields agricultural
482 policies have promoted land cultivation of pollination-dependent crops and the use of
483 managed honeybee colonies, which are not affected by semi-natural habitat. However,
484 these measures reduce the amount of semi-natural area and honeybees cannot
485 compensate for the pollination services of non-managed, wild pollinators (Aizen et al
486 2009, Garibaldi et al 2013). Our model suggests that an alternative to agricultural
487 intensification consists in diminishing crop relative requirement for pollinators with
488 practices that increase the carrying capacity of pollinators in semi-natural habitat, such
489 as higher farmland heterogeneity and floral assemblages, increasing nesting
490 opportunities, and reductions in the use of synthetic pesticides (Garibaldi et al 2014).
491 These measures may not only increase mean crop yield at the landscape scale or per unit
492 of agricultural area, but also its stability.

493

494 Our model has several limitations. For example, our model and the observed trade-offs
495 between biodiversity and crop yield refer to intensively-managed agricultural systems,
496 where crop land does not host important biodiversity levels; however, these trade-offs
497 are not necessarily similar in non-intensive agricultural systems where biodiversity can
498 moderately thrive within crop land (Clough et al 2011). Second, the species-area
499 relationship is stronger at spatial scales larger than that of arable fields, where we might
500 expect more variation around the expected biodiversity values; yet, our simple model
501 captures the expected mean biodiversity at the scale of an arable field in Europe.

502 Besides, the observation that biodiversity loss has either none (stability) or positive
503 (mean) effects on independent crop yield is based on the species-area relationship; these
504 effects are likely to differ if taxonomic groups responsible for other ecosystem services,
505 i.e. pest control, are more specifically included. Also, our model is spatially-implicit,

506 and does not consider the effects of the spatial configuration of semi-natural habitat
507 (Garibaldi et al 2011b, Mitchell et al 2015); future studies should consider space
508 explicitly, as the spatial distribution of semi-natural habitat within the agricultural
509 landscape determines the ecosystem service flows between semi-natural habitat and
510 crop land, including pollination (Brosi et al 2008, Keitt 2009, Serna-Chavez et al 2014).
511 Finally, we find that the amount of semi-natural habitat has no effect on the stability of
512 independent crop yield. This may change, however, if environmental stochasticity of
513 crops increases with decreasing amounts of semi-natural habitat, as suggested by studies
514 linking semi-natural habitat to climate regulation, natural hazard regulation and water
515 flow regulation services (Harrison et al 2010). Despite these limitations, our model is a
516 very useful first step as it successfully reproduces the results of recent empirical studies
517 on the stability of pollination-dependent crop yield and it provides a mechanistic
518 understanding of the trade-offs that are relevant in intensively-managed
519 agroecosystems.

520

521 **Conclusions**

522 Although historically the demand for increased crop production has been satisfied by
523 agricultural practices that promote land conversion to crop land and improvements in
524 crop yield (e.g. fertilizers, pesticides, selection of high-yield crop strains), the benefits
525 of this approach have started to be challenged. The present study sheds new light on this
526 debate. Our model suggests that landscape composition imposes trade-offs on several
527 ecosystem services in intensively-managed agroecosystems. These trade-offs not only
528 affect the mean production of crops, but also their temporal stability, in such a way that
529 high and stable crop yields are not necessarily associated. This suggests that an
530 approach that simultaneously considers the magnitude and stability of multiple

531 ecosystem services is needed to understand and better manage agricultural systems. In
532 order to develop a more efficient agriculture and ensure food security, it is essential to
533 understand the mechanisms driving the trade-offs between multiple ecosystem services.
534

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723 cover long foraging distances. *Biological Conservation* 143:669–76.

724 **Table 1.** Parameters and variables of the model

725

Parameters & Variables	Definition	Dimensions
Parameters		
α_P	Maximum growth rate of pollinators	time ⁻¹
α_W	Maximum growth rate of semi-natural plants	time ⁻¹
α_C	Maximum crop yield derived from pollinator interactions	mass·area ⁻¹
β_P	Half-saturation constant of pollinators	mass
β_W	Half-saturation constant of ‘wild’ plants	mass·area ⁻¹
β_C	Half-saturation constant of crop plants to pollinators	mass·area ⁻¹
k_P	Carrying capacity of pollinators per unit area	mass·area ⁻¹
k_W	Carrying capacity of semi-natural plants per unit area	mass·area ⁻¹
A	Total landscape area	area
ω_{sn}	Proportion of semi-natural habitat	dimensionless
Z_C	Crop yield independent of pollinators	mass·area ⁻¹
c_W	Conversion rate of ‘wild’ plants (from functional to numerical response)	dimensionless
c_P	Conversion rate of pollinators (from functional to numerical response)	dimensionless
Φ_W	Weighting factor for ‘wild’ plants (flux to stock)	dimensionless
Φ_C	Weighting factor for crop plants (flux to stock)	dimensionless
r_P	Intrinsic growth rate of pollinators	time ⁻¹
r_W	Intrinsic growth rate of ‘wild’ plants	time ⁻¹

σ_P^e	Environmental standard deviation of pollinators	time ^{-1/2}
σ_W^e	Environmental standard deviation of ‘wild’ plants	time ^{-1/2}
σ_C^e	Environmental standard deviation of crop production	dimensionless
σ_P^d	Demographic standard deviation of pollinators	mass ^{1/2} ·time ^{-1/2}
σ_W^d	Demographic standard deviation of semi-natural plants	mass ^{1/2} ·time ^{-1/2}
u_P^e, u_P^d	White noise signals with zero mean and standardized variance. u^e = environmental, u^d = demographic P = pollinators; W = ‘wild’ plants; C = crop plants	dimensionless
u_W^e, u_W^d		
u_C^e, u_C^d		

Variables

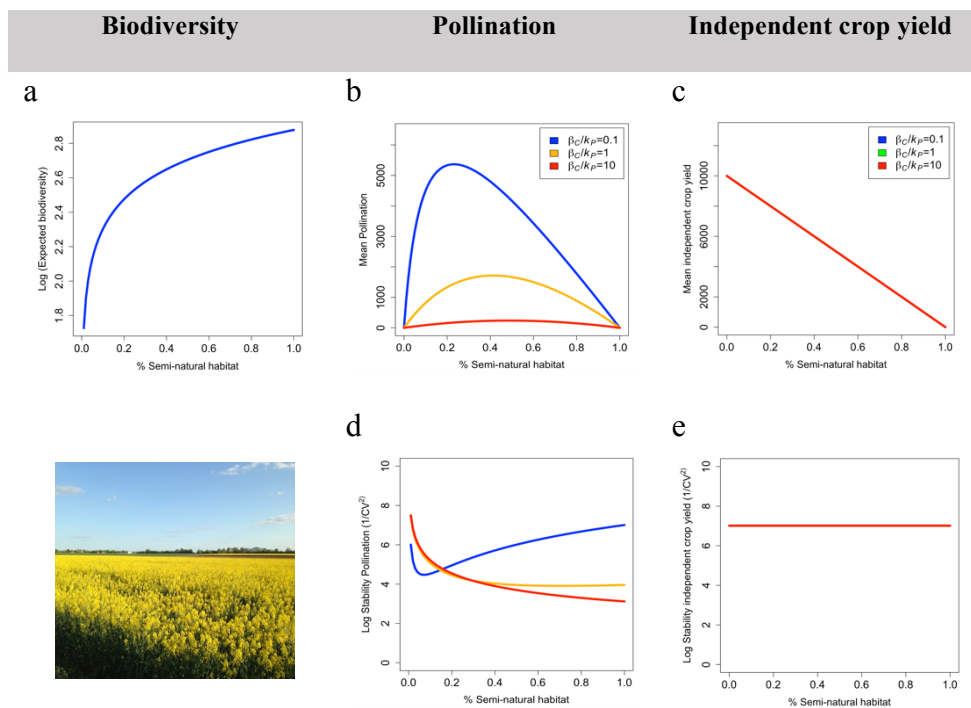
$C(t)$	Biomass of crop plants (crop yield)	mass
$W(t)$	Biomass of semi-natural or ‘wild’ plants	mass
$P(t)$	Biomass of pollinators	mass

726

727

Figure 1. Mean and stability of five ecosystem service components in agroecosystems.

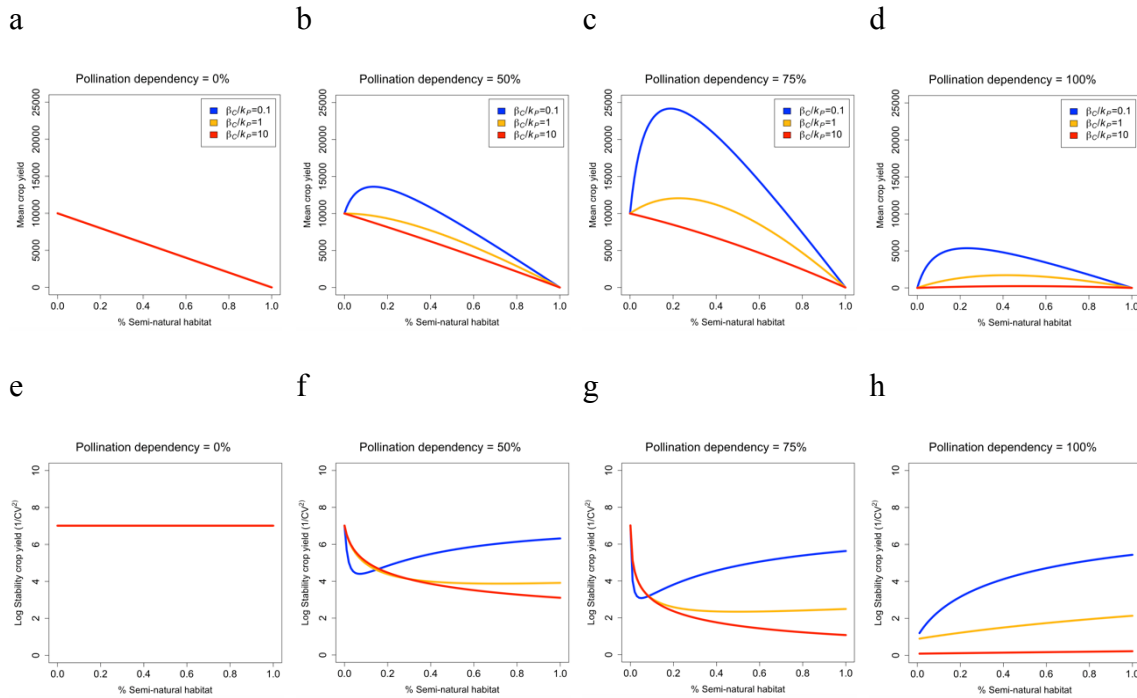
This graph shows the expected biodiversity (a) and the temporal mean (c) and stability (d; $\log[1/CV^2]$) of independent crop yield, and crop pollination (b, d), as functions of the proportion of semi-natural habitat, for different crop relative requirement for pollinators (β_C/k_P). Because β_C/k_P does not affect biodiversity and the mean/stability of independent crop yield, a single line is showed. Picture of an intensive agricultural landscape in the LSTER Zone Atelier Plaine & Val de Sèvre, France (Photo credit: Sabrina Gaba).



(Parameter values: $\alpha_p = 0.9$, $\beta_p = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $k_P = 0.1$, $\sigma_p^c = 0.8$, $\sigma_p^d = 0.1$, $\sigma_C^c = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%; Species-area relationship [$S=c(\omega_{sn}A)^z$]: $c=10$, $z=0.25$)

Figure 2. Mean and stability of total crop yield. Temporal mean and stability

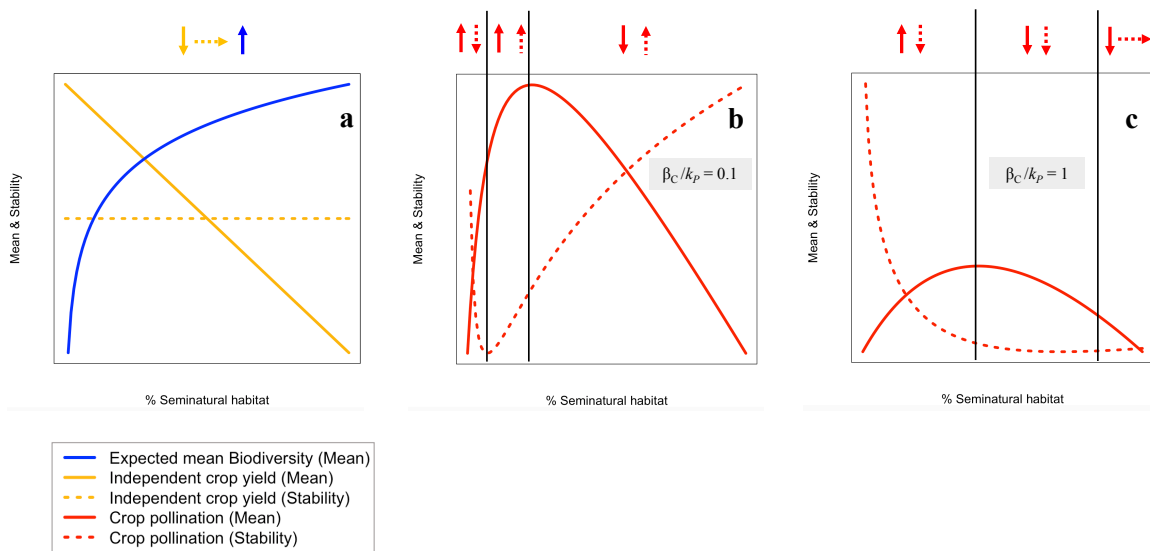
($\log[1/CV^2]$) of total crop yield as functions of pollination dependence and crop relative requirement for pollinators. In (a, e), the three curves overlap.



(Parameter values: $\alpha_p = 0.9$, $\beta_p = 0.6$, $A = 10$, $k_W = 5000$, $\sigma_p^e = 0.8$, $\sigma_p^d = 0.1$, $\sigma_C^e = 0.03$, $\alpha_C = 1000$.)

Because $Z_C = 1000$, α_C is allowed to increase with higher pollination dependences; this is why mean crop yield increases with pollination dependence of crops. In a, e: $\alpha_C = 0$ and $Z_C = 1000$. In d, h: $\alpha_C = 1000$ and $Z_C = 0$)

1 **Figure 3.** A variety of trade-offs and synergies between ecosystem service components
 2 in agroecosystems. This graph shows the expected biodiversity and the temporal mean
 3 and stability ($\log[I/CV^2]$) of independent crop yield (**a**), and crop pollination (**b**, **c**), as
 4 functions of the proportion of semi-natural habitat. The responses of the mean and
 5 stability of the three ecosystem services to increasing proportions of semi-natural
 6 habitat produce different patterns across the gradient of semi-natural habitat, from trade-
 7 offs (negatively correlated responses: opposite arrows) to synergies (positively
 8 correlated responses: similar arrows). Independent crop yield and biodiversity (**a**) are
 9 not affected by crop relative requirement for pollinators (β_C/k_P). Conversely, crop
 10 pollination mean and its stability, and therefore ecosystem service synergies and trade-
 11 offs, are controlled by crop relative requirement for pollinators: (**b**) $\beta_C/k_P = 0.1$, (**c**) β_C/k_P
 12 $/k_P = 1$ (see main text and Supplementary Methods 1). Y axes are unit-less to make
 13 comparison between curves clearer.



14
 15 (Parameter values: $\alpha_P = 0.9$, $\beta_P = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $k_P = 0.1$, $\sigma_P^c = 0.8$, $\sigma_P^d =$
 16 0.1 , $\sigma_C^c = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%; Species-area relationship [$S=c (\omega_{sn} A)^z$]: $c=10$,
 17 $z=0.25$)