1 *For Ecological Applications: Research article*

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4 # Trade-offs in provisioning and stability of multiple ecosystem

5 # services in agroecosystems

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25 production, trade-offs, stability

Abstract

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

Introduction

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

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

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

154

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

156

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

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-ω_{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:

180

181
$$r_P(t) = c_P \frac{\alpha_P(\phi_W W(t) + \phi_C C(t))}{\beta_P + \phi_W W(t) + \phi_C C(t)} \qquad (4)$$

182
$$r_W(t) = c_W \frac{\alpha_W(P(t)/A)}{\beta_W + (P(t)/A)} \qquad (5)$$

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

Results

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:

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

323

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 (Tscharntke 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. Duflot 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

Conclusions

521

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

535 **Acknowledgements**

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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	$mass \cdot area^{-1}$
β_P	Half-saturation constant of pollinators	$mass$
β_W	Half-saturation constant of 'wild' plants	$mass \cdot area^{-1}$
β_C	Half-saturation constant of crop plants to pollinators	$mass \cdot area^{-1}$
k_P	Carrying capacity of pollinators per unit area	$mass \cdot area^{-1}$
k_W	Carrying capacity of semi-natural plants per unit area	$mass \cdot area^{-1}$
A	Total landscape area	$area$
ω_{sn}	Proportion of semi-natural habitat	dimensionless
Z_C	Crop yield independent of pollinators	$mass \cdot area^{-1}$
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^e_P	Environmental standard deviation of pollinators	$\text{time}^{-1/2}$
σ^e_W	Environmental standard deviation of 'wild' plants	$\text{time}^{-1/2}$
σ^e_C	Environmental standard deviation of crop production	dimensionless
σ^d_P	Demographic standard deviation of pollinators	$\text{mass}^{1/2} \cdot \text{time}^{-1/2}$
σ^d_W	Demographic standard deviation of semi-natural plants	$\text{mass}^{1/2} \cdot \text{time}^{-1/2}$
$u^e_P, u^d_P,$ $u^e_W, u^d_W,$ u^e_C, u^d_C	White noise signals with zero mean and standardized variance. u^e = environmental, u^d = demographic P = pollinators; W = 'wild' plants; C = crop plants	dimensionless

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

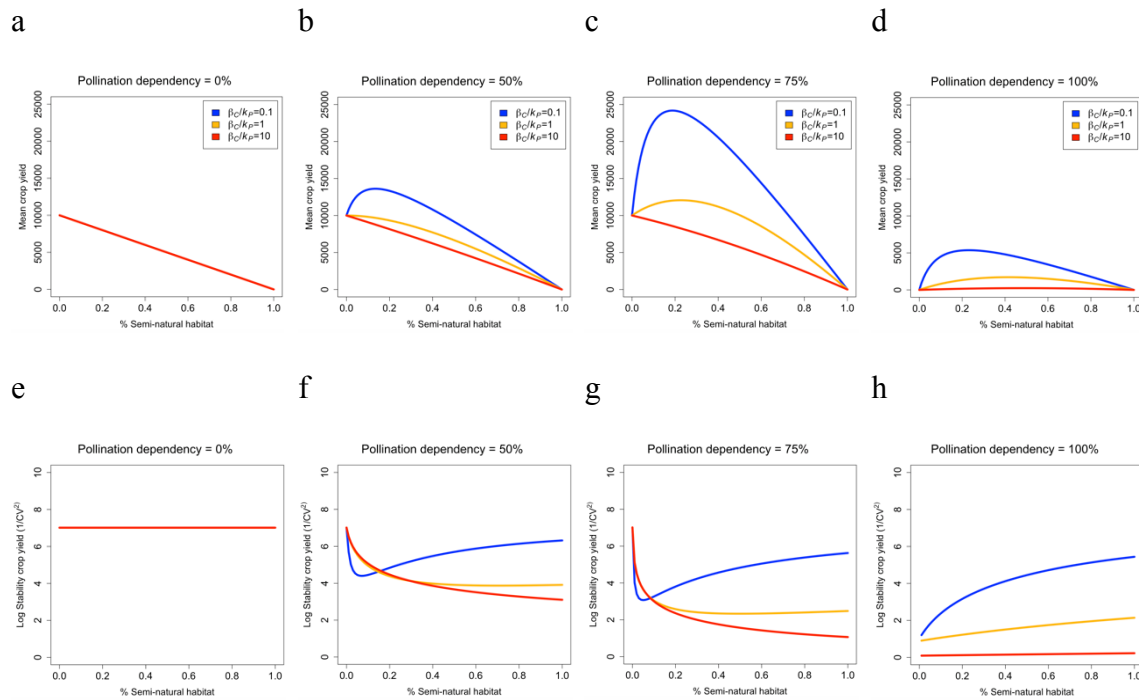**Figure 1**. Mean and stability of five ecosystem service components in agroecosystems. This graph shows the expected biodiversity (a) and the temporal mean (c) and stability (d; log[$1/CV^2$]) of independent crop yield, and crop pollination (b, d), as functions of the proportion of semi-natural habitat, 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).
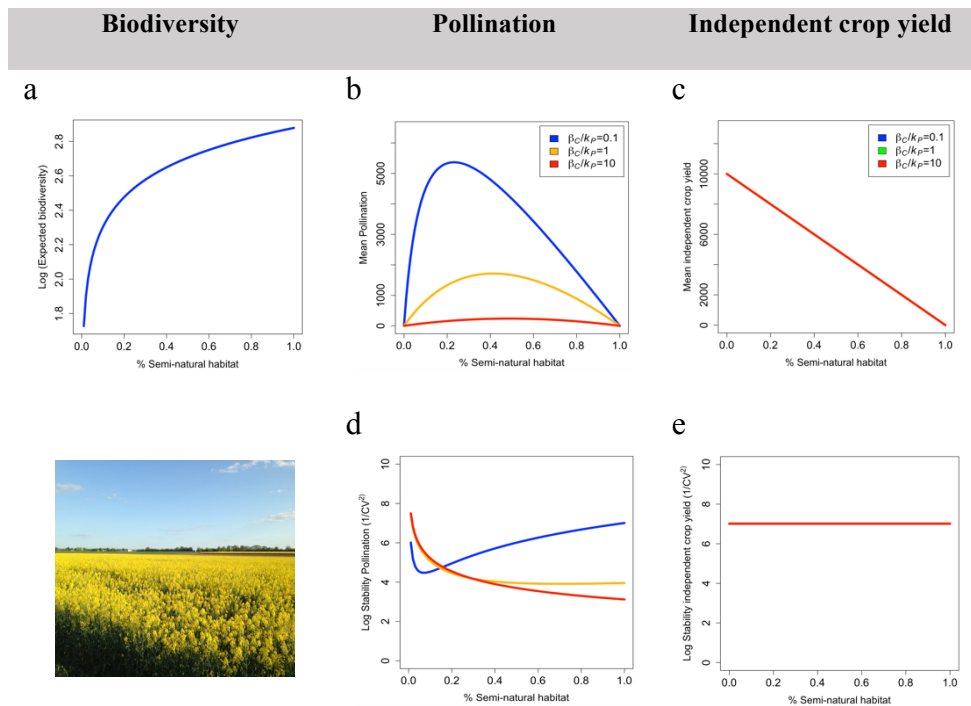
(Parameter values: $\alpha_P = 0.9$, $\beta_P = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $k_P = 0.1$, $\sigma^e_P = 0.8$, $\sigma^d_P = 0.1$, $\sigma^e_C = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%; Species-area relationship [$S = c\,(\omega_{sn}A)^z$]: c=10, z=0.25)

**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: $\alpha_P = 0.9$, $\beta_P = 0.6$, $A = 10$, $k_W = 5000$, $\sigma^e_P = 0.8$, $\sigma^d_P = 0.1$, $\sigma^e_C = 0.03$, $\alpha_C = 1000$.

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 ($\log[1/CV^2]$) 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

12 $/k_P = 1$ (see main text and Supplementary Methods 1). Y axes are unit-less to make

13 comparison between curves clearer.
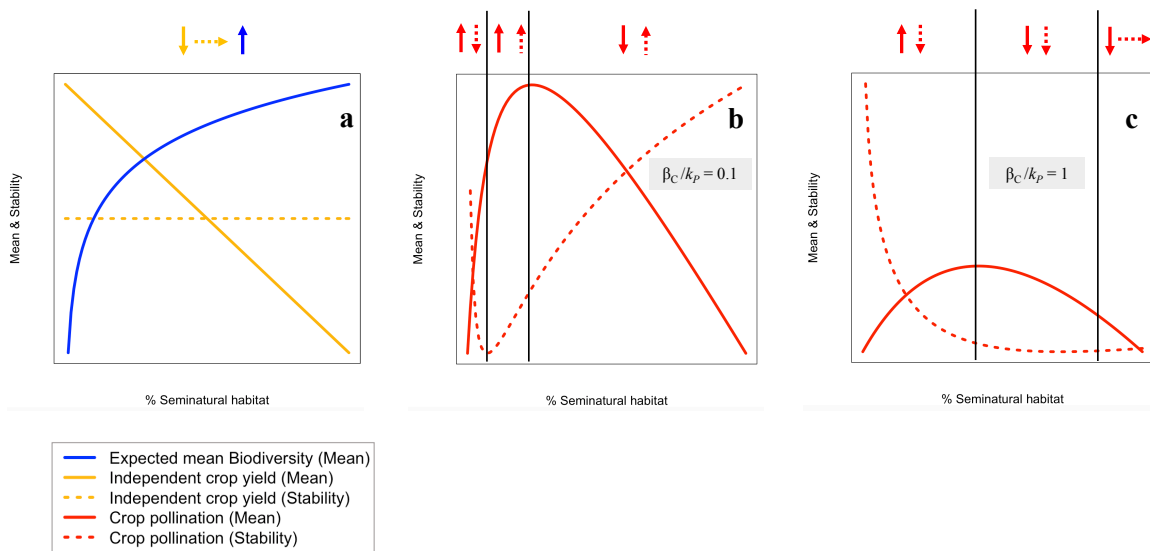
14

15 (Parameter values: $\alpha_P = 0.9$, $\beta_P = 0.6$, $A = 10$, $Z_C = 1000$, $\alpha_C = 1000$, $k_W = 5000$, $k_P = 0.1$, $\sigma^e_P = 0.8$, $\sigma^d_P =$

16 0.1, $\sigma^e_C = 0.03$, $\alpha_C = 1000$, Pollination dependence = 50%; Species-area relationship [$S = c\,(\omega_{sn}A)^z$]: c=10,

17 $z=0.25$)