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1 **Contribution of insect pollinators to crop yield and quality varies with agricultural**  
2 **intensification**

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29

30 **Abstract**

31 **Background.** Up to 75 % of crop species benefit at least to some degree from animal  
32 pollination for fruit or seed set and yield. However, basic information on the level of  
33 pollinator dependence and pollinator contribution to yield is lacking for many crops. Even  
34 less is known about how insect pollination affects crop quality. Given that habitat loss and  
35 agricultural intensification are known to decrease pollinator richness and abundance, there  
36 is a need to assess the consequences for different components of crop production.

37 **Methods.** We used pollination exclusion on flowers or inflorescences on a whole plant basis  
38 to assess the contribution of insect pollination to crop yield and quality in four flowering  
39 crops (spring oilseed rape, field bean, strawberry, and buckwheat) located in four regions of  
40 Europe. For each crop, we recorded abundance and species richness of flower visiting  
41 insects in ten fields located along a gradient from simple to heterogeneous landscapes.

42 **Results.** Insect pollination enhanced average crop yield between 18 and 71% depending on  
43 the crop. Yield quality was also enhanced in most crops. For instance, oilseed rape had  
44 higher oil and lower chlorophyll contents when adequately pollinated, the proportion of  
45 empty seeds decreased in buckwheat, and strawberries' commercial grade improved;  
46 however, we did not find higher nitrogen content in open pollinated field beans. Complex  
47 landscapes had a higher overall species richness of wild pollinators across crops, but  
48 visitation rates were only higher in complex landscapes for some crops. On the contrary, the  
49 overall yield was consistently enhanced by higher visitation rates, but not by higher  
50 pollinator richness.

51 **Discussion.** For the four crops in this study, there is clear benefit delivered by pollinators on  
52 yield quantity and/or quality, but it is not maximized under current agricultural  
53 intensification. Honeybees, the most abundant pollinator, might partially compensate the

54 loss of wild pollinators in some areas, but our results suggest the need of landscape-scale  
55 actions to enhance wild pollinator populations.

## 56 **Introduction**

57 There is growing evidence that ecosystem services, such as biological pest control and crop  
58 pollination, benefit food production (Bommarco et al. 2013). Indeed, 75% of the crop  
59 species used for food depend on insect pollination to some degree (Klein et al. 2007). More  
60 than a decade of active pollination research has led to a greatly improved general  
61 understanding on animal pollination benefits to crop yields worldwide (e.g., Klein et al.  
62 2007; Garibaldi et al 2011, 2013). However, major knowledge gaps remain.

63  
64 First, we have surprisingly little information on the actual degree of pollinator dependence  
65 for some major crops. While some crops depend entirely on insect pollinator visits to set  
66 fruit, many others are only partly dependent on animal pollination and can produce more  
67 than 90% of the maximum seed or fruit yield without pollinators (Klein et al. 2007). The role  
68 of pollinators for crop production has mainly been examined in observational studies,  
69 relying primarily on natural variation in visitation rates among observed sites. Experiments  
70 directly manipulating insect flower visitation (e.g., excluded pollinators vs. open access of  
71 pollinators) are less common for most crops (but see Klein et al. 2003, Höhn et al. 2008).  
72 Assessing pollination dependence with proper controls is needed to correctly estimate the  
73 contribution that insect pollinators can provide to crop yields.

74  
75 Second, most available studies quantify the number of fruits per plant. Fruit number can be  
76 a good proxy for yield (Garibaldi et al. 2013), which is the amount of produce harvested per  
77 unit area. However, the correlation between the number of fruit produced and yield is likely  
78 to be low in some crops. For example, interspecific plant competition can lead to high  
79 variability in plant size and thereby fruit production among plants. This is especially critical

80 for crops with indeterminate flowering and a high compensation capacity such as soybean  
81 (*Glycine max*) and oilseed rape (*Brassica napus*). For these, fruit set measured on a limited  
82 number of isolated plants is unlikely to be representative of the real production in a crop  
83 stand (Stivers & Swearingin 1980, Angadi et al. 2003). Moreover, plants can allocate  
84 resources for producing fruits of variable size based on the number of fruits per plant and  
85 the level of pollination received (e.g., Gonzalez et al. 1998 in kiwifruit *Actinidia deliciosa*),  
86 such that similar levels of fruit set can differ in total crop yield because of difference in fruit  
87 size (Bos et al. 2007). Again, the use of proper control plants from which pollinators are  
88 excluded is a way to better estimate the actual contribution of pollinators to yield in such  
89 crops.

90  
91 Quality is also important in crop production, especially from an economic standpoint. Fruit  
92 quality can be negatively correlated with quantity when the fruit load on a tree or a vine is  
93 too high (e.g., Ferguson & Watkins 1992 in apple *Malus x domestica*), but it is not so  
94 otherwise, especially in crops with indeterminate flowering such as oilseed rape (Bommarco  
95 et al. 2012). Indeed, adequate pollination often leads to produce with enhanced quality in  
96 entomophilous crops such as orchard fruit production (e.g., in apple – Sheffield et al. 2005,  
97 Garratt et al. 2014), as well as in field crops (oilseed rape – Bommarco et al. 2012b) and  
98 small fruits and vegetables (e.g., strawberry *Fragaria x ananassa* – Andersson et al. 2012,  
99 Chagnon et al. 1993, Roselino et al. 2009; tomato *Solanum lycopersicum* – Hogendoorn et al.  
100 2010; bell peppers *Capsicum annuum* – Roldan Serrano and Guerra-Sanz 2006 ; highbush  
101 blueberry *Vaccinium corymbosum* – Isaacs and Kirk 2010).

102  
103 Given the drastic shifts in community composition of insects that visit flowering crops

104 (Winfree et al. 2011, Bommarco et al. 2011, Bartomeus et al. 2013a), and declines in  
105 pollinator species numbers observed in certain regions (Potts et al. 2010, Carvalheiro et al.  
106 2013), it is increasingly important to gather information on the extent to which different  
107 crops depend on insect pollination for yield, and if current pollinator communities fulfill the  
108 demand for pollination services such that both crop quality and yields are maximized  
109 (Breeze et al. 2011). Relationships between land use intensity, pollinator visitation, and fruit  
110 set have been well studied. While pollinator species richness consistently and drastically  
111 decays as agricultural landscapes are deprived of natural habitat and are more intensively  
112 cultivated (Kennedy et al. 2013), this relationship is much weaker for fruit set (Garibaldi et  
113 al. 2011, Chacoff et al. 2008, Ricketts et al. 2008). One explanation for this difference is that  
114 the remaining pollinators provide sufficient visitation even in monotonous, intensively  
115 cultivated landscapes, especially if the crop has a large degree of autonomous self-  
116 pollination. Moreover, intensive landscapes are characterized by harboring just a few  
117 generalist pollinator species (Bartomeus & Winfree 2013), but these might be in sufficient  
118 numbers to deliver enough crop pollination services. In fact, not all pollinator species  
119 respond equally to land use change (Williams et al. 2010, Winfree et al. 2011), and some  
120 even increase in abundance with agricultural intensification (Westphal et al 2003, Carré et  
121 al. 2009). This diversity of responses can in some cropping systems buffer a loss of  
122 pollination function (Cariveau et al. 2013), especially if the pollinators who are the main  
123 ecosystem service providers are adapted to the ephemeral and spatially disassociated  
124 resource distribution that is typical for agricultural landscapes. Moreover, although wild  
125 insects increase fruit set independently of honeybee visits (Garibaldi et al. 2013), honeybees  
126 are less dependent on landscape characteristics because they are mainly managed,  
127 particularly in North America and Europe, and can be moved around in the landscape.



128 Hence, honeybees can also help mitigate against wild pollinator loss in more intensively  
129 used landscapes where pollination services are degraded. In any case, the composition of  
130 the landscape in which the flowering crop field is embedded emerges as an important driver  
131 for pollinator community composition, and the landscape context needs to be considered  
132 when linking land use to pollination provisioning and benefits in field crops.

133

134 Here we used pollinator exclusion on the flowers or inflorescence on a whole plant basis in a  
135 set of crops under standard field conditions, to obtain information on pollinator  
136 dependency for four economically important annual crops in Europe. We assessed  
137 pollinator contribution to both yield quantity and quality. By replicating this experiment  
138 along a landscape gradient for each crop, we were able to assess changes in pollinator  
139 community composition and visitation rate following landscape level land use change and  
140 its consequences for crop pollination services and production.

141

## 142 **Material and Methods**

143

### 144 **Study sites**

145 The fieldwork was conducted in four European countries during May–August 2005 (Table 1).  
146 Spring oilseed rape was assessed in the region around the city of Uppsala, Sweden (see  
147 Bommarco et al. 2012 for details); field bean (*Vicia faba*) in around Reading, UK, strawberry  
148 around Göttingen, Germany; and buckwheat (*Fagopyrum esculentum*) near Krakow, Poland.  
149 For each crop, we selected ten fields that were separated by a minimum distance of 3 km,  
150 corresponding to the maximum foraging range of most bees (Greenleaf et al. 2007). Within  
151 each field, we established a 50 \* 25 m study area (5\*150 m for buckwheat as the fields were

152 long and narrow) with a homogeneous and continuous crop cover. For fields up to two ha in  
153 size, this study site was located in the middle of the field. For larger fields, it was located  
154 between the geometric center of the field and one of its margins (Vaissière et al. 2011).

155

#### 156 **Insect sampling**

157 In each field, we assessed the abundance and species richness of the major groups of  
158 flower-visiting insects, including bees (Hymenoptera: Apoidea: Apiformes), hoverflies  
159 (Diptera: Syrphidae), and butterflies (Lepidoptera). We used standardized transect walks  
160 with an aerial net (Westphal et al. 2008). In each study site, a 150 m transect line was  
161 established in the field near the experimental plots. An observer walked this line for 30 min  
162 identifying visiting insects at species level and catching unidentified species within a corridor  
163 4 m wide. We performed the transect walks between 0900 and 1700 hours only on days  
164 with temperatures at or above 15°C, with no precipitation, dry vegetation, and low  
165 windspeed (<40 km.h<sup>-1</sup>; Westphal et al. 2008). Specimens were pinned, labeled, and  
166 subsequently identified to species level. We returned four times to each study site during  
167 the main flowering period of each study crop.

168

#### 169 **Experimental design and yield analysis**

170 In each of the ten fields, we established a block experiment with four blocks. Each block had  
171 two treatments with one plot per treatment and five to ten tagged contiguous plants  
172 monitored per plot. The first treatment (Open) was open pollinated with all the flowers of  
173 each plant accessible to autonomous self-, wind- and insect-pollination. In the second  
174 treatment (Net), all flowers were enclosed in nylon tulle bags with 1 \* 1 mm openings  
175 (Diatex F510; <http://www.diatex.fr/-Agriculture-.html>) of an appropriate size to cover an

176 inflorescence (buckwheat, field bean & oilseed rape), or an individual flower (strawberry).  
177 Thus, in the Net-treatment all flowers were exposed to wind- and self-pollination, but not to  
178 insect pollination. Because such nets do not hinder the airborne pollen flow (Sacchi and  
179 Price 1988, Wragg and Johnson 2011), the difference between these treatments represents  
180 the contribution from insect pollination. We put the nets over the flower buds before the  
181 onset of flowering. Leaves and plant parts with no flowers were left as much as possible  
182 outside the net bag to minimize any effects of the bag on the photosynthesis (Howpage et  
183 al. 2001). As soon as flowers had wilted, we removed the nets, and the tagged plants were  
184 left to ripen in the field until harvest.

185  
186 For buckwheat, field bean, and oilseed rape, we cut all experimental plants from each plot  
187 and stored them individually in a linen bag just before commercial harvest. For strawberry,  
188 we followed the commercial harvest procedure and harvested the ripe strawberries twice a  
189 week. In each plot, we recorded the number of fruits per plant (field bean, oilseed rape, and  
190 strawberry), and the number and weight of seeds per plant (buckwheat, field bean, and  
191 oilseed rape) were measured using a precision scale and a seed counter. For each crop, we  
192 also measured the specific attributes of quality that affect its marketing value. For oilseed  
193 rape, we analyzed the oil content and chlorophyll contents of the seeds (performed by  
194 Svalof Weibull Lab AB, Svalov, Sweden). High chlorophyll contents decrease the durability  
195 and alter the color of the extracted oil. For field beans, we measured the nitrogen content  
196 of the seed as a proxy of their protein content. The nitrogen content was measured using  
197 oxidative combustion in an automated Dumas type combustion analyzer. For strawberry, we  
198 classified commercial quality as grade 1 (fully developed fruits of good quality), grade 2  
199 (marketable fruits with some changes in colour and shape) and grade 3 (non-marketable

200 fruits) according to guidelines of the German board of trade. For buckwheat, we measured  
201 the proportion of filled seeds since high proportion of empty seeds leads to a penalty in the  
202 market price. For buckwheat, six fields were destroyed due to a hailstorm, and hence we  
203 do not have yield measures for those.

204

## 205 **Landscape context**

206 The ten fields for each crop were located along a gradient of surrounding landscape  
207 complexity. The gradient ranged from intensive agricultural landscapes dominated by large  
208 arable fields with few boundary features, to complex landscapes with smaller average  
209 arable field sizes and more than 40% coverage of semi-natural habitats, such as pastures  
210 and forest patches over 0.5, 1, 2, and 3 km radius around each study field. When selecting  
211 the field sites, the proportion of arable land in the surrounding landscape was measured  
212 around each experimental field and used as a proxy for landscape complexity (Steffan-  
213 Dewenter et al. 2002, Fahrig 2013). The proportion of arable land in the landscape  
214 surrounding each of the ten experimental fields varied depending on the region, with some  
215 regions presenting more intense landscapes (e.g., range of 48 to 97 % of agricultural land for  
216 oilseed rape fields at 1000 m radius), and other regions presenting more complex  
217 landscapes (range of 4 to 45 % of agricultural land for field bean at 1000 m radius).

218

219 For oilseed rape, we used the Swedish digitized land cover terrain map database to  
220 characterize the landscape surrounding each field (Lantmateriet 2008). For buckwheat and  
221 strawberry, we used CORINE data from 2006 (European Environment Agency:  
222 <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-2>). For field  
223 beans we used the CORINE 2000 Land Cover Map

224 (<http://www.ceh.ac.uk/landcovermap2000.html>).

225

## 226 **Data analysis and statistics**

227

### 228 *Landscape effects on bee richness and visitation*

229 Because different organisms act in and react to the landscape at different spatial scales, it is

230 necessary to find a suitable scale at which to measure the surrounding landscape (Steffan-

231 Dewenter et al. 2002; Henry et al. 2012). Before exploring any significances, we ran models

232 for each variable with each of the different radii (0.5–3 km) at which the landscapes had

233 been measured. Hence, for each crop we regressed percentage of agricultural area against

234 pollinator richness and abundance at different radii, and identified the radius that explained

235 the highest proportion of variance (highest  $R^2$ ). For species richness, all crops showed the

236 highest  $R^2$  at a radius of 0.5 km, while abundance was best explained at a 1 km radius with

237 the exception of field bean bee communities, which also responded to a larger scale (1500

238 m). We performed joint models for all crops at 0.5 and 1 km radius for richness and

239 visitation abundance, respectively. Bee species richness showed a similar relation to

240 landscape complexity for all crops, and this permitted us to include 'crop' as random factor

241 in the model to investigate the general influence of landscape on richness. Visitation

242 abundance, however, followed contrasting trajectories in relation to landscape depending

243 on the crop. We therefore included in the model crop and its interaction with landscape as

244 fixed effects. Pollinator abundances were centered and scaled to a mean of zero and a

245 deviation of one within each crop.

246

### 247 *Yield quantity and quality*

248 We first correlated fruit set with yield (i.e., total fruit or seed weight/plant) for each crop.  
249 Block was nested within site and included as random factor in all models. Second, we  
250 constructed two mixed effect model with yield as the response variable. In order to analyze  
251 all crops in the same model, yield and pollinator visitation abundance were centered and  
252 scaled to a mean of zero and a deviation of one within each crop. The first model had  
253 pollination treatment, species richness, total visitation abundance, and the interactions of  
254 treatment with the other two variables as predictors. The second model had treatment,  
255 landscape, and its interaction as predictors. Landscape was investigated at 0.5 and 1 km  
256 radius with similar results and so only models at 1 km are shown. Block, nested within site,  
257 nested within crop was included as a random factor in all models. In both models, a  
258 significant interaction with treatment would indicate that the factor had an effect on yield  
259 only in the open treatment. To account for heteroscedasticity, we added a constant  
260 variance structure (*varIdent* function in package nlme, R) in which the variance was  
261 independently specified for each crop (Cleasby et al. 2011).

262  
263 We also checked if quality was affected by the pollination treatment. Each crop was  
264 analyzed independently due to different measurement units and also because there was no  
265 homogeneous response among the crops. Block nested within site was included as a  
266 random factor in all models. In this case, we tested only for the effect of the pollination  
267 treatment, without including the interactions with species richness, visitation abundance, or  
268 landscape context due to sample size limitations. For buckwheat, we used block as a  
269 constant variance function to control for the different heteroscedasticity among blocks. The  
270 package *nlme* in R was used to fit all models (Pineiro et al. 2013). Residual plots where  
271 used to check for normality and standardized residuals for heteroscedasticity.

272

## 273 **Results**

### 274 *Landscape effects on bee richness and visitation*

275 Pollinator species richness ranged from 2 to 26 species per site (Table 1). The flower visitors  
276 of all crops were highly dominated by one or two species of pollinators, in most cases  
277 managed honeybees. In field beans, the dominant species were bumblebees; *Bombus*  
278 *terrestris/lucorum* complex, followed by *B. hortorum* and *B. lapidarius* (Fig. 1). Simple  
279 landscapes had consistently lower species richness in all crops (GLMM:  $F_{1,35} = 5.39$ ,  $P = 0.02$ ;  
280 Fig. 2A). However, the pollinator abundance trend depended on the crop (Table 2; Fig. 2B).  
281 Visitation patterns were driven by managed honeybee densities in all crops except for field  
282 beans. While in most regions honeybee visits were also higher in complex landscapes (Table  
283 2), in buckwheat there were higher honeybee visits in simple landscapes. For field beans,  
284 this positive relationship between number of visits recorded and landscape was even more  
285 pronounced at larger scales when we analyze the primary pollinators, the bumblebees,  
286 alone ( $F_{1,8} = 6.44$ ,  $P = 0.03$  at 1.5 km radius).

287

### 288 *Yield quantity and quality*

289 Seed numbers were in all cases positively correlated with yield. However, the correlation  
290 was stronger in some crops than others (oilseed rape:  $R^2 = 0.95$ ,  $P < 0.0001$ ; field bean:  $R^2 =$   
291  $0.90$ ,  $P < 0.0001$ ; strawberry:  $R^2 = 0.61$ ,  $P < 0.0001$ ; buckwheat:  $R^2 = 0.67$ ,  $P < 0.0001$ ).

292

293 Open pollination increased fruit set and yield for all crops (Table 3; Fig. 3). We did not detect  
294 an interaction between treatment and species richness, which indicates that higher richness  
295 does not increase yield in any of the treatments. However, total visitation rate increased

296 yield in both treatments (Fig 4A). Interestingly, landscape complexity (both at 0.5 or at 1 km)  
297 also showed a significant interaction with treatment, indicating that simpler landscapes had  
298 lower yields only in the open pollinated plants (Table 3; Fig. 4B). However, landscape did not  
299 affect the yield of net-bagged plants.

300

301 In addition to quantity, the quality of oilseed rape, buckwheat and strawberry increased in  
302 the open pollination treatments (oilseed rape: oil content estimate =  $1.28 \pm 0.31$  %, df = 39,  
303  $t = 4.18$   $P < 0.001$ ; Chlorophyll content estimate =  $-4.15 \pm 1.76$  ppm, df = 39,  $t = -2.37$ ,  $P =$   
304  $0.02$ ; buckwheat: percentage of filled seeds estimate =  $0.08 \pm 0.01$  %, df = 12,  $t = 6.35$ ,  $p <$   
305  $0.001$ ; strawberry: commercial grade estimate =  $-0.32 \pm 0.06$ , df= 67,  $t = -5.36$ ,  $p < 0.001$ ). On  
306 the other hand, the nitrogen content of field beans did not increase on open-pollinated  
307 plants (estimate =  $-0.10 \pm 0.08$  %, df = 37,  $t = -1.16$ ,  $p = 0.25$ ; Fig 3).

308

### 309 Discussion

310 Four economically important entomophilous annual crops in Europe demonstrated highly  
311 different degrees of insect pollination dependence. When open pollinated, mean yield  
312 increases ranged from 18 to 71% depending on the crop. Three of these crops are listed as  
313 having a “modest” positive impact by animal pollination in the comprehensive review by  
314 Klein et al. (2007). However, despite being in the same category, oilseed rape and  
315 strawberry increased around 20 %, while field bean reached a 40 % increase in yield from  
316 insect pollination. The fourth crop, buckwheat is listed as having a large positive impact by  
317 animal pollination, in line of our reported 71 % increase. The Klein et al. (2007) review is  
318 currently the best available, most up to date source of animal pollination dependence on  
319 crops, but our data highlight a disparity of results among crops listed under the same



320 category. Our quantitative data on animal pollination dependence provides a first step to  
321 depart from the uncertainty embedded in a categorical approach. For example, animal  
322 pollination dependence can change by variety and region. Recent reports show variability in  
323 pollinator dependence between 0 to 30% among varieties of oilseed rape (Stanley et al.  
324 2013, Garratt et al. 2013). While we were able to standardize variety for most studied crops,  
325 strawberry fields were planted with four different varieties and the presented data should  
326 be seen as an average across those varieties (but see Klatt et al. 2013).

327 As expected, we found that fruit set per plant was positively correlated with yield. However,  
328 this correlation was rather weak ( $r^2 \sim 0.60$ ) for both strawberry and buckwheat. This  
329 indicates that for these crops, the total fruit weight was quite variable among plants with  
330 similar fruit or seed numbers. Indeed, for strawberry, the size of the receptacle is directly  
331 related to the number of fertilized achenes while for buckwheat, it is the proportion of filled  
332 seeds that can vary considerably and is a major component of yield besides fruit set. While  
333 previous research has focused mainly on exploring the effects of pollinators on fruit or seed  
334 set (e.g. Garibaldi et al. 2011, 2013), which is a more direct measure of plant reproduction,  
335 yield has the potential to better reflect economic value (Bommarco et al. 2012, Klatt et al.  
336 2013), and hence, farmers' interest. For example, while less than 20% in mean yield increase  
337 may seem as a modest advantage from the plant perspective, for the farmers it can  
338 translate into a substantial difference in revenue.

339

340 Similarly, we report that the yield quality component is enhanced to different extents by  
341 open pollination in three out of four crops. For buckwheat, strawberry, and oilseed rape,  
342 quality is directly linked to the pollinating activity of insects. We find this despite the fact  
343 that the measure of quality and underlying mechanisms is specific for each crop, and largely

344 unrelated among crops. Empty seeds in buckwheat accumulate little or no starch (Björkman  
345 1995). The shape of strawberries is also directly related to a complete pollination of all  
346 ovules, resulting in a homogeneously pollinated fruit (Zebrowska 1998). For oilseed rape,  
347 the plant allocate more oil resources to well pollinated seeds. In contrast, for field beans,  
348 the nitrogen content in the seeds was not affected by insect pollination. Other factors such  
349 as soil fertility and availability of the appropriate N-fixing bacteria (*Rhizobium* spp.) may play  
350 a more important role for field beans (Köpke and Nemecek 2010). Is interesting to note that  
351 we do not detect any trade-off between yield and nitrogen content of the seeds, as plants  
352 with more seeds do not present lower nitrogen content. Hence, the overall protein yield (i.e.  
353 nitrogen content at the plant level) was increased with open pollination. On a general note,  
354 it is interesting to observe that many different aspects of a plant's investments in its seed or  
355 fruit are affected by pollination.

356  
357 The treatment with netted flowers gives us estimates for the extreme cases where  
358 pollinators are completely absent, and we show that the current levels of pollination do not  
359 suffice to maximize yield in the open pollinated treatment in all landscapes. As previously  
360 reported, we confirm that agricultural intensification has a drastic effect on bee species  
361 richness (Ricketts et al. 2008, Garibaldi et al. 2011). However, total visitation does not always  
362 follow the same pattern as richness. This is the case for buckwheat and field bean, where  
363 fields presenting higher total visits were located in simple landscapes. For buckwheat, most  
364 of the visits in complex landscapes were due to increased honeybee densities managed for  
365 pollination. In field beans we found that bumblebees respond positively to agricultural  
366 simplification, noting, however, that even the more simple field beans landscapes contain a  
367 fair amount of semi-natural habitats. Overall, we find a general positive relationship

368 between total visitation rates and yield, but not with species richness. If the remaining  
369 species that thrive in intensively cultivated agricultural areas, including the managed  
370 honeybee, are effective pollinators, yield losses can be partly decoupled from losses of  
371 species (Bartomeus and Winfree 2013).

372

373 A recent global meta-analysis highlights the role of wild species in crop systems (Garibaldi et  
374 al. 2013). The flower visitors of three out of four crops were clearly dominated by  
375 honeybees (Fig. 1) and hence, are likely to be key pollinators for those crops. Garibaldi et al.  
376 (2013) show that an increase in wild insect visitation enhanced fruit set by twice as much as  
377 an equivalent increase in honeybee visitation. While this is generally the case in our target  
378 crops (three of which were included as part of Garibaldi's synthesis), the numerical  
379 advantage of honeybees in European agricultural landscapes needs to be acknowledged  
380 when calculating their total contribution to pollinated plants (e.g., as done in Winfree et al.  
381 2007 and Rader et al. 2009). However, increasing or maintaining high pollinator diversity can  
382 enhance yield quantity and stability by improving the pollination efficiency of honeybees  
383 (Greenleaf & Kremen 2006) and reduce the risk of pollination failure due to climate change  
384 (Rader et al. 2013, Bartomeus et al. 2013b), or environmental disturbances such as extreme  
385 weather events (Brittain et al. 2012).

386

387 Overall, we also found a weak negative effect of land use intensity on yield (Garibaldi et al.  
388 2011, but see Ricketts et al. 2008), but this was not directly mediated by increased  
389 pollinator visitation by itself, because the correlation between pollinator total visits and the  
390 proportion of agricultural land in the landscape was weak. The yield of experimental plots  
391 with net bagged flowers also increased in sites with more pollinators (Fig 4A). This suggests

392 that other environmental or biotic factors correlated with insect visitation may have been  
393 operating simultaneously. The release of airborne pollen by foraging bees could be such a  
394 factor (Pierre et al. 2009) (Fig 4B).

395  
396 In order to make efficient management decisions and increase our power to predict the  
397 actual benefit from pollinators in a certain farming situation, we need to estimate the  
398 combined contribution of multiple ecosystem services and agricultural inputs (Boreux et al.  
399 2013), as they may be influenced differently by landscape characteristics or have non-  
400 additive interactions among them (e.g., Lundin et al. 2013, Martin et al. 2013).

401 Information on the benefit delivered by pollinators to yield quantity and quality in relation  
402 to landscape context provides an important baseline for this work.

403  
404

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408 Waldemar C., and P. Williams for bee identifications to species.

409

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650 Table 1. Characteristics of the four study systems.

	Variety	Distance between sites (range in km)	Field sizes (range in ha)	Mean richness of pollinators
Oil seed rape	Stratos	3 - 7	1.0 – 40.4	11.3
Field bean	Clipper	3 - 18	5.0 – 47.0	3.1
Strawberry	Honeye, Korona, Darselect, Symphonie	3 - 26	0.3 – 1.3	12.9
Buckwheat	Kora	4 - 7	0.3 – 4.0	11.4

651

652 Table 2. Effects of land use complexity on total visitation and honeybee visitation (field  
 653 beans excluded from the honeybee model). Visitation is scaled within each crop. Both  
 654 models include block nested in site as random factors. Agriculture is the proportion of  
 655 arable land in the surrounding landscape of each field.

Total visitation	F-value	D.f.	P-value
Crop	3.13	3	<b>0.04</b>
Agriculture 1km	0.05	1	0.81
Agriculture*crop	3.08	3	<b>0.04</b>
Residuals		32	
<hr/>			
Honeybee visitation			
Crop	4.35	2	<b>0.02</b>
Agriculture 1km	0.10	1	0.75
Agriculture*crop	3.87	2	<b>0.03</b>
Residuals		32	

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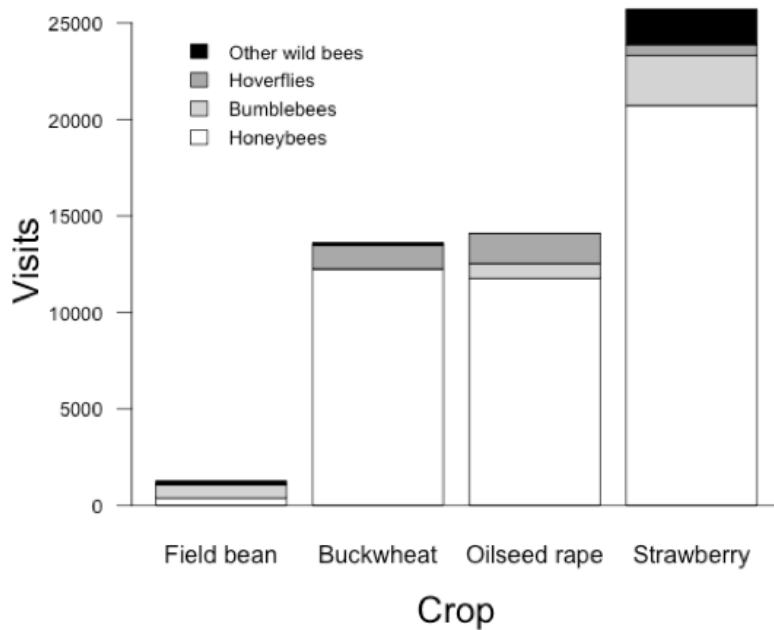


658 Table 3. Effects of open pollination vs pollinator exclusion treatments, visitation and  
 659 landscape context on yield in four entomophilous crops grown over 10 fields in Europe  
 660 (buckwheat, field bean, spring oilseed rape and strawberry). Yield and visitation are scaled  
 661 within each crop. Block, nested in site, nested in crop are included as a random factor.  
 662 Agriculture is the proportion of arable land in the surrounding landscape of each field.

	F-value	Df	P-value
Pollination treatment	67.05	128	< <b>0.001</b>
Pollinator richness	0.51	28	0.482
Total number of visits	7.25	28	<b>0.012</b>
Treatment*Pollinator richness	0.34	128	0.557
Treatment*Total number of visits	0.23	128	0.634
	F-value	Df	P-value
Pollination treatment	10.05	128	<b>0.001</b>
Agriculture 1 km radius	0.18	29	0.671
Treatment*Agriculture	9.73	128	<b>0.002</b>

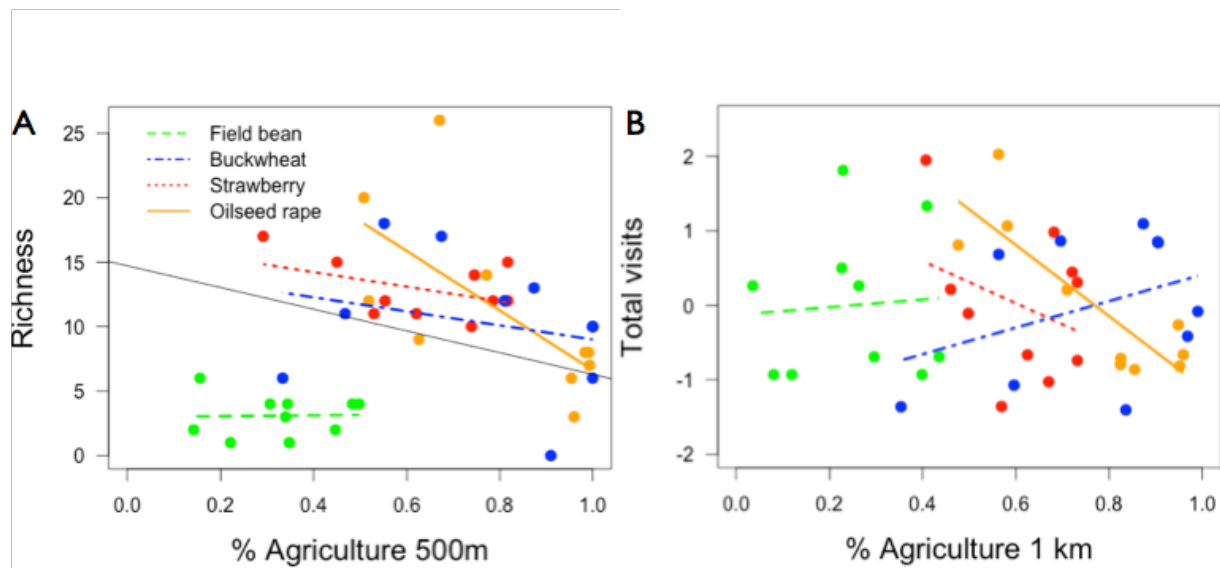
663 **Figures:**

664 Fig 1: Total number of visits recorded per pollinator guild in each crop. All crops received the  
665 same sampling effort (i.e., four 30 minutes visits to 150 m transects). Note the strong  
666 dominance of honeybees in most crops.



667

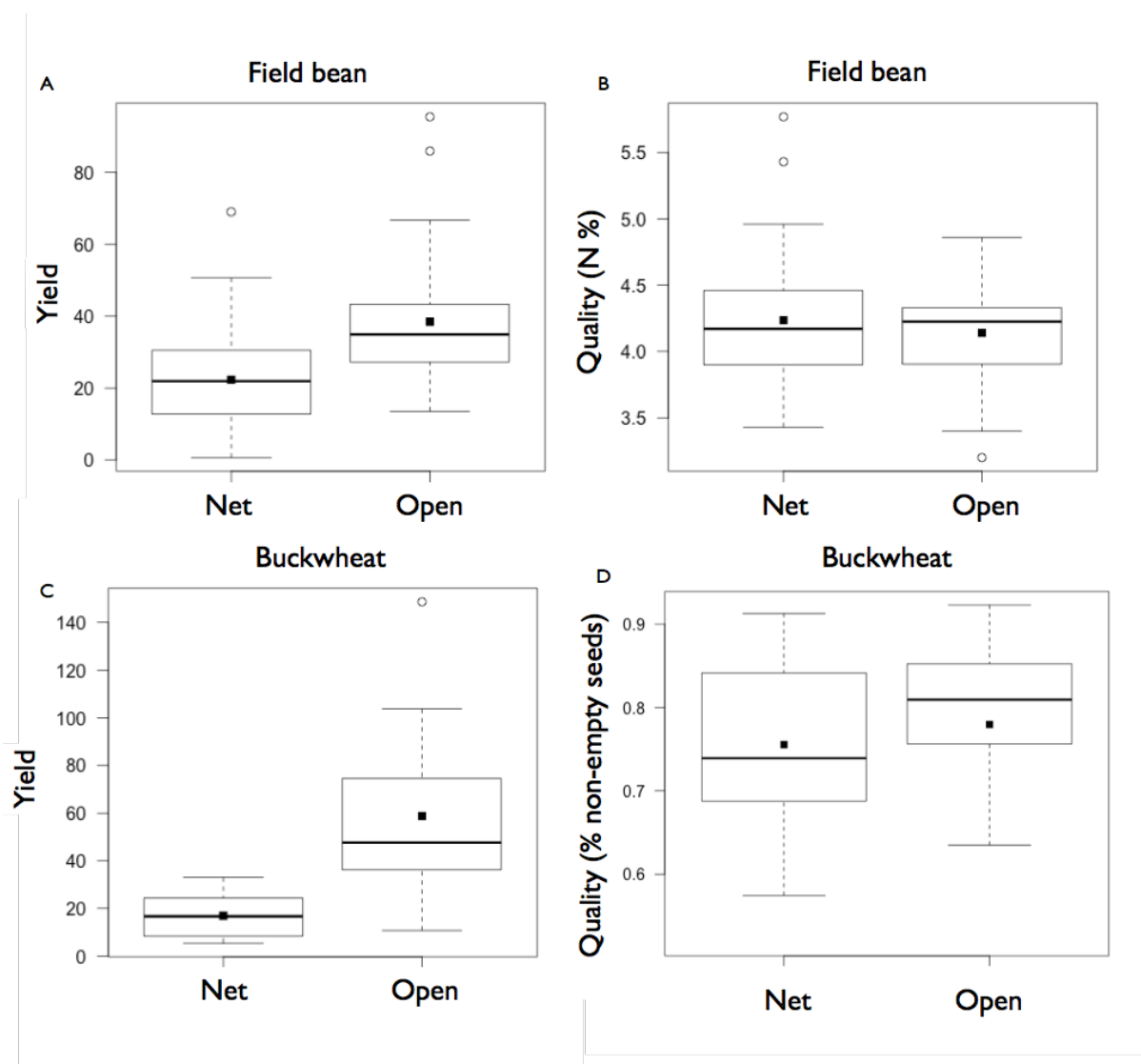
668 Fig 2: Relationship of A) Pollinator richness per field and B) Total number of visits per field  
669 with landscape complexity at the appropriate radii. Each crop individual slope is plotted in a  
670 different color and the overall response, when appropriate, in black. Total visits are scaled  
671 within each crop.



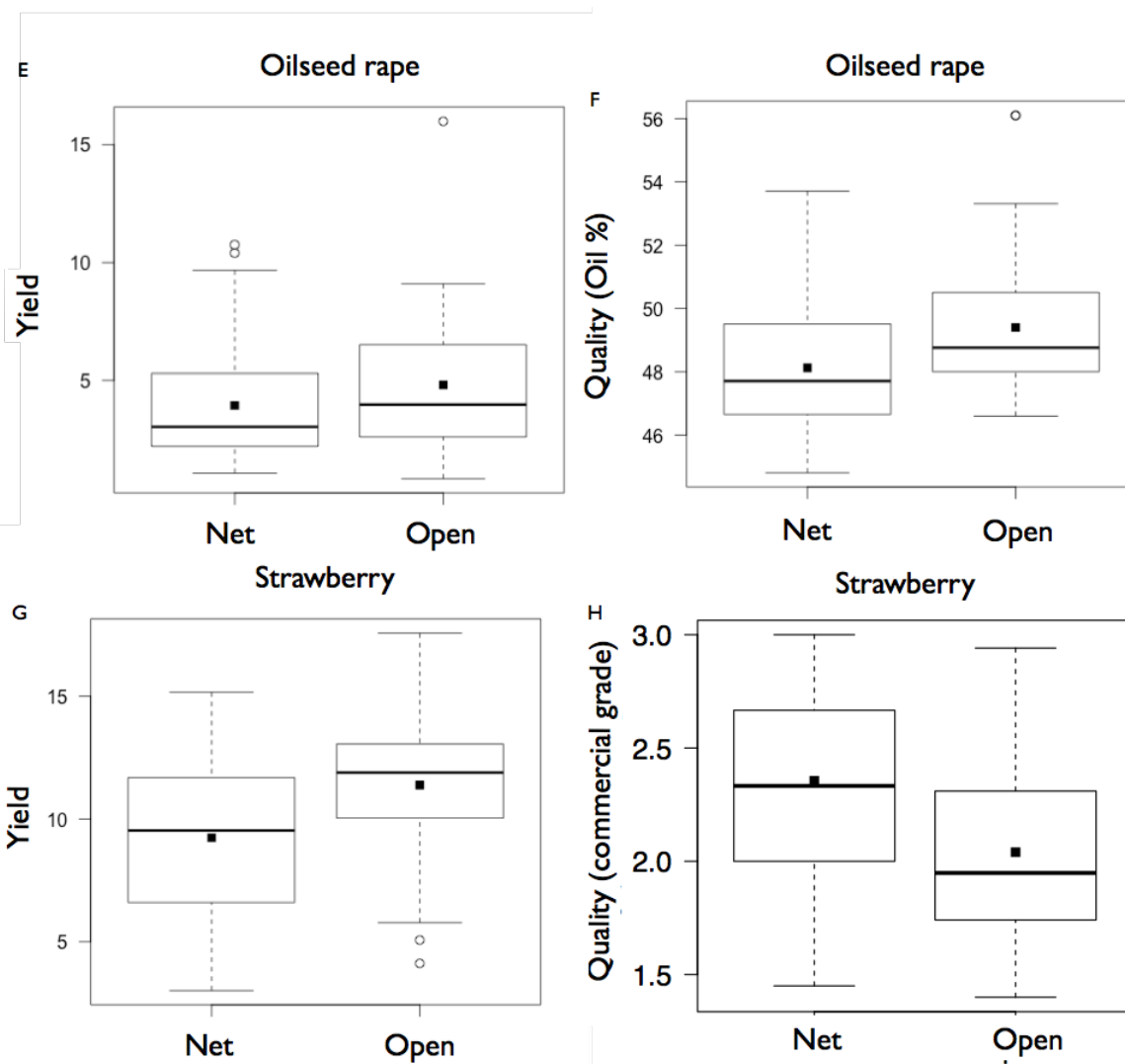
672

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674 Fig 3: Overall yield per plant (A, C, E, G) and quality (B, D, F, H) with pollinator exclusion  
 675 (Net) and open pollination (Open) for each crop. Black dots are the mean values reported in  
 676 the text, and the boxplots reflects the distribution of the data. Yield is measured in seed  
 677 weight per plant (g) for all crops except strawberry, which was measured as fruit weight per  
 678 plant (g). Commercial Grades of 1 and 2 are marketable, while grade 3 is considered non  
 679 marketable.

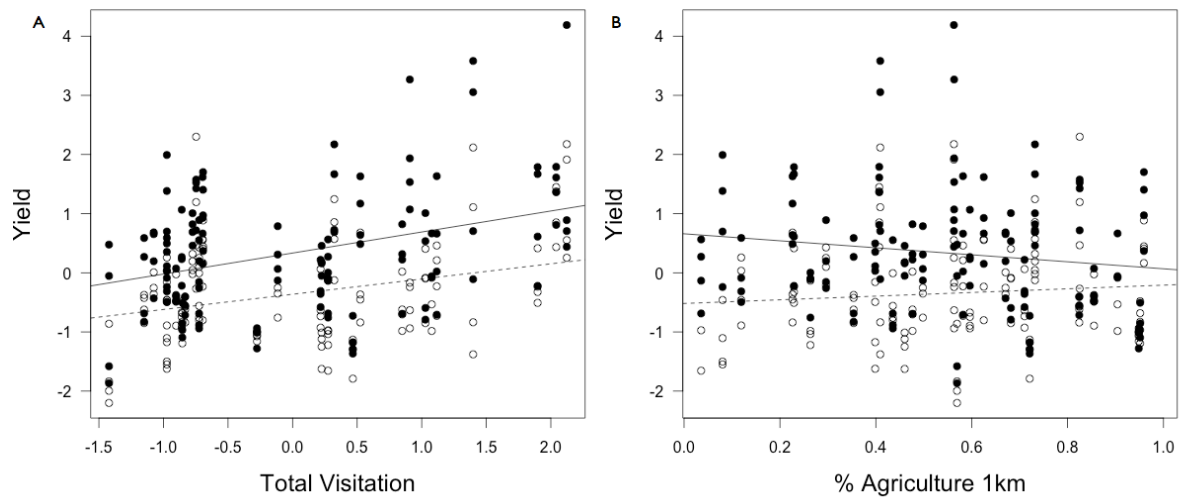


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682 Fig 4: Interaction plots showing the relationships of A) Yield per plant and total visitation  
683 and B) Yield and landscape complexity for pollinator exclusion (open circles, dotted line) and  
684 open pollination (black circles, solid line). Total visitation and yield are scaled to a mean of  
685 zero within each crop.



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