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1 **Title**

2 **Preserving habitat quality at local and landscape scales increases wild bee diversity in**
3 **intensive farming systems**

4

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27

28 **Abstract:**

29 Biological diversity is influenced by many environmental factors, which can act either at a
30 local scale (e.g. quality and quantity of feeding and nesting resources, habitat type) or at a
31 landscape scale (e.g. habitat fragmentation, composition and configuration of landscape
32 features). To effectively manage or promote biodiversity in heterogeneous environments such
33 as intensive agrosystems, a thorough knowledge of the spatial and temporal scale of
34 ecological factor effects is required. This study investigates the effects of ecological correlates
35 on local wild bee diversity in semi-natural farmland habitats, and predicts changes in species
36 richness according to local-scale and landscape-scale correlates to further guide bee
37 conservation practices. Local floral richness, the proportion of semi-natural habitats in the
38 landscape (1000m radius) and the type of semi-natural habitats influenced bee richness at a
39 field scale. However, the magnitude of the effect varied seasonally and according to local bee
40 abundance. Model predictions showed that increasing floral richness on farms had a greater
41 effect on bee richness than increasing the proportion of semi-natural habitats. While
42 increasing the number of semi-natural habitats would be a more effective strategy for
43 promoting bee diversity at the landscape scale, it may not be feasible in intensive farming
44 systems.

45

46 **Key-words**

47 Apoidea, Semi-natural habitat, landscape composition, floral resources, Richness

48

49

50

51 **1. Introduction**

52

53 Diversity and composition of animal communities depend on biotic and abiotic environmental
54 factors, which can interact at different temporal and spatial scales (Holyoak et al., 2005;
55 Moritz et al., 2013). In particular, ecological correlates of diversity for a given biological
56 group may be perceived at the landscape scale (e.g. habitat type, landscape configuration and
57 composition) or the local scale (e.g. predation, competition, feeding and nesting resources). In
58 human-dominated systems such as farmlands, habitat management or agricultural practices
59 may severely affect animal and plant communities through the modification of landscape and
60 local characteristics (Bretagnolle and Gaba, 2015; Gaba et al., 2013). For example, many
61 invertebrates have multiple habitat requirements, such as bees and butterflies that use
62 complementary habitats for nesting and feeding (Holzschuh et al., 2006; Klein et al., 2003;
63 Quin et al., 2004). Highly biodiverse agroecosystems are usually associated with
64 heterogeneous landscapes that have a large diversity of habitats arranged in complex spatial
65 configurations (Fahrig et al., 2011; Hass et al., 2018; Senapathi et al., 2016). Yet, the ongoing
66 intensification of agriculture has led to a decrease in landscape heterogeneity and quality
67 (Benton et al., 2003) due to the reduction of the quantity and diversity of semi-natural habitat
68 remnants, crop homogenisation and the increase in field sizes (Robinson and Sutherland,
69 2002). A decline in habitat quality can also be observed at the local scale with significant
70 modification and loss of the diversity of plants due to the use of external inputs (e.g.
71 herbicides, fertilizers) (Baessler and Klotz, 2006; Rollin et al., 2016; Storkey et al., 2009;
72 Sutcliffe and Kay, 2000). As a consequence, animal and plant diversity have strongly declined
73 in agro-ecosystems (Bretagnolle and Gaba, 2015; Chamberlain et al., 2000; Donald et al.,
74 2001; Sotherton, 1998; Wilson et al., 1999).

75 To reverse these negative trends, alternative management approaches, such as agro-
76 environmental schemes, have been developed during the last few decades for promoting
77 biodiversity, especially bee diversity, and the ecosystem services they deliver (Decourtye et
78 al, 2010; Grass et al, 2016; Senapathi et al., 2016; Sprague et al, 2016). However, the
79 efficiency of these practices is still unclear. Kleijn et al., (2006), for example, have shown that
80 only half of the agro-environmental schemes promoted at the European level had a significant
81 positive effect on biodiversity. The effectiveness can varies according to the type of measure,
82 the focus taxonomic group or the environmental context and spatial scale considered (Batáry
83 et al., 2011; Grass et al., 2015; Henry et al., 2012; Kleijn et al., 2011; Senapathi et al., 2016;
84 Tschardt et al., 2005). We therefore need more studies that evaluate the efficiency and
85 trade-offs between practices developed at the farm and landscape scales and aimed to enhance
86 animal-delivered services (Garibaldi et al., 2017).

87 In intensive agricultural systems, semi-natural vegetation surrounding fields is the
88 habitat most frequently used by bees and promotes a higher local bee diversity than any other
89 source of flowers such as flowering crops (Rollin et al., 2015, 2013). Therefore, conservation
90 of semi-natural habitats at a landscape scale is one of the most promising strategies for
91 preserving wild bee populations (Kleijn and Sutherland, 2003; Knop et al., 2006). However,
92 depending on the context, there might be a minimum threshold of flower cover needed for an
93 herbaceous habitat-oriented management strategy to be more profitable to wild bees than a
94 local, floral-specific resource-oriented management strategy (Rollin et al., 2013). There may
95 be an optimum threshold of wild flower cover, depending on the varying wild bee families,
96 that could result in the best compromise between these two management strategies. Moreover,
97 Rollin et al., (2015) have shown an intermittent turnover of bee species according to the focal
98 spatial scales, with a maximal turnover within 50 km² areas (7 km in diameter) and thus
99 suggest to concentrate conservation efforts within such medium-scale areas, e.g. by

100 maximizing the density of allocated semi-natural habitats. In this context, to develop more
101 effective management practices, it is necessary to consider the effect of landscape
102 composition and structure on the occurrence and spatial organisation of the species or
103 ecologically related species. We need to better understand how ecological correlates shape the
104 diversity of targeted biological groups, and at which optimal spatial scale, in order to conceive
105 efficient conservation and management practices for maintaining or restoring diversity at
106 local and landscape scales.

107 Here we focused on wild bees as an example of a species rich community in an
108 intensive agricultural system in western France, in the buffer area recommended by Rollin et
109 al. (2015). In order to guide conservation efforts, we aimed to understand the relative
110 importance of the floral context at the local scale and the quantity of surrounding semi-natural
111 habitats at the landscape scale that promote wild bee diversity in farmlands.

112

113 **2. Material and Method**

114

115 **2.1. Sampling design**

116

117 Field data is from Rollin et al. (2015, 2013), with a specific focus on those sampling sites
118 surrounded by *semi-natural herbaceous* habitats. This survey was carried out in the springs
119 and summers of 2010, 2011 and 2012 in the LTSER *Zone Atelier Plaine & Val de Sèvre*, a
120 450 km² intensive agricultural territory in western France, that comprises over 16,000 fields
121 (Fig. 1; Bretagnolle et al., 2018). This study area consists mostly of intensive arable land,
122 with annual crops accounted on average for 80% of total land cover (40% for cereals, 9% for
123 oilseed rape, 12% for sunflower and 9% for maize). Temporary and permanent grasslands, as
124 well as small but numerous remnant patches of forest, covered only between 3% and 7% of

125 the total land but permit to provide highly heterogeneous landscapes in some areas. A
126 spatially extensive sampling strategy was therefore favoured to best cover the variety of
127 ecological contexts throughout the study area. Sampling sites were located in 30 grid cells
128 (ten cells sampled per year) randomly drawn without replacement from a 3.3 x 3.3 km
129 spacing grid covering the whole study area (see Rollin et al., 2015, 2013) (Fig. 1). Local bee
130 diversity was sampled using capture surveys of flower-visiting bees in a total of 702 sites in
131 semi-natural herbaceous habitats (permanent grasslands, external field margins and
132 spontaneous weed plants in crops or stubble fields) over the three years, including three
133 relevant periods in the bee activity season: (i) the rapeseed (*Brassica napus*) flowering period
134 in April-May, (ii) the food restriction period, with no mass-flowering crop available, in late
135 spring or early summer and (iii) the sunflower (*Helianthus annuus*) flowering period in July-
136 August. Surveys, for each sampling period during a given year, were conducted for 12-15
137 consecutive days. Sampling sites were surveyed once by capturing flower-visiting bees with a
138 net along walking transects of 50 m long and 2 m wide, in only one direction (i.e. without
139 back and forth), during 15 min sampling sessions. Sites were sampled between 10:00 and
140 19:00, and only during good weather (Hoehn et al., 2010; Westphal et al., 2008). We consider
141 here the local (α) wild bee diversity, which was measured as the bee species richness, i.e. the
142 number of distinct wild bee species, observed at a given sampling site (walking transects). We
143 then applied generalized linear mixed models (GLMMs) to explore how α diversity is affected
144 by a suite of *a priori* relevant ecological correlates, as well as by some potentially
145 confounding variables (mainly due to sampling design).

146

147 **2.2. Local and landscape scale ecological determinants of bee richness**

148

149 The main local-scale variable liable to affect bee diversity was the floral species richness at
150 the sampling site. The main landscape-scale variable considered in this study was the
151 percentage of semi-natural habitats within a given radius around sampling sites. We chose a
152 series of 10 radii, ranging from 200 to 3000 m so as to cover the distance range with the
153 steepest spatial accumulation of bee species (Rollin et al., Unpublished. Data, see
154 Supplementary material). This range also roughly covers the range of wild bee maximum
155 foraging distances reported in the literature (reviewed by Zurbuchen et al., 2010b).
156 Herbaceous and woody semi-natural habitat areas were computed for each site and radius,
157 based on land use maps made available on a Geographic Information System (ArcView®
158 V.9.0.) and up-dated twice a year (see, e.g. Marrec et al., 2014; Rollin et al., 2013). Fallows,
159 permanent and temporary grassland surfaces were recorded throughout the study area and
160 were summed to estimate semi-natural herbaceous habitat areas. Field and road margins were
161 assigned to thin 2 m wide strips on both sides of the road and trail networks, and subsequently
162 handled as an approximation of interstitial semi-natural herbaceous habitats. Likewise, the
163 assignment of linear landscape elements (hedgerows and forest edges) to the confines of
164 ligneous semi-natural habitats followed the procedure in Henry et al. (2012). Regardless of
165 the chosen radius, we combined herbaceous and ligneous semi-natural areas (e.g. hedgerows)
166 under the general denomination of *semi-natural habitat*.

167 In addition to floral species richness we distinguished between two types of sampling
168 sites, namely grassland sampling sites (permanent and temporal grasslands, fallows) vs.
169 marginal sampling sites (external field margins, road margins) at the local scale. We were also
170 concerned that bee diversity at a given sampling site would be partly influenced by two
171 important sampling features, the total number of captured bees and/or the density of floral
172 units (i.e. all open flowers and inflorescences that could be visited by bees; Potts et al., 2003)
173 found along the sampling transect. To assess floral density, all the distinct flower species

174 found along sampling transects were recorded and an abundance score of 1, 10 or 100 was
175 assigned to each of them according to a visually estimated minimal number of floral units.
176 Species scores were then summed within each site (walking transect).

177 Bee foraging activity is also strongly dependent on certain temporal drivers that need
178 be controlled for, particularly temperature variations on a daily scale (Corbet et al., 1993;
179 Kelber et al., 2006; Kwon and Saeed, 2003) and phenological variations across seasons
180 (Michener, 2007; Tylianakis et al., 2005; Westrich, 1989). Both temperature at the time of
181 capture and period of the season were introduced into the analysis as additional explanatory
182 variables. Temperature was coded as a quadratic function because its effect on bee foraging
183 activity has been showed to be non-linear (Rollin et al., 2013). The *Period* of the season refers
184 to the three study periods within a year (i.e. rapeseed in spring, sunflower in early summer,
185 and the food restriction period in-between), and was further tested in statistical interaction
186 with the other ecological correlates assuming that the importance of ecological correlates
187 might not be stationary over time.

188 Finally, special attention was paid to account for inter-annual variation and spatial
189 autocorrelation among neighbouring sampling sites, which are typical sources of random
190 statistical noise, and were taken into account by specifying appropriate random grouping
191 structures within the frame of generalized mixed models (Rollin et al., 2013). Spatially
192 neighbouring sites were grouped by grid cell identity, which were then nested within years
193 (see also below).

194

195 **2.3. Statistical analysis**

196

197 To evaluate the influence of the local and landscape context on bee diversity we used
198 generalized linear mixed model (GLMM) with a zero-inflated negative binomial distribution

199 of errors. This type of model was chosen because no bees were caught in 31.7% of the
200 sampled sites (223 out of a total of 702 sites). Bee richness was used as the response variable.
201 Fixed effects included local- and landscape-scale variables, climatic conditions and season.
202 Local variables were represented by (i) *habitat type* (grasslands vs field margins), (ii) *floral*
203 *richness*, (iii) *floral density* and (iv) interactions between *habitat type* and *floral richness*.
204 Indeed, Öckinger and Smith (2007) have shown that the quality of floral resources can change
205 according to the type of semi-natural habitat (grasslands vs. field margins) and significantly
206 affects bee species richness and density of other insect pollinators. Landscape variables
207 included the *proportion of semi-natural habitats* that we computed at different landscape
208 scales (see above).

209 Possible confounding factors or other sources of significant statistical noise were
210 investigated in our dataset. The possible biases were (i) distribution gradients at the scale of
211 the study area (i.e. non-stationary), (ii) inter-annual variation, (iii) seasonal variation, (iv)
212 temperature-dependent variation in bee foraging activity at the daily time scale and (v) the
213 local abundance of bees. Possible bias due to a large-scale distribution gradient was
214 systematically accounted for by including the grid cell identity as a random factor within the
215 frame of a mixed model structure, i.e. generalized linear mixed models (GLMMs) (Rollin et
216 al., 2013). Likewise, inter- annual variations were considered by including the year as a
217 higher-level random variable, within which grid cells were nested (Rollin et al., 2013). The
218 observed number of species recorded in a sample (or a set of samples) is very sensitive to the
219 number of individuals (Gotelli and Colwell, 2001). For this reason, we added as co-variable
220 the *number of bees* at each sampling site. Seasonal variations were accounted for by including
221 the period as a factor. Moreover, bee foraging activity is affected by temperature but its effect
222 on bee occurrence frequency or bee abundance might not be linear (Corbet et al., 1993;
223 Kelber et al., 2006; Kwon and Saeed, 2003). Thus, temperature dependent variations were

224 considered by introducing standardized and squared temperature data ($^{\circ}\text{C}$) as a fixed variable
225 into the model (Saveliev et al., 2009).

226 Based on AIC values, we determined that 1000 m was the scale at which the
227 proportion of semi-natural habitat returned the best model fit. Accordingly, results and
228 predictions in this study were presented at this landscape scale. All analyses were computed
229 using the R software, version 3.4.2 (R Development Core Team, 2017).

230

231 **3. Result**

232

233 **3.1. Effect of ecological correlates on bee diversity at local and landscape-scales**

234

235 Ecological correlates that explained α diversity were floral richness, proportion of semi-
236 natural habitats in the landscape and type of semi-natural habitats, as well as the period (three
237 levels) and total number of bees per sampling site (Table 1, Fig. 2). Floral richness at the local
238 scale ($Z = 3.61$; $p < 0.01$; Fig. 2A) as well as the proportion of semi-natural habitats at a
239 radius of 1000 m ($Z = 1.892$; $p = 0.05$; Fig. 2B) were positively related to bee richness. Bee
240 richness was higher in grasslands than in field margins ($Z = -2.689$; $p < 0.01$; Fig. 2C). In
241 addition, bee richness was significantly higher during the sunflower flowering period (Fig.
242 2D) than in both the rapeseed ($Z = -4.643$; $p < 0.01$) and the food restriction periods ($Z = -$
243 5.342 ; $p < 0.01$). Finally, bee richness was positively correlated with total bee abundance ($Z =$
244 18.186 ; $p < 0.01$).

245

246 **3.2. Effect of equilibrium between local and regional ecological correlates on bee** 247 **diversity**

248

249 Bee richness was positively related to richness of flowering plants. Moreover, the magnitude
250 of this effect (represented by the difference between upper and lower limits of the shared area
251 in Fig. 3) was overall higher than that predicted for a change in availability of semi-natural
252 habitats within a 1000 m radius, at least for the upper range of semi-natural habitat
253 proportions (20-30%).

254 Furthermore, the magnitude of the effect of the floral species richness was higher
255 during the sunflower flowering period than during the two other periods. Predictions of bee
256 diversity for periods 1 and 3 (respectively during the flowerings of rapeseed and sunflower)
257 were more similar to each other than to those of period 2 (food restriction period), despite
258 overall similarity response pattern between all three periods, which included increasing bee
259 richness with higher floral richness, higher bee abundance and higher proportion of semi-
260 natural habitats. During the sunflower flowering period (July-August), local bee diversity was
261 higher than during other periods. The lowest measure of bee richness would be expected
262 during the food restriction period (June).

263

264 **4. Discussion**

265

266 *Effect of ecological correlates at the local scale*

267 Previous studies have suggested that habitat type and quality are important factors in
268 explaining the diversity of wild bees as they are usually related to the floral richness of
269 resources for pollinators (Biesmeijer et al., 2006; Carvell et al., 2006; Öckinger and Smith,
270 2007). Accordingly, we found that bee diversity increased with increasing richness of floral
271 resources. Moreover, Williams et al. (2012) have shown that an increase in the quantity of
272 flowers in the vicinity of bumble bee colonies had a positive effect on their growth. Increased
273 floral richness promotes higher bee diversity most likely due to the pollen and nectar

274 specialisations of bees. Behavioural and structural adaptations of bee species (e.g. density and
275 localisation of the mass of stiff hairs for collecting pollen grains) can determine the type of
276 pollen collected (Michener, 2007; Thorp, 1979). Likewise, nectar selection is strongly
277 determined by morphological constraints in bee species (e.g. tongue length, body size) and by
278 quality and quantity of nectar rewards delivered by floral resources (Potts et al., 2003; Roubik
279 and Buchmann, 1984).

280 Secondly, we found that grasslands supported higher bee diversity than field margins.
281 Grasslands usually have larger areas than field margins; therefore, they are expected to
282 provide more diverse and greater amounts of floral resources. This is supported by our results
283 that show that floral richness and floral density is greater in grasslands during two of the three
284 studied periods (Rollin et al., Unpublished. Data). In addition, in our study system vegetation
285 of field margins is frequently scythed/mown for security (along the road) or for reducing the
286 risk of propagating pathogens or crop predators (pers. obs.), which may explain the lower bee
287 diversity detected when compared to grasslands. Moreover, field margins can receive various
288 pesticides as drift that come from the neighbouring crops (Botías et al., 2015). Our results are
289 consistent with those found by previous studies that show increased richness of insect
290 pollinators in grasslands with high local floral abundance with relation to field margins (e.g.
291 Öckinger and Smith, 2007).

292

293 *Importance of the quantity of semi-natural areas and the interaction with local bee* 294 *population size*

295 As expected we found a strong effect of the proportion of semi-natural vegetation on
296 wild bee diversity (e.g., Goulson et al., 2008; Le Féon et al., 2010; Senapathi et al., 2016).
297 Semi-natural habitats are the most favourable habitat types for wild bees, providing feeding
298 and nesting resources and therefore acting as population refuges (Goulson et al., 2010;

299 Öckinger and Smith, 2007). They contain the most abundant and diversified wild bee
300 communities (Rollin et al., 2015, 2013) and increasing their proportion in agricultural
301 landscapes may promote bee species diversity (Duelli and Obrist, 2003; Le Féon et al., 2010;
302 Senapathi et al., 2016). Similarly, landscape-scale ecological correlates also affect bee
303 diversity: the loss of natural and semi-natural habitats or the transformation of permanent
304 grasslands into annual crops both have negative effects on wild bee species (Breeze et al.,
305 2012; Goulson et al., 2008; Le Féon et al., 2010; Senapathi et al., 2016).

306 However, the magnitude of the effect of semi-natural habitat proportion on bee
307 richness was higher at high bee abundance than at low bee abundance. This could be
308 explained by the dual function of semi-natural habitats, as a source of both feeding resources
309 and nesting sites (Goulson et al., 2010; Öckinger and Smith, 2007)

310

311 ***Seasonal effect on the magnitude of the ecological correlates***

312 Although predictions of bee diversity trends were similar between periods (bee diversity
313 increasing with floral richness, proportion of semi-natural surrounding sampling sites and bee
314 abundance), we detected a highly significant seasonal effect on bee diversity. Bee diversity
315 during the rapeseed and sunflower flowering periods was higher than during the food
316 restriction period (Fig. 3), while the regional bee diversity γ was higher overall during the
317 food restriction period (Rollin et al., 2015). Competition with the honey bee *Apis mellifera*
318 could explain these results. During mass flowering crop periods, honey bees foraged
319 preferentially in rapeseed and sunflower fields and were found much less frequently and in
320 lower abundance in wild floral resources of herbaceous semi-natural habitats (Rollin et al.,
321 2013). In the absence of mass-flowering crops, however, honey bees foraged more frequently
322 in semi-natural herbaceous resources, a shift in floral resource exploitation that may lead to
323 greater competition for floral resources between wild bees and the honey bee. Despite many

324 studies seeking evidence for competition between honey bees and wild bees and possibly, a
325 negative effect of the honey bee on wild bee communities, current evidence is scarce
326 (Goulson and Sparrow, 2008; Gross, 2001; Henry and Rodet, 2018; Hudewenz and Klein,
327 2013; Roubik, 1978; Shavit et al., 2009; Thomson, 2006, 2004). Yet Magrach et al. (2017)
328 recently showed that honey bee spillover from crops into semi-natural habitats leads to a
329 reassembly of plant–pollinator interactions through increased competition with other
330 pollinator species.

331 In addition, in our study area, it should be noted that the global diversity in semi-
332 natural herbaceous habitats (regional bee diversity; γ) during the food restriction period was
333 similar to that of the sunflower period and even significantly higher than that of the rapeseed
334 period, while local diversity (α) showed the opposite trend (Rollin et al., 2015). This suggests
335 that the among-community diversity changes or the spatial turnover (Crist et al., 2003) was
336 higher at an intermediate period than earlier or later in the season (Rollin et al., 2015). In
337 other words, at the second period, wild bee diversity might be spatially reorganised, with
338 lower local diversity and higher spatial turnover. Interestingly, this scenario would be
339 compatible with the hypothesis that honey bees exclude wild bees by local competition in
340 between the two mass-flowering periods, a period of reduced food availability (Requier et al.,
341 2015). An effect of local competitive exclusion is plausible (Henry and Rodet, 2018) given
342 that foraging honey bees may occur locally at very high abundances owing to their ability to
343 communicate the location of floral resources (Dyer, 2002).

344

345 *Spatial scale and potential species bias*

346 Our results and prediction focus on a 1000m buffer landscape scale, as this was the resolution
347 that better explained the distribution of our data (AIC model selection). This scale is
348 consistent with results found in similar studies (e.g. Connelly et al., 2015; Zurbuchen et al.,

349 2010b) and probably reflects foraging range of most bee species. Recent evidences suggest
350 that maximum foraging range of wild bee species, especially small-size bees, has been
351 underestimated in various previous studies (Zurbuchen et al., 2010b). For example, Castilla et
352 al (2017) found that all bee species sampled in this study (n=10), even very small-sized bees,
353 such as several Halictidae spp. or *Trigonisca buyssony* (Apidae) amongst others, exhibited
354 foraging movements that exceeded the 1000 m. However, evidences found in Europe suggest
355 that only a few bee species are able to exceed this distance (Greenleaf et al., 2007). The
356 majority of wild bee species do not move farther than 500m away from their nests due to the
357 associated energetic costs (Gathmann & Tscharntke, 2002 ; Zurbuchen et al., 2010a). Given
358 the spatial scale considered (1000 m buffer) in this study, our results might thus underestimate
359 species richness and might be biased towards large-sized species.

360

361 ***Implications for conservation and farmland management***

362 The results of our study suggest that promoting local diversity of floral resources may be
363 more efficient in increasing wild bee richness than conserving or restoring adjacent
364 natural/semi-natural habitats (Fig 2). Yet both strategies provided positive effects in
365 increasing bee diversity and are expected to be complementary. On one hand, semi-natural
366 habitats at the landscape scale are fundamental for providing nesting resources to wild bee
367 populations, which are usually scarce in farm fields and surrounding field margins. On the
368 other hand, increasing the proportion of semi-natural vegetation would indirectly promote
369 total floral richness found within these habitats, and accentuate their positive effect on bee
370 diversity. This positive effect could be mitigated by floral abundance in these habitats. In our
371 study, semi-natural patches frequently provided scarce floral resources as measured by floral
372 abundance (pers. observation; Rollin et al., 2013). In our model-prediction approach (Fig. 3),
373 the greatest landscape effect was predicted beyond a 20-25% threshold for herbaceous semi-

374 natural habitats (within a 1000 m radius). However, it might be unrealistic to increase the area
375 of semi-natural habitats in these proportions. In fact, this value far exceeds the land cover
376 farmers may actually sustain at the farm scale. Indeed, areas of ecological interest in arable
377 lands (trees, hedges, fallow land, grass strips, buffer strips at the edge of fields, woods and
378 forests) must be at least 3% of the Useful Agricultural Area (target of 7% of UAA by 2020)
379 (Heidsieck and Allier, 2013). Thus, promoting this type of habitat appears to be a very
380 promising measure for increasing bee diversity, but increasing semi-natural habitats to 25% of
381 the land cover or more would be difficult to implement and its feasibility could vary widely
382 depending on crop type and the initial landscape context. Moreover it is necessary to diversify
383 the types of semi-natural habitat, in order to promote a variety of floral resources and nesting
384 sites, the latter being indispensable in allowing permanent wild bee populations to settle in the
385 landscape (Carrié et al., 2018; Goulson et al., 2010; Senapathi et al., 2016). Therefore, in
386 highly intensive farmland landscapes, a mixed strategy involving improved semi-natural
387 elements as well as promoting floral resources in crops (through, e.g. herbicide reduction) is
388 likely the most promising scenario, whereas in less intensive agricultural contexts, protecting
389 or restoring the diversity of semi-natural herbaceous habitats would be favoured.

390

391

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399

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401 **References**

402 Baessler, C., Klotz, S., 2006. Effects of changes in agricultural land-use on landscape
403 structure and arable weed vegetation over the last 50 years. *Agriculture, Ecosystems &*
404 *Environment* 115, 43–50. <https://doi.org/10.1016/j.agee.2005.12.007>

405 Batáry, P., Báldi, A., Kleijn, D., Tschardt, T., 2011. Landscape-moderated biodiversity
406 effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. B* 278,
407 1894–1902. <https://doi.org/10.1098/rspb.2010.1923>

408 Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat
409 heterogeneity the key? *Trends in Ecology & Evolution* 18, 182–188.
410 [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)

411 Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T.,
412 Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E.,
413 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the
414 Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>

415 Botías, C., David, A., Horwood, J., Abdul-Sada, A., Nicholls, E., Hill, E., Goulson, D., 2015.
416 Neonicotinoid Residues in Wildflowers, a Potential Route of Chronic Exposure for
417 Bees. *Environmental Science & Technology* 49, 12731–12740.
418 <https://doi.org/10.1021/acs.est.5b03459>

419 Breeze, T.D., Roberts, S.P.M., Potts, S.G., 2012. The decline of England's bees : Policy
420 review and recommendations.

421 Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhauer,
422 I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018. Towards sustainable and
423 multifunctional agriculture in farmland landscapes: Lessons from the integrative

424 approach of a French LTSER platform. *Science of The Total Environment* 627, 822–
425 834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>

426 Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agronomy for Sustainable*
427 *Development*. 35, 891-909. <https://doi.org/10.1007/s13593-015-0302-5>

428 Carrié, R., Lopes, M., Ouin, A., Andrieu, E., 2018. Bee diversity in crop fields is influenced
429 by remotely-sensed nesting resources in surrounding permanent grasslands. *Ecological*
430 *Indicators* 90, 606–614.

431 Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F., Nowakowski, M., 2006. Assessing the
432 value of annual and perennial forage mixtures for bumblebees by direct observation
433 and pollen analysis. *Apidologie* 37, 326–340. <https://doi.org/10.1051/apido:2006002>

434 Castilla, A.R., Pope, N.S., O’Connell, M., Rodriguez, M.F., Treviño, L., Santos, A., Jha, S.,
435 2017. Adding landscape genetics and individual traits to the ecosystem function
436 paradigm reveals the importance of species functional breadth. *Proceedings of the*
437 *National Academy of Sciences* 114, 12761-12766. DOI: 10.1073/pnas.1619271114

438 Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubbs, M., 2000. Changes
439 in the abundance of farmland birds in relation to the timing of agricultural
440 intensification in England and Wales. *Journal of Applied Ecology* 37, 771–788.

441 Connelly, H., Poveda, K., Loeb, G., 2015. Landscape simplification decreases wild bee
442 pollination services to strawberry. *Agriculture, Ecosystems and Environment*
443 *Complete*, 51–56. <https://doi.org/10.1016/j.agee.2015.05.004>

444 Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., Smith, K., 1993.
445 Temperature and the pollinating activity of social bees. *Ecological Entomology* 18,
446 17–30. <https://doi.org/10.1111/j.1365-2311.1993.tb01075.x>

447 Crist, T.O., Veech, J.A., Jon C. Gering, Summerville, K.S., 2003. Partitioning species
448 diversity across landscapes and regions: A hierarchical analysis of α , β , and γ
449 diversity. *The American Naturalist* 162, 734–743.

450 Decourtye, A., Mader, E., Desneux, N., 2010. Landscape enhancement of floral resources for
451 honey bees in agro-ecosystems. *Apidologie*, 41, 264–277. doi:10.1051/apido/2010024

452 Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of
453 Europe's farmland bird populations. *Proc. R. Soc. Lond. B* 268, 25–29.
454 <https://doi.org/10.1098/rspb.2000.1325>

455 Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the
456 contribution of seminatural habitat islands. *Basic and Applied Ecology* 4, 129–138.
457 <https://doi.org/10.1078/1439-1791-00140>

458 Dyer, F.C., 2002. The biology of the dance language. *Annual Review of Entomology* 47,
459 917–949. <https://doi.org/10.1146/annurev.ento.47.091201.145306>

460 Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C.,
461 Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and
462 animal biodiversity in agricultural landscapes. *Ecology Letters* 14, 101–112.
463 <https://doi.org/10.1111/j.1461-0248.2010.01559.x>

464 Gaba, S., Fried, G., Kazakou, E., Chauvel, B., Navas, M.-L., 2013. Agroecological weed
465 control using a functional approach: a review of cropping systems diversity. *Agron.*
466 *Sustain. Dev.* 34, 103–119. <https://doi.org/10.1007/s13593-013-0166-5>

467 Garibaldi, L.A., Requier, F., Rollin, O., Andersson, G.K.S., 2017. Towards an integrated
468 species and habitat management of crop pollination. *Current Opinion in Insect Science*
469 21, 105–114.

470 Gathmann, A., Tschardtke, T., 2002. Foraging ranges of solitary bees. *Journal of Animal*
471 *Ecology* 71, 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>

472 Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the
473 measurement and comparison of species richness. *Ecology Letters* 4, 379–391.
474 <https://doi.org/10.1046/j.1461-0248.2001.00230.x>

475 Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L.,
476 Darvill, B., 2010. Effects of land use at a landscape scale on bumblebee nest density
477 and survival. *Journal of Applied Ecology* 47, 1207–1215.
478 <https://doi.org/10.1111/j.1365-2664.2010.01872.x>

479 Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. *Annual*
480 *Review of Entomology* 53, 191–208.
481 <https://doi.org/10.1146/annurev.ento.53.103106.093454>

482 Goulson, D., Sparrow, K.R., 2008. Evidence for competition between honeybees and
483 bumblebees; effects on bumblebee worker size. *Journal of insect conservation* 13,
484 177–181.

485 Grass, I., Albrecht, J., Jauker, F., Diekötter, T., Warzecha, D., Wolters, V., Farwig, N., 2016.
486 Much more than bees - Wildflower plantings support highly diverse flower-visitor
487 communities from complex to structurally simple agricultural landscapes. *Agriculture,*
488 *Ecosystems & Environment* 225, 45–53. <https://doi:10.1016/j.agee.2016.04.001>

489 Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and
490 their relationship to body size. *Oecologia* 153, 589–596. [https://doi:10.1007/s00442-](https://doi:10.1007/s00442-007-0752-9)
491 [007-0752-9](https://doi:10.1007/s00442-007-0752-9)

492 Gross, C.L., 2001. The effect of introduced honeybees on native bee visitation and fruit-set in
493 *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. *Biological conservation*
494 102, 89–95.

495 Hass L.A., Kormann U.G., Tschardtke t., Clough Y., Baillod A.B., Sirami C., Fahrig L.,
496 Martin J-L., Baudry J., Bertrand C., Bosch J., Brotons L., Burel F., Georges R., Giralt

497 D., Marcos-García M.A., Ricarte A., Siriwardena G., Batáry P., 2018. Landscape
498 configurational heterogeneity by small-scale agriculture, not crop diversity, maintains
499 pollinators and plant reproduction in western Europe. *Proceedings of the Royal*
500 *Society B: Biological Sciences*, 285, 20172242. <https://doi.org/10.1098/rspb.2017.2242>

501 Heidsieck, H., Allier, F., 2013. Propositions pour une prise en compte des insectes
502 pollinisateurs dans les politiques agricoles nationales et européennes.

503 Henry, M., Fröchen, M., Maillet-Mezeray, J., Breyne, E., Allier, F., Odoux, J.-F., Decourtye,
504 A., 2012. Spatial autocorrelation in honeybee foraging activity reveals optimal focus
505 scale for predicting agro-environmental scheme efficiency. *Ecological Modelling* 225,
506 103–114. <https://doi.org/10.1016/j.ecolmodel.2011.11.015>

507 Henry, M., Rodet, G., 2018. Controlling the impact of the managed honeybee on wild bees in
508 protected areas. *Sci Rep* 8. <https://doi.org/10.1038/s41598-018-27591-y>

509 Hoehn, P., Steffan-Dewenter, I., Tschardtke, T., 2010. Relative contribution of agroforestry,
510 rainforest and openland to local and regional bee diversity. *Biodiversity and*
511 *Conservation* 19, 2189–2200. <https://doi.org/10.1007/s10531-010-9831-z>

512 Holyoak, M., Leibold, M.A., Holt, R.D., 2005. *Metacommunities: Spatial Dynamics and*
513 *Ecological Communities*. University of Chicago Press.

514 Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tschardtke, T., 2006. Diversity of flower-
515 visiting bees in cereal fields: effects of farming system, landscape composition and
516 regional context. *Journal of Applied Ecology* 44, 41–49.
517 <https://doi.org/10.1111/j.1365-2664.2006.01259.x>

518 Hudewenz, A., Klein, A.-M., 2013. Competition between honey bees and wild bees and the
519 role of nesting resources in a nature reserve. *J Insect Conserv* 17, 1275–1283.
520 <https://doi.org/10.1007/s10841-013-9609-1>

521 Kelber, A., Warrant, E.J., Pfaff, M., Wallén, R., Theobald, J.C., Weislo, W.T., Raguso, R.A.,
522 2006. Light intensity limits foraging activity in nocturnal and crepuscular bees.
523 Behavioral Ecology 17, 63–72. <https://doi.org/10.1093/beheco/arj001>

524 Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D.,
525 Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-
526 Dewenter, I., Tschamtkke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed
527 biodiversity benefits of agri-environment schemes in five European countries.
528 Ecology Letters 9, 243–254. <https://doi.org/10.1111/j.1461-0248.2005.00869.x>

529 Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tschamtkke, T., 2011. Does conservation on
530 farmland contribute to halting the biodiversity decline? Trends in Ecology &
531 Evolution 26, 474–481. <https://doi.org/10.1016/j.tree.2011.05.009>

532 Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in
533 conserving and promoting biodiversity? Journal of Applied Ecology 40, 947–969.
534 <https://doi.org/10.1111/j.1365-2664.2003.00868.x>

535 Klein, A.-M., Steffan-Dewenter, I., Tschamtkke, T., 2003. Fruit set of highland coffee
536 increases with the diversity of pollinating bees. Proceedings of the Royal Society B:
537 Biological Sciences 270, 955–961. <https://doi.org/10.1098/rspb.2002.2306>

538 Knop, E., Kleijn, D., Herzog, F., Schmid, B., 2006. Effectiveness of the Swiss agri-
539 environment scheme in promoting biodiversity. Journal of Applied Ecology 43, 120–
540 127. <https://doi.org/10.1111/j.1365-2664.2005.01113.x>

541 Kwon, Y.J., Saeed, S., 2003. Effect of temperature on the foraging activity of *Bombus*
542 *terrestris* L. (Hymenoptera: Apidae) on greenhouse hot pepper (*Capsicum annuum* L.).
543 Applied Entomology and Zoology 38, 275–280.

544 Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R.,
545 Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition

546 and wild bee communities: A large scale study in four European countries.
547 *Agriculture, Ecosystems & Environment* 137, 143–150.
548 <https://doi.org/10.1016/j.agee.2010.01.015>

549 Magrach, A., González-Varo, J.P., Boiffier, M., Vilà, M., Bartomeus, I., 2017. Honeybee
550 spillover reshuffles pollinator diets and affects plant reproductive success. *Nat Ecol*
551 *Evol* 1, 1299–1307. <https://doi.org/10.1038/s41559-017-0249-9>

552 Marrec, R., Ruault, S., Ribout, C., Plantegenest, M., Gauffre, B., 2014. Isolation and
553 characterization of eleven polymorphic microsatellite markers from the beneficial
554 carabid beetle, *Poecilus cupreus* (Coleoptera: Carabidae), and genetic structuring
555 among three populations from western France. *European Journal of Entomology*.
556 <https://doi.org/10.14411/eje.2014.084>

557 Michener, C.D., 2007. *The Bees of the world*, 2nd Revised edition. ed. Johns Hopkins
558 University Press.

559 Moritz, C., Meynard, C.N., Devictor, V., Guizien, K., Labrune, C., Guarini, J.-M., Mouquet,
560 N., 2013. Disentangling the role of connectivity, environmental filtering, and spatial
561 structure on metacommunity dynamics. *Oikos* 122, 1401–1410.
562 <https://doi.org/10.1111/j.1600-0706.2013.00377.x>

563 Öckinger, E., Smith, H.G., 2007. Semi-natural grasslands as population sources for
564 pollinating insects in agricultural landscapes. *Journal of Applied Ecology* 44, 50–59.
565 <https://doi.org/10.1111/j.1365-2664.2006.01250.x>

566 Ouin, A., Aviron, S., Dover, J., Burel, F., 2004. Complementation/supplementation of
567 resources for butterflies in agricultural landscapes. *Agriculture, Ecosystems &*
568 *Environment* 103, 473–479. <https://doi.org/10.1016/j.agee.2003.11.003>

569 Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003. Linking bees and
570 flowers: How do floral communities structure pollinator communities? *Ecology* 84,
571 2628–2642.

572 R Development Core Team, 2017. R: A language and environment for statistical computing,
573 version 3.4.2. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
574 900051-07-0, URL.

575 Requier, F., Odoux, J.-F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., Bretagnolle, V.,
576 2015. Honey bee diet in intensive farmland habitats reveals an unexpectedly high
577 flower richness and a major role of weeds. *Ecological Applications* 25, 881–890.
578 <https://doi.org/10.1890/14-1011.1>

579 Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity
580 in Great Britain. *Journal of Applied Ecology* 39, 157–176.
581 <https://doi.org/10.1046/j.1365-2664.2002.00695.x>

582 Rollin, O., Benelli, G., Benvenuti, S., Decourtye, A., Wratten, S.D., Canale, A., Desneux, N.,
583 2016. Weed-insect pollinator networks as bio-indicators of ecological sustainability in
584 agriculture. A review. *Agron. Sustain. Dev.* 36, 1–22. [https://doi.org/10.1007/s13593-](https://doi.org/10.1007/s13593-015-0342-x)
585 [015-0342-x](https://doi.org/10.1007/s13593-015-0342-x)

586 Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B.E., Henry, M.,
587 2013. Differences of floral resource use between honey bees and wild bees in an
588 intensive farming system. *Agriculture, Ecosystems & Environment* 179, 78–86.
589 <https://doi.org/10.1016/j.agee.2013.07.007>

590 Rollin, O., Bretagnolle, V., Fortel, L., Guilbaud, L., Henry, M., 2015. Habitat, spatial and
591 temporal drivers of diversity patterns in a wild bee assemblage. *Biodivers Conserv* 24,
592 1195–1214. <https://doi.org/10.1007/s10531-014-0852-x>

593 Roubik, D.W., 1978. Competitive interactions between neotropical pollinators and
594 Africanized honey bees. *Science* 201, 1030–1032.
595 <https://doi.org/10.1126/science.201.4360.1030>

596 Roubik, D.W., Buchmann, S.L., 1984. Nectar selection by *Melipona* and *Apis mellifera*
597 (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical
598 forest. *Oecologia* 61, 1–10. <https://doi.org/10.1007/BF00379082>

599 Saveliev, A.A., Cronin, M., Zuur, A.F., Ieno, E.N., Walker, N.J., Smith, G.M., 2009.
600 Incorporating temporal correlation in seal abundance Data with MCMC, in: *Mixed*
601 *Effects Models and Extensions in Ecology with R, Statistics for Biology and Health.*
602 Springer New York, pp. 503–529.

603 Senapathi, D., Goddard, M.A., Kunin, W.E., Baldock, K.C.R., 2016. Landscape impacts on
604 pollinator communities in temperate systems: evidence and knowledge gaps.
605 *Functional Ecology* 31: 26–37. doi:10.1111/1365-2435.12809

606 Shavit, O., Dafni, A., Ne’eman, G., 2009. Competition between honeybees (*Apis mellifera*)
607 and native solitary bees in the Mediterranean region of Israel-Implications for
608 conservation. *Isr. J. Plant Sci.* 57, 171–183. <https://doi.org/10.1560/IJPS.57.3.171>

609 Sotherton, N.W., 1998. Land use changes and the decline of farmland wildlife: An appraisal
610 of the set-aside approach. *Biological Conservation* 83, 259–268.
611 [https://doi.org/10.1016/S0006-3207\(97\)00082-7](https://doi.org/10.1016/S0006-3207(97)00082-7)

612 Sprague, R., Boyer, S., Stevenson, G.M., Wratten, S.D., 2016. Assessing pollinators’ use of
613 floral resource subsidies in agri-environment schemes: An illustration using *Phacelia*
614 *tanacetifolia* and honeybees. *PeerJ* 4:e2677. <https://doi.org/10.7717/peerj.2677>.

615 Storkey, J., Moss, S.R., Cussans, J.W., 2009. Using Assembly Theory to Explain Changes in
616 a Weed Flora in Response to Agricultural Intensification. *Weed Science* 58, 39–46.
617 <https://doi.org/10.1614/WS-09-096.1>

618 Sutcliffe, O.L., Kay, Q.O.N., 2000. Changes in the arable flora of central southern England
619 since the 1960s. *Biological Conservation* 93, 1–8. <https://doi.org/10.1016/S0006->
620 [3207\(99\)00119-6](https://doi.org/10.1016/S0006-3207(99)00119-6)

621 Thomson, D.M., 2006. Detecting the effects of introduced species: a case study of
622 competition between *Apis* and *Bombus*. *Oikos* 114, 407–418.
623 <https://doi.org/10.1111/j.2006.0030-1299.14604.x>

624 Thomson, D.M., 2004. Competitive interactions between the invasive European honey bee
625 and native bumble bees. *Ecology* 85, 458–470. <https://doi.org/10.1890/02-0626>

626 Thorp, R.W., 1979. Structural, behavioral and physiological adaptations of bees (Apoidea) for
627 collecting pollen. *Annals of the Missouri Botanical Garden* 66, 788–812.

628 Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape
629 perspectives on agricultural intensification and biodiversity – ecosystem service
630 management. *Ecology Letters* 8, 857–874. <https://doi.org/10.1111/j.1461->
631 [0248.2005.00782.x](https://doi.org/10.1111/j.1461-0248.2005.00782.x)

632 Tylianakis, J.M., Klein, A.-M., Tschardtke, T., 2005. Spatiotemporal variation in the diversity
633 of Hymenoptera across a tropical habitat gradient. *Ecology* 86, 3296–3302.
634 <https://doi.org/10.1890/05-0371>

635 Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G.,
636 Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski,
637 M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring
638 bee diversity in different european habitats and biogeographical regions. *Ecological*
639 *Monographs* 78, 653–671. <https://doi.org/10.1890/07-1292.1>

640 Westrich, P., 1989. Die Wildbienen Baden-Württemburgs: Spezieller Teil - Die Gattungen
641 und Arten. Eugen Ulmer, Germany.

642 Williams, N.M., Regetz, J., Kremen, C., 2012. Landscape-scale resources promote colony
643 growth but not reproductive performance of bumble bees. *Ecology* 93, 1049–1058.
644 <https://doi.org/10.1890/11-1006.1>

645 Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B., 1999. A review of the
646 abundance and diversity of invertebrate and plant foods of granivorous birds in
647 northern Europe in relation to agricultural change. *Agriculture, Ecosystems &*
648 *Environment* 75, 13–30. [https://doi.org/10.1016/S0167-8809\(99\)00064-X](https://doi.org/10.1016/S0167-8809(99)00064-X)

649 Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Long foraging
650 distances impose high costs on offspring production in solitary bees. *Journal of*
651 *Animal Ecology* 79 : 674-681. <https://doi.org/10.1111/j.1365-2656.2010.01675.x>

652 Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum
653 foraging ranges in solitary bees: only few individuals have the capability to cover long
654 foraging distances. *Biological Conservation* 143, 669–676.
655 <https://doi.org/10.1016/j.biocon.2009.12.003>

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Type of effect	Estimate	Std.Error	Z value	p-value
Floral diversity	0.067	0.019	3.610	< 0.010
Floral density	0.001	0.001	0.266	0.790
Period 1 vs 2	0.010	0.090	0.113	0.993
Period 1 vs 3	-0.438	0.094	-4.643	< 0.010
Period 2 vs 3	-0.448	0.084	-5.342	< 0.010
Type of SN habitat	-0.346	0.129	-2.689	< 0.010
Quantity of SN habitat (1000m radius)	0.811	0.429	1.892	0.050
Type of SNh x Floral diversity	0.023	0.022	1.055	0.290
Number of bees	0.048	0.002	18.186	< 0.010
Temperature	-0.049	0.061	-0.812	0.420

Table 1. Ecological correlates associated with the local (α) bee richness, based on GLMMs and log-likelihood ratio tests. The “×” denote statistical interactions. Ecological correlates with p-value < 0.050 are strictly significant.

Figure caption

Figure 1. Situation and map of the study area (Zone Atelier “Plaines et Val de Sèvres”) in western France. Dark lines delineate the 3.3 x 3.3-km spacing grid from which 30 grid cells were randomly drawn without replacement for bee sampling. Dark points indicate the 702 sampling sites in the semi-natural habitats in 2010, 2011 and 2012. The number of sampling sites varied among grid cells due to phenological and spatial requirements of wild plant species.

Figure 2. Variation in bee richness according to local floral richness (A), proportion of semi-natural habitat in the landscape (buffer of 1000m radius; B), semi-natural habitat type (C) and flowering periods (D). Shaded areas (A, B) stand for the confidence interval (95%).

Figure 3. Model predictions of the bee richness variation according to (i) local bee abundance (high: top row; third quartile = 23 bees / and low: bottom row; first quartile = 5 bees), (ii) local floral richness (high: black curves; third quartile = 8 species / and low: dashed curves; first quartile = 2 species), (iii) proportion of semi-natural habitats in the landscape (from 1 to 30% of the 1000m radius), for (iv) each period (Column 1: rapeseed flowering period; Column 2: food restriction period; Column 3: sunflower flowering period). Shaded areas stand for the confidence interval (95%).

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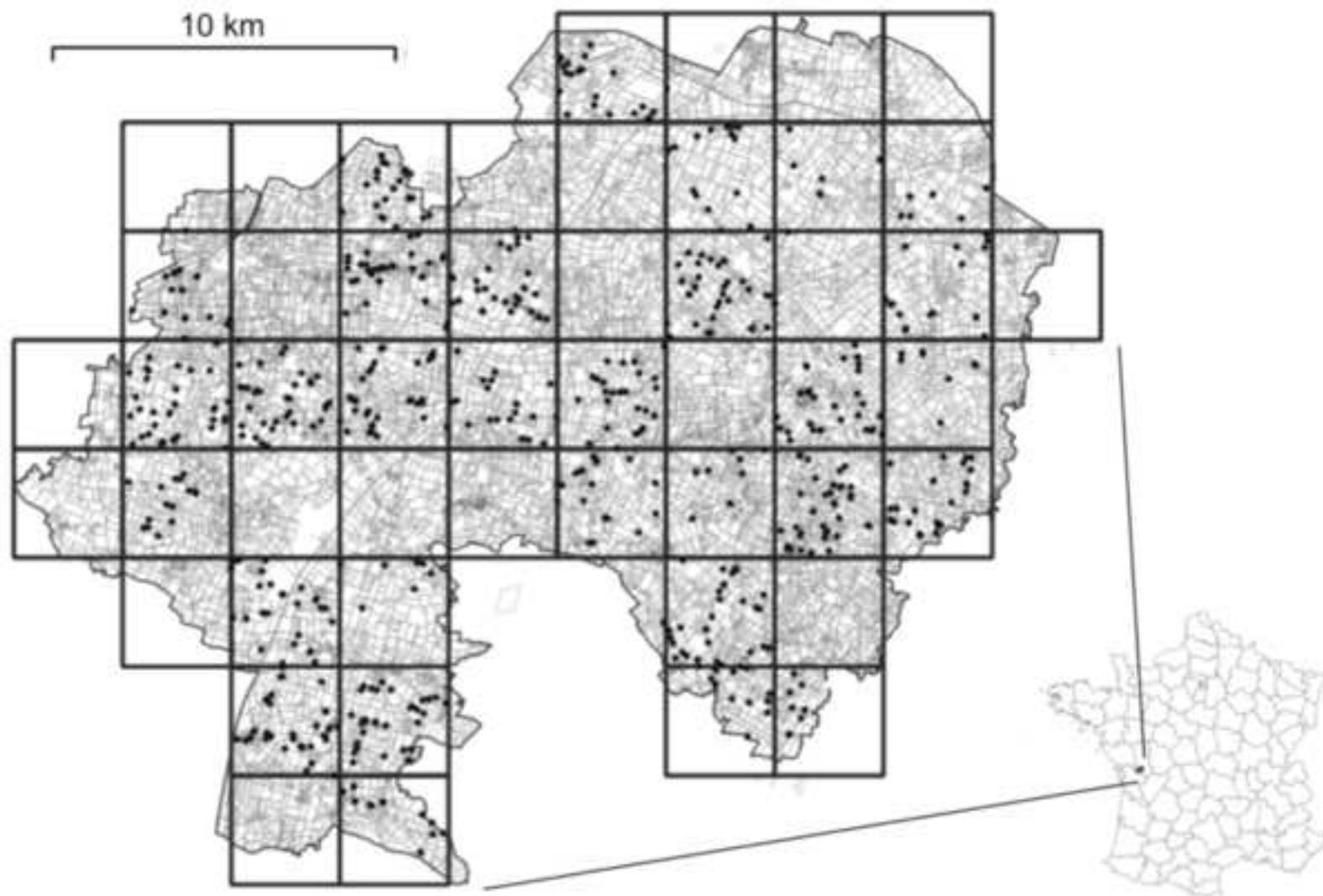


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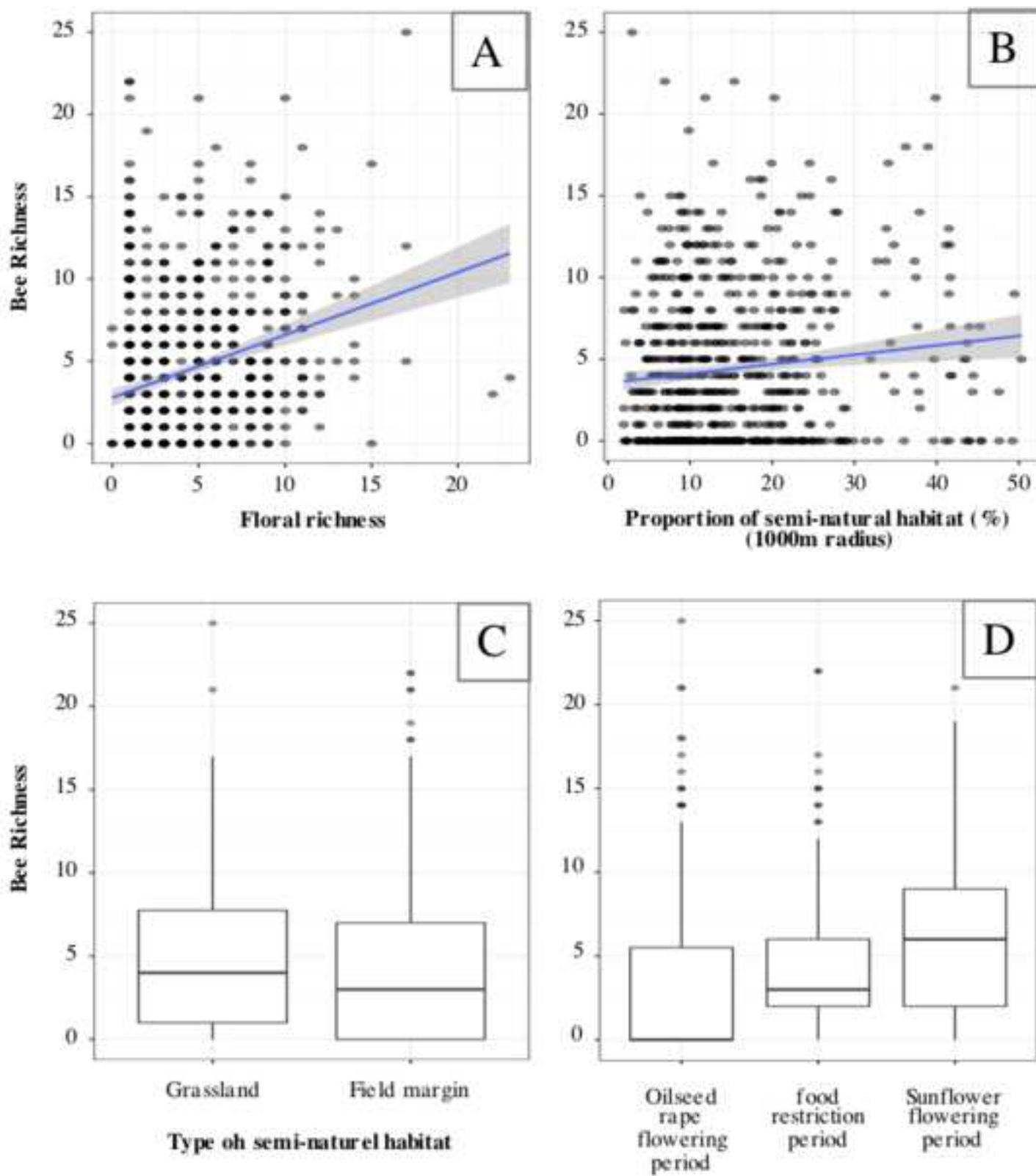
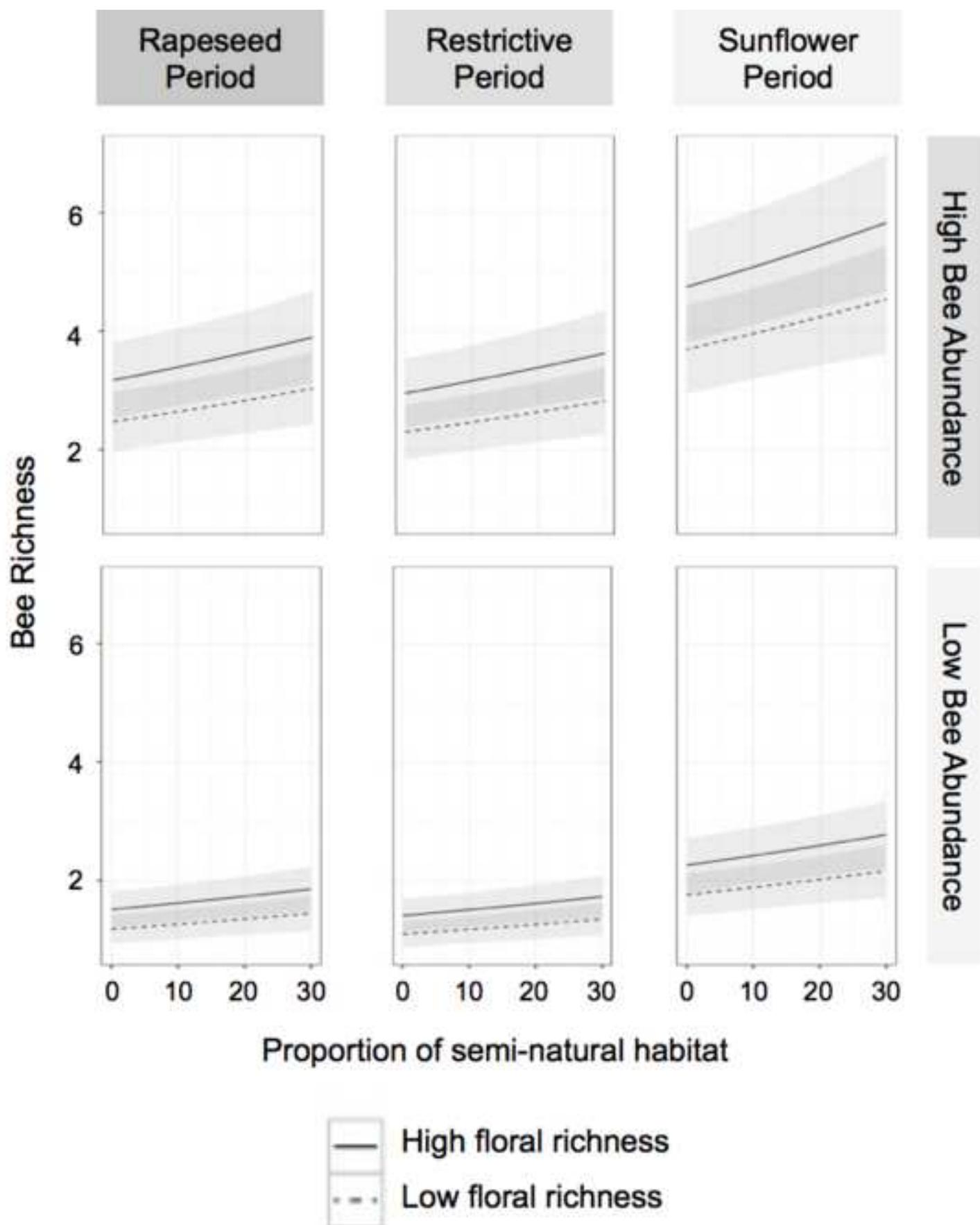


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