



HAL
open science

Floral resource maps: a tool to explain flower-visiting insect abundance at multiple spatial scales

Audrey Alignier, Nathan Lenestour, Emma Jeavons, Joan van Baaren, Stéphanie Aviron, Léa Uroy, Claire Ricono, Cécile Le Lann

► To cite this version:

Audrey Alignier, Nathan Lenestour, Emma Jeavons, Joan van Baaren, Stéphanie Aviron, et al.. Floral resource maps: a tool to explain flower-visiting insect abundance at multiple spatial scales. *Landscape Ecology*, In press, 15p. 10.1007/s10980-023-01643-9 . hal-04056320

HAL Id: hal-04056320

<https://hal.inrae.fr/hal-04056320>

Submitted on 12 Jun 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Floral resource maps : a tool to explain flower-visiting insect abundance at multiple spatial scales**

2 Audrey Alignier^{1,2,*}, Nathan Lenestour¹, Emma Jeavons^{3,4}, Joan van Baaren³, Stéphanie Aviron¹, Léa

3 Uroy^{1,3,5}, Claire Ricono³, Cécile Le Lann³

4

5 ¹ INRAE UMR 0980 BAGAP, 65 rue de St Briec, F-35042 Rennes, France

6 ² LTSER Zone Atelier Armorique, F-35042 Rennes, France

7 ³ Université de Rennes 1 (UNIR), UMR-CNRS 6553 ECOBIO, 35042 Rennes, France

8 ⁴ Laboratoire de Biologie Végétale Yves Rocher, La Croix des Archers, 56200 La Gacilly, France

9 ⁵ Université de Toulouse, École d'Ingénieurs de Purpan, INPT, UMR Dynafor 1201, 75 voie du TOEC, f-
10 31076 Toulouse Cedex, France

11

12 *Corresponding author: Audrey Alignier; INRAE UMR 0980 BAGAP 65 rue de St Briec 35042 Rennes
13 cedex; Tel : +33 2 23 48 57 70; Fax : +33 2 23 48 56 20; audrey.alignier@inrae.fr

14

15 **ORCID numbers**

16 Audrey Alignier: 0000-0002-7619-7124

17 Emma Jeavons: 0000-0002-5934-7872

18 Joan van Baaren: 0000-0002-8552-9645

19 Stéphanie Aviron: 0000-0002-8518-3920

20 Léa Uroy: 0000-0003-4967-4017

21 Cécile Le Lann: 0000-0002-3949-4066

22

23 **Acknowledgements**

24 We warmly thank the farmers who gave permission to perform flower-visiting insects' surveys on
25 their farms. We also thank Gérard Savary, Arnaud Maillard and Jean-Luc Roger for their help in
26 collecting land cover information. The study was supported by the TRY initiative on plant traits
27 (<http://www.try--db.org>). The TRY initiative and database are hosted, developed and maintained by
28 J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is currently
29 supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research
30 (iDiv) Halle---Jena---Leipzig. We also thank Rebecca Spake and the reviewers for their constructive
31 comments on the manuscript.

32 **Abstract**

33 *Context* Flower-visiting insects depend on floral resource availability from both cultivated and semi-
34 natural habitats in agricultural landscapes. Landscape studies exploring insect abundance mainly
35 focus on land cover maps without considering plant species within. Highlighting the functional role of
36 landscapes through the potential floral resources they provide is an overlooked innovative approach.

37 *Objectives* We aimed to identify traits of floral communities that are important, across several spatial
38 scales, for explaining the abundance of flower-visiting insects. Mapping and quantifying potential
39 floral resources according to their attractivity, accessibility and profitability in both crop and non-
40 crop habitats was performed to gain insights into flower-vising insect requirements.

41 *Methods* We translated land-cover maps of 39 landscapes of 250 m, 500 m and 1000 m radius into
42 potential floral resource maps, using pre-existing vegetation surveys and floral traits databases. In
43 the centres of the landscapes, the abundance of flower-visiting insect groups (domestic and wild
44 bees, bumblebees and hoverflies) were recorded in organic winter cereal fields. We then fitted
45 Generalized Linear Models (GLMs) to investigate the effects of flower trait variables (pre-selected
46 with conditional random forests) at both field and landscape scales on the abundance of each flower-
47 visiting insect group.

48 *Results* Floral resource maps explained the abundances of flower-visiting insect groups. Small wild
49 bees (< 1 cm) responded positively to the relative amount of attractive and accessible floral
50 resources at 250 m. The abundance of domestic bees and bumblebees was positively correlated with
51 the relative amount of high nectar producing plants at 1000 m. The abundance of hoverflies was
52 positively influenced by the relative amount of actinomorphic flowers (i.e. those with radial
53 symmetry), at 1000 m.

54 *Conclusion* Resource maps could explain flower-visiting insect abundances, identify which category of
55 floral resources organisms require, and determine in which habitat types these resources prevail.

56 These results open a new research area related to managing the environment by optimising floral
57 resources for flower-visiting insect conservation and pollination maintenance.

58

59 **Keywords:** functional landscape, floral resource, wild bees, domestic bees, pollinators

60 **Introduction**

61 The influence of spatial heterogeneity on ecological processes is central in landscape ecology (Turner
62 1989). Landscape heterogeneity, defined by the amount (landscape composition) and spatial
63 arrangement (landscape configuration) of the habitat patches that compose them (Fahrig et al. 2011;
64 Gustafson 1998) is classically estimated from vegetation types or land covers, with or without
65 explicit consideration of their relevance to species. This structural view has been challenged by many
66 authors who pointed out the need for a functional approach that considers the fundamental
67 ecological requirements of species to better understand biodiversity patterns and functions (Dennis
68 et al. 2003; Dennis et al. 2006; Vanreusel and Van Dyck 2007). Nowadays, few studies have employed
69 a resource-based view of landscape heterogeneity involving mapping habitat patches or land cover
70 as a collection of resources (food, shelter, etc.) required by, and accessible to, organisms (see
71 Ammann et al. 2022; Eckerter et al. 2020; Lonsdorf et al. 2009; Vialatte et al. 2017). Generating such
72 maps requires additional organism-specific information that is not always easy to obtain unlike
73 'classical' habitat mapping. However, resource maps may help to better explain species patterns and
74 identify in which habitat types these resources prevail. It also allows for ecologically-relevant
75 recommendations on agricultural landscape design and habitat restoration/diversification programs
76 for biodiversity conservation and ecosystem service promotion (Ammann et al. 2022).

77 In European agricultural landscapes, maintaining diverse and abundant flower-visiting insects such as
78 domestic bees, wild bees and hoverflies is crucial for sustaining wild plant species diversity and the
79 efficiency and stability of agricultural production (Balzan et al. 2014; Garibaldi et al. 2013; Ollerton et
80 al. 2011). Flower-visiting insects require distinct types of resources including availability and
81 accessibility of nesting sites and floral resources (Potts et al. 2003). In this regard, different types of
82 habitats are associated with different plant communities and therefore provide different floral
83 resources (Cavigliasso et al. 2022). Research on landscape-level effects on pollinating insects has
84 predominantly focused on a binary view (habitat vs. non-habitat) of the landscape, with particular

85 attention to the contributions of semi-natural habitats and mass flowering crops (Diekötter et al.
86 2014; Williams and Kremen 2007). Results show that wild bees and hoverflies seem to depend more
87 on semi-natural habitats (e.g. grasslands, hedgerows, forest edges) for floral resources than on mass
88 flowering crops (e.g. oilseed rape, legume crops) while the opposite is true for domestic bees (Rollin
89 et al. 2013). Nevertheless, few studies have investigated to what extent the amount and diversity of
90 floral resources fulfilled by crop and non-crop habitat types drive flower-visiting insect abundance.
91 Contrasting results observed may indicate that these studies mainly considered the amount of floral
92 resources (i.e. flower density) at a given landscape scale (500 buffer radius, Ammann et al. 2022; 1km
93 buffer radius, Williams et al. 2012; 2km buffer radius, Lonsdorf et al. 2009). Only Vialatte et al. (2017)
94 considered different buffer size. Furthermore, these studies focused on a single flower-visiting insect
95 species (i.e. *Bombus vosnesenskii*, Williams et al. 2012) or group (i.e. hoverflies, Ammann et al. 2022;
96 Vialatte et al. 2017). Studies considering weeds, i.e. plants that spontaneously grow within fields, are
97 even rarer (but see Balfour and Ratnieks 2022; Crochard et al. 2022; Twerski et al. 2022). Targeted by
98 intensive management in cultivated fields, weeds are paradoxically a major asset for biodiversity
99 conservation because they offer resources at various times but especially after blooming of mass-
100 flowering crops. Therefore, weeds may support the maintenance of flower-visiting insects and the
101 provision of crop pollination ecosystem services at the landscape scale (Bretagnolle and Gaba 2015;
102 Requier et al. 2015). Thus, adopting a flower-visiting insect's perspective could overcome this binary
103 view (habitat vs. non-habitat) of the landscape, and calls for a characterisation of the landscape as a
104 continuum of available resources, including neglected resources such as weeds. This approach
105 requires an evaluation of floral resources that habitat types may provide by identifying of plant
106 species and their specific floral traits.

107 To reflect local interactions between flower-visiting insects and floral resources, and depict floral
108 resource heterogeneity, Ricou et al. (2014) proposed three categories of floral traits: (i) visual
109 attractivity of flowers (e.g. flower colour, plant height); (ii) nectar and pollen accessibility (e.g. flower
110 morphology) and (iii) profitability (i.e. reward linked to nectar and pollen levels). Indeed, flowering

111 plant species exhibit particular traits that do not contribute equally in explaining variation among
112 insect groups that visit and successfully pollinate flowers (Fenster et al. 2004). For instance, blue and
113 purple flowers are the most attractive to bees and bumblebees (Ricou et al. 2014) while yellow
114 flowers are preferred by hoverflies (Sutherland et al. 1999). Focusing on legume mixtures, Cole et al.
115 (2022) showed that flower morphology plays a role in coordination with the length of the pollinating
116 insect tongue. Most bumblebees and some solitary bees (Apidae and Megachilidae), all long-tongued
117 pollinators (Rollin et al. 2013), are more likely to forage tube-shaped corolla rather than flat corolla
118 flowers unlike hoverflies (Cole et al. 2022). Plant height is another important discerning factor as
119 many flower-visiting insects tend to fly at a constant height when foraging (Dafni and Potts 2004).
120 For instance, previous work showed that bumblebees avoided short plants (Dafni and Potts 2004).
121 Lastly, the preferential use of plant species by insects might be related to the amount and quality of
122 resources (nectar and pollen) they provide (Balzan et al. 2014). In particular, van Rijn and Wäckers
123 (2016) showed that nectar (but not pollen) availability was the main driver determining flower
124 resource suitability, flower choice and abundance of hoverflies.

125 Since flower-visiting insects move through the landscape to acquire resources, floral resources must
126 be considered at relevant spatial scales. Previous work, based upon land-cover, showed that
127 response scales vary across insect groups, according to their dispersal abilities and foraging
128 behaviour (i.e. scale of effect; Jackson and Fahrig 2012). For instance, domestic bees with a generalist
129 diet and a large foraging range (up to 2 km; Danner et al. 2017) may respond to landscape
130 heterogeneity at large spatial scales. By contrast, wild bees are more specialised to a single host plant
131 species or family and with lower dispersal ability. Thus, they may be more sensitive to landscape
132 heterogeneity at smaller spatial scales (up to several hundred meters; Gathmann and Tschardt
133 2002; Steffan-Dewenter et al. 2002).

134 Mapping and quantifying the presence of flowering species with specific traits across spatial scales,
135 from both crop and non-crop habitats, could provide important insight into flower-visiting insect

136 requirements. Note that our approach did not allow us to accurately measure the availability of floral
137 resources (i.e. the number of flowers). We thus use the term “potential floral resources’. Resource
138 maps could inform about how landscape is exploited and what constitutes a high quality habitat for
139 flower-visiting insects considering their successful conservation in agricultural areas. More
140 particularly, we hypothesised that the abundance of insects visiting wild and crop flowers (i.e. wild
141 bees, honeybees, bumblebees and hoverflies) in arable fields increases with potential floral
142 resources in the landscape. We expected the spatial scale of the responses to floral resources to vary
143 among flower-visiting insect groups, depending on insect morphology. We predicted that the relative
144 amount of flowers with high profitability (nectar directly affecting insect survival and fitness) may
145 explain flower-visiting insect abundances better than flower attractivity and accessibility.

146 **Material and methods**

147 *Study site*

148 The study took place in the Zone Atelier Armorique (Long Term Socio-Ecological Research site, 48° 36’
149 N, 1° 32’ W), located in the southern part of the Ille-et-Vilaine department in Brittany, north-western
150 France. The climate is temperate oceanic with close to 700 mm of annual precipitation. Average
151 annual temperature is about 12 °C (18 °C in summer and about 5 °C in winter). This zone is
152 characterised by a dense hedgerow network and small fields (Burel and Baudry 1990). Agriculture is
153 oriented towards mixed dairy farming and the main cultivated crops are grasslands including leys
154 (about 40 %), maize silage (30 %) and winter cereals (20 % ; Puech et al. 2015).

155 In this area, we selected 39 winter cereal fields, distributed along a gradient of landscape
156 heterogeneity based on the amount of semi-natural elements (including woodland and hedgerows)
157 within circular landscape buffers of 1000 m radius (Fig. 1). The amount of semi-natural elements
158 varied from 0.70 % to 25.83 % (woodland: from 0.19 % to 25.23 %; hedgerows: from 0.38 % to 1.07
159 %). The 39 selected fields had similar soil types and groundwater level, and all were cultivated under
160 organic farming practices. Their area ranged from 1.08 to 5.88 ha and averaged 3.35 ha. The mean

161 distance between selected fields was 24.2 ± 15.2 km. Among fields, 17 were cultivated with a mixture
162 of winter cereal (triticale (*Triticosecale* spp.), oat (*Avena sativa* L.), spelt/wheat (*Triticum* spp) and
163 legume (faba bean (*Vicia faba* L.) or pea (*Pisum sativum* L.); others were cultivated with winter cereal
164 only. No bee hives were observed around selected fields.

165 *Flower-visiting insect monitoring*

166 Observations of flower-visiting insects were made visually by counting all individuals flying or visiting
167 either wild or crop flowers along standardised transect walks, i.e. 50 m long x 2 m width transects
168 (Westphal et al. 2008). Transects were walked at a constant and slow pace, and the average duration
169 of counting surveys was of 9 minutes (min = 5 minutes even in the absence of flower-visiting insects;
170 max = 25 minutes). Variation in observation duration is explained by the fact that we did not stop the
171 timer when scoring abundance; we assumed that net observation duration was comparable between
172 transects. Transects (one per field) were located in the centre of each crop field, parallel to the field
173 margin and 50 m away from it. By doing this, we avoided the edge effect and variability caused by
174 adjoining habitat, which could be another arable field with little or no boundary, a grass strip, a ditch
175 or a hedgerow. Flower-visiting insect surveys were conducted three times between May and July
176 2019, once per month, resulting in 117 transects surveyed during the study. Observations were made
177 on days with wind speeds < 8 m/s and temperatures $> 13^{\circ}\text{C}$ on sunny days and $> 17^{\circ}\text{C}$ on more
178 cloudy days, from 09:00 to 18:00. To limit potential time-of-day bias (Jeavons et al. 2020), we
179 randomised the sampling hour for fields across the three sessions. We also took care to avoid double
180 counting as much as possible by considering only the insects in front of the walker. Observed flower-
181 visiting insects were classified at sight into five easily recognisable morpho-groups: small wild bees ($<$
182 1cm), large wild bees ($> 1\text{cm}$), domestic bees (*Apis mellifera* Linnaeus, 1758), bumblebees (*Bombus*
183 spp.) and hoverflies (Syrphidae). We use the term 'flower-visiting' instead of 'pollinator' or
184 'pollinating' insect since we did not discriminate between true pollinators and insects visiting flowers

185 for other purposes, following Welti and Joern (2018). Abundances (i.e. total number of counted
186 individuals) was summed over the three sessions for each flower-visiting insect group.

187 *Land-cover maps and floral traits*

188 Land-cover maps were digitised in 1000 m radius buffers centred on the centroid of each crop field
189 by ArcGis 10.8.1 using aerial ortho-photographs (BD ORTHO IGN, 2017) and field surveys. This radius
190 is commonly used for assessing landscape effects on pollinators and corresponds to the typical
191 foraging range of the flower-visiting insects considered here, including domestic bees (Rollin et al.
192 2019). Land-cover types were classified into 37 categories, including hedgerows. Hedgerows were
193 digitized as polylines and assigned a standard width of 2 m. The amount (%) of each land-cover type
194 was calculated. We then identified the main land-cover types likely to provide floral resources. We
195 selected seven categories (rather than nine) whose cumulative areas represented more than 82 % of
196 the whole surface of the 39 land-cover maps: grassland, maize, cereal and woodland (altogether
197 covering more than 75% of the whole surface), two mass flowering crops predominant in our study
198 area (i.e. oilseed rape and legume-crop mixture), and hedgerows (Table 1).

199 To list all plant species potentially providing floral resources, we used exhaustive vascular plant data
200 from previous studies conducted in the studied area within 5 years preceding insect monitoring
201 (Table 1; Appendix A). When available, 40 plots (e.g. crop fields, woodlots or hedgerows) per main
202 land-cover type were used (only 30 plots for legume-crop mixture fields). For each plot, 8 to 20
203 quadrats of exhaustive plant species monitoring were performed (Table 1; Appendix B). From these
204 exhaustive plant datasets (see species accumulation curves in Appendix C), we established the list of
205 all dicotyledons, cultivated (e.g. oilseed rape, faba bean, pea) and uncultivated, as well as their
206 occurrence (i.e. presence in quadrats) within each of the seven main land-cover types (Appendix B).
207 No exhaustive vegetation dataset was available for oilseed rape. We thus considered *Brassica napus*
208 to be the only species, present in 100 % of rape fields. Next, we removed species occurring in less

209 than 5 % of all quadrats per main land-cover type. All subsequent analyses were performed on this
210 subset of 95 dicotyledon plant species.

211 Following Ricou et al. (2014), all available plant traits in relation to attractivity (in terms of flower
212 size, colour and mean UV reflection), accessibility (according to flower morphology and symmetry),
213 and profitability (in terms of reward linked to nectar and pollen quantity and quality) of floral
214 resources for flower-visiting insects were gathered. These traits were selected based on (i) their
215 importance in plant-flower-visiting insect interactions and (ii) their availability in databases. Their
216 values were collected from several trait databases including catminat (Julve 1998), TRY Plant Trait
217 Database (Kattge et al. 2011), AgriLand (Baude et al. 2015) and Tela Botanica ([http://www.tela-](http://www.tela-botanica.org/site/accueil)
218 [botanica.org/site/accueil](http://www.tela-botanica.org/site/accueil)), and from Ricou et al. (2014). Among *Attractivity* traits, flower colour plays
219 an important role in the attraction of flower visitors, but due to differences in colour vision and
220 colour preferences of insects (Arnold et al. 2009) and since flowers were assigned one to three
221 colours, we preferred to use the continuous floral trait *Mean UV reflection* instead, to which bees are
222 known to be sensitive (Ricou et al. 2014, Papiorek et al. 2016). Flower size increases plant
223 attractiveness and diminishes insect pollen and nectar search time (Spaethe et al. 2001). Among
224 *Accessibility* traits and as mentioned above, flower morphology (see Appendix D for illustration)
225 conditions insect corolla foraging according to their tongue length. Flower symmetry influences
226 flower handling speed for insects and pollination efficiency (Ricou et al. 2014). Finally, nectar is
227 usually considered to be the main attractive force driving flower-visiting insects, and likely to have a
228 substantial impact on survival and fitness: nectar provides 80 % of sugar required by bees (Ricou et
229 al. 2014). In total, 13 floral traits (five continuous traits and eight trait modalities), for which less than
230 one third of the data across all 95 plant species was missing were considered in subsequent analyses
231 (Table 2).

232 *Functional landscapes*

233 With the aim of translating land-cover maps (Fig. 1) into potential floral resource maps (Fig. 2),
234 Community Weighted Mean (CWM) was calculated for each floral trait and each land-cover type
235 (Appendices B and E) using the R package FD (Laliberté et al. 2014). For qualitative traits, the
236 calculated value corresponded to the presence probability of each trait modality (value between 0
237 and 1). CWM values were calculated for each crop field (N = 39) then extended to the landscape scale
238 by weighting CWM values by the relative area of every land-cover type in each landscape. To take
239 into account the varying dispersal abilities of flower-visiting insect groups, three spatial scales were
240 considered corresponding to 250 m, 500 m and 1000 m radius circle buffers centered on sampled
241 fields.

242 *Statistical analysis*

243 We explored how the abundance of each flower-visiting insect group related to the relative amount
244 of potential floral resources at different spatial scales. Owing to our sample size (N = 39 crop fields), a
245 preselection of explanatory variables was performed to decrease their large number (N = 13 floral
246 traits * 4 spatial scales). As we were interested in disentangling the contribution of floral resources at
247 local (i.e. field) vs. landscape scale, we performed a variable selection in two steps.

248 In the first step, we identified the explanatory variables (i.e. CWM of floral traits) at the field scale
249 most related to the abundance of each flower-visiting insect group using a conditional random forest
250 model (Strobl et al. 2008). Random forests have grown in popularity in many scientific fields due to
251 their robustness in 'small n large p' situations, complex interactions and highly correlated predictor
252 variables (Bradter et al. 2013; Strobl et al. 2008). Random forests are recursive partitioning methods
253 used in ecology for variable selection (see Puech et al. 2014; Bertrand et al. 2016 for examples). By
254 providing a measure of 'variable importance' for each explanatory variable (Strobl et al. 2007, 2008),
255 random forests allow selection of the most relevant variables to be considered in linear models.
256 Herein, random forests were grown based on 500 bootstrap samples (robustness of results was
257 checked with 1000 trees) using the party R package (Hothorn et al. 2006). We fixed the number of

258 input variables randomly sampled as candidates at each node as the square root of the total number
259 of variables (often suggested as a default value in the literature, see Strobl et al. 2007). Model
260 stability was verified by checking that the same ranking was achieved with different random seeds
261 (Puech et al. 2014; Bertrand et al. 2016). Variables were considered as informative and relevant
262 when their conditional score was above the absolute value of the lowest negative-scoring variable
263 (Strobl et al. 2007). In the case of two highly correlated ‘important’ variables (Spearman *rho*
264 coefficient $> |0.70|$, Appendix F), only the most important one (in terms of the conditional
265 importance measure from random forests) was retained in models.

266 In the second step, we repeated the procedure at the landscape scale, including all explanatory
267 variables (i.e. CWM of floral traits) within different spatial scales around sample locations (i.e. at 250,
268 500 and 1000 m. Examination of these variables at three spatial scales each resulted in 39 potentially
269 correlated predictors (see Spearman’s correlation matrix in Appendix G) to select between.

270 In the third step, Generalized Linear Models (GLMs) were run to test for the effects of the important
271 field and landscape variables (pre-selected with conditional random forests) on the abundance of
272 each flower-visiting insect group. Poisson error distribution with a log link function was used for the
273 abundance of insect groups as it represented count data. All explanatory variables were centred and
274 scaled (mean = 0, standard deviation = 1) to allow direct comparison of regression coefficients across
275 variables. Due to overdispersion, models were fitted with a Negative Binomial distribution and a log
276 link using the `glm.nb` function in the MASS R package (Venables and Ripley 2002). We checked for
277 multi-collinearity (Lautenbach 2013) using variance inflation factors (VIFs), and all VIFs were below
278 the collinearity threshold (< 2.5) in all models (Dormann et al. 2013). Visual inspection of residuals
279 revealed no obvious deviations from homoscedasticity or normality. No spatial autocorrelation in
280 model residuals was observed (Appendix H).

281 In a last step, we applied a multi-model inference to build all possible generalized linear models
282 based on all additive combinations of up to four explanatory variables for each flower-visiting insect

283 group. Models were ranked according to Akaike's information criterion corrected for small sample
284 size (AICc) using the MuMIn R package (Bartoń 2020). Model averaging was used to determine the
285 average of models presenting similar relevance, i.e. $\Delta AICc < 4$ (Grueber et al. 2011). We used the
286 natural average approach (*sensu* Burnham and Anderson 2022) in which the parameter estimate of
287 each variable is averaged only over models in which that variable appears. We considered
288 independent variables significant if the 95% confidence intervals did not overlap with zero. Explained
289 variance (R^2) was estimated through the explained variance of the best-fitting model (i.e. with the
290 lowest AIC value) using the rsq function in the rsq R package (Zhang 2022).

291 To identify in which habitat type significant floral traits prevail, we tested for Spearman correlations
292 between significant CWM trait values and the amount of land-cover type at 250, 500 and 1000 m. All
293 statistical analyses were performed in R 4.0.2 (R Core Team 2020).

294 **Results**

295 In total, 1031 flower-visiting insects were observed comprising 148 small wild bees, 129 large wild
296 bees, 156 domestic bees, 239 bumblebees and 359 hoverflies.

297 Using conditional random forests, zero to four variables at the field scale and one to three variables
298 at the landscape scale were selected as 'important' for explaining the abundance of flower-visiting
299 insect groups (Table 3). Among 'important' traits for small wild bees, four (CWM of *Min* and *Max size*
300 *of floral unit*, *Plant height [Intermediate]* and *Flowering duration*) were identified at the field scale,
301 along with three (CWM of *Mean UV reflection*, *Flower morphology [Tube]* and *Empiric nectar*
302 *productivity*) at the landscape scale. Selected floral traits mainly pertained to the *Attractivity*
303 category ($N = 4$). Two of the three floral traits selected at the landscape scale concerned the smallest
304 spatial scale (250 m). Two floral traits were selected for explaining the abundance of large wild bees:
305 CWM of *Mean UV reflection* at the field scale and CWM of *Flower morphology [Tube]* at 1000 m.
306 Three floral traits, one at the field scale (CWM of *Flowering duration*) and two at the landscape scale
307 (CWM of *Flower morphology [Tube]* and *Empiric nectar productivity*) were identified as 'important' to

308 explain the abundance of domestic bees. Two of them pertained to the *Accessibility* category. All
309 floral traits selected at the landscape scale referred to the 1000 m spatial scale. Among ‘important’
310 floral traits for bumblebees, two were retained at the field scale (CWM of *Plant height [Intermediate]*
311 and *Flowering duration*) along with one (CWM of *Empiric nectar productivity*) at 1000 m. None of the
312 floral traits at the field scale were identified as ‘important’ for explaining the abundance of
313 hoverflies. Two of the three floral traits (CWM of *Plant height [Short]*, *Flower symmetry [Actimorphy]*
314 and *Flower morphology [Flat]*) retained at the landscape scale belonged to the *Accessibility* category
315 and all referred to the 1000 m spatial scale. CWM of *Flowering duration* at the field scale and CWM
316 of *Empiric nectar productivity* at 1000 m were the traits most often identified as ‘important’ for
317 explaining insect group abundances (three groups out of five; Table 3).

318 Following this selection by random forests, averaged GLMs showed that the abundance of small wild
319 bees was significantly and negatively correlated with CWM of *Mean UV reflection* at 250 m and
320 positively related to CWM of *Flower morphology [Tube]* at 250 m (Table 4). CWM of *Flower*
321 *morphology [Tube]* at 250 m was highly correlated ($\rho = 0.62$) with the amount of grassland at 250
322 m (Table 5). None of the ‘important’ floral traits significantly influenced the abundances of large wild
323 bees (Table 4). CWM of *Empiric nectar productivity* at 1000 m was significantly and positively
324 correlated with the abundance of domestic bees and bumblebees (Table 4). CWM of *Empiric nectar*
325 *productivity* at 1000 m was very highly correlated ($\rho = 0.72$) with the amount of woodland at 1000
326 m and, to a lesser extent, with the amount of grassland at 1000 m ($\rho = 0.60$) but was negatively
327 correlated with the amount of maize at 1000 ($\rho = -0.60$; Table 5). The abundance of hoverflies was
328 significantly and positively corelated with CWM of *Flower symmetry [Actinomorphy]* at 1000 m (Table
329 4). No major correlations were observed for the amount of any particular habitat amount at 1000 m
330 (Table 5).

331 **Discussion**

332 To our knowledge, our study is the first to investigate the effects of potential floral resources,
333 described in terms of attractiveness, accessibility and profitability at multiple spatial scales, on the
334 abundance of several groups of flower-visiting insects. Our approach goes beyond the binary view of
335 the landscape traditionally used in pollinating insect studies by considering a continuum of potential
336 floral resources, evaluated from crop and wild plants, in both cultivated and semi-natural habitats.
337 We showed that the abundance of most flower-visiting insect groups, except large wild bees,
338 increased with the presence of plant communities possessing certain floral traits in the landscape.
339 Small wild bees responded positively to the relative amount of attractive (i.e. low values of mean UV
340 reflection) and accessible (i.e. tube-shaped corolla) floral resources at the smallest landscape scale
341 (i.e. 250 m) whereas domestic bees and bumblebees responded to the relative amount of profitable
342 resources (i.e. high nectar producing plant species) at the largest landscape scale (i.e. 1000 m).

343 The amount and quality of floral resources are known to be limiting factors for flower-visiting insect
344 development in agricultural landscapes. Nevertheless, studies addressing the role of habitat patch
345 quality, in terms of potential resource provision and at different spatial scales are scarce (but see
346 Ammann et al. 2022). Furthermore, those studies predominantly focused on the role of semi-natural
347 habitats (e.g. Ricketts et al. 2008; Winfree et al. 2009) while ignoring the contribution of wild plants
348 in cultivated habitats (i.e. weeds). Our study highlights the importance of a holistic integration of the
349 diverse potential floral resources provided by crops, wild plants in semi-natural habitats and, weeds
350 in fields, to allow functional characterisation of landscape heterogeneity for flower-visiting insects.

351 Our approach did not allow us to accurately measure the availability of floral resources because we
352 did not assess the number of flowers of each species, nor the variation between plots of the same
353 land-cover type (i.e. due to environmental heterogeneity or management), nor the variation across
354 seasons (i.e. plant phenology). Additionally, estimating floral resources at the landscape scale is
355 challenging and time-consuming. Therefore, our estimation inevitably relies on some generalisations
356 resulting in potential over- or underestimation of the contributions of different flowering species to
357 the landscape scale floral resource availability (Ammann et al. 2022). Additional ecological resources,

358 such as pollen provision, oviposition and nesting sites could not be included in the study because
359 such data are not available. Despite these limitations, we obtained significant results that explicitly
360 linked flower-visiting insect abundance with the amount of floral resources surrounding the focal
361 fields. Moreover, the results allowed us to determine which floral traits are the most important in
362 explaining flower-visiting insect abundance.

363 According to our second hypothesis, we detected variability in the spatial scales of flower-visiting
364 insect responses to potential floral resources. We showed that domestic bees, bumblebees and
365 hoverflies responded to the relative amount of specific floral traits at the largest spatial scale (1000
366 m). These results are in accordance with the foraging distance reported for these insects in the
367 literature: Knight et al. (2005) evaluated the foraging range of bumblebees between 1 to 3 km while
368 Danner et al. (2017) reported foraging range for domestic bees (*Apis mellifera*) up to 2 km. These
369 results also support the findings of Kleijn and van Langevelde (2006), who suggested that hoverflies
370 are optimally related to landscape context at scales of 500–1000 m. By contrast, solitary wild bees
371 are known to have a small foraging range (150 to 600 m) and were found to respond to landscape
372 heterogeneity at smaller scales than bumblebees and domestic bees (Gathmann and Tschardt
373 2002; Steffan-Dewenter et al. 2002). Our results for small wild bees confirmed these observations.
374 Because of the contrasting response scales, it appears necessary to consider taxon-specific
375 differences when predicting the effect of functional landscape heterogeneity (i.e. based on potential
376 floral resource availability) on flower-visiting insects.

377 In partial agreement with our third hypothesis, we showed that *Profitability*, through CWM of
378 *Empiric nectar productivity*, was the best floral trait category for explaining the abundance of
379 domestic bees and bumblebees but not of other flower-visiting insect groups. While many studies
380 have investigated the effect of floral morphology/nectar accessibility on the abundance and
381 behaviour of floral visitors (e.g. van Rijn and Wäckers 2016), few have addressed several categories
382 of floral traits together. A rare example is the study of Mallinger and Prasifka (2017) who examined

383 floral trait variation within cultivated sunflowers and its effects on bee foraging behaviour. They
384 showed that visits by domestic and wild bees increased significantly with nectar sugar amount
385 (determined by nectar volume) and decreased with corolla length. Here, we found that plant
386 communities at 250 m with decreasing *Mean UV reflection* increased the abundances of small wild
387 bees. Red flowers are known to be more attractive to bees if they reflect UV light, and white flowers
388 are more attractive to bees if they absorb UV light, but no difference in bee preference was observed
389 for yellow flowers with differing UV reflectance (Lunau et al. 2011). Thus, we suggest that promoting
390 the presence of low-reflectance white flowers such as *Convolvulus arvensis* or *Daucus carota* in the
391 vicinity of fields could be an effective habitat restoration/diversification measure to support the
392 abundance of small wild bees. The beneficial effect at 250 m of plant communities with tube-shaped
393 corolla is more difficult to explain as bees generally forage on flowers with a corolla depth matching
394 their tongue length (Cole et al. 2022). Although floral traits may provide clues about potential
395 foraging pollinators, they are not always a fail-safe way of predicting the occurrence of specific
396 flower-visiting insect species, or their abundance. Similar patterns could also emerge due to other
397 abiotic factors or biotic relationships not considered here. We found that the CWM of *Empiric nectar*
398 *productivity* in a 1000 m radius buffer around the focal fields significantly increased the abundance of
399 both domestic bees and bumblebees, and it explained up to 20 % of variance. In accordance with
400 previous work (e.g. Mallinger and Prasifka 2017), nectar amount appears to be the main driver of bee
401 abundance. Lastly, we showed that the abundance of hoverflies increased with higher availability of
402 actinomorphic plant species at 1000 m. This result agrees with previous work showing that hoverflies
403 prefer simpler flower structure, with a radial symmetric shape rather than an oblong shape (Cole et
404 al. 2022). Nevertheless, caution should be taken with results because explained variance is relatively
405 low, except for domestic bees.

406 We showed that the presence of tube-shaped corolla species was correlated with the amount of
407 grassland at the 250 m scale. Although the link between tube-shaped flowers and small wild bees is
408 unclear, restoring grasslands would be beneficial for the conservation of these insects. We also found

409 that CWM of *Empiric nectar productivity* at 1000 m was highly correlated with the amount of
410 woodland and, to a lesser extent, with the amount of grassland and maize at 1000 m. Among semi-
411 natural habitats in agricultural landscapes, the beneficial role of grasslands in supporting flower-
412 visiting insects is well known (e.g. Morandin et al. 2007), whereas the contribution of woodlands has
413 received far less attention (but see Öckinger et al. 2012; Proesmans et al. 2019). As a consequence,
414 agri-environmental schemes often focus on the extensification of grassland management, or the
415 conservation/plantation of linear ecological infrastructures such as sown flower strips (Batáry et al.
416 2015). However, our study underlines the importance of also including woodland habitats in
417 management and conservation programs since high nectar producing plant communities are not
418 restricted to grasslands. Furthermore, *Hedera helix*, *Crataegus monogyna* and *Prunus spinosa* were
419 the highest nectar producing species encountered in our woodlands. By flowering early (i.e. from
420 March to May for *Prunus spinosa*) or late in the season (i.e. from August to November for *Hedera*
421 *helix*), these species could provide complementary resources when nectar is otherwise scarce in the
422 landscape. This would suggest that improving woodland quality through the promotion of such highly
423 nectar producing plant species may contribute to increase the abundance of domestic bees and
424 bumblebees, and may consequently lead improved delivery of pollination service. Although we
425 cannot prove this hypothesis, wooded habitats are also beneficial for other flower-visiting insect
426 groups, and can host more specialised bee communities such as *Lasioglossum* sp. (Rivers-Moore et
427 al. 2020).

428 Finally, the fact that the presence of actinomorphic flowers at 1000 m was not strongly correlated
429 with a particular amount of habitat confirms the value of our resource-based approach and suggests
430 that a wide diversity of habitats should be included in pollinating insect conservation programs.
431 Indeed, having a range of complementary habitats in farmlands that provide resources during
432 different periods of the year appears to be an effective measure for conserving pollinators
433 (Timberlake et al. 2019). If wild pollinator populations are known to be limited by floral resources,
434 the timing of these resources is definitely an important factor driving this limitation (Timberlake et al.

435 2019). Taking better account of plant phenology would certainly have improved the explanatory
436 power of our models. Thus, the effects of intra- and inter-annual variation, landscape composition
437 and management on resource phenology are important topics for future studies.

438 **Conclusion**

439 We demonstrated significant relationships between the presence of plant communities exhibiting
440 specific floral traits in the landscape and flower-visiting insects' abundance. We argue that using a
441 resource-based approach can benefit the conservation of flower-vising insects including pollinators
442 by informing efforts to preserve existing habitats within degraded landscapes, and also guiding
443 spatial planning of priorities for habitat restoration. Enhancing habitat quality to sustain flower-
444 visiting insects could be achieved by sowing UV light-absorbing, actinomorphic, and nectar-rich plant
445 species. Interestingly, we found that the presence of highly nectar producing plant species was
446 strongly correlated with the amount of woodland in the vicinity. This result calls for a better
447 consideration of woodlands in flower-visiting insect conservation and landscape management
448 programs.

449 **References**

450 Ammann L, Boser-Baillod A, Eckerter PW, Entling MH, Albrecht M, Herzog F (2022) Comparing floral
451 resource maps and land cover maps to predict predators and aphid suppression on field bean.
452 *Landscape Ecology* 37(2): 431-441

453 ArcGIS [GIS software]. Version 10.8.1. Redlands, CA: Environmental Systems Research Institute, Inc.,
454 2020

455 Arnold SE, Le Comber CS, Chittka L (2009) Flower color phenology in European grassland and
456 woodland habitats, through the eyes of pollinators. *Israel Journal of Plant Sciences* 57(3): 211-230

457 Balfour NJ, Ratnieks FL (2022) The disproportionate value of 'weeds' to pollinators and biodiversity.
458 *Journal of Applied Ecology* 59: 1209-1218

459 Balzan MV, Bocci G, Moonen AC (2014) Augmenting flower trait diversity in wildflower strips to
460 optimise the conservation of arthropod functional groups for multiple agroecosystem services. *Journal*
461 *of Insect Conservation* 18: 713–728

462 Bartoń K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17.

463 Baude M, Kunin WE, Memmott J (2015) Nectar sugar values of common British plant species
464 [AgriLand]. NERC Environmental Information Data Centre

465 Batáry P, Dicks LV, Kleijn D, Sutherland WJ (2015) The role of agri-environment schemes in
466 conservation and environmental management. *Conservation Biology* 29(4): 1006-1016

467 Bertrand C, Burel F, Baudry J (2016) Spatial and temporal heterogeneity of the crop mosaic influences
468 carabid beetles in agricultural landscapes. *Landscape Ecology* 31(2): 451-466

469 Bradter U, Kunin WE, Altringham JD, Thom TJ, Benton TG (2013) Identifying appropriate spatial scales
470 of predictors in species distribution models with the random forest algorithm. *Methods in Ecology*
471 *and Evolution* 4(2): 167-174

472 Bretagnolle V, Gaba S (2015) Weeds for bees? A review. *Agronomy for Sustainable Development*
473 35(3): 891-909

474 Burel F, Baudry J (1990) Structural dynamic of a hedgerow network landscape in Brittany France.
475 *Landscape Ecology* 4(4): 197-210

476 Cavigliasso P, Phifer CC, Knowlton JL, Licata JA, Flaspohler DJ, Webster CR, Chacoff NP (2022)
477 Influence of landscape composition on wild bee communities: Effects of functional landscape
478 heterogeneity. *Agriculture, Ecosystems and Environment* 340: 108150

479 Cole LJ, Baddeley JA, Robertson D, Topp CFE, Walker RL, Watson CA (2022) Supporting wild pollinators
480 in agricultural landscapes through targeted legume mixtures. *Agriculture, Ecosystems and*
481 *Environment* 323: 107648

482 Crochard L, Julliard R, Gaba S, Bretagnolle V, Baude M, Fontaine C (2022) Weeds from non-flowering
483 crops as potential contributors to oilseed rape pollination. *Agriculture, Ecosystems and Environment*
484 336: 108026

485 Dafni A, Potts SG (2004) The role of flower inclination, depth, and height in the preferences of a
486 pollinating beetle (Coleoptera: Glaphyridae). *Journal of Insect Behavior* 17(6): 823-834

487 Danner N, Keller A, Härtel S, Steffan-Dewenter I (2017) Honey bee foraging ecology: Season but not
488 landscape diversity shapes the amount and diversity of collected pollen. *PLOS ONE* 12(8): e0183716

489 Dennis RLH, Shreeve TG, Van Dyck H (2003) Towards a functional resource-based concept for habitat:
490 A butterfly biology viewpoint. *Oikos* 102(2): 417-426

491 Dennis RLH, Shreeve TG, Van Dyck H (2006) Habitats and resources: The need for a resource-based
492 definition to conserve Butterflies. *Biodiversity and Conservation* 15(6): 1943-1966

493 Diekötter T, Peter F, Jauker B, Wolters V, Jauker F (2014) Mass-flowering crops increase richness of
494 cavity-nesting bees and wasps in modern agro-ecosystems. *Gcb Bioenergy* 6(3): 219-226

495 Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré, G, Marquéz JRG, Gruber B, Lafourcade B,
496 Leitão PJ, Münkemüller T, McClean C, Osborne, PE, Reineking B, Schröder B, Skidmore, AK, Zurell D,
497 Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study
498 evaluating their performance. *Ecography* 36: 27-46

499 Eckerter PW, Albus L, Natarajan S, Albrecht M, Ammann L, Gobet E, Herzog F, Tinner W, Entling M
500 (2020) Using temporally resolved floral resource maps to explain bumblebee colony performance in
501 agricultural landscapes. *Agronomy* 10(12): 1993

502 Fahrig L, Baudry J, Brotons L, Burel F, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin JL (2011)
503 Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology*
504 *Letters* 14(2): 101-112

505 Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and
506 floral specialization. *Annual Review of Ecology, Evolution and Systematics* 35:375-403

507 Garibaldi LA, Steffan-Dewenter I, Winfree R et al (2013) Wild pollinators enhance fruit set of crops
508 regardless of honey bee abundance. *Science* 339(6127): 1608-1611

509 Gathmann A, Tscharrntke T (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*
510 71(5):757-764

511 Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and
512 evolution: challenges and solutions. *Journal of Evolutionary Biology* 24(4): 699-711

513 Gustafson EJ (1998) Quantifying landscape spatial pattern: What is the state of the art? *Ecosystems*
514 1(2):143-156

515 Hothorn T, Hornik K, Zeileis A (2006) Unbiased recursive partitioning: A conditional inference
516 framework. *Journal of Computational and Graphical Statistics* 15(3): 651-674

517 Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? *Landscape Ecology* 27(7):
518 929-941

519 Jeavons E, van Baaren J, Le Lann C (2020) Resource partitioning among a pollinator guild: A case
520 study of monospecific flower crops under high honeybee pressure. *Acta Oecologica* 104: 103527.

521 Julve P (1998) *Baseflor. Index botanique, écologique et chorologique de la flore de France. Version :*
522 "20 novembre 2018".

523 Kattge EJ, Diaz S, Lavorel S et al (2011) TRY – a global database of plant traits. *Global Change Biology*
524 17(9): 2905-2935

525 Kleijn D, Van Langevelde F (2006) Interacting effects of landscape context and habitat quality on
526 flower visiting insects in agricultural landscapes. *Basic and Applied Ecology* 7(3): 201-214

527 Knight ME, Martin AP, Bishop S, Hale RJ, Sanderson RA, Goulson D (2005) An interspecific comparison
528 of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology* 14(6):
529 1811-1820

530 Laliberté E, Legendre P, Shipley B (2014) FD: Measuring functional diversity (FD) from multiple traits,
531 and other tools for functional ecology. R package version 1.0-12.

532 Lonsdorf E, Kremen C, Ricketts T, Winfree R, Williams N, Greenleaf S (2009) Modelling pollination
533 services across agricultural landscapes. *Annals of Botany* 103(9): 1589-1600

534 Lunau K, Papiorek S, Eltz T, Sazima M (2011) Avoidance of achromatic colours by bees provides a
535 private niche for hummingbirds. *Journal of Experimental Biology* 214(9): 1607-1612

536 Mallinger RE, Prasifka JR (2017) Bee visitation rates to cultivated sunflowers increase with the
537 amount and accessibility of nectar sugars. *Journal of Applied Entomology* 141(7): 561-573

538 Morandin LA, Winston ML, Abbott VA, Franklin MT (2007) Can pastureland increase wild bee
539 abundance in agriculturally intense areas? *Basic and Applied Ecology* 8: 117–124

540 Mueller-Dombois D, Ellenberg H (1974) *Aims and Methods of Vegetation Ecology*. John Wiley & Sons

541 Öckinger E, Lindborg R, Sjödin NE, Bommarco R (2012) Landscape matrix modifies richness of plants
542 and insects in grassland fragments. *Ecography* 35(3): 259-267

543 Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos*
544 120(3): 321-326

545 Papiorek S, Junker RR, Alves-dos-Santos I, Melo GA, Amaral-Neto LP, Sazima M, Wolowski M, Freitas
546 L, Lunau K (2016). Bees, birds and yellow flowers: pollinator-dependent convergent evolution of UV
547 patterns. *Plant Biology* 18(1): 46-55

548 Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P (2003) Linking bees and flowers: How do floral
549 communities structure pollinator communities ? *Ecology* 84(10):2628-2642

550 Proesmans W, Bonte D, Smagghe G, Meeus I, Verheyen K (2019) Importance of forest fragments as
551 pollinator habitat varies with season and guild. *Basic and Applied Ecology* 34: 95-107

552 Puech C, Baudry J, Joannon A, Poggi S, Aviron S (2014) Organic vs. conventional farming dichotomy:
553 does it make sense for natural enemies? *Agriculture, Ecosystems and Environment* 194: 48–57

554 Puech C, Poggi S, Baudry J, Aviron S (2015) Do farming practices affect natural enemies at the
555 landscape scale? *Landscape Ecology* 30(1): 125-140

556 R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for
557 Statistical Computing, Vienna, Austria: Available at: <https://www.R-project.org/>.

558 Requier F, Odoux J-F, Tamic T, Moreau N, Henry M, Decourtye A, Bretagnolle V (2015) Honey bee diet
559 in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of
560 weeds. *Ecological Applications* 25(4): 881-890

561 Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Gemmill-Herren
562 B, Greenleaf SS, Klein AM, Mayfield MM, Morandin LA, Ochieng' A, Viana BF (2008) Landscape effects
563 on crop pollination services: are there general patterns? *Ecology Letters* 11(5): 499-515

564 Ricou C, Schneller C, Amiaud B, Plantureux S, Bockstaller C (2014) A vegetation-based indicator to
565 assess the pollination value of field margin flora. *Ecological Indicators* 45: 320-331

566 Rivers-Moore J, Andrieu E, Vialatte A, Ouin A (2020) Wooded semi-natural habitats complement
567 permanent grasslands in supporting wild bee diversity in agricultural landscapes. *Insects* 11(11): 812

568 Rollin O, Bretagnolle V, Decourtye A, Aptel J, Michel N, Vaissière BE, Henry M (2013) Differences of
569 floral resource use between honey bees and wild bees in an intensive farming system. *Agriculture,
570 Ecosystems and Environment* 179: 78-86

571 Rollin O, Pérez-Méndez N, Bretagnolle V, Henry M (2019). Preserving habitat quality at local and
572 landscape scales increases wild bee diversity in intensive farming systems. *Agriculture, Ecosystems
573 and Environment* 275: 73-80

574 Spaethe J, Tautz J, Chittka L (2001) Visual constraints in foraging bumblebees: flower size and color
575 affect search time and flight behavior. *Proceedings of the National Academy of Sciences* 98(7): 3898-
576 390

577 Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharnkte T (2002) Scale-dependent effects of
578 landscape context on three pollinator guilds. *Ecology* 83(5): 1421-1432

579 Strobl C, Boulesteix A-L, Zeileis A, Hothorn T (2007) Bias in random forest variable importance
580 measures: illustrations, sources and a solution. *BMC Bioinformatics* 8(1): 25

581 Strobl C, Boulesteix A-L, Kneib T, Augustin T, Zeileis A (2008) Conditional variable importance for
582 random forests. *BMC Bioinformatics* 9(1): 307

583 Sutherland JP, Sullivan MS, Poppy GM (1999) The influence of floral character on the foraging
584 behaviour of the hoverfly, *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata*, 93(2): 157-
585 164

586 Timberlake TP, Vaughan IP, Memmott J (2019). Phenology of farmland floral resources reveals
587 seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology* 56(7): 1585-1596

588 Turner MG (1989) Landscape ecology: The effect of pattern on process. *Annual Review of Ecology*
589 *and Systematics* 20(1): 171-197

590 Twerski A, Albrecht H, Fründ J, Moosner M, Fischer C (2022) Effects of rare arable plants on flower-
591 visiting wild bees in agricultural fields. *Agriculture, Ecosystems and Environment* 323: 107685

592 van Rijn PCJ, Wäckers FL (2016) Nectar accessibility determines fitness, flower choice and abundance
593 of hoverflies that provide natural pest control. *Journal of Applied Ecology* 53(3): 925-933

594 Vanreusel W, Van Dyck H (2007) When functional habitat does not match vegetation types: A
595 resource-based approach to map butterfly habitat. *Biological Conservation* 135(2): 202-211

596 Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*. Fourth edition. Springer.

597 Venturini EM, Drummond FA, Hoshida AK, Dibble AC, Stack LB (2017) Pollination reservoirs for wild
598 bee habitat enhancement in cropping systems: a review. *Agroecology and Sustainable Food Systems*
599 41(2): 101-142

600 Vialatte A, Tsafack N, Hassan DA, Duflot R, Plantegenest M, Ouin A, Villenave-Chasset J, Ernoult A
601 (2017) Landscape potential for pollen provisioning for beneficial insects favours biological control in
602 crop fields. *Landscape Ecology* 32(3): 465-480

603 Welti EAR, Joern A (2018) Fire and grazing modulate the structure and resistance of plant–floral
604 visitor networks in a tallgrass prairie. *Oecologia* 186(2): 517-528

605 Williams NM, Kremen C (2007) Resource distributions among habitats determine solitary bee
606 offspring production in a mosaic landscape. *Ecological applications* 17(3): 910-921.

607 Williams NM, Regetz J, Kremen C (2012) Landscape-scale resources promote colony growth but not
608 reproductive performance of bumble bees. *Ecology* 93(5): 1049-1058

609 Winfree R, Aguilar R, Vázquez DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to
610 anthropogenic disturbance. *Ecology* 90(8): 2068-2076

611 Zhang D (2022) rsq: R-Squared and Related Measures. R package version 2.5.

612

613 **Statements and declarations**

614 *Funding*

615 This work was supported by the Zone Atelier Armorique. Audrey Alignier has received research
616 support for the FLORAG project (2020) and Nathan Lenestour's internship, and Stéphanie Aviron has
617 received research support for the DIVAG project (2019).

618 *Competing interest*

619 The authors declare that they have no known competing financial interests or personal relationships
620 that could have appeared to influence the work reported in this paper.

621 *Author contributions*

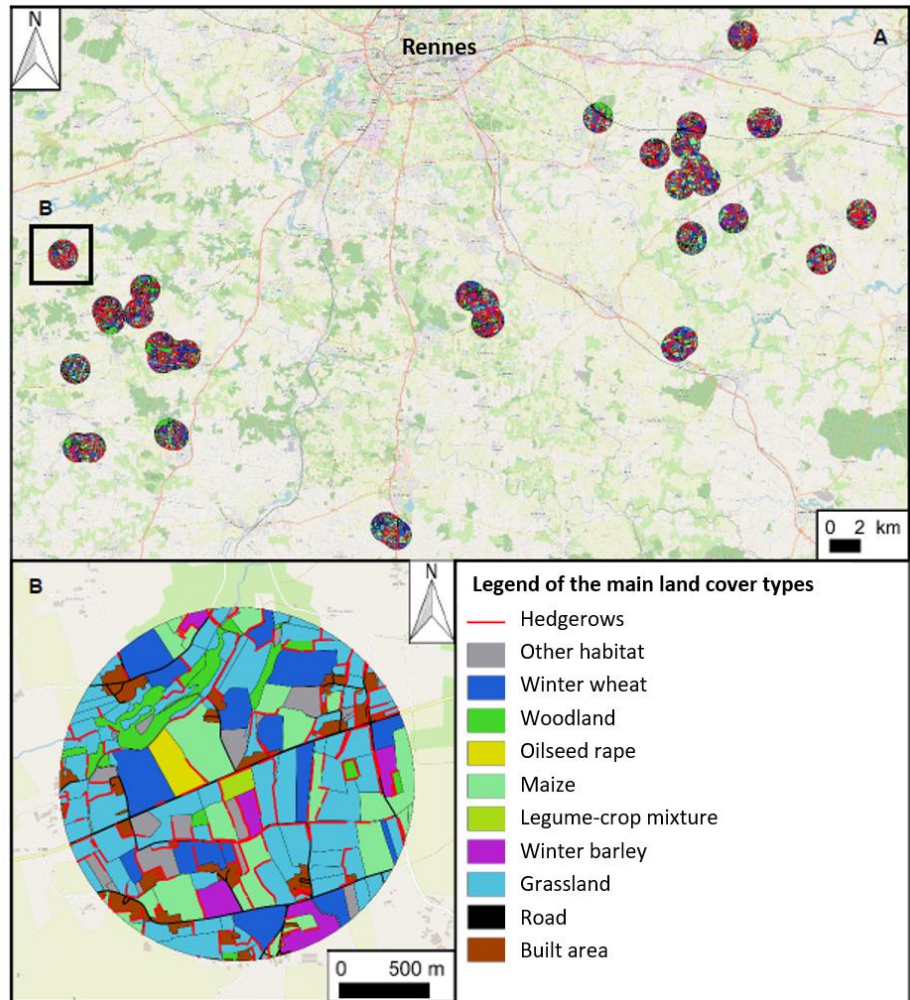
622 Audrey Alignier, Stéphanie Aviron, Cécile Le Lann and Joan van Baaren contributed to the study
623 conception and design. Material preparation and data collection were performed by Nathan
624 Lenestour, Emma Jeavons, Léa Uroy and Claire Ricono. Data analysis was performed by Nathan
625 Lenestour and Audrey Alignier. The first draft of the manuscript was written by Audrey Alignier and all
626 authors commented on previous versions of the manuscript. All authors read and approved the final
627 manuscript.

628 *Consent for publication*

629 All authors gave their consent for publication.

630 *Data availability*

631 The datasets analysed during the current study are available from the corresponding author on
632 reasonable request.



633

634 **Fig. 1** (A) Location of the 39 landscapes in the study area and (B) illustration of the main land-cover

635 types in a 1000 m radius buffer landscape



636

637 **Fig. 2** Representation of a functional landscape (i.e. the empirical nectar productivity in a 1000 m

638 buffer radius landscape). The landscape shown is the same as in Figure 1

639 **Table 1** Main land-cover types (ranked according to their total amount overall in the 39 landscapes)
 640 and information on the data used (sampling year, number of plots [e.g. crop fields, woodlots or
 641 hedgerows], number of quadrats per plot and quadrat size) to characterise their plant communities.
 642 For details of studies, see Appendix A

Land-cover type	Year	No. plots	No. quadrats per plot	Quadrat size ¹	Total amount (%)
Grassland	2018	4	10	1 m × 1 m	29.14
	2018	36	10	2 m × 2 m	
Winter cereal	2019	31	10	1 m × 1 m	22.08
	2018	9	10	1 m × 1 m	
Maize	2013-2014	37	20	1 m × 1 m	17.14
	2018	3	10	1 m × 1 m	
Woodland	2018	40	8	10 m × 5 m	7.74
Built area	/	/	/		7.19
Oilseed rape	/	/	/		3.30
Road	/	/	/		1.97
Legume-cereal mixture	2018	15	10	1 m × 1 m	1.94
	2019	5	10	1 m × 1 m	
	2018	10	10	1 m × 1 m	
Hedgerow	2019	40	10	1 m × 1 m	0.74

643 ¹The sampled area (i.e. number of plots x quadrat size) corresponded to the minimal area recommended for
 644 each land-cover type (Mueller-Dombois and Ellenberg 1974).

645 **Table 2** List of floral traits retained and the trait category to which they belong (attractivity,
 646 accessibility and profitability of floral resources)

Category	Trait	Continuous variable - Unit	Categorical variable - Modality	% data available
Attractivity	Mean UV reflection	%	/	67
	Min size of floral unit	mm	/	100
	Max size of floral unit	mm	/	100
	Plant height	/	Short/Intermediate/Tall	100
Accessibility	Flowering duration	months	/	100
	Flower symmetry	/	Actinomorphy / Zygomorphy	93
	Flower morphology	/	Flat/Tube/Catkin ¹	98
Profitability	Empiric nectar productivity	kg /ha /year	/	70

647 ¹ 'Catkin' refers to flower morphology of some ligneous species such as sweet chestnut (*Castanea sativa*) or hazel
 648 (*Corylus avellana*). See Appendix D for illustration.

649 **Table 3** Results of the selection of ‘important’ variables (i.e. Community Weighted Mean of floral
 650 traits) according to random forests performed at field and landscape scales

Insect group	Scale	Buffer radius	CWM of trait	Trait category
Small wild bees < 1cm	Field		Min size of floral unit ¹	Attractivity
			Max size of floral unit ¹	Attractivity
			Plant height [Intermediate]	Attractivity
			Flowering duration	Accessibility
	Landscape	250	Mean UV reflection	Attractivity
		250	Flower morphology [Tube]	Accessibility
		1000	Empiric nectar productivity	Profitability
Big wild bees > 1cm	Field		Mean UV reflection	Attractivity
	Landscape	1000	Flower morphology [Catkin]	Accessibility
Domestic bees	Field		Flowering duration	Accessibility
	Landscape	1000	Flower morphology [Tube]	Accessibility
		1000	Empiric nectar productivity	Profitability
Bumblebees	Field		Plant height [Intermediate]	Attractivity
			Flowering duration	Accessibility
	Landscape	1000	Empiric nectar productivity	Profitability
Hoverflies	Field		-	-
	Landscape	1000	Plant height [Short] ²	Attractivity
		1000	Flower symmetry [Actinomorphy] ²	Accessibility
		1000	Flower morphology [Flat] ²	Accessibility

651 ¹ Variables highly correlated (Spearman ρ coefficient = 0.96). Only *Min size of floral unit* (the most important
 652 variable according to the random forests results) was introduced into models. ² Variables highly correlated (ρ
 653 ≥ 0.89). Only *Flower symmetry [Actinomorphy]* with a higher ‘importance’ value in random forest was
 654 introduced into further models.

Table 4 Model-averaged standardised estimates from generalised linear models (GLMs) of the abundances of each flower-visiting insect group in relation to the ‘important’ variables selected by random forests. In bold, significant variables i.e. the 95% confidence interval (CI) that do not overlap with zero.

Explained variance (R^2) was calculated for the best fitting model i.e. with the minimum AICc value.

Insect group	Trait category	Variable	Spatial scale	Estimate	St.E	CI 2.5%	CI 97.5%	R^2 best
Small wild bees ¹ < 1cm		Intercept		0.821	0.206	0.403	1.240	0.007
	Attractivity	Min size of floral unit	field	0.535	0.298	-0.057	1.126	
	Accessibility	Flowering duration	field	-0.099	0.215	-0.523	0.326	
	Attractivity	Mean UV reflection	250	-0.821	0.257	-1.342	-0.299	
	Accessibility	Flower morphology [Tube]	250	0.777	0.239	0.292	1.263	
	Profitability	Empiric nectar productivity	1000	0.375	0.337	-0.292	1.043	
Large wild bees > 1 cm		Intercept		1.152	0.215	0.716	1.587	0.04
	Profitability	Mean UV reflection	field	0.166	0.227	-0.285	0.617	
	Accessibility	Flower morphology [Catkin]	1000	0.120	0.205	-0.287	0.528	
Domestic bees		Intercept		1.071	0.227	0.612	1.530	0.22
	Accessibility	Flowering duration	field	0.027	0.133	-0.241	0.295	
	Accessibility	Flower morphology [Tube]	1000	0.169	0.234	-0.297	0.636	
	Profitability	Empiric nectar productivity	1000	0.838	0.255	0.322	1.355	
Bumblebees		Intercept		1.703	0.166	1.366	2.041	0.03
	Attractivity	Plant height [Intermediate]	field	-0.008	0.090	-0.190	0.174	
	Accessibility	Flowering duration	field	-0.122	0.203	-0.525	0.281	
	Profitability	Empiric nectar productivity	1000	0.477	0.244	-0.009	0.963	
Hoverflies		Intercept		2.142	0.167	1.826	2.484	0.11
	Accessibility	Flower symmetry [Actino.]	1000	0.369	0.170	0.064	0.677	

¹ The variable ‘Plant height [Intermediate]’ was not retained in the multi-model inference procedure and thus does not appear.

Table 5 Spearman correlation coefficients between significant traits from the model-averaging procedure and main land-cover types at 250, 500 and, 1000 m. Bold values indicate Spearman *rho* coefficients > |0.7|

	Mean UV reflection 250 m	Flower shape [Tube] 250 m	Flower symmetry [Actino.] 1000 m	Empiric nectar productivity 1000 m
Grassland - 250 m	-0.04	0.62	0.55	0.22
Grassland - 500 m	0.06	0.41	0.57	0.40
Grassland - 1000 m	-0.04	0.24	0.34	0.60
Woodland - 250 m	-0.02	-0.33	-0.32	0.35
Woodland - 500 m	0.18	-0.06	-0.29	0.55
Woodland - 1000 m	0.28	0.06	-0.18	0.72
Hedgerow - 250 m	0.20	0.47	0.48	-0.06
Hedgerow - 500 m	-0.02	0.26	0.35	-0.16
Hedgerow - 1000 m	-0.05	-0.005	0.29	-0.16
Legume-crop mixture - 250 m	0.23	0.49	-0.06	0.07
Legume-crop mixture - 500 m	-0.13	0.07	-0.26	0.05
Legume-crop mixture - 1000 m	-0.16	0.01	-0.16	0.09
Oilseed rape - 250 m	0.41	-0.28	-0.25	-0.16
Oilseed rape - 500 m	0.28	-0.11	-0.09	-0.09
Oilseed rape - 1000 m	0.10	-0.33	-0.40	-0.16
Winter cereal - 250 m	0.42	0.12	-0.04	-0.22
Winter cereal - 500 m	0.25	-0.06	-0.17	-0.26
Winter cereal - 1000 m	-0.05	-0.10	0.12	-0.38
Maize - 250 m	0.19	-0.002	0.24	-0.06
Maize - 500 m	-0.06	0.21	0.51	-0.06
Maize - 1000 m	0.01	0.15	0.46	-0.60

Appendix A Protocol details and references of projects used for exhaustive vegetation data

Land-cover type	Year	Project	Total species richness	No. species 'filtered' ¹	Protocol details	References
Grassland	2018	SEBIOPAG	108	51	Quadrats located 5 m apart, 50 m away from the field margin	Ricci et al. (2019)
	2018	BISCO			Quadrats evenly distributed, at least 5 m away from the field margin	Uroy (2020)
Winter cereal	2019	AGRIM	112	95	Quadrats evenly distributed, at least 10 m away from the field margin	Ricono (2021)
	2018	SEBIOPAG			Quadrats located 5 m apart, 50 m away from the field margin	Ricci et al. (2019)
Maize	2013-2014	FARMLAND	96	45	Quadrats located along two transects, one at 1 m away from the field margin, the other at 25 m away from the field margin	Alignier et al. (2020)
	2018	SEBIOPAG			Quadrats located 5 m apart, 50 m away from the field margin	Ricci et al. (2019)
Woodland	2018	BISCO	146	36	quadrats evenly distributed, at least 5 m away from the field margin	Uroy (2020)
Legume-cereal	2018	DIVAG	124	63	Quadrats located 5 m apart, 25 m away from the field margin	Aviron et al. (in prep)
	2019	AGRIM			Quadrats evenly distributed, at least 10 m away from the field margin	Ricono (2021)
	2018	Berry internship			Quadrats located 5 m apart, 25 m away from the field margin	Aviron et al. (in revision)
Hedgerow	2019	AGRIM	193	76	Quadrats located 5 m apart	Ricono (2021)

¹ Number of species among the 95 dicotyledon species 'filtered'. See Appendix B for details about species selection.

Alignier A, Solé-Senan X, Robleño I, Baraibar B, Fahrig L, Giralte D, Gross N, Martin, J-L, Recasens, J, Sirami C, Siriwardena G, Baillod A, Bertrand C, Carrié R, Hass A, Henckel L., Miguet P, Badenhauer I, Baudry J, Bota G, Bretagnolle V, Brotons L, Burel F, Calatayud F, Clough Y, Georges R, Gibon A, Girard J, Lindsay K, Minano J, Mitchell S, Patry N, Poulin B, Tschardt T, Vialatte A, Violle C, Yaverkovski N., Batáry P (2020) Configurational crop heterogeneity increases within-field plant diversity. *Journal of Applied Ecology* 57(4): 654-663

Aviron S, Berry T, Leroy D, Savary G, Alignier A (in revision) Wild plants in hedgerows and weeds in crop fields are important floral resources for wild flower-visiting insects, independently of the presence of intercrops.

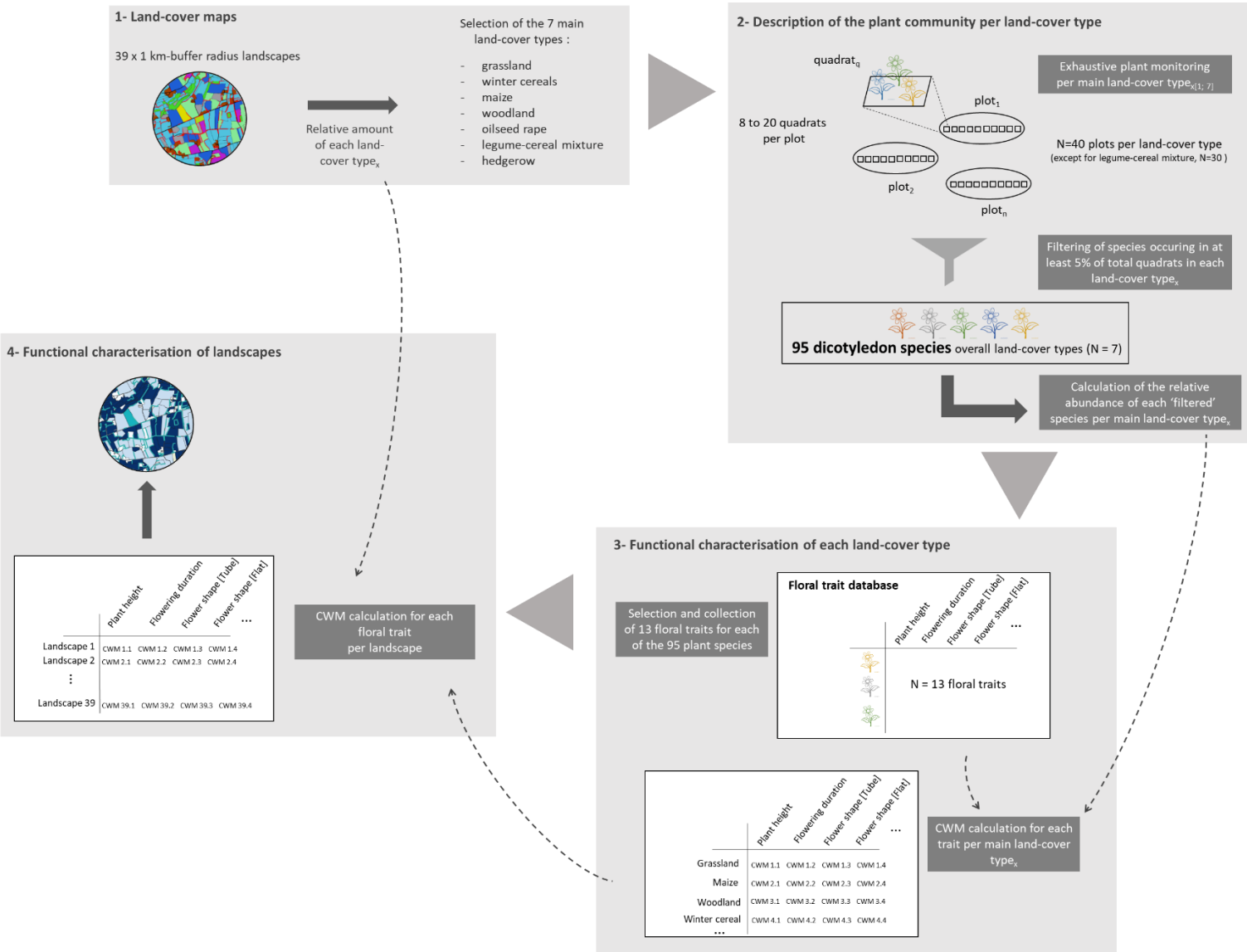
Aviron S, Berry T, Jeavons E, Le Lann C, Leroy D, van Baaren J, Alignier A (in prep) Contribution of floral resources provided by crops, weeds and wild plants in supporting wild pollinating insects in agricultural landscapes

Ricci B, Lavigne C, Alignier A, Aviron S, Biju-Duval L, Bouvier JC, Choisis JP, Franck P, Joannon A, Ladet S, Mezerette F, Plantegenest M, Savary G, Vialatte A, Petit S (2019) Local pesticide use intensity conditions landscape effects on biological pest control. *Proceedings of the Royal Society B* 286(1904) : 20182898

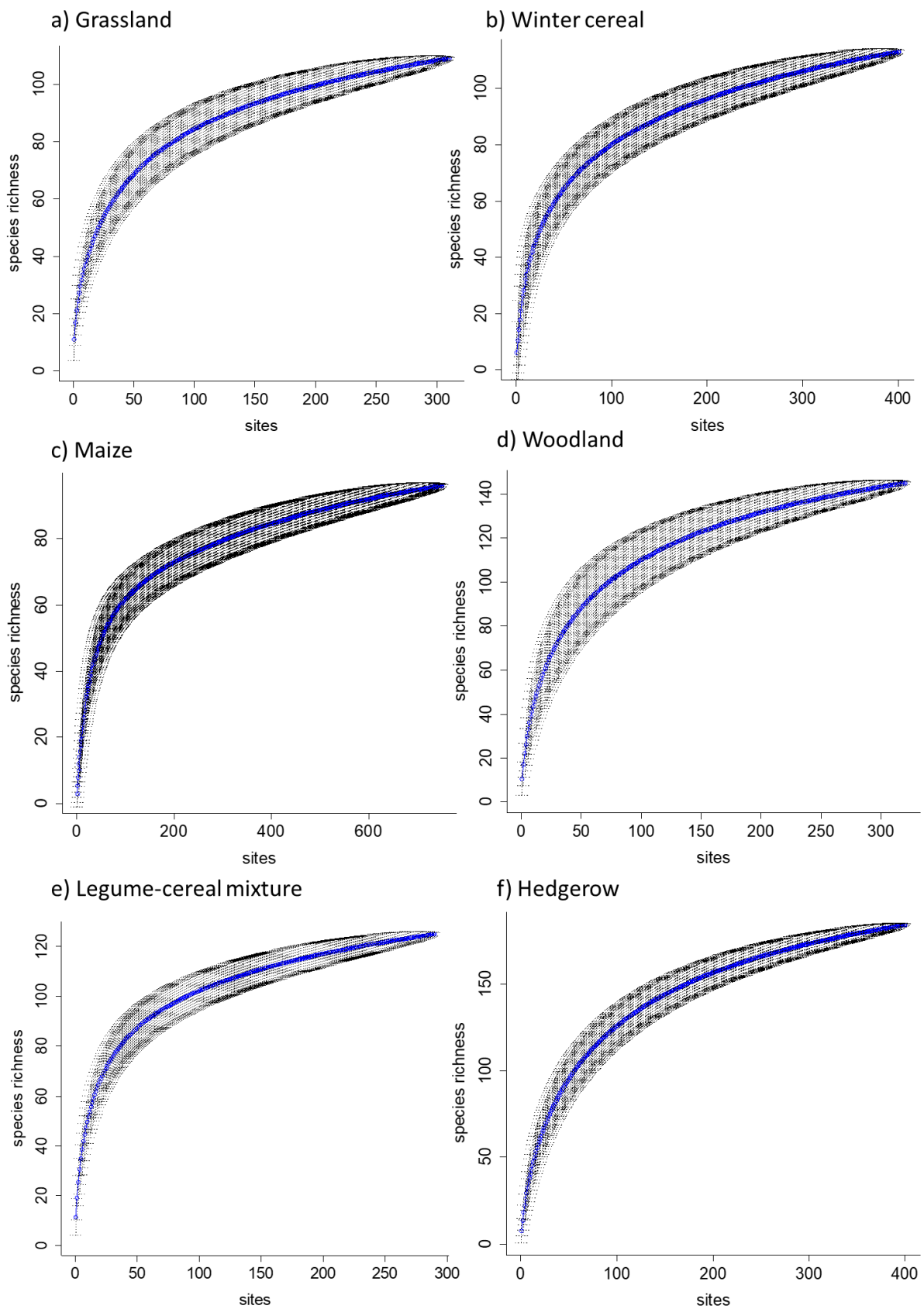
Ricono C (2021) Effets des pratiques agricoles biologiques en contexte bocager sur le microbiote du blé et ses fonctions associées. PhD Dissertation, University of Rennes

Uroy L (2020) Effet de la connectivité et de sa dynamique temporelle sur la structuration taxonomique et fonctionnelle des communautés végétales. PhD Dissertation, University of Rennes

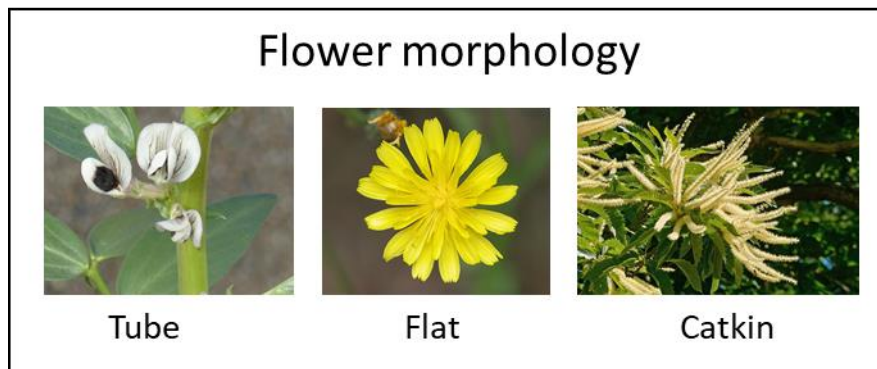
Appendix B Flowchart of the successive steps used to obtain Community Weighted Mean (CWM) values of each floral trait per landscape



Appendix C Species accumulation curves for main land-cover types



Appendix D Illustration of the three traits modalities for *Flower morphology*



Appendix E Community Weighted Mean (CWM) values of each floral trait for each main land-cover type.

	Mean UV reflexion	Min size of floral unit	Max size of floral unit	Plant height [Short]	Plant height [Intermediate]	Plant height [Tall]	Flowering duration	Flower symmetry [Actino.]	Flower symmetry [Zygo.]	Flower morpho. [Catkin]	Flower morpho. [Flat]	Flower morpho. [Tube]	Empiric nectar productivity
Grassland	9.20	17.35	28.02	0.76	0.24	0.00	6.26	0.63	0.37	0.00	0.56	0.37	466.68
Woodland	10.93	24.30	41.45	0.50	0.32	0.18	3.85	0.71	0.09	0.21	0.72	0.07	405.85
Maize	13.40	14.28	23.77	0.90	0.10	0.00	6.66	0.77	0.23	0.00	0.79	0.20	67.16
Legume-crop mix	14.11	14.31	24.04	0.52	0.48	0.00	4.61	0.42	0.58	0.00	0.43	0.57	138.00
Winter cereals	14.40	11.06	18.74	0.86	0.14	0.00	6.54	0.69	0.31	0.00	0.76	0.23	170.46
Hedgerow	12.31	14.74	27.69	0.23	0.62	0.15	4.18	0.75	0.11	0.18	0.71	0.11	199.79
Oilseed rape	21.50	20.00	30.00	0.00	1.00	0.00	5.00	1.00	0.00	0.00	1.00	0.00	268.11

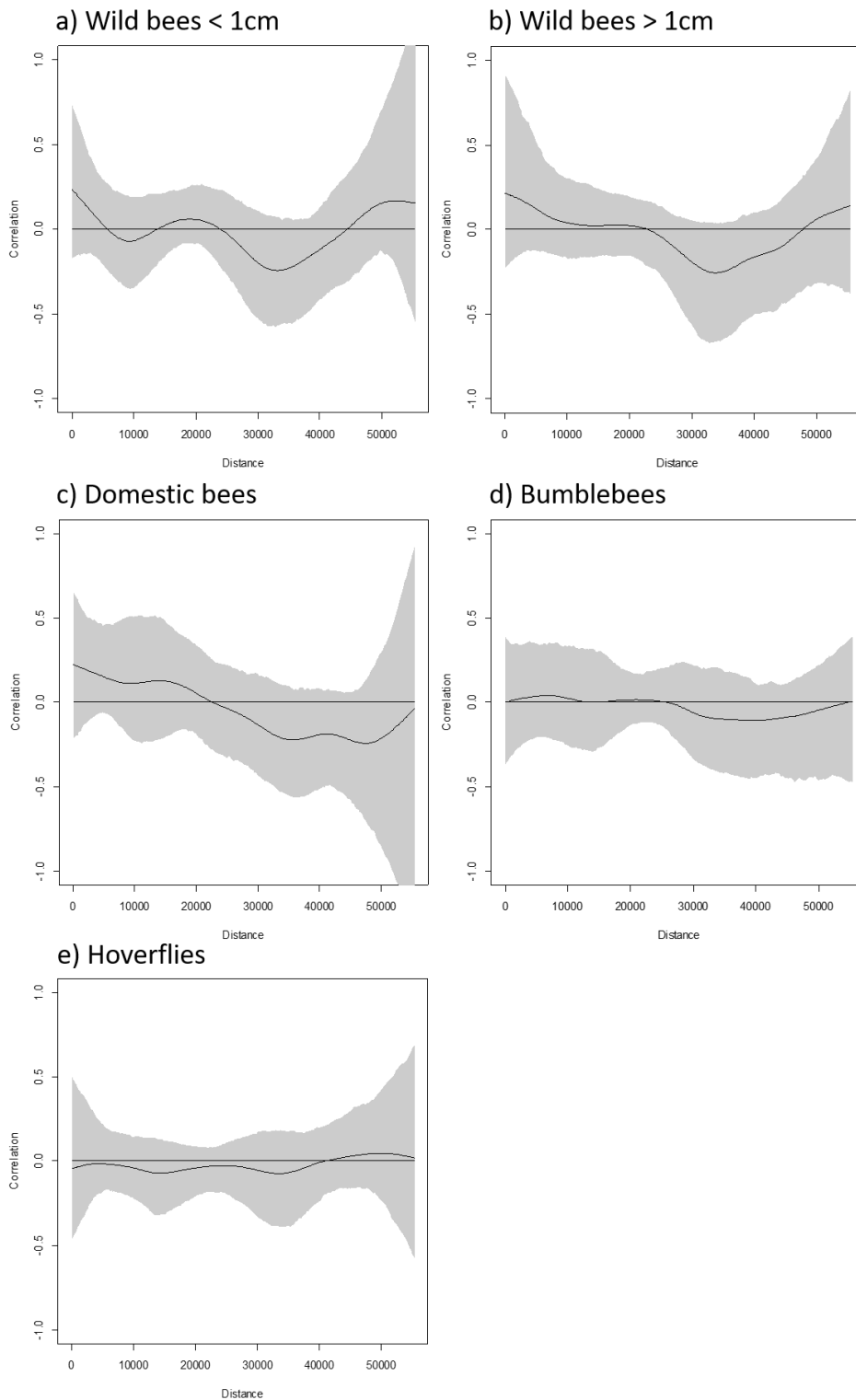
Appendix F Spearman correlation coefficients between Community Weighted Mean (CWM) values of each floral trait, at the field scale. Bold values indicate Spearman *rho* coefficients > |0.7|

	Mean UV reflection	Min size of floral unit	Max size of floral unit	Plant height [Intermediate]	Plant height [Short]	Plant height [Tall]	Flowering duration	Flower symmetry [Actino.]	Flower symmetry [Zygo.]	Empiric nectar productivity	Flower morpho. [Catkin]	Flower morpho. [Flat]	Flower morpho. [Tube]
Mean UV reflection	1.00	0.16	0.17	0.04	-0.04	-0.16	0.10	0.25	-0.25	-0.40	-0.05	0.18	-0.18
Min size of floral unit	0.16	1.00	0.96	0.37	-0.37	0.11	-0.08	-0.01	0.00	0.15	0.27	-0.04	0.02
Max size of floral unit	0.17	0.96	1.00	0.45	-0.46	0.02	-0.24	-0.13	0.12	0.08	0.20	-0.19	0.17
Plant height [Intermediate]	0.04	0.37	0.45	1.00	-1.00	-0.26	-0.66	-0.71	0.70	0.01	-0.09	-0.67	0.66
Plant height [Short]	-0.04	-0.37	-0.46	-1.00	1.00	0.24	0.66	0.70	-0.70	-0.01	0.09	0.66	-0.66
Plant height [Tall]	-0.16	0.11	0.02	-0.26	0.24	1.00	0.41	0.32	-0.33	0.30	0.79	0.44	-0.44
Flowering duration	0.10	-0.08	-0.24	-0.66	0.66	0.41	1.00	0.75	-0.76	0.31	0.33	0.81	-0.81
Flower symmetry [Actino.]	0.25	-0.01	-0.13	-0.71	0.70	0.32	0.75	1.00	-1.00	0.13	0.26	0.92	-0.93
Flower symmetry [Zygo.]	-0.25	0.00	0.12	0.70	-0.70	-0.33	-0.76	-1.00	1.00	-0.14	-0.27	-0.93	0.93
Empiric nectar productivity	-0.40	0.15	0.08	0.01	-0.01	0.30	0.31	0.13	-0.14	1.00	0.25	0.25	-0.24
Flower morpho. [Catkin]	-0.05	0.27	0.20	-0.09	0.09	0.79	0.33	0.26	-0.27	0.25	1.00	0.34	-0.35
Flower morpho. [Flat]	0.18	-0.04	-0.19	-0.67	0.66	0.44	0.81	0.92	-0.93	0.25	0.34	1.00	-1.00
Flower morpho. [Tube]	-0.18	0.02	0.17	0.66	-0.66	-0.44	-0.81	-0.93	0.93	-0.24	-0.35	-1.00	1.00

Appendix G Spearman correlation coefficients between Community Weighted Mean (CWM) values of each floral trait, at the landscape scale (i.e. 250, 500 and 1000 m). Bold values indicate Spearman *rho* coefficients > |0.7|

See attached excel file

- 1 **Appendix H** Spatial correlograms (plotting Moran's I values against distance in metres) of
- 2 Generalized Linear Models residuals for each flower-visiting insect group. The 95 % confidence
- 3 intervals (in grey) always encompass the zero-value, indicating the absence of spatial
- 4 autocorrelation.



5