



**HAL**  
open science

# Nationwide study of the triple landscape gradient across natural, agricultural and urban areas for the richness of flower-visiting insects

James Desaegher, François Chiron, Carmen Bessa-Gomes

## ► To cite this version:

James Desaegher, François Chiron, Carmen Bessa-Gomes. Nationwide study of the triple landscape gradient across natural, agricultural and urban areas for the richness of flower-visiting insects. *Biological Conservation*, 2023, 288, pp.110355. 10.1016/j.biocon.2023.110355 . hal-04295167

**HAL Id: hal-04295167**

**<https://agroparistech.hal.science/hal-04295167>**

Submitted on 17 Jul 2024

**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.

1 **Nationwide study of the triple landscape gradient across natural, agricultural and urban areas**  
2 **for the richness of flower-visiting insects**

3  
4 James Desaegher<sup>1,2\*</sup>, Francois Chiron<sup>1</sup>, Carmen Bessa-Gomes<sup>1</sup>

5  
6 Author affiliations:

7  
8 <sup>1</sup>Laboratoire Ecologie Systématique et Evolution, Université Paris-Saclay, CNRS, AgroParisTech,  
9 91190, Gif-Sur-Yvette, France

10 <sup>2</sup>INRAE, UR406 Abeilles et Environnement, Avignon, 84000, France

11 \*Corresponding author: james.desaegher@inrae.fr, UR 406 Abeilles et Environnement  
12 CS 40509 Domaine St Paul - Site Agroparc 84914 Avignon Cedex 9, France

13

14 **Authors' contributions**

15 James Desaegher: conceptualisation, methodology, formal analysis, writing – original draft,  
16 visualisation. François Chiron: funding acquisition, project administration, conceptualisation, writing –  
17 review & editing. Carmen Bessa-Gomes: conceptualisation, methodology, supervision, writing – review  
18 & editing.

19

20 **Funding**

21 This study is part of the FONTE project ‘Gestion des territoires et biodiversité fonctionnelle’, which is  
22 financially supported by the Agence Française de la Biodiversité (Office Français de la Biodiversité)  
23 and CeMEB Labex.

24

25 **Acknowledgments**

26 The authors would like to thank the SPIPOLL participants for their essential contribution to the data  
27 collection. We are grateful to the members of the Office Pour les Insectes et leur Environnement (OPIE)  
28 and the Muséum National d’Histoire Naturelle (Centre d’Ecologie et des Sciences de la Conservation,  
29 Vigie-Nature) for the scientific and pedagogical organisation of the programme and their validation of  
30 the taxonomic identifications. We also thank Victoria Grace for editing the English text and two  
31 anonymous reviewers for improving quality of the manuscript.

32

33 **Highlights**

- 34 • Urbanisation negatively impacts the total richness of flower visitors
- 35 • Agricultural and semi-natural areas have interactive effects on insect richness
- 36 • Maximum richness occurs in agricultural landscapes with ~30% of semi-natural areas
- 37 • Landscape effects on richness varied according to insect taxa
- 38 • Urban areas were less detrimental to bee richness than intensive agricultural areas

39

40 **Abstract**

41

42 Studies investigating urbanisation effects on pollinator diversity have shown contrasting results, ranging  
43 from predicting urban areas as ecological sinks to possible refuges for pollinators. These divergent  
44 results may stem from the diversity of non-urban areas being compared with urban areas as well as the  
45 existence of interactions among habitats. We tested the interactive effects of urban, agricultural and  
46 semi-natural areas on the richness of flower-visiting insects at the landscape scale. Using the dataset  
47 from a citizen science programme, we investigated how the richness pattern varied (i) along the triple  
48 gradient across urban, agricultural and semi-natural areas and (ii) among the different visitor taxa. We  
49 stratified the dataset to have a balanced landscape composition and spatial distribution of sampling sites  
50 for each plant species sampled. Accounting for general sampling factors (e.g., plant species,  
51 temperature, shading, time of observation), we showed that urbanisation negatively impacted the total  
52 richness of flower visitors, especially when associated with agricultural areas. We observed maximum  
53 richness in agricultural landscapes composed of ~30% of semi-natural areas, thus suggesting synergistic  
54 effects between these land uses on insect richness. Our results showed contrasting richness patterns for  
55 different taxa. For bees, urban areas were less detrimental to richness than agricultural areas. By contrast,  
56 for syrphids and butterflies, richness was highest in agricultural and semi-natural areas, respectively.  
57 Our study revealed the necessity to distinguish among rural areas when studying urbanisation gradients  
58 and highlighted synergistic landscape effects that could help inform landscape planners about how to  
59 attract a diversity of flower visitors.

60

61 **Keywords:** agriculture, urbanization, semi-natural, pollination, Spipoll, citizen science

62

63

64 **1 Introduction**

65 For a quarter of a century, growing evidence has demonstrated that flower-visiting entomofauna is  
66 threatened (Kearns et al. 1998; Biesmeijer et al. 2006; Ollerton et al. 2014; Hallmann et al. 2017; Powney  
67 et al. 2019).<sup>1</sup> For instance, based on data from several European countries with red lists, it was estimated  
68 that nearly 9% of bee and butterfly species are considered threatened (Nieto et al. 2014). Hereafter  
69 ‘flower visitors’ refers to insects that visit flowers, usually to feed on their resources, and mainly belong  
70 to Hymenoptera, Diptera, Lepidoptera and Coleoptera. Changes in the abundance and diversity of flower  
71 visitors, particularly those who are efficient pollinators, are likely to have dramatic cascading effects on  
72 plants, since the vast majority of wild plant species (Ollerton et al. 2011) as well as crops (Klein et al.  
73 2007; Gallai et al. 2009) depend on insects for their reproduction. The cause of flower visitor-species  
74 extinction and population decline is multifactorial, although agricultural intensification and semi-natural  
75 habitat loss are likely to be particularly harmful to species richness and abundance (Winfree et al. 2009).  
76 Urban expansion and agricultural intensification are the two major anthropogenic land-use changes  
77 responsible for the loss of natural habitats (United Nations 2014; Agreste 2021).

78 Although it is frequently shown that urban areas are an adverse environment for flower visitors  
79 compared with the surrounding rural areas (Ahrné et al. 2009; Bates et al. 2011; Deguines et al. 2012;  
80 Geslin et al. 2016; Desaegher et al. 2018), many studies have highlighted that urban areas are a potential  
81 refuge for some taxa (Baldock et al. 2015; Hall et al. 2017; Levé et al. 2019). These contrasting results  
82 may be due to the regional context of the study areas, and particularly, the nature of rural areas that are  
83 compared with urban areas (Wenzel et al. 2020). Rural areas, also known as the countryside, can include  
84 both natural and agricultural areas. Yet it is unclear how landscapes affect the richness of flower visitors  
85 when urban sites are compared with rural areas that have a variable proportion of natural and agricultural  
86 land uses (Verboven et al. 2014).

87 In the context of global insect population declines, partly caused by anthropogenic land-use  
88 changes, it is crucial to identify the specificity and complementarity among habitats in terms of  
89 entomological composition (Collado et al. 2019). Studying landscape gradients, though less frequent  
90 than categorical comparisons in urban ecology (Wenzel et al. 2020), enables the identification of  
91 continuous and non-linear effects (e.g., break points, local maxima; McDonnell and Hahs 2008). Using  
92 a gradient-based experimental design, Fortel et al. (2014) identified the maximum bee diversity at  
93 intermediate levels of urbanisation (~50%), which was interpreted as a possible consequence of the  
94 maximum land-use diversity (known as the *intermediate disturbance hypothesis*; Kolasa and Rollo  
95 1991). Clustering different land uses together, which increases land-use diversity, is often hypothesised  
96 to promote a maximum biodiversity, as it could support species necessitating the complementation and  
97 supplementation among distinct habitats at the landscape scale (Colding 2007) and also allows the

---

<sup>1</sup> Abbreviations: AICc, corrected Akaike information criterion; EDF, effective degree of freedom; GAM, generalised additive model; GLM, generalised linear model; HAC, hierarchical ascendant classification; PCA, principal component analysis; UAN, urban-agricultural-semi-natural.

98 presence of species with different niches. In addition, the *area-heterogeneity trade off hypothesis*,  
99 supposes that increasing heterogeneity in a limited space may initially increase species richness, but  
100 above a certain threshold could lead to a richness decrease due to the reduction of the average habitat  
101 area and the higher risks of stochastic extinctions (Kadmon and Allouche 2007; Allouche et al. 2012).  
102 The likelihood of extinctions would be particularly important for species with narrow niches. In the case  
103 of insect richness along urbanisation gradients, we could also expect that the loss of habitats due to  
104 urbanisation outweighs the increase in land-use diversity and lead to a richness decrease (Desaegher et  
105 al. 2018). Exploring non-linear patterns of insect richness along landscape gradients is essential, since  
106 the maxima of richness may occur in sites where all urban, agricultural and natural areas that are easily  
107 accessible to insects.

108 To date, the effects of anthropogenic disturbance have mostly been studied on bees despite the  
109 important role played by other flower visitors on ecosystem functions and services (i.e., biocontrol,  
110 pollination; Wenzel et al. 2020). Non-bee taxa such as hoverflies and butterflies strongly differ in their  
111 life cycle and niche width compared with bees and may respond differently to anthropogenic  
112 perturbations and complex landscape interactions. For instance, bees act as central place foragers (i.e.,  
113 foraging around a fixed nest) and may particularly depend on landscape  
114 complementation/supplementation compared to other taxa (Verboven et al. 2014). Therefore, we can  
115 expect different richness patterns along landscape gradients according to insect taxa.

116 In the present study, we used a remarkably large dataset generated by an ongoing French citizen  
117 science programme (SPIPOLL) that has been recording flower-visiting insects across the entire country  
118 over a 10-year period (Deguines et al. 2012). We tested the hypothesis of a positive interaction among  
119 three land-cover classes (i.e., urban, agricultural and semi-natural areas) on the richness of flower  
120 visitors at the landscape scale. This large dataset that covers a wide range of landscapes allowed us to  
121 consider for the first time the interactive and non-linear effects of landscape composition variables on  
122 different insect taxa along the triple urban-natural-agricultural gradient. We aimed to respond to the  
123 following questions: (i) What is the average pattern of flower visitor richness along the triple landscape  
124 gradient? (ii) What are the land-use associations responsible for the local maxima or minima of richness?  
125 (iii) How do landscape effects differ among taxa?

126

## 127 **2 Materials and methods**

128

### 129 **2.1 Citizen science programme and protocol**

130

131 In the present study, we used data collected from the French citizen science programme called SPIPOLL  
132 (Suivi Photographique des Insectes POLLinisateurs). This programme was initiated by the Muséum  
133 national d'Histoire naturelle (MNHN) and the Office pour les insectes et leur environnement (OPIE) in

134 2010 and is still ongoing ([www.spipoll.org](http://www.spipoll.org); Deguines et al. 2012, 2016, 2018; Desaegher et al. 2018;  
135 Levé et al. 2019).

136 According to the standard sampling protocol, participants have to choose a location with a plant  
137 species in bloom, regardless of the time and place, in France. The first step is to photograph the plant in  
138 order to identify the species and gather information about the local environment. Participants are then  
139 asked to take photographs of the different insects landing on the flowers of the focal plant species, within  
140 a radius of 5 m for a period of 20 min. Hereafter, a 20 min session is called a ‘collection’. Participants  
141 are also asked to record basic information about the date and location of the collection as well as the  
142 weather conditions (i.e., temperature, cloud cover, wind speed, shading). At home, participants identify  
143 the plant species and flower visitors using online identification tools. Finally, the participants upload all  
144 the photographs and recorded data to the website dedicated to the programme ([www.spipoll.org](http://www.spipoll.org)). The  
145 majority of identifications are checked by experienced entomologists and botanists involved in the  
146 programme (for more details, see Deguines et al. 2012).

147

## 148 **2.2 Flower visitor richness**

149

150 Using the online identification tool available to participants, flower visitors are classified into predefined  
151 ‘morpho-taxa’ with different taxonomic resolution levels according to the traits observable in the  
152 photographs. For insect species with very distinctive traits, identification to the species or genus is  
153 possible (e.g., *Apis mellifera*), although other insects are classified into morpho-groups (e.g., black  
154 bumblebees with yellow stripes and white tail).

155 As not all insects are identified to the same taxonomical resolution, we could not calculate  
156 taxonomic richness but instead richness in morpho-taxa per collection. Using morpho-taxa richness is  
157 not without potential bias, because some morpho-taxa are taxonomically richer than others.  
158 Nevertheless, morpho-taxa richness per collection represents an informative proxy for insect richness  
159 (Renaud et al. 2020), as it is unlikely that distinct species characterised by the same morpho-taxa group  
160 would visit the focal plants during a 20 min session.

161 In the present study, we aimed to quantify the influence of landscape composition on total insect  
162 richness and to identify how it varies according to the main insect categories. We chose to distinguish  
163 seven categories of flower visitors: 1) bees (i.e., Andrenidae, Apidae, Colletidae, Halictidae,  
164 Megachilidae, Melittidae); 2) other hymenopterans; 3) syrphids (i.e., Syrphidae); 4) other dipterans; 5)  
165 coleopterans; 6) lepidopterans; and 7) other insects. Breaking down the total richness into different  
166 groups allows us to distinguish distinct patterns among groups and to eventually identify the dominant  
167 taxa driving the observed pattern along the triple gradient.

168

## 169 **2.3 Geographic information**

170

171 To characterise the landscape composition around the collections, we used the OSO Theia land-cover  
 172 map for 2020 ([www.theia-land.fr/en/product/land-cover-map/](http://www.theia-land.fr/en/product/land-cover-map/)). This map resulted from the processing  
 173 of time series of satellite images (Sentinel-2), for the year 2020, using the *iota*<sup>2</sup> processing chain  
 174 (<https://docs.iota2.net/master/>). This map is a single raster covering the entire French metropolitan  
 175 territory with a spatial resolution of 10 m and a thematic resolution of 23 land-cover categories. Maps  
 176 at this resolution did not exist before 2018, preventing us to use the actualized maps for each sampled  
 177 year between 2010 and 2020.

178 We calculated the proportion of the 23 land-cover categories within a buffer radius of 1000 m  
 179 around the sampled sites. This radius was chosen because it has been shown to be a good compromise  
 180 to detect the maximum landscape effect related to the average flight distance of most flower visitors  
 181 (i.e., *scale of effect*; Krauss et al. 2003; Meyer et al. 2009; Desaegher et al. 2022). To explore correlations  
 182 among the 23 categories, we performed Principal Component Analysis - PCA (*dudi.pca*, *inertia.dudi*,  
 183 *s.corcircle* functions, R package *ade4*). We grouped the 23 land-cover categories into the following three  
 184 classes: urban areas (i.e., dense built-up areas, diffuse built-up areas, industrial and commercial areas),  
 185 agricultural areas (i.e., winter oilseeds, straw cereals, spring oilseeds, soy, sunflower, maize, rice, tubers  
 186 roots, grasslands, orchards, vineyards) and semi-natural areas (i.e., deciduous forests, coniferous forests,  
 187 natural grasslands, heathland, natural mineral surfaces, beaches and dunes, water, glaciers and eternal  
 188 snow). To account for the fact that insects are expected to interact more with nearby landscape elements  
 189 than with those located further away (Miguet et al. 2017), we calculated what is hereafter called the  
 190 ‘accessibility index’ to urban, agricultural and semi-natural areas using a spatial kernel. For a given  
 191 land-cover class, the accessibility index ranges from 0 to 1 and represents the distance-weighted surface  
 192 proportion of that particular land-cover class. For each sampling site, the accessibility to urban,  
 193 agricultural and semi-natural areas adds up to 1 and can be shown in a triangular diagram known as a  
 194 ternary diagram (*triangle.plot* function, R package *ade4*). The accessibility index for a land cover *Class*  
 195 *i* from a map pixel *p* is calculated using the following formula:

$$196 \quad \text{Class } i \text{ Accessibility}_p = \frac{\sum_{p' \in \text{Class } i} e^{-\frac{D}{\alpha}}}{\sum_{p' \in \Omega} e^{-\frac{D}{\alpha}}}$$

197 Where *D* is the Euclidean distance between pixel *p* and *p'*,  $\alpha$  is a scale parameter related to the average  
 198 foraging distance of insects, and  $\Omega$  is the area including all the pixels *p'* used to investigate the landscape  
 199 effects. In our case, we set  $\alpha$  to 400 m and included in  $\Omega$  all the pixels within a buffer radius of 2500 m  
 200 following Desaegher et al. (2022). The distance of 2500 m is the maximum distance beyond which the  
 201 landscape composition was considered to have negligible effects on insect abundance (noted  $\lambda$  in  
 202 Desaegher et al. 2022).

203

## 204 **2.4 Data selection and stratification**

205

206 The biological dataset was composed of all SPIPOLL collections recorded in the French  
207 metropolitan territory between 2010 and 2020 (excluding Corsica). We excluded collections located less  
208 than 3 km from the French borders to ensure that we had the corresponding geographical data. We only  
209 selected the collections made on plant species identified to the species level. Our initial dataset contained  
210 50570 collections. On this dataset we then applied a double stratification to control for heterogeneous  
211 sampling efforts according to the plant species, landscape composition and spatial distribution of the  
212 sites. The double stratification is detailed hereafter.

213 The first stratification involved classifying the collections according to the sampled plant species  
214 and the distribution of the percentage of accessibility to urban, agricultural and semi-natural areas in the  
215 ternary diagram (Fig. 1). We calculated the Euclidean distance matrix among the collections based on  
216 the percentage of accessibility to these three land-cover classes. For each plant species, we iteratively  
217 ran a hierarchical ascendant classification (HAC) based on this distance matrix using the ‘average’  
218 method (*hclust* function, R package *mgcv*). Landscape clusters, hereafter ‘UAN clusters’, were defined  
219 by cutting the dendrogram at a height of 0.05. This means that if the average difference in accessibility  
220 percentages between the sites included in a cluster and a new site exceeded 5%, this site was not included  
221 in the cluster. The 5% threshold appeared to be a good compromise to have a maximum number of UAN  
222 clusters and a homogeneous distribution in the ternary diagram. Once collections were classified into  
223 UAN clusters, we selected randomly one collection per cluster for each plant species in order to avoid  
224 pseudo-replication and simplify statistical modelling design. To ensure a minimum sample size for each  
225 plant species, we removed all collections made on plant species sampled in less than 10 UAN clusters.

226 When the collections selected from the first stratification were combined into a single dataset,  
227 all plant species combined, the spatial distribution of samples was still heterogeneous. We therefore  
228 applied a second stratification to classify the collections according to their spatial distribution and also  
229 to their distribution in the ternary diagram. This second stratification aimed to control for the size of the  
230 spatial clusters, to avoid that landscape effects were biased by a high number of samples spatially  
231 clustered in a few locations. For that, we first calculated the geographic distance between the sampling  
232 sites and then ran a HAC using the ‘average’ method. Spatial clusters were defined by cutting the  
233 dendrogram at 2500 m. We also redefined the UAN clusters, as with the first stratification and using the  
234 same methodology, by running a HAC based on the percentage of accessibility to urban, agricultural  
235 and semi-natural areas. For each spatial cluster, we selected a maximum of five collections per UAN  
236 cluster, made on different plant species. Therefore, each spatial cluster is controlled to have a similar  
237 weight to estimate the effects of landscape variables. To keep as many sampled plant species as possible  
238 in our dataset, we prioritised the collections made on plant species having the smallest sample size but  
239 sampled in at least 10 UAN clusters.

240 After two stratifications, a total of 4045 collections made up the final dataset (Fig. 2). This  
241 dataset provided information on visits to 200 plant species, with at least 10 collections for each plant  
242 species sampled.



243

## 244 **2.5 Statistical analysis**

245

246 To examine the effects of landscape composition on the richness of flower visitors, we had to control  
247 for several botanical, meteorological, geographical and temporal variables. We opted for a two-step  
248 analysis. Using generalised additive models (GAM) to account for non-linear relationships, we first  
249 explored how non-landscape variables affected insect richness (GAM 1) and in a second step, we  
250 estimated the landscape effects on insect richness (GAM 2) while accounting for the richness predicted  
251 from GAM 1.

252

### 253 **2.5.1 Effects of non-landscape variables on the richness of flower visitors**

254

255 To analyse the variation in the richness of flower visitors, the year, Julian day and hour of sampling  
256 were all declared as smooth terms (i.e., non-linear) using generalised additive models (GAM; *gam*  
257 function, R package *mgcv*). Concerning the Julian day and hour of sampling, both characterised by  
258 cyclic effects on insect richness, we modified the basis function of the smooth terms using cubic cyclic  
259 splines. The hour of the day was transformed into a decimal number between 0 and 24 without  
260 considering daylight-saving changes in winter and summer. In the GAM, we also included the shading  
261 of the sampling site (presence/absence), temperature category (< 10°C, 10-20°C, 20-30°C, > 30°C),  
262 cloud cover (0-25%, 25-50%, 50-75%, 75-100%), wind speed (none, light, strong), sampling region (12  
263 French mainland regions) and plant species, as linear terms. Since we observed overdispersion,  
264 characterised by a quadratic relationship between mean and variance of richness, we used a negative  
265 binomial distribution for the residuals. Using the total insect richness as a response variable, we  
266 performed a model selection procedure based on a set of candidate models containing all possible  
267 explanatory variable combinations ranked by the corrected Akaike information criterion (AICc) using  
268 the *dredge* function (R package *MuMIn*). Based on this model selection procedure, we identified the  
269 best model, hereafter called GAM 1 ( $\Delta\text{AICc}=1.9$  with the second-best model). We extracted from GAM  
270 1 the predicted richness of each collection (i.e., fitted values). These predictions were included in the  
271 subsequent model (GAM 2) as a fixed effect and represent standardisation to control for bias in the  
272 detected diversity (e.g., changes made to the photo identification online key in 2014 with a higher  
273 number of taxa). In all GAM, we chose the GCV.Cp as the automatic optimization method to estimate  
274 the smoothing parameters of the models, based on a cross-validation. However, we checked that the  
275 REML (Restricted maximum likelihood) method gave similar results. We were not concerned about  
276 multicollinearity issues because our aim was not to estimate the independent effects of each of these  
277 control variables but rather to use the predictions of the model. Multicollinearity does not influence the  
278 overall fit of the model, nor the model predictions and precision of the predictions (Kutner et al. 2005).  
279 We did not observe strong concurvity among smoothed variables (“worst” value  $\leq 0.8$ , *concurvity*

280 function, R package mgcv). The distribution of the model residuals were visually checked and did not  
281 show issues (*gam.check* function, R package mgcv). We did not observe significant spatial  
282 autocorrelation of residuals (*mantel.rtest*, R package ade4 ; *spline.correlog*, R package ncf).

283

## 284 **2.5.2 Effects of landscape variables on the richness of flower visitors**

285

286 GAM 2 aimed to test the landscape effects on insect richness. We included the observed insect  
287 richness as the response variable and accessibility to the three land-cover classes (urban, agricultural,  
288 semi-natural) as explanatory variables. We used the accessibility to urban, agricultural and semi-natural  
289 areas within the same smooth term, thus accounting for their interactions and non-linear effects on insect  
290 richness. To account for the effects of non-landscape variables modelled with the GAM 1, we also added  
291 the richness predicted by this initial model as a linear term.

292 To identify how landscape effects vary according to insect taxa, we iteratively applied the  
293 GAM1-GAM2 analysis sequence using the richness of the focal taxa (seven categories of flower  
294 visitors) as the response variable. We also performed the analyses on the total insect richness by  
295 removing honeybee *Apis mellifera* observations from the dataset to ensure that any variations in insect  
296 richness were not solely due to beekeeping in the vicinity of sampling sites. Hereafter, we present the  
297 results for total richness, including honeybees, since the results were quantitatively very similar.

298 We predicted the effect of the percentage of accessibility to urban, agricultural and semi-natural  
299 areas on insect richness using the *predict* function on GAM 2, keeping the predicted richness from GAM  
300 1 constant and equal to the mean value. To discriminate the significant variation in insect richness  
301 predicted from GAM 2 according to the three extreme landscape gradients (agricultural to semi-natural,  
302 agricultural to urban, urban to semi-natural), we performed analyses on three subsets of collections based  
303 on their accessibility to the land-cover classes. When studying a gradient between two variables (e.g.  
304 agricultural to semi-natural), we selected all collections with 0 to 15% accessibility of the third variable  
305 (e.g. urban). We selected a threshold of 15%, as it appeared to be a good compromise between the  
306 sample size and the representativity of the studied gradient. We used generalised linear models, GLM,  
307 when the variation in insect richness varied linearly along the landscape gradient, and used GAM when  
308 it varied non-linearly.

309 To discriminate whether the origin of richness hotspots or coldspots in the ternary diagram of  
310 accessibility is due to specific land-cover categories, we also performed complementary analyses. We  
311 tested the individual effects of land-cover categories and interaction effects of pairs of land-cover  
312 categories on total insect richness. As explanatory variables, we used the land-cover percentage (23  
313 categories from OSO Theia), calculated within a buffer radius of 1000 m around the sampled sites. To  
314 estimate individual effects, we only included one land-cover category in the model at a time, to avoid  
315 multicollinearity. We also tested specifically the interaction between aggregated land-cover categories,  
316 the percentage of forest land cover (deciduous, coniferous forests) and the percentage of annual crops

317 (oilseeds, straw cereals, soy, sunflower, maize, rice). When multiple land-cover categories were tested  
318 together we checked that the Variance Inflation Factor was below three (Zuur et al. 2010). Since land-  
319 cover effects were linear on the richness of insects, we used GLM. In these models, we always used the  
320 predicted richness from GAM 1 as an additional explanatory variable to account for the effect of non-  
321 landscape variables.

322

### 323 **3 Results**

324

325 We analysed the results from 4045 collections recorded between 2010 and 2020. A total of 200 plant  
326 species belonging to 155 genera and 45 families were recorded. The most sampled family was  
327 Asteraceae (993 collections). The majority of collections were recorded on plants in sunny locations  
328 during good weather conditions with a temperature between 20 and 30°C, minimal cloud cover (< 25%)  
329 and light wind (for more details, see Table 1).

330 The total richness per collection ranged from 0 to 40 with a mean of 7.2 (sd=5.5). For each taxa,  
331 the mean richness per collection was as follows: bees 1.77 (min=0, max=10), other hymenopterans 0.65  
332 (min=0, max=11), syrphids 0.95 (min=0, max=9), other dipterans 1.27 (min=0, max=14), lepidopterans  
333 0.64 (min=0, max=16), coleopterans 1.01 (min=0, max=12) and other insects 0.92 (min=0, max=9).

334

#### 335 **3.1 Effects of non-landscape variables on total insect richness**

336

337 Based on the model selection procedure, we found that the model with all variables, except for cloud  
338 cover and wind speed, had the lowest AICc ( $\Delta AICc=1.86$  with the second-best model). Using the best  
339 model (GAM 1), we found that all explanatory variables had a significant effect on the variation of total  
340 richness per collection (p-value < 0.001 for all variables). We observed a positive effect of temperature  
341 and a negative effect of shading on total richness (Fig. 3). Temporal variables (year, Julian day and hour  
342 of sampling) also had a non-linear significant effect on total insect richness (Fig. 4), which justifies their  
343 use as smooth terms (p-value < 0.001, respectively, characterised by an effective degree of freedom -  
344 EDF of 4.3, 7.6 and 4.8). Using a linear model, we showed that predicted richness from GAM 1 (fitted  
345 values) explained 44% of the variance ( $R^2$ ) of the observed richness (p-value < 0.001; Fig. 5). The plant  
346 species identity explained most of the variance, because when it was removed from the initial GAM 1,  
347 the predicted richness explained only 20% of the variance of the observed richness.

348

#### 349 **3.2 Landscape effects on total insect richness**

350

351 The PCA on the proportions of the 23 land-cover categories revealed a strong aggregation of variables  
352 into the three land-cover classes (urban, agricultural and semi-natural) (Fig. 6), which justified

353 discriminating the effects of these three major classes on flower visitors. The strongest correlations were  
354 observed among the urban land-cover categories (Fig. 6).

355         Based on GAM 2, we detected a non-linear and significant triple interaction among the three  
356 land-cover classes ( $p$ -value  $< 0.001$ , EDF=13.6, Fig. 7). We observed that urban areas were associated  
357 with the smallest total insect richness. The two gradients of agricultural to urban and semi-natural to  
358 urban were not equivalent. Urbanisation was predicted to be detrimental more rapidly in combination  
359 with agricultural areas than with semi-natural areas (Fig. 7). We also detected a richness maximum for  
360 agricultural landscapes composed of ~30% of semi-natural areas. When the predicted richness from  
361 GAM 1 was removed from GAM 2, landscape effects only accounted for 4.2% of the deviance.

362         Since grasslands have an intermediate status between agricultural and natural areas and are often  
363 associated with other agricultural and semi-natural features (Fig. 6), this land cover was a candidate to  
364 explain the richness hotspot. However, we did not detect any effects of the percentage of grasslands on  
365 total insect richness when the predicted richness from GAM 1 (grasslands  $p$ -value=0.91) or the plant  
366 species sampled (grasslands  $p$ -value=0.42) was included as an explanatory variable. Interestingly, along  
367 the agricultural to semi-natural gradient (i.e., data subset with urban accessibility below 15%), we  
368 observed a significant positive interaction ( $p$ -value=0.039) between the percentage of forest land cover  
369 (deciduous, coniferous forests) and the percentage of annual crops (oilseeds, straw cereals, soy,  
370 sunflower, maize, rice).

371

### 372 **3.3 Landscape effects according to insect taxa**

373

374 The study of the richness of flower visitors revealed that richness patterns varied according to the  
375 different taxa (Fig. 8). Along the agricultural to semi-natural gradient, we detected a significant non-  
376 linear relationship for bees, other hymenoptera and other diptera as well as a significant linear  
377 relationship for syrphids (-) and lepidoptera (+) (Table 2). Along the urban to semi-natural gradient,  
378 we did not detect any significant non-linear relationship, although we observed a significant linear  
379 relationship for lepidoptera (+) and coleoptera (+). Along the agricultural to urban gradient, we  
380 detected a significant non-linear relationship for other diptera and a significant linear relationship for  
381 bees (+), syrphids (-), lepidoptera (-) and coleoptera (-) (Table 2).

382

## 383 **4 Discussion**

384

385 By studying the triple landscape gradient across urban, agricultural and natural areas, we highlighted  
386 distinct richness patterns along the three gradients and according to the different insect taxa. We found  
387 that urbanisation negatively impacts the total richness of flower visitors, especially when associated with  
388 agricultural areas. We identified a maximum richness in agricultural landscapes composed of ~30% of  
389 semi-natural areas, thus pointing to the existence of synergistic effects of agricultural and semi-natural

390 areas on insect richness. When differentiating total richness according to distinct taxa, one striking result  
391 was that urban areas were less detrimental to bee richness than intensive agricultural areas, despite the  
392 major role played by bees in entomophilous crop pollination.

393

#### 394 **4.1 Effects of non-landscape variables**

395

396 Among the variables included in our analyses, plant species identity outweighed the other variables,  
397 including the landscape variables, to explain insect richness per collection. This variable level of  
398 generalisation (Ollerton et al. 2007) among the plant species is explained by differences in their floral  
399 traits such as floral morphology, floral scents and colours, nectar content and floral display (Ramirez  
400 2003; Stang et al. 2006, 2007; Olesen et al. 2007; Dellinger 2020). The study from Desaeagher et al.  
401 (2018), consistently showed that floral morphology traits outweighed the effects of several landscape  
402 and meteorological variables on flower visitor occurrence. More generally, it is often found that the  
403 composition of flower communities and other local microsite factors explain pollinator occurrence and  
404 diversity better than large-scale landscape variables (Ahrné et al. 2009; Everaars et al. 2011; Bates et al.  
405 2011; Shwartz et al. 2013; Wenzel et al. 2020).

406 The observed effects of temperature, shade, hour and Julian day on pollinator activity were  
407 expected and consistent with the existing literature (Vicens and Bosch 2000; Deguines et al. 2016;  
408 Ushimaru et al. 2021). Unexpectedly, however, we detected an increase in insect richness over the 10  
409 years of the study, which was particularly pronounced in the first 3 years (Fig. 4) and never previously  
410 highlighted in the SPIPOLL programme. In the context of the well-documented insect population  
411 decline in several European countries (Biesmeijer et al. 2006; Ollerton et al. 2014; Hallmann et al. 2017;  
412 Powney et al. 2019; van Klink et al. 2020; Desquilbet et al. 2020), this result is particularly surprising.  
413 We do not believe that this trend is related to an overall increase in insect richness. Rather, it could be  
414 explained by the experience gained by volunteers in correctly identifying insects over the years  
415 (Deguines et al. 2018) and the changes made to the photo identification online key in 2014, which  
416 defined a greater number of taxa.

417

#### 418 **4.2 Effects of landscape variables**

419

420 We detected significant landscape effects on total insect richness and on richness for all taxa categories.  
421 Our results were generally consistent with the existing literature, which showed that rural areas are richer  
422 than urban areas (Franks et al. 2007; Ollerton et al. 2009; Zulian et al. 2013; Fortel et al. 2016; Fauviau  
423 et al. 2022; Herrmann et al. 2023). However, in contrast to the frequent result that semi-natural areas are  
424 richer than agricultural areas (Bates et al. 2011; Garibaldi et al. 2011; Verboven et al. 2014; Collado et  
425 al. 2019), we found that it depends on the focal taxa, and that total insect richness is quite similar in  
426 landscapes largely dominated by semi-natural or agricultural areas. Interestingly, the two gradients of

427 urban to agricultural and urban to semi-natural had linear effects on total richness but were not  
428 equivalent, with urbanisation being worse when associated with agricultural areas than semi-natural  
429 areas (e.g., see 25% iso-richness line in Fig. 7). Both bees and other dipterans appear to be driving this  
430 pattern (Fig. 8, Table 2).

431         Along the agricultural to semi-natural gradient, we observed an intermediate maximum, which  
432 was particularly pronounced for bees and other dipterans (Table 2, Fig. 8). This result supports the  
433 *intermediate disturbance* and *area-heterogeneity trade off* hypotheses mentioned above (Kolasa and  
434 Rollo 1991; Kadmon and Allouche 2007; Allouche et al. 2012). Although hump-shaped relationships  
435 were also expected between rural and urban areas (Fortel et al. 2014), our results rather suggest a linear  
436 decrease in richness, probably explained by habitat loss. Concerning the agricultural to semi-natural  
437 gradient, our findings confirm the 20% semi-natural threshold that is often recommended in agro-  
438 ecology guidelines below which it is difficult to maintain ecological functions in agroecosystems (Burel  
439 et al. 2013; Poux and Pointereau 2014; Garibaldi et al. 2021). In the literature, this threshold was  
440 suggested by simulation models showing that when semi-natural patches were reduced by an area  
441 representing less than 20% of the landscape, their isolation increased exponentially (Andr en 1994); this  
442 has nevertheless rarely been confirmed by empirical results (but see Tschardt et al. 2002; Eeraerts  
443 2023). Our analysis suggests that the intermediate maximum resulted from land-cover complementation  
444 (Pope et al. 2000; Colding 2007) between annual crops and forest patches and was not due to a singular  
445 land cover such as grasslands occurring at mid-gradient. Woodlands, especially woodland edges, often  
446 provide nesting habitats and floral resources for wild bees (Osborne et al. 2008; Joshi et al. 2016;  
447 Donkersley 2019; Ulyshen et al. 2023) and can offer various other microhabitats for other taxa such as  
448 syrphids (e.g., Meyer et al. 2009), whereas annual crops provide mass-flowering resources for these taxa  
449 during short periods (Westphal et al. 2003; Timberlake et al. 2019). Semi-natural habitats in  
450 agriculturally dominated landscapes could also mitigate the negative consequences of pesticides and  
451 climate changes on insect populations (Ulyshen et al. 2023). For bees, we observed minimal richness in  
452 agriculturally dominated landscapes, which is possibly related to a higher sensitivity of bees to landscape  
453 simplification and intensive practices (i.e., use of chemicals, reduced crop diversity, short rotations,  
454 large field size), causing a lack of nesting sites and plant diversity with annual flowering discontinuity,  
455 and insect intoxication in these landscapes (Deguines et al. 2014; Ollerton et al. 2014; Sirami et al. 2019;  
456 Dainese et al. 2019). For syrphids, we observed a maximum richness in agriculturally dominated  
457 landscapes. This global trend for syrphids could be driven by crop-dwelling species, whose larvae feed  
458 on aphids, which are possibly more frequent in intensive agricultural landscapes (Meyer et al. 2009;  
459 Dainese et al. 2016). Butterfly richness was lowest in urban areas and highest in semi-natural areas,  
460 which is consistent with the literature (e.g., Deguines et al. 2012). Since most collections were done  
461 during the day, we expect the observed trend to be dominated by diurnal butterflies. Diurnal butterflies  
462 are particularly vulnerable to changes in their environment, especially since the caterpillars of most  
463 species feed on only one or a few specific host plants, which are less frequent in cities than in semi-

464 natural areas (UICN 2014). Recently, it has been shown that the richness of butterflies is particularly  
465 linked to the richness of plant species whose conservation status is of concern (red-listed species),  
466 compared to other arthropod taxa (Tobisch et al. 2023).

467

### 468 **4.3 Limitations and perspectives**

469

470 Our results confirm the necessity to distinguish natural areas from agricultural areas when studying  
471 insect richness along the urbanisation gradient. However, urban, agricultural and semi-natural areas still  
472 represent broad land-use classes, which conceal the high diversity of environments probably responsible  
473 for the large variability in insect richness. For instance, regarding urban areas, the recent review of  
474 Wenzel et al. (2020) emphasises that differentiating urban sprawl from urban densification might be  
475 responsible for the divergence of results among the studies analysed. Unfortunately, in our study we  
476 were unable to differentiate between dense and diffuse built-up areas when calculating the accessibility  
477 to urban areas due to the strong correlation between both land uses (Fig. 6). This point also applies to  
478 agricultural areas, which include diverse cropping systems, and to natural areas such as deciduous and  
479 coniferous forests and heathland. More generally, our study only considered landscape composition and  
480 did not consider single or interactive effects with configurational variables, which have recently been  
481 shown to influence biodiversity and ecosystem services (Martin et al. 2019). For instance, it was shown  
482 that the consequences of urbanisation on butterfly populations can differ for different urban settings  
483 (e.g., land sharing vs land sparing; Soga et al. 2014).

484 It is important to keep in mind that high insect richness may be related to common species and  
485 that some land uses (e.g., natural areas) may be less rich but harbour rare species. In our study, this could  
486 be the case of bees in urban areas, since urbanisation was shown to homogenise plant and insect  
487 communities (Kühn and Klotz 2006; Verboven et al. 2014; Deguines et al. 2016). In our study, we  
488 estimated the landscape effects on insect richness in relation to 200 different plant species, thus  
489 representing an estimation of the  $\alpha$ -diversity of flower-feeding insects along the triple landscape  
490 gradient. However, our approach did not include any assessment of  $\beta$ - and  $\gamma$ -diversity (see diversity  
491 definitions in Whittaker 1972 and a recent example in Collado et al. 2019), which is a fundamental  
492 diversity component to assess the biological conservation value of the different land uses at the  
493 landscape scale. In particular, we did not account for the botanical specificity of each land use in our  
494 analysis, because the citizen science protocol gives participants the freedom to choose the focal plants  
495 and their location, thus possibly leading to the biased representativity of the sampled plants.

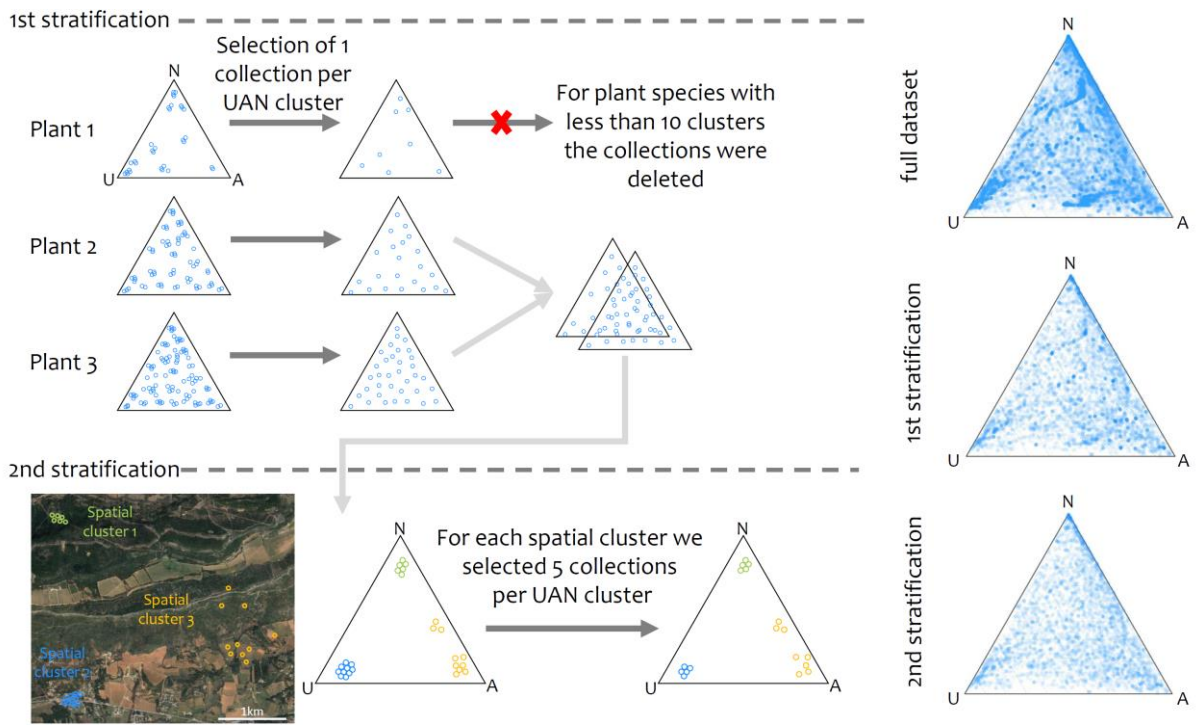
496 In the future, combining our stratification methodology and insect richness predictions for each  
497 plant species together with representative botanical surveys within the different land uses may help to  
498 better estimate the conservation value of the different land uses and their complementarity. This could  
499 inform landscape managers in their decision-making to promote synergies among contiguous land uses.  
500 Furthermore, delving into the diversity of urban morphology (IAURIF 1995) and understanding how it

501 affects biodiversity and ecological connectivity could greatly inform urban planners and policymakers  
502 to make cities more sustainable (Flégeau et al. 2020). The study of urban forms is still largely overlooked  
503 by ecologists and conservation biologists (Wenzel et al. 2020), instead being more the domain of  
504 geographers, urban planners, architects and landscape architects (Flégeau et al. 2020). As a result, this  
505 represents an interdisciplinary and methodological challenge. Finally, based on the observation that  
506 landscape variables only had weak effects on insect richness compared to the variations observed among  
507 plants species, we believe that the effect of plant identity may be promising to investigate further. This  
508 could lead to the optimisation of flower enhancement in urban and agricultural areas to attract pollinator  
509 diversity and maintain ecosystem services.

510



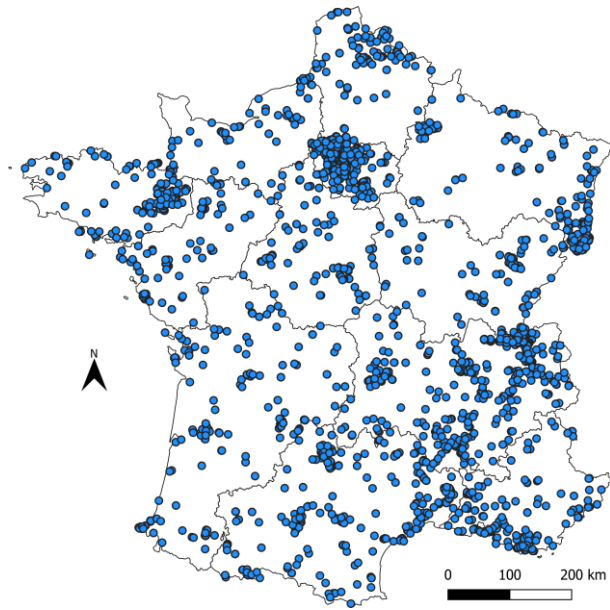
511 **Figures**



512

513 **Fig. 1.** On the left side, the workflow followed during the double stratification of the dataset. On the  
 514 right side, the observed distribution of the collections within the ternary diagram across the urban (U),  
 515 agricultural (A) and semi-natural (N) areas before the stratification and after the first and second  
 516 stratification.

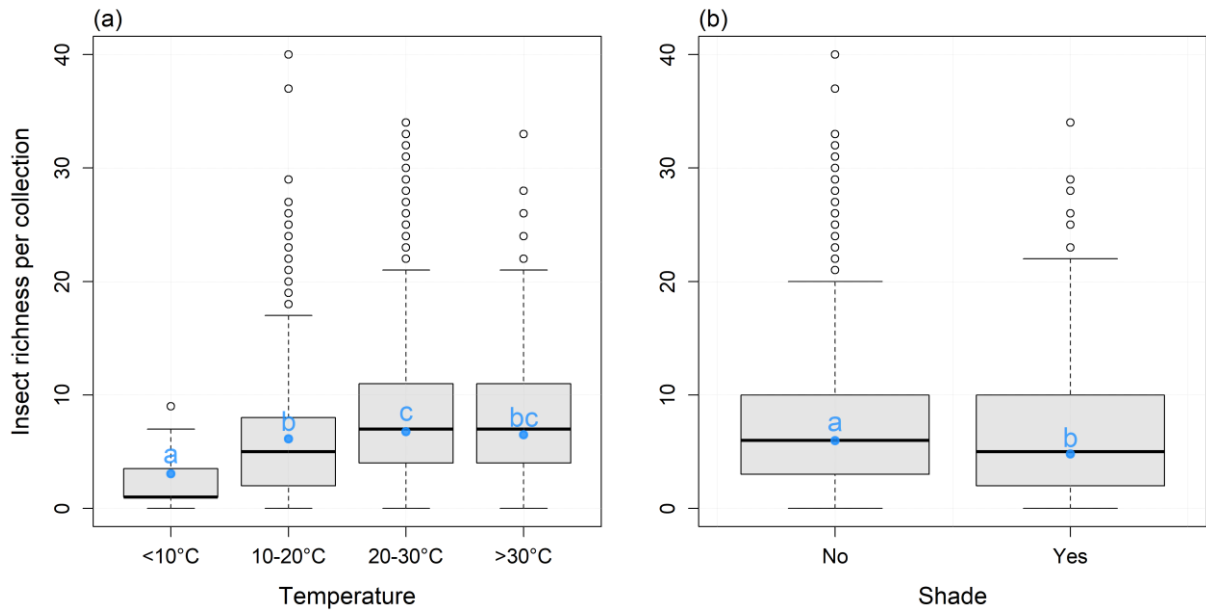
517



518

519 **Fig. 2.** Map of the French metropolitan administrative regions and distribution of the sampling sites  
520 selected after the two sampling stratifications (blue dots).

521



522

523

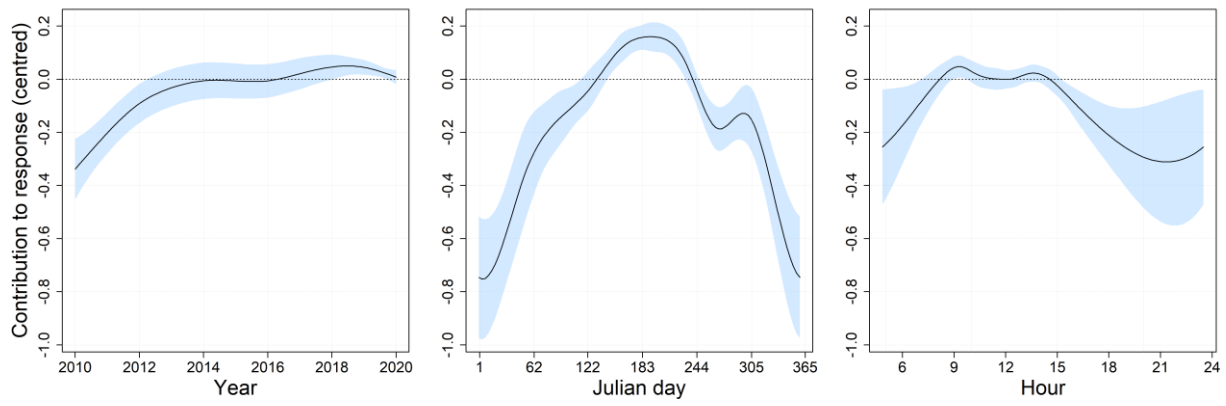
524

525

526

527

**Fig. 3.** Boxplots representing the relationship between the total richness of flower-visiting insects (raw data) and the temperature (a) and the shading of the sampling site (b). Blue dots represent the means for each category and the central bold line the median. For each variable, the categories sharing the same letters do not significantly differ (p-value > 0.05).



528

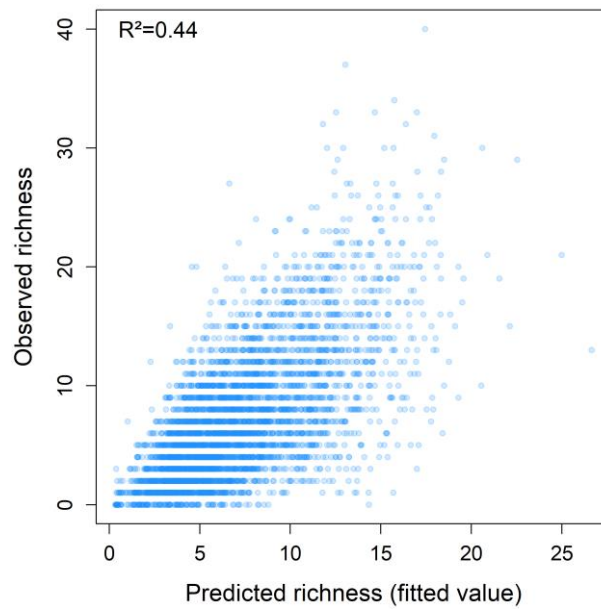
529

530

531

532

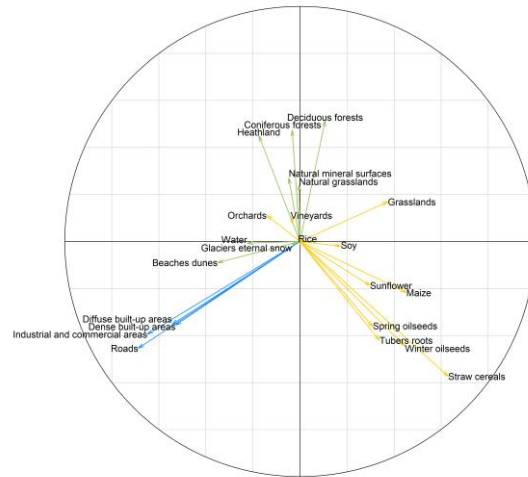
**Fig. 4.** Non-linear contribution of the year (a), Julian day (b) and hour of sampling (c) to total insect richness. If the confidence interval (2 standard errors) overlaps zero for some values of the explanatory variables, the effect is not significant.



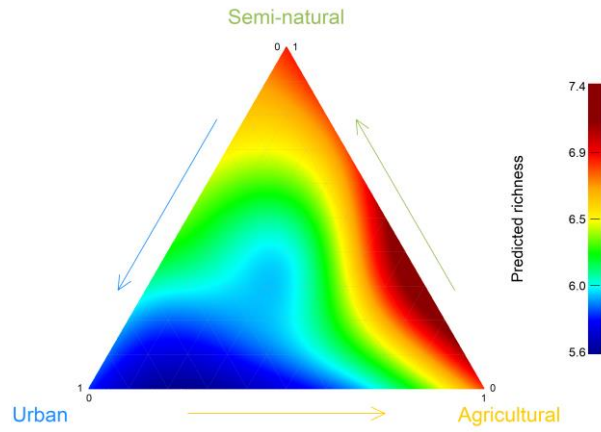
533

534 **Fig. 5.** Observed richness of flower-visiting insects according to the predicted richness using the GAM  
535 based on the non-landscape variables (GAM 1).

536



537  
 538 **Fig. 6.** Projection of the 23 OSO Theia land-cover variables in the correlation circle associated with the  
 539 two first axes of the PCA. The land-cover variables were calculated within a buffer radius of 1000m  
 540 around the 4045 sampled sites. The first two PCA components represent 23.44% of the total inertia. The  
 541 blue, orange and green arrows are associated with the urban, agricultural and semi-natural land-cover  
 542 classes, respectively.  
 543

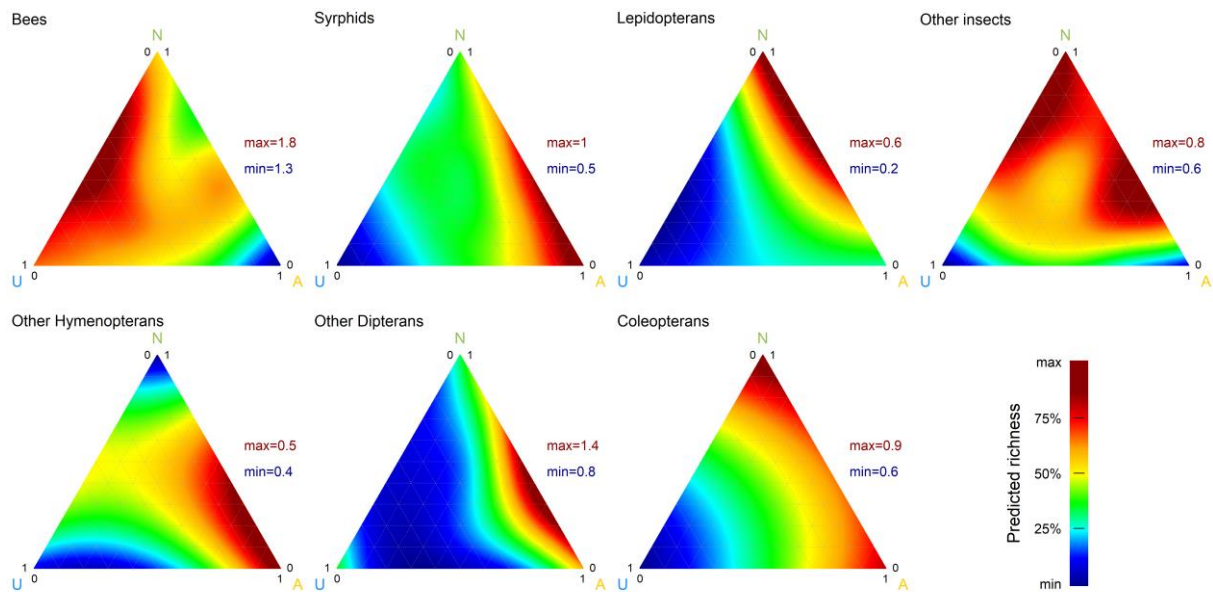


544

545 **Fig. 7.** Ternary diagram of the percentage accessibility to urban, agricultural and semi-natural land-

546 cover classes showing the predicted landscape effect on total insect richness.

547



548  
 549  
 550  
 551  
 552

**Fig. 8.** Ternary diagram of the percentage accessibility to urban (U), agricultural (A) and semi-natural (N) land-cover classes showing the predicted landscape effect on the richness of each insect taxa. The min and max represent the minimum and maximum predicted values, respectively.



553 **Tables**

554

555 **Table 1:** Summary of the categories of the six non-landscape factors. Numbers represent the number of  
 556 collections for each category. For plants, we indicated the top five families, genera, and plant species  
 557 and their associated number of collections.

Variables	Categories and number of collections
Temperature	< 10°C: 91; 10-20°C: 1351; 20-30°C: 2310; > 30°C: 293
Cloud cover	0-25%: 2950; 25-50%: 421; 50-75%: 302; 75-100%: 372
Wind speed	No wind: 977; light: 2407; strong: 661
Region	Auvergne-Rhone-Alpes: 881; Île-de-France: 871; Occitanie: 501; Bretagne: 389; Grand Est: 290; Nouvelle-Aquitaine: 248; Provence-Alpes-Côte d'Azur: 207; Bourgogne-Franche-Comté: 191; Centre-Val de Loire: 131; Hauts-de-France: 127; Pays de la Loire: 122; Normandie: 87
Shading	Yes: 3775; No: 270
Plants	45 families (Asteraceae: 993; Lamiaceae: 408; Rosaceae: 325; Apiaceae:323; Fabaceae: 252); 155 genera (Prunus: 109; Senecio: 106; Ranunculus: 92; Hedera: 82; Solidago: 82); 200 species (Hedera helix: 82; Buddleja davidii: 77; Senecio jacobaea:74; Daucus carota:72; Rosmarinus officinalis: 70)

558

559

560 **Table 2.** Results of the statistical models testing for the effect of the percentage accessibility to land-  
561 cover classes along the three distinct gradients. For each taxon, the first row is the p-value from the  
562 GAM, with the effective degrees of freedom (EDF) between brackets, whereas the second row is the p-  
563 value from the GLM, with estimates between brackets  $\pm$  standard error. In both models, the tested  
564 variable is specified in the column header. Asterisks indicate the level of statistical significance (p-value:  
565  $0 \leq *** < 0.001 \leq ** < 0.01 \leq * < 0.05$ ). The higher the EDF value, the stronger the non-linearity. We  
566 considered the relationship to be linear when  $EDF < 1.5$ ; in this case, only GLM results should be  
567 considered (see bold values).  
568

Taxa	Model	Gradient Agri→SN Access. Semi-natural	Gradient Urban→SN Access. Semi-natural	Gradient Agri→Urban Access. Urban
Total Richness	GAM	<b>0.229</b> (EDF=2.9)	< 0.001*** (EDF=1)	0.005** (EDF=1)
	GLM	0.661 (Est.=-0.021 $\pm$ 0.048)	< <b>0.001</b> *** (Est.=0.21 $\pm$ 0.06)	<b>0.004</b> ** (Est.=-0.191 $\pm$ 0.067)
Bees	GAM	<b>0.014</b> * (EDF=3.6)	<b>0.544</b> (EDF=1.8)	0.003** (EDF=1)
	GLM	0.265 (Est.=0.077 $\pm$ 0.069)	0.751 (Est.=-0.024 $\pm$ 0.075)	<b>0.003</b> ** (Est.=0.259 $\pm$ 0.086)
Other Hymenopterans	GAM	<b>0.036</b> * (EDF=2.1)	0.781 (EDF=1.3)	0.077 (EDF=1)
	GLM	0.026* (Est.=-0.272 $\pm$ 0.122)	<b>0.744</b> (Est.=-0.05 $\pm$ 0.152)	<b>0.076</b> (Est.=-0.322 $\pm$ 0.181)
Syrphids	GAM	0.003** (EDF=1)	0.089 (EDF=1)	< 0.001*** (EDF=1)
	GLM	<b>0.003</b> ** (Est.=-0.294 $\pm$ 0.097)	<b>0.087</b> (Est.=0.236 $\pm$ 0.137)	< <b>0.001</b> *** (Est.=-0.61 $\pm$ 0.146)
Other dipterans	GAM	<b>0.009</b> ** (EDF=2.6)	0.174 (EDF=1)	<b>0.016</b> * (EDF=1.8)
	GLM	0.007** (Est.=-0.225 $\pm$ 0.084)	<b>0.173</b> (Est.=0.148 $\pm$ 0.109)	0.008** (Est.=-0.344 $\pm$ 0.129)
Lepidopterans	GAM	0.001** (EDF=1)	< 0.001*** (EDF=1)	0.057 (EDF=1.4)
	GLM	<b>0.001</b> ** (Est.=0.459 $\pm$ 0.134)	< <b>0.001</b> *** (Est.=1.12 $\pm$ 0.181)	<b>0.025</b> * (Est.=-0.54 $\pm$ 0.241)
Coleopterans	GAM	0.542 (EDF=1)	< 0.001*** (EDF=1)	0.015* (EDF=1)
	GLM	<b>0.535</b> (Est.=0.06 $\pm$ 0.097)	< <b>0.001</b> *** (Est.=0.46 $\pm$ 0.126)	<b>0.014</b> * (Est.=-0.35 $\pm$ 0.143)
Other insects	GAM	<b>0.684</b> (EDF=1.7)	<b>0.172</b> (EDF=1.5)	0.663 (EDF=1)
	GLM	0.588 (Est.=0.054 $\pm$ 0.101)	0.095 (Est.=0.203 $\pm$ 0.122)	<b>0.658</b> (Est.=-0.063 $\pm$ 0.141)

569

570

571

572 **References**

- 573 Agreste (2021) L'occupation du sol entre 1982 et 2018. Les dossiers Avril, n°3:9–10
- 574 Ahrné K, Bengtsson J, Elmquist T (2009) Bumble Bees (*Bombus* spp) along a Gradient of Increasing  
575 Urbanization. *PLoS One* 4:e5574
- 576 Allouche O, Kalyuzhny M, Moreno-Rueda G, et al (2012) Area–heterogeneity tradeoff and the  
577 diversity of ecological communities. *Proc Natl Acad Sci* 109:17495–17500
- 578 Andrén H (1994) Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with  
579 Different Proportions of Suitable Habitat: A Review. *Oikos* 71:355–366
- 580 Baldock KCR, Goddard MA, Hicks DM, et al (2015) Where is the UK's pollinator biodiversity? The  
581 importance of urban areas for flower-visiting insects. *Proc R Soc B Biol Sci* 282:20142849
- 582 Bates AJ, Sadler JP, Fairbrass AJ, et al (2011) Changing Bee and Hoverfly Pollinator Assemblages  
583 along an Urban-Rural Gradient. *PLoS One* 6:e23459
- 584 Biesmeijer JC, Roberts SPM, Reemer M, et al (2006) Parallel declines in pollinators and insect-  
585 pollinated plants in Britain and the Netherlands. *Science* 313:351–354
- 586 Burel F, Aviron S, Baudry J, et al (2013) The Structure and Dynamics of Agricultural Landscapes as  
587 Drivers of Biodiversity BT - Landscape Ecology for Sustainable Environment and Culture. In:  
588 Fu B, Jones KB (eds). Springer Netherlands, Dordrecht, pp 285–308
- 589 Colding J (2007) “Ecological land-use complementation” for building resilience in urban ecosystems.  
590 *Landsc Urban Plan* 81:46–55
- 591 Collado MÁ, Sol D, Bartomeus I (2019) Bees use anthropogenic habitats despite strong natural habitat  
592 preferences. *Divers Distrib* 25:924–935
- 593 Dainese M, Martin EA, Aizen MA, et al (2019) A global synthesis reveals biodiversity-mediated  
594 benefits for crop production. *Sci Adv* 5:eaax0121
- 595 Dainese M, Montecchiari S, Sitzia T, et al (2016) High cover of hedgerows in the landscape supports  
596 multiple ecosystem services in Mediterranean cereal fields. *J Appl Ecol* 54:380–388
- 597 Deguines N, de Flores M, Loïs G, et al (2018) Fostering close encounters of the entomological kind.  
598 *Front Ecol Environ* 16:202–203
- 599 Deguines N, Jono C, Baude M, et al (2014) Large-scale trade-off between agricultural intensification  
600 and crop pollination services. *Front Ecol Environ* 12:212–217
- 601 Deguines N, Julliard R, de Flores M, Fontaine C (2012) The Whereabouts of Flower Visitors:  
602 Contrasting Land-Use Preferences Revealed by a Country-Wide Survey Based on Citizen  
603 Science. *PLoS One* 7:e45822
- 604 Deguines N, Julliard R, de Flores M, Fontaine C (2016) Functional homogenization of flower visitor  
605 communities with urbanization. *Ecol Evol* 6:1967–1976
- 606 Dellinger AS (2020) Pollination syndromes in the 21st century: where do we stand and where may we  
607 go? *New Phytol* 228:1193–1213
- 608 Desaegher J, Nadot S, Fontaine C, Colas B (2018) Floral morphology as the main driver of flower-

609 feeding insect occurrences in the Paris region. *Urban Ecosyst* 21:585–598

610 Desaegher J, Ouin A, Sheeren D (2022) How far is enough? The prediction of the scale of effect for  
611 wild bees. *Ecography (Cop)* 2022:e05758

612 Desquilbet M, Gaume L, Grippa M, et al (2020) Comment on “Meta-analysis reveals declines in  
613 terrestrial but increases in freshwater insect abundances.” *Science (80- )* 370:eabd8947

614 Donkersley P (2019) Trees for bees. *Agric Ecosyst Environ* 270–271:79–83

615 Eeraerts M (2023) A minimum of 15% semi-natural habitat facilitates adequate wild pollinator  
616 visitation to a pollinator-dependent crop. *Biol Conserv* 278:109887

617 Everaars J, Strohbach MW, Gruber B, Dormann CF (2011) Microsite conditions dominate habitat  
618 selection of the red mason bee (*Osmia bicornis*, Hymenoptera: Megachilidae) in an urban  
619 environment: A case study from Leipzig, Germany. *Landsc Urban Plan* 103:15–23

620 Fauviau A, Baude M, Bazin N, et al (2022) A large-scale dataset reveals taxonomic and functional  
621 specificities of wild bee communities in urban habitats of Western Europe. *Sci Rep* 12:18866

622 Flégeau M, Clergeau P, Soubelet H, Carré S (2020) Formes urbaines et biodiversité - Un état des  
623 connaissances. [https://www.urbanisme-](https://www.urbanisme-puca.gouv.fr/IMG/pdf/morgane_flegeau_baumwebv3.pdf)  
624 [puca.gouv.fr/IMG/pdf/morgane\\_flegeau\\_baumwebv3.pdf](https://www.urbanisme-puca.gouv.fr/IMG/pdf/morgane_flegeau_baumwebv3.pdf), PUCA

625 Fortel L, Henry M, Guilbaud L, et al (2014) Decreasing Abundance, Increasing Diversity and  
626 Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an  
627 Urbanization Gradient. *PLoS One* 9:e104679

628 Fortel L, Henry M, Guilbaud L, et al (2016) Use of human-made nesting structures by wild bees in an  
629 urban environment. *J Insect Conserv* 20:239–253

630 Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to  
631 a climate fluctuation. *Proc Natl Acad Sci* 104:1278–1282

632 Gallai N, Salles J-M, Settele J, Vaissière BE (2009) Economic valuation of the vulnerability of world  
633 agriculture confronted with pollinator decline. *Ecol Econ* 68:810–821

634 Garibaldi LA, Oddi FJ, Miguez FE, et al (2021) Working landscapes need at least 20% native habitat.  
635 *Conserv Lett* 14:e12773

636 Garibaldi LA, Steffan-Dewenter I, Kremen C, et al (2011) Stability of pollination services decreases  
637 with isolation from natural areas despite honey bee visits. *Ecol Lett* 14:1062–1072

638 Geslin B, Le Féon V, Folschweiller M, et al (2016) The proportion of impervious surfaces at the  
639 landscape scale structures wild bee assemblages in a densely populated region. *Ecol Evol*  
640 6:6599–6615

641 Hall DM, Camilo GR, Tonietto RK, et al (2017) The city as a refuge for insect pollinators. *Conserv*  
642 *Biol* 31:24–29

643 Hallmann CA, Sorg M, Jongejans E, et al (2017) More than 75 percent decline over 27 years in total  
644 flying insect biomass in protected areas. *PLoS One* 12:e0185809

645 Herrmann J, Buchholz S, Theodorou P (2023) The degree of urbanisation reduces wild bee and

646 butterfly diversity and alters the patterns of flower-visitation in urban dry grasslands. *Sci Rep*  
647 13:2702

648 IAURIF (1995) *Référentiel de Densité et de Formes Urbaines. Contribution Pour Un Référentiel*  
649 *Appliqué à l'habitat Dans La Région Ile-de-France.*  
650 [https://www.institutparisregion.fr/fileadmin/NewEtudes/Etude\\_762/Densites\\_Referentiel.pdf](https://www.institutparisregion.fr/fileadmin/NewEtudes/Etude_762/Densites_Referentiel.pdf)

651 Joshi NK, Otieno M, Rajotte EG, et al (2016) Proximity to Woodland and Landscape Structure Drives  
652 Pollinator Visitation in Apple Orchard Ecosystem. *Front. Ecol. Evol.* 4

653 Kadmon R, Allouche O (2007) Integrating the Effects of Area, Isolation, and Habitat Heterogeneity on  
654 Species Diversity: A Unification of Island Biogeography and Niche Theory. *Am Nat* 170:443–  
655 454

656 Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms : The Conservation of Plant-  
657 Pollinator Interactions. *Annu Rev Ecol Syst* 29:83–112

658 Klein A-M, Vaissière BE, Cane JH, et al (2007) Importance of pollinators in changing landscapes for  
659 world crops. *Proc R Soc B Biol Sci* 274:303–313

660 Kolasa J, Rollo C (1991) Introduction: The Heterogeneity of Heterogeneity: A Glossary. In: Kolasa J,  
661 Pickett S (eds) *Ecological Heterogeneity. Ecological Studies.* Springer New York, pp 1–23

662 Krauss J, Steffan-Dewenter I, Tschardt T (2003) How does landscape context contribute to effects  
663 of habitat fragmentation on diversity and population density of butterflies? *J Biogeogr* 30:889–  
664 900

665 Kühn I, Klotz S (2006) Urbanization and homogenization – Comparing the floras of urban and rural  
666 areas in Germany. *Biol Conserv* 127:292–300

667 Kutner MH, Nachtsheim CJ, Neter J, Li W (2005) *Applied Linear Statistical Models.* 5th Edition.  
668 McGraw-Hill, Irwin, New York

669 Levé M, Baudry E, Bessa-Gomes C (2019) Domestic gardens as favorable pollinator habitats in  
670 impervious landscapes. *Sci Total Environ* 647:420–430

671 Martin EA, Dainese M, Clough Y, et al (2019) The interplay of landscape composition and  
672 configuration: new pathways to manage functional biodiversity and agroecosystem services  
673 across Europe. *Ecol Lett* 22:1083–1094

674 McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our understanding  
675 of the ecology of urbanizing landscapes: Current status and future directions. *Landsc Ecol*  
676 23:1143–1155

677 Meyer B, Jauker F, Steffan-Dewenter I (2009) Contrasting resource-dependent responses of hoverfly  
678 richness and density to landscape structure. *Basic Appl Ecol* 10:178–186

679 Miguet P, Fahrig L, Lavigne C (2017) How to quantify a distance-dependent landscape effect on a  
680 biological response. *Methods Ecol Evol* 8:1717–1724

681 Nieto A, Roberts S, Kemp J, et al (2014) European Red List of Bees

682 Olesen JM, Dupont YL, Ehlers BK, Hansen DM (2007) The Openness of a Flower and Its Number of

683 Flower-Visitor Species. *Taxon* 56:729–736

684 Ollerton J, Alarcón R, Waser NM, et al (2009) A global test of the pollination syndrome hypothesis.  
685 *Ann Bot* 103:1471–1480

686 Ollerton J, Erenler H, Edwards M, Crockett R (2014) Extinctions of aculeate pollinators in Britain and  
687 the role of large-scale agricultural changes. *Science* (80- ) 346:1360 LP – 1362

688 Ollerton J, Killick A, Lamborn E, et al (2007) Multiple Meanings and Modes: On the Many Ways to  
689 Be a Generalist Flower. *Taxon* 56:717–728

690 Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos*  
691 120:321–326

692 Osborne JL, Martin AP, Shortall CR, et al (2008) Quantifying and comparing bumblebee nest  
693 densities in gardens and countryside habitats. *J Appl Ecol* 45:784–792

694 Pope SE, Fahrig L, Merriam HG (2000) Landscape complementation and metapopulation effects on  
695 leopard frog populations. *Ecology* 81:2498–2508

696 Poux X, Pointereau P (2014) L’agriculture à “haute valeur naturelle” en France métropolitaine. Un  
697 indicateur pour le suivi de la biodiversité et l’évaluation de la politique de développement rural. »  
698 Rapport d’étude au Ministère de l’agriculture de l’agroalimentaire et de la forêt. AScA,  
699 SOLAGRO

700 Powney GD, Carvell C, Edwards M, et al (2019) Widespread losses of pollinating insects in Britain.  
701 *Nat Commun* 10:1018

702 Ramirez N (2003) Floral Specialization and Pollination: A Quantitative Analysis and Comparison of  
703 the Leppik and the Faegri and van der Pijl Classification Systems. *Taxon* 52:687–700

704 Renaud E, Baudry E, Bessa-Gomes C (2020) Influence of taxonomic resolution on mutualistic  
705 network properties. *Ecol Evol* 10:3248–3259

706 Shwartz A, Muratet A, Simon L, Julliard R (2013) Local and management variables outweigh  
707 landscape effects in enhancing the diversity of different taxa in a big metropolis. *Biol Conserv*  
708 157:285–292

709 Sirami C, Gross N, Baillod AB, et al (2019) Increasing crop heterogeneity enhances multitrophic  
710 diversity across agricultural regions. *Proc Natl Acad Sci* 116:16442 LP – 16447

711 Soga M, Yamaura Y, Koike S, Gaston KJ (2014) Land sharing vs. land sparing: does the compact city  
712 reconcile urban development and biodiversity conservation? *J Appl Ecol* 51:1378–1386

713 Stang M, Klinkhamer PGL, van der Meijden E (2007) Asymmetric specialization and extinction risk  
714 in plant–flower visitor webs: a matter of morphology or abundance? *Oecologia* 151:442–453

715 Stang M, Klinkhamer PGL, Van Der Meijden E (2006) Size constraints and flower abundance  
716 determine the number of interactions in a plant-flower visitor web. *Oikos* 112:111–121

717 Timberlake TP, Vaughan IP, Memmott J (2019) Phenology of farmland floral resources reveals  
718 seasonal gaps in nectar availability for bumblebees. *J Appl Ecol* 56:1585–1596

719 Tobisch C, Rojas-Botero S, Uhler J, et al (2023) Conservation-relevant plant species indicate

720 arthropod richness across trophic levels: Habitat quality is more important than habitat amount.  
721 Ecol Indic 148:110039

722 Tschardt T, Steffan-Dewenter I, Kruess A, Thies C (2002) Contribution of Small Habitat Fragments  
723 to Conservation of Insect Communities of Grassland-Cropland Landscapes. Ecol Appl 12:354–  
724 363

725 UICN France, MNHN, OPIE & SEF (2014) La Liste rouge des espèces menacées en France - Chapitre  
726 Papillons de jour de France métropolitaine. Paris, France

727 Ulyshen M, Urban-Mead KR, Dorey JB, Rivers JW (2023) Forests are critically important to global  
728 pollinator diversity and enhance pollination in adjacent crops. Biol Rev 98:1118–1141

729 United Nations (2014) World Urbanization Prospects: The 2014 Revision. New York: United Nations

730 Ushimaru A, Rin I, Katsuhara KR (2021) Covering and shading by neighbouring plants diminish  
731 pollinator visits to and reproductive success of a forest edge specialist dwarf species. Plant Biol  
732 23:711–718

733 van Klink R, Bowler DE, Gongalsky KB, et al (2020) Meta-analysis reveals declines in terrestrial but  
734 increases in freshwater insect abundances. Science (80- ) 368:417 LP – 420

735 Verboven H a F, Uyttenbroeck R, Brys R, Hermy M (2014) Different responses of bees and hoverflies  
736 to land use in an urban-rural gradient show the importance of the nature of the rural land use.  
737 Landsc Urban Plan 126:31–41

738 Vicens N, Bosch J (2000) Weather-Dependent Pollinator Activity in an Apple Orchard, with Special  
739 Reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae and Apidae).  
740 Environ Entomol 29:413–420

741 Wenzel A, Grass I, Belavadi V V, Tschardt T (2020) How urbanization is driving pollinator  
742 diversity and pollination – A systematic review. Biol Conserv 241:108321

743 Westphal C, Steffan-Dewenter I, Tschardt T (2003) Mass flowering crops enhance pollinator  
744 densities at a landscape scale. Ecol Lett 6:961–965

745 Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251

746 Winfree R, Aguilar R, Vázquez DP, et al (2009) A meta-analysis of bees’ responses to anthropogenic  
747 disturbance. Ecology 90:2068–2076

748 Zulian G, Maes J, Paracchini ML (2013) Linking Land Cover Data and Crop Yields for Mapping and  
749 Assessment of Pollination Services in Europe. Land 472–492

750 Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical  
751 problems. Methods Ecol Evol 1:3–14

752