

# *Landscape scale drivers of pollinator communities may depend on land use configuration*

Article

Accepted Version

Gillespie, Mark A. K., Baude, Mathilde, Biesmeijer, Jacobus, Boatman, Nigel, Budge, Giles E., Crowe, Andrew, Davies, Nancy, Evans, Rebecca, Memmott, Jane, Morton, R. Daniel, Moss, Ellen, Murphy, Mark, Pietravalle, Stephane, Potts, Simon G. ORCID logo ORCID: <https://orcid.org/0000-0002-2045-980X>, Roberts, Stuart P. M., Rowland, Claire, Senapathi, Deepa ORCID logo ORCID: <https://orcid.org/0000-0002-8883-1583>, Smart, Simon M., Wood, Claire and Kunin, William E. (2022) Landscape scale drivers of pollinator communities may depend on land use configuration. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 377 (1853). ISSN 0962-8436 doi: <https://doi.org/10.1098/rstb.2021.0172>  
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To link to this article DOI: <http://dx.doi.org/10.1098/rstb.2021.0172>

Publisher: The Royal Society

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2 configuration

3

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34

35 **Abstract**

36 Research into pollinators in managed landscapes has recently combined approaches of  
37 pollination- and landscape ecology, because key stressors are likely to interact across wide  
38 areas. While laboratory and field experiments are valuable for furthering understanding,  
39 studies are required to investigate the interacting drivers of pollinator health and diversity  
40 across a broader range of landscapes and a wider array of taxa. Here we use a network of 96  
41 study landscapes in six topographically diverse regions of Britain, to test the combined  
42 importance of honey bee density, insecticide loadings, floral resource availability, and habitat  
43 diversity to pollinator communities. We also explore the interactions between these drivers  
44 and the cover and proximity of semi-natural habitat. We found that among our four drivers,  
45 only honey bee density was positively related to wild pollinator abundance and diversity, and  
46 the positive association between abundance and floral resources depended on insecticide  
47 loadings and habitat diversity. By contrast, our exploratory models including habitat  
48 composition metrics revealed a complex suite of interactive effects. These results demonstrate  
49 that improving pollinator community composition and health is unlikely to be achieved with  
50 general resource enhancements only. Rather, local land-use context should be considered in  
51 fine-tuning pollinator management and conservation.

52

53

54 **Keywords**

55 agriculture, bumblebees, competition, hoverflies, land-use, solitary bees

56

## 57 **Introduction**

58 The health of insect pollinator populations and communities has become a topic of global  
59 importance in recent decades, not least because of widely reported declines [1, 2] and the  
60 reliance of ecosystems on pollination services [3]. Pollinators are under pressure from  
61 multiple interacting stressors [4], with clear physiological and behavioural implications of  
62 management practices such as insecticide application [5, 6], honey bee hive placement [7, 8]  
63 and floral resource enhancement [9]. Laboratory and semi-field studies of these impacts often  
64 focus on individual species such as the managed honey bee or key bumblebee species. Yet  
65 attention is beginning to turn towards the importance of combining the approaches of  
66 pollination ecology and landscape ecology [3, 10], particularly as the key stressors of  
67 pollinator decline are likely to interact across wide areas [11]. In this study, we examine the  
68 combination and interaction of landscape factors that are likely to affect pollinator  
69 populations and communities across the widely varying UK countryside.

70

71 Our understanding of pollinator health has advanced significantly over the past decades by  
72 studies conducted on small groups of species or at small scales. For example, exposure to  
73 toxic pesticides can directly affect health, indirectly impact performance via foraging and  
74 reproduction [12, 13], and also impair immune responses to pathogens [4]. High densities of  
75 managed honey bees may be a stressor for wild bee populations under some conditions [7],  
76 due to competition for floral resources [14], or due to increased risk of pathogen spill over  
77 [15]. Similarly, poor nutrition due to low quality floral resource provision can increase the  
78 incidence of disease in honey bees [16], and pathogens are more likely to be spread in  
79 landscapes with low flower diversity [15, 17]. However, we are also discovering some  
80 interactions between these and other important drivers, such as the moderating influence of  
81 diverse floral resources and semi-natural habitat on the effects of agricultural chemicals on

82 insect development [18, 19]. The stressors to this diverse guild of insects are manifold and  
83 interactive [4], yet we lack comprehensive, standardised field studies to fully demonstrate  
84 how these factors influence the wider pollinator community [3, 20].

85

86 Research into landscape scale drivers of pollination populations and communities has grown  
87 significantly in the last two decades [3, 10, 11, 20-22], to the extent that landscape scale  
88 pollinator conservation is strongly encouraged by governments [3]. However, further research  
89 is needed to synthesise the impacts of widely-diverging land management practices across  
90 topographically diverse countries and to determine context-specific recommendations. Recent  
91 research has made great strides in identifying the important interactive effects of habitat type,  
92 landscape configuration and other drivers, but studies are often only focussed on particular  
93 crop types [23, 24], certain habitat types [25, 26], or limited species groups [27, 28].  
94 However, we require further studies to examine the scenarios in which landscape composition  
95 and configuration are important in mitigating the impacts of drivers such as habitat loss and  
96 fragmentation [29-33]. This information would be of considerable use when identifying  
97 landscape features to be prioritised for safeguarding pollinator communities (e.g., [34]).

98

99 In this study, we use a network of landscape study sites representing the full land use  
100 gradients in six regions of Great Britain. Our site selection protocol was designed to test the  
101 combined importance of four well-documented landscape drivers of pollinator community  
102 health (honey bee density, insecticide loadings, floral resource availability, and habitat  
103 diversity [35]). We surveyed the study sites for a wide range of pollinating insects for two  
104 years and aimed to understand how these land use factors are linked to pollinator density and  
105 diversity, which we use as proxies for community health. We predicted that, in line with

106 previous work, managed honey bee densities and insecticide application would have negative  
107 impacts on wild pollinator community composition across the country [7, 36]. Conversely, we  
108 predict floral resources and habitat diversity to have positive impacts due to their importance  
109 in enhancing pollinator health at individual, population and community levels [10, 26, 37]. In  
110 addition, as resource provision has the potential to offset the negative effects of intensive  
111 agriculture [10, 15, 18], we expected to find similar interactions between our drivers.  
112 Furthermore, during field surveys we observed that the configuration of wide ranging habitat  
113 types are likely to play important roles in pollinator community composition in British  
114 landscapes, as also shown elsewhere [38, 39]. Therefore, we also explore the potential for  
115 these land use factors to enhance our positive drivers and mitigate negative ones [3].

116

117

## 118 **Methods**

### 119 *Pollinator health*

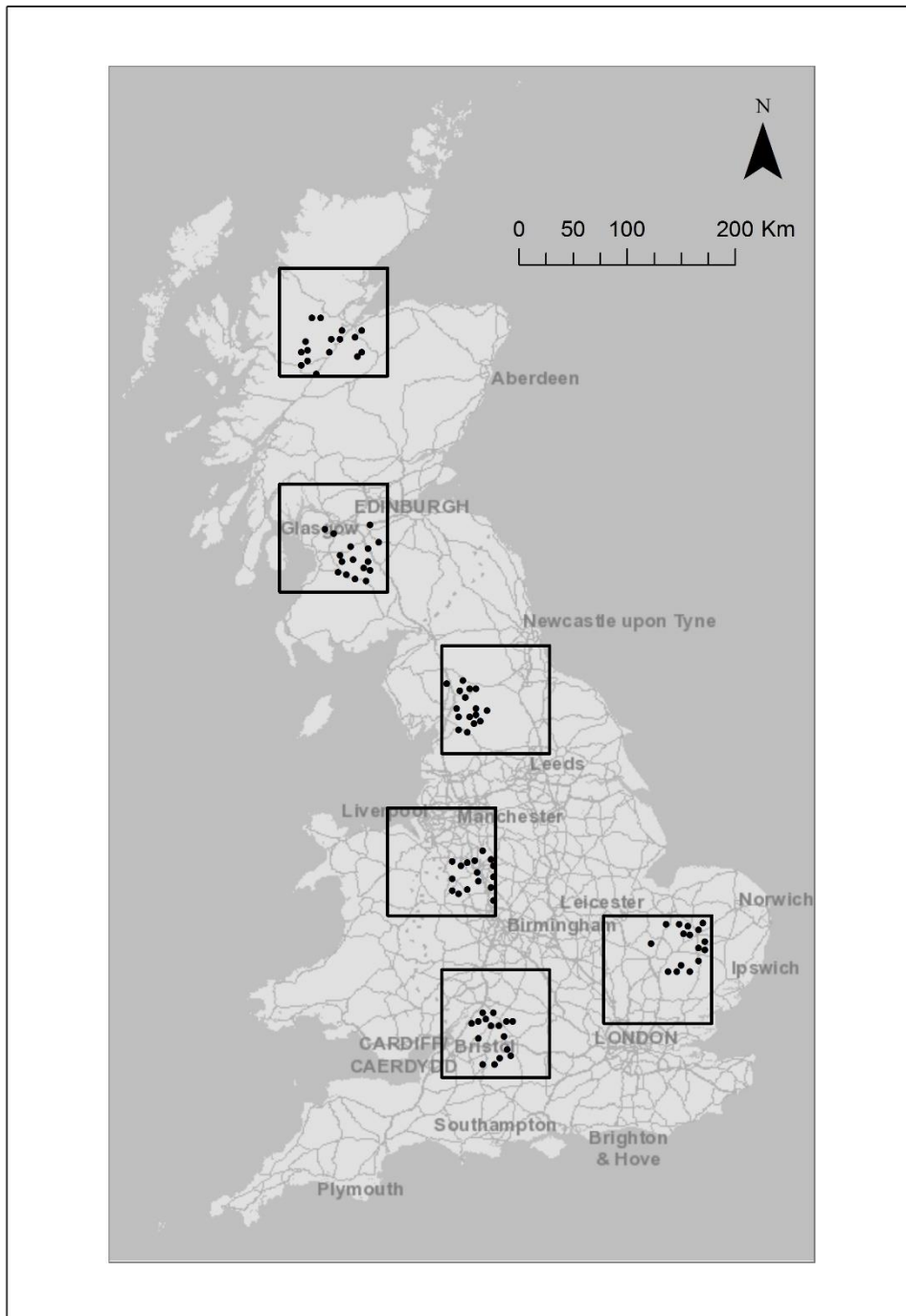
120 In this study we use measures of pollinator community composition, including abundance and  
121 diversity, as proxies for community health. There are limitations to this approach because  
122 community health is typically measured across several years, requires historical baseline data  
123 and/or involves direct measurements of fitness (e.g. longevity, reproductive success) [40].  
124 However, such data are difficult to collect over multiple landscapes and for entire  
125 communities. We therefore use more convenient diversity and abundance measures as  
126 indicators of community health, as it is reasonable to expect that landscapes with many  
127 populations able to optimally utilise resources to improve fitness, are likely to result in diverse  
128 and abundant communities. This is not always true (e.g., [41]), but wild bee abundance and  
129 diversity have been correlated with pollinator success in some systems (e.g., [42]).



130

131 *Study site selection*

132 A detailed account of the selection of our study regions and sites is published elsewhere [35],  
133 but we will provide a brief overview here. We first selected six 100 x 100 km “focal regions”  
134 to represent the vegetation and bioclimatic gradients of Great Britain. All possible  
135 combinations of six 100 km grid squares covering the country were measured in terms of the  
136 proportional area of all broad habitat types (using the 2007 Land Cover Map; [43]). The  
137 process was repeated for the Institute of Terrestrial Ecology (ITE) land classes (a stratification  
138 of all British 1 km squares allowing for representative, unbiased sampling given topography,  
139 climate and human infrastructure; [44]), and the six-region combination that provided the  
140 closest representation of Britain in both respects was selected (Fig 1).



141

142 Figure 1: Map of the six 100 x 100 km study regions (black squares) selected to represent  
 143 Britain in terms of broad habitats, topography and climate. The black dots depict the 16 study  
 144 sites chosen within each region.

145

146 Within each of the six regions, 16 study sites measuring 2 x 2 km were selected along four  
147 gradients: 1) honey bee densities, estimated from Beebase ([www.nationalbeeunit.com](http://www.nationalbeeunit.com))  
148 database information on local colony densities, and weighted by distance using data on honey  
149 bee foraging distances; 2) Insecticide loadings (including the loadings derived from  
150 insecticidal properties of fungicides and herbicides), measured as a summed honey bee hazard  
151 score, estimated from areas of 36 crop groups and insecticides usage data from the Pesticide  
152 Usage Survey; 3) Floral resource availability (kilograms of sugar from nectar per hectare per  
153 year), estimated by combining flowering species cover (insect-pollinated species including  
154 trees and bushes) per unit cover of each habitat from the Countryside Survey 2007 [45] and  
155 models of per-flower nectar quantity parameterised using field measurements of nectar  
156 production [46]; and 4) Habitat diversity values, calculated as Shannon diversity indices using  
157 habitat cover data from the 2007 Land Cover Map [43]. Full details of these estimates can be  
158 found in the Supplementary material.

159

160 To select the 16 sites in each region, we first scored all possible 2,500 grid squares of each  
161 region along the four gradients, standardised the values and applied a selection algorithm to  
162 find the sixteen sites that maximised the difference between high and low values of the four  
163 drivers and the orthogonality between them. For full details on the field site choice, see [35].  
164 The final 16 sites chosen for each region were thus considered to represent every combination  
165 of relatively high and low values for each of the four gradients. The values of the gradients of  
166 the final sites were subject to validation over the two-year survey period [35] and validated  
167 scores are used as predictor variables in this study. Insecticide loadings were adjusted first  
168 with ground referencing habitat and crop types. This resulted in a large number of our sites,  
169 particularly in Scotland and northern England, having insecticide loadings corrected to zero,  
170 because arable fields detected by the LCM 2007 were often reseeded grassland. Loadings for

171 sites with confirmed conventional crops were further validated via questionnaires provided to  
172 some landowners (where land ownership could be identified). For sites with confirmed  
173 chemical applications, the correlation between estimated and validated loadings was  $r_s = 0.67$   
174 [35]. Floral resource availability was validated through flower species surveys collected  
175 during the studying period and statistically modelled nectar availability (see Supplementary  
176 Materials for details; correlation with estimated values:  $r_s = 0.28$ ); and habitat diversity was  
177 validated by field surveyors confirming or correcting maps of broad habitat classes  
178 (correlation with estimated values:  $r_s = 0.77$ ) [35]. However, we were unable to improve on  
179 our original estimates of the honey bee density variable, as honey bees are poorly represented  
180 in pan trap samples ([47]; see below), and so the original modelled estimates of this gradient  
181 were retained.

182

183 We selected sites based on their values at the “tetrad” 2 x 2 km scale because this is the finest  
184 scale at which most datasets are available, and due to the relatively high mobility of many  
185 European pollinators [48]. However, as many solitary bees tend to forage across much smaller  
186 scales, we also calculated floral resource availability and habitat diversity for a central “inner”  
187 square (667 x 667 m) at each site (where pollinator collection was conducted; see below). We  
188 then tested whether these inner square variables were preferable predictors of pollinator  
189 responses to tetrad level variables (see Data analysis below).

190

### 191 *Pollinator collection*

192 In each region, a team of two surveyors was employed each year to collect pollinator  
193 specimens following a standardised protocol. Pollinators were trapped using pan traps  
194 consisting of three bowls painted yellow, white and blue with UV-reflecting paint [47], and

195 attached to a wooden stake at the height of the vegetation. These traps are “activity-based”  
196 with the colours acting as an attractant to foraging insects. It is possible that local flowering  
197 plant context affects the effectiveness of such a method. We attempted to control for this  
198 possibility by measuring floral resources in the area surrounding each trap (1m radius), but the  
199 variable was not significant in statistical modelling (not shown) and was omitted from final  
200 analysis. Furthermore, previous testing has found pan traps to sample pollinator communities  
201 more efficiently than observational methods [47]. Five pan traps were assigned to each site,  
202 and they were placed within a central square (667 x 667 m) of each 2 x 2 km site, and using  
203 the following criteria: away from potential disturbance by livestock and humans, in unshaded,  
204 open habitats, and approximately equidistant and at least 100 m from each other.

205

206 Each time a trap was set up, the bowls were half filled with water and a drop of unscented  
207 detergent was added to break the surface tension. Whenever possible, the traps were placed  
208 out when forecasts predicted clear, dry conditions and left in place for 24 hours before the  
209 bowls were removed and the insect material transferred to plastic bags for later mounting. The  
210 traps were sampled three times (Round 1: May, Round 2: June-July, Round 3: August-  
211 September; see Table S1 for precise dates), randomising the order of survey sites each time.  
212 Due to the geographic spread of the field sites across the region, it was usually only possible  
213 to set up pan traps in four sites at a time, although in some regions with limited access to sites  
214 (e.g. Inverness-shire), fewer sites were sampled in a day. Collected insect material was pinned  
215 and mounted during the summer of collection, and specimens were identified to species by  
216 Hymettus Ltd. Taxonomic resources included [49] for hoverflies, and test keys that formed  
217 the basis of [50] for bees and wasps.

218

219 *Floral resource diversity, habitat composition and habitat configuration*

220 In order to explore the mitigating effect of landscape context on responses to the four key  
221 drivers, we derived three further variables. First, floral resource diversity was calculated using  
222 the flower species and nectar data used to validate the floral resource availability driver. We  
223 first estimated each flowering species' nectar provision in  $\mu\text{g}$  per  $\text{m}^2$  for each of 28 broad  
224 habitat types (the Broad habitat sub-classes listed in Table S6, Supplementary material, plus  
225 the linear features: hedgerows, water edges, stone walls and fencelines). We then scaled this  
226 up to the landscape scale, by multiplying the values by the area of each habitat type for each  
227 site. These values were summed for each species to derive their contribution to the site level  
228 floral resource availability. We used these contributions to calculate the Shannon diversity  
229 index of floral resources for site (see Supplementary materials for full details). We preferred  
230 this measure to a flower species diversity index, because it emphasises the richness and  
231 evenness of nectar sources [46].

232

233 Second, habitat composition was defined as the percentage cover of semi-natural habitat  
234 (SNH) in each site, and was derived from validated land cover data described above. We  
235 included all habitat types not classed as arable, improved grassland, urban and open water in  
236 this calculation. Therefore, our measure of SNH comprises all aspects of forest (including  
237 conifer plantations), and all types of rough, low productivity grassland. Across Britain, these  
238 types of habitat may be subject to varying levels of management, but in comparison to arable  
239 and improved grassland, this can be considered low intensity. Further, while conifer  
240 plantations are not typically useful foraging habitats for wild pollinators, in many of our sites,  
241 particularly in Scotland and Eastern England, the large areas of conifer are managed as nature  
242 reserves and recreational areas and may represent useful nesting habitat, structural diversity  
243 and corridors for movement. We also selected this measure because it provided a broad

244 gradient of data across all six regions, and because use of separate habitat class percentage  
245 covers as individual variables led to problems with collinearity and residual heterogeneity.

246

247 Thirdly, habitat configuration was estimated as an index of habitat proximity following a  
248 method described by [39]. On each site, 100 m buffers contoured around patch boundaries  
249 were created for each SNH patch, including linear features (features found at field margins  
250 such as hedgerows, water features and fence lines). Subsequently, the area of overlapping  
251 buffer zones was calculated and divided by the total buffer area to represent habitat proximity.  
252 Therefore, high values of this index are likely to represent landscapes with many closely  
253 located patches of semi-natural habitat, and low values may represent sites dominated by  
254 intensively managed land types or by large patches of a single SNH type. Spatial calculations  
255 were conducted using QGIS (v3.10.3 [51]).

256

### 257 *Data analysis*

258 We pooled the insect pollinator data from the five pan traps at each site and across the three  
259 rounds and analysed data from both years in the same models (i.e., each site was represented  
260 by two years of sampling data). We used the sampled pollinators to estimate pollinator  
261 abundance, species richness, and the inverse Simpson diversity index ( $1/D$ ). We derived these  
262 measures for the 'full' wild pollinator community (all hoverflies, wasps and bees except  
263 honey bees), as well as separately for bumblebees (*Bombus* spp.), solitary bees (including  
264 cleptoparasitic species) and hoverflies (Diptera: Syrphidae). These community response  
265 measures were then analysed in two ways, using a confirmatory approach to test our original  
266 hypotheses, and an exploratory approach to assess possible mediating roles of habitat cover  
267 and proximity. For the confirmatory models, we fitted generalised linear mixed models

268 (GLMM) to each response with the four drivers (honey bees, insecticides, habitat diversity,  
269 and floral resource availability) and all two-way interactions as fixed explanatory variables.  
270 Higher-order interactions were excluded for clarity and to avoid complex interpretation. To  
271 improve model convergence, insecticides and floral resource availability were log-  
272 transformed, and all drivers were scaled and centred. We tested whether the “inner” scale  
273 variables for floral resource availability and habitat diversity were better predictors than those  
274 at the tetrad scale using AIC, and by comparing residual diagnostic plots. For all response  
275 variables, the choice of variables made negligible difference to model fit ( $\Delta AIC < 2$ ), and we  
276 proceeded with the tetrad scale variables for consistency. The exploratory approach followed  
277 the same procedure, but included the scaled and centred variables SNH, habitat proximity and  
278 floral resource diversity, and all two-way interactions between them and the four main  
279 drivers.

280

281 All data analyses were performed in the R programming environment (v4.1.0 [52]). Mixed  
282 models were fit using the *glmmTMB* package [53], and in all cases, a fixed factor for sampling  
283 year (2012/13) and a fixed integer variable for the number of pan trap bowls successfully  
284 collected (out of a total of 45) were included as covariates to account for differences between  
285 years and for the effect of trap bowls being disturbed by animals or passers-by, respectively.  
286 Random intercepts for ‘site’ (n = 96) nested within ‘region’ (n = 6) were also specified. There  
287 was no collinearity between the explanatory variables, which was checked using variance  
288 inflation factors (VIF) with the *performance* package [54]. The error distribution for each  
289 response variable was determined using residual diagnostic plots and tests applied using the  
290 residual simulation methods of the *DHARMA* package [55]. In most cases for count data  
291 (abundance and species richness), the negative binomial distribution with quadratic  
292 parameterisation (‘nbinom2’ family) provided the best fit to the data, although in some cases



293 (bumblebee and hoverfly species richness) the Poisson distribution provided a better fit. The  
294 Gamma distribution with a log link was used to model the Inverse Simpson diversity index.  
295 All model (simulated) residuals were inspected visually for assumptions of linear modelling  
296 (normality and homoscedasticity). Model residuals were also tested for spatial and temporal  
297 autocorrelation, and the random structure adequately accounted for the clustering and  
298 repeated nature of the sampling. Following model validation, 95% confidence intervals were  
299 calculated for all model estimates using the *confint* function of the *glmmTMB* package, which  
300 computes Wald intervals by default. Significant interactions (those with confidence intervals  
301 not including zero) were plotted with simple slopes, where the predicted effect of one  
302 interacting variable is plotted for several fixed values of the second interacting variable. In  
303 most cases, we chose to keep the second interacting variable constant at the 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup>  
304 quantile values. The exception was for insecticide loadings. Our sites were relatively evenly  
305 distributed between those with and without insecticide loadings. We therefore kept this  
306 variable constant at zero and at the median of those sites with insecticide loadings.

307

## 308 **Results**

309 In total, we collected 20,236 insect pollinators representing 294 species, with a greater  
310 number of individuals and species collected in 2012 (Table 1). Most bee individuals and  
311 species were captured in the two southernmost regions (Cambridgeshire and Wiltshire), and a  
312 high number of hoverflies were caught in the “middle” regions of Ayrshire, Yorkshire, and  
313 Staffordshire. The northernmost region, Inverness-shire, had the lowest numbers of  
314 individuals and species across all groups.

315

316 **Table 1:** Captures of pollinator individuals (and species numbers) across the six focal regions  
 317 and for the three pollinator groups. Individuals identified only to genus were removed from  
 318 the dataset when calculating species numbers.

	All pollinators		Bumblebees		Solitary bees		Hoverflies	
	2012	2013	2012	2013	2012	2013	2012	2013
Suffolk/Cambridgeshire	1,830 (142)	1,224 (116)	474 (10)	420 (9)	884 (66)	331 (45)	342 (35)	424 (43)
Gloucestershire/Wiltshire	1,568 (126)	967 (94)	154 (9)	195 (11)	515 (59)	240 (34)	845 (39)	516 (41)
Staffordshire	2,402 (85)	1,636 (89)	147 (10)	427 (11)	87 (23)	133 (26)	2,159 (46)	1,048 (41)
Yorkshire	1,144 (50)	658 (57)	65 (7)	78 (9)	21 (8)	69 (13)	1,055 (32)	505 (32)
Ayrshire/Renfrewshire	4,961 (78)	2,885 (71)	198 (12)	308 (10)	24 (10)	31 (6)	4,731 (52)	2,496 (49)
Inverness-shire	664 (60)	297 (45)	172 (9)	114 (9)	37 (9)	18 (6)	440 (37)	149 (23)
Total	12,569 (240)	7,667 (205)	1,210 (17)	1,542 (16)	1,568 (86)	822 (67)	9,572 (89)	5,138 (84)

319

320

### 321 *Confirmatory analysis*

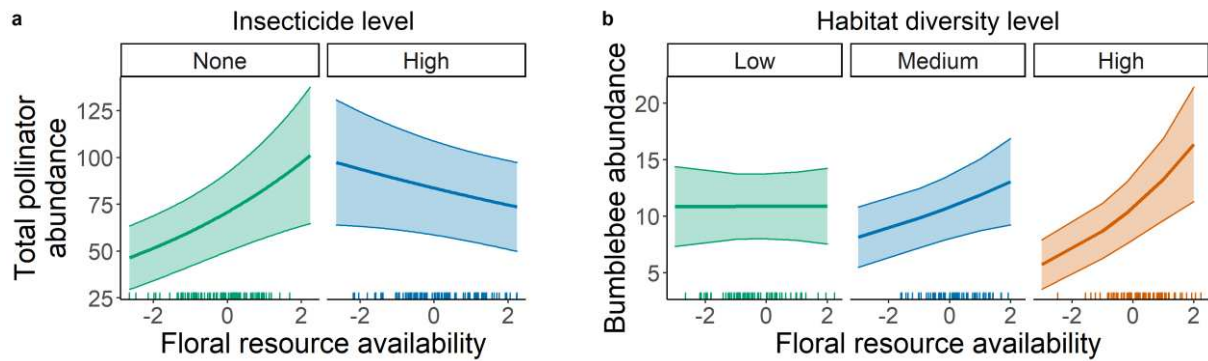
322 The four target drivers as main effects in our GLMMs did not significantly affect abundance  
 323 of total pollinators, or of bumblebees or hoverflies when considered separately (Table S8), but  
 324 there was a positive association between managed honey bee density and solitary bee  
 325 abundance. This relationship was also present for both total pollinator and solitary bee  
 326 richness and diversity (Table S9 & S10).

327

328 We only found two significant interactions between the focal drivers. First, the effect of floral  
 329 resource availability on total pollinator abundance depended on insecticide loadings in the  
 330 surrounding landscape, with the positive influence of floral resource availability most  
 331 pronounced when loadings were absent, and the association apparently reversed at high

332 loadings, although with high uncertainty (Table S8, Fig. 2a). Second, the association between  
333 floral resource availability and bumblebee abundance depended on habitat diversity,  
334 suggesting that floral resources were more beneficial to bumblebees in landscapes with  
335 diverse habitats (Table S8, Fig. 2b).

336



337

338 **Figure 2:** Interaction graphs for a) the abundance of total insect pollinators plotted against  
339 floral resource availability when insecticides are absent, and when insecticides are “high”  
340 (median insecticides for sites with non-zero values), and b) bumblebee abundance for three  
341 levels of habitat diversity at the 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> quartile. Regression lines show the predicted  
342 abundance from the GLMM (in counts) when all other predictors are held constant at mean  
343 values. Shaded areas are  $\pm 1$  SE. See Table S8 for full model results.

344

345

#### 346 *Exploratory analysis*

347 The exploratory models revealed several consistent interactions between focal drivers and  
348 additional variables. Honey bee density was found to interact with habitat diversity for the  
349 abundance of all pollinators (Fig. 3a) and solitary bees separately (Fig. S2, Table S11), as well  
350 as the richness of all pollinators, solitary bees and hoverflies (Fig. S2, Table S12). The

351 positive association between these responses and honey bee density occurred at low to  
352 medium habitat diversity, and the opposite occurred in more diverse landscapes (as illustrated  
353 by Fig. 3a). A similar interaction was found between honey bee density and semi-natural  
354 habitat proximity for some of the same responses (total pollinator abundance: Fig. 3b, Table  
355 S11; Solitary bee abundance: Fig. S2, Table S11, Total richness & hoverfly richness: Fig. S3,  
356 Table S12, hoverfly diversity: Fig. S4, Table S13) . For example, the simple slopes of this  
357 model term suggests that more abundant and diverse pollinator communities occur at high  
358 honey bee densities and when SNH patches are close together, but there may be a negative  
359 relationship with honey bee densities in landscapes with low habitat proximity (Fig. 3b).

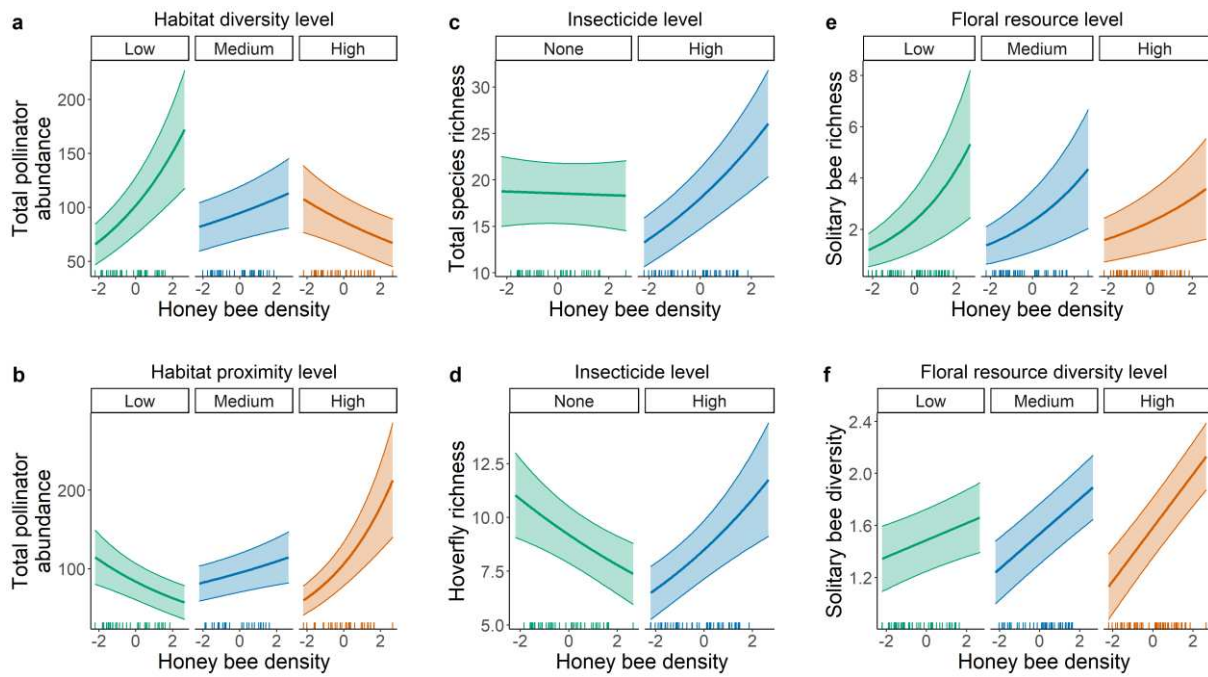
360

361 Honey bee density was also found to interact with insecticide loadings for total and hoverfly  
362 species richness (Fig 3c & d, Table S12), and with floral resource availability for solitary bee  
363 richness (Fig. 3e, Table S12) and solitary bee diversity models (Fig. 3f, Table S13). At high  
364 insecticide loadings, there was a positive association between honey bee density and both  
365 total and hoverfly richness , but the opposite pattern for hoverfly richness in the absence of  
366 insecticides. In addition, honey bee densities were more strongly positively associated with  
367 solitary bee richness at lower levels of floral resource availability, and with solitary bee  
368 diversity at higher levels of floral resource diversity .

369

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373

374 **Figure 3:** Interaction graphs of the significant interactive effects of landscape drivers on a) –  
 375 b) the abundance of total insect pollinators, c) total species richness, d) hoverfly richness, e)  
 376 solitary bee richness, and f) solitary bee diversity. In graphs c) and d), insecticide loadings are  
 377 either absent (“none”) or “high” (median insecticide loadings for sites with non-zero values).  
 378 In all other graphs, the 2<sup>nd</sup> predictor level is held constant at the 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> quartiles.  
 379 Regression lines show the predicted abundance, richness or diversity from the GLMM when  
 380 all other predictors are held constant at mean values. Shaded areas are ± 1 SE. See Tables  
 381 S11-S13 for interaction confidence intervals.

382

383 Insecticides also interacted with floral resources, habitat diversity and the amount of SNH in  
 384 the landscape, and these were mainly found for total pollinator and bumblebee abundance  
 385 (Fig. S2, Fig. 4a, Table S11) and bumblebee diversity (Fig. S4, Table S13). Firstly, total  
 386 pollinator and bumblebee abundance were positively associated with floral resource  
 387 availability when insecticides were absent, and show weak negative relationship when

388 insecticides were present (Fig. 4a). A similar pattern is also shown for the interaction between  
389 insecticide loadings and floral resource diversity (Fig. 4b).

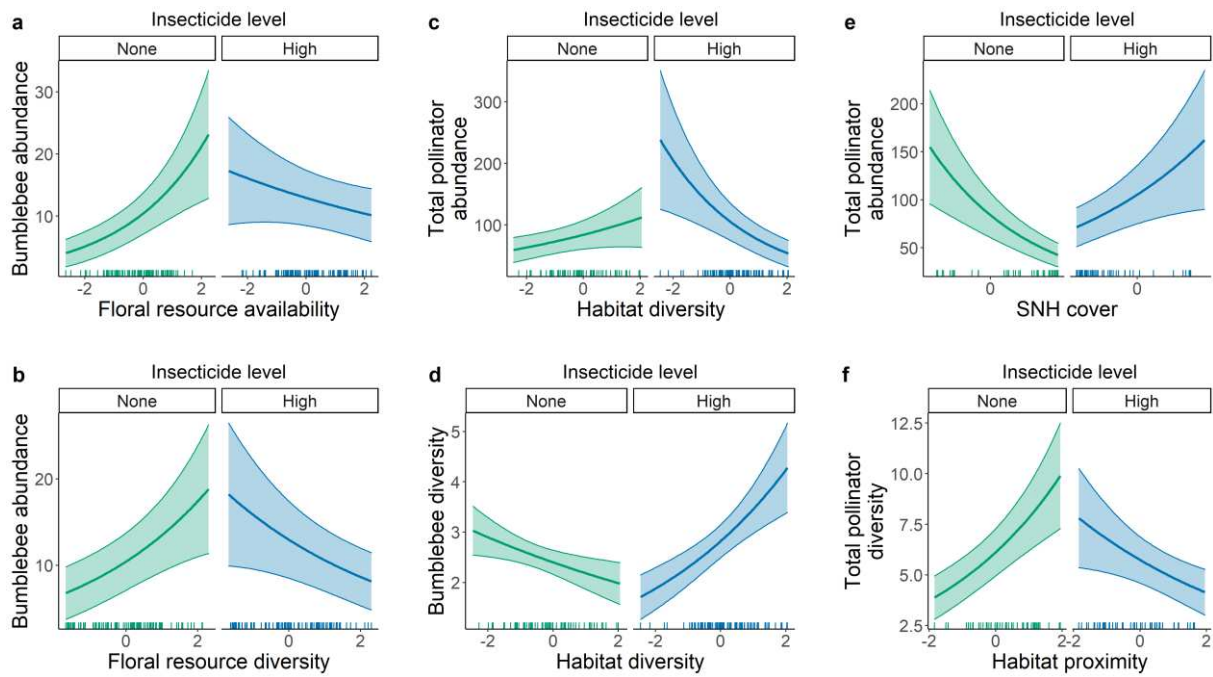
390

391 There was a contrasting interaction between insecticides and habitat diversity for total  
392 abundance and bumblebee diversity. Habitat diversity appears to be negatively associated  
393 with total pollinator abundance in the presence of insecticides, but positive when they were  
394 absent (Fig. 3c, Table S11). Conversely, habitat diversity was positively related to bumblebee  
395 diversity in landscapes where insecticides were applied, and negatively related in the absence  
396 of insecticides (Fig. 3d, Table S13).

397

398 A similar contrasting pattern was found in relation to SNH variables. The abundance of all  
399 pollinators and hoverflies were positively related to SNH cover when insecticides were  
400 present in the landscape, but negatively related in untreated landscapes (Fig. 3e & S2, Table  
401 S11). The interaction between insecticides and habitat proximity showed the opposite pattern  
402 for total pollinator diversity (Fig. 3f, Table S13). Landscapes with no insecticide applications  
403 and SNH patches in close proximity were associated with high species diversity. However,  
404 relatively high diversity was also related to high insecticides and low connection between  
405 habitat patches.

406



407

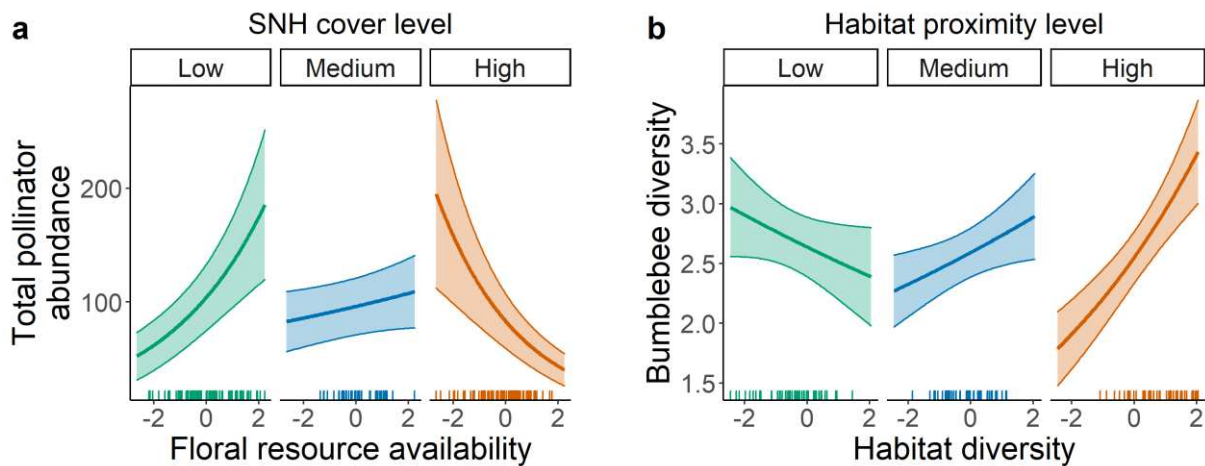
408 **Figure 4:** Interaction plots of the significant interactive effects of landscape drivers on a) – b)  
 409 bumblebee abundance of total insect pollinators, c) & e) abundance of total insect pollinators,  
 410 d) bumblebee diversity and f) total species diversity. In all graphs, insecticide loadings are  
 411 held constant at either absent (“none”) or “high” (median insecticide loadings for sites with  
 412 non-zero values). Regression lines show the predicted abundance or diversity from the  
 413 GLMM when all other predictors are held constant at mean values. Shaded areas are  $\pm 1$  SE.  
 414 See Tables S11-13 for interaction confidence intervals.

415

416 In addition to the interactions detailed above, floral resource availability interacted with SNH  
 417 cover for a number of abundance and richness responses. These patterns were all similar,  
 418 indicating that SNH availability promoted total abundance (Fig 5a, Table S11) and richness  
 419 (Fig S3, Table S12), bumblebee abundance (Fig. S2, Table S11) and the abundance and  
 420 richness of hoverflies when floral resources were scarce (Figs. S2 & S3, Tables S11 & S12).  
 421 Similarly, floral resource availability was important to these responses when SNH cover was  
 422 low. Surprisingly, a combination of both high SNH cover and high floral resource availability

423 lead to some of the lowest number of predicted species. Finally, in addition to the interactions  
424 involving habitat diversity above, bumblebee diversity was predicted to be highest when both  
425 habitat diversity and proximity were high (Fig. 5b, Table S13).

426



427

428

429 **Figure 5:** Interaction plots of selected significant interactive effects of landscape drivers on a)  
430 abundance of total insect pollinators, and b) bumble diversity. In all both graphs, the 2<sup>nd</sup>  
431 predictor level is held constant at the 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> quartiles. Regression lines show the  
432 predicted abundance or diversity from the GLMM when all other predictors are held constant  
433 at mean values. Shaded areas are  $\pm 1$  SE. See Tables S11 and S13 for interaction confidence  
434 intervals.

435

## 436 Discussion

437

438 In this study we have used the most comprehensive nationwide network of study sites to  
439 explore the multiple, interacting drivers of insect pollinator communities in Great Britain. We



440 found that four landscape scale factors considered important to pollinators could not provide  
441 simple explanations for abundance, richness or diversity patterns, except for an unexpected  
442 positive relationship between honey bee density and both total pollinators and solitary bees.  
443 While some factors combined to explain total and bumblebee abundance and richness in our  
444 confirmatory models, we revealed a complex set of responses when incorporating landscape  
445 composition and proximity variables in our exploratory models, supporting previous work  
446 suggesting that improving pollinator population and community health requires an  
447 understanding of local and regional land use factors [7, 10, 31]. We should note that our  
448 project was not designed to test *a priori* hypotheses about these interactions, and we  
449 recommend that further studies seek to confirm these findings. Caution should also be used  
450 when interpreting the results involving two of our four drivers: honey bee density is the one  
451 variable that we could not validate with collected data, and the insecticide loadings variable  
452 did not consist of as wide a range of values within regions as we would have hoped [35].

453

#### 454 *Managed honey bee density*

455 We expected the estimated density of managed honey bees to have a negative relationship  
456 with most functional groups of wild pollinators via either competition for food or the  
457 transmission of pathogens [7]. As a simple effect there were only positive associations of  
458 honey bee density on total richness and diversity, and on all three solitary bee responses.  
459 These may be geographical artefacts, however, because solitary bee abundance and diversity  
460 generally decreased with latitude, and our knowledge of honey bee densities was likely to be  
461 more accurate in the southern regions. It is also possible that the scale of our study sites were  
462 inappropriate for solitary bees, although finer scale measures of floral resource availability  
463 and habitat diversity did not improve our models. Nevertheless, the exploratory models also  
464 suggest that the positive relationship with solitary bee diversity was strongest in landscapes

465 with high floral resource availability and diversity. We expected honey bees to compete with  
466 wild pollinators mainly for floral resources, since honey bee nesting is provided by  
467 beekeepers. However, competition is thought to be context dependent and the majority of  
468 reported negative impacts of honey bees are from territories where the species is not native [7,  
469 26]. *Apis mellifera* is native to the UK [56], which could contribute to the ability of honey  
470 bees and wild pollinators to co-exist in suitable locations when resources are abundant [7, 42].  
471 The placement of honey bee colonies in resource rich environments with coincidental healthy  
472 wild pollinator communities seems an unlikely explanation, given that very few beekeepers in  
473 the UK move their honey bee colonies, instead tending to keep bees close to where they live.

474

475 We also found context dependence in the association, with only weak negative relationships  
476 with abundance in landscapes with low habitat proximity (dominated by arable, grassland or  
477 large single patches of SNH), and high habitat diversity. Sites in our study with this  
478 combination of landscape properties are those with many small isolated patches of semi-  
479 natural habitat, which may provide nesting sites for bees, but require them to forage far into  
480 the agricultural matrix where floral resources may be scarce. Similar patterns have been  
481 reported in Sweden, where competition between honey bees and wild bees and hoverflies  
482 increased with crop field size [57], or when the amount of semi-natural grassland in the  
483 surrounding landscape was low [58]. By contrast, sites in our study with low habitat diversity  
484 but high proximity to SNH, which seem to promote coexistence between managed and wild  
485 pollinators are those with several large patches dominated by a single use such as moorland,  
486 rough grassland or even improved grassland, and divided by linear features (e.g. hedgerows,  
487 ditches and fence lines). These sites may be ideal situations with abundant resources for both  
488 managed honey bee hives and pollinator communities, and we suggest focussed research on  
489 these large habitat types. Interestingly, there remain significant gaps in our understanding of

490 how honey bees can influence population-level responses of plant communities, such as plant  
491 abundance or distribution [7], perhaps masking wider benefits to wild pollinators.

492

### 493 *Insecticide loadings*

494 This variable was less well distributed among the regions because virtually no insecticides  
495 were applied in the three northernmost landscapes, but large amounts were applied in the two  
496 southernmost regions [35]. Nevertheless, in landscapes where insecticides were not applied,  
497 we found positive effects of other drivers such as floral resource availability, resource  
498 diversity and habitat proximity. Interestingly, floral resource availability and diversity  
499 appeared to have a negative association with pollinators in the presence of insecticides. We  
500 interpret this as an increased exposure to insecticide in the presence of abundant and diverse  
501 food resources, such as in chemically treated mass-flowering crops [59], or because forage  
502 plants in adjacent uncultivated habitats can be sources of insecticide exposure for pollinators  
503 via drift or soil pathways [36, 60, 61]. While field microcosm experiments suggest that  
504 diverse forage sources provided as alternatives to mass-flowering crops should offset the  
505 negative impacts of insecticides [18], we did not find evidence of this at the landscape scale.

506

507 There was also a positive relationship between SNH and total pollinator abundance, and  
508 between bumblebee diversity and habitat diversity in the presence of insecticides, in line with  
509 previous findings [19, 62]. These studies suggest that higher amounts of SNH in the landscape  
510 support pollinator communities by providing a refuge from intensive agricultural practices  
511 such as chemical applications [19], although pesticide residues have been found in sites with  
512 up to 89% semi-natural grassland in the surroundings [63]. It is not clear why SNH cover had  
513 a negative impact in the absence of insecticide application, but may be due to our inclusion of

514 conifer plantations in SNH. Untreated sites with high SNH are likely to be those in the  
515 northern regions with high covers of conifer and moorland, and these sites typically had low  
516 pollinator catches. Exclusion of conifer plantations from our SNH variable would have  
517 resulted in these sites scoring very low on the SNH scale, perhaps nullifying the interaction  
518 effects shown here. In any case, as our study design was limited in detecting within-region  
519 relationships between insecticides and pollinators [35], future work on this scale should base  
520 landscape selection on ground-truthed chemical application data. For example, while the  
521 chemical application data we used was of a high standard, our reliance on the LCM 2007 to  
522 select sites with “high” estimated insecticides prevented this gradient from reflecting the full  
523 range of loadings in Britain. Further studies could also focus on the indirect effect of  
524 herbicides via floral resources.

525

#### 526 *Floral resource availability*

527 As well as a positive relationship with pollinator abundance and diversity in the absence of  
528 insecticides, floral resources were important to bumblebee abundance in landscapes with high  
529 habitat diversity. This is unsurprising as a diversity of habitats provides a range of nesting  
530 resources for bumblebees [26], and a correspondingly high level of continuous food supply is  
531 required to support healthy colonies [64]. As central place foragers, bees are more likely to  
532 forage efficiently when flowering plants are abundant within a short distance of the nest [65].  
533 A more surprising result is that we did not find the same synergistic interaction for more  
534 groups. This is perhaps because our scale of study was not appropriate for solitary bees with  
535 shorter foraging ranges, for example.

536

537 In contrast to the above pattern, we found that floral resources were important in landscapes  
538 with low cover of semi-natural habitat. This supports theories of floral provision in  
539 agricultural landscapes, where small patches of nesting resources, such as semi-natural  
540 habitat, should be interspersed with rich floral resources to benefit pollinators [20, 31]. In our  
541 landscapes, the combination of low SNH cover and high floral resource availability  
542 corresponds to sites with high arable cover including mass flowering crops or with a high  
543 cover of improved grassland with flower rich field boundaries. Bumblebees may be  
544 particularly attracted to mass flowering areas over SNH [38, 65], and other bees and  
545 hoverflies may benefit from the connectivity effect provided by floral resources in field  
546 margins [20]. Conversely, the apparent negative relationship between pollinators and SNH  
547 under high floral resources occurs in sites with large areas of heathland and rough grazing. In  
548 such wide, open places, pollinators may concentrate around patches of flowers rather than  
549 disperse [66] and are likely only attracted to our pan trap bowls when resources are low.  
550 Alternatively, floral resources may be relatively homogenous at these sites resulting in low  
551 abundances of pollinating insects [30].

552

### 553 *Habitat diversity*

554 We expected habitat diversity in general to have positive associations with the diversity of the  
555 pollinator community, as a greater array of habitat cover types provide a range of alternative  
556 nesting substrates and niches [26]. However, as we have shown, this can be mediated by  
557 landscape context such as local honey bee densities and insecticide loadings. Furthermore, in  
558 our landscapes low habitat diversity can correspond to large covers of intensive land uses  
559 such as arable or improved grassland, or conversely to a dominance of SNH such as heathland  
560 or low intensity habitat such as coniferous forest. When other habitat variables were included  
561 in models, habitat diversity showed the expected positive relationship with bumblebee

562 diversity when habitat proximity was also high. This supports findings that the provision of  
563 habitat patches *per se* is not always sufficient to promote all aspects of pollinator community  
564 abundance and diversity, but that habitat patches should be connected or at least within  
565 foraging range of a variety of functional groups [20, 31].

566

## 567 *Conclusions*

568 Our results are difficult to distil into simple, generalisable statements. We found rather few  
569 simple effects of the often-cited key drivers of pollinator community composition and  
570 distribution across highly variable topographic areas. This suggests that such variables do not  
571 generalise well across regions that are characterised by their land use, climate and  
572 management. While we have not directly measured pollinator fitness, we infer from these  
573 results that improving pollinator community health at the landscape scale is also unlikely to  
574 have a quick or general fix. When it comes to conservation or restoration of pollinator  
575 communities, our study supports others studies that call for taxon- and context-specific  
576 decisions to be made [7, 32, 67]. Furthermore, unlike other studies that find no effect of SNH  
577 on pollinator communities [29, 68, 69], we find support for studies that include landscape  
578 composition and configuration variables as interactive terms in models [38, 70]. As the reality  
579 of interacting landscape drivers and their effects on pollinator community composition and  
580 health is likely to be even more complex than what we have been able to test, we further  
581 recommend that better policy and practice decisions are likely to be reached by taking multi-  
582 driver, multi-taxa approaches.

583

584 Despite the complexity of our results, some key messages are clear. First, pollinator  
585 community health, if it is indeed correlated with abundant and diverse pollinator assemblages,

586 is likely to be enhanced by increasing the availability and diversity of floral resources, but the  
587 landscape context in terms of insecticide loadings, habitat diversity and habitat proximity  
588 should be considered in their selection and placement. Second, in intensively managed  
589 landscapes, floral resources can be important when SNH cover or proximity is low, and  
590 habitat diversity and configuration can also play important, though complex roles. Third,  
591 while other studies have found that beneficial resources can offset negative influences, we did  
592 not find consistent evidence of this. Thus, instead of simply relying on boosting pollinator  
593 resources to rectify otherwise unhealthy management practices, we recommend that pollinator  
594 conservation should be fine-tuned in relation local land use context. Finally, we re-iterate that  
595 many of our findings were revealed from exploratory data analysis, and we did not have  
596 sufficient data for cross-validation. We therefore further recommend future landscape scale  
597 research confirming the importance of habitat context to the drivers of pollinator  
598 communities.

599

## 600 **Acknowledgements**

601 We would like to extend thanks to our network of farmers, landowners and land managers  
602 who provided access to their land to survey pollinators and to our field assistants for  
603 conducting the field work: Nicole Dunn, Hayley Wiswell, Ewan Munro, Katy Donald, Jessica  
604 Heikkinen, Katherine White, Clare Pemberton, Paul Webb, Mark Tilzey, Sara Iversen, Robin  
605 Curtis, Paul Hill, Sam Bacon, Paul Wilson, Bex Cartwright, John Fitzgerald, Patrick  
606 Hancock, Mel Stone, Robert Day, James McGill, Tracie Evans. We also thank the  
607 taxonomists for identifying insect material: Megan McKercher, George Else, Kirsty  
608 Robertson, A. Ricarte, L. Truslove, M. Smith, M. Kayser, and Z. Nedeljković.

609

610 **Funding**

611 This research was supported by the UK Insect Pollinator Initiative project ‘AgriLand: Linking  
612 agriculture and land use change to pollinator populations’, funded under the Living with  
613 Environmental change programme, a collaboration between Biotechnology and Biological  
614 Sciences Research Council (BBSRC), the Wellcome Trust, Scottish Government, Department  
615 of Environment, Food and Rural Affairs (DEFRA) and Natural Environment Research  
616 Council (NERC): grant BB/H014934/1.

617

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