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1      **Historical nectar assessment reveals the fall and rise of Britain in bloom**

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12    **Summary**

13    **There is considerable concern over declines in insect pollinator communities and potential**  
14    **impacts on the pollination of crops and wildflowers<sup>1–4</sup>. Among the multiple pressures facing**  
15    **pollinators<sup>2–4</sup>, decreasing floral resources due to habitat loss and degradation has been**  
16    **suggested as a key contributing factor<sup>2–8</sup>. However, a lack of quantitative data has**  
17    **hampered testing for historical changes in floral resources. Here we show that overall floral**  
18    **rewards can be estimated at a national scale by combining vegetation surveys and direct**  
19    **nectar measurements. We find evidence for substantial losses in nectar resources in**

20 **England and Wales between the 1930s and 1970s; however, total nectar provision in Great**  
21 **Britain as a whole had stabilised by 1978, and increased from 1998 to 2007. These findings**  
22 **concur with trends in pollinator diversity, which declined in the mid-20th century<sup>9</sup> but**  
23 **stabilised more recently<sup>10</sup>. The diversity of nectar sources declined from 1978 to 1990 but**  
24 **stabilised thereafter at low levels, with four plant species accounting for over 50% of**  
25 **national nectar provision in 2007. Calcareous grassland, broadleaved woodland and neutral**  
26 **grassland are the habitats that produce the greatest amount of nectar per unit area from**  
27 **the most diverse sources, whereas arable land is the poorest in both respects. While agri-**  
28 **environment schemes add resources to arable landscapes, their national contribution is low.**  
29 **Due to their large area, improved grasslands could add substantially to national nectar**  
30 **provision if they were managed to increase floral resource provision. This national-scale**  
31 **assessment of floral resource provision brings new insights into the links between plant and**  
32 **pollinator declines, and offers considerable opportunities for conservation.**

### 33 **Main text**

34 Concerns have been raised about declines in both wild and managed insect pollinators<sup>1–4</sup>. While  
35 several potential drivers have been cited<sup>2–4</sup>, one important factor in pollinator declines may be the  
36 loss of floral resources due to changes in land-use and management<sup>5–8</sup>. Several factors may have  
37 caused decreased floral resources in Great Britain and other developed countries, including  
38 increased use of herbicides<sup>11</sup>, destruction of traditional landscape features such as hedgerows<sup>12</sup>  
39 and loss and degradation of wildflower-rich natural habitats<sup>13–15</sup>. Current strategies to mitigate  
40 pollinator declines focus primarily on enhancing floral resources<sup>4</sup>, including agri-environmental  
41 scheme options such as sowing nectar flower mixtures<sup>16,17</sup>. There is evidence for declines in some

42 key pollinator forage plants in Great Britain<sup>5</sup> and the Netherlands<sup>7</sup>, but the notion that the overall  
43 availability of floral resources has declined is largely based on subjective assessments. Floral  
44 resources have never been quantified at national or even landscape scales.

45 While both nectar and pollen are important floral resources, we focus on nectar because of its  
46 importance as an energy source in the diets of adult bees, and because it provides a common  
47 currency (total sugars) in which we can express the nutritional contribution of all plant species<sup>18</sup>.

48 We quantified the nectar resources in Great Britain by combining directly measured and  
49 modelled nectar productivity data per unit cover for 260 common plant species (Supplementary  
50 Table 1) with historical vegetative cover estimates from the British Countryside Survey<sup>19</sup>, a  
51 representative national-scale survey of plant community composition. Together, the 260 species  
52 comprise the vast majority of British nectar sources as they include virtually all nectar-producing  
53 plants from the set of species covering 99% of the British land area. Using vegetation data from  
54 the latest Countryside Survey (2007), we quantified recent nectar productivity of habitats (nectar  
55 sugar per unit area and time) and the diversity of their nectar sources (considering nectar  
56 production both by species and by floral morphology groups, referred to as “species nectar  
57 diversity” and “functional nectar diversity” respectively). Production was scaled up to estimate  
58 national nectar provision using the estimated area of habitats<sup>19</sup>, allowing the contributions of  
59 species, habitats and agri-environment schemes to national nectar provision to be assessed. We  
60 estimated historical shifts in nectar provision over recent decades using data from earlier  
61 Countryside Survey rounds (1978, 1990, 1998 and 2007), considering both changes in nectar  
62 productivity within habitats and changes in habitat area. We also investigated floral resource  
63 changes from the 1930s onward for England and Wales, based solely on changes in habitat  
64 coverage.

Considering the most recent Countryside Survey (2007), there are significant differences in annual nectar productivity, species nectar diversity and functional nectar diversity among habitats (Extended Data Table 1). Calcareous grassland, broadleaved woodland and neutral grassland are the best in all three respects (as well as shrub heathland for nectar productivity only) whereas arable land is consistently the poorest habitat (Supplementary Table 2). These habitat differences in nectar value create geographical variation in nectar productivity and diversity across Great Britain (Figure 1). After taking into account the national land cover of habitats, improved grassland contributed most (29%) to potential national nectar supply in 2007. Four species of plant, *Trifolium repens*, *Calluna vulgaris*, *Cirsium palustre* and *Erica cinerea* together produce over 50% of nectar nationally (see Extended Data Table 2 and Supplementary Result 1 for further information about these species and their pollinators), and 22 species produce over 90% (Figure 2). Other species may of course be important for pollen provision. Considering flowering phenology reveals seasonal variation nationally (Figure 3): 60% of nectar is provided in July/August when the flower density of British dominant species peaks. Because heathland species are unlikely to contribute as much in other European countries, this seasonal pattern may differ. The relative nectar value of linear features (hedgerows, watersides and road verges) depends on habitat. With the exception of those in shrub heathland and bog, linear features produce more nectar per unit area (and the contrast is particularly high in landscapes dominated by arable land, improved grassland and conifer woodland; Extended Data Figure 1). Of the five types of agri-environment scheme options we investigated, nectar flower mixtures have the highest nectar productivity value, followed by enhanced margins (Extended Data Table 3). Nectar flower mixture options are similar to hedgerows in term of annual nectar productivity per unit area, but they cover a much smaller area, and consequently contribute far less to the national

88 nectar resources (0.1% of nectar supply comes from nectar flower mixtures compared to 3% from  
89 hedgerows in England, Extended Data Table 3).

90 Historical shifts in nectar productivity, species nectar diversity and functional nectar diversity  
91 over recent decades depended on the habitat type and time period considered (Extended Data  
92 Table 1). From 1978 to 1990, annual nectar productivity decreased significantly in arable land  
93 and conifer woodland, but from 1990 to 1998, none of the habitats showed significant changes in  
94 nectar productivity. From 1998 to 2007, nectar productivity increased significantly in arable land  
95 and neutral grassland (Extended Data Figure 2). Nectar diversity, both at the level of plant  
96 species and functional groups decreased significantly in arable land and improved grassland from  
97 1978 to 2007. Species nectar diversity also significantly decreased in conifer woodland and  
98 broadleaved woodland during that period. From 1978 to 1990, species nectar diversity declined in  
99 all habitats (except bog), significantly so in arable land and conifer woodland; thereafter it  
100 remained roughly constant, except in arable land where it rebounded somewhat from 1998 to  
101 2007 (see Extended Data Figure 2 and Supplementary Results 2 for details on functional nectar  
102 diversity). For the 1930s we have information only on shifts in land cover (but not floral  
103 abundances within them), and only for England and Wales<sup>20</sup>. Assuming no change in floral  
104 composition within habitats, we found a strong decline in national nectar provision from 1930s to  
105 1978 (-32%) followed by a period of stagnation from 1978 to 2007 (Figure 4, Supplementary  
106 Table 3). Incorporating shifts in nectar productivity within habitats for recent decades showed an  
107 increase in national nectar provision from 1998 to 2007 (+51% in England & Wales and +25%  
108 for Great Britain as a whole, Figure 4, Supplementary Table 4). While shifts in vegetation  
109 composition within dominant habitats predominate as causes of recent increases, no quantitative  
110 data are available before 1978. This recent upturn could be caused by decreased acidification<sup>21</sup>,

111 decreased nitrogen deposition<sup>22</sup> and agricultural set-asides<sup>23</sup> during this period (Supplementary  
112 Table 5). However, post-war changes in habitat management (e.g. herbicide use in arable land,  
113 cessation of woodland coppicing, nitrogen deposition in grasslands; Supplementary Table 5)  
114 almost certainly resulted in lower nectar per unit area, suggesting that our estimates of losses  
115 based on land use change alone are conservative; actual resource declines may have been much  
116 larger than the recent increases (see Supplementary Discussion). Due to their large area,  
117 improved grassland provided the greatest contribution to the increase in national nectar provision  
118 from 1998 to 2007 (Extended Data Figure 3). After discounting the contribution of *Trifolium*  
119 *repens* in improved grasslands, as it may not flower in heavily grazed fields, the increase in  
120 nectar provision from 1998 to 2007 remained (Supplementary Result 3 and Extended Data Figure  
121 4).

122 The historical pattern of change in nectar resources closely parallels documented shifts in  
123 pollinator communities (Extended Data Figure 5). Substantial declines in floral resources and  
124 their diversity in the mid to late 20th century, when agricultural intensification peaked, coincide  
125 with a period of heightened pollinator extinctions<sup>9</sup>. The stabilization and partial recovery of  
126 resources in recent decades corresponds to concomitant periods of decelerated declines and  
127 partial recovery in some pollinator groups<sup>10</sup>.

128 Our findings provide new evidence based on floral resources to support habitat conservation and  
129 restoration. First, we provide evidence of the high nectar value of calcareous grassland for  
130 pollinating insects. Calcareous grassland area has declined drastically in Great Britain and only a  
131 small fraction of the historical national cover remained by 2007<sup>13,14</sup>. Second, the low availability  
132 and diversity of nectar sources in arable habitats highlights the need to provide supplementary  
133 resources to support pollination services in farmlands, especially as the use of insect-pollinated

134 crops has increased nationally<sup>24</sup> and globally<sup>25</sup>. The conservation and restoration of broadleaf  
135 woodland and neutral grassland as components of the farmland matrix could help to support  
136 diverse flower-visiting insect communities in arable land. The contrast in nectar productivity  
137 between linear features and the surrounding vegetation is particularly high in arable land,  
138 suggesting that linear features, especially hedgerows, provide an efficient means to enhance floral  
139 resources in farmlands if they are managed appropriately to allow flowering<sup>26</sup>. While agri-  
140 environment options such as nectar flower mixtures can also enhance the supply of floral  
141 resources locally, their contribution to nectar provision nationally remains low. The higher profile  
142 given to floral resource provision in the revised Countryside Stewardship guidelines for  
143 England<sup>16</sup> may substantially enhance resources in future. Finally, our results indicate that  
144 improved grassland has the potential to contribute massively to the nectar available nationally.  
145 Small adjustments to the management cycle in improved grasslands, allowing white clover, the  
146 dominant resource species, to flower, would help realize this potential, although its utility might  
147 be restricted to a limited number of pollinator species (Extended Data Table 2). Together, our  
148 results on the nectar values of the commonest British plants and the historical changes in plant  
149 communities provide the evidence base needed to understand recent national changes in nectar  
150 provision and identify the management options needed to restore national nectar supplies.

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207 **End notes**

208 **Supplementary Information** is available in the online version of the paper.

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216 Survey data are owned by NERC – Centre for Ecology & Hydrology  
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218 **Author Contributions**

219 The study was conceived by W.E.K. and J.M. The field survey was carried out by M.B. and N.D.  
220 with the help of J.M. The data were compiled and analysed by M.B. with suggestions from  
221 W.E.K., J.M., S.S., R.D.M. and M.G. Vegetation data from the Countryside Survey database  
222 were extracted by S.S. Agri-environment scheme data were provided and analysed by N.D.B. and  
223 S.C. The national maps were generated by R.D.M. All authors discussed the results and  
224 contributed during manuscript writing.

225 **Author Information**

226 The floral resource database will be made available from the NERC Environmental Information  
227 Data Centre (doi:10.5285/69402002-1676-4de9-a04e-d17e827db93c and doi:10.5285/6c6d3844-  
228 e95a-4f84-a12e-65be4731e934). Reprints and permissions information is available at  
229 [www.nature.com/reprints](http://www.nature.com/reprints). The authors declare no competing financial interests. Correspondence  
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231 **Figure legends**

232 **Figure 1. Nectar productivity and diversity in Great Britain in 2007. a,** Box plots of log10  
233 (x+1) nectar productivity (kg of sugars/ha/year) per habitat. **b,** Box plots of species nectar  
234 diversity (Shannon index of nectar species) per habitat. **c,** Box plots of functional nectar diversity  
235 (Shannon index of nectar flower types) per habitat. Box plots are based on 2007 vegetation data

236 (see Supplementary Table 2 for sample sizes). Habitat types (AR=Arable land, IG=Improved  
237 grassland, AG=Acid grassland, NG=Neutral grassland, CG=Calcareous grassland, CON=Conifer  
238 woodland, BRO=Broadleaf woodland, BOG=Bog, FEN=Fen, BRA=Bracken, SH=Shrub  
239 heathland) significantly different from one another are indicated by different letters. **d**, Map of  
240 nectar productivity. **e**, Map of species nectar diversity. **f**, Map of functional nectar diversity.  
241 Maps are based on 2007 land cover and vegetation data.

242 **Figure 2. Plant species' contributions to Great Britain nectar provision and to habitat**  
243 **nectar provision, based on 2007 land cover and vegetation data.** The dotted line represents the  
244 cumulative contribution of plant species to the national nectar provision in 2007 (only species  
245 that contribute to the first 95% are shown). The pie charts represent the contribution of plant  
246 species towards nectar production in each habitat (only the species that contribute to the first 90%  
247 are shown) in 2007. The size of each pie chart is proportional to the contribution of each habitat  
248 to national nectar provision in 2007.

249 **Figure 3. Seasonal nectar productivity in Great Britain, based on 2007 land cover and**  
250 **vegetation data.** Maps of nectar productivity in kg of sugars/ha from March to October (panels a  
251 to h). Hot colours correspond to high nectar productivity while cold colours correspond to low  
252 nectar productivity (see colours scale). Note that urban areas are assigned with nectar  
253 productivity values equal to zero, hence the blue colours in cities. Nectar productivity values for  
254 mapping correspond to back-transformed estimates of the linear mixed model fitted on  $\log_{10}$   
255 ( $x+1$ ) nectar productivity of 2007 Countryside Survey non-linear plots with habitat, month and  
256 their interaction as fixed effects and plots nested within squares as random effects.

257 **Figure 4. Historical changes in nectar provision (in kg of sugars/year) at the national scale**  
258 **in England & Wales (1930-2007) and in Great Britain (1978-2007):** Nectar provision  
259 partitioned by habitat, based on land cover for 1930 (England & Wales only), 1978, 1990, 1998  
260 and 2007, using vegetation data from 1978 for all years (assuming unchanged nectar productivity  
261 within habitats across time) in **a**, England & Wales and **b**, Great Britain. Nectar provision  
262 partitioned by habitat, based on land cover and vegetation data for 1978, 1990, 1998 and 2007 in  
263 **c**, England & Wales and **d**, Great Britain. See Figure 1 for habitat type codes and Supplementary  
264 Table 6 for habitat land cover values.

265 **Methods**

266 **Stage 1: Constructing the nectar database by scaling up nectar resources from the flower to**  
267 **the vegetative scale**

268 *Identifying the key plant species to be sampled*

269 While there are >2800 plant species in Great Britain<sup>27</sup>, only 1341 of them are common enough to  
270 have been encountered in the Countryside Survey. Of these, the 454 commonest species  
271 accounted for 99% of national plant cover in 2007. More than half of these 454 species are  
272 unrewarding to pollinators (mainly bryophytes, pteridophytes, gymnosperms and wind-pollinated  
273 angiosperms<sup>28</sup>), leaving 220 species that are likely to contribute substantially to floral resources  
274 at a national scale. We focus here on these 220 species, along with an additional 50 species that  
275 we believe to be locally important floral sources (e.g. *Buddleja davidii*, *Impatiens glandulifera*,  
276 *Knautia arvensis*). Together, these 270 plant species provide a focal set of potential importance in  
277 national nectar provision (Supplementary Table 1).

278 Quantifying nectar productivity empirically: the ‘surveyed species’

279 Of the 270 species, 175 were surveyed in the field from February 2011 to October 2012, mainly  
280 in the South of England. When possible (112 species), nectar was collected from plants in at least  
281 two populations in two locations. For three species (*Caltha palustris*, *Lamium purpureum*, and  
282 *Sinapis arvensis*), half the nectar samples, and for *Viola arvensis* all the samples were collected  
283 from pot-grown plants, because insufficient flowering field populations were found. For the  
284 remaining species, nectar was collected from plants in one field population. When possible, the  
285 different populations were sampled on different dates, thus providing some measure of variation  
286 due to differences in location and weather. Note that nectar was collected in only 1-2 sites per  
287 species, and so intraspecific variation in production per flower was not assessed (but see  
288 Supplementary Result 4).

289 Nectar was collected from ten single flowers in each population between 0900-1600 hours  
290 (median: 20 and range: 5-30 flowers collected per species in total; see Extended Data Figure 6  
291 and Supplementary Result 4 for site correlation); these had been bagged (using 1.4 x 1.7mm  
292 fabric mesh) for 24h to prevent depletion by nectar-feeding insects. When possible (76 species),  
293 glass microcapillaries (1 and 5 $\mu$ L Minicaps, Hirshmann, Eberstadt, Germany) were used directly  
294 to collect the nectar, otherwise single flowers were rinsed twice with 1-5  $\mu$ L of distilled water  
295 added to the nectaries with a pipette for one minute, and the diluted nectar solution was collected.  
296 The sugar concentration of nectar (%; g sucrose/100 g solution) was measured by using a hand  
297 held refractometer modified for small volumes (Eclipse, Bellingham and Stanley, Tunbridge  
298 Wells, UK). The amount of sugar produced per flower basis over 24h (s;  $\mu$ g of  
299 sugars/flower/24h) was calculated using the formula<sup>29</sup>

300  $s = 10dvC$

301 where v is the volume collected ( $\mu\text{L}$ ), and d is the density of a sucrose solution at a concentration  
302 C (g sucrose/100 g solution) as read on the refractometer. The density of the sucrose solution was  
303 calculated by the formula<sup>29</sup>

304  $d=0.0037921C+0.0000178C^2+0.9988603$

305 The number of open flowers per unit area of vegetative cover (flower density) was estimated for  
306 179 species by placing five quadrats (0.5m x 0.5m) haphazardly on each flowering population  
307 (median: 10 quadrats, range: 1-20 quadrats; see Extended Data Figure 6 and Supplementary  
308 Result 4 for site correlation). In each quadrat, we counted the number of open floral units of the  
309 focal species (a “floral unit” is one or multiple flowers that can be visited by insects without  
310 flying<sup>30</sup>; for example a composite flowerhead of daisy, *Bellis perennis*). We also counted the  
311 number of open flowers present in one typical open floral unit in each quadrat. Vegetative cover  
312 for each plant species was estimated using a point-quadrat approach with the cross-strings of the  
313 quadrat: cover was expressed as proportional to the number of the 36 cross-points covered by the  
314 foliage of the species of interest in each quadrat. For trees, instead of using quadrats, we counted  
315 the number of floral units in a 3D cube (0.5 × 0.5 × 0.5m) that was placed in the outer areas of  
316 foliage. This was extrapolated to the whole column situated above the unit of vegetative cover by  
317 measuring the height of tree foliage with an inclinometer (PM-5/360 PC Suunto) and by  
318 estimating the distribution of the flowers within the tree foliage (subjectively assessed scores:  
319 from 1 for a strongly biased flower distribution on the outer edges of the foliage to 5 for a  
320 homogeneous full flower distribution). Given that flower density is not constant throughout the  
321 flowering season, we estimated variations in flower density according to a triangular function

322 from the estimated peak of flowering through the flowering season which was documented from  
323 recorded phenologies<sup>28,31,32</sup> (see Supplementary Method 1 and Extended Data Figure 6 for  
324 phenology parameter relationships). An alternative nectar rectangular phenology productivity  
325 database was also generated by keeping nectar productivity of each species constant throughout  
326 the flowering season; this was used to perform sensitivity analyses.

327 The mean nectar sugar content from a single flower (produced over a 24h period) was multiplied  
328 up to the nectar content of a single floral unit (number of flowers in a floral unit), then to the  
329 amount of nectar per unit area (number of flowers per m<sup>2</sup>), to the amount of nectar per unit area  
330 for each month (variation in flower density over the flowering season) and finally to the amount  
331 of nectar per unit area per year. Despite relatively low sample sizes per species compared to  
332 species-specific studies, our estimates of sugar production were well correlated with published  
333 values both per flower/day and per area/year (Extended Data Figure 6 and Supplementary Result  
334 4). This empirical method provided the nectar productivity values for 161 plant species amongst  
335 the 175 initially surveyed (nectar productivity could not be scaled up for some species due to  
336 mismatches with phenological data, see Supplementary Method 1).

337 *Modelling nectar productivity: the ‘unsurveyed species’*

338 To model the nectar productivity of the plant species that could not be surveyed in the field, we  
339 used a predictive modelling approach. We first analysed variation in the nectar values from the  
340 surveyed species. A linear model was fitted to annual nectar sugar productivity ( $\log_{10}(x+1)$   
341 transformed) as a function of plant traits. Plants traits were mainly collected from the BiolFlor  
342 database<sup>33</sup>, and included: “flower shape”, “breeding system”, “life span”, the degree of “dichinity”,  
343 the maximum “height”, the “flowering period” and “family” (see Supplementary Method 2 for

344 definitions). The estimates from the most parsimonious statistical model based on AIC criterion  
345 (Supplementary Table 7, N=153; Adjusted  $r^2=0.55$ ) were used to predict the annual nectar sugar  
346 productivity for the initial list of surveyed and unsurveyed species on the basis of their traits. To  
347 check the validity of the predicted values, we adopted a repeated “leave-one-out” approach to  
348 model successively all the excluded values from the empirically derived datasets. Then, we  
349 applied a standardized major axis regression on the  $\log_{10}(x+1)$  transformed empirically derived  
350 and modelled nectar values of the surveyed species (Extended Data Figure 6). We predicted the  
351 nectar values for 252 species; and giving priority to empirical and default values, we included 94  
352 of them in our database. An alternative nectar productivity database was also generated by  
353 considering only the species with empirical nectar values; this was used to perform sensitivity  
354 testing.

355 *Ascribing default values for nectar productivity*

356 For four crop species harvested before flowering; onion (*Allium cepa*), cabbage (*Brassica*  
357 *oleracea* cultivated), turnip (*Brassica rapa*) and radish (*Raphanus sativus*) we assigned a value of  
358 zero for nectar productivity. A zero-value was also assigned to *Helianthemum nummularium*,  
359 despite the missing flower density data, given that we collected no nectar in flowers. In the  
360 Countryside Survey vegetation dataset, some taxa are only identified at the genus level; we  
361 interpreted these taxa to represent the commonest species in the genus (e.g. *Centaurea* sp. was  
362 interpreted as *Centaurea nigra*). For 10 species out of the initial list of 270 it was not possible to  
363 quantify nectar production, leading to a total of 260 species with quantified annual and monthly  
364 nectar productivity values (161 values from empirical research, 94 modelled values, and 5 default  
365 values, Supplementary Table 1). All the above steps of scaling-up process are summarized in  
366 Supplementary Table 8.

367 ***Stage 2: Using the Countryside Survey vegetation database to scale up nectar resources from***  
368 ***plant species to communities at the habitat and national scales***

369 Spatio-temporal variations in nectar provision at the national scale were calculated by combining  
370 our nectar productivity dataset with vegetation and land cover data already recorded during the  
371 Countryside Survey<sup>19</sup>. The Countryside Survey is a national survey of plant communities  
372 conducted in 1978, 1990, 1998 and 2007 in Great Britain (England, Wales and Scotland). The  
373 survey was conducted by selecting 1-km sample squares at random from 32 Land Classes<sup>19</sup>  
374 representing physiographically similar sampling domains throughout Great Britain, ensuring an  
375 unbiased representation of the British non-urban landscape. Within each square, a random,  
376 stratified sample of five areal (non-linear) square plots (200 m<sup>2</sup>) was established and the presence  
377 and the percentage cover of all vascular plant species were recorded. These plots were classified  
378 to 17 habitat classes, but we only used data from 11 habitats: acid grassland, arable land, bog,  
379 bracken, broadleaf woodland, calcareous grassland, conifer, fen, improved grassland, neutral  
380 grassland and shrub heath (Supplementary Table 9 for habitat description). The habitats not used  
381 were inland rock, littoral rock/supralittoral rock, littoral sediment/supralittoral sediment, montane  
382 and urban habitats; these were excluded due to low sample sizes. Even though urban habitats  
383 probably contribute to the national nectar provision, we were unable to include this habitat in this  
384 study because the Countryside Survey was not designed to survey urban areas. In 1.14% of  
385 Countryside Survey plots, two or more habitats were attributed to the same plot; these were  
386 excluded for this study. Additional plots were used to sample linear features in each 1km square,  
387 covering hedgerows, streamsides and road verges (1x10m and oriented along the linear feature).  
388 Each linear plot was also attributed to its nearest adjacent habitat.

389 To investigate the most recent nectar patterns, we used the most comprehensive vegetation  
390 dataset from the Countryside Survey 2007 that encompasses all non-linear plots (2576 plots in  
391 2007). To focus on linear features, we included vegetation data from linear features plots (1951  
392 plots in 2007). To test for historical changes from 1978 to 2007, we used vegetation data from  
393 non-linear plots shared between the 1978, 1990, 1998 and 2007 Countryside Surveys (529 shared  
394 plots in England & Wales and 768 in Great Britain; Supplementary Table 10). We focussed on  
395 the shared plots across years because the Countryside Survey sampling design was modified over  
396 time (e.g., from fixed to proportional plot number per Land Class from 1978 to 1990).

397 The annual nectar productivity within each plot (kg/ha/year) is the sum of the nectar productivity  
398 of each species (kg/ha cover/year) weighted by their vegetative cover in the plot (%), assuming  
399 that the vegetative cover is representative of floral abundance (see Extended Data Figure 7 and  
400 Supplementary Results 4 for details). Nectar productivity values of plots were used to statistically  
401 estimate the annual nectar productivity for each habitat (kg/ha/year). The annual nectar provision  
402 of each habitat (kg/year) was computed from their annual habitat nectar productivity (kg/ha/year)  
403 multiplied by their respective national land covers for each survey (areas of habitats in ha from  
404 Countryside Surveys<sup>19,34,35</sup>; Supplementary Table 6). These were summed to estimate the annual  
405 national nectar provision in 1978, 1990, 1998 and 2007. For the 1930s period, areas of habitats  
406 (only available for England and Wales) were derived from the digitalised Dudley Stamp land  
407 utilisation survey maps<sup>20</sup>; see Supplementary Method 3 and Supplementary Table 6). Because  
408 nectar productivity can't be assessed for this period, we quantified nectar provision in 1930,  
409 1978, 1990, 1998 and 2007 assuming unchanged nectar productivity within habitats but using  
410 observed shifts in land cover among habitats across time. The national nectar provision of  
411 hedgerows was calculated from their mean nectar productivity (kg/ha/year) multiplied by their

412 estimated area in England (length of hedgerows from Countryside Survey 2007 for England<sup>35</sup>,  
413 assuming a 1m width).

414 The contribution of habitat or species to the national nectar provision in 2007 is the fraction of  
415 nectar provided by these entities (in %). The amount of nectar offered by each habitat in 2007 is  
416 calculated from habitat nectar productivity (estimated value of habitat productivity) multiplied by  
417 its national area. The amount of nectar offered by each species in 2007 is calculated from the sum  
418 of its average nectar productivity stratified by habitat and multiplied by habitat national area. The  
419 contribution of habitat or species to the historical changes in national nectar provision is  
420 expressed by the absolute change (in kg of sugars), which is the difference in the amount of  
421 nectar produced by the entity during the time period considered. Relative change (in %) which is  
422 the absolute change multiplied by 100 and divided by the amount of nectar produced at the initial  
423 date, refers to the magnitude of change for each entity.

424 Nectar diversity was estimated through two Shannon indexes (using ‘vegan’ package in R<sup>36</sup>) that  
425 encompass both the richness and the evenness of nectar producing sources (see Supplementary  
426 Method 4). The species nectar diversity index, based on the proportion of nectar produced by  
427 each species, was calculated as follows:

$$428 H_{sp}' = - \sum_{i=1}^S p_i \times \ln(p_i)$$

429 where  $p_i$  is the proportional nectar contribution of plant species  $i$  and  $S$  is the total number of  
430 plant species in each plot.

431 The functional nectar diversity index, based on the proportion of nectar produced by each floral  
432 morphology group, reflects the diversity of nectar sources in terms of resource accessibility for

433 flower-visiting insects. Flower types were derived from Müller flower classification system  
434 recorded from the BiolFlor database<sup>33</sup> which was condensed into five classes: pollen rewarding  
435 flowers, open, partly-hidden, hidden, and bee flowers (see Supplementary Method 4). The  
436 functional nectar diversity index was computed as follows:

$$437 H_{fun}' = - \sum_{i=1}^S p_i \times \ln(p_i)$$

438 where  $p_i$  is the proportional nectar contribution of flower type  $i$  and  $S$  is the total number of  
439 flower types in each plot.

440 The annual nectar productivity (kg of sugars/ha/year), species nectar diversity (Shannon index of  
441 nectar contribution of plant species) and functional nectar diversity (Shannon index of nectar  
442 contribution of floral morphology groups) in 2007 were mapped at the British national scale  
443 using the Great Britain Land Cover Maps of 2007<sup>37</sup>.

444 ***Stage 3: Using Agri-environment scheme flower abundance data to estimate nectar provision  
445 within agri-environment scheme options at the national scale***

446 Various options are available for managing habitats to provide floral resources for pollinators,  
447 some of which are eligible for grant aid under European Union funded agri-environment  
448 schemes. Agri-environment options within the English ‘Environmental Stewardship’ scheme  
449 included sowing nectar flower mixtures (EF4/HF4), sowing wild bird seed mixtures (EF2/HF2),  
450 creation or enhancement of floristically-enhanced buffer strips (HE10), re-introduction or  
451 continuation of haymaking (haymaking supplement HK18) and creation, restoration and  
452 maintenance of species-rich semi-natural grassland (HK6/7/8). These five options were selected  
453 as the most likely to provide floral resources for pollinators.

454 Field study sites were located on farmland and nature reserves in which the following replicates  
455 of the pollinator habitats were present: nectar flower mixtures (n=32), wild bird seed mixtures  
456 (n=4), enhanced field margins/road verges (n=7), hay meadows (n=5) and species-rich grasslands  
457 (n=7). These were existing habitats representing ongoing management by the land owners or land  
458 managers concerned. Transects 100m long x 6m wide were established in each habitat. The  
459 number of floral units of each flowering species was recorded on 1 to 3 occasions, in 20 x 1m<sup>2</sup>  
460 quadrats per transect. Annual nectar productivity (kg of sugars/ha/year) was calculated for each  
461 species at each site from the average estimated nectar productivity at the peak of the flowering  
462 season derived from the several counts of floral units across the flowering period (analogous to  
463 Supplementary Method 1). The values for the species present in each habitat were then summed  
464 to estimate productivity for each habitat.

465 National areas of options providing floral resources in the English agri-environment scheme  
466 “Environmental Stewardship” were extracted for 2007 for England (data for Great Britain was  
467 unavailable) from data supplied by Natural England<sup>38,39</sup>. Mean nectar productivity per unit area  
468 was multiplied by the national area of each option to give nectar provision by that option (kg of  
469 sugars/year). The total contribution of nectar provision provided by Environmental Stewardship  
470 in England is a minimum value, as it has been compared to national provision estimated from  
471 vegetative cover rather than direct flower counts and we did not take into account the more  
472 limited floral resources potentially provided by other options.

473 ***Stage 4: Statistical analyses***

474 Statistical analyses were carried out with Linear Mixed-Effect Models (lme function from ‘nlme’  
475 package) in R 3.0.1<sup>(36)</sup>. To investigate the most recent nectar variations (2007), we analysed the

476 log<sub>10</sub>(x+1) annual nectar productivity, species nectar diversity and functional nectar diversity  
477 according to the type of habitat (“HABITAT”; 11 habitats) of the non-linear plots. The  
478 differences in log<sub>10</sub>(x+1) nectar productivity, species nectar diversity and functional nectar  
479 diversity between non-linear and linear features were analysed according to the type of habitat  
480 (“HABITAT”; 11 habitats), the type of vegetation surveyed (“TYPE”; non-linear vs linear  
481 features) and the interaction between these two terms. Countryside Survey square (“SQUARE”)  
482 was included as a random term in these models in order to account for the spatial auto-correlation  
483 of plots nested into 1km squares. In order to investigate historical changes over recent decades  
484 (1978-2007), we analysed the log<sub>10</sub>(x+1) annual nectar productivity, species nectar diversity and  
485 functional nectar diversity computed from the shared non-linear plots in 1978, 1990, 1998 and  
486 2007 according to the type of habitat (“HABITAT”), the year (“YEAR”) considered as a  
487 categorical factor, and the interaction between these two terms. We included plots nested within  
488 square (“SQUARE/PLOTS”) as random terms to account for the spatial and temporal auto-  
489 correlation of the data in this latter model. This latter statistical test was repeated considering all  
490 shared plots in Great Britain or only those in England & Wales to provide estimates of habitat  
491 nectar productivity across time for distinct areas, allowing comparisons with earlier (1930s)  
492 habitat information only available for that latter area. Significant differences among modalities  
493 were analysed with multiple comparisons (single-step method adjusted p-values from glht  
494 function in “multcomp” package in R<sup>36</sup>). Model residuals were plotted to visually check that  
495 normality and homoscedasticity assumptions were satisfied. We re-ran the same analyses with the  
496 Countryside Survey vegetation data combined with (i) the alternative nectar rectangular  
497 phenology productivity database (created by keeping constant nectar productivity of each species  
498 during the flowering season); and (ii) using only the empirical nectar productivity database, as  
499 sensitivity tests (Extended Data Figure 4, Supplementary Result 3). Plots were performed with

500 ggplot2 package in R<sup>36</sup>. All box plots show the median, 25<sup>th</sup> and 75<sup>th</sup> percentiles (lower and upper  
501 hinges), trimmed ranges that extend from the hinges to the lowest and highest values within 1.5 x  
502 inter-quartile range of the hinge (lower and upper whiskers) plus outliers (filled circles). Notches  
503 that extend 1.58 x inter-quartile range / square root of the number of observations were  
504 represented to give a roughly 95 interval for comparing medians.

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538 **Extended Data Legends**

539 **Extended Data Table 1. ANOVA results for annual nectar productivity, species nectar**  
540 **diversity and functional nectar diversity. a,** 2007 values according to habitat. The linear mixed  
541 effect models were performed on data from 2576 non-linear plots surveyed in 2007. **b,** 2007  
542 values according to habitat and location. The linear mixed effect models were performed on data  
543 from 4527 plots (2576 non-linear plots and 1951 linear plots) surveyed in 2007. **c,** 1978-2007  
544 values according to habitat and year. The linear mixed effect models were performed on data  
545 from 768 shared plots surveyed in 1978, 1990, 1998 and 2007. The annual nectar productivity  
546 was systematically log10 (x+1) transformed. See Supplementary Table 2 and Supplementary  
547 Table 4 for sample sizes.

548 **Extended Data Table 2. Flower morphology and flower-visiting insects of the four main**  
549 **nectar providing species.** Flower morphology parameters (mean and standard error for depth  
550 and width of flower tubes) were measured on 20-40 flowers per species in the field. Flower-  
551 visiting insects were listed from published and unpublished plant-insect visiting networks from

552 Memmott's group to which recorded interactions from a review of literature have been added  
553 (see Supplementary Table 12 for reference list).

554 **Extended Data Table 3. Agri-environment schemes and linear features: nectar productivity**  
555 **and provision in England in 2007.** **a,** Mean nectar productivity values of agri-environment  
556 schemes were estimated from our nectar productivity database combined with flower counts in  
557 these options. Areas of options providing floral resources in the English agri-environment scheme  
558 "Environmental Stewardship" were extracted for 2007 from data supplied by Natural  
559 England<sup>38,39</sup>. **b,** Mean nectar productivity values of linear features correspond to back-  
560 transformed ( $10^{\hat{x}} - 1$ ) estimates of the linear mixed model fitted on  $\log_{10}(x+1)$  nectar  
561 productivity of all Countryside Survey linear plots surveyed in England in 2007. National areas  
562 of hedgerows were estimated from the length given in Countryside Survey 2007 for England<sup>35</sup>  
563 and assuming a 1m width.

564 **Extended Data Figure 1. Annual nectar productivity and diversity in linear features in**  
565 **2007.** **a,** Box plots of  $\log_{10}(x+1)$  nectar productivity according to the location of the vegetation  
566 surveyed (non-linear vs linear features) in each habitat. **b,** Box plots of species nectar diversity  
567 according to the location of the vegetation surveyed (non-linear vs linear features) in each habitat.  
568 **c,** Box plots of functional nectar diversity according to the location of the vegetation surveyed  
569 (non-linear vs linear features) in each habitat. Significant differences of locations (linear vs non-  
570 linear) in habitats are indicated by asterisks as follows: \* for  $p \leq 0.05$ ; \*\* for  $p \leq 0.01$ ; \*\*\* for  $p \leq$   
571 0.001. Statistical model were re-run without calcareous grassland habitat (to meet residuals  
572 homoscedasticity constraint) in order to check that significant effects remained. See Extended  
573 Data Table 1 for ANOVA results.

574 **Extended Data Figure 2. Historical changes in nectar productivity and diversity per habitat**  
575 **over recent decades (1978 to 2007). a,** Box plots of log 10 (x+1) nectar productivity per habitat,  
576 based on vegetation data for 1978, 1990, 1998 and 2007. **b,** Box plots of species nectar diversity  
577 per habitat, based on vegetation data for 1978, 1990, 1998 and 2007. **c,** Box plots of functional  
578 nectar diversity per habitat, based on vegetation data for 1978, 1990, 1998 and 2007. Significant  
579 differences of time periods per habitats are indicated by stars (\* for  $p \leq 0.05$ ; \*\* for  $p \leq 0.01$ ; \*\*\*  
580 for  $p \leq 0.001$ ). See Extended Data Table 1 for ANOVA results.

581 **Extended Data Figure 3. Habitat contributions to the national nectar provision shifts and**  
582 **species contributions to habitats over recent decades (1978 to 2007).** Habitat contributions to  
583 the national nectar provision changes from **a**, 1978 to 1990 **b**, 1990 to 1998 and **c**, 1998 to 2007.  
584 All barplots represent the absolute changes (in 000 000 kg of sugars) for each habitat during the  
585 time period considered. Numbers in brackets indicate the relative changes (in %). Species  
586 contributions to nectar provision in 1978, 1990, 1998 and 2007 per habitat type (panels **d-n**).  
587 Only species that contribute to the first 90% are shown. See Supplementary Table 11 for main  
588 contributing species to the national changes from 1978 to 2007.

589 **Extended Data Figure 4. Sensitivity analyses of historical trends from 1978 to 2007 in**  
590 **nectar productivity and species diversity with alternative datasets. a,** Box plots of log 10  
591 (x+1) nectar productivity and **b,** Box plots of species nectar diversity per habitat based on  
592 vegetation data for 1978, 1990, 1998 and 2007 discounting the contribution of grazed white  
593 clover in improved grassland. **c,** Box plots of log 10 (x+1) nectar productivity and **d,** Box plots of  
594 species nectar diversity per habitat, based on vegetation data for 1978, 1990, 1998 and 2007 and  
595 computed with the alternative rectangular phenology function. **e,** Box plots of log 10 (x+1) nectar  
596 productivity and **f,** Box plots of species nectar diversity per habitat, based on vegetation data for

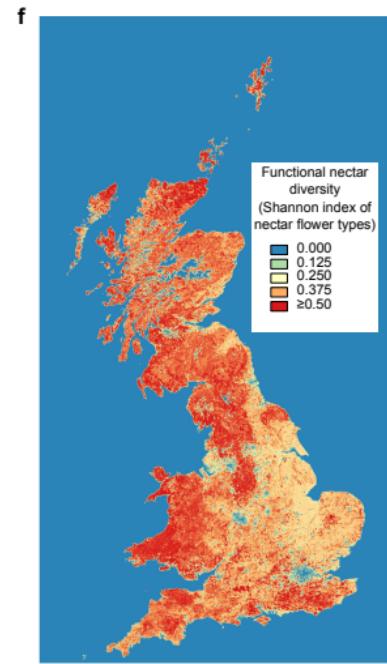
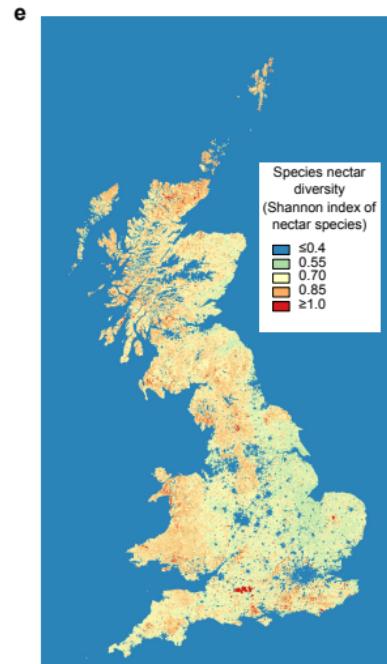
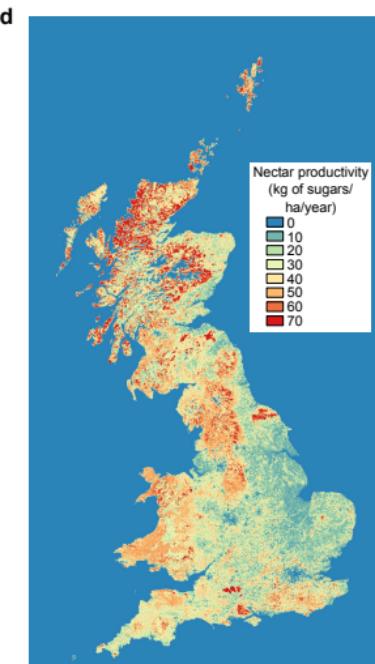
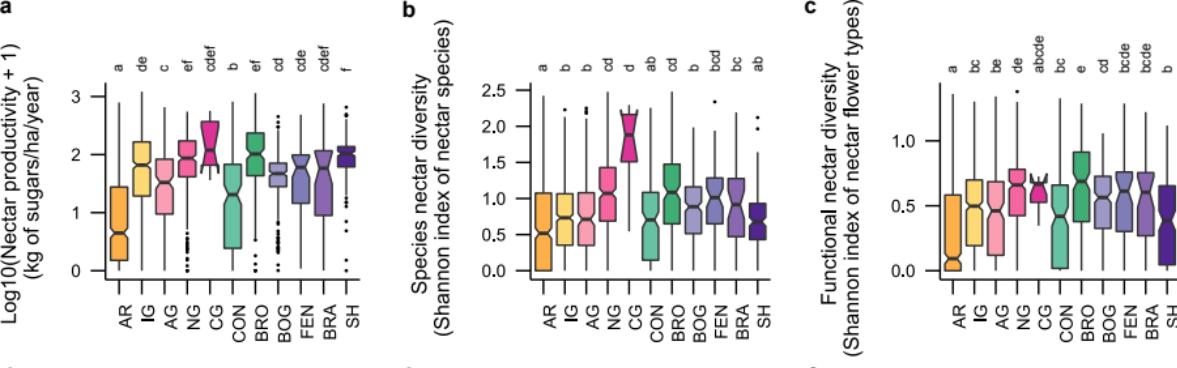
597 1978, 1990, 1998 and 2007 and computed considering only the species with empirical nectar  
598 values. Significant differences of time periods per habitats are indicated by stars (\* for  $p \leq 0.05$ ;  
599 \*\* for  $p \leq 0.01$ ; \*\*\* for  $p \leq 0.001$ ). See Supplementary Table 4 for sample sizes and  
600 Supplementary Result 3 for details.

601 **Extended Data Figure 5. Historical timeline in changes in nectar resources and flower-**  
602 **visiting insects in Great Britain.** Historical periods with the greatest negative changes in nectar  
603 resources and flower-visiting insects are indicated in red, those with intermediate changes are in  
604 orange and those with the lowest (or even reversing) changes are in green. Main historical trends  
605 from this study (Baude et al.) are presented in regard to those described in Carvalheiro et al.  
606 2014<sup>10</sup> and Ollerton et al. 2014<sup>9</sup> studies. The white chevron indicates a provisional extinction rate  
607 that needs to be confirmed on a 20 year period of time (see supplementary materials from  
608 Ollerton et al. 2014<sup>9</sup>).

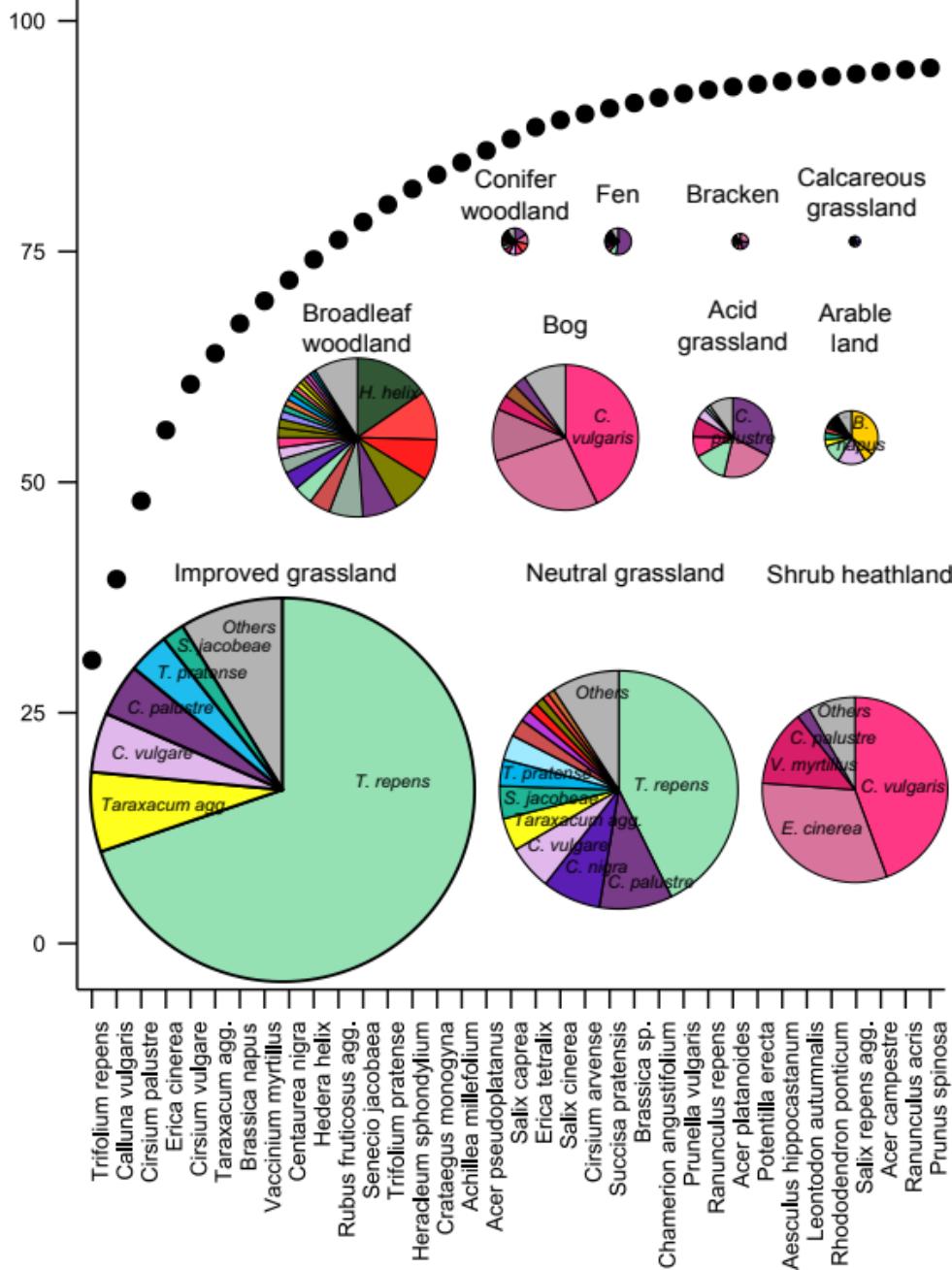
609 **Extended Data Figure 6. Validity of the datasets.** **a**, Major axis linear regression of  $\log_{10}$   
610 ( $x+1$ ) nectar values per flower obtained in the second location against those obtained in the first  
611 one. **b**, Major axis linear regression of  $\log_{10}$  ( $x+1$ ) flower density values obtained in the second  
612 location against those obtained in the first one. **c**, Major axis linear regression of  $\log_{10}$  ( $x+1$ )  
613 peak flower density values obtained in the second location against those obtained in the first one.  
614 **d**, Standardized major axis regression of the  $\log(x+1)$  length of the flowering period used for  
615 analyses with those derived from IPI AgriLand floral transects. **e**, Standardized major axis  
616 regression of peak date of flowering season used for analyses with those derived from IPI  
617 AgriLand floral transects. **f**, Major axis linear regression performed on the  $\log_{10}$  ( $x+1$ ) empirical  
618 (empirical dataset) and published nectar values (literature dataset from Raine & Chittka 2007<sup>40</sup>)  
619 at the flower scale. **g**, Standardized major axis linear regression performed on the  $\log_{10}$  ( $x+1$ )

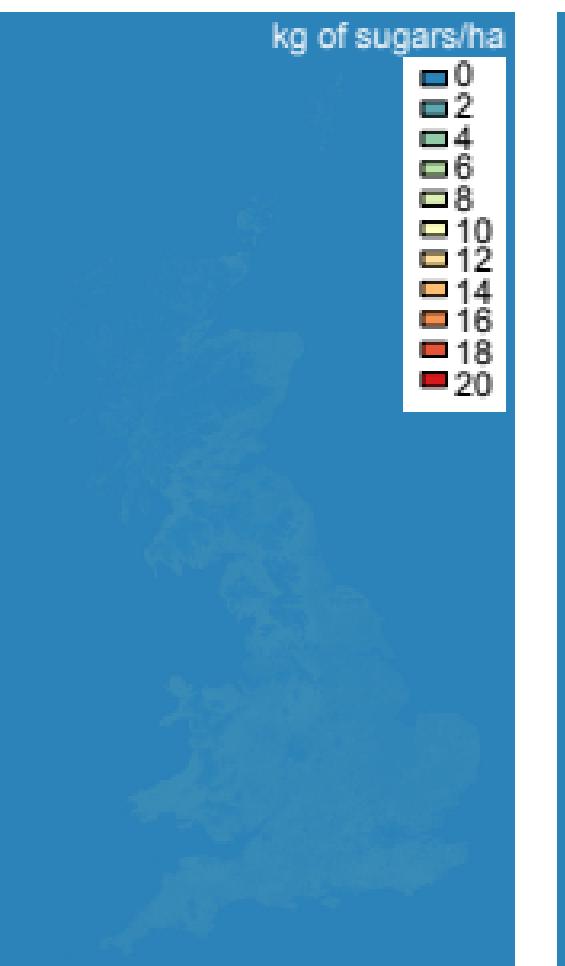
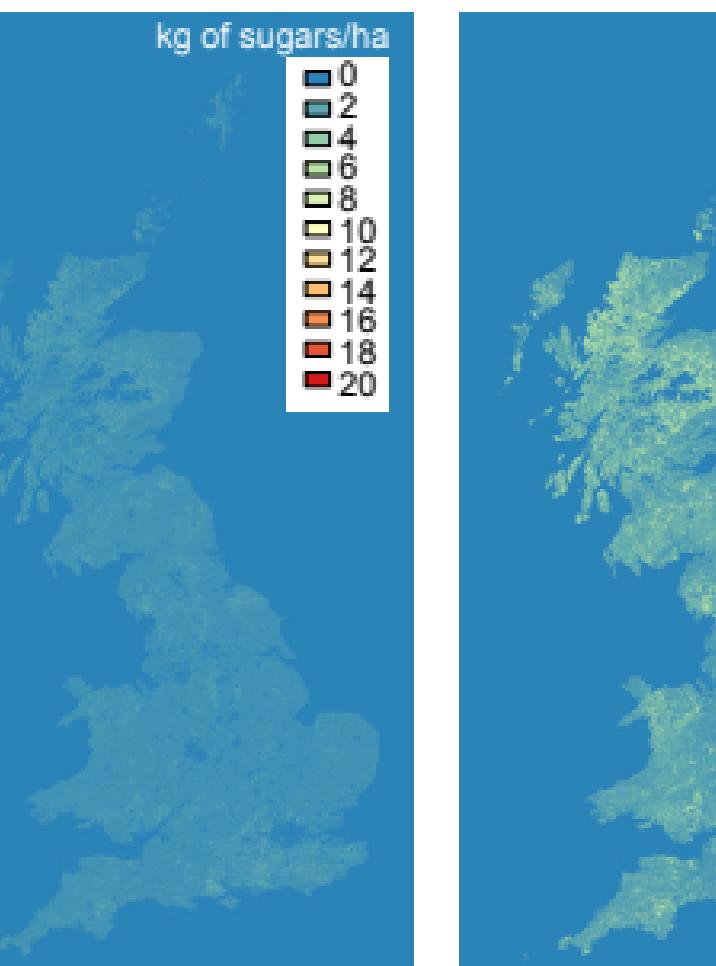
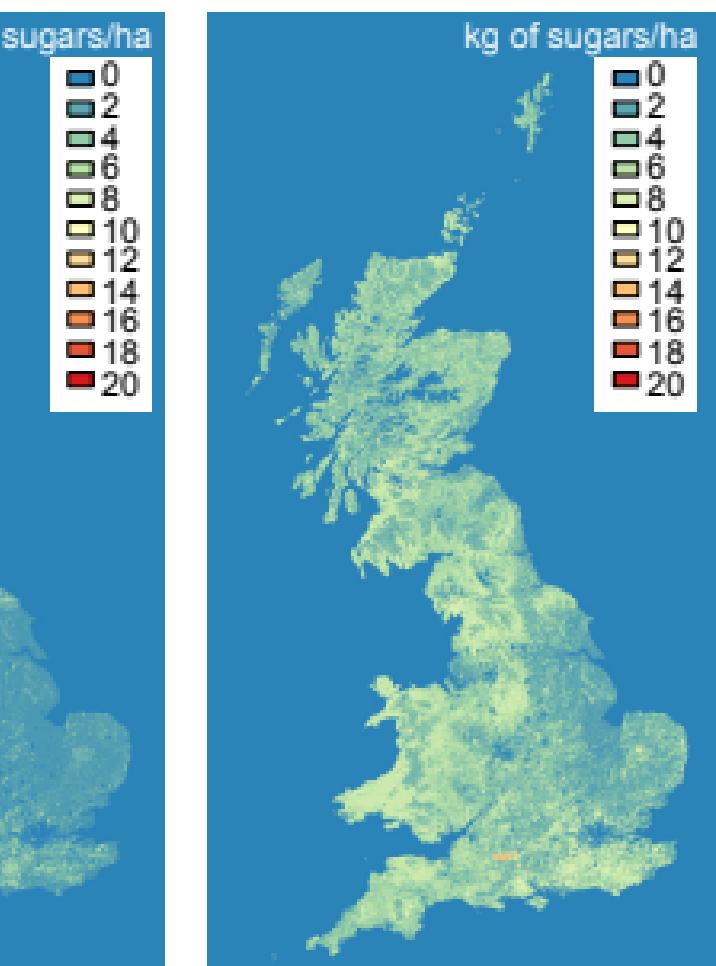
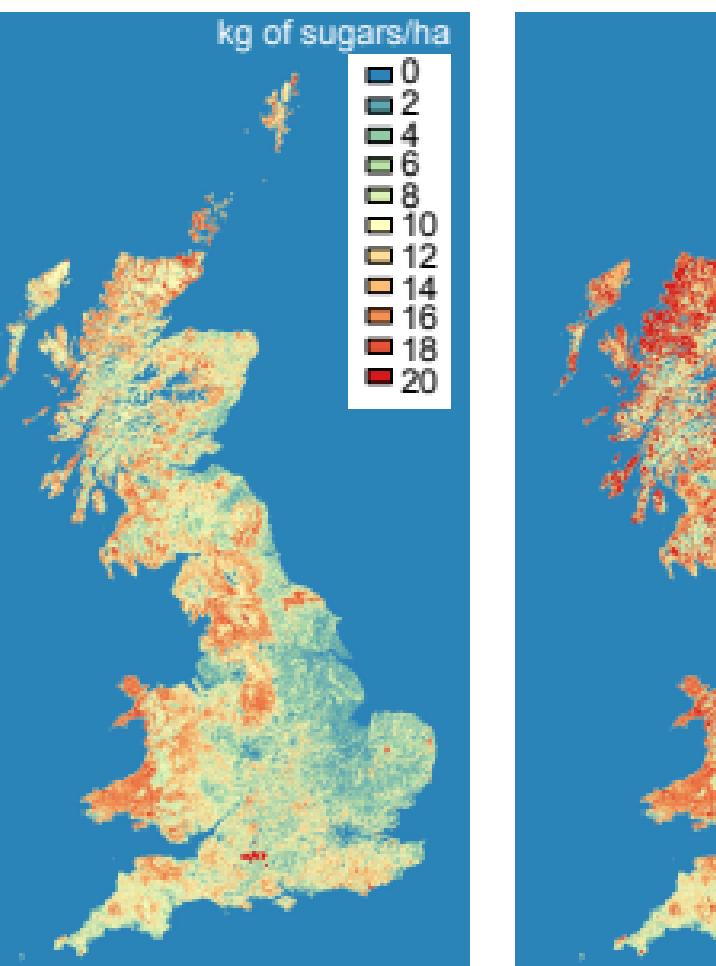
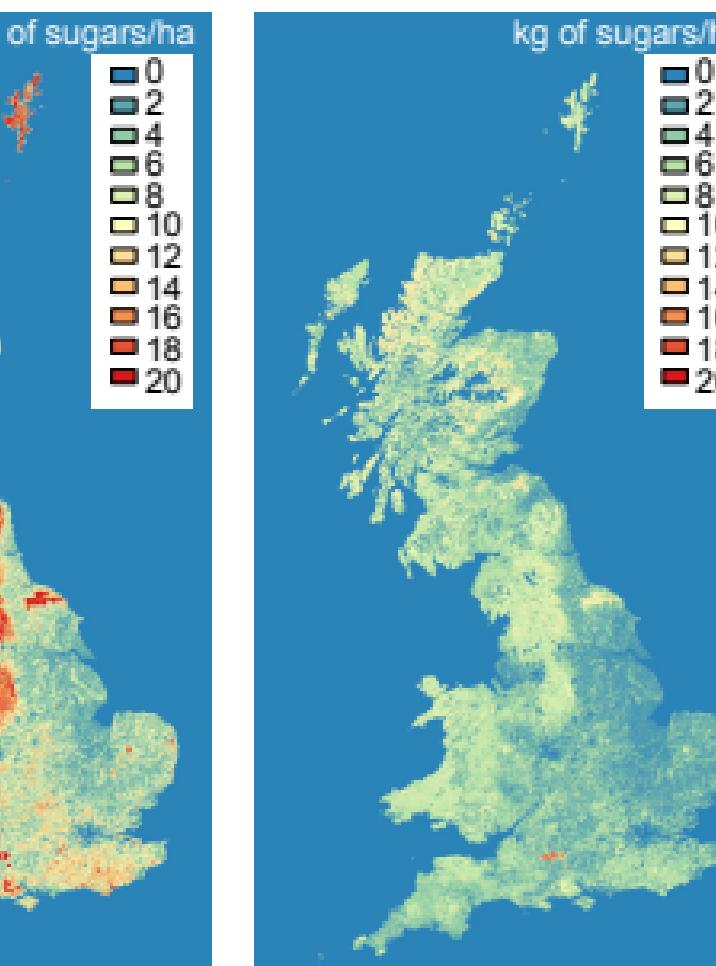
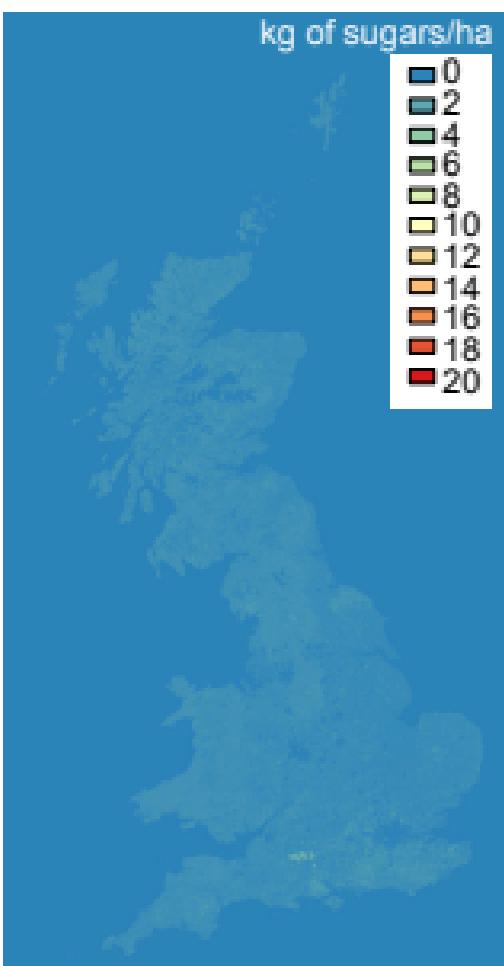
620 empirical (empirical dataset) and published nectar values (literature dataset, see Supplementary  
621 Table 13 for references) at the vegetative scale. **h**, Standardized major axis linear regression  
622 performed on the log10 (x+1) empirical and modelled nectar values generated by a leave-one-out  
623 approach. Estimates of all equations are derived from (standardized) major axis regression (ma  
624 and sma function from ‘smatr’ package in R<sup>36</sup>; see Supplementary Result 4 for details).

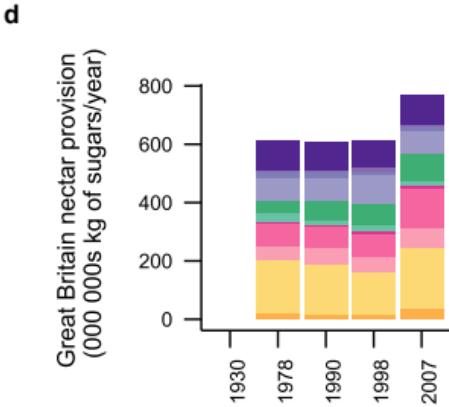
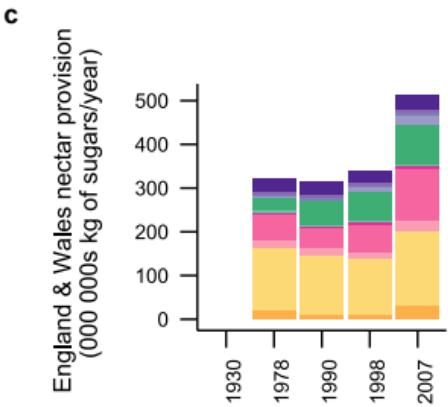
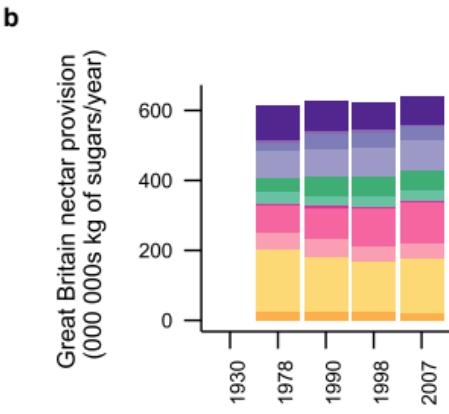
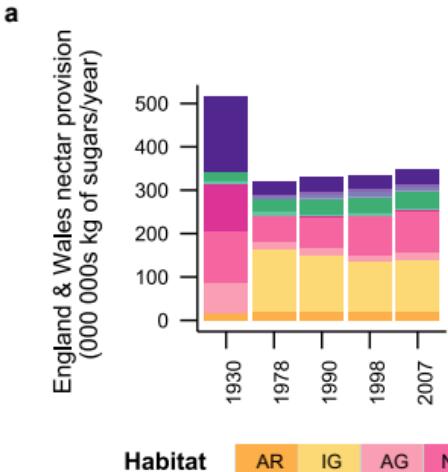
625 **Extended Data Figure 7. Flower number and vegetative cover relationships.** Linear  
626 regressions between the number of open flowers counted in a quadrat of 0.5m<sup>2</sup> according to the  
627 vegetative cover of the focus species in the quadrat (in %). Data are extracted from IPI AgriLand  
628 floral transects survey in 2012 for 23 (panels **a-w**) out of the 35 main nectar contributing species.  
629 The number of flowers was analyzed according to the vegetative cover (“Cover”), the month of  
630 the survey (“Month”) and the interaction between these two terms (“Cover:Month”) using  
631 negative binomial generalized linear models (see Supplementary Result 4 for details). Colored  
632 lines represent the linear regression between flower abundance and vegetative cover for each  
633 month of the survey. Black lines represent the overall linear regression between flower  
634 abundance and vegetative cover when the “Month” covariate cannot be included in the model.  
635 Line equations were derived from statistical intercept and slope estimates.



Contribution to national nectar provision in 2007 (%)



**a March****b April****c May****d June****e July****f August****g September****h October**



a

Response variable	Effect	df	F value	P-value
Nectar productivity	Habitat	10	69.643	<.0001
Species nectar diversity	Habitat	10	19.923	<.0001
Functional nectar diversity	Habitat	10	24.150	<.0001

b

Response variable	Effect	df	F value	P-value
Nectar productivity	Habitat	10	75.081	<.0001
	Location	1	0.560	0.455
	Habitat:Location	10	63.519	<.0001
Species nectar diversity	Habitat	10	22.061	<.0001
	Location	1	0.147	0.701
	Habitat:Location	10	10.396	<.0001
Functional nectar diversity	Habitat	10	23.677	<.0001
	Location	1	2.158	0.142
	Habitat:Location	10	15.810	<.0001

c

Response variable	Effect	df	F value	P-value
Nectar productivity	Habitat	10	26.860	<.0001
	Year	3	1.473	0.220
	Habitat:Year	30	1.793	0.005
Species nectar diversity	Habitat	10	5.137	<.0001
	Year	3	2.600	0.050
	Habitat:Year	30	2.523	<.0001
Functional nectar diversity	Habitat	10	3.517	0.0001
	Year	3	1.987	0.114
	Habitat:Year	30	1.725	0.009

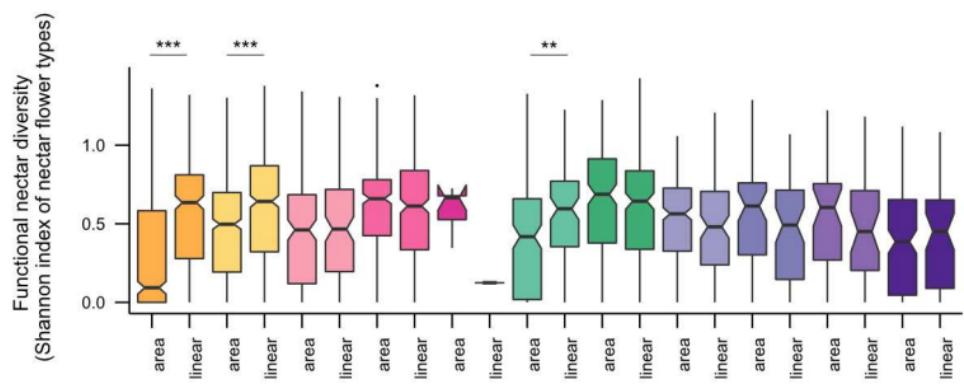
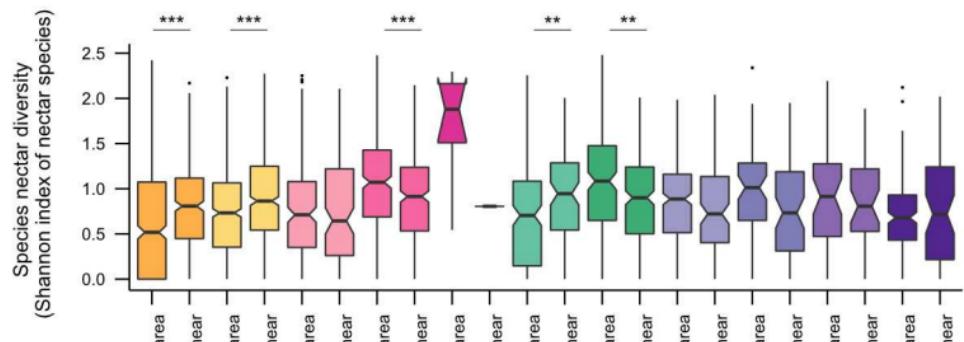
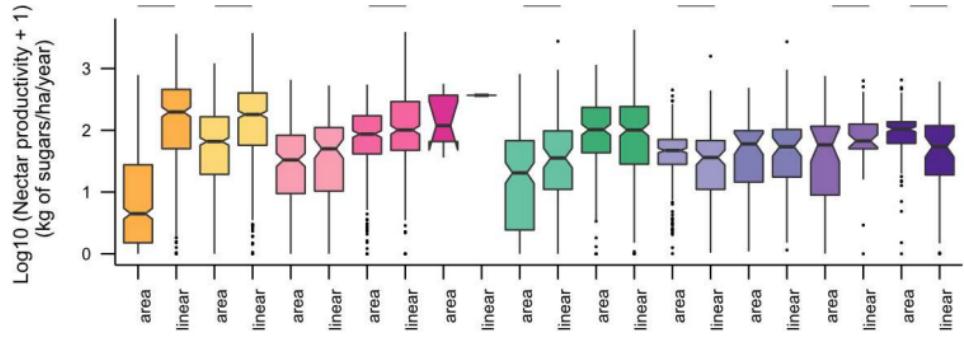
	Depth of nectar tube		Width of nectar tube		Number of visiting insect species					Frequent visiting insect species	Number of sources
	mean	sem	mean	sem	All	Diptera	Hymeno	Lepido	Coleo		
<i>Trifolium repens</i>	4.84	0.19	1.36	0.04	54	22	16 (13 species of <i>Bombus</i> )	8	8	<i>Bombus pascuorum, Bombus lucorum/terrestris, Bombus lapidarius</i>	21
<i>Calluna vulgaris</i>	2.23	0.10	1.93	0.07	139	96	29 (9 species of <i>Bombus</i> )	13	1	<i>Bombus lucorum/terrestris, Bombus pascuorum, Apis mellifera, Bombus jonellus</i>	9
<i>Cirsium palustre</i>	3.63	0.07	1.42	0.07	12	5	7 (6 species of <i>Bombus</i> )	0	0	<i>Bombus pascuorum, Bombus lucorum/terrestris, Bombus pratorum</i>	6
<i>Erica cinerea</i>	5.81	0.11	1.67	0.06	49	19	27 (10 species of <i>Bombus</i> )	2	1	<i>Bombus jonellus, Bombus lucorum/terrestris, Bombus pascuorum</i>	6

a

Option	Option code	Mean nectar productivity (kg of sugars/ha/year)	England land cover (000s ha)	England nectar provision (000 000s kg of sugars/year)
Wild bird seed mixture	EF2/HF2	56.00	2.97	0.17
Enhanced grass buffer strip	HE10	166.80	0.62	0.10
Nectar flower mixture	HF4/HF4	244.00	1.61	0.39
Haymaking supplement	HK18	18.60	1.12	0.02
Species-rich semi-natural grassland	HK6/7/8	31.90	2.77	0.09

b

Linear features	Linear code	England mean nectar productivity (kg of sugars/ha/year)	England land cover (000s ha)	England nectar provision (000 000s kg of sugars/year)
Hedgerows	H	341.59	40.20	13.73
Watersides	S	60.97	/	/
Road verges	R	60.63	/	/

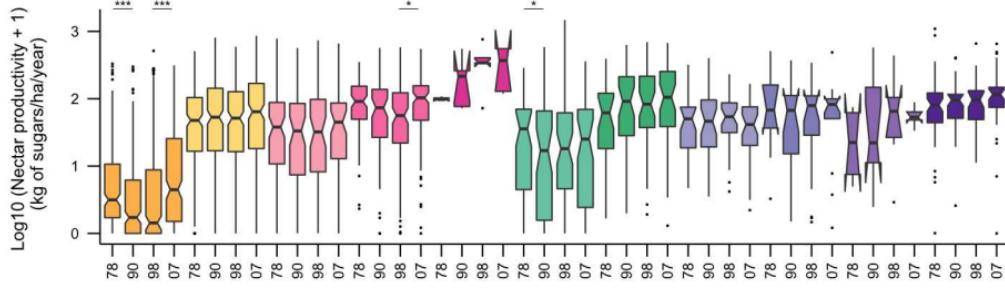


a

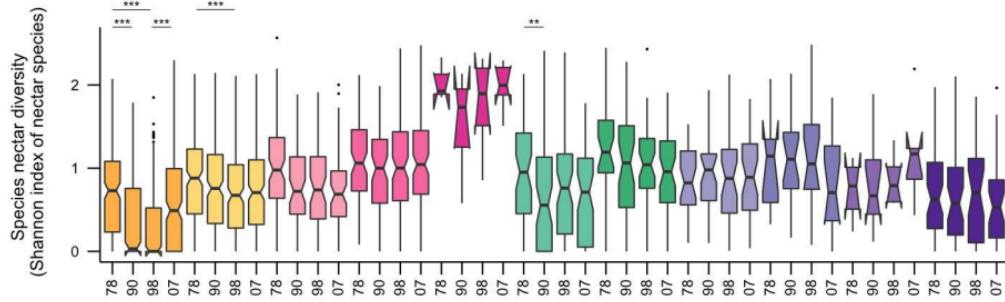
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C

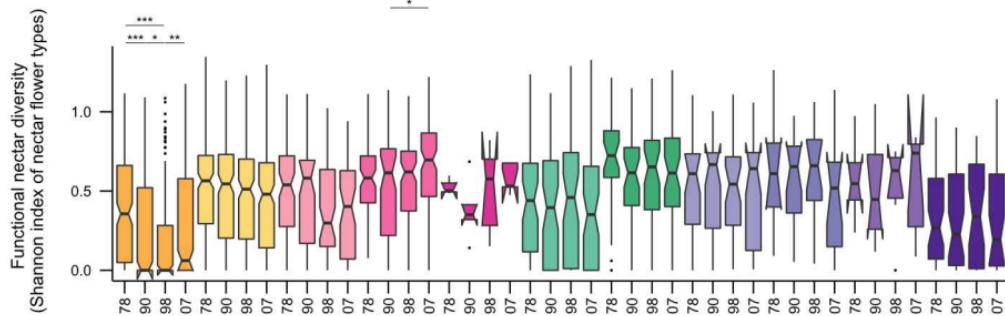
## Habitat



b



C



## Habitat

An orange rectangular icon with two horizontal lines inside, representing arable land.

## Improved Gra

 Acid Grass

A small rectangular icon with a vertical axis, divided into three horizontal sections: top, middle, and bottom.

Neutral Grade

## Calcareous Grass

Conifer

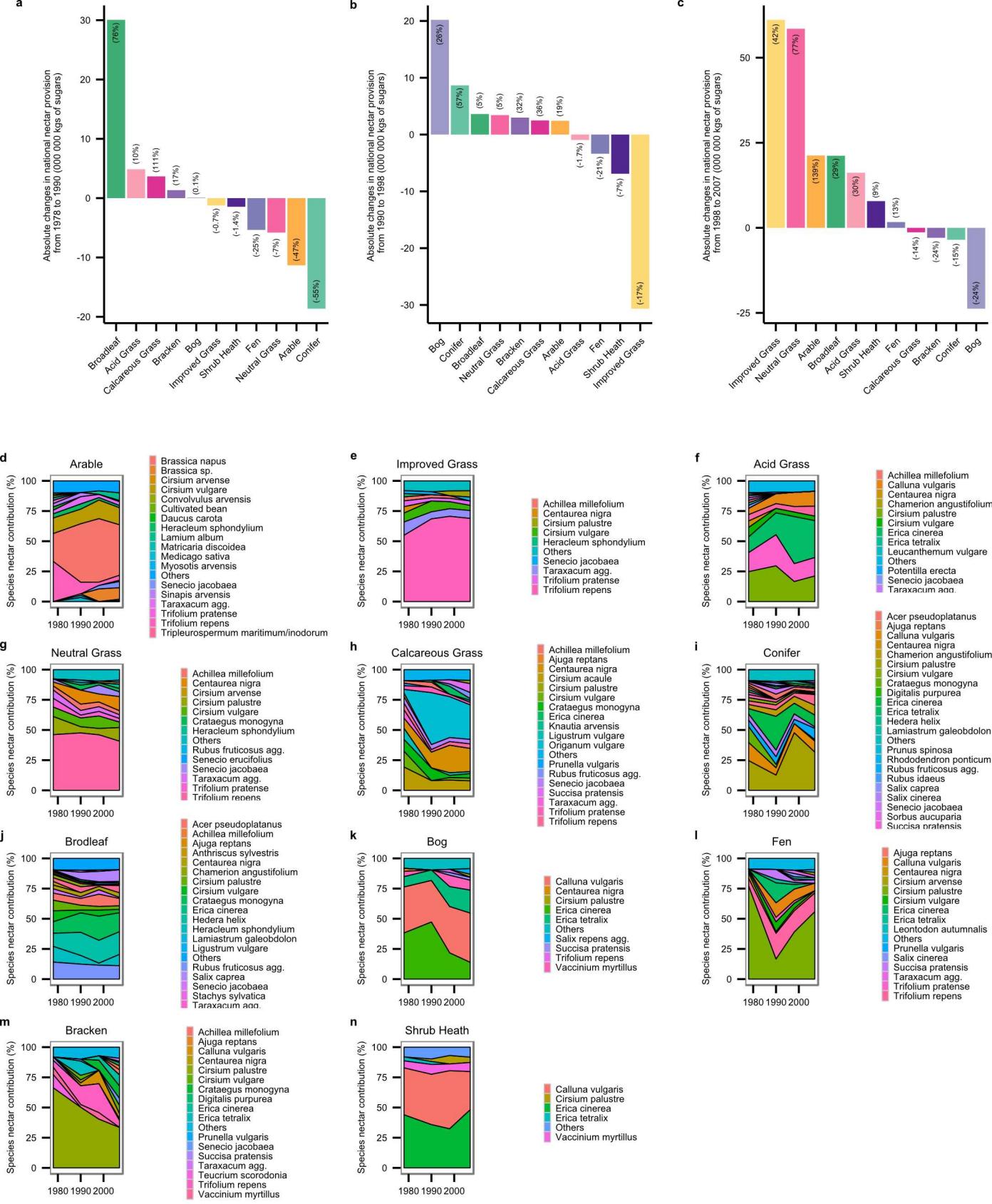
Broadle

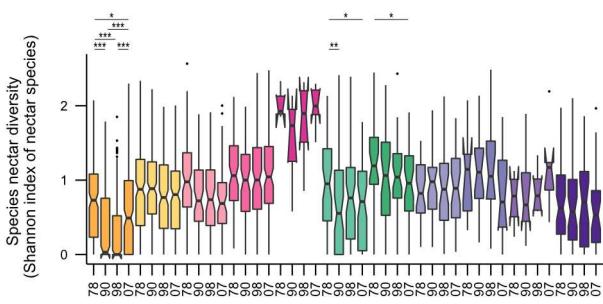
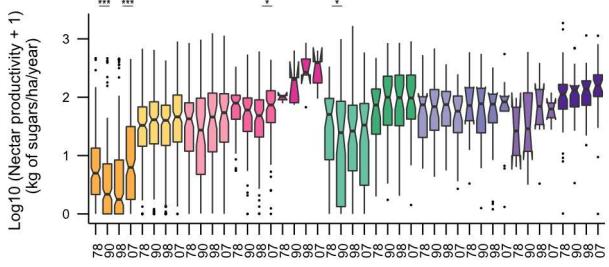
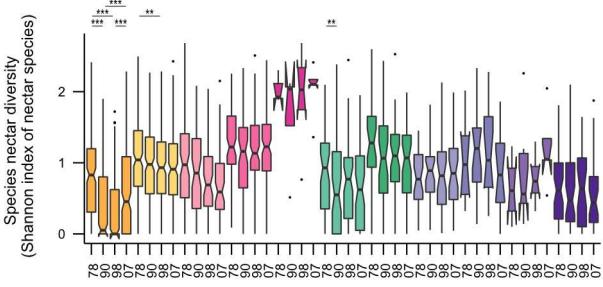
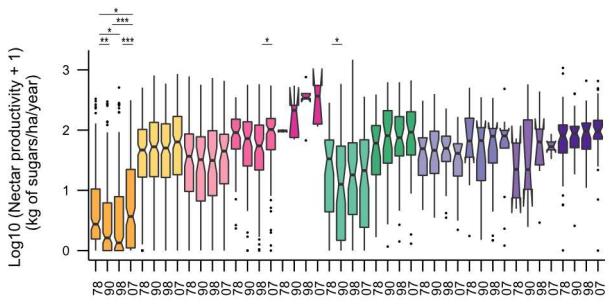
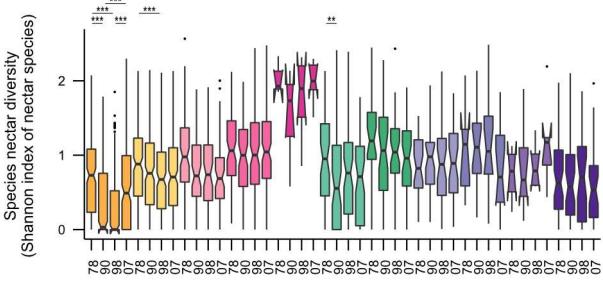
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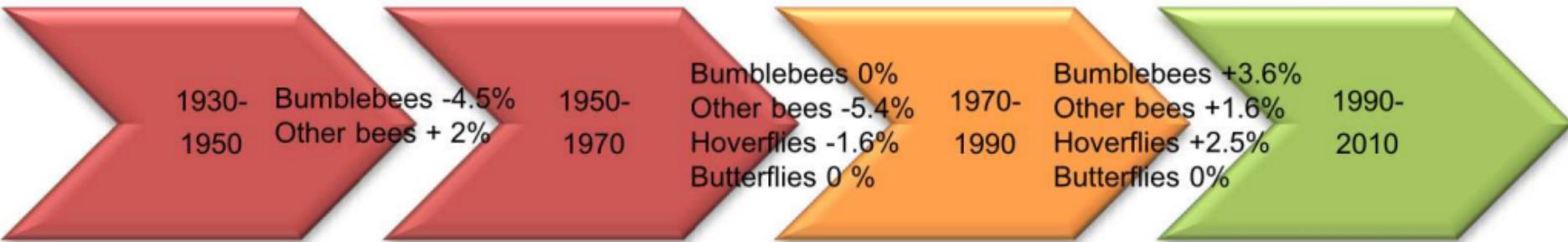
#### Shrub Heath



**b****c****d****e****f**

**Habitat** Arable Improved Grass Acid Grass Neutral Grass Calcareous Grass Conifer Broadleaf Bog Fen Bracken Shrub Heath

Carvalheiro et al. 2014  
What? Changes in species richness at the national scale  
Where? Great Britain  
Database? UK Biological Records Centre



Ollerton et al. 2014  
What? Extinction rates of bees and flower-visiting wasps  
Where? Britain  
Database? BWARS



Baude et al. 2015  
What? Changes in nectar provision at the national scale  
Where? Great Britain  
Database? Plant species nectar productivity combined to national vegetation and land covers surveys

