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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 wildflowers¹⁻⁴. Among the multiple pressures facing**
15 **pollinators²⁻⁴, decreasing floral resources due to habitat loss and degradation has been**
16 **suggested as a key contributing factor²⁻⁸. 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 century⁹ but**
23 **stabilised more recently¹⁰. 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 pollinators¹⁻⁴. While
35 several potential drivers have been cited²⁻⁴, one important factor in pollinator declines may be the
36 loss of floral resources due to changes in land-use and management⁵⁻⁸. Several factors may have
37 caused decreased floral resources in Great Britain and other developed countries, including
38 increased use of herbicides¹¹, destruction of traditional landscape features such as hedgerows¹²
39 and loss and degradation of wildflower-rich natural habitats¹³⁻¹⁵. Current strategies to mitigate
40 pollinator declines focus primarily on enhancing floral resources⁴, including agri-environmental
41 scheme options such as sowing nectar flower mixtures^{16,17}. There is evidence for declines in some

42 key pollinator forage plants in Great Britain⁵ and the Netherlands⁷, 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 species¹⁸.
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 Survey¹⁹, 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 habitats¹⁹, 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.

65 Considering the most recent Countryside Survey (2007), there are significant differences in
66 annual nectar productivity, species nectar diversity and functional nectar diversity among habitats
67 (Extended Data Table 1). Calcareous grassland, broadleaved woodland and neutral grassland are
68 the best in all three respects (as well as shrub heathland for nectar productivity only) whereas
69 arable land is consistently the poorest habitat (Supplementary Table 2). These habitat differences
70 in nectar value create geographical variation in nectar productivity and diversity across Great
71 Britain (Figure 1). After taking into account the national land cover of habitats, improved
72 grassland contributed most (29%) to potential national nectar supply in 2007. Four species of
73 plant, *Trifolium repens*, *Calluna vulgaris*, *Cirsium palustre* and *Erica cinerea* together produce
74 over 50% of nectar nationally (see Extended Data Table 2 and Supplementary Result 1 for further
75 information about these species and their pollinators), and 22 species produce over 90% (Figure
76 2). Other species may of course be important for pollen provision. Considering flowering
77 phenology reveals seasonal variation nationally (Figure 3): 60% of nectar is provided in
78 July/August when the flower density of British dominant species peaks. Because heathland
79 species are unlikely to contribute as much in other European countries, this seasonal pattern may
80 differ. The relative nectar value of linear features (hedgerows, watersides and road verges)
81 depends on habitat. With the exception of those in shrub heathland and bog, linear features
82 produce more nectar per unit area (and the contrast is particularly high in landscapes dominated
83 by arable land, improved grassland and conifer woodland; Extended Data Figure 1). Of the five
84 types of agri-environment scheme options we investigated, nectar flower mixtures have the
85 highest nectar productivity value, followed by enhanced margins (Extended Data Table 3).
86 Nectar flower mixture options are similar to hedgerows in term of annual nectar productivity per
87 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 Wales²⁰. 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 acidification²¹,

111 decreased nitrogen deposition²² and agricultural set-asides²³ 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 extinctions⁹. 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 groups¹⁰.

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^{13,14}. 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 nationally²⁴ and globally²⁵. 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 flowering²⁶. 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 England¹⁶ 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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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. 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 \log_{10}
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 Britain²⁷, 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 angiosperms²⁸), 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 μ L Minicaps, Hirshmann, Eberstadt, Germany) were used directly
294 to collect the nectar, otherwise single flowers were rinsed twice with 1-5 μ 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; μ g of
299 sugars/flower/24h) was calculated using the formula²⁹

300 $s = 10dvC$

301 where v is the volume collected (μL), 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 formula²⁹

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

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 flying³⁰; 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^{28,31,32} (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 m²), 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 database³³, and included: “flower shape”, “breeding system”, “life span”, the degree of “dicliny”,
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 Survey¹⁹. 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 Classes¹⁹
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 m²) 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^{19,34,35}; 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 maps²⁰; 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 England³⁵,
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 R³⁶) 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:

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

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 BioFlor database³³ 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:

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

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 2007³⁷.

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 1m²
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^{38,39}. 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⁽³⁶⁾. To investigate the most recent nectar variations (2007), we analysed the

476 $\log_{10}(x+1)$ 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 $\log_{10}(x+1)$ 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 $\log_{10}(x+1)$ 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 R³⁶). 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 R³⁶. All box plots show the median, 25th and 75th 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 $\log_{10}(x+1)$ 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^{38,39}. **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 England³⁵

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

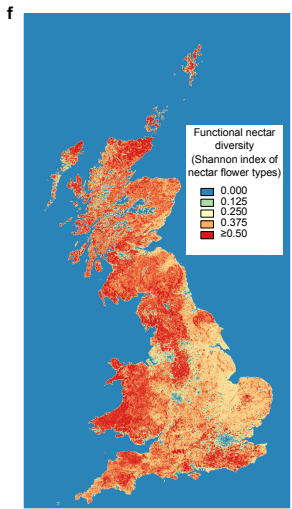
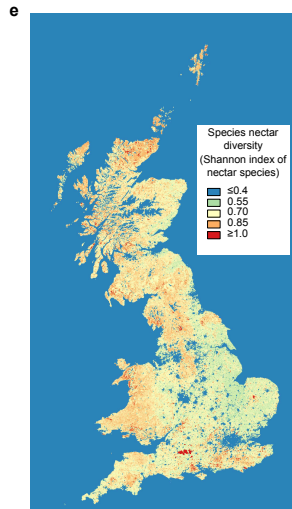
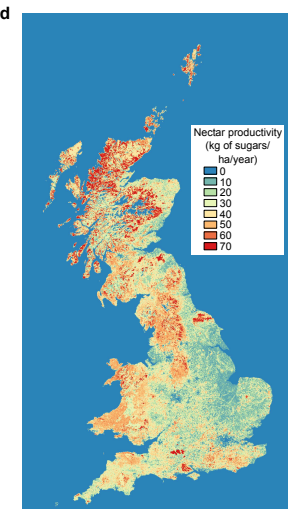
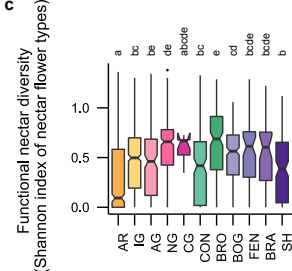
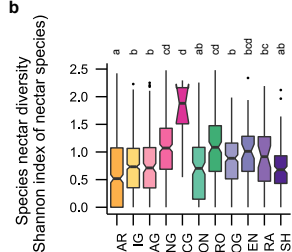
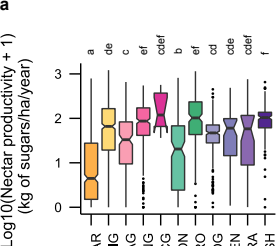
597 1978, 1990, 1998 and 2007 and computed considering only the species with empirical nectar
598 values. Significant differences of time periods per habitats are indicated by stars (* for $p \leq 0.05$;
599 ** for $p \leq 0.01$; *** for $p \leq 0.001$). See Supplementary Table 4 for sample sizes and
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 2014¹⁰ and Ollerton et al. 2014⁹ 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. 2014⁹).

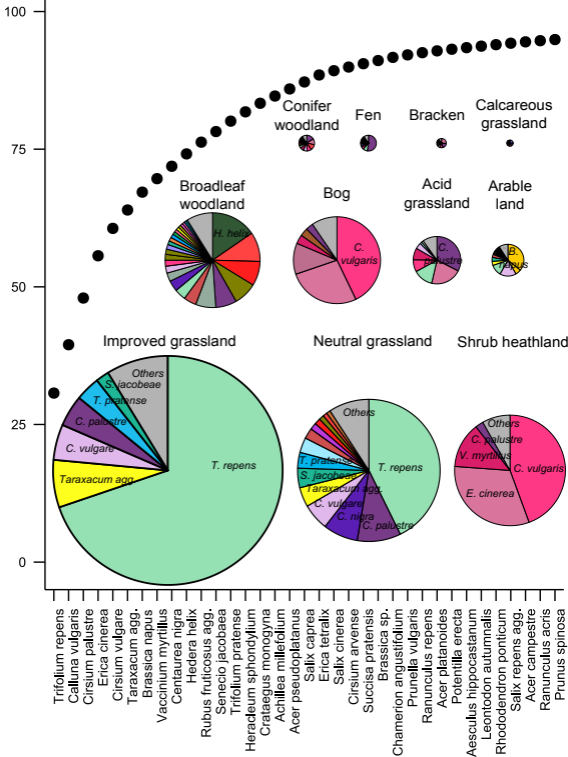
609 **Extended Data Figure 6. Validity of the datasets. a,** Major axis linear regression of \log_{10}
610 $(x+1)$ nectar values per flower obtained in the second location against those obtained in the first
611 one. **b,** Major axis linear regression of $\log_{10} (x+1)$ flower density values obtained 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 2007⁴⁰)
619 at the flower scale. **g,** Standardized major axis linear regression performed on the $\log_{10} (x+1)$

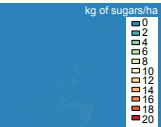
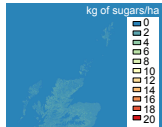
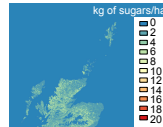
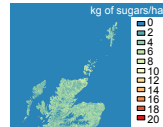
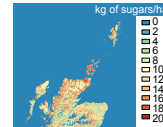
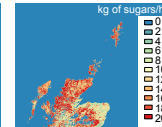
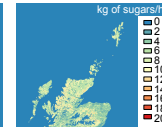
620 empirical (empirical dataset) and published nectar values (literature dataset, see Supplementary
621 Table 13 for references) at the vegetative scale. **h**, Standardized major axis linear regression
622 performed on the $\log_{10}(x+1)$ empirical and modelled nectar values generated by a leave-one-out
623 approach. Estimates of all equations are derived from (standardized) major axis regression (ma
624 and sma function from ‘smatr’ package in R³⁶; 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 0.5m² 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

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

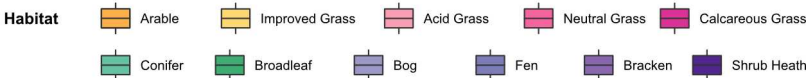
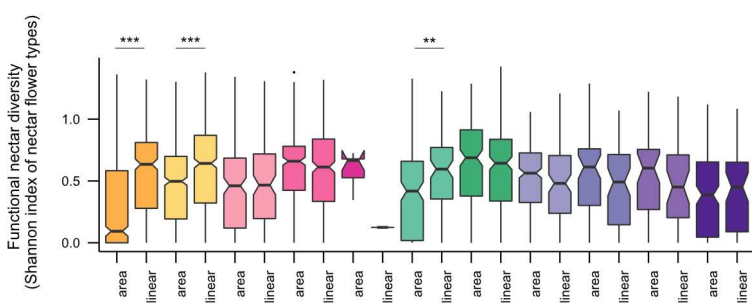
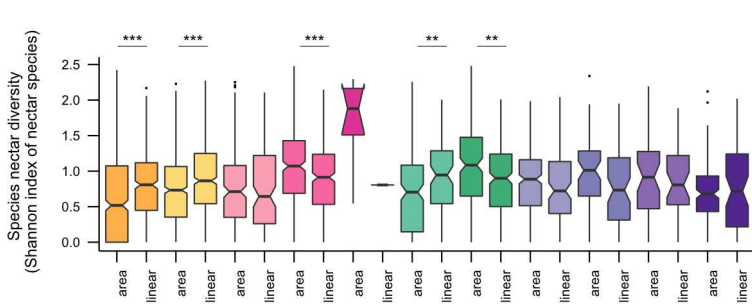
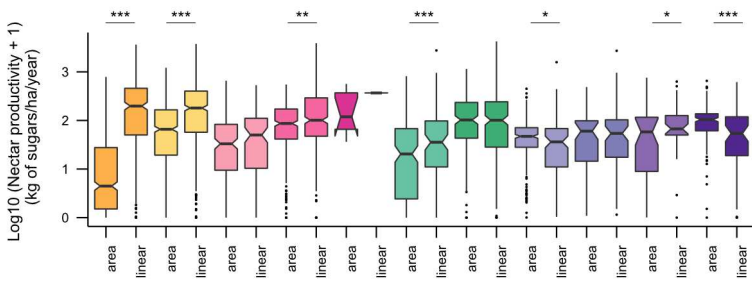
	Depth of nectar tube		Width of nectar tube		Number of visiting insect species					Frequent visiting insect species	Number of sources
	mean	sem	mean	sem	All	Diptera	Hymeno	Lepido	Coleo		
<i>Trifolium repens</i>	4.84	0.19	1.36	0.04	54	22	16 (13 species of <i>Bombus</i>)	8	8	<i>Bombus pascuorum</i> , <i>Bombus lucorum/terrestris</i> , <i>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</i> , <i>Bombus pascuorum</i> , <i>Apis mellifera</i> , <i>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</i> , <i>Bombus lucorum/terrestris</i> , <i>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</i> , <i>Bombus lucorum/terrestris</i> , <i>Bombus pascorum</i>	6

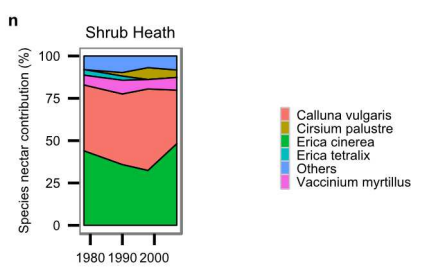
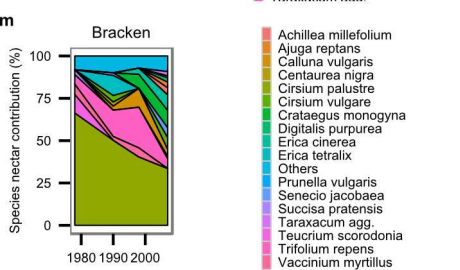
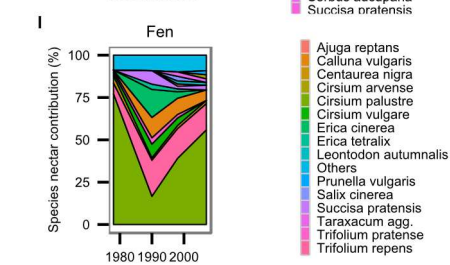
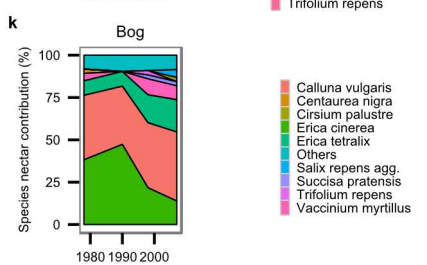
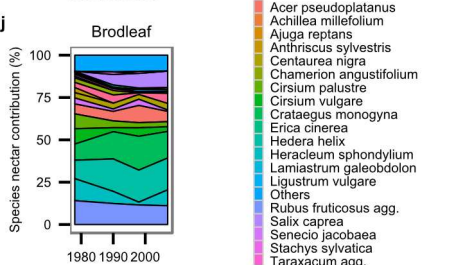
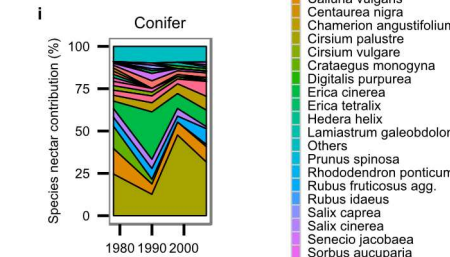
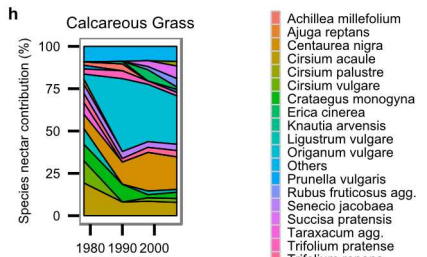
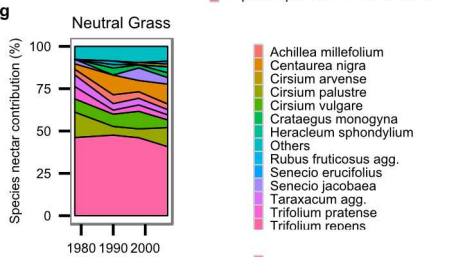
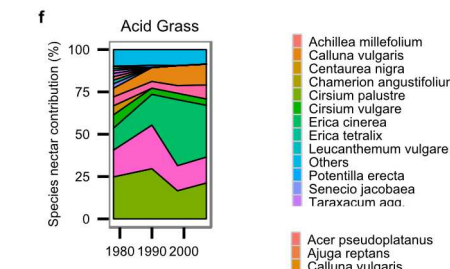
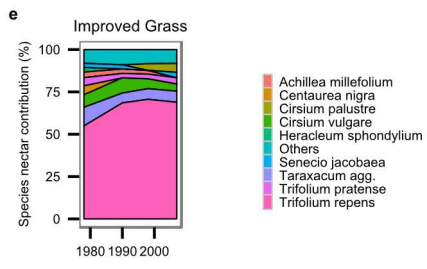
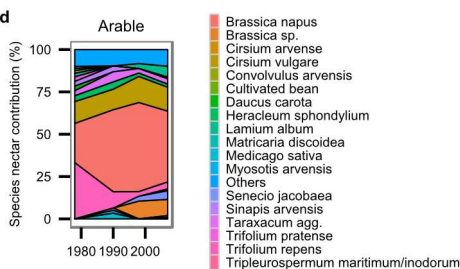
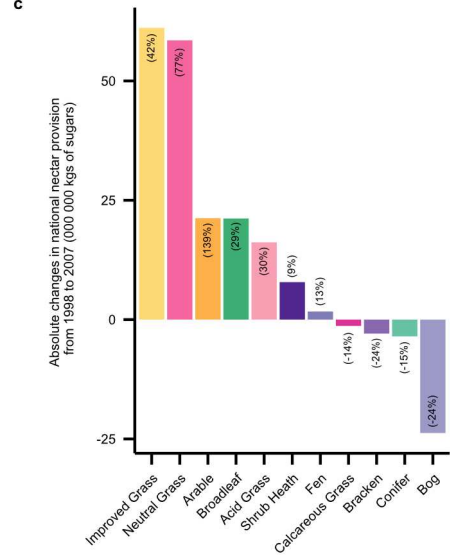
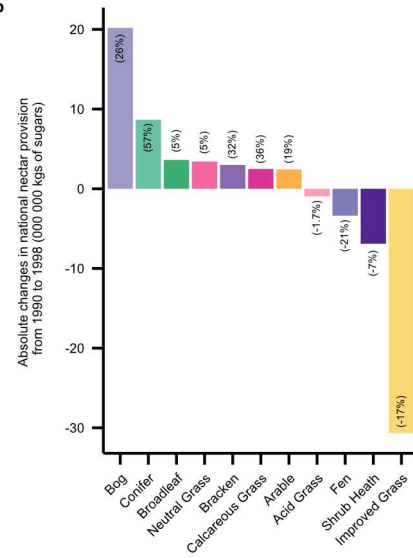
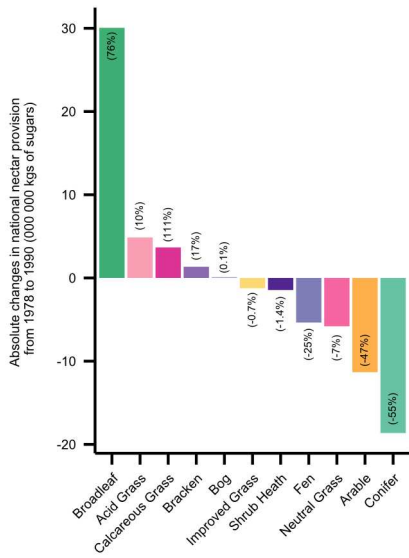
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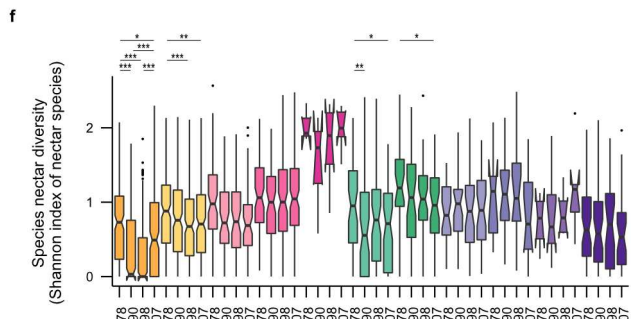
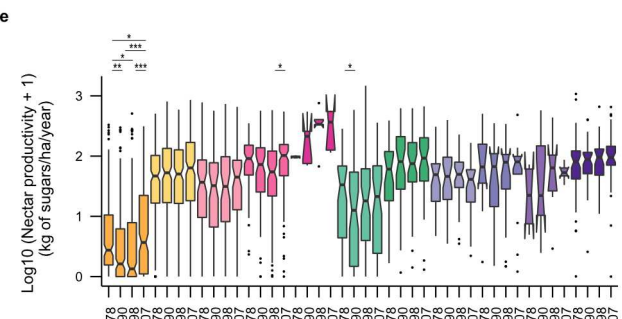
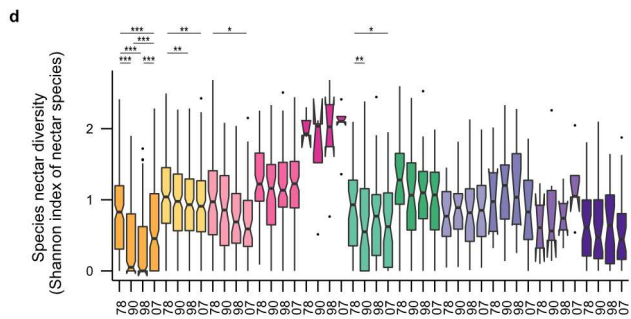
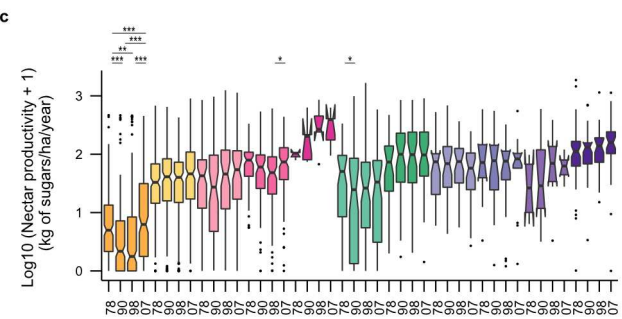
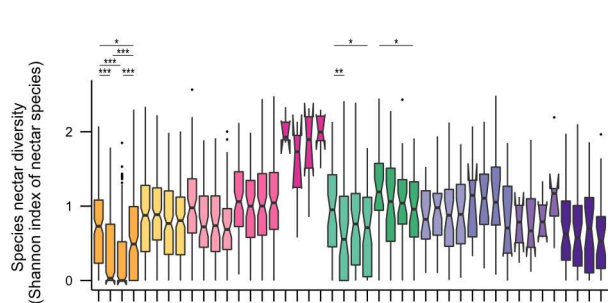
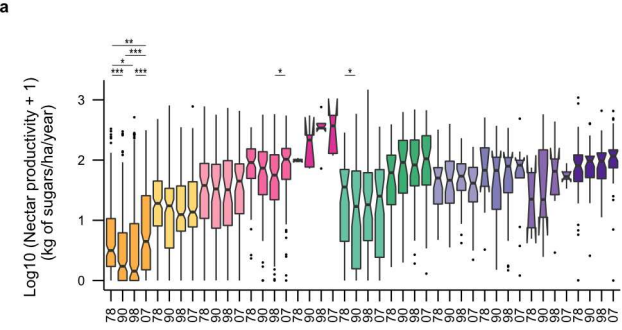
Option	Option code	Mean nectar productivity (kg of sugars/ha/year)	England land cover (000s ha)	England nectar provision (000 000s kg of sugars/year)
Wild bird seed mixture	EF2/HF2	56.00	2.97	0.17
Enhanced grass buffer strip	HE10	166.80	0.62	0.10
Nectar flower mixture	HF4/HF4	244.00	1.61	0.39
Haymaking 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	/	/

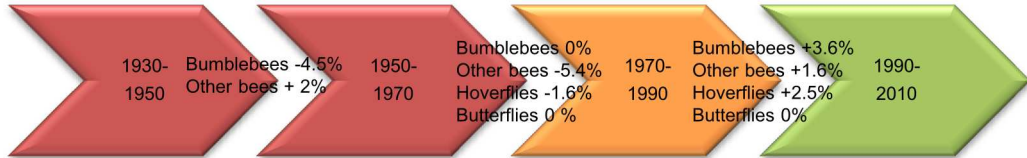






Habitat Arable Improved Grass Acid Grass Neutral Grass Calcareous Grass Conifer Broadleaf Bog Fen Bracken Shrub Heath

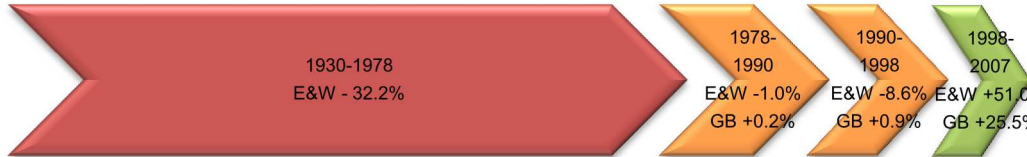
Carvalho et al. 2014
 What? Changes in species richness at the national scale
 Where? Great Britain
 Database? UK Biological Records Centre



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



1930

1950

1970

1990

2010

