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Historical nectar assessment reveals the fall and rise of floral resources in Britain

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There is considerable concern over declines in insect pollinator communities and potential impacts on the pollination of crops and wildflowers[1–4]. Among the multiple pressures facing pollinators[2–4], decreasing floral resources due to habitat loss and degradation has been suggested as a key contributing factor[2–8]. However, a lack of quantitative data has hampered testing for historical changes in floral resources. Here we show that overall floral rewards can be estimated at a national scale by combining vegetation surveys and direct nectar measurements. We find evidence for substantial losses in nectar resources in England and Wales between the 1930s and 1970s; however, total nectar provision in Great Britain as a whole had stabilized by 1978, and increased from 1998 to 2007. These findings concur with trends in pollinator diversity, which declined in the mid-twentieth century[9] but stabilized more recently[10]. The diversity of nectar sources kept declining in most habitats, with four plant species accounting for over 50% of national nectar provision in 2007. Calcareous grassland, broadleaved woodland and neutral grassland are the habitats that produce the greatest amount of nectar per unit area from the most diverse sources, whereas arable land is the poorest with respect to amount of nectar per unit area and diversity of nectar sources. Although agri-environment schemes add resources to arable landscapes, their national contribution is low. Owing to their large area, improved grasslands could add substantially to national nectar provision if they were managed to increase floral resource provision. This national-scale assessment of floral resource provision affords new insights

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into the links between plant and pollinator declines, and offers considerable opportunities for conservation.

Concerns have been raised about declines in both wild and managed insect pollinators[1–4]. Although several potential drivers have been cited[2–4], one important factor in pollinator declines may be the loss of floral resources due to changes in land use and management[5–8]. Several factors may have caused decreased floral resources in Great Britain and other developed countries, including increased use of herbicides[11], destruction of traditional landscape features such as hedgerows[12] and loss and degradation of wildflower-rich natural habitats[13–15]. Current strategies to mitigate pollinator declines focus primarily on enhancing floral resources[4], including agri-environmental scheme options such as sowing nectar flower mixtures[16,17]. There is evidence for declines in some key pollinator forage plants in Great Britain[5] and The Netherlands[7], but the notion that the overall availability of floral resources has declined is largely based on subjective assessments. Floral resources have never been quantified at national or even landscape scales.

While both nectar and pollen are important floral resources, we focus on nectar because of its importance as an energy source in the diets of adult bees, and because it provides a common currency (total sugars) in which we can express the nutritional contribution of all plant species[18]. We quantified the nectar resources in Great Britain by combining directly measured and modelled nectar productivity data per unit cover for 260 common plant species (Supplementary Table 11) with historical vegetative cover estimates from the British Countryside Survey[19], a representative national-scale survey of plant community composition. Together, the 260 species comprise the vast majority of British nectar sources as they include virtually all nectar-producing plants from the set of species covering 99% of the British land area. Using vegetation data from the latest Countryside Survey (2007), we quantified recent nectar productivity of habitats (nectar sugar per unit area and time) and the diversity of their nectar sources (considering nectar production both by species and by floral morphology groups, referred to as ‘species nectar diversity’ and ‘functional nectar diversity’, respectively). Production was scaled up to estimate national nectar provision using the estimated area of habitats[19], allowing the contributions of species, habitats and agri-environment schemes to national nectar provision to be assessed. We estimated historical shifts in nectar provision over recent decades using data from earlier Countryside Survey rounds (1978, 1990, 1998 and 2007), considering both changes in nectar productivity within habitats and changes in habitat area. We also investigated floral resource

changes from the 1930s onward for England and Wales, based solely on changes in habitat 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 1). These habitat differences in nectar value create geographical variation in nectar productivity and diversity across Great Britain (Fig. 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 Information for further information about these species and their pollinators), and 22 species produce over 90% (Fig. 2). Other species may of course be important for pollen provision. A consideration of flowering phenology reveals seasonal variation nationally (Fig. 3): 60% of nectar is provided in July and August when the flower density of British dominant species peaks. Because heathland species are unlikely to contribute as much to nectar provision**[Author: 'contribute as much to nectar provision'?]** 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 compared with nonlinear features **[Author: compared with nonlinear features correct?]** (the contrast is particularly high in landscapes dominated by arable land, improved grassland and conifer woodland; Extended Data Fig. 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 terms of annual nectar productivity per unit area, but they cover a much smaller area, and consequently contribute far less to the national nectar resources (0.1% of nectar supply comes from nectar flower mixtures compared to 3% from hedgerows in England; Extended Data Table 3).

Historical shifts in nectar productivity, species nectar diversity and functional nectar diversity over recent decades depended on the habitat type and time period considered (Extended

Data Table 1). From 1978 to 1990, annual nectar productivity decreased significantly in arable land and conifer woodland, but from 1990 to 1998, none of the habitats showed significant changes in nectar productivity. From 1998 to 2007, nectar productivity increased significantly in arable land and neutral grassland (Extended Data Fig. 2). Nectar diversity, both at the level of plant species and functional groups, decreased significantly in arable land and improved grassland from 1978 to 2007. Species nectar diversity also significantly decreased in conifer woodland and broadleaved woodland during that period. From 1978 to 1990, species nectar diversity declined in all habitats (except bog), significantly so in arable land and conifer woodland; thereafter it remained roughly constant, except in arable land where it increased significantly**[Author: Please clarify 'rebounded' in this context.]** from 1998 to 2007 (see Extended Data Fig. 2 and Supplementary Informationfor details on functional nectar diversity). For the 1930s we have information only on shifts in land cover (but not floral abundances within them), and only for England and Wales[20]. Assuming no change in floral composition within habitats, we found a strong decline in national nectar provision from the 1930s to 1978 (−32%), followed by a period of stagnation from 1978 to 2007 (Fig. 4 and Supplementary Table 2). Incorporating shifts in nectar productivity within habitats for recent decades showed an increase in national nectar provision from 1998 to 2007 (+51% in England and Wales and +25% for Great Britain as a whole; Fig. 4 and Supplementary Table 3). While shifts in vegetation composition within dominant habitats predominate as causes of recent increases, no quantitative data are available before 1978. This recent upturn could be caused by decreased acidification[21], decreased nitrogen deposition[22] and agricultural set-asides[23] during this period (Supplementary Table 4). However, post-war changes in habitat management (for example, herbicide use in arable land, cessation of woodland coppicing, nitrogen deposition in grasslands; Supplementary Table 4) almost certainly resulted in lower nectar per unit area, suggesting that our estimates of losses based on land use change alone are conservative; actual resource declines may have been much larger than the recent increases (see Supplementary Information). Owing to their large area, improved grassland provided the greatest contribution to the increase in national nectar provision from 1998 to 2007 (Extended Data Fig. 3). After discounting the contribution of *Trifolium repens* in improved grasslands, as it may not flower in heavily grazed fields, the increase in nectar provision from 1998 to 2007 remained (Supplementary Information and Extended Data Fig. 4).

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The historical pattern of change in nectar resources closely parallels documented shifts in pollinator communities (Extended Data Fig. 5). Substantial declines in floral resources and their diversity in the mid to late twentieth century, when agricultural intensification peaked, coincide with a period of heightened pollinator extinctions[9]. The stabilization and partial recovery of resources in recent decades corresponds to concomitant periods of decelerated declines and partial recovery in some pollinator groups[10].

Our findings provide new evidence based on floral resources to support habitat conservation and restoration. First, we provide evidence of the high nectar value of calcareous grassland for pollinating insects. Calcareous grassland area has declined drastically in Great Britain, and only a small fraction of the historical national cover remained by 2007 (refs 13, 14). Second, the low availability and diversity of nectar sources in arable habitats highlights the need to provide supplementary resources to support pollination services in farmlands, especially as the use of insect-pollinated crops has increased nationally[24] and globally[25]. The conservation and restoration of broadleaf woodland and neutral grassland as components of the farmland matrix could help to support diverse flower-visiting insect communities in arable land. The contrast in nectar productivity between linear features and the surrounding vegetation is particularly high in arable land, suggesting that linear features, especially hedgerows, provide an efficient means to enhance floral resources in farmlands if they are managed appropriately to allow flowering[26]. While agri-environment options such as nectar flower mixtures can also enhance the supply of floral resources locally, their contribution to nectar provision nationally remains low. The higher profile given to floral resource provision in the revised Countryside Stewardship guidelines for England[16] may substantially enhance resources in future. Finally, our results indicate that improved grassland has the potential to contribute massively to the nectar available nationally. Small adjustments to the management cycle in improved grasslands, allowing white clover, the dominant resource species, to flower, would help realize this potential, although its utility might be restricted to a limited number of pollinator species (Extended Data Table 2). Together, our results on the nectar values of the commonest British plants and the historical changes in plant communities provide the evidence base needed to understand recent national changes in nectar provision and identify the management options needed to restore national nectar supplies.

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

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

Author Information The floral resource database will be made available from the NERC Environmental Information Data Centre (http://dx.doi.org/10.5285/69402002-1676-4de9-a04e-d17e827db93c and http://dx.doi.org/10.5285/6c6d3844-e95a-4f84-a12e-65be4731e934). Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to

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comment on the online version of the paper. Correspondence and requests for materials should be addressed to M.B. (mathilde.baude@univ-orleans.fr).

Figure 1 Nectar productivity and diversity in Great Britain in 2007. a, Box plots of $\log_{10}$ (x+1) nectar productivity (kg of sugars per ha per year) per habitat. **b**, Box plots of species nectar diversity (Shannon index of nectar species) per habitat. **c**, Box plots of functional nectar diversity (Shannon index of nectar flower types) per habitat. Box plots are based on 2007 nonlinear vegetation data (see Supplementary Table 1 for sample sizes). Habitat types (AR, arable land; IG, improved grassland; AG, acid grassland; NG, neutral grassland; CG, calcareous grassland; CON, conifer woodland; BRO, broadleaf woodland; BOG, bog; FEN, fen; BRA, bracken; SH, shrub heathland) significantly different from one another are indicated by different italicised letters (Tukey multiple comparisons tests). **[Author: Please provide a more specific explanation of the statistical difference, as it is currently not clear from the legend. Can *P* values be described for each letter to clarify statistical difference, and would adding brackets on the figure clarifying statistical difference be clearer?]** See Extended Data Table 1 for ANOVA results. See 'Statistical analyses' section of the Methods for detailed statistical methods and definition of box plot elements. **[Author: Inserted sentence ok?] d**, Map of nectar productivity. **e**, Map of species nectar diversity. **f**, Map of functional nectar diversity. Maps are based on 2007 land cover and nonlinear vegetation data. Habitat nectar values for mapping correspond to statistical estimates from linear mixed effects models (Supplementary Table 1).

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

Figure 3 Seasonal nectar productivity in Great Britain, based on 2007 land cover and nonlinear vegetation data. a–h, Maps of nectar productivity in kg of sugars per ha from March to October 2007. Hot colours correspond to high nectar productivity while cold colours

correspond to low nectar productivity (see colours scale). Note that urban areas are assigned with nectar productivity values equal to zero, hence the blue colours in cities. Nectar productivity values for mapping correspond to back-transformed estimates of the linear mixed model fitted on $\log_{10}(x + 1)$ nectar productivity of 2007 Countryside Survey nonlinear plots with habitat, month and their interaction as fixed effects and plots nested within squares as random effects.

Figure 4 Historical changes in nectar provision (in 1 X 10^6 kg of sugars per year) at the national scale in England and Wales (1930–2007) and in Great Britain (1978–2007). a, **b**, Nectar provision partitioned by habitat, based on land cover for 1930 (England and Wales only), 1978, 1990, 1998 and 2007, using vegetation data from 1978 for all years (assuming unchanged nectar productivity within habitats across time) in England and Wales (**a**) and Great Britain (**b**). **c**, **d**, Nectar provision partitioned by habitat, based on land cover and vegetation data for 1978, 1990, 1998 and 2007 in England and Wales (**c**) and Great Britain (**d**). See Fig. 1 for habitat type codes and Supplementary Table 5 for habitat land cover values.

METHODS

Constructing the nectar database by scaling up nectar resources from the flower to the vegetative scale

Identifying the key plant species to be sampled. Although there are >2,800 plant species in Great Britain[27], only 1,341 of them are common enough to have been encountered in the Countryside Survey. Of these, the 454 commonest species accounted for 99% of national plant cover in 2007. More than half of these 454 species are unrewarding to pollinators (mainly bryophytes, pteridophytes, gymnosperms and wind-pollinated angiosperms[28]), leaving 220 species that are likely to contribute substantially to floral resources at a national scale. We focus here on these 220 species, along with an additional 50 species that we believe to be locally important floral sources (for example, *Buddleja davidii*, *Impatiens glandulifera*, *Knautia arvensis*). Together, these 270 plant species provide a focal set of potential importance in national nectar provision (Supplementary Table 11).

Quantifying nectar productivity empirically: the 'surveyed species'. Of the 270 species, 175 were surveyed in the field from February 2011 to October 2012, mainly in the south of England. When possible (112 species), nectar was collected from plants in at least two populations in two locations. For three species (*Caltha palustris*, *Lamium purpureum* and *Sinapis arvensis*), half the

nectar samples, and for *Viola arvensis* all the samples, were collected from pot-grown plants, because insufficient flowering field populations were found. For the remaining species, nectar was collected from plants in one field population. When possible, the different populations were sampled on different dates, thus providing some measure of variation due to differences in location and weather. Note that nectar was collected in only 1–2 sites per species, and so intraspecific variation in production per flower was not assessed (but see Supplementary Information).

Nectar was collected from ten single flowers in each population between 09:00 and 16:00 h (median 20 and range 5–30 flowers collected per species in total; see Extended Data Fig. 6 and Supplementary Information, for site correlation); these had been bagged (using 1.4 × 1.7 mm fabric mesh) for 24 h to prevent depletion by nectar-feeding insects. When possible (76 species), glass microcapillaries (1 and 5 µl Minicaps, Hirshmann, Eberstadt, Germany) were used directly to collect the nectar, otherwise single flowers were rinsed twice with 1–5 µl of distilled water added to the nectaries with a pipette for 1 min, and the diluted nectar solution was collected. The sugar concentration of nectar (%; g sucrose per 100 g solution) was measured by using a hand-held refractometer modified for small volumes (Eclipse, Bellingham and Stanley, Tunbridge Wells, UK). The amount of sugar produced per flower basis over 24 h (s; µg of sugars per flower per 24 h) was calculated using the formula[29] $s = 10dvC$ where v is the volume collected (µl), and d is the density of a sucrose solution at a concentration C (g sucrose per 100 g solution) as read on the refractometer. The density of the sucrose solution was calculated by the formula[29] $d = 0.0037921C + 0.0000178C^2 + 0.9988603$.

The number of open flowers per unit area of vegetative cover (flower density) was estimated for 179 species by placing five quadrats (0.5 m × 0.5 m) haphazardly on each flowering population (median 10 quadrats, range 1–20 quadrats; see Extended Data Fig. 6 and Supplementary Information for site correlation). In each quadrat, we counted the number of open floral units of the focal species (a 'floral unit' is one or multiple flowers that can be visited by insects without flying[30]; for example a composite flower head of daisy, *Bellis perennis*). We also counted the number of open flowers present in one typical open floral unit in each quadrat. Vegetative cover for each plant species was estimated using a point-quadrat approach with the cross-strings of the quadrat: cover was expressed as proportional to the number of the 36 cross-points covered by the foliage of the species of interest in each quadrat. For trees, instead of using

quadrats, we counted the number of floral units in a 3D cube (0.5 × 0.5 × 0.5 m) that was placed in the outer areas of foliage. This was extrapolated to the whole column situated above the unit of vegetative cover by measuring the height of tree foliage with an inclinometer (PM-5/360 PC Suunto) and by estimating the distribution of the flowers within the tree foliage (subjectively assessed scores: from 1 for a strongly biased flower distribution on the outer edges of the foliage to 5 for a homogeneous full flower distribution). Given that flower density is not constant throughout the flowering season, we estimated variations in flower density according to a triangular function from the estimated peak of flowering through the flowering season which was documented from recorded phenologies[28,31,32] (see Supplementary Information and Extended Data Fig. 6 for phenology parameter relationships). An alternative nectar rectangular phenology productivity database was also generated by keeping nectar productivity of each species constant throughout the flowering season; this was used to perform sensitivity analyses.

The mean nectar sugar content from a single flower (produced over a 24 h period) was multiplied up to the nectar content of a single floral unit (number of flowers in a floral unit), then to the amount of nectar per unit area (number of flowers per m^2), to the amount of nectar per unit area for each month (variation in flower density over the flowering season) and finally to the amount of nectar per unit area per year. Despite relatively low sample sizes per species compared to species-specific studies, our estimates of sugar production were well correlated with published values both per flower per day and per area per year (Extended Data Fig. 6 and Supplementary Information). This empirical method provided the nectar productivity values for 161 plant species among the 175 initially surveyed (nectar productivity could not be scaled up for some species due to mismatches with phenological data, see Supplementary Information).

Modelling nectar productivity: the 'unsurveyed species'. To model the nectar productivity of the plant species that could not be surveyed in the field, we used a predictive modelling approach. We first analysed variation in the nectar values from the surveyed species. A linear model was fitted to annual nectar sugar productivity ($\log_{10}(x + 1)$ transformed) as a function of plant traits. Plants traits were mainly collected from the BiolFlor database[33], and included: 'flower shape', 'breeding system', 'life span', the degree of 'dicliny', the maximum 'height', the 'flowering period' and 'family' (see Supplementary Information for definitions). The estimates from the most parsimonious statistical model based on AIC criterion (Supplementary Table 6, $N = 153$; adjusted $r^2 = 0.55$) were used to predict the annual nectar sugar productivity for the initial list of

surveyed and unsurveyed species on the basis of their traits. To check the validity of the predicted values, we adopted a repeated 'leave-one-out' approach to model successively all the excluded values from the empirically derived data sets. Then, we applied a standardized major axis regression on the $\log_{10}(x + 1)$ transformed empirically derived and modelled nectar values of the surveyed species (Extended Data Fig. 6). We predicted the nectar values for 252 species; and giving priority to empirical and default values, we included 94 of them in our database. An alternative nectar productivity database was also generated by considering only the species with empirical nectar values; this was used to perform sensitivity testing.

Ascribing default values for nectar productivity. For four crop species harvested before flowering—onion (*Allium cepa*), cabbage (*Brassica oleracea* cultivated), turnip (*Brassica rapa*) and radish (*Raphanus sativus*)—we assigned a value of zero for nectar productivity. A zero value was also assigned to *Helianthemum nummularium*, despite the missing flower density data, given that we collected no nectar in flowers. In the Countryside Survey vegetation data set, some taxa are only identified at the genus level; we interpreted these taxa to represent the commonest species in the genus (for example, *Centaurea* sp. was interpreted as *Centaurea nigra*). For 10 species out of the initial list of 270 it was not possible to quantify nectar production, leading to a total of 260 species with quantified annual and monthly nectar productivity values (161 values from empirical research, 94 modelled values, and 5 default values, Supplementary Table 11). All the above steps of scaling-up process are summarized in Supplementary Table 7.

Using the Countryside Survey vegetation database to scale up nectar resources from plant species to communities at the habitat and national scales

Spatio-temporal variations in nectar provision at the national scale were calculated by combining our nectar productivity data set with vegetation and land cover data already recorded during the Countryside Survey[19]. The Countryside Survey is a national survey of plant communities conducted in 1978, 1990, 1998 and 2007 in Great Britain (England, Wales and Scotland). The survey was conducted by selecting 1-km sample squares at random from 32 land classes[19] representing physiographically similar sampling domains throughout Great Britain, ensuring an unbiased representation of the British non-urban landscape. Within each square, a random, stratified sample of five areal (nonlinear) square plots (200 m^2) was established and the presence and the percentage cover of all vascular plant species were recorded. These plots were classified to 17 habitat classes, but we only used data from 11 habitats: acid grassland, arable land, bog,

bracken, broadleaf woodland, calcareous grassland, conifer, fen, improved grassland, neutral grassland and shrub heath (Supplementary Table 8 for habitat description). The habitats not used were inland rock, littoral rock/supralittoral rock, littoral sediment/supralittoral sediment, montane and urban habitats; these were excluded due to low sample sizes. Even though urban habitats probably contribute to the national nectar provision, we were unable to include this habitat in this study because the Countryside Survey was not designed to survey urban areas. In 1.14% of Countryside Survey plots, two or more habitats were attributed to the same plot; these were excluded for this study. Additional plots were used to sample linear features in each 1 km square, covering hedgerows, streamsides and road verges (1 × 10 m and oriented along the linear feature). Each linear plot was also attributed to its nearest adjacent habitat.

To investigate the most recent nectar patterns, we used the most comprehensive vegetation data set from the Countryside Survey 2007 that encompasses all nonlinear plots (2,576 plots in 2007). To focus on linear features, we included vegetation data from linear features plots (1,951 plots in 2007). To test for historical changes from 1978 to 2007, we used vegetation data from nonlinear plots shared between the 1978, 1990, 1998 and 2007 Countryside Surveys (529 shared plots in England and Wales and 768 in Great Britain; Supplementary Table 9). We focused on the shared plots across years because the Countryside Survey sampling design was modified over time (for example, from fixed to proportional plot number per land class from 1978 to 1990).

The annual nectar productivity within each plot (kg per ha per year) is the sum of the nectar productivity of each species (kg per ha cover per year) weighted by their vegetative cover in the plot (%), assuming that the vegetative cover is representative of floral abundance (see Extended Data Fig. 7 and Supplementary Information for details). Nectar productivity values of plots were used to statistically estimate the annual nectar productivity for each habitat (kg per ha per year). The annual nectar provision of each habitat (kg per year) was computed from their annual habitat nectar productivity (kg per ha per year) multiplied by their respective national land covers for each survey (areas of habitats in ha from Countryside Surveys[19,34,35]; Supplementary Table 5). These were summed to estimate the annual national nectar provision in 1978, 1990, 1998 and 2007. For the 1930s period, areas of habitats (only available for England and Wales) were derived from the digitalized Dudley Stamp land utilization survey maps[20]; see Supplementary Information and Supplementary Table 5). Because nectar productivity can’t be

assessed for this period, we quantified nectar provision in 1930, 1978, 1990, 1998 and 2007 assuming unchanged nectar productivity within habitats but using observed shifts in land cover among habitats across time. The national nectar provision of hedgerows was calculated from their mean nectar productivity (kg per ha per year) multiplied by their estimated area in England (length of hedgerows from Countryside Survey 2007 for England[35], assuming a 1 m width).

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

Nectar diversity was estimated through two Shannon indexes (using 'vegan' package in R[36]) that encompass both the richness and the evenness of nectar producing sources (see Supplementary Information). The species nectar diversity index, based on the proportion of nectar produced by each species, was calculated as follows:

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

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

The functional nectar diversity index, based on the proportion of nectar produced by each floral morphology group, reflects the diversity of nectar sources in terms of resource accessibility for flower-visiting insects. Flower types were derived from Müller flower classification system recorded from the BiolFlor database[33], which was condensed into five classes: pollen rewarding flowers, open, partly hidden, hidden, and bee flowers (see Supplementary Information). The functional nectar diversity index was computed as follows:

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

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

The annual nectar productivity (kg of sugars per ha per year), species nectar diversity (Shannon index of nectar contribution of plant species) and functional nectar diversity (Shannon index of nectar contribution of floral morphology groups) in 2007 were mapped at the British national scale using the Great Britain Land Cover Maps of 2007[37].

Using Agri-environment scheme flower abundance data to estimate nectar provision within agri-environment scheme options at the national scale

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

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

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

Statistical analyses

Statistical analyses were carried out with Linear Mixed-Effect Models (lme function from 'nlme' package) in R 3.0.1 (ref. 36). To investigate the most recent nectar variations (2007), we analysed the $\log_{10}(x + 1)$ annual nectar productivity, species nectar diversity and functional nectar diversity according to the type of habitat ("HABITAT"; 11 habitats) of the nonlinear plots. The differences in $\log_{10}(x + 1)$ nectar productivity, species nectar diversity and functional nectar diversity between nonlinear and linear features were analysed according to the type of habitat ("HABITAT"; 11 habitats), the type of vegetation surveyed ("TYPE"; nonlinear vs linear features) and the interaction between these two terms. Countryside Survey square ("SQUARE") was included as a random term in these models in order to account for the spatial auto-correlation of plots nested into 1 km squares. In order to investigate historical changes over recent decades (1978–2007), we analysed the $\log_{10}(x + 1)$ annual nectar productivity, species nectar diversity and functional nectar diversity computed from the shared nonlinear plots in 1978, 1990, 1998 and 2007 according to the type of habitat ("HABITAT"), the year ("YEAR") considered as a categorical factor, and the interaction between these two terms. We included plots nested within square ("SQUARE/PLOTS") as random terms to account for the spatial and temporal auto-correlation of the data in this latter model. This latter statistical test was repeated considering all shared plots in Great Britain or only those in England and Wales to provide estimates of habitat nectar productivity across time for distinct areas, allowing comparisons with earlier (1930s) habitat information only available for that latter area. Significant differences among modalities were analysed with multiple comparisons (single-step method adjusted *P*-values from glht function in 'multcomp' package in R[36]). Letter based representation of all multiple comparisons was achieved from multcompLetters function in 'multcompView' package in R[36]. Model

residuals were plotted to visually check that normality and homoscedasticity assumptions were satisfied. We re-ran the same analyses with the Countryside Survey vegetation data combined with (1) the alternative nectar rectangular phenology productivity database (created by keeping constant nectar productivity of each species during the flowering season); and (2) using only the empirical nectar productivity database, as sensitivity tests (Extended Data Fig. 4 and Supplementary Information). Plots were performed with ggplot2 package in R[36]. All box plots show the median, 25th and 75th percentiles (lower and upper hinges), trimmed ranges that extend from the hinges to the lowest and highest values within 1.5× inter-quartile range of the hinge (lower and upper whiskers) plus outliers (filled circles). Notches that extend 1.58× inter-quartile range/square root of the number of observations were represented to give a roughly 95 interval for comparing medians.

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Extended Data Figure 1 Annual nectar productivity and diversity in linear features in 2007. **a**, Box plots of $\log_{10}(x + 1)$ nectar productivity according to the location of the vegetation surveyed (area versus linear features) in each habitat. **b**, Box plots of species nectar diversity according to the location of the vegetation surveyed (area versus linear features) in each habitat. **c**, Box plots of functional nectar diversity according to the location of the vegetation surveyed (area versus linear features) in each habitat. Significant differences of locations (area versus linear features) in habitats are indicated by asterisks as follows: $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$. Statistical models were re-run without calcareous grassland habitat (to meet residuals homoscedasticity constraint) in order to check that significant effects remained. See Extended Data Table 1 for ANOVA results. See ‘Statistical analyses’ section of the Methods for

detailed statistical methods and definition of box plot elements. **[Author: Inserted sentence ok?]**

Extended Data Figure 2 Historical changes in nectar productivity and diversity per habitat over recent decades (1978 to 2007). a, Box plots of $\log_{10}(x + 1)$ nectar productivity per habitat, based on vegetation data for 1978, 1990, 1998 and 2007. **b**, Box plots of species nectar diversity per habitat, based on vegetation data for 1978, 1990, 1998 and 2007. **c**, Box plots of functional nectar diversity per habitat, based on vegetation data for 1978, 1990, 1998 and 2007. Significant differences of time periods per habitats are indicated by asterisks ($*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$). See Extended Data Table 1 for ANOVA results and Supplementary Table 3 for sample sizes. See 'Statistical analyses' section of the Methods for detailed statistical methods and definition of box plot elements. **[Author: Inserted sentence ok?]**

Extended Data Figure 3 Habitat contributions to the national nectar provision shifts and species contributions to habitats over recent decades (1978 to 2007). **a**–**c**, Habitat contributions to the national nectar provision changes from **a**, 1978 to 1990, **b**, 1990 to 1998, and **c**, 1998 to 2007. All bar plots represent the absolute changes (in 1 X 10^6 kg of sugars) **[Author: would 'in 1 X 10^5 kg of sugars' also be correct?]** for each habitat during the time period considered. Numbers in brackets indicate the relative changes (in %). **d**–**n**, Species contributions to nectar provision in 1978, 1990, 1998 and 2007 per habitat type. Only species that contribute to the first 90% are shown. See Supplementary Table 10 for main contributing species to the national changes from 1978 to 2007.

Extended Data Figure 4 Sensitivity analyses of historical trends from 1978 to 2007 in nectar productivity and species diversity with alternative data sets. a, **b**, Box plots of $\log_{10}(x + 1)$ nectar productivity (**a**) and box plots of species nectar diversity per habitat (**b**) based on vegetation data for 1978, 1990, 1998 and 2007 discounting the contribution of grazed white clover in improved grassland. **c**, **d**, Box plots of $\log_{10}(x + 1)$ nectar productivity (**c**) and box plots of species nectar diversity per habitat (**d**), based on vegetation data for 1978, 1990, 1998 and 2007 and computed with the alternative rectangular phenology function. **e**, **f**, Box plots of $\log_{10}(x + 1)$ nectar productivity (**e**) and box plots of species nectar diversity per habitat (**f**), based on vegetation data for 1978, 1990, 1998 and 2007 and computed considering only the species with empirical nectar values. Significant differences of time periods per habitats are indicated by

asterisks (*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$). See Supplementary Table 3 for sample sizes and Supplementary Information for details. See 'Statistical analyses' section of the Methods for detailed statistical methods and definition of box plot elements. **[Author: Inserted sentence ok?]**

Extended Data Figure 5 Historical timeline in changes in nectar resources and flower-visiting insects in Great Britain. Historical periods with the greatest negative changes in nectar resources and flower-visiting insects are indicated in red, those with intermediate changes are in orange, and those with the lowest (or even reversing) changes are in green. Main historical trends from this study (Baude *et al.*) are presented in regard to those described in Carvalheiro *et al.*[10] and Ollerton *et al.*[9] studies. The white chevron indicates a provisional extinction rate that needs to be confirmed on a 20 year period of time (see Supplementary Information from Ollerton *et al.*[9]).

Extended Data Figure 6 Validity of the data sets. a, Major axis linear regression of $\log_{10}(x + 1)$ nectar values per flower obtained in the second location against those obtained in the first one. **b**, Major axis linear regression of $\log_{10}(x + 1)$ flower density values obtained in the second location against those obtained in the first one. **c**, Major axis linear regression of $\log_{10}(x + 1)$ peak flower density values obtained in the second location against those obtained in the first one. **d**, Standardized major axis regression of the $\log_{10}(x + 1)$ length of the flowering period used for analyses with those derived from IPI AgriLand floral transects (unpublished data). **e**, Standardized major axis regression of peak date of flowering season used for analyses with those derived from IPI AgriLand floral transects (unpublished data). **f**, Major axis linear regression performed on the $\log_{10}(x + 1)$ empirical (empirical data set) and published nectar values (literature data set from Raine and Chittka[40]) at the flower scale. **g**, Standardized major axis linear regression performed on the $\log_{10}(x + 1)$ empirical (empirical data set) and published nectar values (literature data set, see Supplementary Table 13 for references) at the vegetative scale. **h**, Standardized major axis linear regression performed on the $\log_{10}(x + 1)$ empirical and modelled nectar values generated by a leave-one-out approach. Estimates of all equations are derived from (standardized) major axis regression (ma and sma function from 'smatr' package in R[36]; see Supplementary Information for details).

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Extended Data Figure 7 Flower number and vegetative cover relationships. Linear regressions between the number of open flowers counted in a quadrat of 0.5 m^2 according to the vegetative cover of the focus species in the quadrat (in %). Data are extracted from IPI AgriLand floral transects survey in 2012 (unpublished data) for 23 out of the 35 main nectar contributing species (panels **a**–**w**). The number of flowers was analysed according to the vegetative cover ('Cover'), the month of the survey ('Month') and the interaction between these two terms ('Cover:Month') using negative binomial generalized linear models (see Supplementary Information for details). Coloured lines represent the linear regression between flower abundance and vegetative cover for each month of the survey. Black lines represent the overall linear regression between flower abundance and vegetative cover when the 'Month' covariate cannot be included in the model. Line equations were derived from statistical intercept and slope estimates.

Extended Data Table 1 Type III ANOVA (F-tests) results for annual nectar productivity, species nectar diversity and functional nectar diversity
a, 2007 values according to habitat. The linear mixed effect models were performed on data from 2,576 nonlinear plots surveyed in 2007. **b**, 2007 values according to habitat and location. The linear mixed effect models were performed on data from 4,527 plots (2,576 nonlinear plots and 1,951 linear plots) surveyed in 2007. **c**, 1978–2007 values according to habitat and year. The linear mixed effect models were performed on data from 768 shared plots surveyed in 1978, 1990, 1998 and 2007. The annual nectar productivity was systematically $\log_{10}(x + 1)$ transformed. See Supplementary Table 1 and Supplementary Table 3 for sample sizes.

Extended Data Table 2 Flower morphology and flower-visiting insects of the four main nectar-providing species
Flower morphology parameters (mean and standard error for depth and width of flower tubes) were measured on 20–40 flowers per species in the field. Flower-visiting insects were listed from plant–insect visiting networks from Jane Memmott (published and unpublished data)**[Author: Please clarify 'Memmott's group'. Do you mean unpublished data from Jane Memmott?]** to which recorded interactions from a review of literature have been added (see Supplementary Table 12 for reference list).

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