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1 **Phenology of farmland floral resources reveals**
2 **seasonal gaps in nectar availability for bumblebees**

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16

17 **Abstract**

- 18 1. Floral resources are known to be important in regulating wild pollinator populations and are
19 therefore an important component of agri-environment and restoration schemes which aim to
20 support pollinators and their associated services. However, the phenology of floral resources is
21 often overlooked in these schemes – a factor which may be limiting their success.
- 22 2. Our study characterises and quantifies the phenology of nectar resources at the whole-farm
23 scale on replicate farms in Southwestern UK throughout the flowering season. We quantify the
24 corresponding nectar demands of a subset of common wild pollinators (bumblebees) to
25 compare nectar supply and pollinator demand throughout the year, thereby identifying periods
26 of supply-demand deficit.
- 27 3. We record strong seasonal fluctuations in farmland nectar supplies, with two main peaks of
28 nectar production (May and July) and a considerable ‘June Gap’ in-between. March and
29 August/September are also periods of low nectar availability.
- 30 4. Comparing the phenology of nectar supply with the phenology of bumblebee nectar demand
31 reveals ‘hunger gaps’ during March and much of August/September when supply is unlikely to
32 meet demand.
- 33 5. Permanent pasture and woodland produced the greatest share of farmland nectar because of
34 their large area, however linear features such as hedgerows and field margins provided the
35 greatest nectar per unit area. 50% of total nectar was supplied by just three species (*Allium*
36 *ursinum*, *Cirsium arvense* and *Trifolium repens*), but some less productive species (e.g. *Hedera*
37 *helix* and *Taraxacum* agg.) were important in ensuring phenological continuity of nectar supply.
- 38 6. *Synthesis and applications.* Our results suggest the phenology of nectar supply may be as
39 important as total nectar production in limiting farmland pollinator populations. Considering
40 phenology in the design of agri-environment or restoration schemes is therefore likely to
41 improve their suitability for pollinators. Plant species which flower during periods of resource

42 deficit (early spring and late summer) should be prioritised in schemes which aim to conserve or
43 restore pollinator populations. Maintaining a range of semi-natural habitats with
44 complementary flowering phenologies (e.g. woodland, hedgerows and field-margins) will ensure
45 a more continuous supply of nectar on farmland, thereby supporting pollinators for their entire
46 flight season.

47 **Keywords:** agri-environment, bumblebees, floral resources, flowering phenology, nectar,
48 pollination, pollinator conservation, restoration

49

50 **Introduction**

51 The service that pollinators provide to a majority of the world's wild flowering plants (Ollerton *et al.*
52 2011) and 75% of world crop species (Klein *et al.* 2007) makes their conservation a high priority.
53 Understanding the factors that limit pollinator populations on farmland is critical in designing
54 conservation schemes that ensure their long-term survival. Wild pollinator populations are limited
55 by several factors including floral nectar and pollen resources (Potts *et al.* 2003; Goulson *et al.* 2015),
56 nesting sites (Steffan-Dewenter & Schiele 2008) and various other factors such as disease, pesticides
57 and predators (Roulston & Goodell 2011; Goulson *et al.* 2015). In the UK, nectar levels fell by 32%
58 between 1930 and 1978, in line with trends in pollinator diversity and agricultural intensification
59 since the Second World War (Baude *et al.* 2016). Changes in the last 30 years, likely due to
60 decreased acidification, decreased nitrogen deposition and the uptake of Environmental
61 Stewardship Schemes, have led to modest increases in nectar production. However, nectar
62 production remains lower than pre-1930s levels and significant losses in nectar diversity remain
63 (Baude *et al.* 2016).

64 The large-scale coverage of agricultural land in the UK (70.8%) (WorldBank 2015), makes it
65 an important consideration for any programme aiming to conserve biodiversity at a national level. In

66 the UK, Environmental Stewardship Schemes provide annual payments to farmers and land
67 managers for managing their land in an environmentally-friendly way, including for the benefit of
68 pollinators (Natural England 2009). Nectar rich field margins are an important component of these
69 schemes and there are data on the best floral mixtures for supporting farmland bumblebees e.g.
70 (Carvell *et al.* 2004; Pywell *et al.* 2005). It is known that the addition of floral resources can increase
71 bumblebee colony growth and nest density (Wood *et al.* 2015; Crone & Williams 2016; Carvell *et al.*
72 2017), and increase species diversity and abundance of trap nesting bees (Dainese *et al.* 2018).
73 However, the timing of resource availability (i.e. the phenology) is also important (Williams *et al.*
74 2012; Carvell *et al.* 2017), but this aspect is much less understood.

75 For pollinators to persist and thrive at the landscape level, they must have sufficient floral
76 resources for the entire duration of their flight season (Menz *et al.* 2011; Russo *et al.* 2013; Scheper
77 *et al.* 2015). ‘Phenological gaps’ of just 15 days severely affect modelled honeybee colony
78 development (Horn *et al.* 2016), a finding empirically supported by Requier *et al.* (2017). Such gaps
79 are likely to be even more detrimental to bee species which do not have honey reserves. The
80 importance of a season-long supply of floral resources has so far not been given sufficient
81 consideration in the design of Environmental Stewardship schemes (Carvell *et al.* 2007). It is similarly
82 overlooked in the restoration of natural habitats which rely on pollinators to ensure the
83 reproductive continuity of the restored plant community (Dixon 2009). These oversights could
84 ultimately be limiting the success of both types of scheme.

85 Identifying periods of the year in which floral resources most strongly limit pollinator
86 populations will be key to addressing this issue in a targeted and cost-effective way. This requires an
87 understanding of both flowering phenology and pollinator floral needs at a landscape-scale over
88 their entire flight season. Our study addresses these knowledge needs via the following three
89 objectives: (i) characterising and quantifying the phenology of nectar resources at the whole-farm
90 scale on replicate farms throughout the flowering season (late February – early November); (ii)
91 quantifying the corresponding nectar demands of common farmland bumblebees to compare nectar

92 supply and pollinator demand throughout the year, thereby identifying periods when there is a
93 supply-demand deficit; (iii) identifying habitats and plant species which may fill these gaps and
94 thereby provide sufficient resources for the entire pollinator flight season on farmland. Our methods
95 provide a novel approach to plant-pollinator phenological matching (Russo *et al.* 2013) and enable
96 targeted planting strategies for the restoration of nectar supplies on farmland, an approach that
97 could be applied to other anthropogenic habitats.

98

99 **Materials and Methods**

100 **Study sites**

101 The study was conducted in 2016 and 2017 on four medium-sized (140-280 hectare) mixed
102 (dairy, sheep and arable) farms in North Somerset, none of which were in Environmental
103 Stewardship. Sites were surrounded by mixed farmland and rural villages, typical of Southwest UK.
104 The substantial time demands of recording floral abundance at a farm scale regularly from late
105 February to early November restricted further replication. There is a trade-off in phenology studies
106 between the amount and resolution of data that can be gathered at a site and the number of sites
107 that can be sampled. Here we adopted a dual approach whereby one site was sampled intensively to
108 capture the fine-scale temporal variation in flowering phenology and three other sites were sampled
109 less intensively to capture the spatial variation.

110 The intensive study site, Birches Farm in Somerset, England (51°25'19.04"N, 2°40'49.93"W)
111 was sampled twice per week in 2016 from late February until early November, providing the
112 intensive component of the study. There were two components to the extensive part of our study.
113 First, in 2016, three further farms in Somerset - Eastwood Farm (51°29'41.71"N, 2°60'56.74"W),
114 Chestnut Farm (51°24'22.94"N, 2°91'08.96"W) and Elmtree Farm (51°21'58.04"N, 2°85'44.36"W) -
115 were sampled each fortnight from March until November in 2016. The four farms were 6-20 km
116 from each other and differed slightly in their habitat composition, with varying proportions of

117 pasture and arable fields, hedgerows, margins and woodland (Supporting Table A1 and Fig. A1). The
118 nectar production and habitat composition of all four farms were broadly representative of the
119 wider landscape, based upon unpublished data from 11 farms in Southwest UK (Supporting Methods
120 A1 and Fig. A2). These four farms were used to compare the plant species and habitat contributions
121 to farmland nectar supply. Second, in 2017, three of the four farms (Birches, Eastwood and Elmtree
122 farms, referred to hereafter as the phenology farms) were sampled every week throughout the
123 flowering season; this providing both phenologically informative data and temporal replication for
124 Birches farm.

125

126 **Objective 1: Characterising and quantifying the phenology of nectar resources at the whole-farm**
127 **scale.**

128 *Nectar measurements:*

129 On each sampling occasion, six randomly located 50 m transects were conducted within
130 each habitat type (e.g. 24 transects in total, for a farm with four habitat types). On each transect, the
131 number of open floral units of each flowering plant species was recorded in a 1 m² quadrat at 5
132 metre intervals along its entire length (i.e. 10 quadrats per transect). For trees and shrubs, all
133 flowers in a 5 m vertical column above the quadrat were counted. Above this, the tree's height
134 within the vertical column was estimated with a clinometer and the floral abundance values were
135 multiplied up accordingly, as in Baude *et al.* (2016). Values for the nectar sugar production of each
136 species were from Baude *et al.* (2016) who measured or modelled the sugar (sucrose) production of
137 305 plant species in the UK, including the 175 most common species. The sugar production of eight
138 species encountered in the study but not covered by Baude *et al.* (2016) were measured according
139 to their methods (Supporting Method A2).

140

141 *Quantifying flowering phenology*

142 Each visit to a farm generated an estimate of the number of open flowers per square metre
143 in each habitat for that point in time. When multiplied by the mean floral sugar production of each
144 species, an estimate of the grams of sugar per unit area per 24-hour period was obtained for each
145 habitat. This was multiplied by the area of that habitat on the farm (calculated using QGIS v.2.12.3)
146 to give an estimate of sugar availability on the whole farm. A generalised additive model (GAM), was
147 used to model a smooth, non-linear trend in sugar availability by time, with separate analyses
148 performed at a farm and habitat level. GAMs provide a useful way of fitting a smooth curve to data
149 with non-linear patterns, thus allowing interpolation between data points. To incorporate
150 uncertainty associated with estimates of individual species' nectar production, high and low
151 estimates of farmland nectar provisioning were calculated using upper (mean+SE) and lower (mean-
152 SE) estimates of each species' sugar production. These three estimates (upper, lower and mean)
153 were modelled separately. A Gamma error family with log link function gave the best fit for the zero-
154 inflated count data. The extent of smoothing was varied between candidate models and guided by
155 Vaughan and Ormerod (2012) who advise values around 0.3 of the number of time points, as a
156 compromise to capture both season-long trends and shorter term variation. Akaike's Information
157 Criterion (AIC) was used to compare candidate models and select the top-ranking one (with lowest
158 AIC value). In addition to modelling sugar production at the whole farm scale and the habitat level,
159 the 20 most common plant species in each habitat were modelled separately using the approach
160 outlined above. This allowed us to compare the sequence of species flowering between farms and
161 between years and identify particularly important species – both in terms of total sugar production
162 and phenological importance. All statistical analyses, figure plotting, and models were performed
163 with R version 3.2.2 (R Core Team), using the *mgcv* package (Wood 2011).

164

165

166 **Objective 2: Quantifying the nectar demands of three common bumblebee species to compare**
167 **nectar supply and pollinator demand throughout the year.**

168 To identify periods in which farmland nectar supplies are likely to be limiting pollinator
169 populations, we compared the total sugar availability of Birches, Eastwood and Elmtree farms (using
170 the GAM predictions) with the estimated population-level, farm-scale sugar demands of the three
171 most common bumblebees on UK farmland (*Bombus terrestris*, *B. pascuorum* and *B. lapidarius*).
172 Bumblebees were chosen as a focal group as they were the only taxon with sufficient data on energy
173 consumption, colony density and phenology to make the necessary calculations. They are also
174 known to be important pollinators of wild plants (Kovacs-Hostyanszki *et al.* 2013) and a range of
175 crops (Garratt *et al.* 2014) and yet are in decline across various parts of the world (Goulson *et al.*
176 2008).

177 Energy demand data came from Rotheray *et al.* (2017) who recorded the grams of sugar
178 consumed each week by captive *Bombus terrestris audax* colonies as they grew from single wild-
179 collected queens to full colonies. To account for the extra energy expended during foraging flight,
180 0.312 grams of sugar were added per individual foraging bee per day (Rotheray *et al.* 2017), based
181 on calorific calculations from Heinrich (1979). We followed the assumptions of Rotheray *et al.*
182 (2017), that half of the workers forage four days a week, the others remaining in the nest as house
183 bees, and that the queen forages up to the point at which five workers are produced. Sugar
184 consumption data was only available for *B. terrestris*, but *B. pascuorum* and *B. lapidarius* were
185 assumed to have similar consumption rates because their body sizes (Intertegular span (mm) for: *B.*
186 *terrestris* (3.5); *B. lapidarius* and *B. pascuorum* (5.2)) (Greenleaf *et al.* 2007), and total colony sizes
187 (400 individuals for *B. terrestris* and *B. lapidarius* and 300 for *B. pascuorum*) (Dicks *et al.* 2015) are
188 broadly similar.

189 Colony densities were taken from Dicks *et al.* (2015) who summarise (from a range of
190 studies) the nest density estimates of the three most common *Bombus* species on agricultural land:

191 *B. terrestris* (mean nest density: 32/km²), *B. pascuorum* (83/km²) and *B. lapidarius* (78/km²). Worker
192 numbers per colony and their changes through the year were taken from Rotheray *et al.* (2017).

193 To estimate the timing of colony foundation in our study area, we used BeeWalk transect
194 data (Bumblebee Conservation Trust 2016 & 2017) from 31 recording sites in North Somerset. The
195 proportions of *B. terrestris*, *B. pascuorum* and *B. lapidarius* queens emerging in different months of
196 the year were calculated, allowing us to match the timing of colony development and nectar
197 demand with the timings of farmland nectar availability.

198

199 **Objective 3: Identifying habitats and plant species which fill the gaps in nectar production.**

200 The relative importance of different farmland habitats was assessed by comparing the GAM
201 predictions for each habitat on the four farms recorded in 2016. The phenological importance of
202 each plant species in each habitat was calculated by summing the proportional contribution to total
203 weekly sugar supply made by the species, for each week of the year. The metric captures both the
204 temporal uniqueness of a species' nectar supply and its length of flowering time.

205

206 **Results**

207 **Objective 1: Characterising and quantifying the phenology of nectar resources at the whole-farm** 208 **scale.**

209 During 137 visits to the four farms over two years, nearly half a million (494291) individual
210 floral units from 176 flowering plant species were counted in 2664 transects (761 hedgerow
211 transects, 759 pasture, 576 woodland and 568 margins). The daily sugar production of eight new
212 species were recorded and added to the nectar database of Baude *et al.* (2016) (Supporting Table
213 A2). The top-ranking generalised additive model (Supporting Table A3) described a non-linear trend
214 in sugar availability which fluctuated greatly through the year, creating the six flowering periods

215 highlighted in Fig. 1. Although total yearly sugar production per kilometre squared varied up to
216 threefold between farms in 2017 (342 kg of sugar/km²/year on Birches Farm, 461 on Eastwood Farm
217 and 131 on Elmtree Farm), the phenological pattern of sugar production was relatively consistent
218 among the farms (Fig. 2).

219

220 **Objective 2: Quantifying the nectar demands of a subset of common wild pollinators to compare**
221 **nectar supply and pollinator demand throughout the year.**

222 The strong seasonality of nectar supply did not synchronise well with the sugar demand of
223 common bumblebee species (Fig. 3). On each of the three phenology farms, the pollinator flight
224 season was characterised by alternating periods of nectar deficit and surplus which were relatively
225 consistent in their timings, though differed somewhat in the magnitude of their peaks and troughs.
226 In early March when queens emerge, sugar demand per individual bee was high while farmland
227 nectar production was at its lowest for the flowering season. This left a mean deficit of 12.3 grams of
228 sugar/km²/day (± 1.7 SE) between what was available and our estimates of bumblebee needs. This
229 'hunger gap' lasted from the start of the pollinator flight season until late March. During this time,
230 the only species producing ecologically meaningful quantities of sugar on the farms were *Taraxacum*
231 *agg.*, *Prunus spinosa*, *Glechoma hederacea*, *Ranunculus ficaria*, and *Bellis perennis*. Together, these
232 species contributed a mean of 13.1 grams of sugar/km²/day (± 6.8 SE) during the hunger gap. Just
233 one foraging queen requires an estimated 0.7 grams of sugar per day, meaning that for most of
234 March, a maximum of 19 queen bumblebees could be supported on 1 km² of farmland. This does not
235 account for any young workers that have been produced, or other pollinator species competing for
236 nectar such as early species of solitary bees or hoverflies.

237 In late summer (August-October), the three study farms had a mean deficit of 1053 grams of
238 sugar/km²/day (± 81.4 SE) lasting between one and three months (Fig. 3). Although sugar production
239 was relatively high at this time, *Bombus* colonies were reaching their maximum size, generating a

240 high demand for nectar which could not be met by the farmland landscape, resulting in a second
241 hunger gap. A very small proportion of the farmland sugar was produced by plants species unlikely
242 to be utilised by *Bombus*, (e.g. *Stellaria media*) implying nectar availability may be even lower than
243 predicted.

244 From late March until mid-late May, there was a mean surplus of 2196 grams of
245 sugar/km²/day (± 986 SE) on the three study farms. Mass flowering oil seed rape was not present on
246 any of the study farms but normally flowers during this period and would therefore be expected to
247 add to the nectar surplus recorded on our farms rather than fill a hunger gap.

248

249 **Objective 3: Identifying habitats and plant species which fill the gaps in nectar production.**

250 Habitats differed greatly in their sugar production value at a farm scale but their relative
251 values among farms were similar (Fig. 4). Hedges produced the greatest sugar per unit area (1.88
252 grams of sugar/m²/year ± 0.24 SE) and with a mean coverage of 1% of farm area, they made up 9.4%
253 (± 3 SE) of total sugar. Their phenological continuity was also highest, being the most nectar-rich
254 habitat per unit area 62% (± 3 SE) of the year. Field margins were also a rich habitat for nectar, with a
255 mean of 1.68 grams of sugar/m²/year (± 0.09 SE). However, their period of nectar production was
256 relatively short-lived (Supporting Information Fig. A3). With a coverage of 1% of farm area, they
257 made up 3.1% (± 4 SE) of total sugar production. The nectar production of pasture was substantial
258 (54% of total sugar production, ± 12 SE) because of its large area on the farm (mean 64% coverage),
259 but per unit area it produced only 0.27 grams of sugar/m²/year (± 0.12 SE). Where woodland was
260 present it covered an average of 8% of the farm, producing 1.08 grams of sugar/m²/year (± 0.06 SE)
261 and making up 33.1% (± 12 SE) of total farm nectar supply. However, approximately 90% of this
262 supply was produced in just one month (May) and it was almost exclusively provided by *Allium*
263 *ursinum* (89%). Figure 5 shows the sugar contributions of the most productive plant species in each
264 of the four habitats.

265 Although up to 59 plant species produced ecologically meaningful quantities of sugar at
266 some point in the year (> 0.3 grams of sugar/km²/day), 50% of total sugar was supplied by just three
267 species and 80% of the sugar was supplied by eight species (Fig. 6). These were: *Allium ursinum*
268 (18%), *Cirsium arvense* (16%), *Trifolium repens* (14%), *Trifolium pratense* (12%), *Heracleum*
269 *sphondylium* (6%), *Ranunculus acris* (5%), *Rubus fruticosus* agg. (5%) and *Taraxacum* agg. (4%).
270 Several less productive species made important contributions to the phenological continuity of
271 nectar supply, due to their unusual flowering times (Table 1). *Hedera helix* provided over half of all
272 sugar from mid-September until the end of the flowering season, while *Taraxacum* agg. provided the
273 majority of sugar from mid-March until the end of April.

274

275 **Discussion**

276 Our study quantifies the flowering phenology of four UK farms at a high temporal resolution
277 throughout the flowering season. The results show strong seasonal fluctuations in farmland nectar
278 supplies and suggest the phenology of nectar supply could be as important as total nectar
279 production in limiting farmland pollinator populations, though this remains to be tested. Comparing
280 nectar supply with the energy demands of a subset of common *Bombus* species reveals gaps
281 between nectar supply and demand during March and much of August and September. Habitats on
282 the farms differed greatly in their pattern of nectar production but tended to complement each
283 other's nectar supply. Permanent pasture and woodland produced the greatest share of farmland
284 nectar because of their large area, however linear features such as hedgerows and field margins
285 provided the greatest nectar per unit area, reflecting findings by Baude *et al.* (2016) in their UK-wide
286 analysis. Most of the farmland nectar was supplied by a small number of plant species, but some less
287 productive species were important in ensuring phenological continuity of nectar supply.

288

289 **Limitations**

290 There were three main limitations to our work. First, the practical and time constraints of
291 recording flowering phenology at a high resolution in multiple locations meant that our study was
292 limited to four farms across one region of the UK. While the pattern of nectar supply was relatively
293 consistent across these four farms, this pattern will differ according to geography, inter-annual
294 variation and agricultural practices. For example, farms with many earlier-flowering tree species or
295 late-flowering hay meadows, are likely to have a different phenological pattern of nectar production.
296 The phenomenon of nectar gaps however, is likely to be a feature of many human-altered
297 landscapes, particularly those that have been heavily simplified. Second, while we model *Bombus*
298 nectar demands on each farm, a lack of data means that we cannot include the demands of the
299 many solitary bees, honey bees, hoverflies etc. It is therefore a conservative estimate of demand and
300 should be viewed as a minimum baseline requirement for bumblebees alone, rather than an ideal
301 level. However, this approach still allows us to identify the most severe nectar gaps which are likely
302 to affect all pollinator groups. And finally, while we have detailed data on nectar, we did not quantify
303 pollen. Although both are important resources, we focus on nectar because of its importance as an
304 energy source in the diets of adult bees and other pollinator groups. It also allows us to directly
305 compare the nutritional contribution of all plant species and habitats through the common currency
306 of total sugars (Willmer 2011). It is possible however that pollen resources (which are known to limit
307 brood production and colony size of honeybees (Requier *et al.* 2017) and bumblebees (Rotheray *et*
308 *al.* 2017)), may differ from nectar resources in their phenology, resulting in a different timing of
309 resource gaps. This is an important topic for future research.

310

311 **Flowering and pollinator phenology**

312 The highly seasonal nectar supply detected in our study on farmland in South West UK is
313 likely to have important implications for wild and managed pollinators. The large differences
314 between the flowering phenology of different habitats (Supporting Information Fig. A1), suggests

315 that pollinators need to move between habitats, tracking the changing resource supplies, to ensure
316 a continuous supply of nectar. This effect has been demonstrated in agricultural areas of the U.S.
317 where complementary habitats provide resources at different times of the year and the pollinator
318 community tracks these resources (Mandelik *et al.* 2012). This highlights the importance of having a
319 range of distinct habitat types present on farmland.

320 Various studies have identified a food deficit for honeybees in June/July (Couvillon *et al.*
321 2014; Requier *et al.* 2015) which coincides with the period between the spring floral resources
322 (including mass-flowering oil seed rape which is known to be important for wild pollinators
323 (Westphal *et al.* 2003)) and summer floral resources. This period of the year has been anecdotally
324 named the 'June Gap' by beekeepers. With the large dip in nectar resources recorded between the
325 spring (May) and summer (July) wildflower blooms and the modest gap between nectar supply and
326 bumblebee demand recorded in June, our study provides strong empirical evidence for the existence
327 of the 'June Gap' on farmland in this region.

328 The early spring season (late February to late March) is a period of very low nectar
329 availability. This coincides with a period of high energy demand by queen bumblebees which are
330 foraging, establishing nests and heating their brood (Heinrich 1972), resulting in a nectar deficit for
331 most of March. This modest gap could be having a marked effect on the survival of queens – an
332 effect which is likely to cascade through the year by limiting the number of colonies established.
333 Indeed, our data help explain the finding by Carvell *et al.* (2017) that availability of early spring
334 resources on farmland strongly influences bumblebee colony densities. Early *Bombus* colonies grow
335 very little under food limitation (Rotheray *et al.* 2017), suggesting the effects of this gap may extend
336 beyond colony establishment, affecting colony size too.

337 Compared with the early spring gap, the late-season gap is greater in magnitude and lasts
338 longer (one-three months), which is likely to threaten the survival of late-emerging bumblebee
339 species on farmland. This is consistent with Balfour *et al.* (2018) who found significantly greater

340 numbers of extinctions in late-summer flying British pollinator species, and Fitzpatrick *et al.* (2007),
341 who found a disproportionate decline in late-emerging bumblebee species in Ireland and Britain.
342 They attribute these declines to a reduction in late-summer floral resources, partially driven by the
343 shift in agricultural practices from hay to silage production. Other wild pollinators such as solitary
344 bees and hoverflies have shorter flight seasons, so may not be affected by all the same resource
345 gaps. However, the populations of most pollinator species peak in late summer (Balfour *et al.* 2018),
346 suggesting this may be a period of nectar deficit for many different pollinator taxa. Horn *et al.* (2016)
347 demonstrated that badly timed gaps in nectar supplies can greatly affect the resilience of modelled
348 honey bee colonies; bumblebees, which don't accumulate significant resource reserves, are likely to
349 be more strongly affected by such gaps. More vulnerable still will be species with short flight seasons
350 (e.g. many solitary bees) whose emergence times coincide with a nectar deficit. Resource gaps
351 differed slightly between sampling years, with an order of magnitude greater spring nectar deficit in
352 2017 than 2016 on Birches Farm (Fig. 3a-b), likely due to the warmer spring and earlier emergence
353 times of queen bumblebees in 2017 (Bumblebee Conservation Trust 2016 & 2017). Variation in
354 resource gaps between sites (Fig. 3b-d) was likely due to different habitat composition and
355 management of the farms, particularly pasture, the most variable habitat (Fig. 4a), which is likely to
356 offer the greatest potential for improvement. The effects of inter-annual variation and landscape
357 composition on nectar phenology are important topics for future study.

358 With climate change advancing the flowering phenology of many plant species (e.g. Fitter
359 and Fitter (2002)), and the potential for resulting phenological mismatches between plants and
360 pollinators (Hegland *et al.* 2009; Forrest 2015), it will become increasingly important to understand
361 how the timing of resource supplies affect pollinator populations. By quantifying the current
362 phenology of nectar resources, we can make more informed predictions about how this resource
363 supply might change and which species are most likely to be affected.

364

365 **Management implications**

366 We have demonstrated that it may not be just the availability of nectar resources limiting
367 *Bombus* populations, but also the timing of these resources, though this remains to be tested. March
368 and August/September are periods of greatest nectar deficit for *Bombus* populations and should
369 therefore be prioritised to ensure a sufficient annual nectar supply. Plant species which flower
370 during these periods of deficit – so-called ‘bridging species’ (Menz *et al.* 2011) - should be prioritised
371 in schemes which aim to conserve or restore pollinator populations on farmland. The early hunger
372 gap we observed on the four farms could theoretically be ‘plugged’ by adding just 12.3 extra grams
373 of sugar each day across 1 km² of farmland, the equivalent of c.1000 willow catkins for example
374 (data from Baude *et al.* 2016). Willows *Salix* spp. could be readily added to UK farming systems,
375 delivering pollen and nectar in the early spring when floral resources are particularly scarce (Moquet
376 *et al.* 2015). The late-season gap however would require between 500 and 2000 extra grams of sugar
377 per day, which equates to approximately one hectare of late-flowering red clover *Trifolium pratense*
378 (Rundlof *et al.* 2014), or an extra 40 bramble *Rubus fruticosus* agg. flowers per metre squared of
379 hedgerow (based on a mean farm coverage of 1% hedgerow area).

380 On all four study farms, half of the total nectar supply was provided by three species or
381 fewer, a finding in accord with Baude *et al.* (2016) in their UK wide analysis. With just a few plant
382 species dominating farmland nectar supply for most of the year, there is the potential for these
383 species to dominate the diets of pollinators, reducing their diet diversity. The immunocompetence of
384 honeybees has been shown to reduce with a less varied diet (Alaux *et al.* 2010; Di Pasquale *et al.*
385 2013) and it is likely that the same is true for bumblebees. Resource diversity should therefore be
386 considered alongside total resource availability in the design of any schemes aiming to restore or
387 conserve healthy pollinator communities.

388

389 **Conclusions**

390 Wild pollinator populations are known to be limited by floral resources and we have
391 demonstrated why the timing of these resources may be an important factor driving this limitation.
392 The temporal mismatch between pollinator resource demand and phenology of farmland resource
393 supply detected in this study, is likely to be a feature of many other human-altered landscapes;
394 though this remains to be tested. Our results suggest that in any agri-environment or restoration
395 scheme which aims to support pollinators and the provisioning of pollination services, considering
396 the phenology of both plants and pollinators will be critical.

397

398 **Authors' contributions**

399 JM and TT conceived the ideas and designed the methodology; TT collected the data; TT and IV
400 analysed the data; TT and JM led the writing of the manuscript. All authors contributed critically to
401 the drafts and gave final approval for publication.

402

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406 assistants: Emma Ball, Izzy Carpenter and Rowan Hookham, along with the four farmers who gave
407 permission to use their land.

408

409 **Data accessibility**

410 Data available via the Dryad Digital Repository

411

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577 **Figures & Tables**

578

579 **Table 1.** The ten most phenologically important species on Birches farm in 2016, ranked in order of
 580 decreasing score. The phenological importance metric gives the proportional contribution to total
 581 weekly nectar supply made by the species, summed across each week of the year. High scoring
 582 species are those which flower at times when little else is in bloom, contributing a very high
 583 proportion of total nectar. Their date of peak flowering is shown, alongside the date at which they
 584 are making the greatest proportional contribution to total nectar supply i.e. the point at which their
 585 provisioning is most important.

| Species | Phenological importance metric | Peak flowering date | Peak phenological importance |
|------------------------------|---------------------------------------|----------------------------|-------------------------------------|
| <i>Hedera helix</i> | 8.0 | 05 October | 02 November |
| <i>Taraxacum</i> agg. | 6.6 | 04 May | 06 April |
| <i>Cirsium arvense</i> | 3.6 | 13 July | 13 July |
| <i>Allium ursinum</i> | 3.3 | 11 May | 11 May |
| <i>Rubus fruticosus</i> agg. | 2.5 | 20 July | 17 August |
| <i>Heracleum sphondylium</i> | 2.5 | 15 June | 08 June |
| <i>Trifolium repens</i> | 2.5 | 13 July | 03 August |
| <i>Bellis perennis</i> | 1.1 | 11 May | 02 March |
| <i>Glechoma hederacea</i> | 1.1 | 18 May | 02 March |
| <i>Centaurea nigra</i> | 1.0 | 29 June | 29 June |

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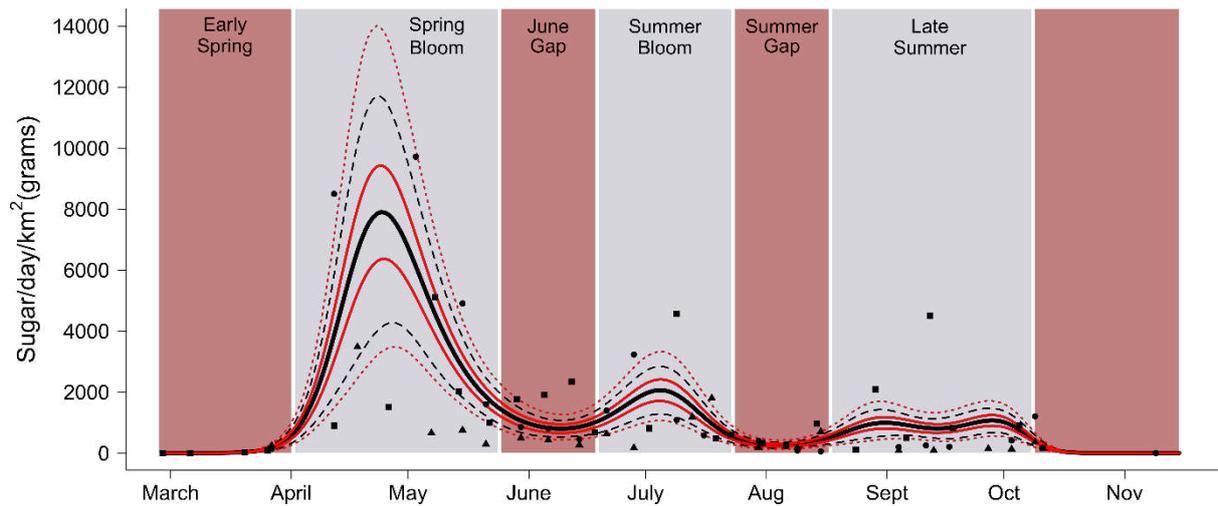
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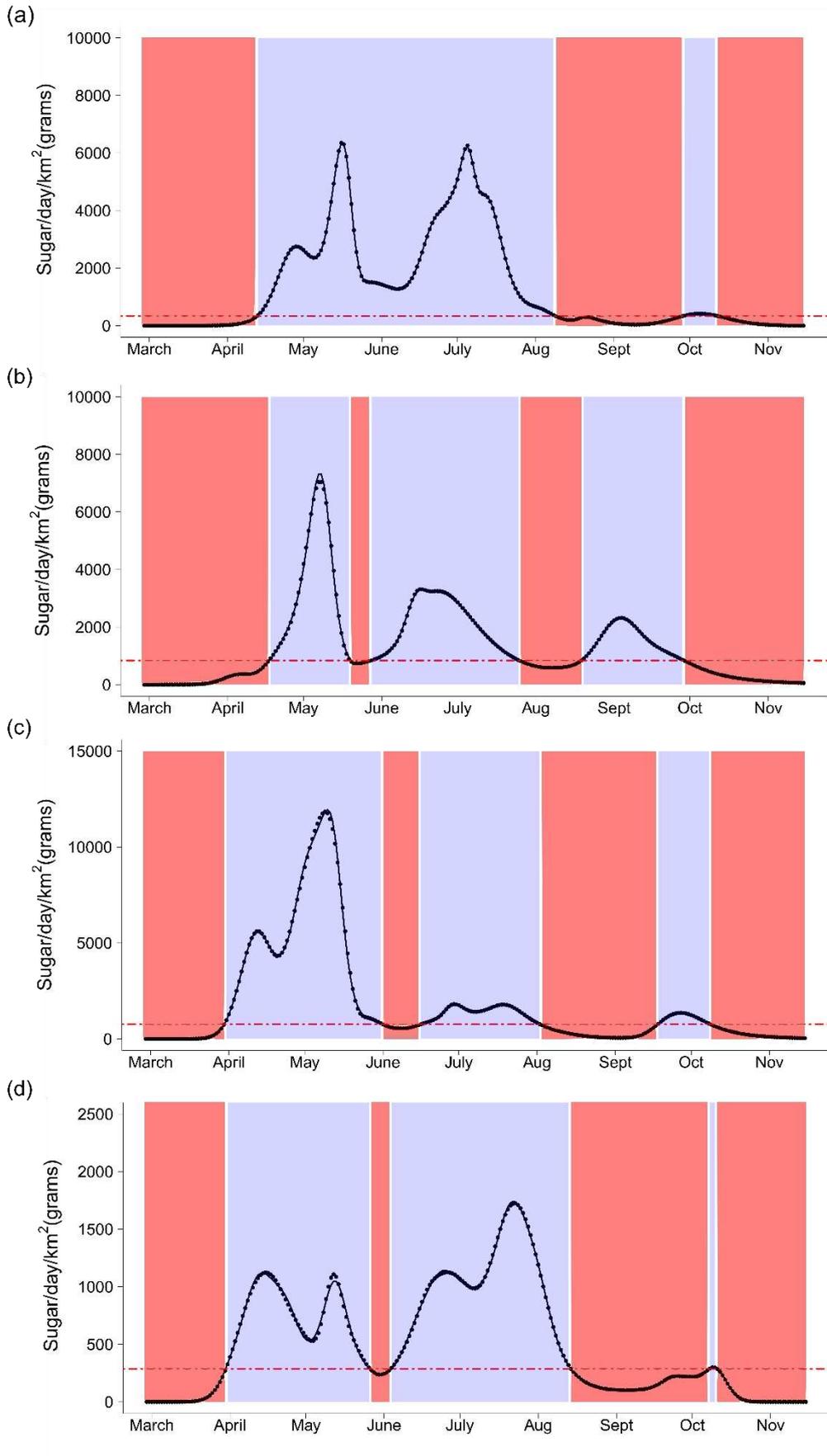
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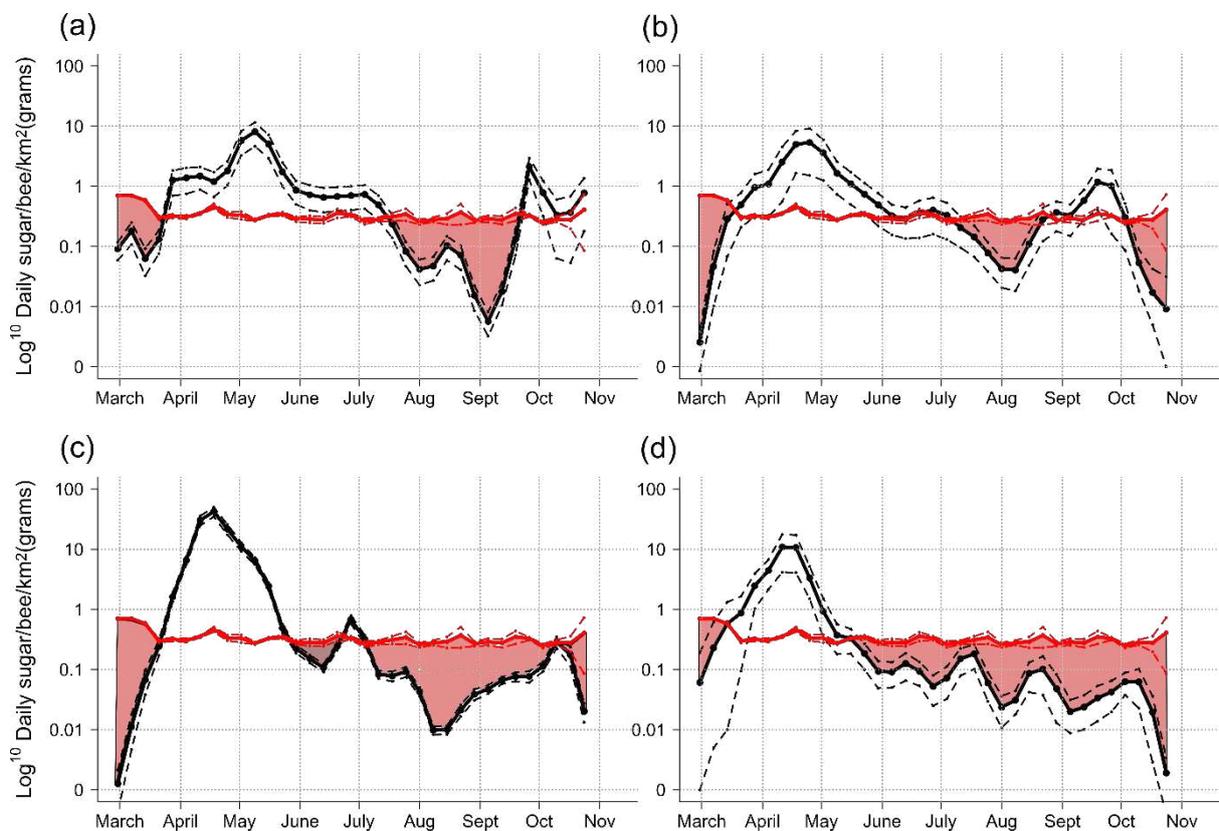
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594 **Figure 1.** Daily sugar production of Birches Farm (squares), Eastwood Farm (circles)
 595 Farm (triangles) during individual visits over an entire flowering season in 2017. Data are smoothed
 596 with a Generalised Additive Model. The curve based upon the mean sugar production of each plant
 597 species (\pm standard error; dashed lines) is shown in black, while the curves based upon low and high
 598 estimates of each species' sugar production are shown in red (\pm standard error; dotted lines). The
 599 year is divided into what is visually perceived as the main flowering seasons, with pink representing
 600 troughs and purple representing peaks.



602 **Figure 2.** Nectar phenology profiles of a. Birches Farm 2016, b. Birches Farm 2017, c. Eastwood Farm
 603 2017 and d. Elmtree Farm 2017. Results are taken from summing the outputs of individual species
 604 models for each farm. Red dotted lines show median daily sugar production for the year. Peaks of
 605 nectar production ($>$ median) are marked in purple, while troughs or gaps ($<$ median) are shown in
 606 pink. Note the different scale for each graph. The June Gap on Birches Farm 2016 (plot A) is evident
 607 from the curve but does not register as a formal trough as it does not cross the median line.

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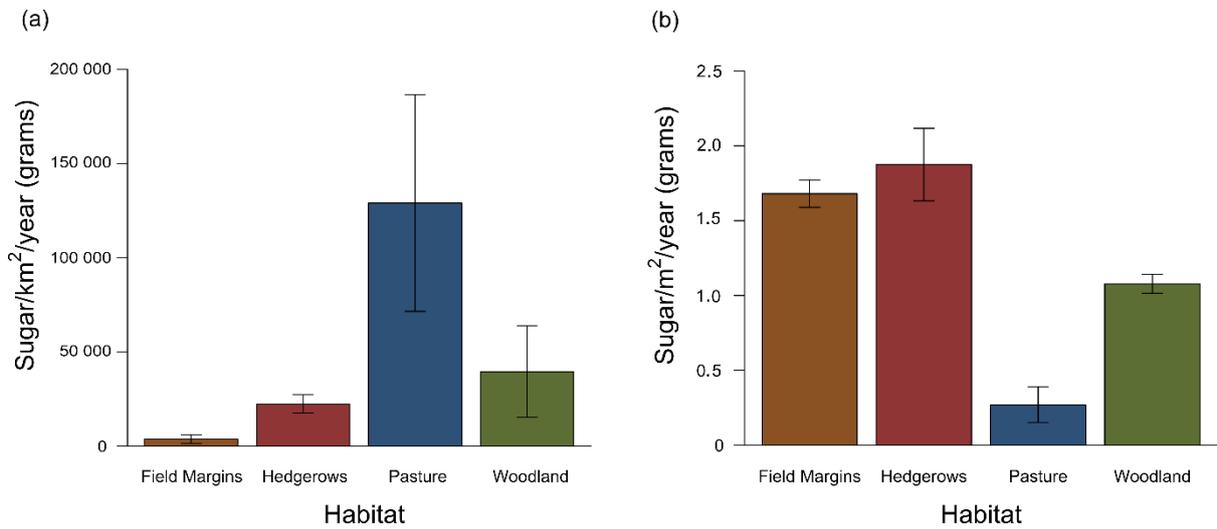


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610 **Figure 3.** Comparison between daily nectar supply and daily demand of three common bumblebee
 611 species present on 1km² of farmland on: a. Birches Farm 2016, b. Birches Farm 2017, c. Eastwood
 612 Farm 2017 and d. Elmtree Farm 2017. Black lines show grams of sugar available each day on 1km²
 613 farmland, divided by the number of common bumblebees present on the landscape at that time i.e.
 614 sugar available per individual bee (\pm SE). The red line shows the estimated mean daily sugar
 615 requirement of a *Bombus terrestris* individual at each point in the year (\pm SE), from Rotheray *et al.*

616 (2017). Note that energy demand per individual is highest in early spring when queens are foraging
617 and establishing colonies. Shaded regions highlight periods of nectar deficit where demand (red line)
618 exceeds supply (black line). Note the y-axis is plotted on a \log_{10} scale.

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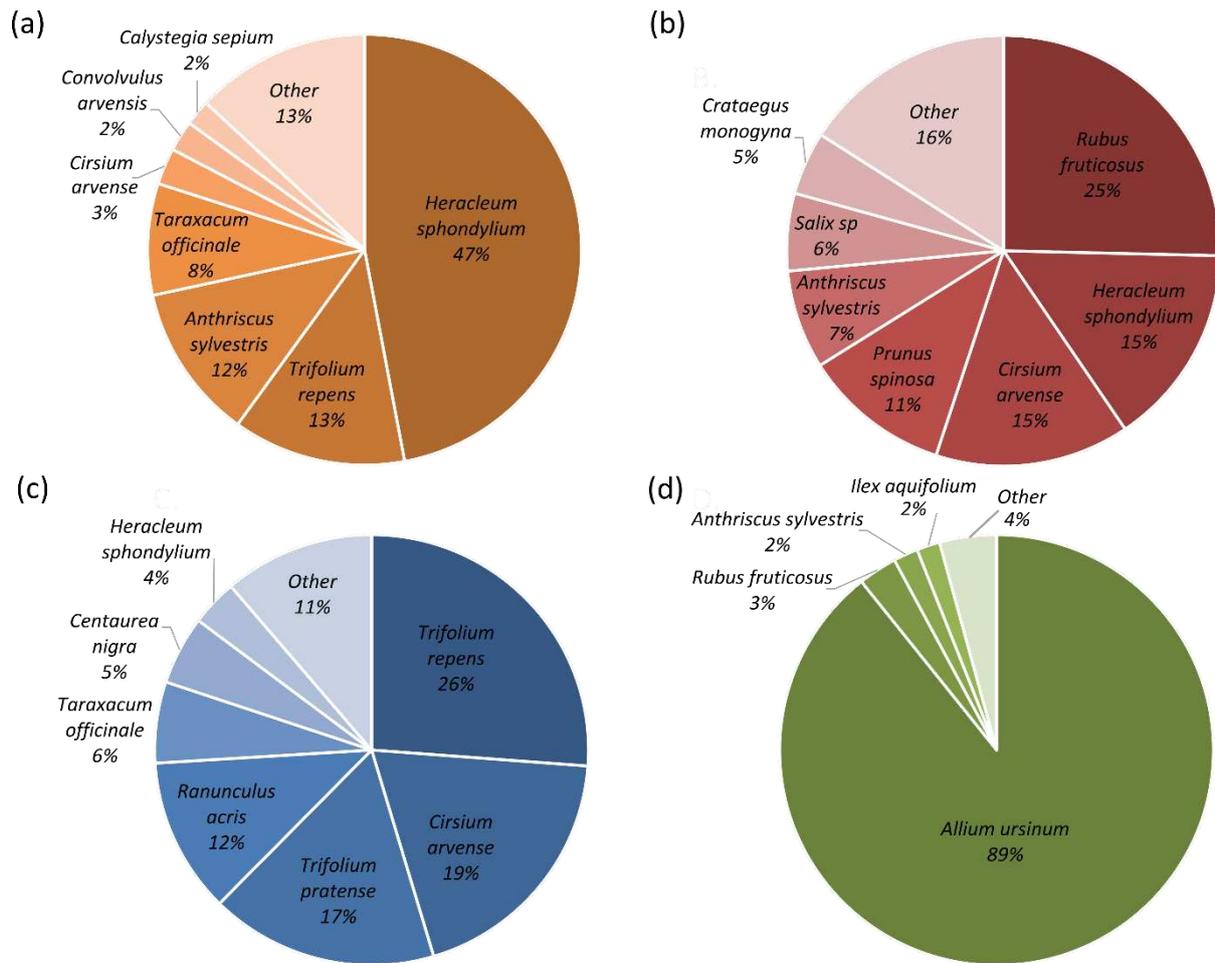
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622 **Figure 4.** Total yearly nectar production of the four main habitat types present on a) a typical 1km²
623 area of farmland (including values from farms where that habitat was not present) and b) a square
624 metre of the given habitat. Values for each habitat are expressed as a mean of the four study farms
625 (Birches, Eastwood, Elmtree and Chestnut) \pm standard error.

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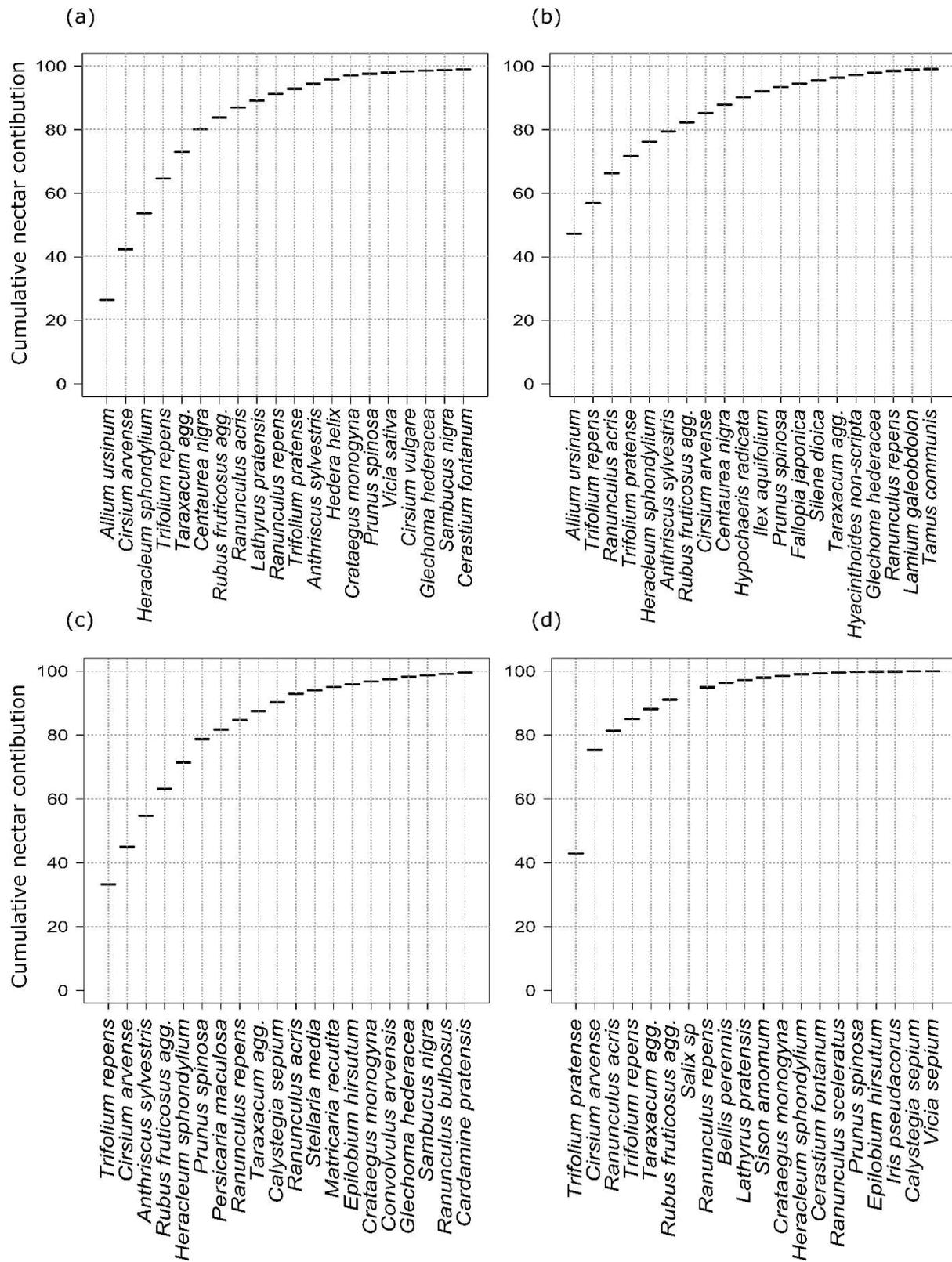
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630 **Figure 5.** Nectar contributions of the most productive plant species in a. field margins, b. hedgerows,
 631 c. pasture and d. woodland. Values shown are a mean of the four study farms (Birches, Chestnut,
 632 Eastwood and Elmtree).



633

634 **Figure 6.** Plant species' contributions to total farmland nectar supply on a. Birches Farm, b.

635 Eastwood Farm, c. Elmtree Farm and d. Chestnut Farm in 2016. Lines show the cumulative

636 contribution of each species. Only the 20 most productive species on each farm are shown.