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

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Abstract

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

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

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

Introduction

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

The large-scale coverage of agricultural land in the UK (70.8%) (WorldBank 2015), makes it an important consideration for any programme aiming to conserve biodiversity at a national level. In the UK, Environmental Stewardship Schemes provide annual payments to farmers and land managers for managing their land in an environmentally-friendly way, including for the benefit of pollinators (Natural England 2009). Nectar rich field margins are an important component of these schemes and there are data on the best floral mixtures for supporting farmland bumblebees e.g. (Carvell *et al.* 2004; Pywell *et al.* 2005). It is known that the addition of floral resources can increase bumblebee colony growth and nest density (Wood *et al.* 2015; Crone & Williams 2016; Carvell *et al.* 2017), and increase species diversity and abundance of trap nesting bees (Dainese *et al.* 2018). However, the timing of resource availability (i.e. the phenology) is also important (Williams *et al.* 2012; Carvell *et al.* 2017), but this aspect is much less understood.

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

Identifying periods of the year in which floral resources most strongly limit pollinator populations will be key to addressing this issue in a targeted and cost-effective way. This requires an understanding of both flowering phenology and pollinator floral needs at a landscape-scale over their entire flight season. Our study addresses these knowledge needs via the following three objectives: (i) characterising and quantifying the phenology of nectar resources at the whole-farm scale on replicate farms throughout the flowering season (late February – early November); (ii) quantifying the corresponding nectar demands of common farmland bumblebees to compare nectar supply and pollinator demand throughout the year, thereby identifying periods when there is a supply-demand deficit; (iii) identifying habitats and plant species which may fill these gaps and thereby provide sufficient resources for the entire pollinator flight season on farmland. Our methods provide a novel approach to plant-pollinator phenological matching (Russo *et al.* 2013) and enable targeted planting strategies for the restoration of nectar supplies on farmland, an approach that could be applied to other anthropogenic habitats.

Materials and Methods

Study sites

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

The intensive study site, Birches Farm in Somerset, England (51°25'19.04"N, 2°40'49.93"W) was sampled twice per week in 2016 from late February until early November, providing the intensive component of the study. There were two components to the extensive part of our study. First, in 2016, three further farms in Somerset - Eastwood Farm (51°29'41.71"N, 2°60'56.74"W), 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) - were sampled each fortnight from March until November in 2016. The four farms were 6-20 km from each other and differed slightly in their habitat composition, with varying proportions of pasture and arable fields, hedgerows, margins and woodland (Supporting Table A1 and Fig. A1). The nectar production and habitat composition of all four farms were broadly representative of the wider landscape, based upon unpublished data from 11 farms in Southwest UK (Supporting Methods A1 and Fig. A2). These four farms were used to compare the plant species and habitat contributions to farmland nectar supply. Second, in 2017, three of the four farms (Birches, Eastwood and Elmtree farms, referred to hereafter as the phenology farms) were sampled every week throughout the flowering season; this providing both phenologically informative data and temporal replication for Birches farm.

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

Nectar measurements:

On each sampling occasion, six randomly located 50 m transects were conducted within each habitat type (e.g. 24 transects in total, for a farm with four habitat types). On each transect, the number of open floral units of each flowering plant species was recorded in a 1 m^2 quadrat at 5 metre intervals along its entire length (i.e. 10 quadrats per transect). For trees and shrubs, all flowers in a 5 m vertical column above the quadrat were counted. Above this, the tree's height within the vertical column was estimated with a clinometer and the floral abundance values were multiplied up accordingly, as in Baude *et al.* (2016). Values for the nectar sugar production of each species were from Baude *et al.* (2016) who measured or modelled the sugar (sucrose) production of 305 plant species in the UK, including the 175 most common species. The sugar production of eight species encountered in the study but not covered by Baude *et al.* (2016) were measured according to their methods (Supporting Method A2).

Quantifying flowering phenology

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

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

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

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

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

B. terrestris (mean nest density: 32/km^2), *B. pascuorum* (83/km^2) *and B. lapidarius* (78/km^2). Worker numbers per colony and their changes through the year were taken from Rotheray *et al.* (2017).

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

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

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

Results

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

During 137 visits to the four farms over two years, nearly half a million (494291) individual floral units from 176 flowering plant species were counted in 2664 transects (761 hedgerow transects, 759 pasture, 576 woodland and 568 margins). The daily sugar production of eight new species were recorded and added to the nectar database of Baude *et al.* (2016) (Supporting Table A2). The top-ranking generalised additive model (Supporting Table A3) described a non-linear trend in sugar availability which fluctuated greatly through the year, creating the six flowering periods highlighted in Fig. 1. Although total yearly sugar production per kilometre squared varied up to threefold between farms in 2017 (342 kg of sugar/km^2/year on Birches Farm, 461 on Eastwood Farm and 131 on Elmtree Farm), the phenological pattern of sugar production was relatively consistent among the farms (Fig. 2).

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

The strong seasonality of nectar supply did not synchronise well with the sugar demand of common bumblebee species (Fig. 3). On each of the three phenology farms, the pollinator flight season was characterised by alternating periods of nectar deficit and surplus which were relatively consistent in their timings, though differed somewhat in the magnitude of their peaks and troughs. In early March when queens emerge, sugar demand per individual bee was high while farmland nectar production was at its lowest for the flowering season. This left a mean deficit of 12.3 grams of sugar/km^2/day (±1.7 SE) between what was available and our estimates of bumblebee needs. This 'hunger gap' lasted from the start of the pollinator flight season until late March. During this time, the only species producing ecologically meaningful quantities of sugar on the farms were *Taraxacum* agg.*, Prunus spinosa, Glechoma hederacea, Ranunculus ficaria,* and *Bellis perennis*. Together, these species contributed a mean of 13.1 grams of sugar/km^2/day (±6.8 SE) during the hunger gap. Just one foraging queen requires an estimated 0.7 grams of sugar per day, meaning that for most of March, a maximum of 19 queen bumblebees could be supported on 1 km^2 of farmland. This does not account for any young workers that have been produced, or other pollinator species competing for nectar such as early species of solitary bees or hoverflies.

In late summer (August-October), the three study farms had a mean deficit of 1053 grams of sugar/km^2/day (±81.4 SE) lasting between one and three months (Fig. 3). Although sugar production was relatively high at this time, *Bombus* colonies were reaching their maximum size, generating a high demand for nectar which could not be met by the farmland landscape, resulting in a second hunger gap. A very small proportion of the farmland sugar was produced by plants species unlikely to be utilised by *Bombus*, (e.g. *Stellaria media*) implying nectar availability may be even lower than predicted.

From late March until mid-late May, there was a mean surplus of 2196 grams of sugar/km^2/day (±986 SE) on the three study farms. Mass flowering oil seed rape was not present on any of the study farms but normally flowers during this period and would therefore be expected to add to the nectar surplus recorded on our farms rather than fill a hunger gap.

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

Habitats differed greatly in their sugar production value at a farm scale but their relative values among farms were similar (Fig. 4). Hedges produced the greatest sugar per unit area (1.88 grams of sugar/m^2/year ±0.24 SE) and with a mean coverage of 1% of farm area, they made up 9.4% (±3 SE) of total sugar. Their phenological continuity was also highest, being the most nectar-rich habitat per unit area 62% (±3 SE) of the year. Field margins were also a rich habitat for nectar, with a mean of 1.68 grams of sugar/m^2/year (±0.09 SE). However, their period of nectar production was relatively short-lived (Supporting Information Fig. A3). With a coverage of 1% of farm area, they made up 3.1% (±4 SE) of total sugar production. The nectar production of pasture was substantial (54% of total sugar production, ±12 SE) because of its large area on the farm (mean 64% coverage), but per unit area it produced only 0.27 grams of sugar/m^2/year (±0.12 SE). Where woodland was present it covered an average of 8% of the farm, producing 1.08 grams of sugar/m^2/year (±0.06 SE) and making up 33.1% (±12 SE) of total farm nectar supply. However, approximately 90% of this supply was produced in just one month (May) and it was almost exclusively provided by *Allium ursinum* (89%). Figure 5 shows the sugar contributions of the most productive plant species in each of the four habitats.

Although up to 59 plant species produced ecologically meaningful quantities of sugar at some point in the year (> 0.3 grams of sugar/km^2/day), 50% of total sugar was supplied by just three species and 80% of the sugar was supplied by eight species (Fig. 6). These were: *Allium ursinum* (18%), *Cirsium arvense* (16%), *Trifolium repens* (14%), *Trifolium pratense* (12%), *Heracleum sphondylium* (6%), *Ranunculus acris* (5%), *Rubus fruticosus* agg. (5%) and *Taraxacum* agg. (4%). Several less productive species made important contributions to the phenological continuity of nectar supply, due to their unusual flowering times (Table 1). *Hedera helix* provided over half of all sugar from mid-September until the end of the flowering season, while *Taraxacum* agg. provided the majority of sugar from mid-March until the end of April.

Discussion

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

Limitations

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

Flowering and pollinator phenology

The highly seasonal nectar supply detected in our study on farmland in South West UK is likely to have important implications for wild and managed pollinators. The large differences between the flowering phenology of different habitats (Supporting Information Fig. A1), suggests that pollinators need to move between habitats, tracking the changing resource supplies, to ensure a continuous supply of nectar. This effect has been demonstrated in agricultural areas of the U.S. where complementary habitats provide resources at different times of the year and the pollinator community tracks these resources (Mandelik *et al.* 2012). This highlights the importance of having a range of distinct habitat types present on farmland.

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

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

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

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

Management implications

We have demonstrated that it may not be just the availability of nectar resources limiting *Bombus* populations, but also the timing of these resources, though this remains to be tested. March and August/September are periods of greatest nectar deficit for *Bombus* populations and should therefore be prioritised to ensure a sufficient annual nectar supply. Plant species which flower during these periods of deficit – so-called ‘bridging species’ (Menz *et al.* 2011) - should be prioritised in schemes which aim to conserve or restore pollinator populations on farmland. The early hunger gap we observed on the four farms could theoretically be ‘plugged’ by adding just 12.3 extra grams of sugar each day across 1 km^2 of farmland, the equivalent of c.1000 willow catkins for example (data from Baude *et al*. 2016). Willows *Salix* spp. could be readily added to UK farming systems, delivering pollen and nectar in the early spring when floral resources are particularly scarce (Moquet *et al.* 2015). The late-season gap however would require between 500 and 2000 extra grams of sugar per day, which equates to approximately one hectare of late-flowering red clover *Trifolium pratense (*Rundlof *et al.* 2014*)*, or an extra 40 bramble *Rubus fruticosus* agg. flowers per metre squared of hedgerow (based on a mean farm coverage of 1% hedgerow area).

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

Conclusions

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

Authors’ contributions

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

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Data accessibility

Data available via the Dryad Digital Repository

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Figures & Tables

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

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

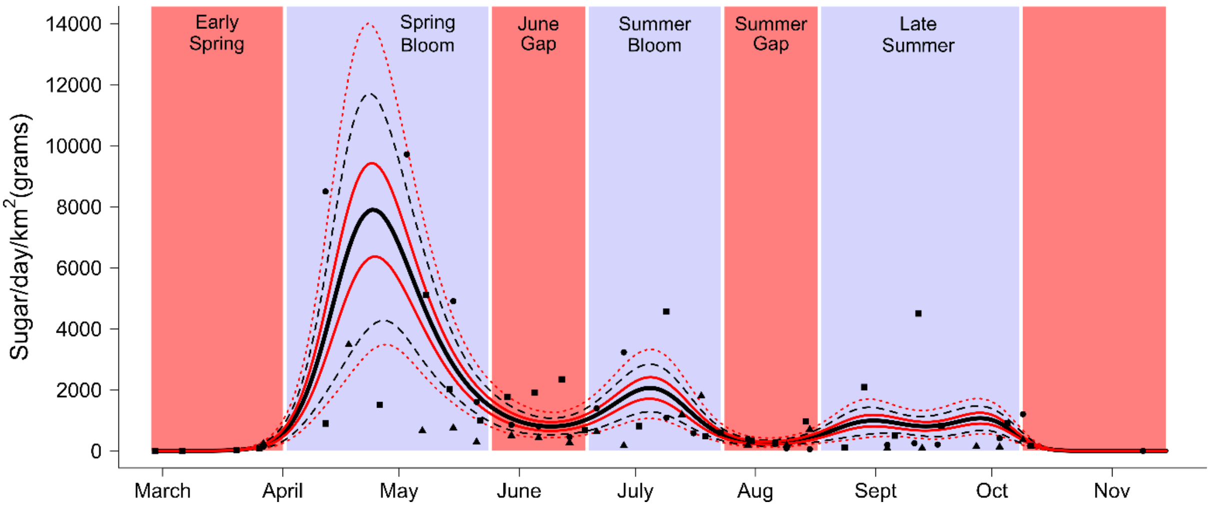
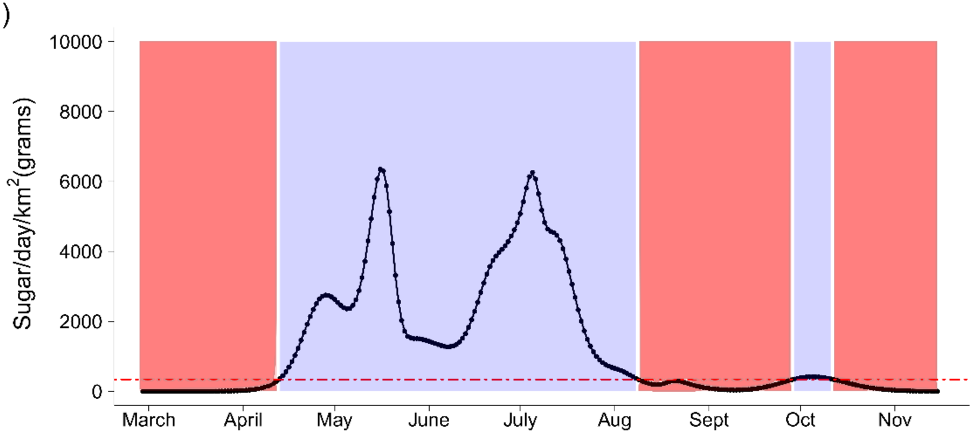
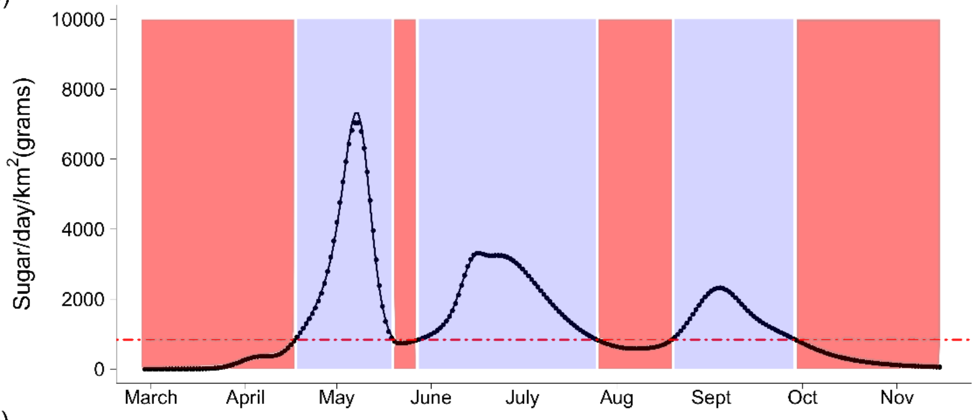


Figure 1. Daily sugar production of Birches Farm (squares), Eastwood Farm (circles) and Elmtree Farm (triangles) during individual visits over an entire flowering season in 2017. Data are smoothed with a Generalised Additive Model. The curve based upon the mean sugar production of each plant species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

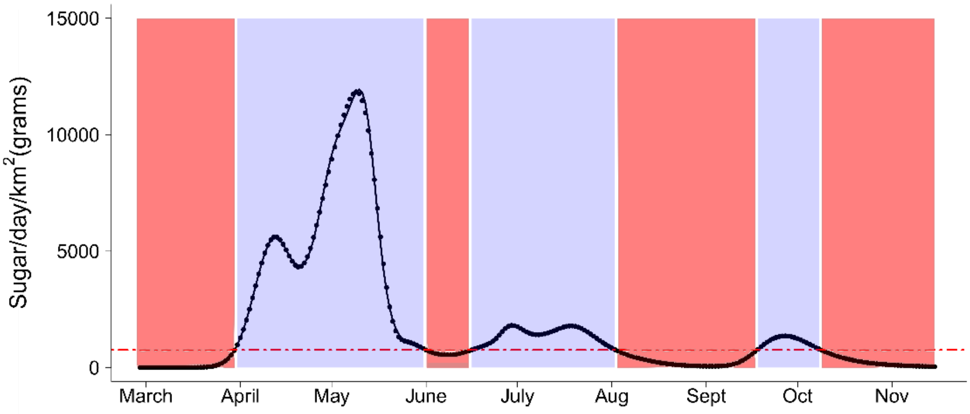
(a)


Sugar/day/km^2(grams)
10000
8000
6000
4000
2000
0
March
April
May
June
July
Aug
Sept
Oct
Nov

(b)


Sugar/day/km^2(grams)
10000
8000
6000
4000
2000
0
March
April
May
June
July
Aug
Sept
Oct
Nov

(c)


Sugar/day/km^2(grams)
15000
10000
5000
0
March
April
May
June
July
Aug
Sept
Oct
Nov

(d)

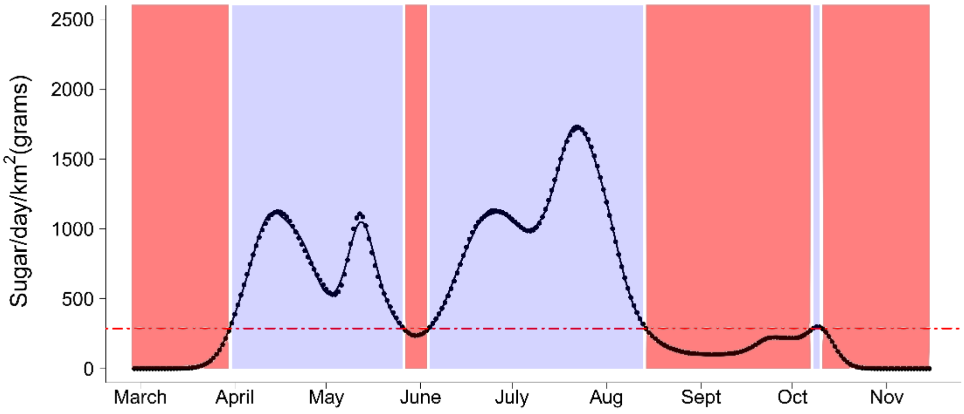

Sugar/day/km^2(grams)
2500
2000
1500
1000
500
0
March
April
May
June
July
Aug
Sept
Oct
Nov

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

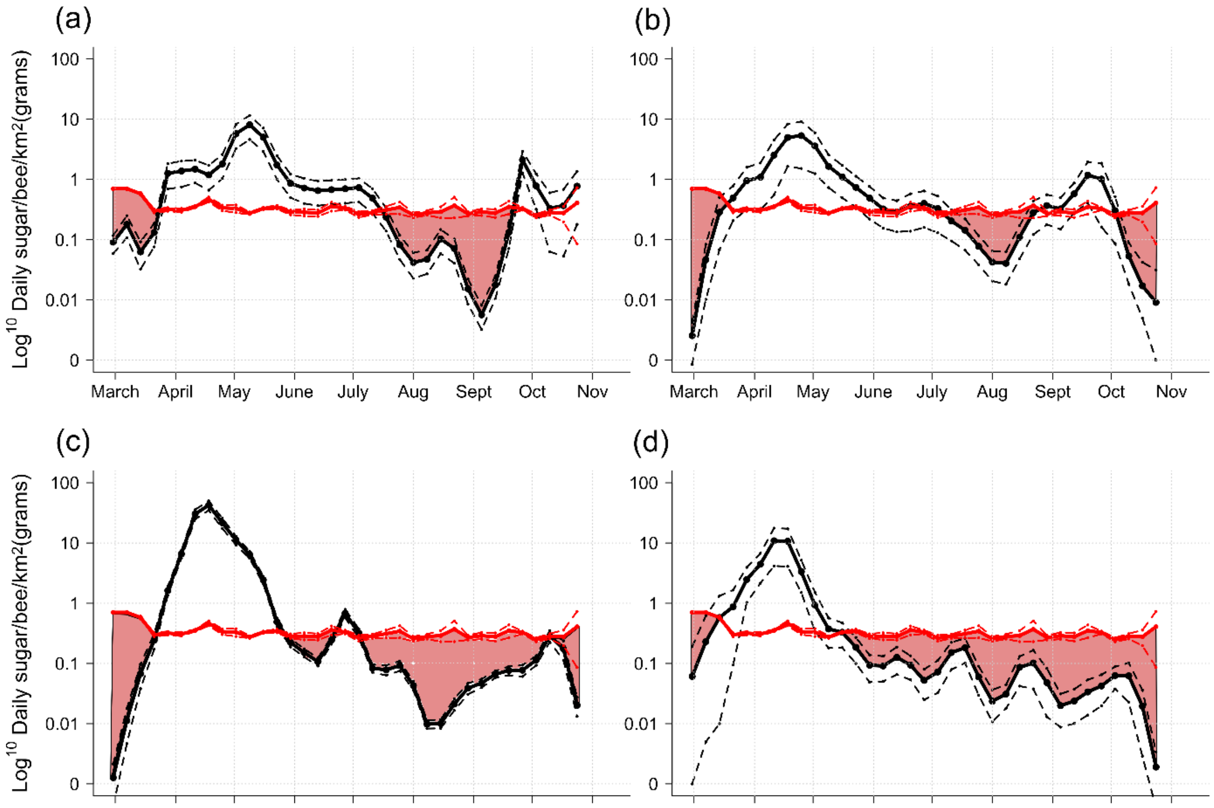


Figure 3. Comparison between daily nectar supply and daily demand of three common bumblebee species present on 1km^2 of farmland on: a. Birches Farm 2016, b. Birches Farm 2017, c. Eastwood Farm 2017 and d. Elmtree Farm 2017. Black lines show grams of sugar available each day on 1km^2 farmland, divided by the number of common bumblebees present on the landscape at that time i.e. sugar available per individual bee (±SE). The red line shows the estimated mean daily sugar requirement of a *Bombus terrestris* individual at each point in the year (±SE), from Rotheray *et al.*

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

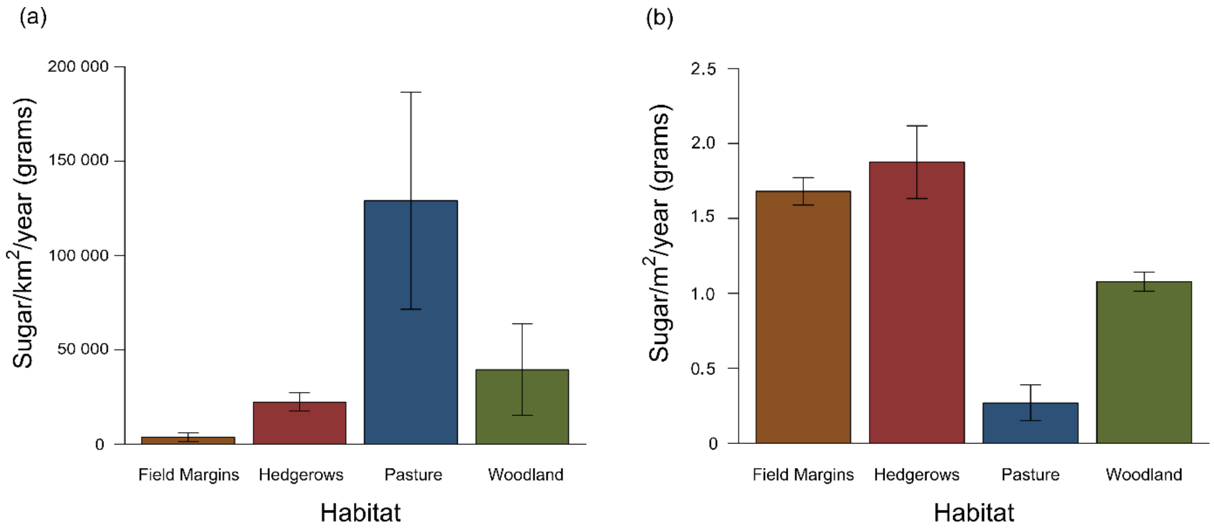


Figure 4. Total yearly nectar production of the four main habitat types present on a) a typical $1km^2$ area of farmland (including values from farms where that habitat was not present) and b) a square metre of the given habitat. Values for each habitat are expressed as a mean of the four study farms (Birches, Eastwood, Elmtree and Chestnut) ± standard error.

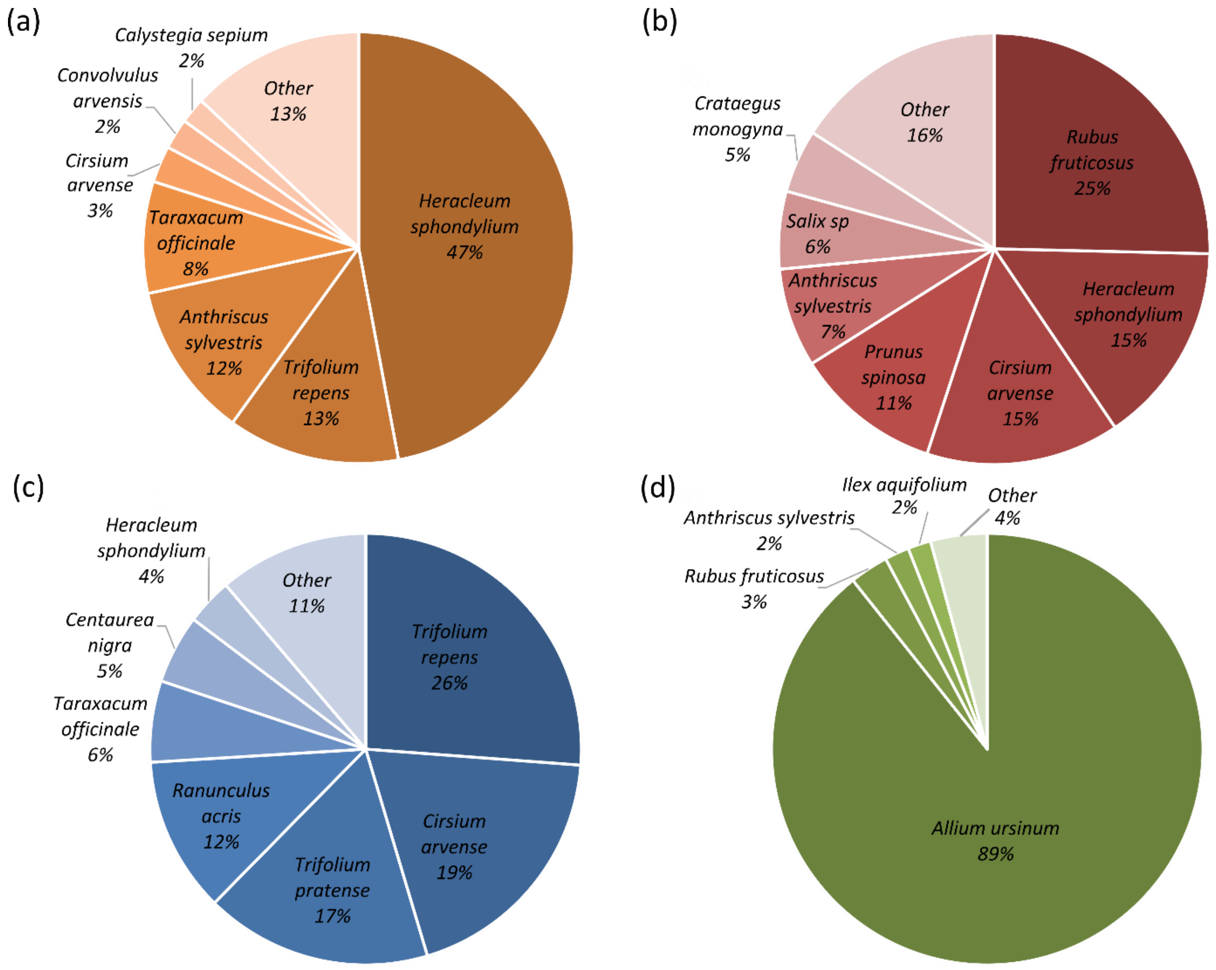


Figure 5. Nectar contributions of the most productive plant species in a. field margins, b. hedgerows, c. pasture and d. woodland. Values shown are a mean of the four study farms (Birches, Chestnut, Eastwood and Elmtree).

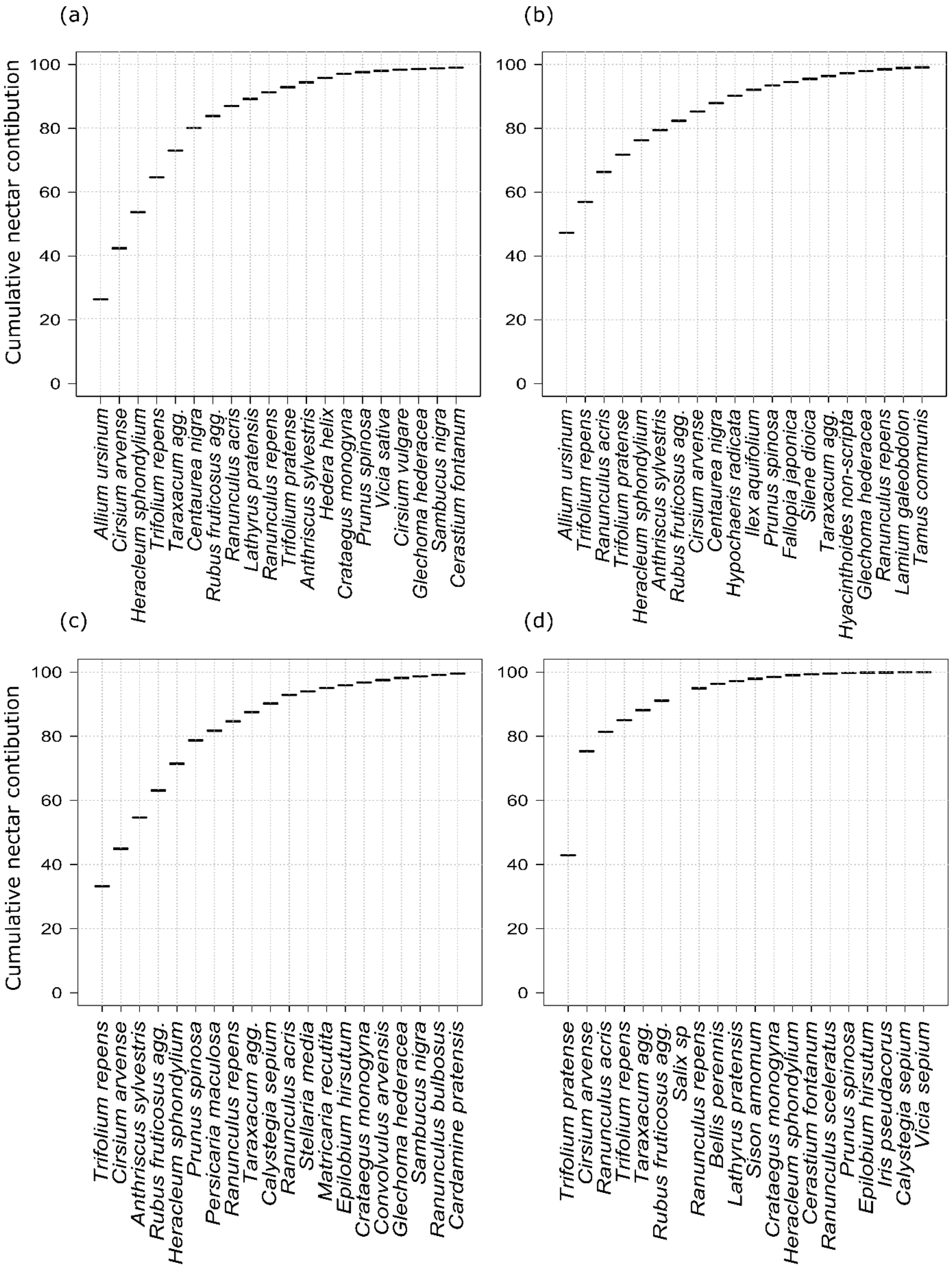


Figure 6. Plant species' contributions to total farmland nectar supply on a. Birches Farm, b. Eastwood Farm, c. Elmtree Farm and d. Chestnut Farm in 2016. Lines show the cumulative contribution of each species. Only the 20 most productive species on each farm are shown.