High rates of nectar depletion in summer grasslands indicate competitive conditions for pollinators

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Abstract

Competition among pollinators for floral resources is a phenomenon of both basic and applied importance. While competition is difficult to measure directly under field conditions, it can be inferred indirectly through the measurement of floral resource depletion. In this study, we conducted a pollinator exclusion experiment to calculate nectar depletion rates in summer across 16 grassland sites in the German regions of Franconia and Saxony-Anhalt. Overall depletion rates were estimated at 95% in Franconia and 79% in Saxony-Anhalt, indicating strong nectar limitation and, by implication, competition among pollinators. Despite being ubiquitous in our study regions, honey bees were scarce at our sites at the time of nectar sampling. This demonstrates that wild pollinators alone are capable of massive nectar depletion, and the addition of managed honey bees to wild pollinator communities may intensify already competitive conditions. Nevertheless, the manifest diversity of the pollinator communities at our sites indicates that other factors, such as non-trophic constraints or temporal variation in food limitation, can mitigate competitive exclusion despite immediate conditions of acute food scarcity.
A

Region

Franconia

Saxony-Anhalt

56°N
54°N
52°N
50°N
48°N
46°N
5°E
10°E
15°E

B

C

Centaurea scabiosa  Dianthus carthusianorum  Echinops sphaerocephalus  Knautia/Scabiosa

Origanum vulgare  Scabiosa ochroleuca  Teucrium chamaedrys
Depletion (%)  25  50  75  100

Proportional abundance

Group
BB
BF
HB
SF
WB

A
F1  F2
F3  F4
F5  F6
F7  F8
May  Jun  Jul  Aug

B
S1  S2
S3  S4
S5  S6
S7  S8
May  Jun  Jul  Aug
High rates of nectar depletion in summer grasslands indicate competitive conditions for pollinators.
Competition among pollinators for floral resources is a phenomenon of both basic and applied importance. While competition is difficult to measure directly under field conditions, it can be inferred indirectly through the measurement of floral resource depletion. In this study, we conducted a pollinator exclusion experiment to calculate nectar depletion rates in summer across 16 grassland sites in the German regions of Franconia and Saxony-Anhalt. Overall depletion rates were estimated at 95% in Franconia and 79% in Saxony-Anhalt, indicating strong nectar limitation and, by implication, competition among pollinators. Despite being ubiquitous in our study regions, honey bees were scarce at our sites at the time of nectar sampling. This demonstrates that wild pollinators alone are capable of massive nectar depletion, and the addition of managed honey bees to wild pollinator communities may intensify already competitive conditions. Nevertheless, the manifest diversity of the pollinator communities at our sites indicates that other factors, such as non-trophic constraints or temporal variation in food limitation, can mitigate competitive exclusion despite immediate conditions of acute food scarcity.

KEYWORDS: coexistence; floral resources; honey bees; trophic ecology; foraging
INTRODUCTION

It is widely appreciated that nearly 90% of flowering plant species rely on animals for pollination (Ollerton et al. 2011). Yet the flipside of this relationship—the trophic ecology of flowers-as-food—remains poorly understood, despite the fact that more than a third of all described and extant animal species subsist on floral resources (Mora et al. 2011, Wardhaugh 2015, Ollerton 2017, Sponsler et al. 2023).

Recently, the ecology of floral resources has been brought to the fore by concerns about competition between managed honey bees and wild pollinators (Geldmann and González-Varo 2018). Empirical studies suggest that competitive effects of honey bees on wild pollinators are common but not ubiquitous (Iwasaki and Hogendoorn 2022), and it remains unclear how the occurrence and severity of competition are modulated by ecological context.

Resource competition is predicated on resource limitation, yet while claims about competition abound, the phenomenon of limitation is rarely given explicit consideration (though see Timberlake et al. 2019, Jachula et al. 2021). The apparent contingency of resource competition (Iwasaki and Hogendoorn 2022) is likely caused by underlying variation in resource limitation, and understanding when, where, and why floral resources are limiting is central both to the applied problem of managing competition and the basic question of population regulation in nectar- and pollen-feeding animals (Sponsler et al. 2023).

While the phenomenon of floral resource limitation per se is difficult to approach empirically, it can be treated as a latent phenomenon represented by an easily-measured proxy: floral resource depletion. While limitation and depletion are not synonymous, the likelihood of resource limitation—and its severity when it occurs—increases with the degree to which foragers deplete the pool of available resources (Sponsler et al. 2023).

In this study, we estimated floral resource depletion rates in semi-natural grassland habitats in two regions of Germany. Based on estimates of resource depletion, we evaluate the plausibility of resource limitation and, by extension, competition among pollinator species.

MATERIALS AND METHODS

Study regions and field sites

Our study was set in the German regions of Franconia and Saxony-Anhalt (Figure 1A). In each region, we selected eight semi-natural grassland sites for sampling. The sites in Franconia were calcareous grasslands, while those of Saxony-Anhalt were set in the distinctive porphyry substrate of that region. In both regions, semi-
natural grasslands are highly fragmented and embedded in a predominantly agricultural matrix characterized by field crops, vineyards (in Franconia), deciduous forest patches, and small settlements. Neighboring sites were separated by a minimum of 2.6 km in Franconia and 5.7 km in Saxony-Anhalt.

**Sampling protocols**

Sampling protocols differed across regions to accommodate local floristics and field work logistics.

In Franconia, we sampled from 4-19 July, 2022. On each sampling day, we arrived at a given site around sunrise (5:00-6:00), prior to the onset of foraging by diurnal pollinators, and bagged flowers from the top 1-3 most abundant flower species. Bags were constructed of synthetic mesh similar to mosquito netting, which has a minimal influence on the microclimate of the flower (Kearns et al. 1993) (Figure 1B).

The most ubiquitous species in Franconia was Centaurea scabiosa, which we sampled at all but one of our sites. Other species, sampled opportunistically, include Dianthus carthusianorum (one site), Echinops sphaerocephalus (two sites), Origanum vulgare (one site), Teucrium chamaedrys (one site), and a species complex of Knautia arvensis and Scabiosa columbaria (three sites) (Figure 1C). Since we failed to distinguish Knautia and Scabiosa reliably in the field, we lumped them under the subfamily Dipsacoideae in all analyses.

Only flowers visibly intact and in good condition were selected for bagging. Since flowers tended to be patchily distributed, we selected flowers opportunistically rather than in a spatially systematic fashion, with the goal of representing the major patches within each site. The number of flowers bagged at each site varied with the abundance of the target species and was constrained by time, but we aimed for at least 10 flowers per species (mean: 12, range: 7-20). Approximately 5 hours after sunrise (~10:30), we sampled nectar from bagged and open flowers using 0.5- or 1.0-µL microcapillary tubes (Hirschmann, Eberstadt). Where possible, we selected open flowers belonging to the same individual plant as a corresponding bagged flower. In all cases, open flowers were selected according to the same standard of intactness and condition as the bagged flowers, and we similarly aimed to sample at least 10 flowers per species (mean: 14, range: 10-27). For species with compound flowers (Knautia, Scabiosa, Centaurea, and Echinops), samples for each inflorescence were pooled across 5 florets. Nectar volumes were measured in mm using a digital caliper (HaWe, Aschheim) and converted to µL nectar by multiplying the maximum capacity of the tube by the proportion of its length that was filled.

In Saxony-Anhalt, flowers were bagged around 9:00 and sampled around 17:00, thus capturing most of the foraging day but allowing some morning foraging prior to bagging. The only species sampled in Saxony-Anhalt was Scabiosa ochroleuca, which was common at all sites. Sampling was conducted from 13-28 July, 2022.
Aside from these differences, sampling in Saxony-Anhalt followed the same methods described above for Franconia.

By midsummer in Germany, the flowering seasons of forests and crops are largely past, and floral resources are mostly restricted to grasslands and settlements (i.e. gardens). Thus, our sampling can be understood to reflect the floral resource conditions of the main foraging habitat available to pollinators at the time of our study.

At all sites, we surveyed pollinator communities using standardized 45-minute transect walks. While insects of many taxonomic groups can function as pollinators (Ollerton 2017), our surveys focused on those most characteristically associated with diurnal flower visitation, namely bees (Hymenoptera: Anthophila), butterflies and burnets (Lepidoptera), and hover flies (Diptera: Syrphidae). Specimens were identified live in the field when possible, and specimens that could not be identified to species-level in the field were euthanized and identified later in the laboratory. In Franconia, pollinator surveys began in mid-April and were repeated at monthly intervals until early-August. In Saxony-Anhalt, surveys were performed in mid-May, early-June, and late-July.

**Data analysis**

Our analytical objective was to calculate floral resource depletion rate \( D \), which we defined as the proportional difference between the mean resource volume of bagged \( V_{bagged} \) and open \( V_{open} \) flowers:

\[
D = 1 - \frac{V_{open}}{V_{bagged}}
\]  

(1)

Simply using the empirical estimates for \( V_{bagged} \) and \( V_{open} \), however, would ignore the dependencies in our sampling structure, thereby underestimating the uncertainty in our estimate of \( D \). Specifically, our measurements of \( V_{bagged} \) and \( V_{open} \) are nested within individual plants, which in turn are nested within species and sites.

To account for this sampling structure in a principled way, we estimated \( V_{bagged} \) and \( V_{open} \) using hierarchical Bayesian regression models with resource volume as the response variable, treatment (bagged vs. open) as a constant (i.e. “fixed”) effect, and plant, species (in Franconia), and site as varying (i.e. “random”) effects, following the nomenclature recommended by Gelman (2005). Since our measurements of resource volume are continuously non-negative but include zeros, we specified hurdle-gamma models consisting of gamma and binomial submodels, each with the effects structure described above. We fit a separate model for the
Franconia and Saxony-Anhalt datasets since the former required the inclusion of the species term. After validating our models, we calculated \( D \) by applying (1) to the posterior predictive distributions of \( V_{\text{bagged}} \) and \( V_{\text{open}} \).

Prior to modeling, we normalized the nectar measurements by dividing each reading by the mean reading of the bagged flowers within each site and species. This facilitated prior selection and dampened variation across sites and species that was extraneous to the task of comparing relative volumes across treatments. All models were specified with regularizing and weakly informative priors (Wesner and Pomeranz 2021) following the modeling workflow described by Gabry et al. (2019).

All data operations were done in R (R Core Team 2021). Geospatial data (Figure 1) were processed using \( \text{sf} \) (Pebesma 2018) and visualized using \( \text{ggplot2} \) (Wickham 2016). Data handling was performed with the \( \text{tidyverse} \) package suite (Wickham et al. 2019). Bayesian models were fit with Stan (Stan Development Team 2022) accessed via \( \text{brms} \) (Bürkner 2017). Marginal predictions were extracted using \( \text{tidybayes} \) (Kay 2021a), and models were visualized using \( \text{ggplot2} \) (Wickham 2016) and \( \text{ggdist} \) (Kay 2021b). A complete workflow including all code needed to reproduce and validate our models is provided in Appendices 1 and 2.

RESULTS and DISCUSSION

In Franconia, the overall marginal mean depletion rate (i.e. averaged across the grouping variables of site, species, and plant) was distributed tightly around a median of 95% (95% credible interval = 92%–97%) (Figure 2). In Saxony-Anhalt, the depletion rate was distributed more broadly around a considerably lower median of 79% (95% credible interval = 71.5%–85.9%) (Figure 2). The lower depletion rates in Saxony-Anhalt compared to Franconia could be due to the difference in sampling time between the two regions. In studies of diel patterns of nectar production and consumption, the lowest levels of standing crop are often reached within a few hours of the onset of foraging, corresponding to the time of day we sampled in Franconia; by afternoon or evening, nectar levels can begin to recover, probably due to a decline in foraging rate (Brown et al. 1981, Roubik and Buchmann 1984, Collins et al. 1984).

Site-level marginal mean depletion rates (i.e. averaged over species and plant) were broadly consistent within each study region, though markedly lower depletion rates were seen at sites F4 and S4 (Figure 3). In the case of site F4, this effect is attributable to the influence of \( \text{Dianthus carthusianorum} \), which was sampled only at this site and which exhibited far lower depletion than any other species in the Franconia study region (Figure 4). The deep and narrow corollas of \( \text{Dianthus} \) flowers (Figure 1) exclude virtually all but Lepidopteran visitors; even prospective robbers (e.g. \( \text{Bombus terrestris} \)) are likely foiled by the thick, leathery
sepals that guard the nectaries. Thus, where Dianthus occurs at appreciable abundance, butterflies and moths probably enjoy a partition of the floral resource community that is free from competition with bees and other flower visitors.

Site- and species-level variation notwithstanding, depletion rates of these magnitudes are evidence of strong resource limitation, and under such conditions competition among foraging pollinators can be expected to be severe. Even at the low end of the depletion estimate for Saxony-Anhalt, a 70% depletion in nectar standing crop could substantially reduce foragers’ rate of resource acquisition, which should translate into net fitness costs. At the extremes of depletion seen in Franconia, where the majority of open flowers contained no detectable nectar, the impact of competition could rise to the level of outright starvation.

Is the food limitation of pollinators typically as severe as our data suggest, or are our findings an extreme case? Our sampling occurred during the hottest month of a severe drought that affected much of Europe in 2022, and this almost certainly stunted the productivity of the floral community (Waser and Price 2016, Phillips et al. 2018). Had we sampled earlier in the year — for example, during the mass flowering of wild and cultivated Prunus trees in early spring — it is likely that we would have seen lower rates of nectar depletion. Nevertheless Heinrich (1976), while noting strong temporal variation in depletion rates, reported an average of 92% depletion of nectar sugars across three years in the relatively moist environment of central Maine, demonstrating that high rates of floral resource depletion can occur apart from exceptionally adverse weather conditions. Moreover, as mentioned earlier, studies monitoring nectar availability through diel time have shown that it is not uncommon for the standing crop of nectar to decline rapidly within the first few hours of foraging activity (Ford 1979, Brown et al. 1981, Roubik and Buchmann 1984, Collins et al. 1984, Laverty and Plowright 1985, Buys 1987), consistent with our findings in Franconia. Even if the degree of resource depletion we observed is a rare event in our system, the competition induced by such conditions could cause persistent local extinctions (MacArthur 1984).

Given the apparent severity of resource limitation and, by implication, resource competition in our system, it is noteworthy that we did not see any evidence of single-species dominance in the pollinator community. To the contrary, our sites hosted bees, butterflies, and hover flies representing at least 95 genera in Franconia and 42 genera in Saxony-Anhalt, and these are conservative estimates because some specimens remain undetermined at the genus level — in particular, due to limited taxonomic resources, hover flies in the Saxony-Anhalt samples were not identified below family level. Granted, a snapshot of floral resource availability may not capture the prevailing conditions that constrain the coexistence of species in a given locality. Nevertheless, if we allow that the depletion rates we observed are broadly similar to those found on average in summer grasslands in our study regions, it would appear that — as is so often the case (Simha et al. 2022) — factors
other than competition for limited supplies of food intervene to prevent the formal expectation of competitive
exclusion from being realized. In our study system, it is possible that unobserved temporal fluctuations in
resource limitation at diel, seasonal, or interannual scales — in combination with other constraints, such as
disease, nesting substrate availability, or the top-down pressure of predators and parasites (Roulston and
Goodell 2011) — could explain the observed coexistence of a diverse pollinator community under immediate
conditions of severe nectar scarcity.

Far from displacing other pollinators, honey bees constituted a small minority of the pollinator community,
and they were virtually absent from many of our sites at the time of nectar sampling (Figure 5). There
is, moreover — in contrast with the recent findings of Page and Williams (2023) in the California Central
Valley — no indication that site-level variation in nectar depletion was driven by honey bee density (Figure
6). Why did honey bees evidently play such a marginal role in our study system? Unlike the other species
in our study, honey bees forage not for subsistence but for accumulation. Under the conditions of nectar
scarcity that we observed, it is likely more economical for honey bees to subsist on stored honey than to
forage for trace amounts of nectar. Given their long foraging range, it is also possible that the honey bees
around our study sites were foraging at distant patches, such as gardens or ornamental trees in settlements
(Rutschmann et al. 2023). Alternatively, honey bees have exclusive access to a special kind of resource
patch to which they readily resort when floral resources are scarce: neighboring honey bee colonies. Indeed,
robbing behavior is known to beekeepers as a consistent summer phenomenon, corresponding to the “summer
dearth” of floral resources typical of temperate regions (Sponsler et al. 2020). The near-absence of honey
bees from our sites, despite their known presence in the vicinity, suggests that there may exist a threshold of
resource standing crop that functions as a sort of release valve for honey- bee-induced competition. This
would be reminiscent of Heinrich’s (1976) observation of small bee species collecting the trace amounts of
nectar left behind by foraging bumble bees, a phenomenon he aptly characterized as a special case of the
classical fugitive species concept (Hutchinson 1951) in which coexistence is facilitated by a tradeoff between
dominance and colonization (in this case, the exploitation of a floral patch).

One question raised by our findings is how the depletion of nectar compares to that of pollen. Unlike nectar,
which plants can actively replenish (sometimes on the scale of minutes) in response to removal by pollinators
(Luo et al. 2014), flowers contain a finite stock of pollen grains, though flowers of some plants can stagger the
release of pollen over the course of hours or days to prolong its presentation to pollinators (Percival 1950).
While we did not measure pollen in our study, we noted during our field work that many flowers from which
we could not extract nectar still bore visible pollen on their anthers, suggesting that nectar was the more
limiting resource in our study system. This question, however, deserves careful scrutiny, since it has been
shown that a single colony of honey bees can collect annually a mass of pollen equivalent to 100,000 larval provisions of an average solitary bee (Cane and Tepedino 2017).

An important caveat of our study is that, due to time constraints and the difficulty of measuring the concentration of very small nectar volumes, we measured nectar solely in terms of volume rather total sugar content. Since our inferences concern the proportional depletion of nectar rather than its absolute energy content, volume is a sufficient proxy for total sugar content insofar as nectar concentration can be assumed constant across bagged and open treatments within each species per site per date. The factors governing nectar concentration dynamics in response to nectar depletion are not well-understood, and it is possible that our volume-based calculations over- or underestimate true depletion rates (Roubik and Buchmann 1984, Luo et al. 2014). We are also aware that microcapillary tubes systematically under-estimate nectar content relative to other sampling methods (Morrant et al. 2009), but this should have no effect on our calculation of proportional depletion.

**CONCLUSION**

Our study demonstrates that, in summer, the floral resources of grassland habitats can be severely limiting to pollinators. Under these conditions, competition for food is almost certainly a strong constraint on pollinator fitness and, ultimately, on the coexistence of pollinator species. That such high rates of nectar depletion were observed in the absence of substantial honey bee activity suggests that competition between pollinator species in our study system is not just an artifact of managed honey bees; rather, when honey bees are introduced to a given locality, it is likely that they intensify already competitive conditions. Nevertheless, the scarcity of honey bees at our sites despite their known presence in the vicinity provides at least circumstantial evidence for the existence of a resource threshold below which honey bees cease competing for locally scarce floral resources and opt instead to subsist on stored honey, resort to inter-colony robbing, or exploit distant resource patches. We also found evidence that, as expected, flowers with restrictive morphologies — in this case, those of *Dianthus carthusianorum* — can function as competition refugia for the species that can access them. Future research should focus on elucidating spatial and temporal patterns of resource limitation, linking resource limitation explicitly to fitness outcomes, and integrating these findings into conceptual and quantitative models of species coexistence.
REFERENCES


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Stan Development Team 2022. The Stan Core Library.


FIGURES

A

![Map of Region]

B

![Photo of Plant]

C

Centaurea scabiosa  Dianthus carthusianorum  Echinops sphaerocephalus  Knautia/Scabiosa

Origanum vulgare  Scabiosa ochroleuca  Teucrium chamaedrys
Centaurea scabiosa -
Dianthus carthusianorum -
Dipsacoideae -
Echinops sphaerocephalus -
Origanum vulgare -
Teucrium chamaedrys -

Depletion (%)
FIGURE CAPTIONS

Figure 1
Study areas (A), each consisting of eight sites, were located in the German regions of Franconia and Saxony-Anhalt. At each site, flowers in the bagged treatment were covered with fine mesh bags to exclude insect visitors (B). Nectar was sampled from a total of seven plant species (B). Illustrations are modifications of public domain works obtained from http://www.plantillustrations.org (Appendix 3).

Figure 2
Normalized nectar volume (A) and mean nectar depletion rates (B) across treatment and study region. Estimated mean depletion rates are visualized with half-eye plots, which use shaded curves to depict the full posterior distribution and point-intervals to summarize the posterior in terms of the highest density interval of the median, with the inner and outer intervals representing 66% and 95% of the posterior, respectively.

Figure 3
Depletion rates by site. Point-intervals summarize the posterior in terms of the highest density interval of the median, with the inner and outer intervals representing 66% and 95% of the posterior, respectively.

Figure 4
Depletion rate by species in Franconia. Point-intervals summarize the posterior in terms of the highest density interval of the median, with the inner and outer intervals representing 66% and 95% of the posterior, respectively.

Figure 5
Area plots depicting the relative abundances of pollinator guilds in Franconia (A) and Saxony-Anhalt (B). Dotted vertical lines indicate the date of nectar sampling at each site. Guild abbreviations: BB = bumble bees, BF = butterflies and burnets, HB = honey bees, SF = hover flies, WB = wild bees excluding bumble bees.

Figure 6
Site-level depletion rate plotted against the square-root of honey bee density (individuals per 45-minute transect). Point-intervals summarize the posterior in terms of the highest density interval of the median,
with the inner and outer intervals representing 66% and 95% of the posterior, respectively. Honey bee counts represent the July transect sample for each site, which is the sample that occurred nearest the date of nectar sampling. For Franconia, depletion rates are shown for *Centaurea scabiosa* only, since this species was sampled across all sites but one. Note that the four sites with the lowest honey bee density all had zero honey bees per transect, but the interval plots are offset slightly to avoid overplotting.