

ARTICLE

Nectar robbing rather than pollinator availability constrains reproduction of a bee-flowered plant at high elevations

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Handling Editor: Debra P. C. Peters**Abstract**

Abiotic factors are generally assumed to determine whether species can exist at the extreme ends of environmental gradients, for example, at high elevations, whereas the role of biotic interactions is less clear. On temperate mountains, insect-pollinated plant species with bilaterally symmetrical flowers exhibit a parallel elevational decline in species richness and abundance with bees. This suggests that the lack of mutualistic interaction partners sets the elevational range limits of plants via a reduction in reproductive success. We used the bee-pollinated mountain plant *Clinopodium alpinum* (Lamiaceae), which blooms along a continuous 1000-m elevational gradient and has bilaterally symmetrical flowers, as a model to test the predicted parallel elevational decline in flower visitation and seed production. Although the community of flower visitors changed with elevation, the flower visitation rate by the most frequent visitors, bumble bees (33.8% of legitimate visits), and the overall rate of flower visitation by potential pollinators did not vary significantly with elevation. However, we discovered that nectar robbing by bumble bees and nectar theft by ants, two interactions with potentially negative effects on flowers, sharply increased with elevation. Seed set depended on pollinators across elevations and followed a weak hump-shaped pattern, peaking at mid-elevations and decreasing by about 20% toward both elevational range edges. Considering the mid- and high elevations, elevational variation in seed production could not be explained by legitimate bee visitation rates but was inversely correlated with the frequency of nectar robbing. Our observations challenge the hypothesis that a decrease in the availability of pollinators limits seed production of bee-flowered plants at high elevations but suggest that an increase in negative interactions (nectar robbing and larceny) constrains reproductive success.

KEYWORDS

altitudinal gradients, bee pollination, chalcidoid wasps, climatic gradients, elevational diversity patterns, *Empis*, floral larceny, fly pollination, mountain ecosystems, plant–pollinator interactions, range limits, zygomorphy

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INTRODUCTION

The potential geographic range of a species is determined by local abiotic conditions and biotic interactions, and the factors responsible for limiting a range can differ depending on which range limit is considered. According to a general hypothesis, abiotic factors are more likely to limit distributional ranges at harsh ends of environmental gradients, while biotic interactions should limit distributions at benign ends of environmental gradients (Louthan et al., 2015). Along elevational gradients, plant species will compete more strongly for space, nutrients, or light at lower elevations, where physical conditions are more favorable, and are likely to be primarily stressed by cold temperatures, weather extremes, or a lack of nutrients on mountain peaks (Körner, 1999). However, in the cases of species that obligatorily depend on specific partners, the biotic environment might also explain current distributional limits at abiotically harsh locations (Neuschulz et al., 2018). For example, most flowering plant species depend on animals, predominantly insects, as pollinators for mating and sexual reproduction (Ollerton et al., 2011). The extant diversity of both flower-visiting insects and angiosperms is thought to be the product of a coevolutionary process in which flower visitors evolve distinct floral preferences and different plants evolve different flower types to make the best use of their respective visitors (Gervasi & Schiestl, 2017; Willmer, 2011). As a result, the distribution of plant species with a specialized pollination system can be subject to biotic filtering by pollinators: The lack of specific flower visitors may hamper the recruitment of plant offspring and set the geographic limit of a population although local abiotic conditions are still suitable (Armbruster, 2017; Sargent & Ackerly, 2008).

Parallel diversity patterns of flowering plants and pollinating insects suggest that such a process of biotic filtering by pollinators is involved in structuring plant communities along elevational gradients on temperate mountains (Pellissier et al., 2010). With increasing elevation, the abundance and diversity of bees decrease, and flies become the dominant group of flower visitors (Arroyo et al., 1982; Classen et al., 2015; Hodkinson, 2005; Hoiss et al., 2012, 2015; Kearns, 1992; Lefebvre et al., 2018; McCabe et al., 2019; Warren et al., 1988; see Figure 1a). In parallel to the decline in bees, the diversity of plant species with bilaterally symmetrical flowers decreases from the foothills to the alpine zone (Pellissier et al., 2010; Fantinato et al., 2016; Hoiss et al., 2013; see Figure 1b). Bilaterally symmetrical flowers (i.e., monosymmetric flowers, including zygomorphic and bilabiate flowers) as opposed to radially symmetrical flowers are generally associated with pollination by bees (Neal et al., 1998; Westerkamp & Classen-Bockhoff, 2007). They often provide ample nectar

rewards which bees specifically forage for, and nectar is usually concealed so that it is only available to visitors with extendable mouthparts, such as bees. Furthermore, the bilateral flower symmetry makes visitors approach the flower in a specific way, allowing the flower to apply pollen grains to specific regions of the insect body where they are not easily reached by the cleaning legs of the insect. This is especially adaptive in the case of visitation by bees since it prevents complete pollen removal from the insect body and thus guarantees its transfer to the next flower (Koch et al., 2017; Reyes et al., 2016; Westerkamp & Classen-Bockhoff, 2007; Willmer, 2011; Yoder et al., 2020). The pollinator-mediated elevational filtering hypothesis therefore proposes that there is a causal link between the parallel elevational decline in bees and bee-flowered plants (Pellissier et al., 2010). The predictions are that decreasing abundance of bees leads to decreased flower visitation rates and hence reduced pollination and outcrossed seed set in the bee-pollinated flowers (Hargreaves et al., 2015). The reduction in seed set, in turn, would cause plant offspring numbers to fall beyond a critical threshold needed to maintain the population. However, the available evidence for pollinator-mediated filtering is only correlational (Pellissier et al., 2010), and it might well be that communities of bees and bee-flowered plant species simply exhibit parallel elevational patterns because both groups of organisms are affected by the same abiotic clines along elevation, for example, the reduction in temperature.

To directly test the predictions of the pollinator-filtering hypothesis, we need to examine whether individuals of the same plant species that grow at different elevations exhibit different rates of bee visitation per flower, and whether seed production is reduced or the level of autonomous self-pollination is increased at high elevations (Hargreaves et al., 2015; Mertens et al., 2020; Moeller et al., 2012; Theobald et al., 2016). We used a population of the labiate plant *Clinopodium alpinum* from the Northern Alps (Berchtesgaden National Park, Germany) to study such intraspecific elevational patterns of flower–insect interactions and seed set. *Clinopodium alpinum* occurs across a large elevational range of about 1000-m elevation from montane meadows to alpine grasslands and exhibits typical bilaterally symmetrical flowers associated with bee pollination (Knuth, 1898). Since the mountain slopes in our study area are steep, we could study plant patches that grow at different elevations but were geographically close, making it a suitable natural experiment. We tested the following specific predictions: (1) The pollinator communities of *C. alpinum* change with elevation; specifically, the flower visitation rate of bee pollinators decreases toward the high-elevation range limit; and (2a) seed production declines toward the high-elevation range limit, and/or (2b) the

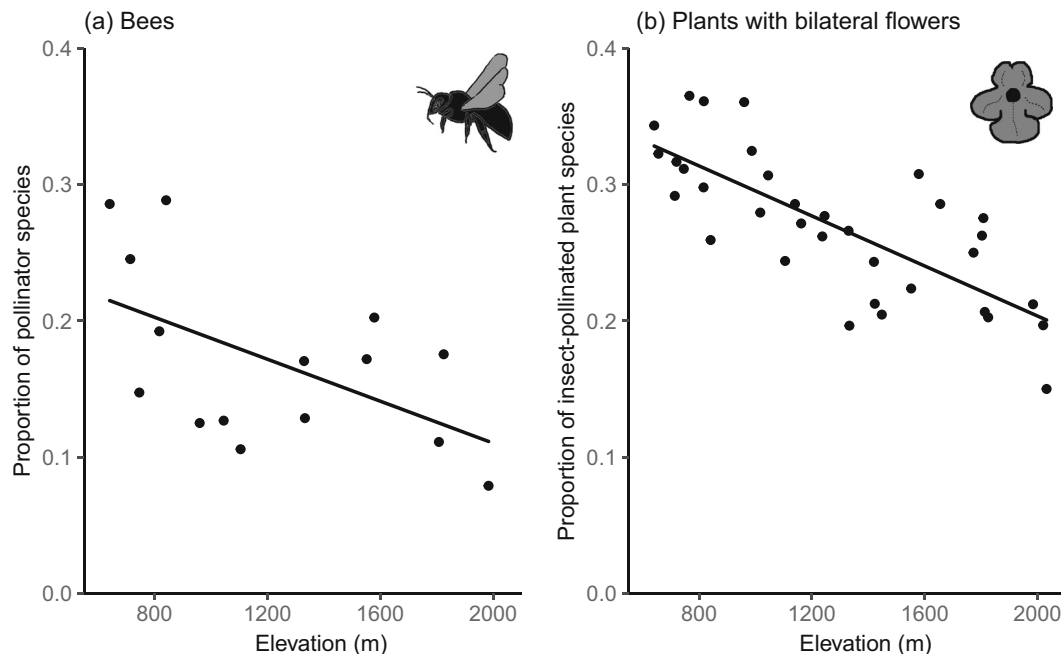


FIGURE 1 Parallel elevational decline in the share of bees among all flower visitors (a), and in the proportion of plants with bilaterally symmetrical flowers among insect-pollinated plants (b), in the Berchtesgaden National Park, Germany. Linear regression for bees: $y = 0.2641 - 0.000077x$, $p = 0.038$, $n = 15$; and for plants: $y = 0.3871 - 0.000092x$, $p < 0.001$, $n = 34$. Data from Hoiss et al. (2013, 2015) (see Appendix S1: Text 1)

ability to produce seeds based on autonomous self-pollination, as a measure of reproductive assurance under limited pollination (Erhardt & Jäggi, 1995; Kalisz & Vogler, 2003; Ling et al., 2017; Morgan & Wilson, 2005), increases toward the high-elevation range limit.

METHODS

Study species and study sites

Clinopodium alpinum (L.) Kuntze (= *Acinos alpinus* [L.] Moench, *Calamintha alpina* [L.] Lam.) is a perennial plant of the Lamiaceae family native to mountain areas from the Mediterranean region to Central Europe. It produces basally ramified and partially woody stems close to the soil surface. The flowers are arranged around the stems of young, vertical shoots in one or several whorl-like clusters, each with up to eight flowers (“verticillasters,” from here on we refer to the whole vertical shoots with flowers as “inflorescences”; see Figure 2a). The violet lip flowers have a conspicuous display and a tubular corolla, which conceal abundant nectar. The flowers are usually hermaphrodite; two short stamens terminate dorsally at the midpoint of the corolla tube, and two long stamens reach the corolla opening, as does the pistil. Pollen is released in advance or in synchrony with stigma receptivity, and

selfing is possible. Each ovary bears four ovules that may develop into 4 one-seeded nutlets upon successful fertilization (for simplicity, from here on we refer to “nutlets” as “seeds”). Bees are thought to be the main pollinators, but hoverflies and lepidopterans were also reported to be common flower visitors (Müller, 1881; Knuth, 1898; Owens & Uibera-Jimenez, 1992; and information from the TRY plant traits database, Kattge et al., 2011).

We conducted this study at the Berchtesgaden National Park in southeast Germany (N 47.55, E 12.92). The area is situated in the Northern Limestone Alps and encompasses mountain massifs with elevations of 600–2700 m above sea level. As the mountain slopes are steep, plant communities change over small spatial scales. Montane mixed forests dominate up to elevations of about 1500 m. They are interspersed with old mountain pastures, many of which are grazed by cattle or sheep. Subalpine krummholz vegetation ranges up to elevations of about 1800 m and is followed by (sub)alpine grasslands. The vegetation limit is between 2000 and 2300 m. In the study region, *C. alpinum* is common but patchily distributed. It grows in meadows and scree slopes, along paths and in rock fissures. We considered 21 localities at elevations between 910 and 1940 m representing the species’ main elevational range in the area. The sites were situated along four trails on different mountain slopes and distributed over an area of about 90 km² (see Figure 2b and

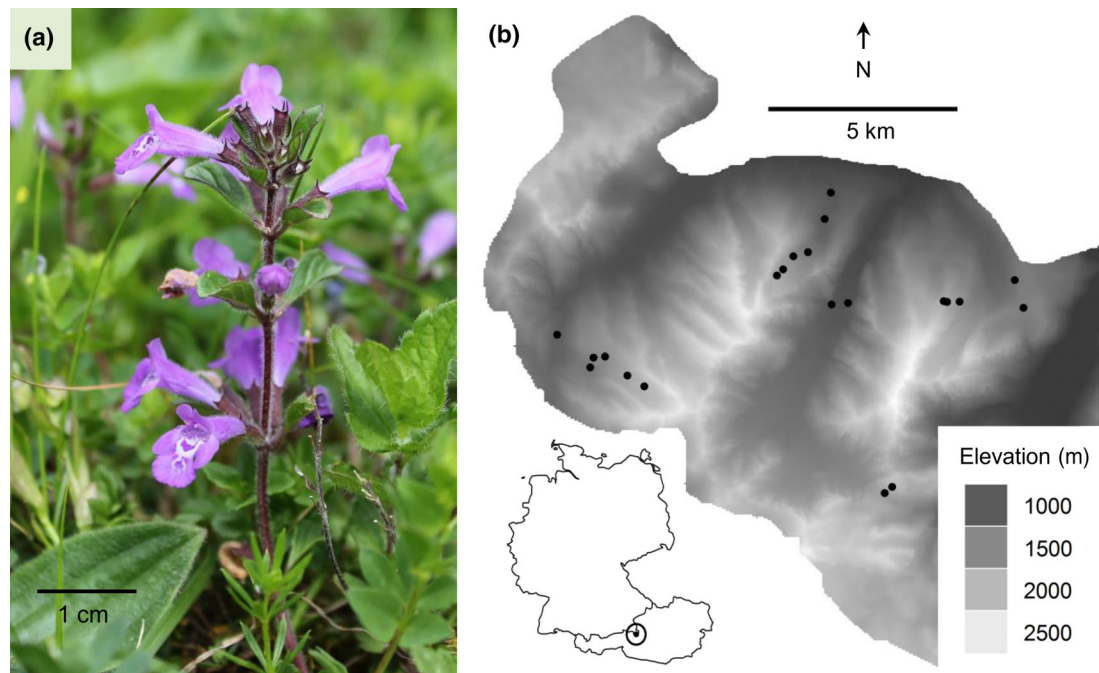


FIGURE 2 (a) Shoot with flowers of *Clinopodium alpinum*. (b) Topographic map of the Berchtesgaden National Park at the German–Austrian border with the 21 study sites indicated as black dots (map data source: Bayerische Vermessungsverwaltung, www.geodaten.bayern.de)

Appendix S1: Table S1). At each site, based on the criteria of accessibility and protection from grazing cattle or hikers, we chose single patches of flowers for observation. There was no elevational variation with respect to basic flowering traits (the number of flowers per inflorescence, the corolla tube length, and the flower display diameter; see Appendix S1: Text 2.2 and Figure S1), so the study population suited as a “natural experiment.”

Flower–insect interactions

Flower visitor observations

We determined the average visitation rate of all insect visitors to flowers of *C. alpinum* by making site-specific flower observations. In the study year, the flowering period started around mid-June and lasted until the end of August, but most flowers were in bloom during July. Between 15 June and 17 August 2017, we conducted 50 flower observation units, one to four observations per study site. Each lasted at least 20 min depending on visitor activities (Fijen & Kleijn, 2017), totaling 60–160 min of observation time per site (mean: 88.8 ± 29.3 min; here and in the following, we provide SDs alongside mean values). As we studied natural plant patches, these were not homogeneous in terms of size and density so that the number of simultaneously observed flowers per patch

ranged from 28 to 173 (mean: 94.6 ± 43.6). The local abundance of conspecific flowers can directly affect flower visitation rates and can indirectly affect seed production (via an effect on visitation and on the amount of available outcross pollen, e.g., Dauber et al., 2010). To take this factor into account, we also determined the number of conspecific open flowers within a radius of 2 m around the focal flowering patch. Data were only gathered on sunny or moderately clouded days with foothill temperatures above 20°C and during suitable light conditions (between 9:00 AM and 6:30 PM). We organized the observation units as such that the elevational distribution of observations was unbiased with respect to the day of the year (Spearman’s rank correlation: $n = 50$, $\rho = 0.197$, $p = 0.169$), daytime ($\rho = -0.012$, $p = 0.933$), and the observation exposure (observed flowers \times hours) ($\rho = -0.018$, $p = 0.903$). We noted the behavior and counted the number of flower visits of any insect at the observation patch during the observation time. For each visitor, we recorded its taxonomic group to the best possible level in the field. After observation, we captured some representative specimens for more detailed identification using specific identification keys (Amiet, 1996; Gokcezade et al., 2010; Grisell & Schauff, 1997; Hackston, 2012; Schaefer, 2009; Unwin, 1981; van Veen, 2004). We also classified each flower visit as being either “legitimate” or “illegitimate.” The first category applied when a visitor approached the flower frontally

and touched the reproductive organs, so it potentially contributed to pollination. The second category applied to nectar robbing (by short-tongued bumble bees), which is the extraction of nectar via lateral perforations bitten through the corolla tubes (including both primary nectar robbing, the making of a hole in the corolla to obtain nectar, and secondary nectar robbing, the use of existing holes to obtain nectar), and to nectar theft, which is the consumption of nectar without touching the anthers and/or the stigma of the flowers (Inouye, 1983).

Recording flower perforation by nectar robbers

Apart from direct visitor observations, we assessed the incidence of nectar robbing by determining the proportion of perforated corolla tubes among each of 12–20 (mean: 18.8 ± 2.9) randomly chosen flowers from different plants at the focal flower patches. These data were gathered once on each of 20 sites ($n = 376$ flowers).

Seed production

We determined the natural seed set and the ability to produce seeds through autonomous selfing in plants from the same sites for which we had gathered flower visitor observations. We considered seed set on the level of whole inflorescences for the analyses (and not on the level of individual flowers) since the seed set of flowers from the same inflorescence might not have been independent. Before flowering started, we covered 6–12 virgin inflorescences from different plants per study site with bags of nylon mesh to exclude insect visitors from the flowers during the whole flowering period (Kearns & Inouye, 1993). Between mid-July and the end of August, we collected 11–37 (mean: 21.9 ± 6.1) open-pollinated inflorescences from different plants and 3–11 bagged inflorescences (mean: 6.3 ± 2.8 ; some insect-exclusion bags were lost by wind and damage by cattle) per study site. We opened the ripened fruits with forceps under a stereomicroscope and counted the number of developed seeds. We only considered flowers for which the fate of each of the four ovules could be determined (i.e., those in which the seeds were not already dispersed). Of all flowers, 16.4% were infested with the larvae of an eulophid wasp species, which fed on the tissue of the flower base (see Appendix S1: Figure S2a). However, since seeds could still develop and be counted, and since infestation was independent of elevation ($p = 0.780$, Appendix S1: Figure S2b), flower herbivory by Eulophidae did not affect our results and conclusions.

Data analysis

We primarily analyzed whether insect–flower interactions and seed production varied in relation to elevation. As there was considerable variation in the patch-scale flower abundance among study sites, we also considered this variable as an explanatory factor (we used the log of flower abundance in the models). The patch-scale flower abundance tended to increase with elevation, but the correlation was not significant, so we considered elevation and patch-scale flower abundance as independent factors (Pearson’s correlation test: $n = 21$, $r = 0.269$, $p = 0.239$; Appendix S1: Figure S3). All statistical tests were performed with R 3.6.2 (R Core Team, 2019), and data figures were created using the graphics package “ggplot2” (Wickham, 2009).

As the general procedure, for each response variable we first compared up to three models with different combinations of explanatory factors, and the study site as a random factor using the Akaike information criterion (AIC; Burnham & Anderson, 1998; Bolker et al., 2017): a model with elevation as the sole explanatory factor; a model with the patch-scale flower abundance as a cofactor; and a model containing the interaction between elevation and the patch-scale flower abundance. For the respective best models (i.e., with the lowest AIC value), we inferred the significance of the fixed factors using likelihood-ratio tests (“anova” function).

We used separate models to analyze whether the pooled flower visitation rate of all legitimate flower visitors and the visitation rates of separate groups of visitors varied with elevation (analyses were not performed for visitors, which accounted for less than 5% of all flower visits and which were observed at less than half of the study sites). We modeled the original visitation count data and accounted for the number of flowers observed and the observation time (the observation exposure) using an offset variable (Reitan & Nielsen, 2016). Being a common problem with time-limited flower observations, our visitation counts contained many zeros and were highly variable. To reduce the part of the variation that was likely caused by the mode of data collection (limited observation times per observation unit; Martin et al., 2005), we pooled the observations per study site and used the data of the $n = 21$ study sites for the analyses. We fit generalized linear models with a quasi-Poisson error structure using the “glmmTMB” function (Brooks, Kristensen, & Benthem, 2017). For model comparison, we used the quasi-Akaike information criterion for overdispersed data with small sample sizes (“QAIC_c” function from the R-package “MuMIn”; Barton, 2018). To analyze the elevational pattern of nectar robbing (as determined by the absence or presence of corolla

perforations, binary variable), we used generalized linear mixed models with a binomial error structure (“glmmTMB” function; Brooks, Kristensen, van Benthem, et al., 2017).

We analyzed the seed/ovule ratios of open-pollinated inflorescences using linear mixed effect models (“lmer” function from the “lme4” package; Bates et al., 2015). To account for a hump-shaped pattern along the elevational gradient, we also considered models with elevation as a quadratic predictor. Since the seed counts of bagged inflorescences were low and resulting seed/ovule ratios were heteroscedastic and not normally distributed, we modeled the selfed seed counts as a function of elevation using a generalized linear mixed model with a quasi-Poisson error structure and the number of fertilizable ovules per inflorescence as an offset variable using “glmmTMB.”

RESULTS

Flower–insect interactions

Visitor observations

We recorded a total of 2392 interactions of insects with the flowers of *C. alpinum*, of which 87% were legitimate visits and 13% were visits in which insects stole or robbed

nectar, probably without pollinating (Inouye, 1980). On average, flowers received a legitimate visit every 80–90 min (0.68 visits/flower/h). The species composition and behavior of flower visitors were diverse (see Figure 3 for examples, and Appendix S1: Table S2 for an overview of recorded taxa). In descending order of visitation frequency, we distinguished the following species groups (the percentages in brackets give the share in legitimate visits and the share in all visits): bees (40.1% and 43.6%), of which we further distinguished bumble bees (33.8% and 38.1%) and solitary bees (6.3% and 5.5%); hoverflies (30.9% and 26.9%); “other flies” (that were neither hoverflies nor *Empis* flies; 15.8% and 13.8%); flies of the genus *Empis* (7.8% and 6.8%); ants (0% and 4.3%); and, to a minor extent, lepidopterans (4.4% and 3.8%), and beetles and wasps (both <1% of all visits). Variation in the patch-scale flower density among observation sites did not affect the estimated flower visitation rates as indicated by models with elevation as the sole explanatory factor being most parsimonious in every case (see Appendix S1: Table S3).

Although there were considerable elevational changes in the community composition of flower visitors (Figure 4a), the combined flower visitation rates of all legitimate visitors ($\chi^2 = 0.291$, df: 1, $p = 0.59$; Figure 4b) and the legitimate visitation by the most frequent visitor group, bumble bees ($\chi^2 = 0.366$, df: 1, $p = 0.545$), did not vary significantly with elevation. Bumble bees including



FIGURE 3 Representative flower visitors of *C. alpinum*. (a) A bumble bee (*Bombus pascuorum*) legitimately foraging. (b) The short-tongued bumble bee *B. wurflenii* robbing nectar. (c) A hoverfly feeding on pollen. (d) A muscoid fly licking the inner corolla surface. (e) *Empis* specimen sitting on the lower petal lobe. (f) The same specimen as in (e) sucking nectar. Photos by P. L. Kohl

Bombus pascuorum, *B. pratorum*, *B. hortorum*, *B. cf. terrestris*, and *B. wurflenii* collected nectar and/or pollen in the legitimate way at estimated rates between 0.2 and 0.3 visits/flower/h throughout the elevational range (Figures 3a and 4c). Visitation by solitary bees, in turn, decreased with elevation from an estimated 0.15 to almost zero visits/flower/h from the foothills to the sub-alpine grasslands ($\chi^2 = 5.695$, df: 1, $p = 0.017$; Figure 4d). When considering all legitimate visits by bumble bees and solitary bees together, the estimated visitation rates declined with elevation, but given the dominance by bumble bees, this pattern was not significant ($\chi^2 = 0.871$, df: 1, $p = 0.351$; see Appendix S1: Figure S4a). Apart from legitimate visitation, short-tongued bumble bees, especially *B. wurflenii* but also *B. pratorum* and *B. cf. terrestris*, robbed nectar (Figure 3b). Nectar robbing made up 8.7% of all observed visits, and in contrast to legitimate visitation, robbing rates sharply increased with

elevation ($\chi^2 = 17.433$, df: 1, $p = 0.020$; Figure 4e). While we did not observe any robbing visits up to the mid-elevation sites, individual flowers were robbed on average every 3–4 h at the high (sub)alpine grassland sites. When pooling legitimate visits and nectar-robbing visits, the average interaction rates of all bees tended to increase with elevation, but again, this was statistically insignificant ($\chi^2 = 1.346$, df: 1, $p = 0.246$; see Appendix S1: Figure S4b).

Hoverflies were represented both by species with short mouthparts (e.g., *Syrphus* species), which presumably fed on pollen provided at the corolla openings (Figure 3c), and by species with long mouthparts (e.g., *Volucella bombylans*), which fed on nectar. Visitation by hoverflies steadily increased with elevation from an estimated rate of 0.1 at the lowest sites to more than 0.3 visits/flower/h at high elevations ($\chi^2 = 4.224$, df: 1, $p = 0.040$; Figure 4f). Visitation by “other flies” (Diptera:

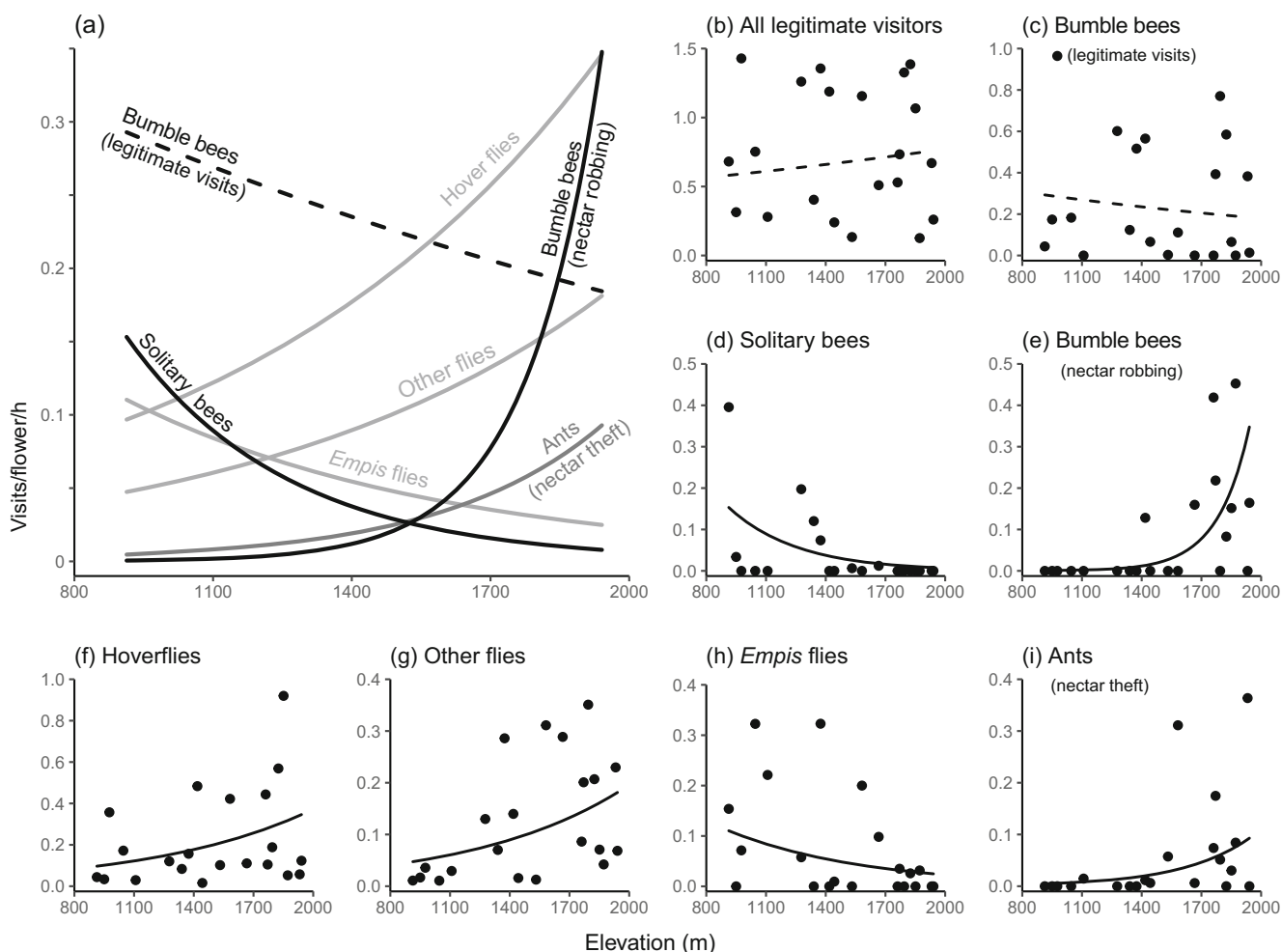


FIGURE 4 Elevational patterns of insect visitation to the flowers of *C. alpinum*. (a) Comparison of predicted flower visitation rates by different visitor groups. (b)–(i) Observed flower visitation rates per study site ($n = 21$, dots) and model prediction (lines) of all legitimate flower visitors pooled, and of different taxonomic groups or types of interactions. Dashed lines are presented when the factor elevation was not significant. See text and Appendix S1: Table S3 for statistics

superfamily Muscoidea and family Otitidae), which occasionally lapped the inner corolla surfaces and stamens with their sponge-like mouthparts (Figure 3d), also increased with elevation from an estimated 0.05 at the low edge to about 0.2 visits/flower/h at the high edge of the elevational range ($\chi^2 = 5.303$, df: 1, $p = 0.021$; Figure 4g). A rather distinct behavior was shown by flies of the genus *Empis* (Diptera: Empididae), which we therefore treat separately (Figure 3e,f). They moved from flower to flower in slow flight and consumed nectar with their long sucking mouthparts. In contrast to syrphids and other flies, visitation rates by *Empis* decreased with elevation ($\chi^2 = 6.722$, df: 1, $p = 0.010$; Figure 4h): They made about 0.1 visits/flower/h at low elevations but were rarely observed above the tree line.

Ant visitation showed a clear elevational increase with almost no observations at the lower half of the elevational range, but with an average rate of about 0.1 visits/flowers/h at subalpine sites ($\chi^2 = 8.507$, df: 1, $p = 0.004$; Figure 4i). By crawling into the corolla tubes without touching the reproductive structures, they stole nectar from *C. alpinum* flowers.

Flower perforation by nectar robbers

The incidence of nectar robbing, quantified as the proportion of flowers perforated by bumble bees, was best predicted by a model with elevation and the patch-scale flower abundance as interacting factors (whole model: $\chi^2 = 31.178$, df: 3, $p = 0.007$; Appendix S1: Table S4). The proportion of robbed flowers steadily increased with elevation (factor elevation: $\chi^2 = 21.805$, df: 1, $p = 0.007$). At sites below 1300 m, between 0% and 40% of corolla tubes were perforated; at mid-elevations, the proportion was about 50%; and at subalpine sites, up to 100% of flowers were robbed. There was a significant interaction between elevation and the patch-scale flower abundance in that the elevational increase in nectar robbing was more pronounced at patches with higher flower abundance (interaction: $\chi^2 = 6.902$, df: 1, $p = 0.009$; Figure 5).

Seed production

The seed/ovule ratios of inflorescences with open-pollinated flowers ranged between 0.39 and 0.81 per study site with an overall mean of 0.60 ± 0.10 seeds per ovule. The natural seed set followed a weak hump-shaped pattern along the elevational range: It peaked at mid-elevations (~ 0.65 seeds per ovule) and declined by about 20% toward both the high- and the low-elevation

range limit (~ 0.52 seeds per ovule) (Figure 6). The model with elevation as a quadratic predictor was significantly better than a model with elevation as a simple linear term ($\chi^2 = 5.803$, df: 1, $p = 0.016$), and the quadratic elevation model was marginally better than the intercept-only model assuming no elevational variation ($\chi^2 = 5.945$, df: 2, $p = 0.051$; see Appendix S1: Table S5).

The seed/ovule ratios of inflorescences from which insects were experimentally excluded ranged from 0.004 to 0.28 per study site with a mean of 0.10 ± 0.08 seeds per ovule, thus reaching on average about 16% (range: 1%–43%) of the seed set of open-pollinated inflorescences at the respective study sites. Seed set based on self-pollination only marginally increased with elevation from an estimated 0.06 seeds per ovule at the foothills to about 0.14 seeds per ovule at high elevations ($\chi^2 = 2.753$, df: 1, $p = 0.097$; Figure 6).

DISCUSSION

Species numbers and abundance of both bees and bee-flowered plants decrease with increasing elevation, leading to the hypothesis that the lack of bee pollinators sets elevational range limits of plants (Pellissier et al., 2010). Contrary to the prediction of the pollinator-filtering hypothesis, we found that the flowers of the bee-pollinated plant *C. alpinum* were visited by bees at similar rates throughout a large elevational range due to a

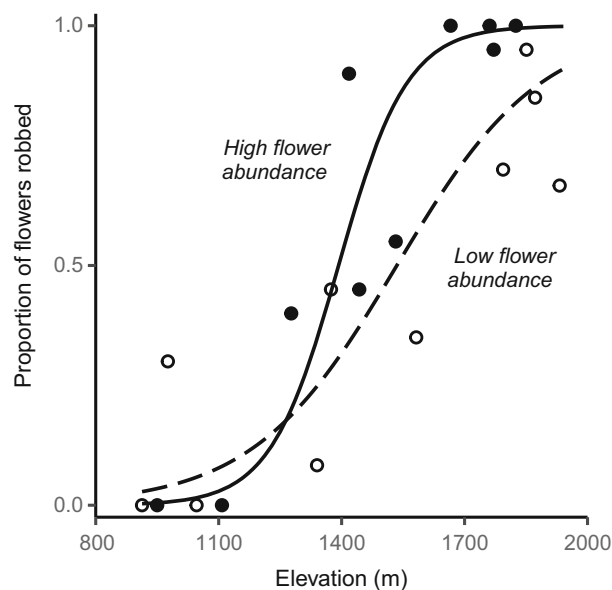


FIGURE 5 Proportion of flowers robbed by short-tongued bumble bees on $n = 20$ study sites in relation to elevation. Lines are logistic regressions. Data were grouped post hoc into two categories of flower abundance to illustrate the interactive effect of elevation and flower abundance. See text for statistics

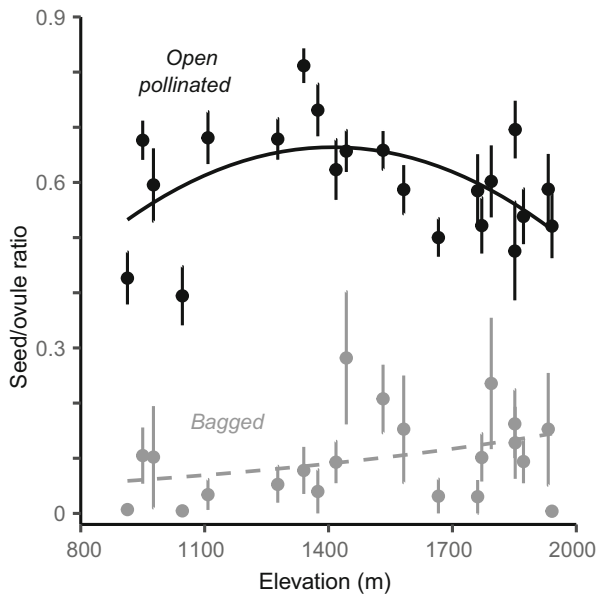


FIGURE 6 Elevational patterns of seed production in open-pollinated (black) and bagged (visitors excluded, gray) inflorescences of *C. alpinum*. Dots and vertical lines show mean seed/ovule ratios \pm SE for $n = 21$ study sites. The lines are predictions by a quadratic LMM (open-pollinated) and a quasi-Poisson GLMM (bagged). See text for statistics

high share in visitation by bumble bees. Furthermore, elevational variation in seed set was not associated with variation in legitimate flower visitation. These data cast doubt on whether the parallel elevational declines in species numbers of bees and of bee-flowered plants are functionally related.

Considering legitimate visitation, the elevational variation in flower visitor composition of the single plant species *C. alpinum* partly reflected the general elevational patterns of flower visitor communities: Visitation rates by most dipterans increased, and visitation rates by solitary bees decreased with elevation. However, the visitation rates by all bees declined only insignificantly with elevation since bumble bees, which accounted for around 85% of all legitimate bee visits, visited flowers at high rates across elevations. Bumble bees are special among bees since they bear a set of adaptations that enable them to forage under cold and adverse weather conditions, which often prevail at high elevations (Heinrich, 1979; Peters et al., 2016). Given that bumble bees are generally among the most effective pollinators (Gorenflo et al., 2017; Willmer et al., 2017), it seems unlikely that *C. alpinum* experiences a lack of effective pollinators at its high-elevation range limit. Furthermore, if the small elevational reduction in visitation by bees made a difference at all, it was probably leveled out by the elevational increase in visitation by dipterans (Larson

et al., 2001). Particularly, hoverflies, who have the potential to be effective pollen vectors (Doyle et al., 2020; Goulson & Wright, 1998; Willmer, 2011), probably contributed to pollination of *C. alpinum* since they were the most frequent visitors at high elevations and often made several visits between conspecific flowers.

In contrast to legitimate flower visitation, we discovered that there was a substantial variation in the frequency of nectar robbing and nectar theft along the elevational gradient: While there was no nectar robbing at many low-elevation sites, the nectar of virtually all flowers was robbed at the highest elevations. Since the flowers of *C. alpinum* are similar in shape across their elevational range, and since the three bumble bee species observed robbing nectar (*B. wurflenii*, *B. cf. terrestris* and *B. pratorum*) are all common across the whole elevational range (Hoiss et al., 2012), the reason for the increase in nectar robbing must be a shift in the behavior of the bumble bees. A likely cause is a change in the ratio between their energetic requirements and the availability of nectar along the elevational gradient (Heinrich & Raven, 1972). At higher elevations, foraging bumble bees need to fly in cooler and thinner air, which should boost their energetic needs (Hodkinson, 2005). If their nests are located up the mountains, they will also have higher energetic needs to keep the brood warm. Both factors should lead to a higher energy demand per foraging bumble bee at higher elevations. In turn, since species richness and abundance of nectar-producing plants species decrease with elevation (Hoiss et al., 2013), the absolute nectar availability likely decreases. This would mean that, at higher elevations, the nectar produced by *C. alpinum* flowers has a larger share in all nectar produced by the plant community. Under these circumstances, it would make sense that bumble bees visit *C. alpinum* flowers more often at higher elevations to rob its nectar if it is otherwise inaccessible. The scenario of an elevational shift in the behavior of flower visitors is independently supported by the elevational increase in the visitation rates of nectar-thieving ants, since ants are typically less abundant at higher elevations and would therefore, all else being equal, be expected to show lower visitation rates at higher elevations (Fontana et al., 2020; Glaser, 2006; Peters et al., 2014). The more pronounced elevational increase in nectar robbing in plant patches with higher flower densities than in plant patches with lower flower densities further suggests that the absolute reward density plays a role in determining robbing rates of *C. alpinum* flowers (Rojas-Nossa et al., 2016). Compared with the small elevational changes in legitimate visitation, it seems that variation in nectar robbing and nectar theft could have a relatively stronger effect on floral reproduction in *C. alpinum*.

The prediction of the pollinator-filtering hypothesis regarding plant reproductive success is that a reduction in flower visitation rates leads to suboptimal pollination at the high-elevation range edge so that plants fail to produce enough seeds to propagate at higher elevations. An alternative, nonexclusive prediction is that subpopulations at high elevations compensate for reduced insect pollination by an enhanced capacity to produce seeds via autonomous self-pollination—a strategy, however, that bears potential long-term fitness cost through inbreeding depression (Erhardt & Jäggi, 1995; Kalisz & Vogler, 2003; Kühn et al., 2006; Ling et al., 2017; Morgan & Wilson, 2005). We found a marginal elevational increase in autonomous seed set; however, seed production of bagged inflorescences was generally substantially lower than that of open-pollinated inflorescences, showing that *C. alpinum* highly depended on pollinators across elevations. Seed production of open-pollinated flowers followed a hump-shaped elevational pattern and therefore indeed declined from mid- to high elevations. However, this reduction in natural seed could not be explained by changes in legitimate visitation rates by bees, since these were similar between mid- and high-elevations: There was no significant correlation between the average seed set per site and the observed bee visitation rates (Figure 7a). Therefore, it seems unlikely that the population of *C. alpinum* is primarily pollinator-limited at its high-elevation range edge, an outcome in line with several other studies that investigated pollination and floral reproduction of different plant species at

environmentally harsh (high-elevation or high-latitude) range edges (Bingham & Orthner, 1998; Hargreaves et al., 2015; Koch et al., 2020). Interestingly, the only marked difference to the mid-elevations with respect to insect visitation is the clear increase in nectar robbing by bumble bees and nectar theft by ants. On the one hand, nectar robbers might directly reduce fitness by damaging flowers. On the other hand, both nectar robbers and nectar thefts might indirectly reduce fitness by rendering flowers less attractive to legitimate visitors (Hanna et al., 2015; Irwin et al., 2010; Irwin et al., 2015; Levan & Holway, 2015; Traveset et al., 1998). Indeed, when directly contrasted, there was a significant negative correlation between the average seed set and the proportion of robbed flowers per study site (Figure 7b). Although we cannot exclude the possibility that the elevational variation in seed set in *C. alpinum* was caused by abiotic factors, such as resource limitation (Straka & Starzomski, 2015), the striking elevational increase in both nectar robbing and theft suggests that there is a causal link to the drop in seed set toward the high-elevation range edge (Irwin et al., 2010). The validity of this hypothesis can be tested with rigorous robber exclusion experiments (Irwin et al., 2010; Morris, 1996; Rojas-Nossa et al., 2021; Traveset et al., 1998; Ye et al., 2017a, 2017b; Zhang et al., 2007; Zhang et al., 2014).

Against the expectation, our study showed that a plant species with typical bilaterally symmetrical, bee-pollinated flowers does not experience a significant shortage of legitimate flower visits at high elevations, making

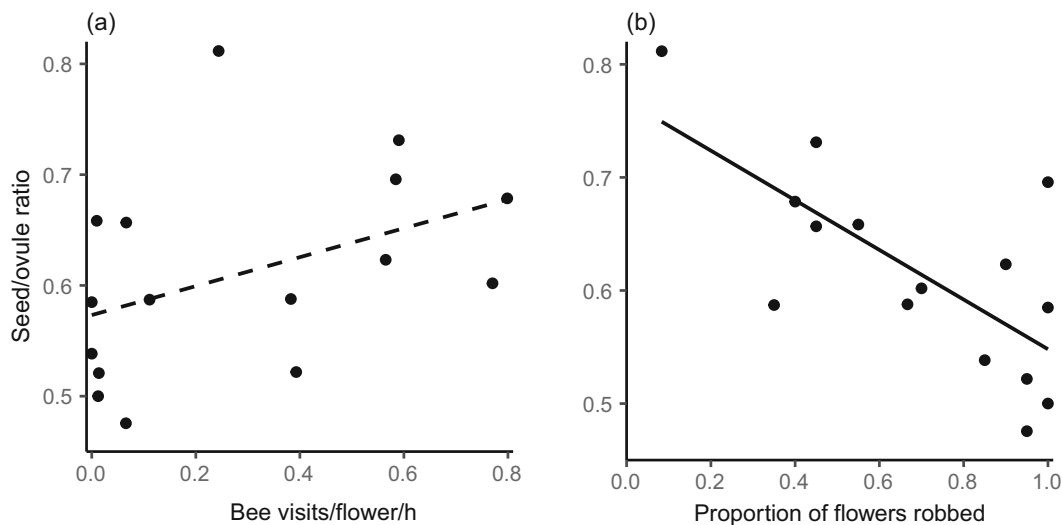


FIGURE 7 Legitimate bee visitation and nectar robbing as potential factors explaining the decline in seed production from mid- to high elevations. (a) Average seed set per study site in relation to the observed average legitimate flower visitation rate by bees ($n = 16$). (b) Average seed set per study site in relation to the proportion of flowers perforated by nectar robbers ($n = 15$). Only study sites covering the mid- to high-elevation range of *C. alpinum* (c. 1200–2000 m) are considered. Lines are predictions by simple linear regression models (bee visitation: $F_{1,14} = 3.014$, adjusted $R^2 = 0.118$, $p = 0.105$; nectar robbing: $F_{1,13} = 12.8$, adjusted $R^2 = 0.457$, $p = 0.003$)

it unlikely that reduced pollinator availability affects its reproduction and high-elevation range limits. Therefore, under the assumption that our study plant is a good representative, our results challenge the hypothesis of a functional relationship between the parallel elevational decline in bees and plants with bilaterally symmetrical flowers. It seems more likely that the parallel patterns are caused by an abiotic cline to which both groups of organisms react similarly (Louthan et al., 2015; Pellissier et al., 2010). Since most extant bee species are thermophilous and can be found in relatively warm areas (Classen et al., 2015; Michener, 2000), it can be assumed that the first bees originated in regions with mild climates. Consequently, plant lineages that evolved a bilateral flower symmetry as an adaptation to bee pollination must also have originated in warm-climate regions. It is therefore conceivable that both groups of organisms incidentally share phylogenetically rooted temperature constraints, which makes them less likely to colonize regions with cold climate such as high mountain areas (McCabe et al., 2019). However, even though our data cast doubt on the pollinator-filtering hypothesis in the way it was proposed (Pellissier et al., 2010), biotic interactions with flower visitors might still play a role in determining the elevational range limitations of plants with bilateral flowers. Insects foraging at colder temperatures have higher energetic needs (Heinrich & Raven, 1972) so that they will try to increase their sugar intake rate (Guariento et al., 2018). It is therefore likely that an elevational increase in the rates of nectar robbing and theft, as we reported it here, is a general phenomenon on temperate mountains (see Utelli & Roy, 2001, who found higher frequencies of nectar robbing in *Aconitum lycoctonum* at two high-elevation populations compared with two low-elevation populations in Switzerland). The potential consequence could be the overexploitation of the usually reward-rich bilateral, bee-pollinated flowers at high elevations and a breakdown of their mutualism with legitimate visitors.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Kohl & Steffan-Dewenter, 2022) are available from Dryad: <https://doi.org/10.5061/dryad.73n5tb2wz>.

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REFERENCES

- Amiet F. 1996. Hymenoptera Apidae, 1. Teil. Allgemeiner Teil, Gattungsschlüssel, Die Gattungen Apis, Bombus und Psithyrus. *Insecta Helvetica* 12.
- Armbruster, W. S. 2017. "The Specialization Continuum in Pollination Systems: Diversity of Concepts and Implications for Ecology, Evolution and Conservation." *Functional Ecology* 31: 88–100.
- Arroyo, M. T. K., R. Primack, and J. Armesto. 1982. "Community Studies in Pollination Ecology in the High Temperate Andes of Central Chile. I. Pollination Mechanisms and Altitudinal Variation." *American Journal of Botany* 69: 82.
- Barton, K. 2018. MuMIn: Multi-Model Inference R package version 1.43.6. <https://cran.r-project.org/package=MuMIn>.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Bingham, R. A., and A. R. Orthner. 1998. "Efficient Pollination of Alpine Plants." *Nature* 391: 238–9.
- Bolker, B., and RDCT. 2017. bbmle: Tools for General Maximum Likelihood Estimation. R package version 1.0.20. <https://cran.r-project.org/package=bbmle>.
- Brooks, M. E., K. Kristensen, and K. J. V. Benthem. 2017. "Modeling Zero-Inflated Count Data with glmmTMB." *bioRxiv*: 132753. doi: <https://doi.org/10.1101/132753>.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. "glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9: 378–400.
- Burnham, K. P., and D. R. Anderson. 1998. "Practical Use of the Information-Theoretic Approach." In *Model Selection and Inference* 75–117. New York, NY: Springer.
- Classen, A., M. K. Peters, W. J. Kindeketa, T. Appelhans, C. D. Eardley, M. W. Gikungu, A. Hemp, T. Nauss, and I. Steffan-Dewenter. 2015. "Temperature Versus Resource Constraints: Which Factors Determine Bee Diversity on Mount Kilimanjaro, Tanzania?" *Global Ecology and Biogeography* 24: 642–52.
- Dauber, J., J. C. Biesmeijer, D. Gabriel, W. E. Kunin, E. Lamborn, B. Meyer, A. Nielsen, et al. 2010. "Effects of Patch Size and Density on Flower Visitation and Seed Set of Wild Plants: A Pan-European Approach." *Journal of Ecology* 98: 188–96.
- Doyle, T., W. L. S. Hawkes, R. Massy, G. D. Powney, M. H. M. Menz, and K. R. Wotton. 2020. "Pollination by Hoverflies in the Anthropocene." *Proceedings of the Royal Society B: Biological Sciences* 287: 20200508.
- Erhardt, A., and B. Jäggi. 1995. "From Pollination by Lepidoptera to Selfing: The Case of *Dianthus glacialis* (Caryophyllaceae)." *Plant Systematics and Evolution* 195: 67–76.

- Fantinato, E., M. Giovanetti, S. Del Vecchio, and G. Buffa. 2016. "Altitudinal Patterns of Floral Morphologies in Dry Calcareous Grasslands." *Plant Sociology* 53: 83–90.
- Fijen, T. P. M., and D. Kleijn. 2017. "How to Efficiently Obtain Accurate Estimates of Flower Visitation Rates by Pollinators." *Basic and Applied Ecology* 19: 11–8.
- Fontana, V., E. Guariento, A. Hilpold, G. Niedrist, M. Steinwandter, D. Spitale, J. Nascimbene, U. Tappeiner, and J. Seeber. 2020. "Species Richness and Beta Diversity Patterns of Multiple Taxa along an Elevational Gradient in Pastured Grasslands in the European Alps." *Scientific Reports* 10: 1–11.
- Gervasi, D. D. L., and F. P. Schiestl. 2017. "Real-Time Divergent Evolution in Plants Driven by Pollinators." *Nature Communications* 8: 14691.
- Glaser, F. 2006. "Biogeography, Diversity, and Vertical Distribution of Ants (Hymenoptera: Formicidae) in Vorarlberg, Austria." *Myrmecological News* 8: 263–70.
- Gokcezade, J. F., B. A. Gereben-Krenn, J. Neumayer, and H. W. Krenn. 2010. "Feldbestimmungsschlüssel für die Hummeln Österreichs, Deutschlands und der Schweiz (Hymenoptera, Apidae)." *Linzer biologische Beiträge* 42: 5–42.
- Gorenflo, A., T. Diekötter, M. van Kleunen, V. Wolters, and F. Jauker. 2017. "Contrasting Pollination Efficiency and Effectiveness among Flower Visitors of *Malva sylvestris*, *Borago officinalis* and *Onobrychis vicifolia*." *Journal of Pollination Ecology* 21: 62–70.
- Goulson, D., and N. Wright. 1998. "Flower Constancy in the Hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae)." *Behavioral Ecology* 9: 213–9.
- Grisell, E., and M. E. Schauff. 1997. *A Handbook of the Families of Nearctic Chalcidoidea (Hymenoptera)*. Washington, DC: Entomological Society of Washington.
- Guariento, E., J. Martini, and K. Fiedler. 2018. "Bait Visitation by *Formica lemni* (Hymenoptera: Formicidae) Indicates Shortage of Carbohydrates in Alpine Grasslands." *European Journal of Entomology* 115: 217–22.
- Hackston, M. 2012. Key to Genera of Empididae. <https://sites.google.com/site/mikesinsectkeys2/home/brachycera/empididae>.
- Hanna, C., I. Naughton, C. Boser, R. Alarcón, K. L. J. Hung, and D. Holway. 2015. "Floral Visitation by the Argentine Ant Reduces Bee Visitation and Plant Seed Set." *Ecology* 96: 222–30.
- Hargreaves, A. L., J. L. Weiner, and C. G. Eckert. 2015. "High-Elevation Range Limit of an Annual Herb Is neither Caused nor Reinforced by Declining Pollinator Service." *Journal of Ecology* 103: 572–84.
- Heinrich, B. 1979. *Bumblebee Economics*. Cambridge: Harvard University Press.
- Heinrich, B., and P. H. Raven. 1972. "Energetics and Pollination Ecology." *Science* 176: 597–602.
- Hodkinson, I. D. 2005. "Terrestrial Insects along Elevation Gradients: Species and Community Responses to Altitude." *Biological Reviews* 80: 489.
- Hoiss, B., J. Gavrira, A. Leingärtner, J. Krauss, and I. Steffan-Dewenter. 2013. "Combined Effects of Climate and Management on Plant Diversity and Pollination Type in Alpine Grasslands." *Diversity and Distributions* 19: 386–95.
- Hoiss, B., J. Krauss, S. G. Potts, S. Roberts, and I. Steffan-Dewenter. 2012. "Altitude Acts as an Environmental Filter on Phylogenetic Composition, Traits and Diversity in Bee Communities." *Proceedings of the Royal Society B: Biological Sciences* 279: 4447–56.
- Hoiss, B., J. Krauss, and I. Steffan-Dewenter. 2015. "Interactive Effects of Elevation, Species Richness and Extreme Climatic Events on Plant-Pollinator Networks." *Global Change Biology* 21: 4086–97.
- Inouye, D. W. 1980. "The Terminology of Floral Larceny." *Ecology* 61: 1251–3.
- Inouye, D. W. 1983. "The Ecology of Nectar Robbing." In *The Biology of Nectararies*, edited by B. Bentley and T. Elias, 153–73. New York, NY: Columbia University Press.
- Irwin, R. E., J. L. Bronstein, J. S. Manson, and L. Richardson. 2010. "Nectar Robbing: Ecological and Evolutionary Perspectives." *Annual Review of Ecology, Evolution, and Systematics* 41: 271–92.
- Irwin, R. E., P. Howell, and C. Galen. 2015. "Quantifying Direct vs. Indirect Effects of Nectar Robbers on Male and Female Components of Plant Fitness." *Journal of Ecology* 103(6): 1487–97.
- Kalisz, S., and D. W. Vogler. 2003. "Benefits of Autonomous Selfing under Unpredictable Pollinator Environments." *Ecology* 84: 2928–42.
- Kattge, J., S. Diaz, S. Lavorel, C. Prentice, P. Leadley, G. Boenisch, E. Garnier, et al. 2011. "TRY – A Global Database of Plant Traits." *Global Change Biology* 17: 2905–35.
- Kearns, C. A. 1992. "Anthophilous Fly Distribution across an Elevation Gradient." *The American Midland Naturalist* 127: 172–82.
- Kearns, C. A., and D. W. Inouye. 1993. *Techniques for Pollination Biologists*. Boulder, CO: University Press of Colorado.
- Knuth, P. 1898. *Handbuch der Blütenbiologie*. Leipzig.
- Koch, L., K. Lunau, and P. Wester. 2017. "To Be on the Safe Site – Ungroomed Spots on the Bee's Body and Their Importance for Pollination." *PLoS One* 12: 1–16.
- Koch, V., L. Zoller, J. M. Bennett, and T. M. Knight. 2020. "Pollinator Dependence but No Pollen Limitation for Eight Plants Occurring North of the Arctic Circle." *Ecology and Evolution* 10: 13664–72.
- Kohl, P. L., and I. Steffan-Dewenter. 2022. "Data From: Nectar Robbing Rather Than Pollinator Availability Constrains Reproduction of a Bee-Flowered Plant at High Elevations." Dryad. Dataset. <https://doi.org/10.5061/dryad.73n5tb2wz>.
- Körner, C. 1999. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Berlin, Heidelberg: Springer-Verlag.
- Kühn, I., S. M. Bierman, W. Durka, and S. Klotz. 2006. "Relating Geographical Variation in Pollination Types to Environmental and Spatial Factors Using Novel Statistical Methods." *New Phytologist* 172: 127–39.
- Larson, B. M. H., P. G. Kevan, and D. W. Inouye. 2001. "Flies and Flowers: Taxonomic Diversity of Anthophiles and Pollinators." *The Canadian Entomologist* 133: 439–65.
- Lefebvre, V., C. Villemant, C. Fontaine, and C. Daugeon. 2018. "Altitudinal, Temporal and Trophic Partitioning of Flower-Visitors in Alpine Communities." *Scientific Reports* 8(1): 1–12.
- Levan, K. E., and D. A. Holway. 2015. "Ant-Aphid Interactions Increase Ant Floral Visitation and Reduce Plant Reproduction via Decreased Pollinator Visitation." *Ecology* 96: 1620–30.
- Ling, T. C., L. Wang, Z. Zhang, A. Dafni, Y. Duan, and Y. Yang. 2017. "High Autonomous Selfing Capacity and Low Flower

- Visitation Rates in a Subalpine Population of *Prunella vulgaris* (Lamiaceae)." *Plant Ecology and Evolution* 150: 59–66.
- Louthan, A. M., D. F. Doak, and A. L. Angert. 2015. "Where and When Do Species Interactions Set Range Limits?" *Trends in Ecology and Evolution* 30: 780–92.
- Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. "Zero Tolerance Ecology: Improving Ecological Inference by Modelling the Source of Zero Observations." *Ecology Letters* 8: 1235–46.
- McCabe, L. M., N. S. Cobb, and B. J. Butterfield. 2019. "Environmental Filtering of Body Size and Darker Coloration in Pollinator Communities Indicate Thermal Restrictions on Bees, but Not Flies, at High Elevations." *PeerJ* 7: e7867.
- Mertens, J. E. J., Š. Janeček, F. F. Dzekashu, E. Chmelová, E. B. Fokam, and R. Tropek. 2020. "Changes in Pollinator Community of *Scadoxus cinnabarinus* (Amaryllidaceae) along its Elevational Range on Mount Cameroon." *Arthropod-Plant Interactions* 14: 215–26.
- Michener, C. D. 2000. *The Bees of the World*. Baltimore, MD: JHU Press.
- Moeller, D. A., M. A. Geber, V. M. Eckhart, and P. Tiffin. 2012. "Reduced Pollinator Service and Elevated Pollen Limitation at the Geographic Range Limit of an Annual Plant." *Ecology* 93: 1036–48.
- Morgan, M. T., and W. G. Wilson. 2005. "Self-Fertilization and the Escape from Pollen Limitation in Variable Pollination Environments." *Evolution* 59: 1143.
- Morris, W. F. 1996. "Mutualism Denied? Nectar-Robbing Bumble Bees Do Not Reduce Female or Male Success of Bluebells." *Ecology* 77: 1451–62.
- Müller, H. 1881. *Alpenblumen, ihre Befruchtung durch Insekten und ihre Anpassungen an dieselben*. Leipzig.
- Neal, P. R., A. Dafni, and M. Giurfa. 1998. "Floral Symmetry and Its Role in Plant-Pollinator Systems: Terminology, Distribution, and Hypotheses." *Annual Review of Ecology and Systematics* 29(1): 345–73.
- Neuschulz, E. L., D. Merges, K. Bollmann, F. Gugerli, and K. Böhning-Gaese. 2018. "Biotic Interactions and Seed Deposition Rather than Abiotic Factors Determine Recruitment at Elevational Range Limits of an Alpine Tree." *Journal of Ecology* 106(3): 948–59.
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. "How Many Flowering Plants Are Pollinated by Animals?" *Oikos* 120: 321–6.
- Owens, S. J., and J. L. Ubers-Jimenez. 1992. "Breeding Systems in Labiatae." In *Advances in Labiatae Science*, edited by R. M. Harley and T. Reynolds, 257–80. London: Kew.
- Pellissier, L., J. Pottier, P. Vittoz, A. Dubuis, and A. Guisan. 2010. "Spatial Pattern of Floral Morphology: Possible Insight into the Effects of Pollinators on Plant Distributions." *Oikos* 119: 1805–13.
- Peters, M. K., A. Mayr, J. Röder, N. J. Sanders, and I. Steffan-Dewenter. 2014. "Variation in Nutrient Use in Ant Assemblages along an Extensive Elevational Gradient on Mt Kilimanjaro." *Journal of Biogeography* 41: 2245–55.
- Peters, M. K., J. Peisker, I. Steffan-Dewenter, and B. Hoiss. 2016. "Morphological Traits Are Linked to the Cold Performance and Distribution of Bees along Elevational Gradients." *Journal of Biogeography* 43: 2040–9. <https://doi.org/10.1111/jbi.12768>.
- R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reitan, T., and A. Nielsen. 2016. "Do Not Divide Count Data with Count Data; a Story from Pollination Ecology with Implications Beyond." *PLoS ONE* 11: e0149129.
- Reyes, E., H. Sauquet, and S. Nadot. 2016. "Perianth Symmetry Changed at Least 199 Times in Angiosperm Evolution." *Taxon* 65: 945–64.
- Rojas-Nossa, S. V., J. M. Sánchez, and L. Navarro. 2016. "Nectar Robbing: A Common Phenomenon Mainly Determined by Accessibility Constraints, Nectar Volume and Density of Energy Rewards." *Oikos* 125: 1044–55.
- Rojas-Nossa, S. V., J. M. Sánchez, and L. Navarro. 2021. "Nectar Robbing and Plant Reproduction: An Interplay of Positive and Negative Effects." *Oikos* 130(4): 601–8.
- Sargent, R. D., and D. D. Ackerly. 2008. "Plant-Pollinator Interactions and the Assembly of Plant Communities." *Trends in Ecology and Evolution* 23: 123–30.
- Schaefer, M., ed. 2009. *Brohmer – Fauna von Deutschland*. Wiebelsheim: Quelle & Meyer.
- Straka, J. R., and B. M. Starzomski. 2015. "Fruitful Factors: What Limits Seed Production of Flowering Plants in the Alpine?" *Oecologia* 178: 249–60.
- Theobald, E. J., H. Gabrielyan, and J. HilleRisLambers. 2016. "Lilies at the Limit: Variation in Plant-Pollinator Interactions across an Elevational Range." *American Journal of Botany* 103: 189–97.
- Traveset, A., M. F. Willson, and C. Sabag. 1998. "Effect of Nectar-Robbing Birds on Fruit Set of *Fuchsia magellanica* in Tierra Del Fuego: A Disrupted Mutualism." *Functional Ecology* 12: 459–64.
- Unwin, D. M. 1981. "A Key to the Families of British Diptera." *Field Studies* 5: 513–33.
- Utelli, A. B., and B. A. Roy. 2001. "Causes and Consequences of Floral Damage in *Aconitum lycoctonum* at High and Low Elevations in Switzerland." *Oecologia* 127(2): 266–73.
- van Veen, M. P. 2004. *Hoverflies of the Northwest Europe – Identification Keys to the Syrphidae*. Zeist: KNNV Publishing.
- Warren, S. D., K. T. Harper, and G. M. Booth. 1988. "Elevational Distribution of Insect Pollinators." *American Midland Naturalist* 120: 325–30.
- Westerkamp, C., and R. Classen-Bockhoff. 2007. "Bilabiate Flowers: The Ultimate Response to Bees?" *Annals of Botany* 100: 361–74.
- Wickham, H. 2009. *Ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Willmer, P. 2011. *Pollination and Floral Ecology*. Princeton, NJ: Princeton University Press.
- Willmer, P. G., H. Cunnold, and G. Ballantyne. 2017. "Insights from Measuring Pollen Deposition: Quantifying the Pre-Eminence of Bees as Flower Visitors and Effective Pollinators." *Arthropod-Plant Interactions* 11: 411–25.
- Ye, Z. M., X. F. Jin, Q. F. Wang, C. F. Yang, and D. W. Inouye. 2017a. "Nectar Replenishment Maintains the Neutral Effects of Nectar Robbing on Female Reproductive Success of *Salvia przewalskii* (Lamiaceae), a Plant

- Pollinated and Robbed by Bumble Bees.” *Annals of Botany* 119(6): 1053–9.
- Ye, Z. M., X. F. Jin, Q. F. Wang, C. F. Yang, and D. W. Inouye. 2017b. “Pollinators Shift to Nectar Robbers When Florivory Occurs, with Effects on Reproductive Success in *Iris Bulleyana* (Iridaceae).” *Plant Biology* 19(5): 760–6.
- Yoder, J. B., G. Gomez, and C. J. Carlson. 2020. “Zygomorphic Flowers Have Fewer Potential Pollinator Species.” *Biology Letters* 16: 2–7.
- Zhang, Y. W., G. W. Robert, Y. Wang, and Y. H. Guo. 2007. “Nectar Robbing of a Carpenter Bee and Its Effects on the Reproductive Fitness of *Glechoma longituba* (Lamiaceae).” *Plant Ecology* 193(1): 1–13.
- Zhang, Y. W., J. M. Zhao, and D. W. Inouye. 2014. “Nectar Thieves Influence Reproductive Fitness by Altering Behavior of Nectar Robbers and Legitimate Pollinators in *Corydalis ambigua* (Fumariaceae).” *Journal of Ecology* 102: 229–37.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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