

Research

Floral preferences of mountain bumble bees are constrained by functional traits but flexible through elevation and season

Douglas Sponsler, Katharina Kallnik, Fabrice Requier, Alice Classen, A. Fabienne Maihoff, Johanna Sieger and Ingolf Steffan-Dewenter

D. Sponsler (<https://orcid.org/0000-0002-4892-9332>) ✉ (douglas.sponsler@uni-wuerzburg.de), K. Kallnik, A. Classen, A. F. Maihoff and I. Steffan-Dewenter, Univ. of Würzburg, Dept of Animal Ecology and Tropical Biology, Würzburg, Germany. – F. Requier, Univ. Paris-Saclay, Évolution, Génomes, Comportement et Écologie, Gif-sur-Yvette, France. – J. Sieger, Naturpark Frankenhöhe, Ansbach, Germany.

Oikos

2022: e08902

doi: 10.1111/oik.08902

Subject Editor: Ignasi Bartomeus

Editor-in-Chief: Dries Bonte

Accepted 22 November 2021



Patterns of resource use by animals can clarify how ecological communities have assembled in the past, how they currently function and how they are likely to respond to future perturbations. Bumble bees (Hymenoptera: *Bombus* spp.) and their floral hosts provide a diverse yet tractable system in which to explore resource selection in the context of plant–pollinator networks. Under conditions of resource limitation, the ability of bumble bees species to coexist should depend on dietary niche overlap. In this study, we report patterns and dynamics of floral morphotype preferences in a mountain bumble bee community based on ~13 000 observations of bumble bee floral visits recorded along a 1400 m elevation gradient. We found that bumble bees are highly selective generalists, rarely visiting floral morphotypes at the rates predicted by their relative abundances. Preferences also differed markedly across bumble bee species, and these differences were well-explained by variation in bumble bee tongue length, generating patterns of preference similarity that should be expected to predict competition under conditions of resource limitation. Within species, though, morphotype preferences varied by elevation and season, possibly representing adaptive flexibility in response to the high elevational and seasonal turnover of mountain floral communities. Patterns of resource partitioning among bumble bee communities may determine which species can coexist under the altered distributions of bumble bees and their floral hosts caused by climate and land use change.

Keywords: coexistence, competition, foraging, niche, pollinator, resource selection

Introduction

Resource selection by animals is instrumental in community assembly, species coexistence and ecosystem function (Chesson 2000, Bascompte and Jordano 2007). Understanding patterns of resource selection in biological communities is also key to anticipating the effects of climate and land use change, which can be expected to reorganize species interactions and niche relationships (Tylianakis et al. 2008).



www.oikosjournal.org

© 2021 The Authors. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Bumble bee (Hymenoptera: *Bombus* spp.) communities and their floral hosts raise interesting questions of resource selection and coexistence that have attracted the attention of ecologists for decades (Heinrich 1976, Inouye 1977). All bumble bee species are grossly similar in morphology and behavior, and all share the same general diet of floral nectar and pollen. The most important trait that distinguishes bumble bee species with respect to dietary niche is tongue length. Bumble bee species can differ markedly in tongue length, and floral handling time increases when tongue length and corolla depth are poorly matched (Inouye 1980, Harder 1983), leading to an association between tongue length and floral choice in bumble bee communities (Brian 1954, Heinrich 1976, Teräs 1976, Inouye 1978, Pyke 1982). Under conditions of food limitation, the coexistence of bumble bee species should be limited by their similarity in tongue length, insofar as it is a proxy for dietary niche. Based on field studies in the Rocky Mountains, Inouye (1977) concluded that, assuming food limitation, four bumble bee species can be expected to persist in any given locality: a long-tongued species, a medium-tongue species, a short-tongued species and a nectar-robber (i.e. a species that accesses nectaries by biting through the corolla, thus bypassing the ordinary constraint of tongue length). In many places, though, considerably more than four bumble bee species coexist, often with overlapping tongue lengths, indicating either that food is often not limiting or that competitive conditions can be too variable in time and space to be detected at the scale of field observations (Ranta and Vepsäläinen 1981, Williams 1989, Goulson et al. 2008).

The most species rich bumble bee communities are found in the mountainous regions of Eurasia in which *Bombus* initially arose and diversified (Williams 1998, Hines 2008) and where the predictions of competitive exclusion are rarely realized (Ranta and Vepsäläinen 1981, Goulson et al. 2008). Nevertheless, climate and land use change in these regions have the potential to alter and intensify competitive relationships between bumble bee species. Warming climates have already caused measurable upslope shifts in some bumble bee species and their floral hosts (Ploquin et al. 2013, Pyke et al. 2016, Fourcade et al. 2019, Marshall et al. 2020), which could introduce novel competitive interactions between bumble bee species that experience increased co-occurrence. At the same time, socioeconomic factors are causing widespread abandonment and reforestation of mountain meadows, particularly in the European Alps, which dramatically reduces floral resource abundance and diversity (Tappeiner et al. 2006, Tasser et al. 2007, Walcher et al. 2017). The consequences of reshuffled species distributions and declining floral resources for the coexistence of mountain bumble bees will depend in part on how bumble bee species select and partition available flora.

Under competitive conditions, species coexistence is possible when intraspecific competition exceeds interspecific competition, and this stabilizing inequality is favored to the extent that species differ in dietary niche (Abrams 1977, Hanski 1995, Chesson 2000). Estimating dietary niche overlap from field observations of resource use is problematic,

though, because resource selection is usually a function not only of species' intrinsic preferences but also of the relative abundances of the available resources (Beyer et al. 2010). Diet overlap observed in a particular time and place may, therefore, be a poor predictor of diet overlap under different conditions of resource abundance. A more robust measure of competition potential between species can be obtained by isolating the process of resource preference from the neutral effects of resource abundance, and one way to do this is to compare observed patterns of resource selection to those predicted by a null model in which resources are selected at random in proportion to their relative abundance (Vázquez and Aizen 2003, Blüthgen et al. 2008).

In this study, we explore the floral morphotype preferences of a mountain bumble bee community using ~13 000 records of bumble bee visits to wildflowers collected over three years along a 1400 m elevation gradient. First, we use null model analysis to compare floral morphotypes in terms of community-level preferences, identifying morphotypes that are consistently over- or under-visited relative to their abundance. Next, we compare morphotype preferences across bumble bee species and model species-level preferences as a function of tongue length. Then, we analyze preference similarity across species to identify species among which competition is most likely under conditions of resource limitation. Finally, we explore the flexibility of floral preferences in bumble bees by modeling the variation of morphotype preferences through elevation and time.

Methods

Field sampling

Field sampling was conducted 2010–2012 in Berchtesgaden National Park (47°55'N, 12°92'E), located in the northern Limestone Alps of southeast Germany. The landscape is composed of a coniferous forest matrix embedded with pastures either currently or historically maintained by extensive (i.e. low intensity) agricultural management. We selected a total of 25 study sites (60 × 60 m) located on pastures along a ~1400 m elevation gradient ranging from 641 to 2032 m a.s.l.

We recorded bumble-bee–wildflower interactions during repeated visits to each study site at approximately weekly intervals. Sampling at each site began upon snowmelt in the spring and continued until the effective end of the bumble bee colony cycle in early September, thus encompassing approximately the full foraging season. Sampling was only conducted during periods without rain and with an air temperature of at least 6°C. Each 60 × 60 m study plot was divided into 10 evenly-spaced 60 × 6 m transects. During each visit, the observer walked each transect in a zig-zag pattern for 5 min and recorded all bumble bee visits to flowers, resulting in a total of 50 min of observation. Queens were identified to species level in the field to avoid destructively sampling colony foundresses, but workers and males were collected and

identified in the lab following Amiet (1996). Prior to analysis, we pooled the cryptic *Bombus lucorum/terrestris* species complex and the parasitic *Bombus (Psithyrus)* species, respectively, into species-groups. Males were recorded, but we analyzed only the pooled visitation of queens and workers. In conjunction with each bumble bee visitation sample, we visually estimated the flower cover of herbaceous and shrubby plant species within each 60 × 60 m study plot to the nearest 0.01 m² and identified the plant species according to Oberndorfer (2001) and Lauber and Wagner (2007). Floral cover estimation was performed by exhaustive visual inspection of each study plot, and the same investigator (K. Kallnik) performed all floral surveys to avoid observer bias.

Bumble bee tongue length and floral morphology

Bumble bee tongue-length data (for the worker caste) were obtained from the literature values compiled and summarized by Arbetman et al. (2017). Values for *B. gerstaeckeri* and *B. mendax*, which were not included in Arbetman et al. (2017), were obtained from Obeso (1992) and Durieux (2000), respectively.

To summarize floral morphology, we relied on the synthesis of Kugler (1970), who developed a typology consisting of ten primary morphotypes and nested subdivisions of each. Morphotypes were simplified to the primary classes numbered 0–10: 0 = null (includes wind-pollinated flora such as grasses), 1 = disc- and bowl-shaped flowers, 2 = funnel flowers, 3 = bell-shaped flowers, 4 = stalk-disc flowers, 5 = lip flowers, 6 = flag flowers, 7 = flower heads, 8 = spike flowers, 9 = brush flowers, 10 = trap flowers (Fig. 1). In a few cases, a plant species in our data set was not found in the BIOFLOR database. In most cases, morphotypes are constant at the genus level, and missing morphotypes were added based on the morphotypes found for congeners. In the case of the genus *Phyteuma*, we followed Neumayer and Paulus (1999) and classified it as a group 7 flower head. Morphotypes 9 and 10 were extremely rare in our study system and morphotype 8 was completely absent, so these morphotypes were omitted from all analyses. Plants belonging to morphotype 0 were typically not recorded during floral surveys due to their lack of conspicuous floral displays, and they were rarely visited by bumble bees, so this morphotype was also omitted from all analyses. Kugler morphotype classifications of the plants in our study system were accessed via the BIOFLOR database (Klotz et al. 2002).

Kugler's typology was informed by laboratory studies of bumble bee flower choice (Kugler 1943), and there is a precedent for analyzing bumble bee visitation in terms of Kugler's morphotypes (Farnberger and Paulus 1996, Neumayer and Paulus 1999, Schneller et al. 2014). It must be noted, though, that the use of a morphotypology in lieu of quantitative data on corolla depth (which are lacking for most species in our system) precludes strong statements about trait-matching, since there is no quantitative measure of fitness between a given morphotype and bumble bee tongue length. Nevertheless, the morphotypology we use captures

qualitatively much of the information concerning the accessibility of floral rewards that would otherwise require quantitative measurement not only of corolla depth, but also of floral shape, openness, etc. Thus, it is reasonable to expect a functional link between morphotype and tongue length, even if this link is not mechanistically quantifiable.

Data analysis

For the purposes of our study, we define 'preference' as the difference between the observed visitation rate to a given resource and visitation rate predicted by a null model in which the probability of a resource being chosen is proportional to its relative abundance (Agustí et al. 2003). In other words, preferences are null model residuals, and thus take negative values for under-visited resources and positive values for over-visited resources. For more nuanced definitions of preference, we refer the reader to Beyer et al. (2010) and references therein.

We constructed null models following Vaughan et al. (2018). In this modeling approach, resource selection is simulated for individual consumers – in our case, individual bumble bees. By simulating the visitation of individual consumers rather than species in aggregate, the abundance of each resource, and therefore its probability of visitation, can vary across samples (i.e. site-dates), thus preserving the within-sample correspondence between visitation and abundance. Simulated interactions are then summarized for each consumer species by taking the mean number of interactions with each resource across all individuals of the consumer species and all samples of the dataset. As this process is iterated, the result is a distribution of visitation rates of each consumer species to each resource under the null assumption that resource selection is determined only by resource abundance. The visitation distributions of the null model can then be compared to observed visitation rates to infer positive or negative preference of each consumer toward each resource. Since the mean of the null distribution can be interpreted as the expected value under null assumptions, the difference between the mean null value and the observed value can be interpreted as a magnitude of preference (Vaughan et al. 2018), and statistical significance can be estimated as the proportion of simulated null values more extreme than the observed value.

We followed the procedure described above, simulating our entire dataset in one modeling process to infer aggregate preferences of bumble bee species for each floral morphotype. Using the results of this analysis, we modeled preferences for each floral morphotype as a function of bumble bee tongue length with hierarchical generalized additive modeling (HGAM), following the type I effect structure described by Pedersen et al. (2019). To verify that our inference of preference was not sensitive to our decision to pool queen and worker visitation, we recalculated the null model and tongue length HGAM using only data from workers. Finally, we compared morphotype preferences across bumble bee species by performing a principal components analysis on the

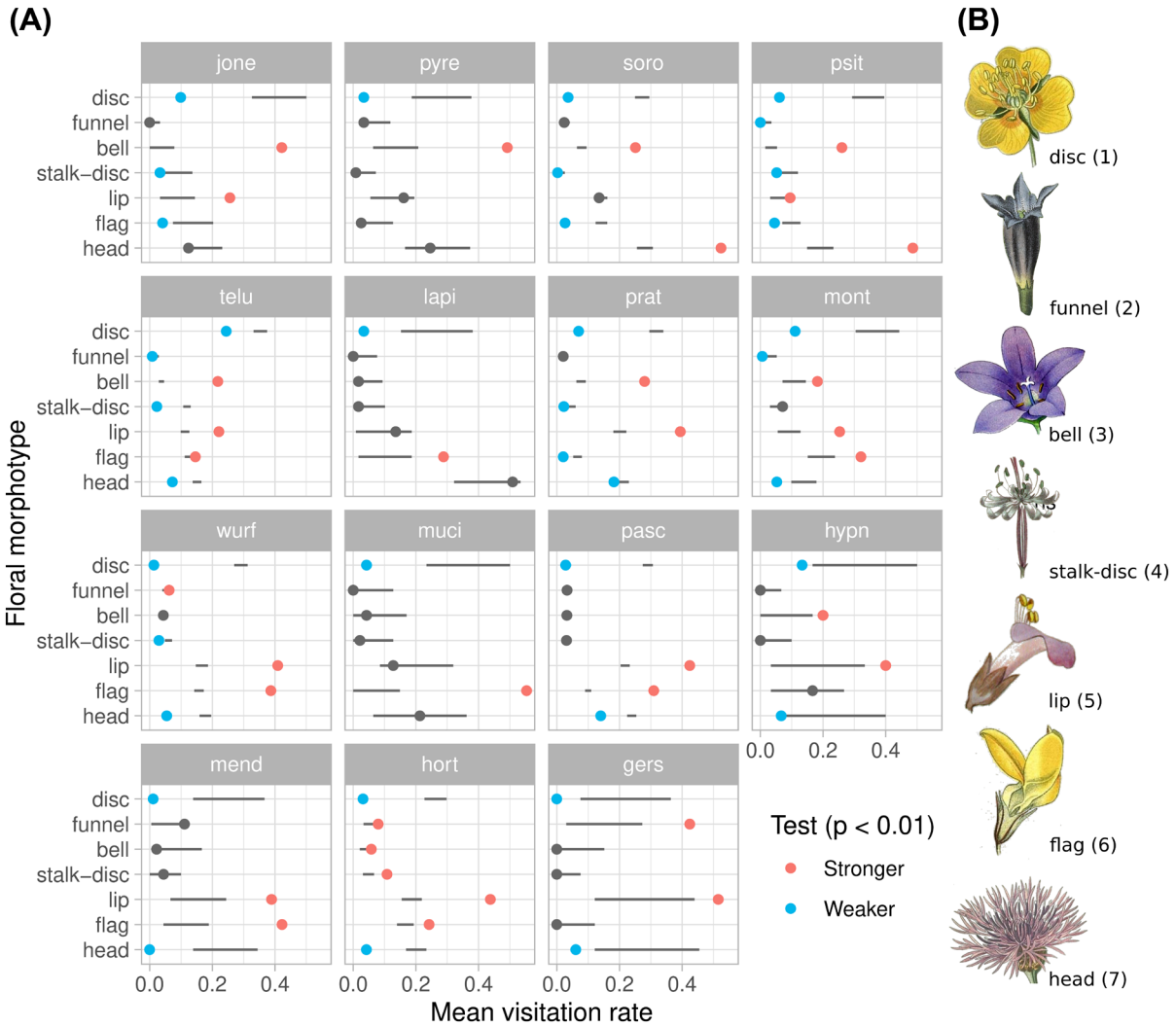


Figure 1. Observed visitation rates compared to null model simulations for each bumble bee species and floral morphotype (A). Gray bars depict 99% intervals of null model simulations and points depict observed visitation rates. Points are color-coded according to where they fall with respect to the 99% interval of the null model: red=above (positive preference), blue=below (negative preference), gray=within (nonsignificant preference). The difference between the observed value and the center of the null model interval can be interpreted as magnitude of preference. Each floral morphotype is illustrated (B) with a representative species common in our study system: 1 = *Potentilla erecta*, 2 = *Gentiana asclepiadea*, 3 = *Campanula glomerata*, 4 = *Silene nutans*, 5 = *Ajuga reptans*, 6 = *Lotus corniculatus*, 7 = *Centaurea jacea*. Illustrations are modifications of public domain works obtained from <www.plantillustrations.org>. See the Supporting information for details of original sources.

bumble bee species × floral morphotype preference matrix, and we mapped bumble bee tongue length onto the ordination space by fitting a 2-dimensional GAM surface to the first two principal components.

To explore temporal and elevational variation in floral preference, we repeated the null model analysis described above but this time for each site-date individually, so that the preference of each bumble bee species toward each floral morphotype could be modeled as a variable through elevation and time. For this analysis, we included only the six most abundant and widespread bumble bee species in our study system (*B. hortorum*, *B. pascuorum*, *B. pratorum*, *B. soroeensis*, *B. terrestris-lucorum* and *B. wurflenii*) to ensure sufficient data

points through elevation and time, and we modeled their preference only toward the four most visited floral morphotypes (bell, lip, flag and head flowers). Preference for each bumble-bee–morphotype pair was modeled together in a single HGAM with an interaction smooth between elevation and time. We also included bee–morphotype pair as a fixed intercept effect and the interactions between bee–morphotype pair and site and bee–morphotype pair and year as random effects.

An inherent problem with modeling sample-wise variation in preference is that the bounds of preference are strictly dependent on floral abundance (Beyer et al. 2010). A morphotype present at very low relative abundance would,

under the null model, be expected to receive very low visitation, which sets the lower bound of preference near zero (i.e. neutrality) but allows the upper bound to approach 1. Conversely, a morphotype present at very high relative abundance would receive very high visitation under the null model, and its upper bound of preference would fall near zero and its lower bound near -1 . This creates some confoundedness between preference and floral abundance. With this limitation in mind, we fit HGAMs of the same form to the relative abundance of each floral morphotype, and we present the results together to be interpreted jointly.

All data processing and analyses were conducted in R (<www.r-project.org>). Data handling and visualization were performed with the tidyverse suite (Wickham et al. 2019). Null models were constructed using econullnetr (Vaughan et al. 2018). GAM analyses were performed with mgcv (Wood 2017) and visualized with mgcViz (Fasiolo et al. 2020) and tidymv (Coretta 2021). PCA was performed with the vegan (Oksanen et al. 2019) and visualized using ggplot2 (Wickham 2016) and ggvegan (Simpson 2019). Annotated R code and complete output of our analytical workflow is available in the Supporting information.

Results

Bumble bee and floral communities

A total of 13 293 bumble-bee–flower interactions were included in our final data set, comprising 15 bumble bee species, 163 plant species (110 genera, 37 families) and 730 unique bumble-bee–plant interaction pairs. Most sites hosted 8 or more species per year (Supporting information), suggesting that interspecific competition was not the main driver of community assembly. *Bombus pascuorum* ('pasc'), *B. pratorum* ('prat'), *B. soroensis* ('soro'), *B. terrestris-lucorum* ('telu') and *B. wurflenii* ('wurf') were the most abundant species, and they occurred at all sites. *Bombus hortorum* ('hort'), *B. jonellus* ('jone'), *B. monticola* ('mont') and *B. psithyrus* ('psit') occurred at moderate abundance. The remaining species – *B. gerstaeckeri* ('gers'), *B. hypnorum* ('hypn'), *B. lapidarius* ('lapi'), *B. mendax* ('mend'), *B. mucidus* ('muci') and *B. pyrenaicus* ('pyre') – were relatively rare. *Bombus humilis* ('humi') was recorded only three times and only in one year, so we omitted it from all analyses. Floral surveying yielded a total of 354 plant species (194 genera, 53 families).

Bumble bee preferences toward floral morphotypes

Preferences were generally strong, with the visitation rates of most bumblebee species to most floral morphotypes falling significantly above or below the 99% interval of the null model (Fig. 1). Nonsignificant preference was observed mainly among the rarer bumblebee species, likely because their small samples sizes lead to wide null model confidence intervals. Notably, bumble bees showed strong species-specific

variation in their relative preferences of different floral morphotypes (Fig. 1). The omission of queens from the calculation of overall preference did not yield qualitatively different results (Supporting information).

When floral morphotypes are compared to one another in terms of preference across all bumble bee species, clear patterns emerge (Fig. 2A). All species exhibited negative preference toward disc flowers, while most species exhibited positive preference toward bell, lip and flag flowers. Preference toward funnel and stalk-disc flowers tended to be neutral (with one strong positive outlier – *B. gerstaeckeri* – for funnel flowers), reflecting the fact that these morphotypes tended to be rarely visited while also occurring at low abundance. Preference toward head flowers varied widely across bumble bee species, ranging from strongly positive (*B. psithyrus*, *B. soroensis*) to strongly negative (e.g. *B. gerstaeckeri*, *B. mendax*).

Tongue length as a predictor of floral choice

Tongue length was a strong predictor of preference (Fig. 3). Preference toward funnel, bell, lip, flag and head flowers exhibited significant GAM curves in response to bumble bee tongue length, and the model explained 77% of total deviance (adj. $R^2 = 0.728$). For funnel and lip flowers, preference increased linearly with tongue length. Preference toward bell flowers and head flowers exhibited approximately quadratic responses with preference peaking among short-tongued species and declining sharply with increasing tongue length before leveling off. Preference toward flag flowers exhibited a unimodal peak among medium-tongued species. Again, these results did not differ when preference was based on the worker-only null model (Supporting information).

PCA of bumble bee floral preferences captured more than 80% of total variance in the first two axes (Fig. 4), and the GAM surface fit to the first two axes explained most of the variance in tongue length (deviance explained = 94.7%, adj. $R^2 = 0.893$, $p < 0.001$), reflecting the importance of compatibility between tongue length and floral morphotype as a mechanistic basis of preference. Longer tongue length was associated with more closed flower morphotypes (lip, funnel, flag), while shorter tongue length was associated with more open flower morphologies (disc, stalk-disc, bell, head). The strong affinity of *B. soroensis* and *B. psithyrus* for head flowers is especially salient.

Variation of morphotype abundance and preference through elevation and season

The relative abundance of the most visited floral morphotypes – bell, lip, flag and head flowers – was strongly patterned by elevation and season (Fig. 5). Bell flowers peaked in relative abundance early in the season and at mid-elevation, and lip flowers peaked late in the season and at low elevation. Flag flowers peaked in mid-season and exhibited two distinct elevational peaks, the lower at around 1000 m a.s.l. and the higher at around 1800 m a.s.l. Head flowers exhibited

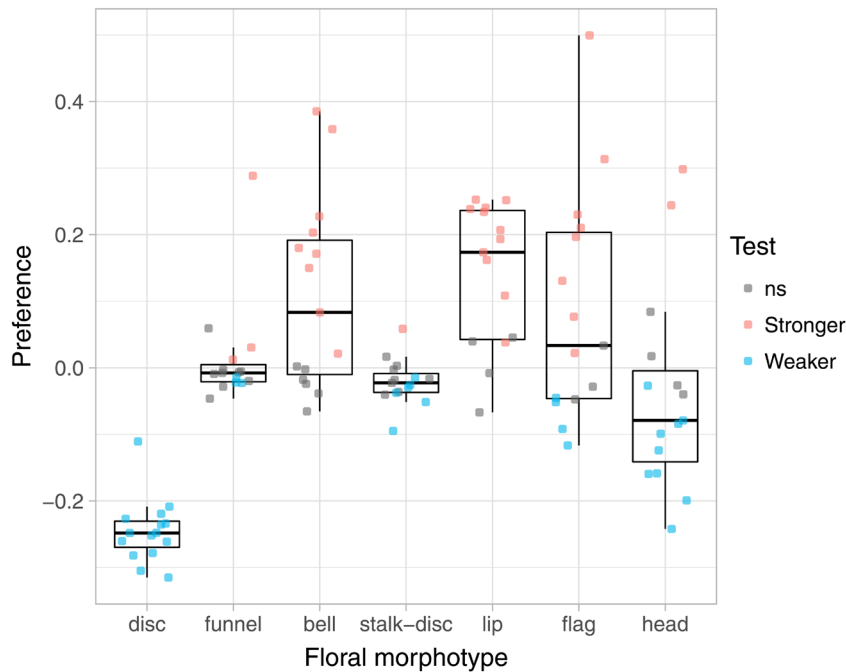


Figure 2. Preference of the bumble bee species toward each floral morphotype. Each point represents the preference of one bumble bee species toward the corresponding floral morphotype. The colors of each point are retained from Fig. 2, indicates whether preference is significantly ($p < 0.01$) positive or negative with respect to null model simulations.

a mid-season peak at low elevation and a broad late season peak at around 1600 m a.s.l. All smooths were significant ($p \ll 0.0001$), and the model explained 64.3% of total deviance ($\text{adj. } R^2 = 0.554$).

The morphotype preferences of bumble bee species were also strongly patterned through elevation and season. In some cases, though, patterns of preference mirrored patterns of floral availability, suggesting that bumble bees may exhibit functional responses (Myerud and Ims 1998) to floral abundance not entirely accounted for by null models that assume a linear proportionality between abundance and visitation. Preference for flag flowers was strongly associated with high elevation, except among the species that tended to avoid flag flowers (*B. pratorum* and *B. soroensis*) (Fig. 1). It is also apparent that preference tends to be more dynamic where it is also higher overall. Bell flowers, which were positively selected overall by the short-tongued bumble bee species *B. pratorum*, *B. terrestris-lucorum* and *B. soroensis* (Fig. 1), also exhibited the most complex patterns of preference in elevation and time for these bumble bee species (Fig. 6). In contrast, the long and medium-tongued species *B. hortorum*, *B. pascuorum* and *B. wurflenii*, which exhibited neutral or weakly positive overall selection toward bell flowers (Fig. 1), also show weak patterns of variation in preference toward bell flowers (Fig. 5). Nearly the reverse pattern is evident for flag flowers, reflecting their association with longer-tongued bumble bee species. Smooths were significant ($p < 0.05$) for all bee–morphotype pairs except hort-head, prat-flag, telu-head and soro-flag, and the model explained 36.4% of total deviance ($\text{adj. } R^2 = 0.33$).

Discussion

Based on complementary bumble bee flower visitation and floral abundance data, we used null model analysis to reveal patterns and dynamics of floral morphotype preference in a mountain bumble bee community. Our results underscore that bumble bees are highly selective generalists, rarely visiting floral morphotypes at the rates predicted by their relative abundances. Floral morphotype preferences also differed markedly across bumble bee species, and these differences were well-explained by variation in bumble bee tongue length. Ordination of species preferences corroborated the role of tongue length in explaining preference and revealed the resulting patterns of preference similarity that should be expected to predict competition under conditions of resource limitation. Within species, though, morphotype preferences varied by elevation and season, possibly representing adaptive flexibility of foraging behavior in response to the high elevational and seasonal turnover of mountain floral communities.

The most preferred morphotypes in our system were bell, lip and flag flowers, which is broadly consistent with visitation patterns reported by previous studies in central Europe (Farnberger and Paulus 1996, Neumayer and Paulus 1999, Schneller et al. 2014). These previous studies tended to find a stronger role of head flowers than indicated by our preference analysis, but this is probably because they characterized foraging in terms of simple visitation rates rather than null-model-inferred preference. We saw similarly high visitation rates toward head flowers, but our null-model analysis reveals that while head flowers were highly visited, they tended to

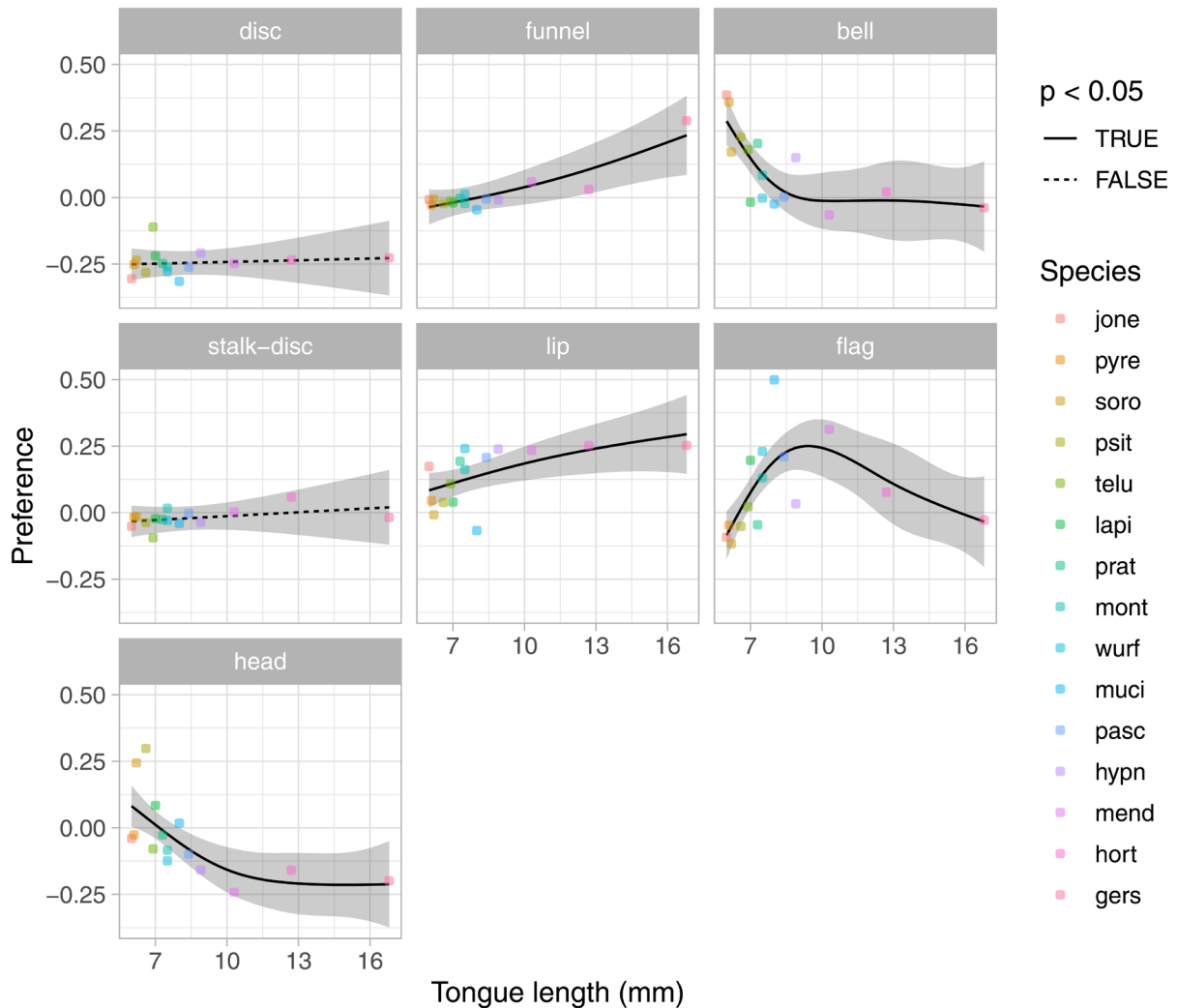


Figure 3. Preference for each morphotype regressed against bumble bee tongue length. Each point represents the preference of one bumble bee species toward the corresponding floral morphotype. Curves depict fitted GAM smooths with 95% confidence bands. Solid lines indicate curves differing significantly ($p < 0.05$) from a flat line while dashed lines indicated nonsignificant curves. Points are color-coded by species, and species are presented in the legend in order of increasing tongue length.

be under-visited relative to their abundance. When considering these community-level patterns of preference and visitation from the perspective of pollination services to mountain flora, it is important to note that while bumble bees are the dominant Hymenopteran pollinators in our study system, flies (Diptera) are also abundant flower visitors in mountain ecosystems, and their visitation is mainly restricted to the open flower morphotypes (e.g. disc flowers) that receive less attention from bumble bees (Neumayer and Paulus 1999). In the context of our research question, we have emphasized the differences in tongue length between bumble bee species, but all bumble bees have relatively long tongues compared to the overall pollinator community, and it is not surprising that their foraging tends to be focused on the deeper and more closed flower morphotypes. The process of floral resource partitioning among bumble bee species is nested within the process of floral partitioning between bumble bees and other flower visitors.

While bell, lip and flag flowers were the most preferred morphotypes on average, preference toward these morphotypes varied broadly across bumble bee species. Moreover, while average preference toward funnel and head flowers was low, each was strongly preferred by one or two bumble bee species. The majority of variation in preference toward floral morphotypes could be explained by bumble bee tongue length, with the more open bell and head morphotypes preferred by short-tongued bumble bee species and the more restrictive funnel, lip and flag morphotypes preferred by medium- and long-tongued bumble bee species. The failure of tongue length to explain preference toward disc and stalk-disc flowers reflects the fact that these flowers were almost unanimously ignored by the bumble bees in our study system. We cannot say from our data why disc and stalk-disc flowers received such consistently low visitation, but the pattern may be driven in part by the fact that some disc flowers offer pollen but little or no nectar; indeed, Kugler's (1970)

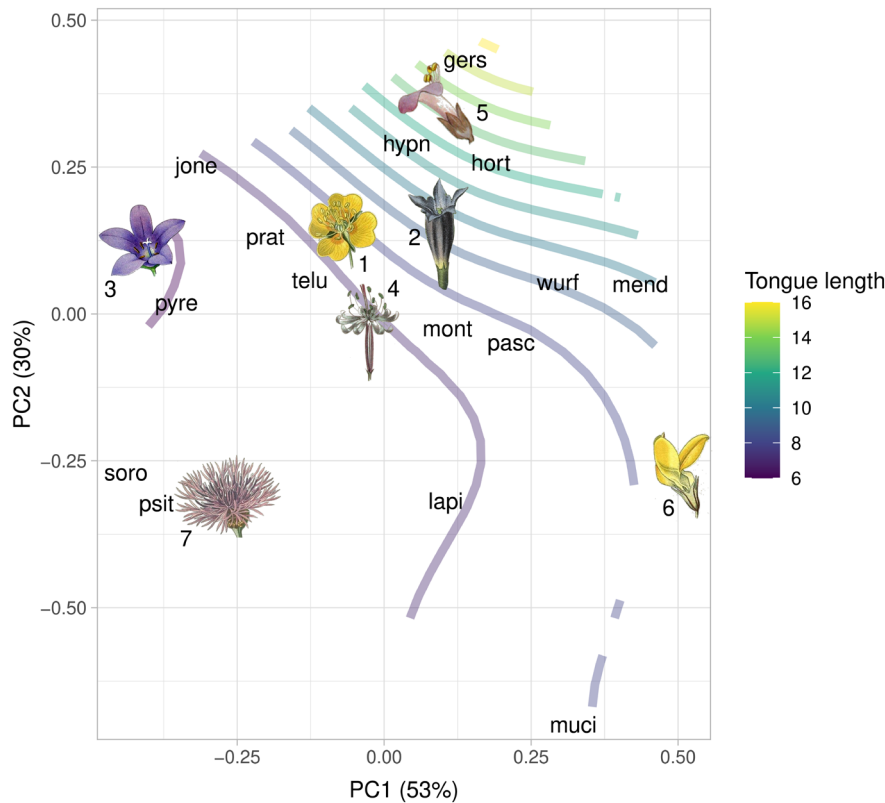


Figure 4. Principal components biplot of bumble bee species according to their preference toward each floral morphotype. Floral morphotypes are abbreviated with their numerical codes and illustrated as in Fig. 1. Colored bands depict a 2-dimensional GAM smooth representing the relationship between the first two principal components and bumble bee tongue length.

typology recognizes this distinction with subdivisions of the disc morphotype into those with (class 1.2) and without (class 1.1) nectar rewards. A limitation of our study is that we could not reliably distinguish pollen- and nectar-foraging bumble bees, and it is likely that this distinction would shed further light on the mechanisms underlying the selection patterns we observed.

The strong explanatory power of tongue length with respect to preference in our study corroborates the established link between tongue length and floral choice (Brian 1954, Heinrich 1976, Teräs 1976, Inouye 1978, Pyke 1982). Moreover, our study shows that bumble bee tongue length can predict floral choice even when a simple morphotypology is used in lieu of quantitative floral traits, which could streamline the prediction of floral choice in systems where quantitative floral trait data is missing. It is important, though, to consider the species that appear as outliers with respect to the smooth dependency of preference on tongue length. *Bombus terrestris/lucorum* showed comparatively high (though still negative) preference toward disc flowers. *Bombus mucidus* exhibited unusually low preference toward lip flowers, complemented by unusually high preference toward flag flowers. *Bombus soroensis* and the *B. psithyrus* species-group were anomalous in their high preference for head flowers. Such unexplained variation in preference may indicate that traits not captured by Kugler's (1970) morphotypology

are also important in governing floral selection by bumble bees. Floral color, in particular, is known to be involved in the process of flower detection by foraging bumble bees (Spaethe et al. 2001), and some bumble bee species exhibit marked color preferences (Teräs 1976, Neumayer and Paulus 1999, Raine and Chittka 2007). Bumble bees floral choice is also influenced by pollen nutritional parameters (Vaudo et al. 2016a, b), and floral preferences may be conserved in phylogenetic lineages within *Bombus* (Wood et al. 2021).

Species of similar tongue length will, on average, be more likely to compete for resources than species of dissimilar tongue length. Our ordination analysis, though, suggests that there may be significant patterns of similarity and divergence even among species of similar tongue length. Among short-tongued species, *B. jonellus* and *B. pyrenaicus* cluster tightly around bell flowers, while *B. psithyrus* and *B. soroensis* cluster tightly around head flowers. Medium- and long-tongued species differ in their allocation of preference across funnel, lip and flag flowers. *B. gerstaeckeri*, for example, is associated with lip and funnel flowers but eschews flag flowers, while *B. mucidus* does the opposite. With respect to the question of climate-induced competition, the case of *B. gerstaeckeri* deserves special consideration. A red-listed vulnerable species, *B. gerstaeckeri* is a pollen specialist on the lip flowers of the genus *Aconitum* (Ponchau et al. 2006, Schneller et al. 2014), and there is evidence that joint elevational shifts of

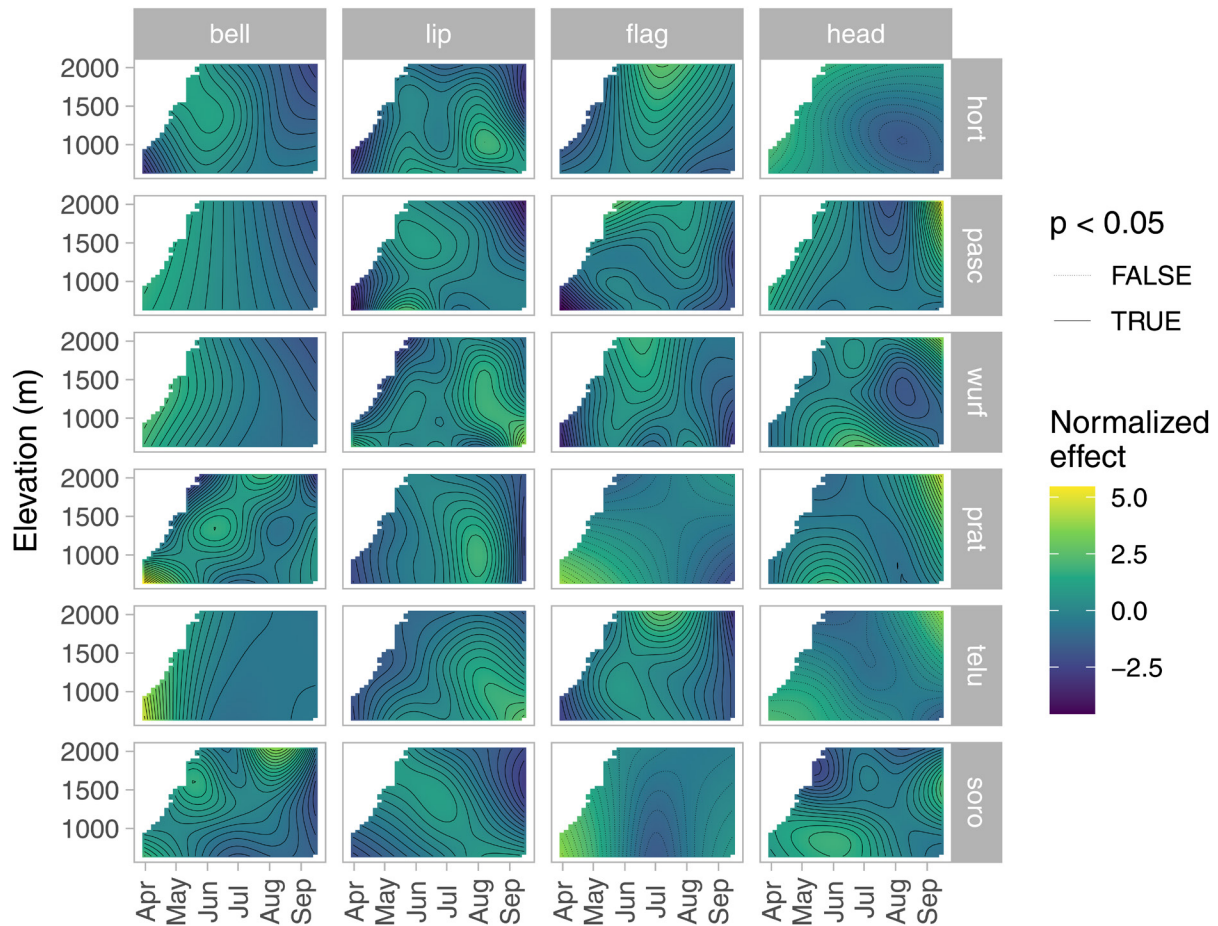


Figure 5. Variation in preference through elevation and time modeled as HGAM surfaces. Color ramps depict z-normalized effects to allow the range of effect size to be compared across panels, but contour lines are set at the same fixed density across all panels to emphasize the within-panel patterns. Significant ($p < 0.05$) smooths are depicted with solid contour lines and nonsignificant smooths with dashed contour lines.

bumble bees and floral resources over the past century have generated more intense exploitation of *Aconitum*, which may indicate nascent competitive conditions for *B. gerstaeckeri* (Marshall et al. 2020).

Intraspecific variation of bumble bee foraging preferences has been demonstrated under laboratory conditions (Ings et al. 2009, Maharaj et al. 2019); our study reveals the in situ variation of preference for multiple bumble bee species through elevational and temporal gradients of floristic turnover. At least three mechanisms could underlie the variation of preferences we observed. First, variation in preference toward a given morphotype could be driven by changes in the intrinsic reward of that focal morphotype, which could be caused by 1) shifts in species composition of the focal morphotype (e.g. the occurrence of a particularly rewarding flag flower at high-elevation sites), 2) shifts in the reward levels of individual species (e.g. increased nectar production in a particular flag flower under high elevation conditions) or 3) changes in nutritional requirements of bumble bees (e.g. an increased need for concentrated nectar to support thermoregulation at colder ambient temperatures). Alternatively,

preference toward a given morphotype could vary due to changes in the relative reward of the focal morphotype with respect to changing background resource conditions. For example, it could be that flag flowers are selected more positively at high elevation because they must compete for visitation with highly attractive lip flowers at lower elevation. Finally, it is possible that patterns of resource selection could vary due to competitive interactions within or between bumble bee species. For example, the increased selection of flag flowers at high elevation could be driven by competition release from *B. pascuorum*, which tends to be the most abundance bumble bee species at lower elevations but becomes relatively scarce above 1500 m (Sponsler et al. unpubl.). Under this hypothesis, an organism's resource selection is the product of exogenous constraint rather than endogenous preference (Brosi and Briggs 2013). As we have noted previously, the high numbers of coexisting species at our study sites suggest that interspecific competition is currently not the main driver of community assembly in our system, but competition is likely to intensify as flower-rich abandoned meadows revert to flower-poor coniferous forest. All the

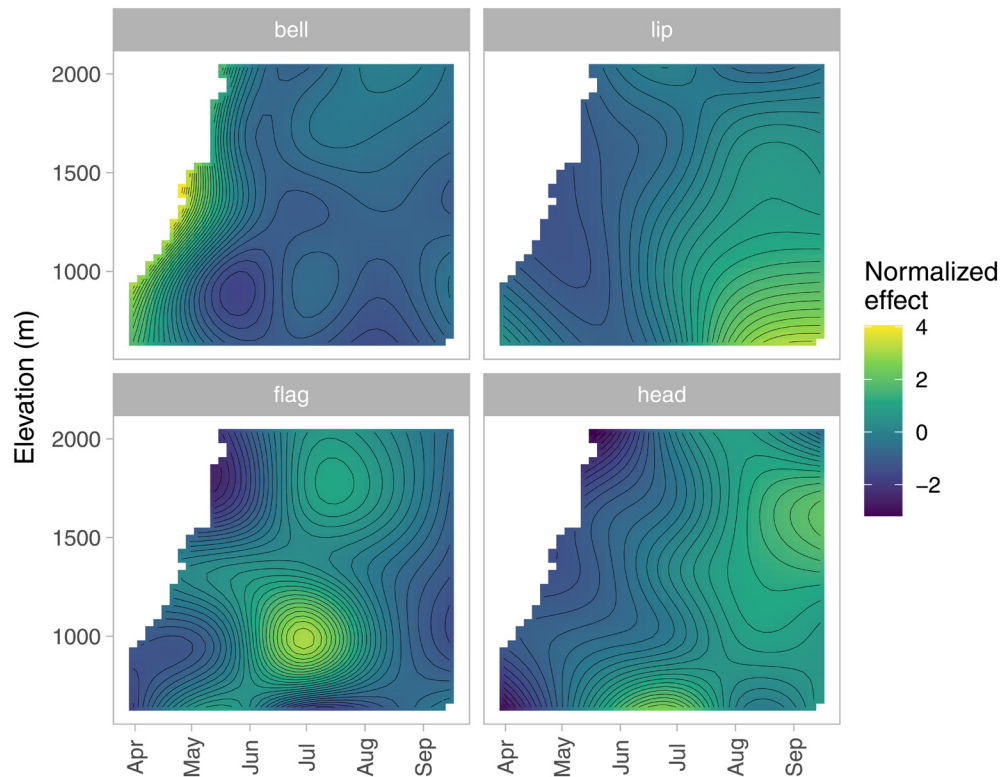


Figure 6. Variation in relative floral abundance through elevation and season modeled as HGAM surfaces. Color ramps depict z-normalized effects to allow the range of effect size to be compared across panels, but contour lines are set at the same fixed density across all panels to emphasize the within-panel patterns. All smooths are significant ($p < 0.05$).

potential scenarios explaining the variability of preference in our study underscore the importance of accounting for environmental (Tylianakis and Morris 2017) and temporal (CaraDonna et al. 2021) heterogeneity in the study of plant pollinator networks.

Clarifying the patterns and processes of bumble floral selection sheds light on how bumble bee communities have evolved with respect to their mountain habitats and how they might respond to the incipient forcings of climate and land use change. Perhaps the most salient finding of our study is the remarkable marriage of generalism and selectivity in bumble bee foraging ecology. While most bumble bees (with the exception of true specialists like *B. gerstaeckeri*) can and do visit most floral morphotypes, they allocate their visitation according to strong preferences; yet, these preferences are themselves flexible, evidently adapting to changes in ecological context. Such flexible selectivity among generalist foragers might make enable bumble bee communities to adaptively partition resources under varying competitive conditions, which could make them relatively robust to new competitive pressures introduced by species range shifts. Moreover, the dynamics of preference in our study suggest adaptive tuning of floral choice consistent with the ecological hurdles that have shaped the evolution of bumble bees in the mountain habitats in which they arose and diversified (Williams 1985, Hines 2008). Where steep temperature gradients and short growing seasons generate extreme spatiotemporal turnover of

floral resources, adaptive flexibility of morphological preferences should be favored over fixed biases.

Acknowledgments – We thank the National Park Berchtesgaden for their support and the permission to work in the national park, and we thank the owners of the study sites outside the national park for access to their land. D. J. McNeil provided for helpful conversations during data analysis. O. Mitesser kindly provided a high-performance computing environment to expedite null modeling.

Funding – The field work of this study was performed within the framework of the joint research center FORKAST as part of the ‘Bavarian Climate Programme 2020’, with funds awarded to ISD. A. Classen, A. F. Maihoff and I. Steffan-Dewenter acknowledge further funding from the Bavarian Climate Research Network (bayklif).

Author contributions

Douglas Sponsler: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Katharina Kallnik:** Conceptualization (equal); Data curation (supporting); Investigation (lead); Methodology (lead); Writing – review and editing (supporting). **Fabrice Requier:** Conceptualization (supporting); Data curation (equal);

Writing – review and editing (supporting). **Alice Classen**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Visualization (supporting); Writing – review and editing (supporting). **A. Fabienne Maihoff**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting). **Johanna Sieger**: Investigation (equal); Methodology (equal); Writing – review and editing (supporting). **Ingolf Steffan-Dewenter**: Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

All data used in this study have been archived on Dryad digital repository (<<https://datadryad.org/stash/dataset/doi:10.5061/dryad.7d7wm37wp>>). Related software is published at Zenodo: <<https://doi.org/10.5281/zenodo.5724496>>, and supplemental information is also published at Zenodo: <<https://doi.org/10.5281/zenodo.5724498>>.

Supporting information

The supporting information associated with this article is available from the online version.

References

- Abrams, P. A. 1977. Density-independent mortality and interspecific competition: a test of piñka's niche overlap hypothesis. – *Am. Nat.* 111: 539–552.
- Agustí, N. et al. 2003. Collembola as alternative prey sustaining spiders in arable ecosystems: prey detection within predators using molecular markers. – *Mol. Ecol.* 12: 3467–3475.
- Amiet, F. 1996. Hymenoptera apidae, 1. Teil. Allgemeiner teil, gattungsschlüssel, die Gattungen *Apis*, *Bombus* und *Psithyrus*. – *Insecta Helv. Fauna* 12: 1–98.
- Arbetman, M. P. et al. 2017. Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. – *Proc. Biol. Sci.* 284: 20170204.
- Bascompte, J. and Jordano, P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 38: 567–593.
- Beyer, H. L. et al. 2010. The interpretation of habitat preference metrics under use–availability designs. – *Phil. Trans. R. Soc. B* 365: 2245–2254.
- Blüthgen, N. et al. 2008. What do interaction network metrics tell us about specialization and biological traits? – *Ecology* 89: 3387–3399.
- Brian, A. D. 1954. The foraging of bumble bees part II. Bumble bees as pollinators. – *Bee World* 35: 81–91.
- Brosi, B. J. and Briggs, H. M. 2013. Single pollinator species losses reduce floral fidelity and plant reproductive function. – *Proc. Natl Acad. Sci. USA* 110: 13044–13048.
- CaraDonna, P. J. et al. 2021. Seeing through the static: the temporal dimension of plant–animal mutualistic interactions. – *Ecol. Lett.* 24: 149–161.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annu. Rev. Ecol. Syst.* 31: 343–366.
- Coretta, S. 2021. Tidymv: tidy model visualisation for generalised additive models. <<https://stefanocoretta.github.io/tidymv/>>.
- Durieux, E.-A. 2000. Etude des choix floraux des bourdons (hyménoptera, apidae) de la commune d'eyne (france, Pyrénées-Orientales). – PhD thesis, Univ. de Mons-Hainaut, France.
- Farnberger, C. and Paulus, H. F. 1996. Hummelgemeinschaften und blumengesellschaften am eichkogel in niederösterreich (hymenoptera, apoidea). – *Linz. Biol. Beitr.* 28: 1083–1116.
- Fasiolo, M. et al. 2018. Scalable visualisation methods for modern generalized additive models. – *J. Comput. Graph. Stat.* 29: 78–86.
- Fourcade, Y. et al. 2019. Climate and land-cover change alter bumblebee species richness and community composition in subalpine areas. – *Biodivers. Conserv.* 28: 639–653.
- Goulson, D. et al. 2008. Diet breadth, coexistence and rarity in bumblebees. – *Biodivers. Conserv.* 17: 3269–3288.
- Hanski, I. 1995. Effects of landscape pattern on competitive interactions. – In: Hansson, L. et al. (eds), *Mosaic landscapes and ecological processes*. Springer, pp. 203–224.
- Harder, L. D. 1983. Flower handling efficiency of bumble bees: morphological aspects of probing time. – *Oecologia* 57: 274–280.
- Heinrich, B. 1976. Resource partitioning among some eusocial insects: bumblebees. – *Ecology* 57: 874–889.
- Hines, H. M. 2008. Historical biogeography, divergence times and diversification patterns of bumble bees (Hymenoptera: Apidae: *Bombus*). – *Syst. Biol.* 57: 58–75.
- Ings, T. C. et al. 2009. A population comparison of the strength and persistence of innate colour preference and learning speed in the bumblebee *bombus terrestris*. – *Behav. Ecol. Sociobiol.* 63: 1207–1218.
- Inouye, D. 1977. Species structure of bumblebee communities in north america and europe. – In: Mattson, W. J. (ed.), *The role of arthropods in forest ecosystems*. Springer, pp. 35–40.
- Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. – *Ecology* 59: 672–678.
- Inouye, D. W. 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. – *Oecologia* 45: 197–201.
- Klotz, S. et al. 2002. BIOLFLOR – eine datenbank zu biologisch-ökologischen merkmalen der gefäßpflanzen in deutschland. – Bundesamt für Naturschutz.
- Kugler, H. 1943. Hummeln als blütenbesucher. – *Ergebn. Biol.* 19: 143–323.
- Kugler, H. 1970. Blütenökologie. – Gustav Fischer.
- Lauber, K. and Wagner, G. 2007. *Flora helvetica*. – Haupt.
- Maharaj, G. et al. 2019. Influence of preexisting preference for color on sampling and tracking behavior in bumble bees. – *Behav. Ecol.* 30: 150–158.
- Marshall, L. et al. 2020. Bumblebees moving up: shifts in elevation ranges in the Pyrenees over 115 years. – *Proc. R. Soc. B* 287: 20202201.
- Mysterud, A. and Ims, R. A. 1998. Functional responses in habitat use: availability influences relative use in tradeoff situations. – *Ecology* 79: 1435–1441.
- Neumayer, J. and Paulus, H. F. 1999. Ökologie alpiner hummelgemeinschaften: blütenbesuch, ressourcenaufteilung und energiehauhalt. – *Stapfia* 67: 5–246.
- Oberndorfer, E. 2001. *Pflanzensoziologische exkursionsflora für deutschland und angrenzende gebiete*. – Verlag Eugen Ulmer, Stuttgart.

- Obeso, J. R. 1992. Geographic distribution and community structure of bumblebees in the northern iberian peninsula. – *Oecologia* 89: 244–252.
- Oksanen, J. et al. 2019. Vegan: community ecology package. – <<https://cran.r-project.org/web/packages/vegan/index.html>>.
- Pedersen, E. J. et al. 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. – *PeerJ* 7: e6876.
- Ploquin, E. F. et al. 2013. Bumblebee community homogenization after uphill shifts in montane areas of northern spain. – *Oecologia* 173: 1649–1660.
- Ponchau, O. et al. 2006. Is the caste-ratio of the oligolectic bumblebee *bombus gerstaeckeri morawitz* (Hymenoptera: Apidae) biased to queens? – *Ann. Soc. Entomol. Fr.* 42: 207–214.
- Pyke, G. H. 1982. Local geographic distributions of bumblebees near crested butte, colorado: competition and community structure. – *Ecology* 63: 555–573.
- Pyke, G. H. et al. 2016. Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. – *Ecosphere* 7: 1.
- Raine, N. E. and Chittka, L. 2007. The adaptive significance of sensory bias in a foraging context: floral colour preferences in the bumblebee *bombus terrestris*. – *PLoS One* 2: e556.
- Ranta, E. and Vepsäläinen, K. 1981. Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. – *Oikos* 36: 28–34.
- Schneller, B. et al. 2014. Diversität, lebensraumpräferenzen und blütenbesuch der hummeln (hymenoptera: Apidae: *Bombus*) in vorarlberg (Österreich). – *Acta ZooBot. Austria* 150: 135–156.
- Simpson, G. L. 2019. Ggvegan: ‘ggplot2’ plots for the ‘vegan’ package.
- Spaethe, J. et al. 2001. Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. – *Proc. Natl Acad. Sci. USA* 98: 3898–3903.
- Sponsler, D. 2020. Data from: Floral preferences of mountain bumble bees are constrained by functional traits but flexible through elevation and season. – Dryad Digital Repository, <<http://datadryad.org/stash/dataset/doi:10.5061/dryad.7d7wm37wp>>
- Tappeiner, U. et al. 2006. Landnutzung in den alpen: historische entwicklung und zukünftige szenarien. – In: Psenner, R. and Lackner, R. (eds), *Die alpen in jahr 2020*. Innsbruck Univ. Press, pp. 23–39.
- Tasser, E. et al. 2007. Land-use changes and natural reforestation in the eastern central alps. – *Agric. Ecosyst. Environ.* 118: 115–129.
- Teräs, I. 1976. Flower visits of bumblebees, *Bombus* Latr. (Hymenoptera, Apidae), during one summer. – *Ann. Zool. Fenn.* 13: 200–232.
- Tylianakis, J. M. and Morris, R. J. 2017. Ecological networks across environmental gradients. – *Annu. Rev. Ecol. Evol. Syst.* 48: 25–48.
- Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. – *Ecol. Lett.* 11: 1351–1363.
- Vaudo, A. D. et al. 2016a. Bumble bees regulate their intake of the essential protein and lipid pollen macronutrients. – *J. Exp. Biol.* 219: 3962–3970.
- Vaudo, A. D. et al. 2016b. Macronutrient ratios in pollen shape bumble bee (*bombus impatiens*) foraging strategies and floral preferences. – *Proc. Natl Acad. Sci. USA* 113: E4035–E4042.
- Vaughan, I. P. et al. 2018. Econullnet: an r package using null models to analyse the structure of ecological networks and identify resource selection. – *Methods Ecol. Evol.* 9: 728–733.
- Vázquez, D. P. and Aizen, M. A. 2003. Null model analyses of specialization in plant–pollinator interactions. – *Ecology* 84: 2493–2501.
- Walcher, R. et al. 2017. Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both: abandonment and extensive management of mountain meadows in three regions across the austrian and swiss alps. – *Landscape Ecol.* 32: 1937–1951.
- Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – Springer.
- Wickham, H. et al. 2019. Welcome to the tidyverse. – *J. Open Source Softw.* 4: 1686.
- Williams, P. H. 1985. A preliminary cladistic investigation of relationships among the bumble bees (hymenoptera, apidae). – *Syst. Entomol.* 10: 239–255.
- Williams, P. H. 1989. Why are there so many species of bumble bees at dungeness? – *Bot. J. Linn. Soc.* 101: 31–44.
- Williams, P. H. 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). – *Bull. Nat. Hist. Mus. Entomol.* 67: 79–152.
- Wood, S. N. 2017. Generalized additive models: an introduction with r. – Chapman; Hall/CRC.
- Wood, T. J. et al. 2021. Global patterns in bumble bee pollen collection show phylogenetic conservation of diet. – *J. Anim. Ecol.* 90: 2421–2430.