OIKOS

Research article

Bumble bee niche overlap along an elevation gradient: how traits can inform novel competitive pressures under climate change

Kaitlyn Barthell and Julian Resasco

Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO, USA

Correspondence: Kaitlyn Barthell (barthell3@gmail.com)

Oikos
2025: e10650
doi: 10.1111/oik.10650
Subject Editor: Matthew Symonds
Editor-in-Chief: Dries Bonte
Accepted 29 October 2024

Climate change-induced range shifts can disrupt interactions among species by moving them in and out of ecological communities. These disruptions can include impacts on competition for shared resources. Bumble bees (*Bombus* spp.) are important pollinators shifting their range upwards in elevation in response to climate change. These shifts could lead to altered competition among species and threaten co-existence. This could be particularly worrying at the tops of mountain ranges where bumble bees may no longer be able to move up to higher elevations to track climate change. To better understand this issue, we investigated changes in diet niche overlap among bumble bee species along a 2296 m elevation gradient in the southern Rocky Mountains. Additionally, we investigated how morphological and phenological traits impact diet composition (flower species visited) among bumble bee species and explored a simple simulation to understand how the continued upward movement of bumble bee species under climate change into the mountaintop may affect trait overlap of newly co-occurring species. We found that diet niche overlap among bumble bee species increased with elevation. We also found that differences in morphological and phenological traits (body size, tongue length, date of activity) were correlated with differences in diet composition among bumble bee species. Finally, we described how the co-occurrence of bumble bee species from lower elevations with mountaintop species would lead to increased trait overlap and likely more species sharing similar flowers. These shifts could lead to increased competition for high-elevation restricted species on mountaintops and exacerbate the effects of climate change on high-elevation bumble bees.

Keywords: alpine, montane, plants, pollinators, Rocky Mountains

Introduction

Climate change is causing many species to move their ranges upwards in elevation and towards the poles to track changing environmental conditions (Hughes 2000, Walther et al. 2002). Range shifts can modify community structure and disrupt ecosystems through the turnover of species in and out of ecological communities (Wardle et al. 2011). The rearrangement of competing species in communities may threaten coexistence, considering the ability of species competing for a shared resource

NORDIC SOCIETY OIKOS

www.oikosjournal.org

to co-exist is facilitated by each competitor having distinct patterns of resource use, or a distinct 'niche' (Chesson 2000). To more fully account for the effects of climate change on species, it is important to study how biotic interactions like competition may change in addition to the impacts of abiotic factors.

Insects are critical to the pollination of over 85% of flowering plant species (Ollerton et al. 2011). Insect pollinator communities may be especially vulnerable to species' range shifts that may occur under climate change, considering their strong dependence on host flower species for food (Michener 2007) and their high sensitivity to changing environmental variables (Kingsolver 2013). Range-shift caused spatial mismatches between pollinators and their host plants threaten pollination success (Gomez-Ruiz and Lacher 2019) and affect competition for both groups (Richman et al. 2020). Understanding how pollinator species partition their diet and how range changes may impact these interactions is important for understanding the impacts of climate change on plant–pollinator communities.

Mountain elevation gradients provide an opportunity to study how plant–pollinator communities change with elevation and how range shifts under climate change may alter competitive interactions. Mountains are climatically heterogeneous, making them hotspots for biodiversity and useful as 'natural experiments' for understanding ecological responses to climatic change (Körner 2007). As elevation changes, different factors such as temperature, precipitation, productivity, area and species interactions also change, supporting different numbers of species (McCain and Grytnes 2010). Species richness for plants and pollinators typically peak within middle elevations along mountain ranges, with plants often having species richness peaks at higher elevations than pollinators (Wohlgemuth et al. 2008, Gallou et al. 2017, Chesshire et al. 2021, Sponsler et al. 2022b). As the richness of host flowers and their associated pollinators change, the spectrum of available resources and the number of species competing for those resources also change, potentially altering the competitive pressures within a community (Doublet et al. 2022). As plant and pollinator species move in and out of communities to track climate change, competitive pressures will likely be affected. This could be particularly worrying at the tops of mountain ranges, where species may no longer be able to move upwards in elevation in response to climate change.

Bumble bees (*Bombus* spp.) are shifting their ranges in response to climate change (Kerr et al. 2015, Marshall et al. 2020). Bumble bees are essential pollinators of native plants in mountain ecosystems (Bingham and Orthner 1998, Gorenflo et al. 2017, Minachilis et al. 2021); however, studies have documented dramatic bumble bee declines across the Northern Hemisphere (Kosior et al. 2007, Cameron et al. 2011). Climate change is a distinct driver of these losses, and its effects are independent of other important drivers such as land-use change and pesticide use (Kerr et al. 2015, Soroye et al. 2020). In response to climate change, bumble bees are moving upwards in elevation to remain within a habitable range of environmental conditions (Kerr et al. 2015). However, at mountaintops, bumble bee species can no longer move upward to track suitable climate. The upward movement of colonizing species into the same environment as high-elevation species at mountaintops will likely cause novel competitive interactions for shared floral resources that could exacerbate the effects of changing climate. Accounting for these novel competitive interactions is important for a better understanding of how species will respond to climate change (Alexander et al. 2015).

Competition among co-occurring bumble bee species is heavily influenced by their dependence on the flowers that they visit for pollen and nectar food resources (Heinrich 1976). Exploitative competition, wherein species compete indirectly for a shared resource, is the primary mechanism for resource partitioning among bumble bee species (Inouye 1978). Since closely related species are similar in life history and morphology, they are likely to compete more strongly with each other for limited resources than more distantly related taxonomic groups (Burns and Strauss 2011). Co-existence among bumble bee species may be facilitated by traits that allow for niche partitioning of floral resources. For example, morphological trait variation among species, such as body size and tongue length, also may influence diet niche partitioning. Past research has found that bumble bee morphological traits influence which flowers species visit (Harder 1985, Sponsler et al. 2022a). Longer-tongued bumble bees, for example, are more likely to visit flowers that are more closed in shape (lip, funnel, and flag-shaped flowers) than their shorter-tongued counterparts that prefer more open-shaped flowers (disc, stalk-disc, bell, head-shaped flowers; Sponsler et al. 2022a). This difference in visitation may be attributed to species visiting flowers that are most energetically efficient for their morphology (Balfour et al. 2021). Phenology, or the timing of bumble bee activity, differs among species during the season and can also be a mechanism for diet niche partitioning since bumble bees can only access flowers that are open when they are actively foraging. Therefore, variation in morphology and phenology may be important indicators of variation in diet composition and niche partitioning among bumble bee species.

Past research on bumble bee competitive interactions along elevation gradients has shed light on the patterns and mechanisms underlying niche overlap. Using historical data collected between 1966 and 1969 by Macior (1974) in the Colorado Rocky Mountains, Miller-Struttmann and Galen (2014) found high niche overlap in the lowest and highest elevation zones of their study, with niche overlap peaks attributed to disturbance in the lowest zone (1600–2700 m) and a shortened flowering window in the highest zone (3500–4300 m). Additionally, they found that long-tongued bumble bees altered their foraging behavior in the alpine by becoming more generalized, suggesting that tongue length plays a role in determining which flowers species visit at different elevations (Miller-Struttmann and Galen 2014). Another study in the Rocky Mountains found that lower-elevation bumble bee species that have recently colonized alpine environments are likely to take better advantage of foraging early and late in the season, potentially making them more likely to outcompete resident species in a warming alpine environment (Miller-Struttmann et al. 2022). Still, patterns of niche overlap along elevation gradients, traits' influence in determining diet, and how climate change may impact competition among mountain bumble bees are poorly understood.

In this study, we investigated bumble bee distributions and host floral diet niche overlap along the elevation gradient of Pikes Peak in the Colorado Front Range. Further, we examined how bumble bee traits relate to host flower diet composition to better understand niche overlap and how it might change with elevational range shifts under climate change. We asked the following questions: Q1**:** how does bumble bee diet niche overlap change along the elevation gradient?; Q2: is variation in phenology, body size, and tongue length correlated with variation in bumble bee diet composition?; and Q3: how might the upward movement of bumble bee species impact phenological and morphological trait overlap at the top of the mountain? For Q1, we predicted that bumble bee diet niche overlap would increase with elevation, considering high-elevation mountain environments have short flowering seasons and greatly lowered plant species richness (McCain and Grytnes 2010, Stephens et al. 2022). For Q2, we predicted that variation in phenology, body size, and tongue length values would positively correlate with variation in diet composition for species, considering bumble bees should make foraging choices that are most efficient for their morphology (Balfour et al. 2021) and should only be able to visit flowers that are open during their foraging period. For Q3, we predicted that the co-occurrence of mountain-top species with species found at lower elevations would create increased trait space overlap in phenology, body size and tongue length.

Material and methods

To test our questions, we conducted a four-year survey of bumble bee and host flower interactions along a 2295 m elevation gradient on Pikes Peak (Fig. 1A), a mountain in the southern Front Range of the Rocky Mountains in Colorado, USA. We categorized the elevation gradient into five zones of equal elevational length (Fig. 1B). We estimated bumble bee and host flower species richness and diet niche overlap within each elevation zone. Next, we assessed if phenology, body size, and tongue length are related to diet composition in bumble bees by testing for correlations between variation in diet composition and trait values among bumble bee species. Finally, we performed a simple simulation through data manipulation to explore how trait space overlap may change in the mountaintop if species are to continue moving upwards in elevation under climate change by simulating the co-occurrence of mountaintop species with species found at lower elevations.

Study area

The Front Range of Colorado, USA, in the southern Rocky Mountains, is a hotspot for bumble bee diversity; half of the United States' 48 bumble bee species reside in Colorado, most of which occupy counties within or bordering the Front Range (Wright et al. 2017). The Front Range's natural transition from low-elevation short-grass prairie, which begins around 1000 m, to high-elevation mountain environments, that peak around 4300 m, encompasses suitable habitat for many bumble bee species. The high species richness of the Front Range is useful for understanding bumble bee community patterns in niche partitioning along an elevation gradient as well as making predictions about the consequences of the upward movement of bumble bee species.

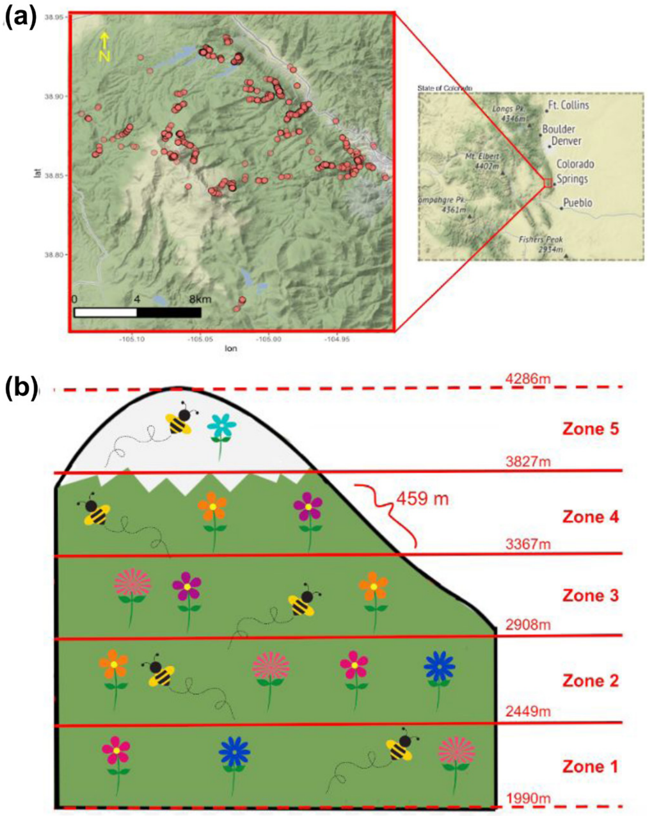


Figure 1. (A) Map of bumble bee and host flower observations surrounding Pikes Peak, Colorado (2019–2022). Each point represents a GPS location used to observe bumble bee and host flower interactions. (B) Figure of the five elevational zones used in this study. Each zone encompassed 459 m of the elevational landscape.

We carried out our study between May and September for four years (2019–2022) on Pikes Peak, the highest mountain (4302 m) in the southern Front Range of Colorado (38°50'15.59''N, 105°02'23.40"W). Observations were made along an elevation gradient ranging from 1990 to 4286 m on Pikes Peak (Fig. 1A). The United States Department of Agriculture Forest Service manages most of the study area. Vegetation varies considerably along the elevation gradient: at the base of the mountain in the foothills (1981–2438 m), Gambel oak shrubs *Quercus gambelii* dominate dry, rocky slopes; as elevation increases, ponderosa pine *Pinus ponderosa* and aspen *Populus tremuloides* begin to dominate in the montane (2438–3048 m); in the subalpine (3048–3474 m), Engelmann spruce *Picea engelmannii* and limber pine *Pinus flexilis* predominate; finally, in the alpine (3475–4302 m), trees disappear and are replaced by tundra vegetation such as sedges and mat-forming plants (Kelso 2012).

Study design

Bumble bee and host flower interaction data were used to characterize bumble bee niche overlap along the elevational gradient. The bumble bee interaction data used in this study were a subset of those from a concurrent study on plant–pollinator interactions on Pikes Peak (Resasco 2021). Bumblebees are conspicuous flower visitors. We defined interactions as observations of bumble bees touching the stamen or pistil of flowers. Interactions were recorded through observing flowers along hiking trails, meadows, roadsides and other accessible areas throughout the elevation gradient. We sampled in ecologically diverse areas to represent the diversity of flowers available in each zone. Flowering forb and shrub species found with mature, open flowers were chosen for observation. Bumble bees found interacting with flowers were collected through waiting and observation, as well as collected opportunistically as encountered. Some flower species *Aconitum columbianum*, *Chamerion angustifolium*, *Delphinium ramosum*, *Frasera speciosa*, *Geranium caespitosum*, *Mertensia lanceolata*, *Monarda fistulosa*, *Penstemon glaber*, *Penstemon secundiflorus*, *Penstemon virens*, *Rosa acicularis*, *Rubus deliciosus* and *Rubus idaeus* were observed for long periods (varying between 30 min and 2 h) as part of the study design of Resasco (2021) and likely have a better representation of bumble bee interactions. Bumble bees found interacting with flowers in the field were usually collected via aspirator or net, frozen, and mounted for later identification. Individuals that could confidently be identified on sight, including the western bumble bee *Bombus occidentalis*, which is declining in western North America, were released. All host flowers observed were identified to species using Ackerfield's Flora of Colorado (Ackerfield 2015). Each collected interaction data point had an associated number of flowers observed, date, WGS84 GPS coordinates, and elevation recorded. We sampled on weekdays during the span of the flowering period between late May and mid-August from 2019–2022. Two additional sampling days occurred in September of 2022 to include late-season plant-pollinator interaction data. Observation effort varied by year and elevation (see the Supporting information for details). Bumble bee observations in the highest elevation zones were restricted by shorter flowering seasons and a lower frequency of bumble bee and flower interactions observed compared to lower elevation zones. Bumble bee habitat suitability varied depending on the areas visited in each elevation zone.

All collected bumble bees were identified to species and caste in the lab using a stereozoom microscope, taxonomic keys and references (Byron 1980, Williams et al. 2014, Wright et al. 2017). In addition to our collected data, we also obtained species-level minimum, maximum, and average worker tongue length (mm, labium: prementum + glossa) from Macior 1974's 'Pollination ecology of the Front Range of the Colorado Rocky Mountains' and Medler 1962's 'Morphometric studies on bumble bees'; as well as species-level minimum, maximum and midpoint body size (mm) data from Williams et al. 2014's 'Bumble bees of North America' guidebook (Medler 1962, Macior 1974, Williams et al. 2014) for our trait analyses. Our trait-based analyses in Question 2 and 3 used worker bee data only since their primary role is foraging for food and their foraging behavior impacts colony success. *Bombus insularis*, a cuckoo bumble bee, was excluded from all trait-based analyses because this species does not produce workers. For three bumble bee species used in Question 3's analysis for which we did not have tongue length data available from Macior 1974 (*Bombus fervidus*, *B. huntii* and *B. rufocinctus*), we estimated minimum and maximum values by taking the mean +/− 2SD from Medler 1962.

We divided observations along the elevation gradient into five zones of equal elevational length (459 m), between the lowest (1990 m) and highest (4286 m) bumble bee–flower interaction observation (Fig. 1B). Zone 1 was our lowest zone in the elevation gradient (1990–2449 m), followed by zone 2 (2449–2908 m), zone 3 (2908–3367 m), zone 4 (3367–3827 m), and zone 5 (3827–4286 m). The zone classifications used in this study were selected equidistantly along the elevation gradient and do not correspond directly with specific ecotypes (foothills, montane, subalpine and alpine). However, ecotypes are difficult to delineate at specific elevations as they vary with slope and aspect (Resasco et al. 2024). Similar to these ecotypes, the five elevation zones used in this study have high plant species turnover, providing a range of varying floral resources that bumble bees can use along the elevation gradient. We pooled data collected from all four years for our analyses since our dataset is too limited to examine temporal patterns. Therefore, generalized results across all years helped us better understand the overall trends among elevation zones.

Statistical analysis

We conducted all analyses in R ver. 4.0.3 (www.r-project.org). We checked the data for GPS errors by mapping data points using the 'ggmap' package ver. 3.0.0 (Kahle and Wickham 2013) and checking elevation correspondence with latitude and longitude using the 'elevatr' package ver. 0.4.2 (Hollister et al. 2021). Bumble bee observations were dropped from the dataset if their GPS points were incorrect (seven points), if their elevations appeared as outliers (> 300 m different from the elevation points within the USGS Elevation Point Query Service; four points), or if we were unable to identify the host flower species (two points). We used the packages 'bipartite' ver. 2.16, 'ggridges' ver. 0.5.4, and 'ggplot2' ver. 3.4.1 for data visualization (Dormann et al. 2009, Wickham 2016, Wilke 2022).

Assessing elevational patterns of species richness and sampling completeness

To help inform our understanding of diet niche partitioning among bumble bee species, we calculated the richness of host flower species and bumble bee species within each elevational zone. Host flower and bumble bee species richness estimates give us insight into the breadth of available flower species and the number of bumble bees competing for them. Species richness for host flowers and bumble bees was estimated for each of the five elevational zones using rarefaction and extrapolation from the 'iNEXT' package ver. 3.0.0 (Hsieh et al. 2022). To account for uneven sampling within each zone, we compared species richness estimates and their confidence intervals at n = 270 observations, the median number of samples among zones. We ran both asymptotic and sample size-based richness estimates. To assess the thoroughness of sampling at each elevation zone, we estimated sample completeness for bumble bee and host flower species visited and their unique interactions using the 'iNEXT' package (Hsieh et al. 2022).

Q1: how does bumble bee diet niche overlap change along the elevation gradient?

We used Horn's index (Horn 1966) to calculate niche overlap in diet composition among bumble bee species, where 0 indicates no niche overlap and 1 indicates perfect niche overlap. We estimated niche overlap for bumble bees across the elevation gradient using non-parametric bootstraps that sampled without replacement using the 'bootstrapnet' package ver. 1.0.0 (Stefan and Knight 2023). This approach allowed us to account for uneven samples across the elevation gradient by comparing niche overlap estimates at equivalent observations and estimating uncertainty within each elevational zone. We chose to bootstrap without replacement to avoid the potential bias of overrepresenting common interactions between bumble bees and host flowers. In our bootstrap, we estimated niche overlap at a starting interval of n = 50 observations (approximately 10% of 491 unique flower and bumble bee interactions) and continued at n = 1 intervals until no more samples were left in each zone. This sampling procedure was replicated 1000 times. The mean niche overlap values for each zone were compared at n = 117 observations. We chose n = 117 since our least sampled zone (zone 5) had 118 interactions, and sampling below this value gave us confidence intervals for all zones. To test whether niche overlap increased with elevation (Q1), we ran a linear regression on each elevation zone's mean niche overlap estimates. To visualize differences in host flower diet composition among bumble bee species, we used nonmetric multidimensional scaling (NMDS) of diet compositions of bumble bees across all elevation zones, as well as within each zone using the 'vegan' package ver. 2.5.7 (Oksanen et al. 2020).

Q2: is variation in phenology, body size, and tongue length correlated with variation in bumble bee diet composition?

We used Mantel tests to examine the relationship between species traits (phenology, body size and tongue length) and diet composition (plant species visited and weighted by the frequency of these interactions) among all worker bumble bee species observations. Workers reliably contribute resources acquired during foraging back to an established colony, whereas queens spend some time foraging while searching for an area to establish a colony, and males do not return to the colony upon leaving. We felt that focusing on the relationship of worker traits and diet composition would best capture interactions from an established colony.

We created a matrix of Bray–Curtis dissimilarity values for frequency and composition of diet, as well as matrices of Euclidean distances of trait values (mean phenology, midpoint of minimum and maximum body size range and mean tongue length) between each pairwise combination of bumble bee species. We used diet and trait values of workers only for this analysis. Bray–Curtis dissimilarity values, which range from 0 (complete similarity) to 1 (complete dissimilarity), were calculated using the 'vegan' package (Oksanen et al. 2020). Euclidean distance dissimilarity values were calculated using the 'stats' package ver. 4.0.3 (www.r-project.org). In total, four matrices were created. We tested for correlation between the diet dissimilarity matrix and each trait matrix using Mantel tests in the 'vegan' package (Oksanen et al. 2020). Mantel tests determine correlation by comparing observed matrices to a null model, where the matrix values are shuffled at random and tested for significance based on these permutations (Oksanen et al. 2020). The resulting Mantel test statistic value varies between −1 and 1, with −1 indicating perfect negative correlation and 1 indicating perfect positive correlation. To investigate whether body size variation correlates with tongue length variation, we ran Pearson's correlation on available worker bumble bee tongue length and corresponding body size values in base R. Pearson's correlation coefficient varies between −1 and 1, with −1 indicating perfect negative correlation and 1 indicating perfect positive correlation. Finally, to visualize diet composition in relation to trait variables, we created NMDS plots of species diet composition pooled across all elevation zones and overlaid with the average trait values for each species in multidimensional space using the 'vegan' package (Oksanen et al. 2020). In these plots, contour lines indicate the relationship between diet composition and trait values.

Q3: how might the upward movement of bumble bee species impact phenological and morphological trait overlap at the top of the mountain?

To explore the effects that the continued upward movement of bumble bee species from lower elevations may have on competition with mountaintop bumble bee species, we simulated the co-occurrence of workers found in zone 4 with those found in zone 5 and examined phenological and morphological trait overlap between colonizing species from zone 4 and species that are most restricted to high elevations in zone 5.

To do this, we moved all zone 4 observations into the highest elevation zone, zone 5. Next, to identify colonizing species and high elevation species that may have high trait similarity under this hypothetical scenario, we calculated the percent overlap of phenology, body size, and tongue length ranges between each unique pairing of high-elevation species occurring in zone 5 and colonizing bumble bee species from zone 4, as well as species that we found most restricted to high elevations in our study (*Bombus balteatus*, *B. frigidus* and *B. sylvicola*) and colonizing bumble bee species from zone 4. These three high-elevation restricted species were selected because they had the highest average elevation across all observed species. Trait overlap was calculated by dividing the shared trait space by the total trait space for both species. We highlighted bumble bee pairings with high trait overlap (> 65%) as more likely to have high competition for floral resources under climate change.

This simulation holds the assumption that bumble bees would become trapped at the highest elevation zone under climate change, due to the possible inability to further move upwards to track warming temperatures. We also assumed that bumble bees would move upwards but not their plant resources. This assumption was made on the basis that bumble bees will likely be able to respond to warming temperatures with range shifts more quickly than plants (Pyke et al. 2016). Therefore, plant shifts were not included in this exploratory model. To visualize changes in the mountaintop's bumble bee community trait overlap under this simulation, line segment graphs representing the range of occupied trait space between each pairing of high elevation species from zone 5 and colonizing bumble bee species from zone 4 were plotted using the 'ggplot' package (Wickham 2016).

Results

We observed 19 out of Colorado's 24 bumble bee species interacting with 148 host flowering plants, totaling in 491 unique bumble bee and host flower interactions (Supporting information). We observed a total of 2951 bumble bees, and determined the sex for 2793 bumble bees, which included 2137 workers, 526 males and 130 queens. *Bombus centralis*, *B. bifarius* and *B. flavifrons* were the most dominant bumble bee species in our flower–bumble bee network (Supporting information). *Geranium caespitosum* (GERCAE), *Chamerion angustifolium* (CHAANG), *Frasera speciosa* (FRASPE) and *Aconitum columbianum* (ACOCOL) were the most dominant host flower species in our network (Supporting information). Bumble bee species varied in their elevation range, phenology, as well as in their body size and tongue length values (Fig. 2A–B). Bumble bee phenology is constrained by elevation; with longer phenological windows at lower elevations (Fig. 2A). *Bombus griseocollis*, *B. nevadensis*, *B. huntii* and *B. rufocinctus* interacted with flowers for most of the summer study periods, whereas *B. pensylvanicus*, *B. occidentalis*, *B. mixtus*, *B. balteatus* and *B. sylvicola* had narrow foraging windows from collected data (Fig. 2A). *Bombus griseocollis* emerged and was abundant relatively early in the summer seasons compared to the rest of the species observed and was also most concentrated at the lowest elevations in the study (Fig. 2A–B).

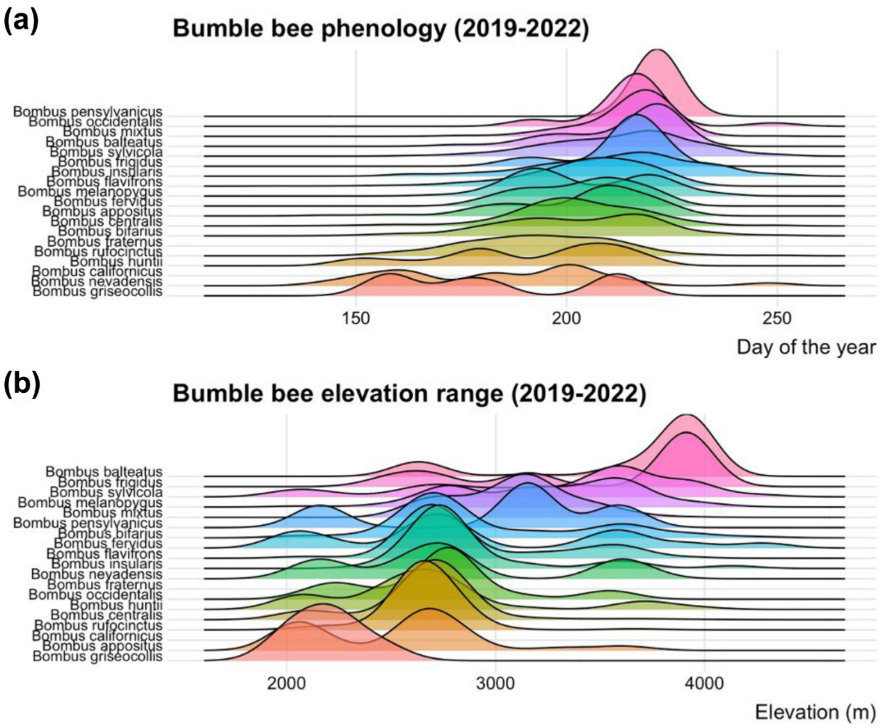
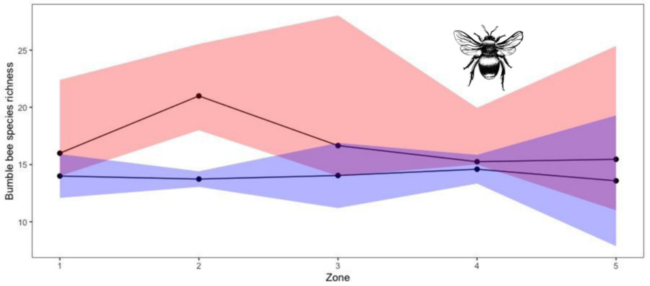


Figure 2. (A) Bumble bee phenology across all elevational zones pooled for 2019–2022. (B) Bumble bee elevational range pooled for 2019–2022.

(a) Bumble bee species richness estimates across elevation zones



(b) Flower species richness estimates across elevation zones

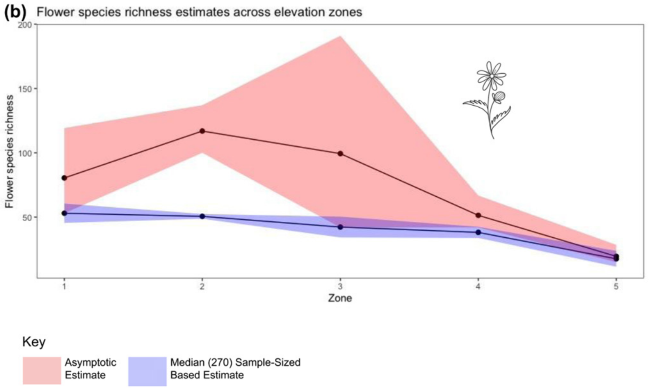


Figure 3. (A) Bumble bee species richness estimates and (B) host flower species richness estimates across the elevation gradient. Error polygons represent the 95% upper and lower confidence limits.

Assessing elevational patterns of species richness and sampling completeness

Asymptotic bumble bee rarefied species richness estimates were unimodal, with a peak in lower to middle elevational zones. Bumble bee species richness was greatest in zone 2 (21 species, 95% CI [18, 25.54]) and lower in zone 1 (16 species, 95% CI [14, 22.39]), zone 3 (17 species, 95% CI [14, 28.03]), zone 4 (15 species, 95% CI [15, 19.95]), and zone 5 (15 species, 95% CI [11, 25.37]) (Fig. 3A). Bumble bee sample size-based species richness estimates at an endpoint of 270 were similar across all five elevation zones (Fig. 3A).

Asymptotic host flower rarefied species richness estimates were also unimodal, with lower richness estimates in zone 1 (84 species, 95% CI [56.02, 112.40], and zone 2 (111 species, 95% CI [95.00, 130.39]) a peak in zone 3 (136 species, 95% CI [40.00, 284.48]), then lower richness estimates into zone 4 (51 species, 95% CI [40.00, 78.41]), and zone 5 (19 species, 95% CI [15.00, 30.00]) (Fig. 3B). Host flower sample size-based estimates at an endpoint of 270 had a negative trend, peaking in zone 1 and decreasing with elevation to its lowest richness in zone 5 (Fig. 3B). The sample completeness for bumble bee and host flower species in each zone was generally high. Sample completeness for bumble bee and host flower interactions was lower, varying between 70 and 95% for the elevation zones (Supporting information).

Q1: how does bumble bee diet niche overlap change along the elevation gradient?

Bumble bee diet niche overlap increased linearly with elevation zone (t = 13.43, p-value = < 0.001; Fig. 4, Supporting information). Niche overlap values in the highest elevational zone (zone 5) were over three times greater than the lowest elevational zone (zone 1). Zone 1 and 2 were significantly different from zone 5. Niche overlap measurements compared at n = 117 included zone 1: 0.11 (lower 95% CI: 0.06, upper 95% CI: 0.18), zone 2: 0.15 (lower 95% CI: 0.08 upper 95% CI: 0.26), zone 3: 0.22 (lower 95% CI: 0.14, upper 95% CI: 0.36), zone 4: 0.26 (lower 95% CI: 0.17, upper 95% CI: 0.39), and zone 5: 0.35 (lower 95% CI: 0.33, upper 95% CI: 0.36). NMDS plots showed differences in bumble bee species' diet composition relative to one another, with longer distances between species representing less similar diets and shorter distances representing more similar diets (Fig. 5).

Q2: is variation in phenology, body size and tongue length correlated with variation in bumble bee diet composition?

Euclidean distance values in phenology, body size, and tongue length among bumble bee workers were all positively correlated with differences in diet composition (Bray–Curtis dissimilarity). The Mantel test statistic showed a positive correlation of 0.25 (p-value = 0.013) for phenology and diet differences, a positive correlation of 0.26 (p-value = 0.02) for body size and diet differences, and a positive correlation of 0.13 (p-value = 0.07) for tongue length and diet differences. Pearson's product moment correlation coefficient between available worker bumble bee tongue length and body size values were positively correlated at 0.73 (p-value < 0.001). Relationships among traits and diet are also illustrated by contours in NMDS plots for diet overlaid with continuous data for phenology, body size, and tongue length (Fig. 6).

Q3: how might the upward movement of bumble bee species impact phenological and morphological trait overlap at the top of the mountain?

Worker observations from ten species were recorded in the mountaintop zone (zone 5) before simulating

Figure 4. Average niche overlap (Horn's index) values among bumble bee species across the elevation gradient. A niche overlap value of 0 indicates no niche overlap, or no similarity in diet and a niche overlap value 1 indicates perfect niche overlap, or perfect similarity in diet.

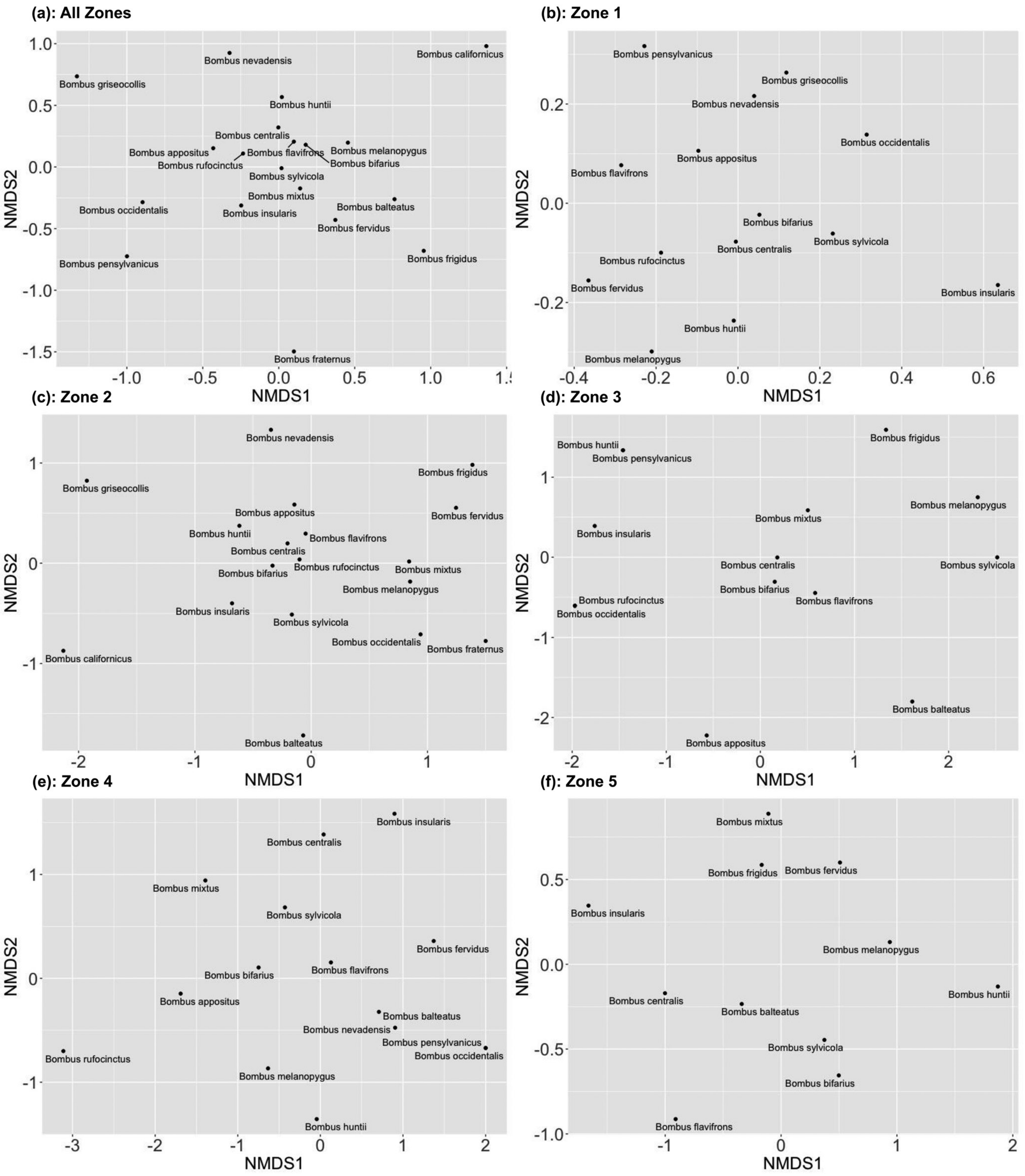


Figure 5. NMDS plots of the dissimilarity of diet among bumble bee species within all zones combined (A) and within each individual zone (B–F).

the colonization of lower elevation species from zone 4 upwards: *Bombus balteatus*, *B. bifarius*, *B. centralis*, *B. fervidus*, *B. flavifrons*, *B. frigidus*, *B. huntii*, *B. melanopygus*, *B. mixtus* and *B. sylvicola*. Four additional bumble bee species, *Bombus appositus*, *B. nevadensis*, *B. occidentalis* and *B. rufocinctus*, were unique to zone 4 and colonized the mountaintop under our simulation, resulting in 14 different species co-occurring together (Fig. 7).

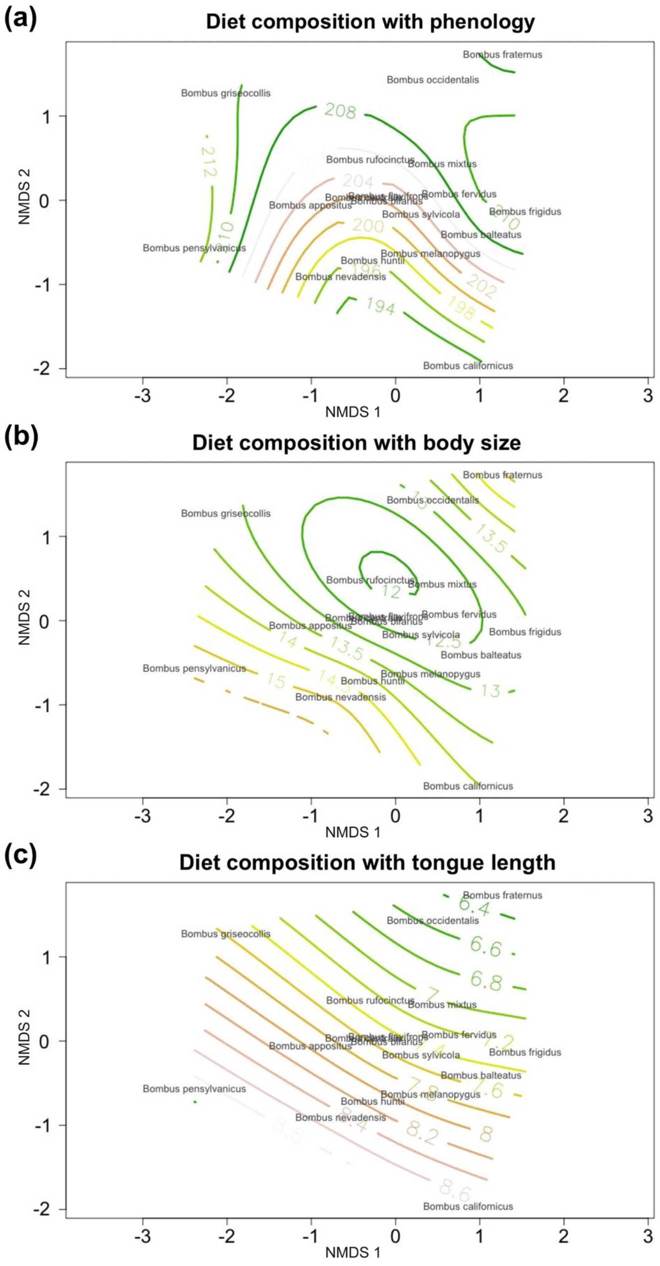


Figure 6. NMDS plots showing differences in diet composition of bumble bee species with overlaid continuous data for (A) phenology, (B) body size and (C) tongue length data.

Percent phenological overlap between high-elevation restricted species (*Bombus balteatus*, *B. frigidus*, *B. sylvicola*; yellow bars in Fig. 7) and colonizing bee species from zone 4 (blue bars in Fig. 7) was greatest (>75%) for the combination *of B. balteatus* and *B. appositus* (81.4%) as well as *B. sylvicola* and *B. rufocinctus* (79.7%) (Table 1). Percent body size overlap between species restricted to high elevations (*Bombus balteatus*, *B. frigidus*, *B. sylvicola*) and colonizing bee species from zone 4 was greatest (> 65%) for the combinations of *B. balteatus* and *B. appositus* (87.5%) as well as *B. sylvicola* and *B. occidentalis* (66.7%) (Table 1). Percent tongue length overlap between high-elevation restricted species in zone 5 (*Bombus balteatus*, *B. frigidus*, *B. sylvicola*) and colonizing bee species from zone 4 was greatest (>70%) for the combination of *B. balteatus* and *B. nevadensis* (81.8%) as well as for *B. frigidus* and *B. rufocinctus* (72.5%) (Table 1).

Discussion

Overview

Our results show that 1) bumble bee species diet niche overlap increases with elevation, 2) phenology and morphology are correlated with diet among species, and 3) future mountaintop bumble bee species may have increased competition under climate change due to more species occupying similar morphological and phenological trait space. These results present new patterns of bumble bee niche overlap across an elevation gradient and suggest that morphological and phenological traits can be important for explaining diet composition, which can be used to inform the consequences of future upward movement of bumble bee species into mountaintop environments on competitive interactions.

Assessing elevational patterns of species richness and sampling completeness

Asymptotic species richness estimates for both bumble bees and host flowers had unimodal peaks in species richness at middle-lower elevations. After peaking in zone 2, species richness for both taxa continued to decline with elevation. Sample-based species richness estimates at an endpoint of 270 had a relatively flattened estimation across the elevation gradient for bumble bees, and a negative linear trend for plant species in comparison.

The unimodality in our asymptotic estimations is generally consistent with past studies that have investigated bumble bee and host flower species richness along elevation gradients across the globe (Goulson et al. 2008, Miller-Struttmann and Galen 2014, Sponsler et al. 2022b). Our estimates of bumble bee species richness were similar to Miller-Struttmann and Galen (2014), who found that bumble bee communities in the Colorado Front Range generally decreased in species richness with elevation. However, our estimates of nectar and pollen host flower richness were different from Miller-Struttmann and Galen (2014), who found increases in pollen host-flower species richness with elevation. The difference in results may be due to our sampling methodology involving nectar and pollen foraging interactions and Miller-Struttmann and Galen's study involving solely pollen foraging interactions. There is evidence that bumble bees vary in their probability of carrying pollen from one or multiple flower species with elevation (Miller-Struttmann and Galen 2014) and tend to visit a broader range of flowers for nectar resources than pollen (Goulson and Darvill 2004), which would explain differences in our results. Our estimates of bumble bee and host flower richness are valuable in informing niche overlap (Costa-Pereira et al. 2019) as they determine the availability of the shared resource.

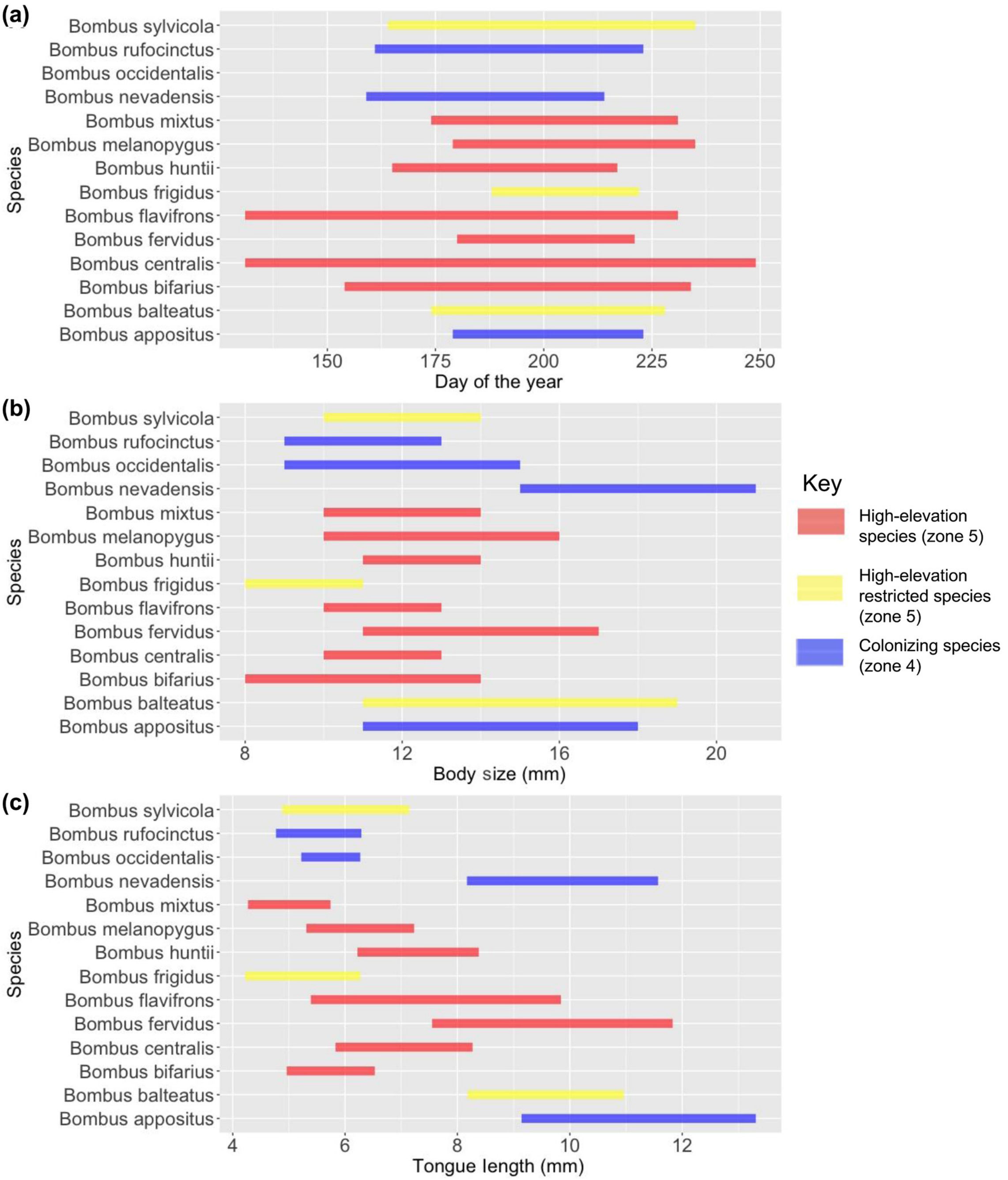


Figure 7. (A) Bumble bee phenology, (B) body size, and (C) tongue length trait overlap at the mountaintop (zone 5) after shifting zone 4 worker observations into zone 5. Lines represent the range of trait measurements possible for each respective species. 'Colonizing' species new to zone 5 are represented in blue, and 'high elevation' species already found in zone 5 are represented by pink and yellow, with the species most restricted to the mountaintop in yellow.

Q1: how does bumble bee diet niche overlap change along the elevation gradient?

As predicted, bumble bee diet niche overlap increased with elevation and was greatest at the mountaintop, likely due to a restricted temporal flowering window and low plant species richness. Our results differ from Miller-Struttmann and Galen's (2014) historical niche overlap analysis in the Colorado Front Range, which found high diet niche overlap at the top and bottom of the elevation gradient (Miller-Struttmann and Galen 2014). This may be explained by differences in host flower species richness patterns between our study and Miller-Struttmann and Galen's study, as they had much lower host flower species richness in their lowest elevational zone compared to our lowest zones. Additionally, Miller-Struttmann and Galen (2014) attributed high niche

Table 1. Percent of phenology, body size and tongue length trait overlap for each unique pairing of bumble bee species restricted to high elevations and colonizing bumble bee *Bombus* species that were moved into the mountaintop from zone 4. Interactions in bold are over 65% trait overlap.

	B. appositus (%)	*B. nevadensis* (%)	*B. occidentalis* (%)	*B. rufocinctus* (%)
Phenology				
B. balteatus	**81.5**	58.0	0.0	**73.1**
B. frigidus	**77.3**	41.3	0.0	54.8
B. sylvicola	62.0	**65.8**	0.0	**79.7**
Body size				
B. balteatus	**87.5**	40.0	40.0	20.0
B. frigidus	0.0	0.0	28.6	40.0
B. sylvicola	37.5	0.0	**66.7**	60.0
Tongue length				
B. balteatus	35.5	**81.8**	0.0	0.0
B. frigidus	0.0	0.0	51.2	**72.5**
B. sylvicola	0.0	0.0	46.5	59.5

overlap at the bottom of their elevation gradient to disturbance. The extent of our study is largely protected from intensive land use and human development. Therefore, disturbance along the elevation gradient may be less of an influence than in Miller-Struttmann and Galen (2014).

Competition is logistically difficult to test in nature as it requires experimentally excluding bumble bee species from one another (Goulson et al. 2008, Brosi et al. 2017). Our niche overlap estimates are not a direct measure of competition but rather a statistic that measures the shared use of a resource. Past research has suggested that exploitative competition is the primary mechanism driving niche partitioning among bumble bee species (Inouye 1978). Therefore, niche overlap is a valuable tool for identifying species utilizing a limited resource similarly and identifying potential novel competitive interactions under climate change.

Q2: is variation in phenology, body size and tongue length correlated with variation in bumble bee diet composition?

Differences in both morphological (body size and tongue length) and phenological traits were correlated with differences in diet among species. This supports the idea that morphological and phenological traits mediate diet niche partitioning (Goulson et al. 2008, Balfour et al. 2021, Sponsler et al. 2022a), likely due to resource accessibility and the energetic efficiency of visiting certain flowers depending on morphology (Balfour et al. 2021). There is evidence that body size can increase with elevation within bee species (McCabe et al. 2019), which highlights a limitation in using a single species-wide metric to define the entire bumble bee species across the elevation gradient. It is likely that the correlation between morphological traits and diet varies along the elevation gradient, which was not accounted for in our analysis.

Phenological windows for bumble bee species were created from the date that individuals were collected in the field. Therefore, some phenological windows we created for species were limited to few observations and may not entirely capture their phenology. *Bombus pensylvanicus*, which is in decline and categorized as vulnerable by the International Union for the Conservation of Nature (IUCN), appeared to have a narrow foraging window (Hatfield et al. 2015b); however, observations of this species were limited to four occurrences, and this limited sample size may be responsible for the narrow foraging window we observed (Fig. 2A). In addition, *Bombus californicus*, which is treated as a conspecific with *B. fervidus* and listed as vulnerable by the IUCN (Hatfield et al. 2015a), had one observation, and its phenology is not well captured from our data.

We found that tongue length and body size were correlated. The non-independence of these traits makes it difficult to determine which trait is driving diet composition in bumble bees (de Keyzer et al. 2016, Christmas et al. 2022). Notwithstanding, our findings indicate the value that morphological variation has in helping to predict the diet of bumble bee species. Body size and tongue length (labium: prementum + glossa) values used in this analysis were taken from bumble bees used for past scientific research and from guidebooks (Medler 1962, Macior 1974, Williams et al. 2014). We assumed that while tongue length and body size may be different at Pikes Peak or may have changed since these past measurements, the relative relationships of these traits among species have likely remained similar, and therefore our findings from these data are still valuable to understanding trait impacts on diet.

Q3: how might the upward movement of bumble bee species impact phenological and morphological trait overlap at the top of the mountain?

Simulating the movement of bumble bees upwards into the mountaintop created the addition of new species and pairs of co-occurring bumble bee species that may compete with one another under climate change. Of the three high-elevation restricted species, *B. sylvicola* and *B. balteatus* had the greatest number of high trait overlap interactions with colonizing species from zone 4 across all three traits. High-elevation restricted species have lower tolerances for warming temperatures (Oyen et al. 2016) and may be less well adapted to take advantage of a longer foraging window in the alpine under climate change compared to colonizing species (Miller-Struttmann et al. 2022). *Bombus sylvicola* is classified by the International Union for the Conservation of Nature as ‘least concern’ (Hatfield et al. 2015c). However, recent genomic analysis of specimens initially identified as *B. sylvicola* has revealed the presence of a cryptic species, *‘incognitus’* (Christmas et al. 2022). While this species isn’t formally recognized, two species being categorized as *B. sylvicola* may be conflating their population status. *Bombus balteatus* has recently been reclassified as *B. kirbiellus* for North American populations (Williams et al. 2015). More information on the population status of this species is needed to fully understand the how *B. balteatus* could be impacted by climate change (Hatfield et al. 2014). However, relative abundance of this species has declined from historic measures in North America (Hatfield et al. 2014). Increased competitive pressures in addition to these pre-existing disadvantages may exacerbate the effects of climate change on species restricted to high elevations.

Our approach to this simulation was simple and only considered individual comparisons of traits among co-occurring bumble bee species. We did not consider how the range shifts of host flowers might impact potentially novel competitive interactions at the tops of mountain ranges since we assumed bumble bees will be more mobile in their response to warming temperatures than plants. In addition, we assumed that all zone 4 bumble bees would move upwards into zone 5 in response to climate change at the same rate. This may not be realistic, as past research has documented species variation in bumble bee elevation shifts (Pyke et al. 2016, Marshall et al. 2020). We also assumed that bumble bee species' phenology would not change as they move upwards in elevation. We acknowledge that our model is simplistic and that it is unlikely that bumble bees will have unchanged phenology as they move upwards into a new habitat. However, past research has found that bumble bees that have already colonized the alpine tend to be less genetically constrained, or ‘canalized,’ in their phenology than resident bumble bees (Miller-Struttmann et al. 2022), so it may be reasonable to assume that phenology will not change drastically between colonizing and resident species. With simple models we were able to infer potential species-specific competitive impacts. These could be expanded (e.g. with species distribution modeling) to better understand potential changes in competitive pressures under climate change.

Our findings highlight the value of using trait measurements to predict potential novel competitive interactions under climate change. However, future research is needed to predict the outcomes of these potential novel competitive interactions. Additionally, considering the relative fitness of the different trait values species may have, rather than trait values alone, would also be valuable for predicting competitive outcomes (Funk and Wolf 2016) for future predictive models of novel competitive pressures under climate change.

Conclusion

In summary, our study shows that bumble bee diet niche overlap increases with elevation, morphological and phenological traits (phenology, body size, tongue length) are correlated with diet composition among bumble bee species, and the upward movement of bumble bees under climate change may lead to new pairs of species with very similar trait values, increasing the likelihood that they will have a similar diet at the mountaintop under climate change. The effects of climate change may be exacerbated by the movement of species to remain within habitable environmental conditions. Our findings highlight the utility of using species traits to predict expected novel competitive interactions under climate change.

Acknowledgements – Thank you to Dr Deane Bowers and Dr Adrian Carper for their intellectual contributions to this research. Thank you to members of the Resasco and Bowers lab for their thoughtful feedback.

Funding – This research was funded by the National Science Foundation (NSF-DEB 2102974) and National Geographic Explorer award given to JR and the CanBee Cocktails grant given to KB.

Author contributions

Kaitlyn Barthell: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (equal); Resources (supporting); Supervision (supporting); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (supporting). **Julian Resasco**: Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Resources (lead); Supervision (lead); Validation (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1g1jwsv6d (Barthell and Resasco 2024).

Supporting information

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

References

Ackerfield, J. 2015. The flora of Colorado, 4th edn. – Lipscomb B. Bo. Res. Inst. of Texas.

Alexander, J. M., Diez, J. M. and Levine, J. M. 2015. Novel competitors shape species' responses to climate change. – Nature 525: 515–518.

Balfour, N. J., Shackleton, K., Arscott, N. A., Roll-Baldwin, K., Bracuti, A., Toselli, G. and Ratnieks, F. L. 2021. Energetic efficiency of foraging mediates bee niche partitioning. – Ecology 102: e03285.

Barthell, K. and Resasco, J. 2024. Data from: Bumble bee niche overlap along an elevation gradient: how traits can inform novel competitive pressures under climate change. – Dryad Digital Repository, https://doi.org/10.5061/dryad.1g1jwsv6d.

Bingham, R. A. and Orthner, A. R. 1998. Efficient pollination of alpine plants. – Nature 391: 238–239.

Brosi, B. J., Niezgoda, K. and Briggs, H. M. 2017. Experimental species removals impact the architecture of pollination networks. – Biol. Lett. 13: 20170243.

Burns, J. H. and Strauss, S. Y. 2011. More closely related species are more ecologically similar in an experimental test. – Proc. Natl Acad. Sci. USA 108: 5302–5307.

Byron, P. A. 1980. On the ecology and systematics of coloradan bumblebees. – PhD thesis, Dept of Environmental, Population and Organismic Biology, Univ. of Colorado, Boulder, CO, USA.

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F. and Griswold, T. L. 2011. Patterns of widespread decline in North American bumble bees. – Proc. Natl Acad. Sci. USA 108: 662–667.

Chesshire, P. R., McCabe, L. M. and Cobb, N. S. 2021. Variation in plant–pollinator network structure along the elevational gradient of the San Francisco Peaks, Arizona. – Insects 12: 1060.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. – Annu. Rev. Ecol. Syst. 31: 343–366.

Christmas, M. J., Jones, J. C., Olsson, A., Wallerman, O., Bunikis, I., Kierczak, M., Whitley, K. M., Sullivan, I., Geib, J. C., Miller-Struttmann, N. E. and Webster, M. T. 2022. A genomic and morphometric analysis of alpine bumblebees: ongoing reductions in tongue length but no clear genetic component. – Mol. Ecol. 31: 1111–1127.

Costa-Pereira, R., Araújo, M. S., Souza, F. L. and Ingram, T. 2019. Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. – Proc. R. Soc. B 286: 20190369.

de Keyzer, C. W., Colla, S. R., Kent, C. F., Rafferty, N. E., Richardson, L. L. and Thomson, J. D. 2016. Delving deeper: questioning the decline of long-tongued bumble bees, long-tubed flowers and their mutualisms with climate change. – J. Pollination Ecol. 18: 36–42.

Dormann, C. F., Fründ, J., Blüthgen, N. and Gruber, B. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. – Open Ecol. J. 2: 7–24.

Doublet, V., Doyle, T., Refoy, I., Hedges, S., Carvell, C., Brown, M. J. and Wilfert, L. 2022. Increasing flower species richness in agricultural landscapes alters insect pollinator networks: implications for bee health and competition. – Ecol. Evol. 12: e9442.

Funk, J. L. and Wolf, A. A. 2016. Testing the trait-based community framework: do functional traits predict competitive outcomes? – Ecology 97: 2206–2211.

Gallou, A., Baillet, Y., Ficetola, G. F. and Després, L. 2017. Elevational gradient and human effects on butterfly species richness in the French Alps. – Ecol. Evol. 7: 3672–3681.

Gómez-Ruiz, E. P. and Lacher Jr, T. E. 2019. Climate change, range shifts, and the disruption of a pollinator–plant complex. – Sci. Rep. 9: 14048.

Gorenflo, A., Diekötter, T., van Kleunen, M., Wolters, V. and Jauker, F. 2017. Contrasting pollination efficiency and effectiveness among flower visitors of *Malva sylvestris*, *Borago officinalis* and *Onobrychis viciifolia*. – J. Pollination Ecol. 21: 62–70.

Goulson, D. and Darvill, B. 2004. Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? – Apidologie 35: 55–63.

Goulson, D., Lye, G. C. and Darvill, B. 2008. Diet breadth, coexistence and rarity in bumblebees. – Biodivers. Conserv. 17: 3269–3288.

Harder, L. D. 1985. Morphology as a predictor of flower choice by bumble bees. – Ecology 66: 198–210.

Hatfield, R., Colla, S., Jepsen, S., Richardson, L., Thorp, R. and Foltz, S. 2014. IUCN assessments for North American *Bombus* spp. for the North American IUCN bumble bee specialist group. – IUCN.

Hatfield, R., Jepsen, S., Thorp, R., Richardson, L., Colla, S. and Folts, J. 2015a. *Bombus fervidus*. – The IUCN Red List of Threatened Species.

Hatfield, R., Jepsen, S., Thorp, R., Richardson, L., Colla, S. and Foltz, J. 2015b. *Bombus pensylvanicus*. – The IUCN Red List of Threatened Species.

Hatfield, R., Jepsen, S., Thorp, R., Richardson, L. and Colla, S. 2015c. *Bombus sylvicola*. – The IUCN Red List of Threatened Species.

Heinrich, B. 1976. Resource partitioning among some eusocial insects: bumblebees. – Ecology 57: 874–889.

Hollister, J., Shah, T., Robitaille, A., Beck, M. and Johnson, M. 2021. elevatr: access elevation data from various APIs. – R package ver. 0.4.2, https://cran.r-project.org/web/packages/elevatr/index.html.

Horn, H. S. 1966. Measurement of 'overlap' in comparative ecological studies. – Am. Nat. 100: 419–424.

Hsieh, T. C., Ma, K. H. and Chao, A. 2022. iNEXT: iNterpolation and EXTtrapolation for species diversity. – R package ver. 3.0.0, https://cran.r-project.org/web/packages/iNEXT/index.html.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? – Trends Ecol. Evol. 15: 56–61.

Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. – Ecology 59: 672–678.

Kahle, D. and Wickham, H. 2013. ggmap: spatial visualization with ggplot2. – R J. 5: 144–161.

Kelso, T. 2012. Peak to prairie: botanical landscapes of the Pikes Peak region. – Colorado College.

Kerr, J. T., Pindar, A., Galpern, P., Packer, L., Potts, S. G., Roberts, S. M., Rasmont, P., Schweiger, O., Colla, S. R., Richardson, L. L., Wagner, D. L., Gall, L. F., Sikes, D. S. and Pantoja, A. 2015. Climate change impacts on bumblebees converge across continents. – Science 349: 177–180.

Kingsolver, J. G., Diamond, S. E. and Buckley, L. B. 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. – Funct. Ecol. 27: 1415–1423.

Körner, C. 2007. The use of 'altitude' in ecological research. – Trends Ecol. Evol. 22: 569–574.

Kosior, A., Celary, W., Olejniczak, P., Fijał, J., Król, W., Solarz, W. and Płonka, P. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe. – Oryx 41: 79–88.

Macior, L. W. 1974. Pollination ecology of the front range of the Colorado Rocky Mountains. – Melanderia 15: 1–59.

Marshall, L., Perdijk, F., Dendoncker, N., Kunin, W., Roberts, S. and Biesmeijer, J. C. 2020. Bumblebees moving up: shifts in elevation ranges in the Pyrenees over 115 years. – Proc. R. Soc. B 287: 20202201.

McCabe, L. M., Cobb, N. S. and Butterfield, B. J. 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.

McCain, C. M. and Grytnes, J. A. 2010. Elevational gradients in species richness. – Encyclopedia of Life Sciences, pp. 1–10.

Medler, J. T. 1962. Morphometric studies on bumble bees. – Ann. Entomol. Soc. Am. 55: 212–218.

Michener, C. D. 2007. The bees of the world, 4th edn. – Johns Hopkins Univ. Press

Miller-Struttmann, N. E. and Galen, C. 2014. High-altitude multi-taskers: bumble bee food plant use broadens along an altitudinal productivity gradient. – Oecologia 176: 1033–1045.

Miller-Struttmann, N., Miller, Z. and Galen, C. 2022. Climate driven disruption of transitional alpine bumble bee communities. – Global Change Biol. 28: 6165–6179.

Minachilis, K., Kantsa, A. and Petanidou, T. 2021. Bumblebees, the proficient mountain pollinators: evidence from *Stachys germanica* (Lamiaceae) along the altitudinal gradient of Mount Olympus, Greece. – Biol. J. Linn. Soc. 134: 732–744.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P. and Stevens, M. H. 2020 Vegan: community ecology package. – R package ver. 2.5-7, https://cran.r-project.org/web/packages/vegan/index.html.

Ollerton, J., Winfree, R. and Tarrant, S. 2011. How many flowering plants are pollinated by animals? – Oikos 120: 321–326.

Oyen, K. J., Giri, S. and Dillon, M. E. 2016. Altitudinal variation in bumble bee (*Bombus*) critical thermal limits. – J. Therm. Biol. 59: 52–57.

Pyke, G. H., Thomson, J. D., Inouye, D. W. and Miller, T. J. 2016. Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. – Ecosphere 7: e01267.

Resasco, J. 2021. Award abstract # 2102974: understanding changes in a plant–pollinator network over a century of global change. – National Science Foundation.

Resasco, J., Vázquez, D. P., McCain, C. M. and Olson, S. D. 2024. Revisiting Clements and Gleason: insights from plant distributions on Pikes Peak, Clements's life-long study site. – Am. Nat. https://doi.org/10.1086/732808.

Richman, S. K., Levine, J. M., Stefan, L. and Johnson, C. A. 2020. Asynchronous range shifts drive alpine plant–pollinator interactions and reduce plant fitness. – Global Change Biol. 26: 3052–3064.

Soroye, P., Newbold, T. and Kerr, J. 2020. Climate change contributes to widespread declines among bumble bees across continents. – Science 367: 685–688.

Sponsler, D., Kallnik, K., Requier, F., Classen, A., Maihoff, A. F., Sieger, J. and Steffan-Dewenter, I. 2022a. Floral preferences of mountain bumble bees are constrained by functional traits but flexible through elevation and season. – Oikos 2022: e08902.

Sponsler, D. B., Requier, F., Kallnik, K., Classen, A., Maihoff, F., Sieger, J. and Steffan-Dewenter, I. 2022b. Contrasting patterns of richness, abundance, and turnover in mountain bumble bees and their floral hosts. – Ecology 103: e3712.

Ştefan, V. and Knight, T. M. 2023. bootstrapnet: bootstrap network metrics. – R package ver. 1.0.0, https://github.com/valentinitnelav/bootstrapnet?tab=readme-ov-file.

Stephens, R. E., Sauquet, H., Guerin, G. R., Jiang, M., Falster, D. and Gallagher, R. V. 2022. Climate shapes community flowering periods across biomes. – J. Biogeogr. 49: 1205–1218.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J., Hoegh-Guldberg, O. and Bairlein, F. 2002. Ecological responses to recent climate change. – Nature 416: 389–395.

Wardle, D. A., Bardgett, R. D., Callaway, R. M. and Van der Putten, W. H. 2011. Terrestrial ecosystem responses to species gains and losses. – Science 332: 1273–1277.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis, 2nd edn. – Springer.

Wilke, C. S. 2022. ggridges: ridgeline plots in 'ggplot2'. – R package ver. 0.5.4, https://cran.r-project.org/web/packages/ggridges/index.html.

Williams, P., Thorp, R., Richardson, L. and Colla, S. 2014. The bumblebees of North America. – Princeton Univ. Press

Williams, P. H., Byvaltsev, A. M., Cederberg, B., Berezin, M. V., Ødegaard, F., Rasmussen, C., Richardson, L. L., Huang, J., Sheffield, C. S. and Williams, S. T. 2015. Genes suggest ancestral colour polymorphisms are shared across morphologically cryptic species in Arctic bumble bees. – PLoS One 10: e0144544.

Wohlgemuth, T., Nobis, M. P., Kienast, F. and Plattner, M. 2008. Modeling vascular plant diversity at the landscape scale using systematic samples. – J. Biogeogr. 35: 1226–1240.

Wright, A., Boyd, C. L., Bowers, M. D. and Scott, V. L. 2017. The bumble bees of Colorado. – Princeton Univ. Press.