



## ARTICLE

# Contrasting patterns of richness, abundance, and turnover in mountain bumble bees and their floral hosts

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## Abstract

Environmental gradients generate and maintain biodiversity on Earth. Mountain slopes are among the most pronounced terrestrial environmental gradients, and the elevational structure of species and their interactions can provide unique insight into the processes that govern community assembly and function in mountain ecosystems. We recorded bumble bee–flower interactions over 3 years along a 1400-m elevational gradient in the German Alps. Using nonlinear modeling techniques, we analyzed elevational patterns at the levels of abundance, species richness, species  $\beta$ -diversity, and interaction  $\beta$ -diversity. Though floral richness exhibited a midelevation peak, bumble bee richness increased with elevation before leveling off at the highest sites, demonstrating the exceptional adaptation of these bees to cold temperatures and short growing seasons. In terms of abundance, though, bumble bees exhibited divergent species-level responses to elevation, with a clear separation between species preferring low versus high elevations. Overall interaction  $\beta$ -diversity was mainly caused by strong turnover in the floral community, which exhibited a well-defined threshold of  $\beta$ -diversity rate at the tree line ecotone. Interaction  $\beta$ -diversity increased sharply at the upper extreme of the elevation gradient (1800–2000 m), an interval over which we also saw steep decline in floral richness and abundance. Turnover of bumble bees along the elevation gradient was modest, with the highest rate of  $\beta$ -diversity occurring over the interval from low- to mid-elevation sites. The contrast between the relative robustness bumble bee communities and sensitivity of plant communities to the elevational gradient in our study suggests that the strongest effects of climate change on mountain bumble bees may be indirect effects mediated by the responses of their floral hosts, though bumble bee species that specialize in high-elevation habitats may also experience significant direct effects of warming.

## KEYWORDS

alpine plants,  $\beta$ -diversity, *Bombus*, climate, elevation gradient, mountain ecology, pollination network

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## INTRODUCTION

Environmental gradients regulate the assembly of biological communities, and they have likely played a central role in generating and maintaining Earth's biological diversity (Hutchinson, 1953). Patterns of species- and community-level responses to environmental gradients can shed light on the underlying mechanisms that govern community assembly and function (e.g., Beals, 1969). In addition to its basic significance, such insight is important for anticipating and managing the effects of climate and land-use change, which can modify existing environmental gradients and reorganize the biological communities that inhabit them.

Mountain slopes generate steep environmental gradients over short geographical distances, facilitating the assembly of biological communities with high species richness and turnover (Rahbek et al., 2019). Perhaps the most salient environmental condition that changes along a mountain elevation gradient is air temperature, which declines according to a linear lapse rate of approximately  $-0.6^{\circ}\text{C}$  per 100 m (Rolland, 2003), but mountain slopes also generate variation in other conditions, including precipitation, atmospheric pressure, atmospheric turbulence, substrate characteristics, and exposure to solar radiation (Hodkinson, 2005; Körner, 1995).

Ecologists have long viewed mountain slopes as natural laboratories for the study of community assembly, and particular attention has been given to elevational patterns of species richness and composition. Species richness along mountain slopes tends to exhibit either a midelevation peak or a monotonic decline (Guo et al., 2013; Rahbek, 1995), though the exact shape of these responses can vary considerably across taxonomic groups (e.g., Peters et al., 2016). Species composition along mountain slopes, best studied in plant communities, can exhibit a range of patterns from smooth gradations to relatively abrupt transitions, with steeper slopes tending to exhibit more discrete patterns of species turnover (Beals, 1969). For example, many mountains have a well-defined tree line ecotone, where plant communities exhibit accelerated species turnover and declining diversity as multiple abiotic conditions become more extreme away from the shelter of tree canopy, as discussed by Slatyer & Noble (1992), Becker et al. (2007), and Descombes et al. (2017), though see Odland & Birks (1999).

Though elevational patterns in overall species richness and composition are informative, the functional significance of mountain slopes can be explored more deeply by focusing on the responses of interacting guilds of species. For example, studies of plants and insect herbivores along mountain elevation gradients have revealed a positive correlation between elevation and herbivore niche breadth, suggesting an extension of the classical latitude–niche–breadth hypothesis to the analogous case

of elevational gradients (Rasmann et al., 2018). Similarly, plant–pollinator interactions along mountain slopes have been found to become less specialized as elevation increases, which may reflect a reciprocal relationship between the processes of competition and environmental filtering in community assembly (Classen et al., 2020; Hoiss et al., 2015). A unifying theme of such studies is the understanding of species interactions as ecological entities per se, dependent upon but not reducible to the species-level richness and composition of the interacting guilds.

Bumble bees (Hymenoptera: *Bombus* spp.) and their floral hosts provide an excellent system in which to study elevational patterns at both the species and interaction levels. Bumble bees are believed to have arisen in the mountains of Asia during the cooling climate of the Eocene–Oligocene boundary, and their subsequent spread and diversification along mountain corridors and into lowland habitats was likely driven by alternating range expansion during cooling periods and retreat to higher elevations during warming periods (Hines, 2008; Martinet et al., 2018; Stewart et al., 2010). Today, they remain characteristically cold-adapted organisms (Heinrich & Esch, 1994), with peak abundance and diversity in mountain ranges and northern latitudes (Williams, 1998). In these habitats, they are often the dominant guild of flower-visiting insects and the principal pollinators of entomophilous flora (Goulson, 2010). As in the past, so now are mountain habitats critical theaters of ecological change for bumble bees. Warming climates are expected to cause habitat loss and potentially novel competitive pressures (Kerr et al., 2015; Soroye et al., 2020; though see Guzman et al., 2021). At the same time, socioeconomic drivers are causing succession to forest in pastures on mountain slopes and the intensification of agriculture in lowlands, both of which entail a loss of floral resources for bumble bees (Tappeiner et al., 2006; Tasser et al., 2007; Tasser & Tappeiner, 2002; Walcher et al., 2017).

In this paper, we present a study based on ~13,000 interactions between bumble bees and their floral hosts recorded along a 1400-m elevation gradient, complemented by corresponding surveys of floral abundance. Using this data set, we investigate elevational responses of richness, abundance, and  $\beta$ -diversity, at the level of species (bumble bees and flowering plants) and at the level of interactions (bumble bee–flower pairs). Our results reveal nonlinear and, in some cases, contrasting elevational patterns, underscoring the fact that mountain slopes are complex ecological systems where multiple processes interact to produce biological responses. These patterns shed light on the basic ecology of the mountain mutualism between bumble bees and wildflowers and suggest how this mutualism might be reshaped by ongoing processes of climate and land use change.

## METHODS

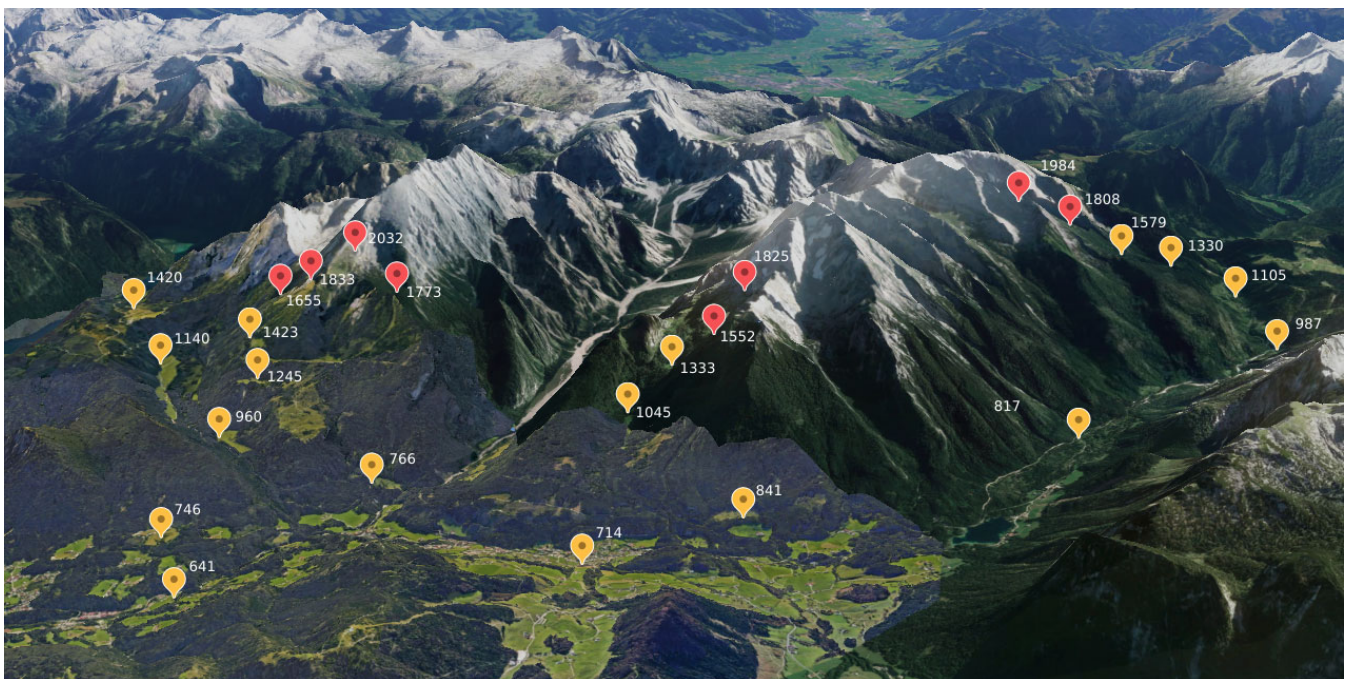
### Field system

The study was conducted from 2010 to 2012 in Berchtesgaden National Park, located in the Northern Limestone Alps of southeast Germany (47.55° N, 12.92° E). The landscape is composed of mountain pastures surrounded mainly by coniferous forest. We selected 25 study sites (60 × 60 m) on mountain pastures at elevations ranging from 641 to 2032 m above sea level (a.s.l.) (Figure 1). Of these pastures, 14 are extensively grazed by cattle or sheep, 3 are mowed for hay production, and 8 have been abandoned throughout the last century and are no longer subjected to any human management. Study sites were classified as lying either above or below the tree line based on an examination of Google Earth imagery corroborated by field experience at our study sites. Eight sites were located above the tree line, which generally fell at an elevation of around 1500 m a.s.l., consistent with the previous descriptions of the tree line in the Berchtesgadener Alps (Köstler & Mayer, 1970; Mayer, 1970).

Sampling in each year of the study consisted of repeated visits to each site at approximately weekly intervals. Samples were only collected during periods without rain and when the air temperature was at least 6°C. We divided each 60 × 60 m study plot into 10 evenly spaced 60 × 6 m transects. During each visit, the observer

walked each transect in a zigzag pattern for 5 min and recorded all interactions between bumble bees and flowers; thus, each sampling event consisted of a total of 50 min of observation. Bumble bees observed on a given flower were counted as floral visitors. Bumble bee queens were identified to species level in the field, whereas workers and males were collected and stored in individually labeled tubes in the freezer for later identification in the laboratory according to Amiet (1996). Floral visitation by male bumble bees was recorded during visitation sampling, but we chose to analyze only visitation by queens and workers. Males are often found resting on flowers, particularly late in the year, so their presence on a flower cannot necessarily be interpreted as a foraging visit. In conjunction with bumble bee observations, we estimated the flower cover of each herbaceous or shrubby plant species within the study plot to the nearest 0.01 m<sup>2</sup> by exhaustive visual inspection of the study plot. To avoid observer bias, floral cover estimates were always performed by the same investigator (K. Kallnik). Plant species were identified following Lauber and Wagner (2007) and Oberndorfer (2001).

Although per-sample effort was standardized across all years, the total number of samples (i.e., site dates) and of bumble bee observations varied across years. Since the start of field sampling each year was determined by snowmelt, lower sites were sampled as early as April, though higher sites could not be sampled until June or July. This resulted in a temporally staggered pattern of



**FIGURE 1** Study sites in Berchtesgadener Alps plotted over Google Earth imagery (<https://earth.google.com/>). Sites above the tree line are in red and sites below the tree line in yellow. The elevation of each site is given in meters above sea level

sampling in 2010 and 2012, though in 2011 a combination of early snowmelt and a late start to field activities resulted in sampling that was approximately aligned in time across the whole elevation gradient. See Appendix S1 for a detailed description of sampling patterns.

## Data analysis

### Data processing

We quantified bumble bee abundance as the total number of recorded floral visits per bumble bee species per site date. We treated the cryptic *Bombus terrestris/lucorum* species pair as a single morphospecies, since these two species cannot be visually distinguished, and we pooled representatives of the parasitic *Psithyrus* subgenus—*Bombus barbutellus*, *B. bohemicus*, *B. campestris*, *B. flavidus*, *B. quadricolor*, and *B. sylvestris*—into the species group *B. psithyrus*.

To focus our analysis on the subset of flowering plant species that are relevant to bumble bee foraging, we omitted from analysis all plant species that received no visits from bumble bees during the course of our study. Eight plant species—*Rubus idaeus*, *Rosa canina*, *Juniperus communis*, *Larix decidua*, *Salix* sp., *Caltha palustris*, *Pulmonaria officinalis*, and *Rheum barbarum*—were recorded as visited during interaction sampling but were missed during floral surveying. Each accounted for no more than four visits in total over the 3 years of our study, so they were also omitted from analysis.

### Elevational patterns of richness and abundance

We analyzed the richness and abundance of bumble bees, flowering plants, and their interactions using hierarchical generalized additive models (HGAMs) (Wood, 2011; Pedersen et al., 2019). To focus on elevational patterns, we collapsed within-year variation of richness and abundance at each site into annual summary values of cumulative richness and peak abundance. We then modeled these summary values, respectively, as smooth responses to elevation. Following the global-independent model form described by Pedersen et al. (2019), we specified both a global smoother and year-specific smoothers, with the latter understood as *random* deviations from the global effect. In each model, we also included year and management as fixed intercept effects, and we included site as a random intercept effect to avoid pseudoreplication due to repeated sampling of sites across years. In the richness models, we also added number of transects as a smoother to account for the effect of

sampling intensity on observed richness. For all models, we used the quasipoisson (log link) distribution family.

To explore species-level elevational responses in bumble bees, we fit a model with a specieswise elevation smoother and no global smoother, corresponding to the I model form of Pedersen et al. (2019). Year and management were included as fixed intercept effects, and site and species were included as random intercept effects. For this model, we used the negative binomial (log link) distribution family.

To facilitate clear interpretation with respect to our focal questions, the aforementioned models focus on elevational patterns of abundance by summarizing across seasonal time. Within-season abundance patterns and their interaction with elevation were explored with more complex tensor-product generalized additive models (GAMs), and these are included in Appendix S1.

### Species and interaction $\beta$ -diversity

For our analyses of species and interaction  $\beta$ -diversity, we pooled all samples by site irrespective of year. After pooling, we calculated  $\beta$ -diversity between all pairs of sites for bumble bees, flowering plants, and their interactions using the binary Jaccard index. We then partitioned total interaction  $\beta$ -diversity into its components of species turnover (changes in species composition) and interaction rewiring (interaction turnover despite species constancy) (Novotny, 2009; Poisot et al., 2012).

As an initial analysis, we visualized the relationship between sitewise elevation difference and each metric of  $\beta$ -diversity, fitting each response with a binomial regression. We then used generalized dissimilarity modeling (GDM) (Ferrier et al., 2007) to ask whether the relationship between  $\beta$ -diversity and elevation exhibits thresholds or other nonlinearities. In addition to estimating the relationship between differences in a response variable and differences in a predictor variable, GDM captures the slope of this relationship over the range of the predictor variable, revealing potential variation in the amount of change in the response induced by a given change in the predictor (Ferrier et al., 2007). We fit separate generalized dissimilarity models for bumble bees, flora, and their (unpartitioned) interactions, respectively. To control for potential confounding effects of sampling intensity, we included sampling days per site as a covariate, and we included the geographic distances between sites as a covariate to account for potential spatial autocorrelation. The importance of the variables in each model was assessed by a permutation test (Fitzpatrick et al., 2021).

## Software

All analyses were conducted in R (R Core Team, 2021). Data handling and visualization were performed with the *tidyverse* suite (Wickham et al., 2019). GAM analyses were performed with the packages *mgcv* (Wood, 2017), *mgcViz* (Fasiolo et al., 2018), and *gratia* (Simpson, 2021).  $\beta$ -diversity was calculated with the package *vegan* (Oksanen et al., 2019) and visualized using the packages *ggplot2* (Wickham, 2016) and *ggvegan* (Simpson, 2019). Calculation and partitioning of interaction  $\beta$ -diversity were performed with the package *bipartite* (Dormann et al., 2008; Dormann et al., 2009). GDM analysis of  $\beta$ -diversity was performed with the package *gdm* (Fitzpatrick et al., 2021). The full workflows of our analyses are available in Appendix S1 (analysis of sampling patterns), Appendix S2 (analysis of abundance and richness), and Appendix S3 (analysis of  $\beta$ -diversity).

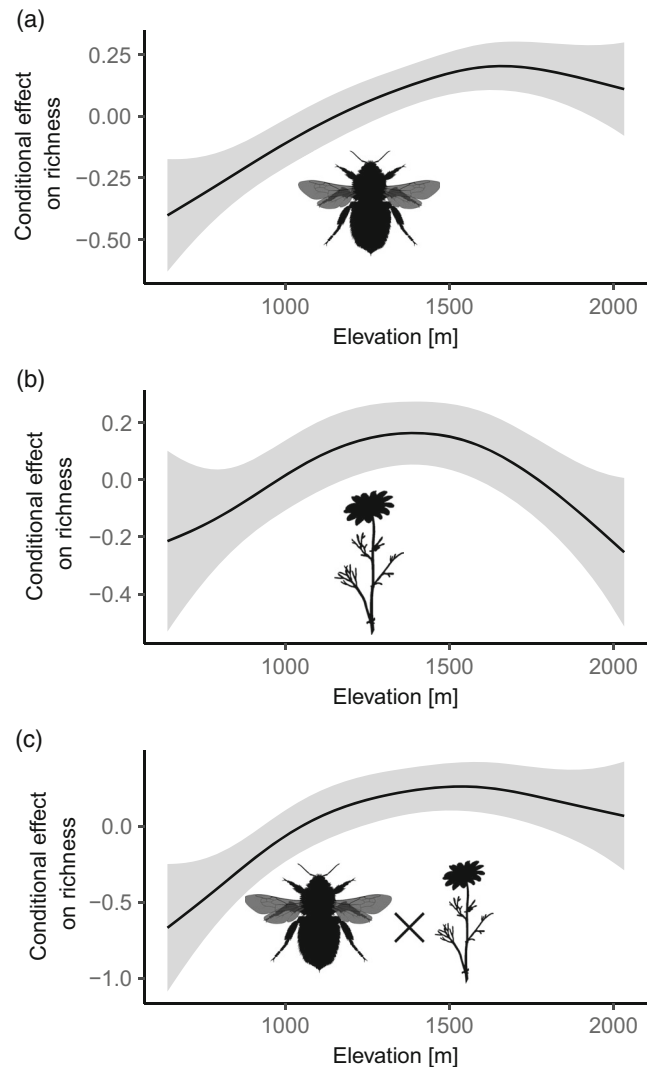
## RESULTS

### Bee–flower interactions and floral survey data

We recorded a total of 12,918 bumble bee–flower interactions (excluding males) over the 3 years of our study. The metaweb across all sites and dates consisted of 16 bumble bee species, 163 plant species (110 genera, 37 families), and 736 unique bumble bee–plant interaction pairs. *Bombus pascuorum* (“pasc”), *B. pratorum* (“prat”), *B. soroeensis* (“soro”), *B. terrestris/lucorum* (“telu”), and *B. wurflenii* (“wurf”) accounted for the bulk of overall bumble bee abundance, whereas *B. hortorum* (“hort”), *B. jonellus* (“jone”), *B. psithyrus* (“psit”), *B. monticola* (“mont”), *B. mendax* (“mend”), *B. mucidus* (“muci”), *B. pyrenaes* (“pyre”), and *B. gerstaeckeri* (“gers”) were present at moderate to low abundance. *Bombus hypnorum*, *B. humilis*, and *B. lapidarius* were recorded only sporadically. See Appendix S1 for a summary of specieswise abundances.

### Elevational patterns of richness and abundance

The response of bumble bee richness to elevation exhibited an approximately linear increase up to 1600–1700 m and then leveled off and declined slightly at the upper limit of the gradient (Figure 2a). The year 2012 had a negative effect ( $p = 0.04$ ) on bumble bee richness relative to the reference year 2010, but neither mowing nor abandonment had a significant effect on bumble bee richness



**FIGURE 2** Conditional effects of elevation on richness of (a) bumble bee species, (b) floral species, and (c) bumble bee–flower interactions. Effects are plotted on link scale, and shaded bands depict 95% confidence intervals. Bumble bee and plant illustrations were obtained from <http://phylopic.org/>; see Appendix S1 for details and licensing

relative to the reference management level of grazing ( $p > 0.05$ ) (Table 1). In contrast, the response of floral richness exhibited a clear unimodal pattern, peaking between 1300 and 1500 m (Figure 2b). The years 2011 ( $p < 0.001$ ) and 2012 ( $p < 0.03$ ) had negative effects on floral richness relative to the reference year 2010, but again management type had no significant effect ( $p > 0.1$ ) (Table 1). The response of interaction richness to elevation was intermediate to that of bumble bee and floral richness, peaking around 1500 m and leveling off at higher elevation (Figure 2c). The effect of year 2011 on interaction richness was positive ( $p < 0.05$ ) and that of year 2012 negative ( $p < 0.001$ ), but management type did not have a significant effect ( $p > 0.1$ ) (Table 1).

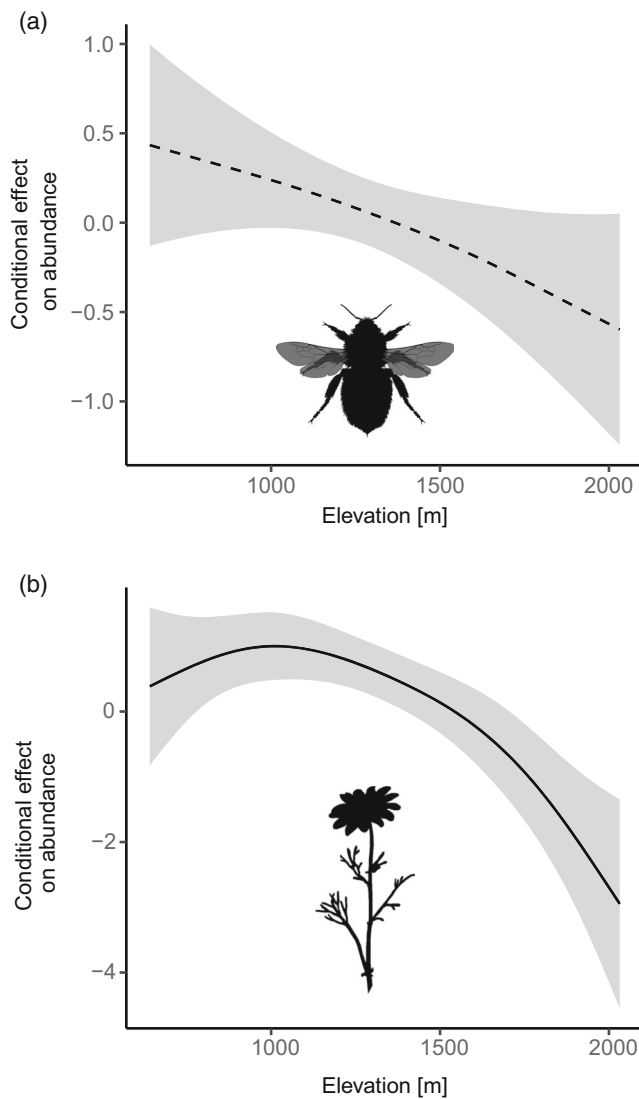
**TABLE 1** Tabular output of richness generalized additive models

Class	Term	Estimate	Lower 95	Upper 95	edf	p.value	Significance
Model: Bumble bees							
Parametric	Intercept	2.15	2.05	2.25		<0.001	***
	mgmt:none	0.01	-0.13	0.15		0.885	
	mgmt:mowing	0.22	-0.02	0.46		0.072	
	year:2011	0.09	-0.01	0.18		0.089	
	year:2012	-0.19	-0.37	-0.01		0.044	*
Smoothe	s(site)				6.54	0.074	
	s(samples)				1	<0.001	***
	s(elevation)				2.77	<0.001	***
	s(elevation:2010)				0.99	0.065	
	s(elevation:2011)				<0.001	0.35	
	s(elevation:2012)				<0.001	0.709	
Model: Flora							
Parametric	Intercept	4.20	4.06	4.34		<0.001	***
	mgmt:none	-0.10	-0.31	0.11		0.362	
	mgmt:mowing	-0.13	-0.46	0.21		0.471	
	year:2011	-0.15	-0.19	-0.10		<0.001	***
	year:2012	-0.35	-0.64	-0.05		0.026	*
Smooth	s(site)				18.17	<0.001	***
	s(samples)				2.35	0.033	*
	s(elevation)				2.78	0.023	*
	s(elevation:2010)				<0.001	0.743	
	s(elevation:2011)				<0.001	0.343	
	s(elevation:2012)				1.41	0.012	*
Model: Interactions							
Parametric	Intercept	3.89	3.69	4.08		<0.001	***
	mgmt:none	-0.14	-0.41	0.14		0.326	
	mgmt:mowing	0.14	-0.31	0.59		0.534	
	year:2011	0.15	0.00	0.30		0.049	*
	year:2012	-0.84	-1.17	-0.51		<0.001	***
Smooth	s(site)				14.81	<0.001	***
	s(samples)				3.61	<0.001	***
	s(elevation)				2.75	0.003	**
	s(elevation:2010)				<0.001	0.907	
	s(elevation:2011)				<0.001	0.461	
	s(elevation:2012)				<0.001	0.525	

Note: Parametric model terms are summarized with an estimated intercept effect (“estimate”), whereas smooth terms are summarized with their effective degrees of freedom (“edf”), the latter representing the complexity (i.e., “wiggleness”) of the fitted spline. Elevation:year smoothers represent year-specific deviations from the global elevation smoothers calculated across years. \*  $0.01 < p < 0.05$ ; \*\*  $0.001 < p < 0.01$ ; \*\*\*  $p < 0.001$ .

Cumulative bumble bee abundance did not respond significantly to elevation ( $p > 0.1$ ) (Figure 3a) or management type ( $p > 0.1$ ), but the year 2011 had a positive effect ( $p = 0.03$ ) on bumble bee abundance relative to the

reference year of 2010 (Table 2). Floral abundance, however, peaked around 1000 m and exhibited an approximately quadratic decline with increasing elevation ( $p = 0.003$ ) (Figure 3b). The effect of year 2012 on floral



**FIGURE 3** Conditional effects of elevation on peak abundance of (a) bumble bees and (b) flower cover. Effects are plotted on link scale, and shaded bands depict 95% confidence intervals. The dashed line for the bumble bee abundance smoother indicates that this smoother did not differ significantly from a flat line ( $p > 0.1$ )

abundance was negative ( $p = 0.002$ ) relative to the reference year 2010 ( $p = 0.02$ ), and the effect of abandoned meadows on floral abundance was positive compared to the reference level of grazed meadows (Table 2).

At the species level, bumble bee abundance exhibited variable and sometimes divergent responses to elevation (Figure 4 and Table 3). *B. pyrenaicus*, *B. mendax*, *B. monticola*, and *B. mucidus* exhibited approximately linear increases with elevation. In contrast, *B. psithyrus* and *B. pascuorum* exhibited approximately linear decreases with elevation. *B. pratorum* was unique in exhibiting a strongly unimodal abundance pattern with a well-defined peak between 1500 and 1600 m, approximately at the tree

line ecotone, similar to the abundance pattern of *B. pratorum* described by Iserby et al. (2008) in the Eyne Valley of the Pyrenees. The remaining species did not respond significantly to elevation ( $p > 0.05$ ). It must be noted, however, that the pooling of *B. terrestris* and *B. lucorum* might have masked distinct elevational responses of these species (Geue & Thomassen, 2020).

### Species and interaction $\beta$ -diversity

Floral  $\beta$ -diversity among our study sites was very high overall and responded steeply to elevation difference between sites (Figure 5a). Even sites at similar elevation exhibited  $\sim 40\%$  species turnover, and the most vertically distant sites (elevation difference  $> 1250$  m) differed by more than 85%. Bumble bee  $\beta$ -diversity was, in comparison to floral  $\beta$ -diversity, both lower overall and less responsive to elevational difference between sites (Figure 5a). Sites at similar elevation exhibited  $\sim 25\%$  species turnover, and species turnover between the most vertically distant sites remained less than 50%.

Total interaction  $\beta$ -diversity was  $> 75\%$  between sites at similar elevation and approached perfect dissimilarity in the most vertically distant sites (Figure 5a). Partitioning (Figure 5b) revealed that total interaction  $\beta$ -diversity was driven primarily by turnover of floral hosts, which accounted for  $\sim 50\%$  of total interaction turnover for sites at similar elevation and nearly 75% of interaction turnover for the most vertically distant sites. The contribution of bumble bee species turnover alone to interaction turnover was minimal, but the importance of joint turnover of plants and bumble bees increased from less than 5% between sites at similar elevation to 25% of interaction turnover between the most vertically distant sites. The importance of interaction rewiring exhibit the opposite pattern, accounting for  $\sim 30\%$  of interaction turnover between sites at similar elevation but only  $\sim 10\%$  between the most vertically distant sites.

Bumble bees, flora, and their interactions exhibited marked differences in their rates of  $\beta$ -diversity in response to elevation (Figure 6). Bumble bee turnover was relatively high from  $\sim 600$  to 1100 m, briefly leveled off, and then accelerated again around 1250 m. Floral turnover was high from  $\sim 600$  to 1000 m, gradually leveled off from  $\sim 1000$ –1500 m, and then accelerated again around the tree line ecotone at  $\sim 1500$  m. Interaction turnover mirrored the high rates of bumble bee and floral  $\beta$ -diversity from  $\sim 600$  to 1000 m, but it exhibited a markedly different pattern above 1000 m, with relatively low turnover between 1000 and 1750 m and then a sharp acceleration from  $\sim 1750$  to 2000 m. The conditional effect of elevation was significant ( $p < 0.001$ ) in all models, and

**TABLE 2** Tabular output of abundance generalized additive models

Class	Term	Estimate	Lower 95	Upper 95	edf	p.value	Significance
Model: Bumble bees							
Parametric	Intercept	3.68	3.42	3.95		<0.001	***
	mgmt:none	-0.04	-0.46	0.38		0.848	
	mgmt:mowing	-0.48	-1.09	0.12		0.124	
	year:2011	0.33	0.04	0.62		0.028	*
	year:2012	-0.30	-0.64	0.03		0.082	
Smooth	s(site)				4.28	0.281	
	s(elevation)				1.41	0.128	
	s(elevation:2010)				1	0.155	
	s(elevation:2011)				1.54	0.172	
	s(elevation:2012)				<0.001	0.991	
Model: Flora							
Parametric	Intercept	1.58	1.10	2.07		<0.001	***
	mgmt:none	1.23	0.48	1.98		0.002	**
	mgmt:mowing	0.62	-0.39	1.63		0.232	
	year:2011	0.36	-0.02	0.74		0.067	
	year:2012	-0.59	-1.06	-0.13		0.015	*
Smooth	s(site)				9.52	0.003	**
	s(elevation)				2.89	0.001	**
	s(elevation:2010)				1.25	0.029	*
	s(elevation:2011)				1	0.887	
	s(elevation:2012)				<0.001	0.982	

Note: Parametric model terms are summarized with an estimated intercept effect (“estimate”), whereas smooth terms are summarized with their effective degrees of freedom (“edf”), the latter representing the complexity (i.e., “wiggleness”) of the fitted spline. Elevation:year smoothers represent year-specific deviations from the global elevation smoothers calculated across years. \*  $0.01 < p < 0.05$ ; \*\*  $0.001 < p < 0.01$ ; \*\*\*  $p < 0.001$ .

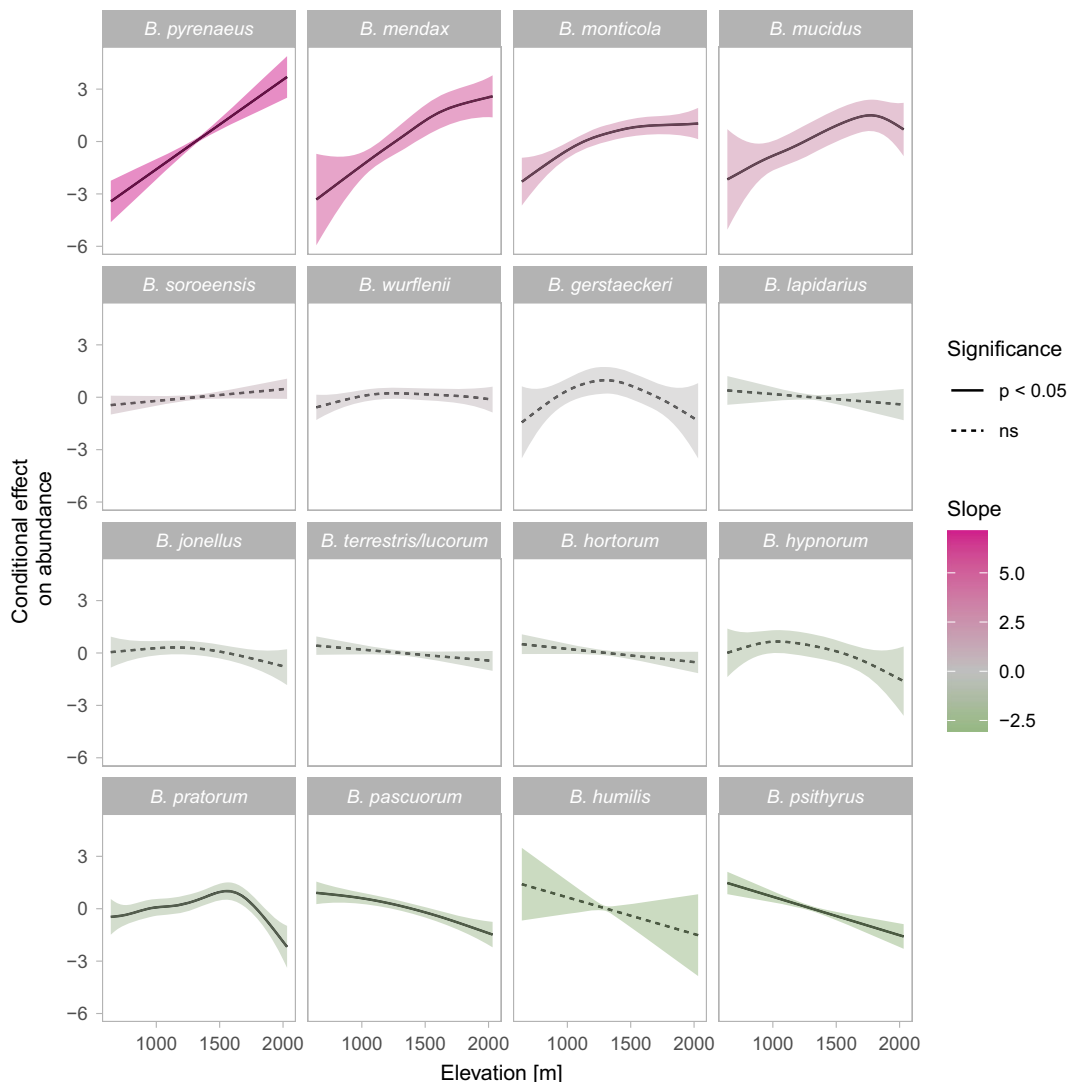
its importance was 4–20 times higher than that of sampling intensity and geographic distance (Table 4). Nevertheless, geographic distance was a significant predictor in all models ( $p < 0.001$ ), and sampling intensity was a significant predictor in the bumble bee ( $p = 0.004$ ) and interaction models ( $p < 0.001$ ). Our generalized dissimilarity models explained 31% of total deviance in bumble bee  $\beta$ -diversity, 73% of floral  $\beta$ -diversity, and 71% of interaction  $\beta$ -diversity.

## DISCUSSION

Our study revealed strong and sometimes contrasting patterns of elevational structure in the richness, abundance, and  $\beta$ -diversity of mountain bumble bees and wildflowers. By extending our analysis to the level of species interactions, we show how the elevational patterns within bumble bee and wildflower communities are propagated to the functional relationships between these two guilds.

Though floral richness exhibited the expected unimodal response to elevation, bumble bee richness responded positively to elevation for nearly the whole gradient, showing only a slight declining trend at the highest sites. The positive response of bumble bee species richness to elevation sets bumble bees apart from most other taxa (Guo et al., 2013; Peters et al., 2016; Rahbek, 1995), underscoring their exceptional adaptation to mountain environments. In particular, it stands in sharp contrast to the monotonic decline of overall bee richness with elevation in the Berchtesgadener Alps (Hoiss et al., 2012), highlighting the special importance of bumble bees as pollinators where few other bees persist. On higher mountains, the increase of bumble bee richness with elevation eventually gives way to a unimodal response, but peak richness is often found above 3000 m (e.g., Paul Hugh Williams, 1991; Streinzer et al., 2019). In the Berchtesgadener Alps, which reach just over 2000 m, the positive response of bumble bee richness to elevation encompasses almost the entire mountain slope, echoing the findings of Minachilis et al. (2020)





**FIGURE 4** Conditional effects of elevation on peak abundance of each bumble bee species. Effects are plotted on link scale, and shaded bands depict 95% confidence intervals. Confidence bands are colored to indicate the linear slope of the response curve, and species are plotted in order of decreasing slope

along a comparable elevation gradient (300–2700 m) at Mt. Olympus, Greece.

The response of overall bumble bee abundance to elevation was approximately flat, but this aggregate pattern concealed divergent species-level responses. The strongly positive responses of *B. mendax*, *B. monticola*, *B. mucidus*, and *B. pyrenaeus* are consistent with the known affinity of these species for high-elevation habitats (Rasmont & Iserbyt, 2010–2014). At the other extreme, *B. pascuorum* and the *B. psithyrus* species group exhibited strongly negative responses to elevation. In the case of *B. pascuorum*, this pattern is likely driven by its exceptionally long nesting cycle, which limits its fitness in the short growing seasons of higher elevations (Neumayer, 2009). Growing season length may also explain the lower abundance of the Psithyrus species group at high elevation since cuckoo

bumble bees must emerge later than the queens of their host species and then successfully usurp host nests before they can begin to raise brood (Goulson, 2010). Nevertheless, though the divergent responses of bumble bee species to elevation are informative, it is important to emphasize the overall robustness of bumble bees to elevational variation. Of the 16 species in our study system, 9 did not respond significantly to elevation, and 8 were observed across the full span of the gradient.

The relative stability of the bumble bee community in our study stands in stark contrast to the extreme dynamism of the floral community, as illustrated by the dominance of total interaction  $\beta$ -diversity by floral species turnover. This pattern is consistent with the findings of Simanonok and Burkle (2014) in the Rocky Mountains of North America, and it is perhaps unsurprising given the

**TABLE 3** Tabular output of species-level abundance generalized additive models

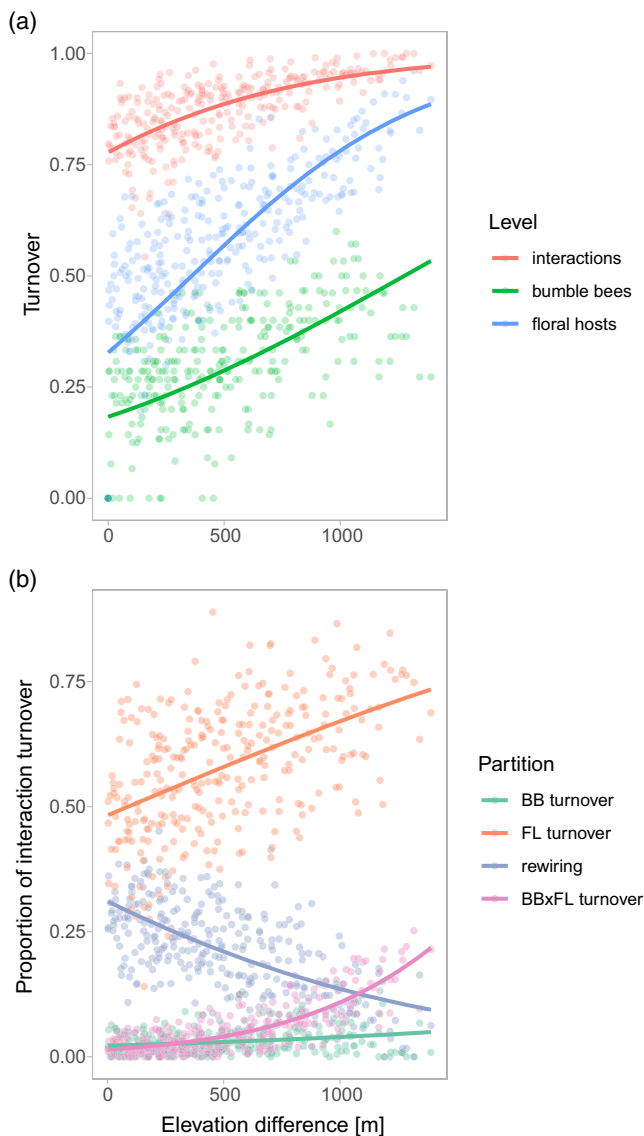
Class	Term	Estimate	Lower 95	Upper 95	edf	p.value	Significance
Parametric	Intercept	−0.26	−1.22	0.69		0.588	
	year:2011	0.65	0.48	0.82		<0.001	***
	year:2012	0.16	−0.01	0.34		0.063	
	mgmt:mowing	−0.36	−0.96	0.24		0.243	
	mgmt:none	−0.06	−0.54	0.41		0.792	
Smooth	s(site)				16.70	<0.001	***
	s(species)				14.68	<0.001	***
	s(elevation: gers)				2.62	0.092	
	s(elevation:hort)				1.00	0.067	
	s(elevation:humi)				1.00	0.186	
	s(elevation:hypn)				2.22	0.217	
	s(elevation:jone)				1.92	0.225	
	s(elevation:lapi)				1.00	0.339	
	s(elevation: mend)				2.08	<0.001	***
	s(elevation: mont)				2.48	0.001	**
	s(elevation:muci)				2.79	0.018	*
	s(elevation:pasc)				1.85	<0.001	***
	s(elevation:prat)				4.36	<0.001	***
	s(elevation:psit)				1.00	<0.001	***
	s(elevation: pyre)				1.00	<0.001	***
	s(elevation:soro)				1.00	0.084	
	s(elevation:telu)				1.00	0.099	
s(elevation:wurf)				2.33	0.252		

Note: Parametric model terms are summarized with an estimated intercept effect (“estimate”), whereas smooth terms are summarized with their effective degrees of freedom (“edf”), the latter representing the complexity (i.e., “wiggleness”) of the fitted spline. \*  $0.01 < p < 0.05$ ; \*\*  $0.001 < p < 0.01$ ; \*\*\*  $p < 0.001$ .

exceptional cold hardiness of bumble bees and the sensitivity of plants to temperature gradients. Nevertheless, it highlights the behavioral challenge that bumble bees have presumably faced for the entirety of their evolutionary history as mountain florivores—how to forage efficiently in a diverse floral community that exhibits rapid spatial and temporal turnover. A fascinating question that could not be answered by our sampling approach is the extent to which mountain bumble bees actively exploit the elevational dynamics of floral communities by adaptively foraging up- or downslope, as suggested by Lundberg and Ranta (1980). Bumble bees have large foraging ranges and have been shown both to track resources through space and time (Devoto et al., 2014) and to cross forest matrices to reach patches of foraging habitat (Mola et al., 2020). Assuming an average slope of  $20^\circ$  and a foraging range of 1 km, a bumble bee could travel up- or downslope by more than 340 m, thereby spanning an elevation band nearly 700 m wide. Such three-dimensional foraging would enable bumble bees

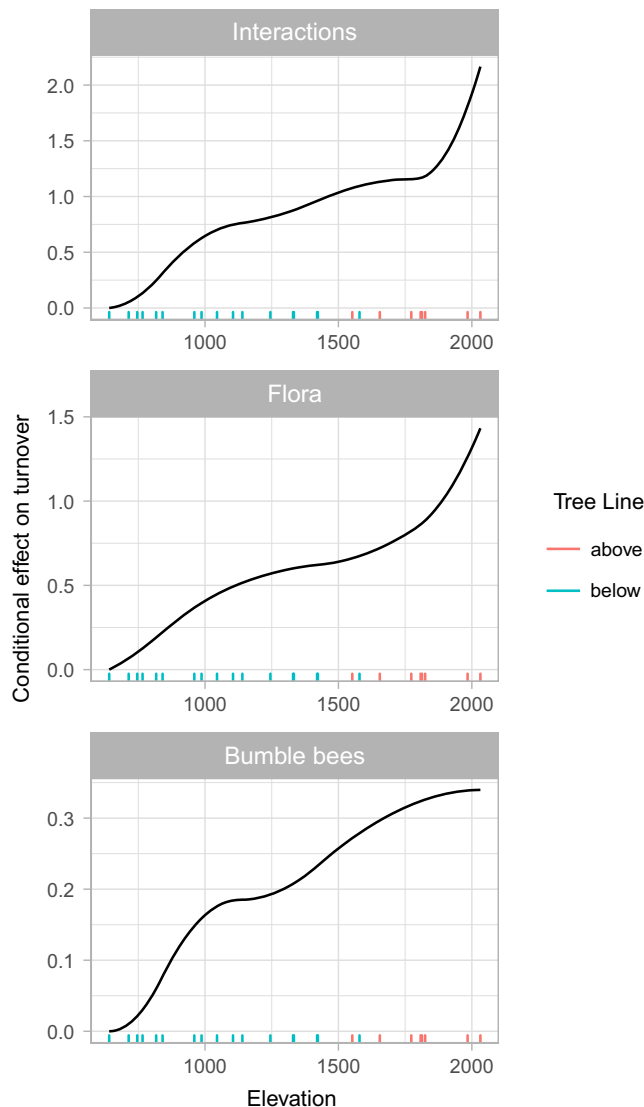
both to exploit the elevational turnover of floral species and to track preferred species through their elevationally staggered phenology, the latter constituting a sort of physiological time travel (van Straalen, 1983).

The roughly sigmoidal pattern of bumble bee  $\beta$ -diversity rate in response to elevation, revealed by our GDM analysis, probably reflects both the reciprocal abundance patterns of high- and low-elevation species and the occurrence of certain rarer species only at middle-elevation sites. As discussed earlier, though, bumble bee turnover was low overall, demonstrating the robustness of bumble bees to the environmental variation encompassed by our elevation gradient. The floral  $\beta$ -diversity rate also exhibited a sigmoidal pattern, and its inflection point coincides with the tree line ecotone at  $\sim 1500$  m. The floristic importance of the tree line has been noted by previous researchers (e.g., Descombes et al., 2017; Pellissier et al., 2010), and our study corroborates these findings specifically for the subset of flora visited by bumble bees. Interestingly, the tree line did not



**FIGURE 5** (a)  $\beta$ -diversity (in terms of proportional turnover) plotted against elevational difference for bumble bees (BB), floral hosts (FL), and their interactions (BBxFL). (b) Partitioned interaction  $\beta$ -diversity showing proportional contribution of bumble bee turnover, floral host turnover, joint bumble bee and floral host turnover, and interaction rewiring. Each point represents the turnover (or partition of turnover) between a pair of sites, and lines represent the overall relationship between turnover and elevation difference using binomial regression smoothers

constitute a discrete transition to a new equilibrium of species composition, but rather a threshold marking the beginning of a process of  $\beta$ -diversity acceleration that continued for the remainder of the elevation gradient. Though the most obvious effect of the tree line may be the relatively discrete transition from forest to scrub/grassland, the tree line also initiates a process of angiosperm species attrition that proceeds at a rate of about 40 species per 100 m (Christian Körner, 2003), and the



**FIGURE 6** GDM splines of species- and interaction-level  $\beta$ -diversity (i.e., turnover) in response to elevation. The maximum height of each spline represents the conditional effect of elevation on  $\beta$ -diversity, and the shape of each spline represents the rate of species/interaction turnover as it varies along the elevation gradient, with steeper parts of the curve indicating regions of the gradient over which species/interaction turnover is more rapid. Rug plots depict the locations of sites along the elevation axis and are color coded to indicate whether each site fell above or below the tree line

accelerated  $\beta$ -diversity we observed above the tree line mirrors simultaneous patterns of decreasing floral richness and abundance (Figures 2b and 3b).

In contrast, the rate of interaction  $\beta$ -diversity exhibited a late and very pronounced acceleration at ~1800 m, indicating that the two highest sites at 1984 and 2032 m differed strongly in interaction composition from the sites ~200 m below them. At these highest sites, the growing season is very short and vegetation is sparse, giving way to bare rock and scree landscapes, and it may be

**TABLE 4** Summary of GDM results for each model (bumble bees, flora, and interactions)

Variable	Importance (%)	Var.pval	Model.pval	Model.dev.exp (%)
Model: Bumble bees				
Elevation	73.38	<0.001	<0.001	31.10
Distance	12.41	<0.001	...	...
Samples	13.49	0.004	...	...
Model: Flora				
Elevation	78.29	<0.001	<0.001	72.74
Distance	3.92	<0.001	...	...
Samples	3.47	0.068	...	...
Model: Interactions				
Elevation	52.08	<0.001	<0.001	71.29
Distance	10.25	<0.001	...	...
Samples	12.66	<0.001	...	...

Note: Variable importance represents the percentage of explained deviance lost when the focal variable is permuted. The  $p$ -value of each variable (Var.pval) is based on comparing the deviance explained by the unpermuted model (Model.dev.exp) with the distribution of deviance explained when the focal variable is permuted. Similarly, the model  $p$ -value (Model.pval) is based on a comparison between the deviance explained by the unpermuted model and the distribution of deviance explained when the entire predictor matrix is permuted.

that the last 200-m interval of our elevation gradient imposes the most stringent environmental filter. It is interesting that interaction  $\beta$ -diversity did not exhibit the inflection point at the tree line ecotone (~1500 m) that we saw for floral  $\beta$ -diversity, despite the fact that overall interaction  $\beta$ -diversity was driven primarily by the turnover of the floral community. A possible explanation for this pattern is that there could be an elevational lag in bumble bee floral selection such that most bumble bee species do not switch to supra-tree-line floral species when these species first appear but rather maintain associations with flora whose ranges span the tree line until the extreme species turnover between 1800 and 2000 m forces them to adopt new floral hosts.

The paucity of floral resources at the highest elevations raises the question of why bumble bees choose to forage at such elevations at all. For some species, the selection of high-elevation habitats may be influenced by thermal tolerances (Oyen et al., 2016), but that fails to explain the presence of elevation-generalist species (including the majority of the species in our study system) in resource-poor high-elevation habitats. It is possible that nest site limitation at lower elevations drives some bumble bees to establish nests at high elevations, and their ability to forage downslope is subsequently constrained by their flight range, which may be reduced due to the energetic costs of flight in cold environments (Kovac et al., 2015). It is also possible that high-elevation landscapes, though sparse in absolute floral resources, offer an escape from more competitive conditions at lower elevations where forager density is higher and other bee genera peak in diversity

(Classen et al., 2020; Hoiss et al., 2015). Similarly, higher elevations could also offer an escape from density-dependent parasite and pathogen pressure (Parsche & Lattorff, 2018). Finally, it is worth speculating that an affinity for open, high-elevation habitats might be an evolutionary legacy in mountain bumble bees since the existence of flower-rich meadows in the forest matrix below the tree line is largely an artifact of human land use arising in the last 500 years of bumble bees' evolutionary history (Hejcman et al., 2013).

Mountains are unique ecological theaters in which the extrinsic forces of climate and land-use change interact with intrinsic environmental gradation to shape the ecology of species and their interactions (Peters et al., 2019). Given the elevational patterns of richness, abundance, and  $\beta$ -diversity among bumble bees and wildflowers in our study, what can be said about the response of these communities, and their functional relationships, to climate and land-use change? If the process of mid-elevation pasture abandonment continues, the flower-rich meadows that now perforate the forest matrix will eventually close into flower-poor coniferous forest, and bumble bees will be pushed either into the more agriculturally intensified land at lower elevation or the relatively resource-poor open habitat above the tree line. This land-use-driven redistribution of bumble bees will interact with the concomitant process of climate warming, which has already generated measurable upslope shifts in some bumble bee species (Marshall et al., 2020; Ploquin et al., 2013; Pyke et al., 2016), sometimes resulting in increased species richness at higher

elevations (Fourcade et al., 2019). Under this scenario, high-elevation bumble bees can be expected to face increased densities of low-elevation or elevation-generalist species, and the introduction of competing bumble bee species in a given habitat can have strong effects on both the fitness of their congeners and the patterns of floral visitation (Brosi & Briggs, 2013; Ishii, 2013; Nagamitsu et al., 2010). Nevertheless, the tolerance of most bumble bee species (excluding high-elevation specialists) for a relatively broad climate envelope, together with their long flight, range may enable them to cope with climate and land-use change better than their floral mutualists. The flowering plant community in our study system was strongly structured by elevation, and turnover in the plant community was the main driver of network-level turnover in bumble bee–flower interactions. There is evidence that the upslope movement of plants in response to warming temperatures may outpace that of bumble bees (Marshall et al., 2020; though see Pyke et al., 2016), and it is the plant community that experiences the direct effects of land-use change. Thus, it may be that the strongest effects of climate and land-use change on mountain bumble bees will be indirect effects mediated by changes in the floral community.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Sponsler, 2022a) are available in Dryad at <https://doi.org/10.5061/dryad.s1rn8pk7f>. Code (Sponsler, 2022b) is available in Zenodo at <https://doi.org/10.5281/zenodo.5897095>.

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