The tree line ecotone punctuates the elevational turnover of plants, pollinators, and their interactions

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# ABSTRACT

The structuring of biological communities along mountain slopes is complex, and the elevational range shifts that are now occurring in response to climate change involve more than merely tracking suitable temperature envelopes. When species move, they do so in the context of biological communities, and the outcomes of these movements depend on how and to what extent biotic interactions are reordered. Bumble bees (Hymentopera: *Bombus* spp.) are cold-adapted species associated with mountain habitats, and they have already exhibited measurable upslope range shifts that are expected to result in habitat loss, novel competitive interactions, and the rewiring of pollination networks. Predicting and interpreting these shifts, however, requires an understanding of the current elevational patterns of bumble bees and the floral mutualists that are being acted upon by climate change. In this study, we sampled bumble bees, flowering plants, and their interactions over three consecutive years along an 1400 m elevational gradient in the German Alps. Using nonlinear modeling techniques, we analyze the elevational patterns of this community at three levels of biological organization: species abundance, species β-diversity, and interaction β-diversity. We demonstrate complex, nonlinear responses to elevation at all three levels of organization. In particular, we identify the tree line ecotone as (1) a distributional interface between low/mid- and high-elevation bumble bee species, (2) a threshold above which floral resource availability sharply decreases, and (3) a zone of accelerated turnover of flowering plants and bumble- bee-flower interactions. The implications of these findings extend beyond the particular case of bumble bees to demonstrate that linear elevational temperature gradients are ecologically punctuated, and the outcomes of climate-induced range shifts with depend on how species and species-interactions change as they cross — or fail to cross — thresholds like the tree line ecotone.

*Keywords*: climate, elevation gradient, pollinator, *Bombus*, mountain, tree line

# INTRODUCTION

Mountains are unique ecological theaters in which extrinsic climate dynamics interact with intrinsic climate gradation to shape the distributions of species and biotic interactions (Telwala et al. 2013, CaraDonna et al. 2014, Miller-Struttmann and Galen 2014, Rafferty et al. 2020). The rate of recent climate change is forcing species to adapt ecologically within the constraints of gene pools shaped by cooler climates (Visser 2008). As temperatures rise, species are expected to track suitable conditions to higher elevations, and such effects are already measurable across a broad range of taxa (Lenoir and Svenning 2015). Elevational range shifts, however, are not merely abstract translations along the linear lapse of temperature generated by mountain slopes; they are movements *in situ*, involving the advent, extinction, and reorganization of biological interactions (Tylianakis et al. 2008, Blois et al. 2013) as well as the concomitant variation of abiotic conditions other than temperature (Körner 1995, Hodkinson 2005). Thus, when species move along continuous, linear climate gradients, they can experience punctuated and nonlinear ecological transitions. A salient example is the tree line ecotone that marks the elevational transition between forest and grassland. At this relatively discrete band within a continuous elevational temperature gradient, plant communities exhibit rapid species turnover (Descombes et al. 2017) and declining diversity (Becker et al. 2007) as abiotic conditions become more extreme away from the shelter of tree canopy (Slatyer and Noble 1992).

Bumble bees (Hymenoptera: *Bombus* spp.) are classic model organisms in the field of community ecology, but they have more recently become conservation priorities due to well-documented population declines and vulnerability to climate change (Goulson et al. 2008, Soroye et al. 2020). Bumble bees are characteristically cold-adapted species (Heinrich and Esch 1994), with peak abundance and diversity in mountain ranges and northern latitudes, where they are often the dominant guild of flower-visiting insects and the principal pollinators of entomophilous flora (Williams 1998, Goulson 2010). Upslope movement of bumble bee species in response to climate change has already been documented, and this is expected to cause the declines or extinction of some bumble bee species (Ploquin et al. 2013, Kerr et al. 2015, Pyke et al. 2016, Fourcade et al. 2019, Soroye et al. 2020, Marshall et al. 2020). From a purely geometric perspective, populations of bumble bee species already restricted to the highest elevation zones can be expected to suffer habitat shrinkage (Dirnböck et al. 2011), possibly accompanied by increasing genetic isolation (though see Fijen 2020). But the outcomes of elevational range shifts on bumble bees also hinge upon the current elevational distributions of bumble bees and their floral resources that will be acted upon by climate change. The upward advance of lowland bumble bee species, for example, may introduce novel competitive pressures on highland species and rewire the pollination networks in which they participate (Nagamitsu et al. 2010, Ishii 2013, Brosi and Briggs 2013), and elevational (Lenoir et al. 2008) and/or phenological (Pyke et al. 2016) shifts in the floral community could generate mismatches between bumble bee species and their floral hosts. When range shifts are considered in this complex biotic context, it is especially important to understand nonlinearities or thresholds in species-, community-, and interaction-level responses to elevational climate gradients, such as the floristic threshold effect that has been documented at the tree line ecotone (Descombes et al. 2017), since these could produce dramatic ecological consequences that would not be predicted by geometric considerations alone.

The outcomes of range shifts in mountain bumble bee and floral communities have obvious significance from a conservation perspective (Soroye et al. 2020), but they also provide a model system in which to study the basic phenomenon of community assembly under climate change, a phenomenon of both historical interest and prospective urgency. In the present study, set along ~1400 m elevation gradient in the German Alps, we investigate elevational patterns in a community of bumble bees and wildflowers at three levels of biological organization. First, we ask how elevation shapes the abundances of bumble bee species and their floral resources. Then, we move from the level of individual species to that of community composition and explore the elevational structure of species turnover (i.e. β-diversity) in bumble bees and flowering plants. Finally, we advance to the level of species interactions, investigating the turnover of bumble- bee-flower interaction partners through elevation. In each of these analyses, we employ flexible modeling techniques designed to capture nonlinear responses to elevation, with a particular emphasis on the tree line ecotone as a key threshold that structures the biological communities of mountains slopes.

# METHODS

## Field system

The study was conducted 2010-2012 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 mainly surrounded by coniferous forests. We selected 25 study sites (60 x 60 m) on mountain pastures at elevations ranging from 641-2032 meters above sea level (m.s.l.) **(Figure 1)**. Fourteen of these pastures 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 subject 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 and corroborated by the authors with field experience at our study sites (K. Kallnik, A. F. Maihoff, A. Claßen). Eight sites were located above the tree line, which generally fell at an elevation of around 1500 m.s.l., consistent with the previous descriptions of the tree line in the Berchtesgadener Alps (Köstler and Mayer 1970, Mayer 1970).



Figure 1: Study sites in the Berchtesgadener Alps plotted over Google Earth imagery. Sites above the tree line are depecited in red and sites below the tree line in yellow. The elevation of each site is given in meters above sea level.

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 when the air temperature was at least 6°C. During each visit, bumble bees and their activity were recorded during a 50-minute transect walk. Bumblebees observed on or a given flower were counted as floral visitors. Bumble bee queens were identified to species level in the field, while workers and males were stored in individually labeled tubes in the freezer for later identification in the laboratory after (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, so their “visits” cannot necessarily be interpreted in the same way as those of queens and workers. In conjunction with visitation observations, we estimated the flower cover of each herbaceous or shrubby plant species within each 60 x 60 m study plot to the nearest 0.01 m2. Species identification followed 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) varied: 153 in 2010, 212 in 2011, and 539 in 2012. Since the start of field sampling each year was determined by snowmelt, lower sites were sampled as early as April while higher sites could not be sampled until June or July. This resulted in a temporally staggered pattern of sampling in 2010 and 2012, while 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 X for details of sampling patterns.

## Data analysis

### Data processing

Bumble bee abundance was quantified as the total number of recorded floral visits per bumble bee species per site-date. To represent floral abundance from the perspective of each bumble bee species in our network, we first scored each plant genus in our data set as either visited or not visited by each bumble bee species. We then calculated the total floral resource availability for each bumble bee species for each site-date by summing the observed flower cover of visited genera. We opted to work at the genus level based on the reasoning that if a bumble bee species visits one member of a given genus, other members of the same genus should also be considered potential floral hosts. This approach was intended to dampen the effects of false non-detection on the estimation of floral resource abundance, particularly for rare bumble bee species whose diet breadth would tend to be underestimated simply due to sparsity of observations (Williams 2005). We also opted to treat the cryptic *B. terrestris/lucorum* species pair as a single morphospecies, since these two species cannot be visually distinguished reliably, and we similarly pooled representatives of the parasitic *Psithyrus* subgenus — *B. barbutellus*, *B. bohemicus*, *B. campestris*, *B. flavidus*, *B. quadricolor*, and *B. sylvestris* — into the species group *B. psithryus*.

### Elevational distribution of bumble bees and floral resources

We analyzed the abundance of bumble bees and floral resources using separate hierarchical generalized additive models (HGAMs) fit with the Tweedie distribution family (log link function) (Wood 2011, Pedersen et al. 2019). We opted in both models to collapse the temporal variation of abundance within sites and focus on elevational patterns. For bumble bees, we modeled *peak* abundance at each site as a smooth response to elevation, with bumble bee species as a smoothing factor and a random intercept term. We also included species:year as a random intercept term because exploratory analysis indicated that species varied differently across years. For floral resources, we modeled *mean* flower cover, weighted per bumble bee species, as a smooth response to elevation, with year and bumble bee species as random intercept terms. Both models are follow the “type I” model form described in Pedersen et al. (2019).

### Species and interaction β-diversity

For our analyses of species and interaction β-diversity, we again opted to focus on elevational patterns by pooling samples within sites, since the sparse observations of individual sampling events tended to inflate β-diversity and its variance to a degree that impaired model fitting and interpretation. After pooling, we calculated the species and interaction β-diversity between all pairs of sites and partitioned total interaction β-diversity into its components of species turnover (changes in species composition) and interaction rewiring (identical species interacting in different ways) (Novotny 2009, Poisot et al. 2012). As an initial analysis, we plotted the relationship between site-wise elevation difference and each metric of β-diversity and verified the significance of the relationship using logistic matrix regression (Goslee 2009), with the difference in number of sampling dates between sites as a covariate to control for potential confounding effects of sampling frequency.

To investigate the relationship between elevation and β-diversity more deeply, we performed a second analysis using generalized dissimilarity modeling (GDM) (Ferrier et al. 2007) to analyze the elevational variation in the β-diversity of bumble bees, flora, and (unpartitioned) interactions. In addition to estimating the relationship between differences in the response variable and differences in the predictor variables, GDM captures the slope of this relationship over the range of each predictor variable, revealing potential variation in the amount of change in the response induced by a given change in a predictor. This enabled us to ask whether the relationship between β-diversity and elevation exhibits thresholds or other nonlinearities. To control for potential confounding effects of geographic proximity and number of sampling dates per site, these terms were added as covariates in the GDM.

### 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 packages mgcv (Wood 2017) and mgcViz (Fasiolo et al. 2018). PCoA and species β-diversity calculation were performed 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 β-diversity were performed with the package bipartite [Dormann et al. (2008); Dormann2009-aa]. Matrix regression was performed with the package ecodist (Goslee and Urban 2007). GDM analysis of β-diversity was performed with the package gdm (Fitzpatrick et al. 2021). Annotated R code is available in the Supplementary Material.

# RESULTS

## Summary of visitation and floral survey data

We recorded a total of 12,918 bumble- bee-flower interactions (excluding males) over the three 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. *B. 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, while *B. hortorum* (“hort”), *B. jonellus* (“jone”), *B. psithyrus* (“psit”), *B. monticola* (“mont”), *B. mendax* (“mend”), *B. mucidus* (“muci”), *B. pyrenaeus* (“pyre”), and *B. gerstaeckeri* (“gers”) . *B. hypnorum*, *B. humilis*, and *B. lapidarius* were recorded only sporadically and at low abundance, so we omitted them from all analyses.

Floral surveying yielded a total of 352 plant species, representing 191 genera and 52 families. Of these, 155 species from 103 genera and 35 families were observed to be visited by bumble bees. Eight species — *Rubus idaeus*, *Rosa canina*, *Juniperus communis*, *Larix decidua*, *Salix* sp., *Caltha palustris*, *Pulmonaria officinalis*, and *Rheum barbarum* — were recorded in visitation data but not recorded during floral surveying. Each accounted for no more than 4 visits in total over the three years of our study, and they were omitted from the analysis of floral abundance.

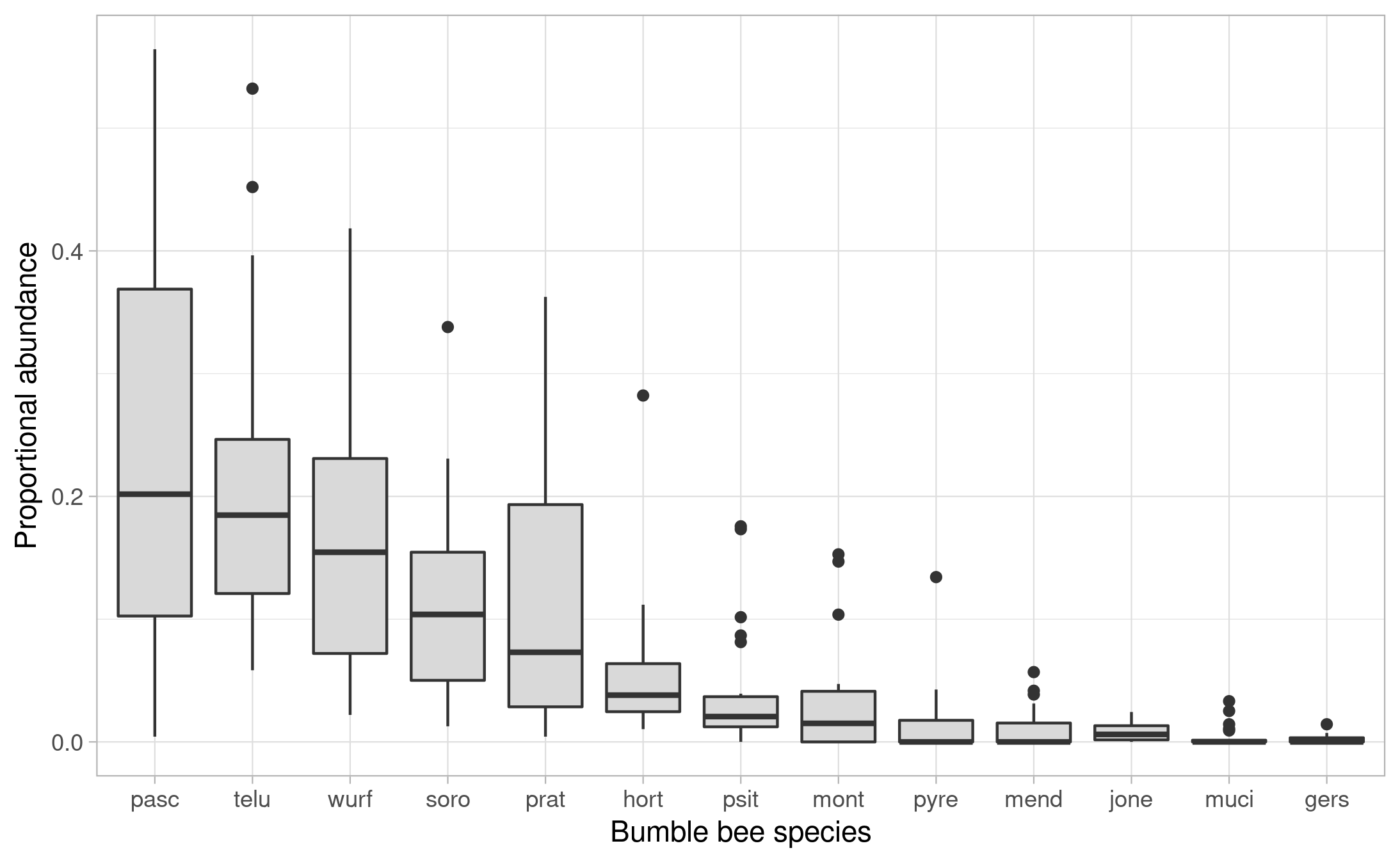


Figure 2: Proportional abundances (cumulative within site) of bumble bee species in our study system, ordered by mean proportional abundance.

## Elevational distribution of bumble bees and floral resources

The peak abundance of all bumble bee species responded significantly to elevation (p ≤ 0.04) **(Figures 3, 4)**. *B. mendax*, *B. monticola*, *B. mucidus*, and *B. pyrenaeus* exhibited a positive response to elevation and peaked in abundance above the tree line (~ 1500 m.s.l.), consistent with their known affinity for high elevation habitats (Rasmont and Iserbyt 2010-2014). The abundance of *B. soroeensis* also tended to increase with elevation and peaked above the tree line, but it was also abundant at lower elevations. In contrast, the abundance of *B. hortorum*, *B. pascorum*, and *B. psithyrus* declined with elevation. This effect was especially pronounced in *B. pascuorum*, which was also the most abundant species in our study system overall. *B. gerstaeckeri*, *B. jonellus*, *B. terrestris-lucorum*, and *B. wurflenii* peaked at mid-elevation below the tree line, while *B. pratorum* was unique in exhibiting a sharp peak of abundance directly *at* the tree line.

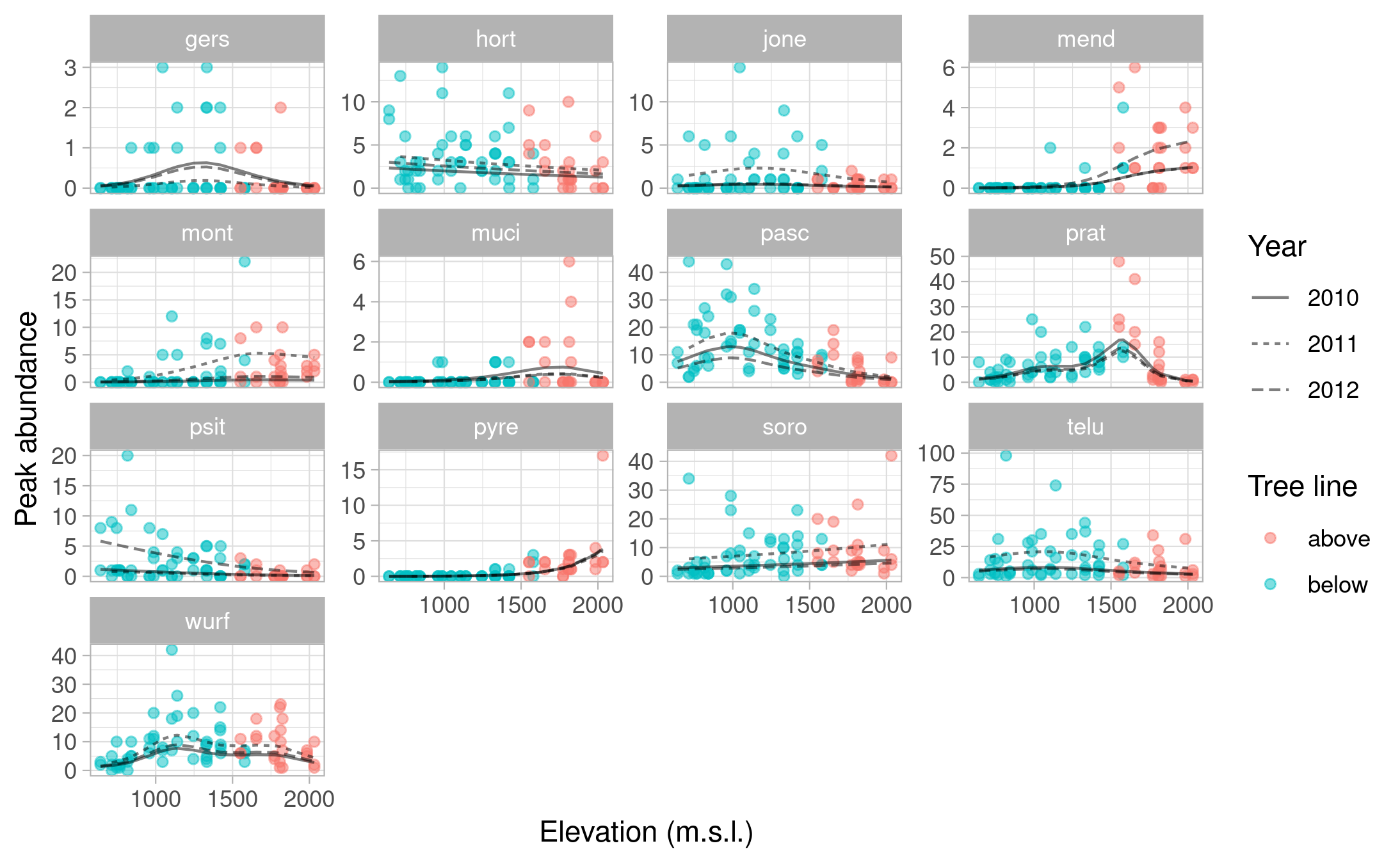


Figure 3: Fitted GAM smooths of bumble bee abundance on elevation, faceted by bumble bee species and plotted over original data. Data points are color-coded to indicate whether they represent sites above (red) or below (blue) the tree line. Note the different scales of the y-axes.

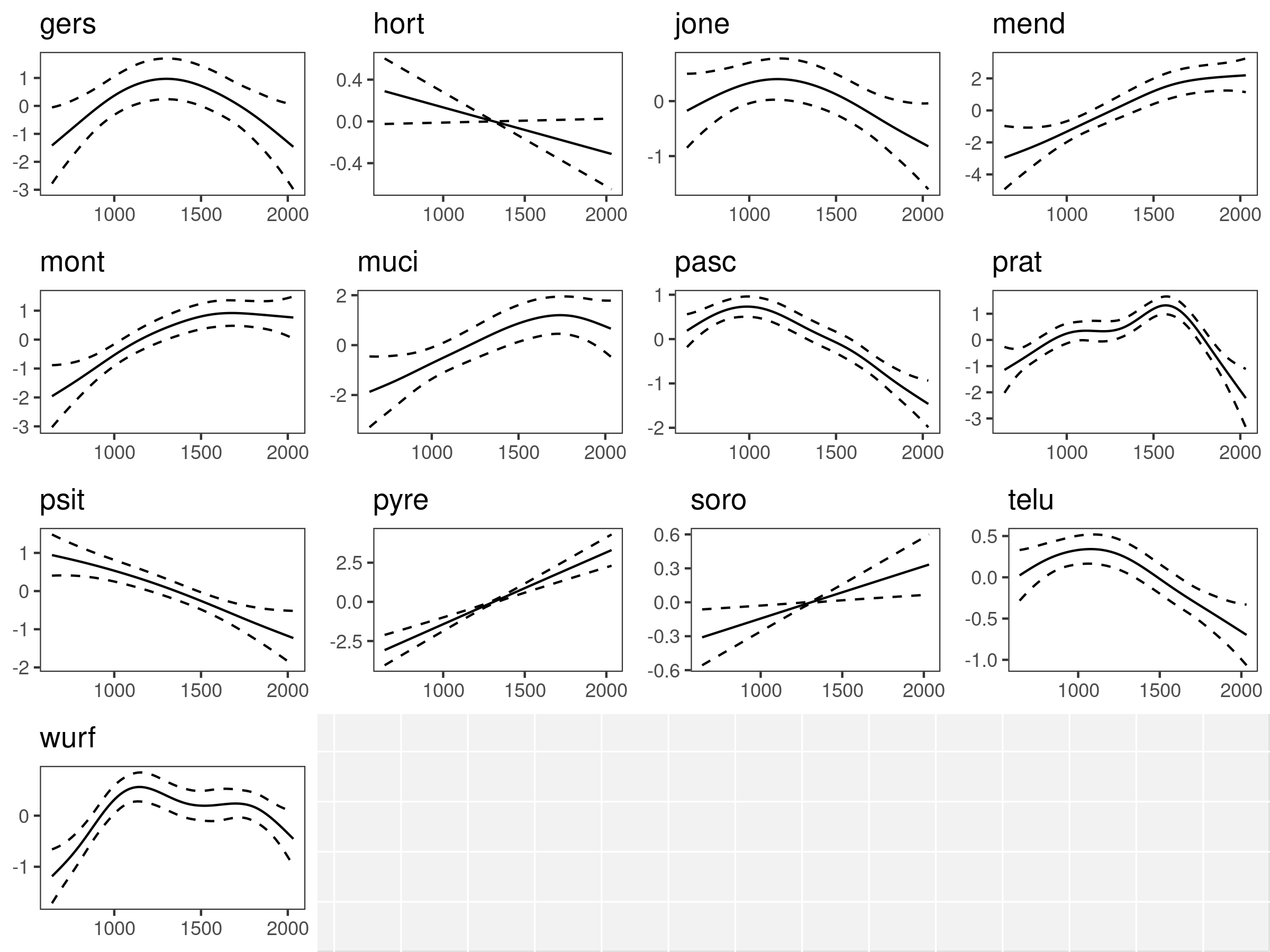


Figure 4: Conditional effect of elevation on the peak abundance of each bumble bee species. Effects are plotted on the link scale, and dashed lines depict 95% confidence intervals.

Mean floral resource abundance likewise responded significantly (p << 0.0001) to elevation for all bumble bee species **(Figures 5, 6)**. *B. mendax*, *B. monticola*, *B. mucidus*, *B. soroeensis*, and *B. wurflenii* exhibited a weakly to strongly bimodal pattern of flora resource abundance, with peaks around 1000 m.s.l. and 1600 m.s.l., the latter peak corresponding closely to the location of the tree line. *B. jonellus* and *B. pyrenaeus* exhibited a unimodal pattern peaking near 1600 m.s.l. The remaning species — *B. gerstaeckeri*, *B. hortorum*, *B. pascuorum*, *B. pratorum*, *B. psithyrus*, and *B. terrestris-lucorum* experienced linear or quadratic decline in floral resource abundance with increasing elevation. Floral resource abundance was low for all species at elevations above ~1600 m.s.l.

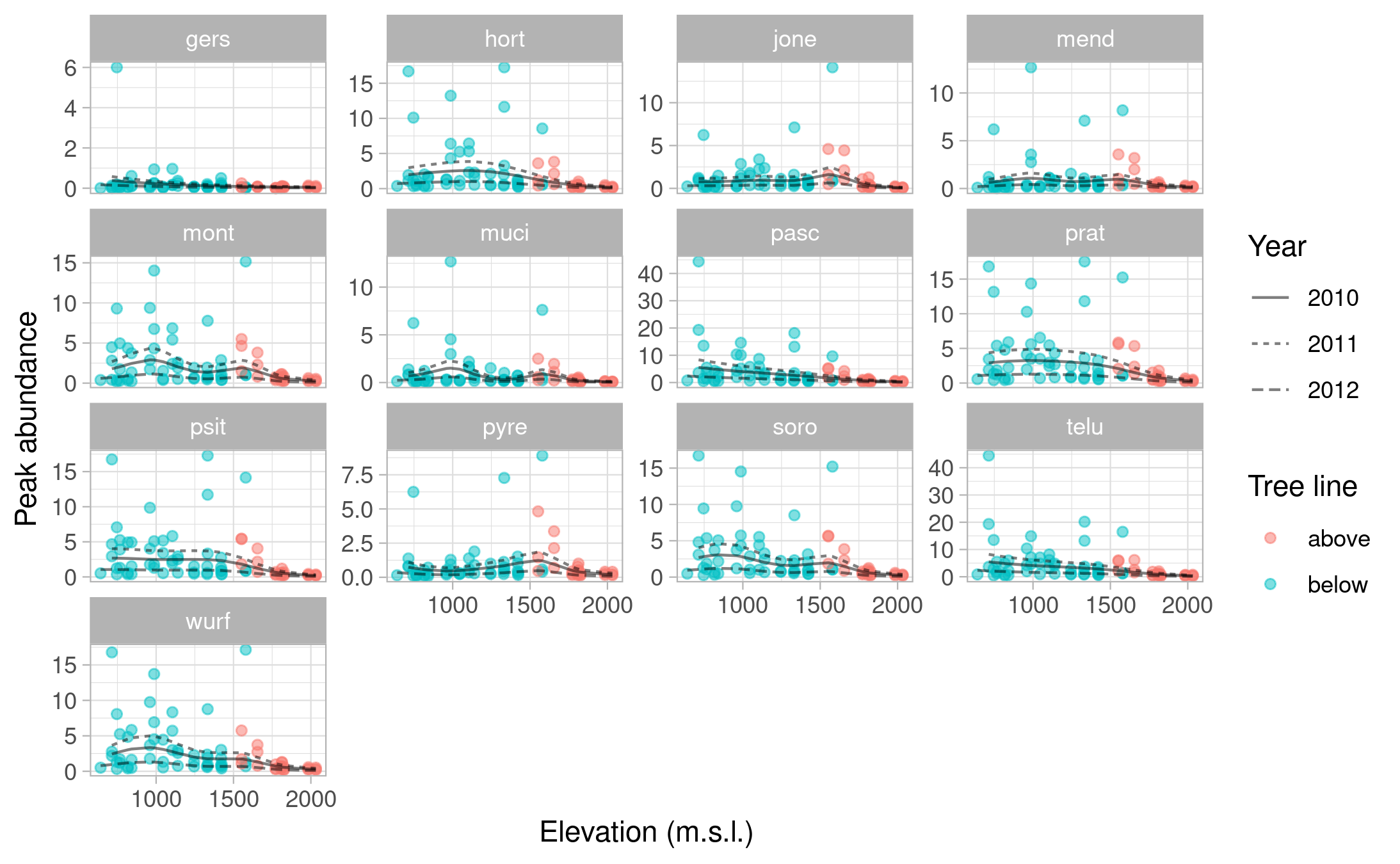


Figure 5: Fitted GAM smooths of floral abundance on elevation, faceted by bumble bee species and plotted over original data. Data points are color-coded to indicate whether they represent sites above (red) or below (blue) the tree line. Note the different scales of the y-axes.

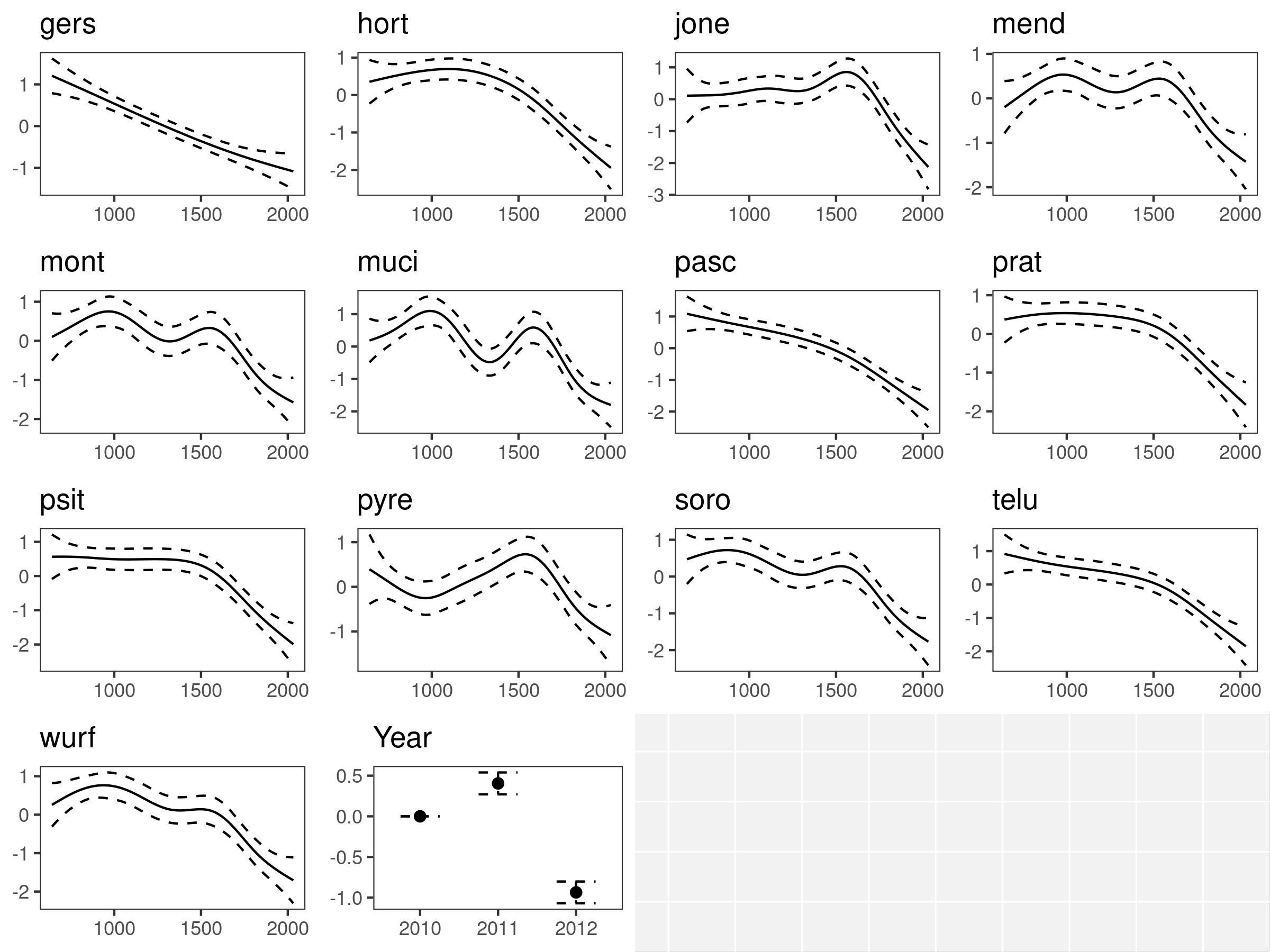


Figure 6: Conditional effects of elevation on mean flower cover by bumble bee species and year. Effects are plotted on the link scale and dashed lines depict 95% confidence intervals.

## Species and interaction β-diversity

Floral β-diversity among our study sites was very high overall and responded steeply to elevation difference between sites **(Figure 3A)**. Even sites at similar elevation exhibited ~40% species turnover, and the most widely separated sites (elevation difference > 1250 m) differed by more than 85%.

Bumble bee β-diversity was, in comparison to floral β-diversity, both lower overall and less responsive to elevational difference between sites **(Figure 3A)**. Sites at similar elevation exhibited ~25% species turnover, and species turnover between the most widely separated sites remained less than 50%.

Total interaction β-diversity was >75% between sites at similar elevation and approached perfect dissimilarity in the most widely separated sites **(Figure 3B)**. Partitioning revealed that total interaction β-diversity was driven primarily by species turnover, which accounted for ~50% of total β-diversity for sites at similar elevation and ~90% of total β-diversity for the most widely separated sites. Species turnover consisted mainly of turnover in the floral community **(Figure 3C)**, though the joint turnover of plants and bumble bees accounted for ~25% of total species turnover between the most widely separated sites. Interaction rewiring was most significant between sites at similar elevation, where it accounted for ~30% of total β-diversity, but its share of total β-diversity declined to ~10% in the most widely separated sites **(Figure 3B)**.

Logistic matrix regression confirmed the significance (p < 0.01) of the relationship between each β-diversity metric and elevation **(Table 1)**.

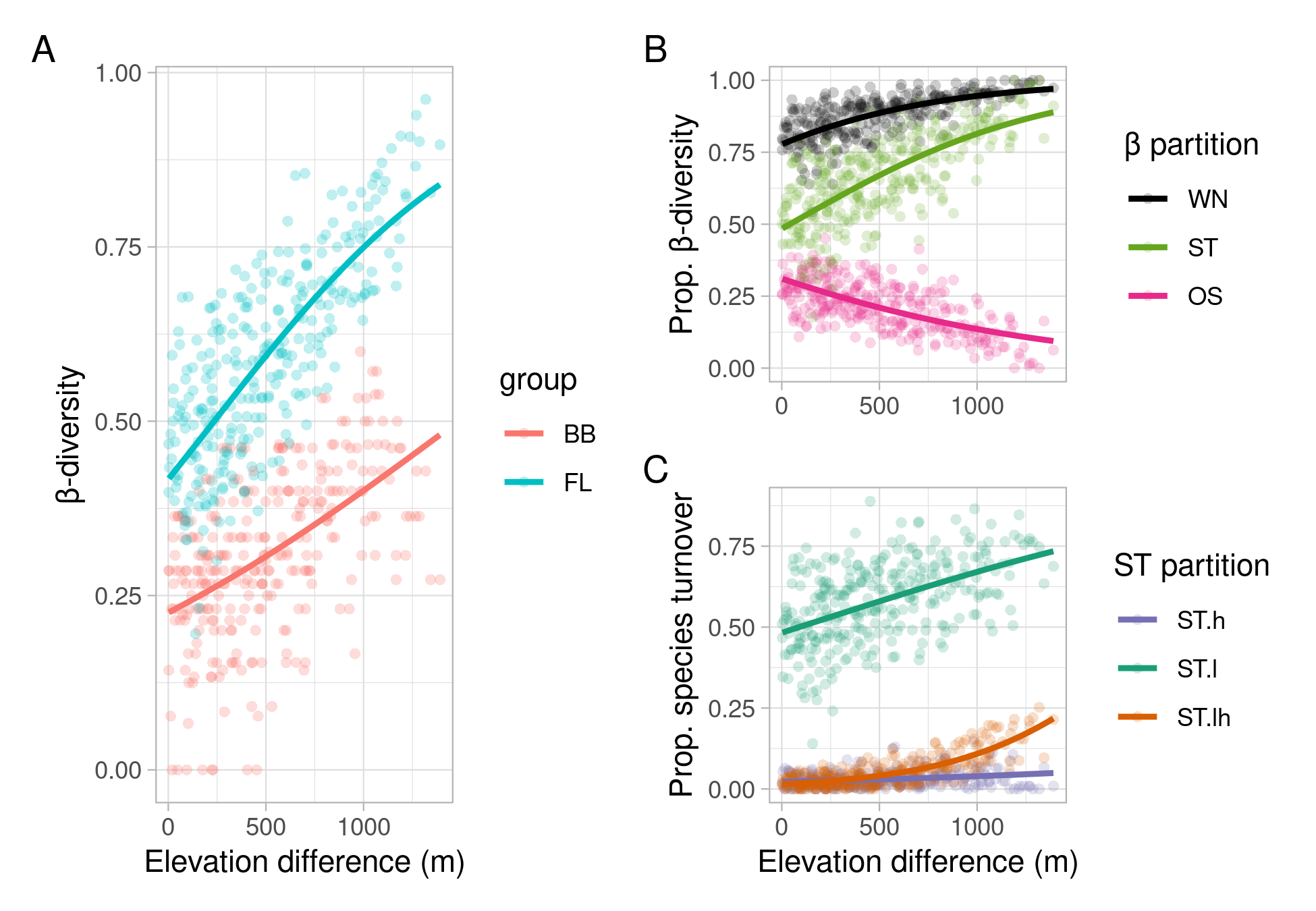


Figure 7: Species-level (A) and interaction-level (B, C) plotted against elevational difference. Each point represents the β-diversity (or β-diversity partition) between a pair of sites, and lines represent the overall relationship between β-diversity and elevation difference using binomial regression smooths. Standard errors are not plotted because they would be misleading due to the non-independence inherent to distance matrix regression, but all regressions were significant (p < 0.01). Interaction β-diversity (B, C) is partitioned using Poisot et al.’s (2012) notation: WN = unpartitioned β-diversity, ST = β-diversity due to species turnover, OS = β-diversity due to interaction rewiring, ST.h = β-diversity due to species turnover in the higher trophic level (bumble bees), ST.l = β-diversity due to species turnover in the lower trophic level (plants), and ST.lh = β-diversity due to joint species turnover in higher and lower trophic levels.

GDM analysis reproduced the finding that overall β-diversity was dominated by floral turnover, but it also revealed a strongly nonlinear response of floral and interaction β-diversity to elevation **(Figure 4)**. Turnover was high from ~600-1000 m, representing the transition from valley floor to lower slopes, and then leveled off from ~1000-1500 m. At around 1500 m, turnover accelerated sharply and remained steep for the remainder of the elevation gradient. The partial effects of geographic proximity and sampling intensity were negligible in all cases.

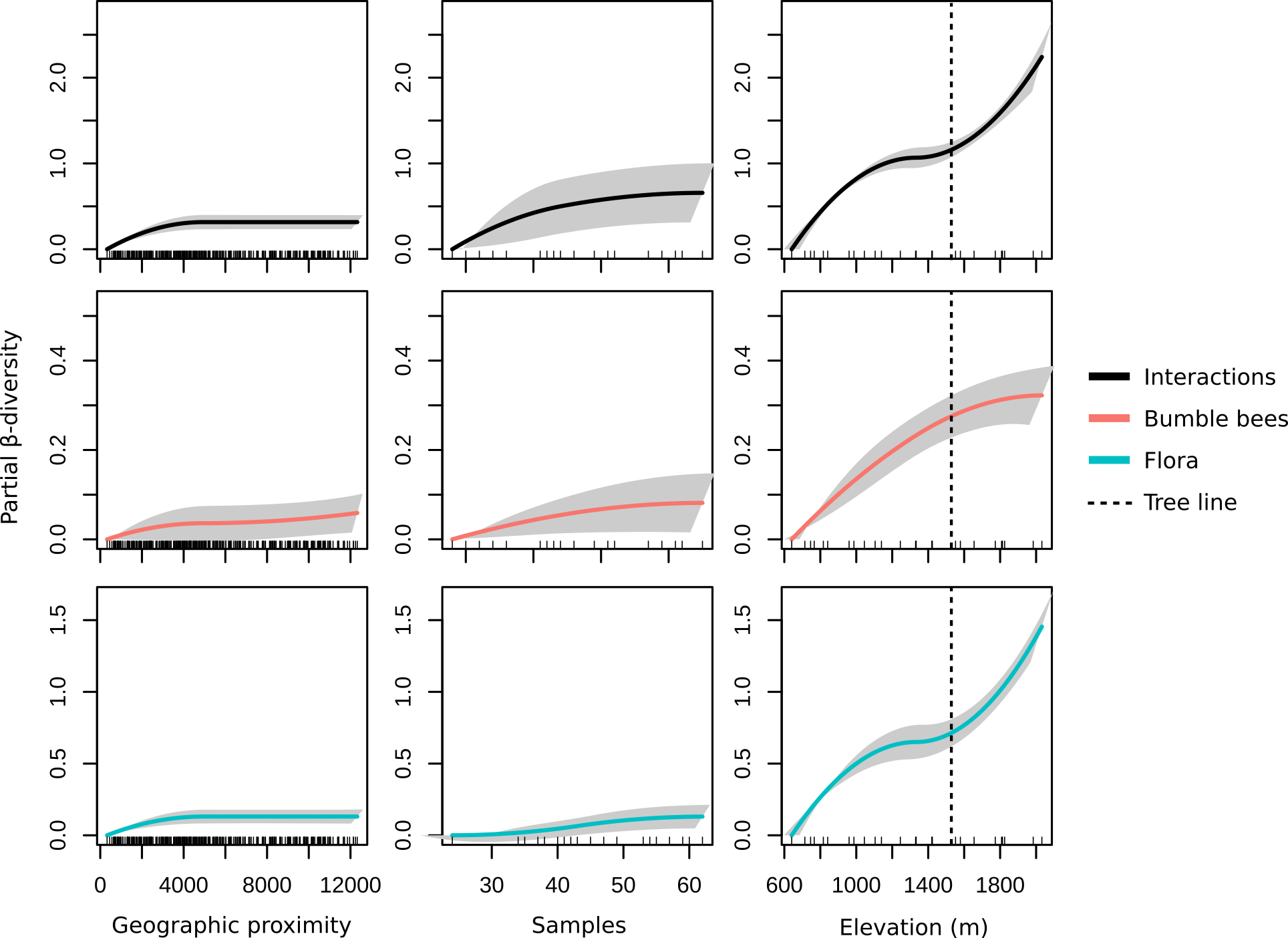


Figure 8: GDM splines of species-level and interaction-level β-diversity in response to elevational, controlling for geographic proximity and number of sampling dates. The maximum height of each spline represents a given variable’s partial effect on β-diversity (its effect when covariates are held constant), and the shape of each spline represents to the rate of species turnover as it varies along the corresponding gradient, with steeper parts of the curve indicating regions of the gradient over which species/interaction turnover is more rapid. Dotted vertical lines in the elevation panels indicates the location of the tree line. Within-site comparisons were omitted from GDM analysis to avoid pseudoreplication. Shaded bands depict the uncertainty of each partial effect curve (+/- one standard deviation) based on bootstrapping. Note the differences in scale between the y-axes of each variable.

# DISCUSSION

The core finding of our study, evident in each of our analyses, is that a linear elevation gradient can generate complex and nonlinear biological responses in a mountain bumble- bee-wildflower community in terms of both abundance and β-diversity, and the latter both at the level of community composition and at the level of species interactions. As a rule, these responses are punctuated by the tree line ecotone, which constitutes a discrete ecological threshold along the linear elevation gradient of a mountain slope.

We found a clear distinction between bumble bee species with low- or mid-elevation abundance peaks (*B. gerstaeckeri*, *B. hortorum*, *B. jonellus*, *B. pascorum*, *B. pratorum*, *B. psithyrus*, *B. terrestris-lucorum*, *B. wurflenii*) and those with high-elevation abundance peaks (*B. mendax*, *B. monticola*, *B. mucidus*, *B. pyrenaeus*, and *B. soroeensis*). The tree line forms an important zone of overlap at which the declining abundance of low- and mid-elevation species intersects with the rising abundance of high-elevation species. The tree line was also important in the elevational structure of floral resource abundance. For some (mostly high-elevation) bumble bee species, the tree line marked a distinct peak of floral resource availability, often mirrored by a second peak at lower elevation (~1000 m.s.l.). It is notable that, for some of the high-elevation species that exhibited this bimodal pattern of floral resource abundance — *B. mendax*, *B. monticola*, and *B. mucidus* — the lower peak of floral resource abundance is almost entirely outside their elevational range. The tree line, therefore, functions as critical foraging habitat for high-elevation bumble bees. Above the tree line, flora resource availability declined sharply as flower-rich grassland and shrubland transitioned to sparse alpine scree. The observation that the upslope advancement of alpine tree lines often lags behind climate warming (Dullinger et al. 2004) suggests that high elevation bumble bees could move upslope faster than their floral resources, increasingly confined to resource-poor habitat, though the opposite pattern could also occur if the climate-tracking of bumble bees is limited by other factors, such as nest site availability (Marshall et al. 2020). Moreover, several studies have found that the introduction or removal of bumble bee species from a community can have strong effects on the fitness of other species and on patterns of floral visitation (Nagamitsu et al. 2010, Ishii 2013, Brosi and Briggs 2013); if elevational range shifts introduce new competitive pressures via the encroachment of low-elevation species into the historic ranges of high-elevation species, this effect might be expected to be most pronounced at the tree line. The significance of the tree line ecotone as a threshold of floral resource availability and as a zone of overlapping bumble bee distributions corroborates the recent findings of Minachilis et al. (2020) in the Mediterranean system of Mount Olympus, indicating that these patterns are likely to generalize well across mountain ecosystems.

The tree line not only punctuated patterns of abundance but also those of species-level and interaction-level β-diversity. While the turnover rate of bumble bee species was low across the whole elevation gradient and showed no response to the tree line, the turnover rate of the floral community was an order of magnitude higher and exhibited a marked inflection point at the tree line, above which it increased steeply. This floristic importance of the tree line has been noted in previous work (Pellissier et al. 2010, Descombes et al. 2017), but our study provides a functional extension to this pattern, demonstrating that the tree line also marks a zone of rapid acceleration in the turnover of bumble- bee-flower interactions that is evidently driven by the underlying turnover of the floral community. The picture that emerges is a striking contrast between a relative stable bumble bee community and an extremely dynamic floral community. The dominance that we observed of total interaction β-diversity by floral species turnover is consistent with the findings of Simanonok and Burkle (2014) in the Rocky Mountains of North America, and it is perhaps unsurprising given the 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 turns over so rapidly. Indeed, the remarkable flexibility and intelligence of bumble bee foraging (Heinrich 1979, Loukola et al. 2017), which have been interpreted as side-effects of their sociality (Dukas and Real 1991), could be interpreted alternatively as an adaptation to precisely this problem of foraging in the context of extreme β-diversity. A fascinating question that could not be answered by our sampling approach is whether mountain bumble bees adaptively forage 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 matrix to reach patches of foraging habitat (Mola et al. 2020). Assuming an average slope of 20° and a foraging range of 1 km, a bumble bee could travel up- or downslope by more than 340 m, thus spanning an elevation belt nearly 700 m wide. Such 3-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 (Straalen 1983).

The central finding of our study, that elevation gradients are characterized by complex and nonlinear responses of species, communities, and biotic interactions — punctuated by the tree line — is almost certainly not an idiosyncrasy of bumble bees and their floral hosts but rather a pattern emerging from fundamental physical constraints that should be expected to obtain broadly across the biotic communities of mountains worldwide. Species interactions along tree line ecotones, therefore, deserve special consideration in research and conservation management, since climate-induced range shifts at tree lines should be expected to have disproportionate ecological consequences relative to range shifts at other elevation bands.

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