



Smaller, more diverse and on the way to the top: Rapid community shifts of montane wild bees within an extraordinary hot decade

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Abstract

Aim: Global warming is assumed to restructure mountain insect communities in space and time. Theory and observations along climate gradients predict that insect abundance and richness, especially of small-bodied species, will increase with increasing temperature. However, the specific responses of single species to rising temperatures, such as spatial range shifts, also alter communities, calling for intensive monitoring of real-world communities over time.

Location: German Alps and pre-alpine forests in south-east Germany.

Methods: We empirically examined the temporal and spatial change in wild bee communities and its drivers along two largely well-protected elevational gradients (alpine grassland vs. pre-alpine forest), each sampled twice within the last decade.

Results: We detected clear abundance-based upward shifts in bee communities, particularly in cold-adapted bumble bee species, demonstrating the speed with which mobile organisms can respond to climatic changes. Mean annual temperature was identified as the main driver of species richness in both regions. Accordingly, and in large overlap with expectations under climate warming, we detected an increase in bee richness and abundance, and an increase in small-bodied species in low- and mid-elevations along the grassland gradient. Community responses in the pre-alpine forest gradient were only partly consistent with community responses in alpine grasslands.

Main Conclusion: In well-protected temperate mountain regions, small-bodied bees may initially profit from warming temperatures, by getting more abundant and diverse. Less severe warming, and differences in habitat openness along the forested gradient, however, might moderate species responses. Our study further highlights the utility of standardized abundance data for revealing rapid changes in bee communities over only one decade.

KEYWORDS

Alps, altitudinal gradient, body size, climate change, global warming, hymenoptera, pollinator, range shifts

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1 | INTRODUCTION

Anthropogenic climate change can be especially pronounced in mountain regions (Pepin et al., 2015), where it is expected to disrupt some of the world's richest biological communities (Rahbek et al., 2019). Cold-adapted species for which mountains serve as climate-refugia are particularly vulnerable to warming along elevational temperature gradients (Noroozi et al., 2018; Trew & Maclean, 2021). However, how climate change alters mountain communities is hardly understood (McCain & Garfinkel, 2021)—especially for pollinators such as wild bees. This is due to the lack of standardized long-term data (Halsch et al., 2021), and because insect communities are often recorded in agricultural contexts, in which the negative impacts of land use may mask the responses of insect communities to climate change (Potts et al., 2010).

This empirical gap notwithstanding, there are theoretical reasons to expect the responses of mountain communities to climate change to be more complex than simply the loss of biodiversity. Warming in mountain ecosystems could even *increase* species richness—at least transiently—by raising rates of metabolism, activity and reproduction (Belmaker & Jetz, 2015; Brown, 2014; Frazier et al., 2006; Savage et al., 2004), yielding larger populations and reduced risk of local extinction (O'Grady et al., 2004). Higher temperatures can also create the *appearance* of increased species richness, since larger populations and more active individuals are more likely to be detected during surveying (Corbet et al., 1993; Kenna et al., 2021).

The effects of temperature per se, however, can be confounded with the influence of resource availability on population persistence and species coexistence (Hurlbert & Stegen, 2014; Hutchinson, 1978). Interactions between temperature effects and resource-effects might explain why species richness and abundance often exhibit non-linear responses to temperature gradients (Peters, Hemp, et al., 2016) but temperature–resource interactions remain largely unstudied. Furthermore, at the global scale, minimum and maximum humidity levels can restrict bees (Danforth, 1999; Minckley & Radke, 2021; Orr et al., 2021).

In addition to affecting species richness and abundance, temperature can also affect the distribution of body sizes in a community. Among bees, for example, the thermal niche of small bees should be narrow than that of large bees due to the physiological constraints of flight activity (Kenna et al., 2021; Peters, Peisker, et al., 2016). With increasing temperature, we expect that smaller species will be less restricted in rather cold mountain environments, what should lead to a mean body size decrease in the community. Other mechanisms, such as temperature-dependent reductions in individual growth rates or competitive and predatory interactions within communities, are still debated (Gérard et al., 2018) and might also contribute to the expected decline in bee body sizes under warming temperatures.

Another commonly used approach to predict the fate of species communities under climate change is to look at current community

patterns along spatial temperature gradients, using this comparison as the so-called space-for-time substitutions. Wild bee community assessments along spatial temperature gradients indeed detected more species and higher abundance under higher temperatures (Arroyo et al., 1985; Classen et al., 2015; Mayr et al., 2020; Osorio-Canadas et al., 2021; Perillo et al., 2017). There is also evidence that the mean body size of wild bee communities varies with climate, increasing in cool highlands and decreasing in warmer lowlands (Hoiss et al., 2012; Peters, Peisker, et al., 2016). Thus, both theory and spatial gradient studies predict an increase in bee abundance and species richness and a decrease in average community body sizes under climate change. However, and importantly, species are known to respond very specifically to long-term temperature changes, which could influence community responses and weaken community-level predictions drawn from space-for-time substitution approaches. Individual species may either adapt or acclimatize to new temperatures, change their spatial distribution or phenology or even go extinct (Feeley et al., 2012; Hoffmann & Sgrò, 2011; Maebe et al., 2021; Thomas et al., 2004). Changes in species-specific distributions, such as the upslope shifts reported for a variety of taxa (Bässler et al., 2013; Chen et al., 2011; Freeman et al., 2018; Lenoir et al., 2008; Menéndez et al., 2014) can lead to rapid restructuring of communities (Cerrato et al., 2019; Lindström et al., 2013; Princé & Zuckerberg, 2015; Wilson et al., 2007; Zografou et al., 2014), with potential cascading effects on species interactions. Studies reporting upwards shifts in bee communities are limited to the bee genus *Bombus* (Kerr et al., 2015; Marshall et al., 2020; Ploquin et al., 2013; Pyke et al., 2016). Other bee genera have been thus far neglected regarding elevational shifts. In addition, previous studies with historic data require corrections for sampling effort differences during recaptures (Bartomeus et al., 2013; Marshall et al., 2020), thus underestimating the actual expected temperature-induced increase in abundance. Understanding the real impact of temperature changes on bee species communities requires an abundance-based monitoring of real-world communities, considering both species and community responses in space and time, together with regional drivers of bee assemblages.

In this study, we empirically investigated the restructuring of wild bee communities along two independent elevational gradients in largely protected mountain areas, each sampled twice within an exceptionally hot decade (see Appendix S1 for regional temperature pattern since 1880). The methodologically precise repeated sampling along each gradient provided a unique opportunity to test whether bee community responses to increasing temperatures over time reflect expectations derived from theories and observations along spatial temperature gradients. We here (a) disentangle the potential drivers of community responses (i.e. temperature increase across sample periods, absolute temperature differences between sample years, local temperature, food resource availability and bee abundance) and (b) compare the observed responses with predictions from theory and spatial diversity patterns. Specifically, we addressed the following research questions:

1. How did wild bee abundance and species richness change along elevation gradients and within an extraordinary hot decade?
2. What are the drivers shaping wild bee abundance and species richness along the elevational gradients?
3. Do single bee species and even substantial parts of the bee community shift along the elevation gradient in magnitudes that, on average, mirror the changes in temperature?
4. How did temperature changes influence the body size composition of bee communities?

2 | METHODS

2.1 | Study regions

The study was conducted along two elevational gradients in two different mountainous regions, both in southeastern Germany: Berchtesgaden (BGL in the figures and tables) and the Bavarian Forest (BF in the figures and tables; [Figure 1a–c](#)).

The Berchtesgaden gradient was located in the National Park Berchtesgaden and its vicinity and ranged from 641 to 2032 m above sea level (m.a.s.l.). Its landscape consists of calcareous grassland patches embedded in a coniferous forest matrix, transitioning to scree above the tree line. Along this gradient, 33 grassland sites were selected, each 60×60 m, distributed across five elevational transects. Eighteen of these sites were extensively managed (grazed by livestock or mowed once in late summer), and 15 were not managed (abandoned during last century or above the treeline). These sites were initially sampled in 2009 (Hoiss et al., 2012), and we resampled them in 2019. During this 10-year interval, only one site underwent a change in management practices as it was irregularly used as pasture (confirmed through personal communication with farmers).

The Bavarian Forest gradient ranges from 297 to 1368 m.a.s.l., with predominantly beech forest at lower elevations yielding to mixed forest (spruce, beech and fir) in the montane zone. Along this gradient, 47 study sites were selected across four elevational slopes within the Bavarian Forest National Park (BF in the figures and tables) and outside the park (<650 m.a.s.l.), extending the elevational gradient down to the Danube River. All sites were located within continuous pre-alpine forest or forest patches, varying in canopy cover as a measure of the summarized canopy cover of the tree layers and the shrub layer (details are described below). The sites were first sampled in 2007 and 2008, then resampled in 2016 (Bässler et al., 2015).

Maps of the study regions ([Figure 1](#)) were produced in QGIS. GIS data was obtained from <https://www.lfu.bayern.de/umweltdaten> and <https://search.earthdata.nasa.gov>.

2.2 | Pollinator monitoring

At Berchtesgaden, wild bees and honeybees were recorded from May to September, thus encompassing approximately the full foraging season. Sampling was conducted in standardized 50 min transect walks,

repeated six times in sites below 1200 m.a.s.l. and, five times in higher elevations due to a later snowmelt. Transect walks took place from 9:30 to 18:00 under conditions suitable for insect flight: either sunny weather or, if cloudy, when the temperature at 650 m.a.s.l. was at least 17°C. We used sweep nets to catch insects for later determination to species level in the laboratory. Bumble bees, however, were partly identified in the field, and *Bombus lucorum* and *Bombus terrestris* were summarized as *Bombus sensu stricto* complex.

In the Bavarian Forest, wild bees and honeybees were sampled each month during May and September by deploying one flight-interception trap and one malaise trap per site. While flight interception traps were activated over 4 weeks (continuously over the study period), malaise traps were activated over a period of 2 weeks each month. Insects were identified to species level.

2.3 | Environmental variables

As resource availability may affect the occurrence of bees (Araújo et al., 2010; Classen et al., 2015; Escobedo-Kenefic et al., 2020), we recorded flower cover of insect pollinated flowering plants (according to Klotz et al., 2002) in Berchtesgaden in parallel with each bee survey (for details see [Appendix S2](#)). In the Bavarian Forest, where we lacked replicated flower cover estimates, annual canopy cover was used as a proxy for resource availability, as varying light conditions generally correlate with flower cover (Rhoades et al., 2018). To estimate the effect of canopy cover in the Bavarian Forest, we calculated canopy cover for each site per year by summarizing the estimated proportional cover of the tree layer 1 (>5 to 15 m height), tree layer 2 (>15 m) and shrub layer (up to 5 m height). The proportion of cover of each layer was estimated by visual estimation (for details see Bässler et al., 2009). Note that for the monitoring in 2007, we used canopy data from 2006, but no major differences in the canopy cover are expected between these years.

Using interpolated data from neighbouring climate stations (Section S1.2 in [Appendix S1](#)), we calculated for each study plot (1) temperature during sampling (only for Berchtesgaden), (2) mean annual temperature (MAT) and (3) temperature change between sampling years. The temperature change between years was calculated from the slope of the linear model $MAT \sim \text{year}$ (see Section S1.4 in [Appendix S1](#)). Note that the use of modelled data comes with some limitations as microclimate variation caused by air currents or vegetation structure is not captured in our temperature data. As one climate station per region was directly installed on a study site, we could verify that the quality of our predicted data is high (Pearson $R^2 = .99$ in both regions; see Section S1.2 in [Appendix S1](#)).

2.4 | Body size assessment

We assigned female body size values per bee species (using the worker caste for bumble bees) based on data Hofmann et al. (2019) and Westrich (2019). To calculate the abundance-weighted

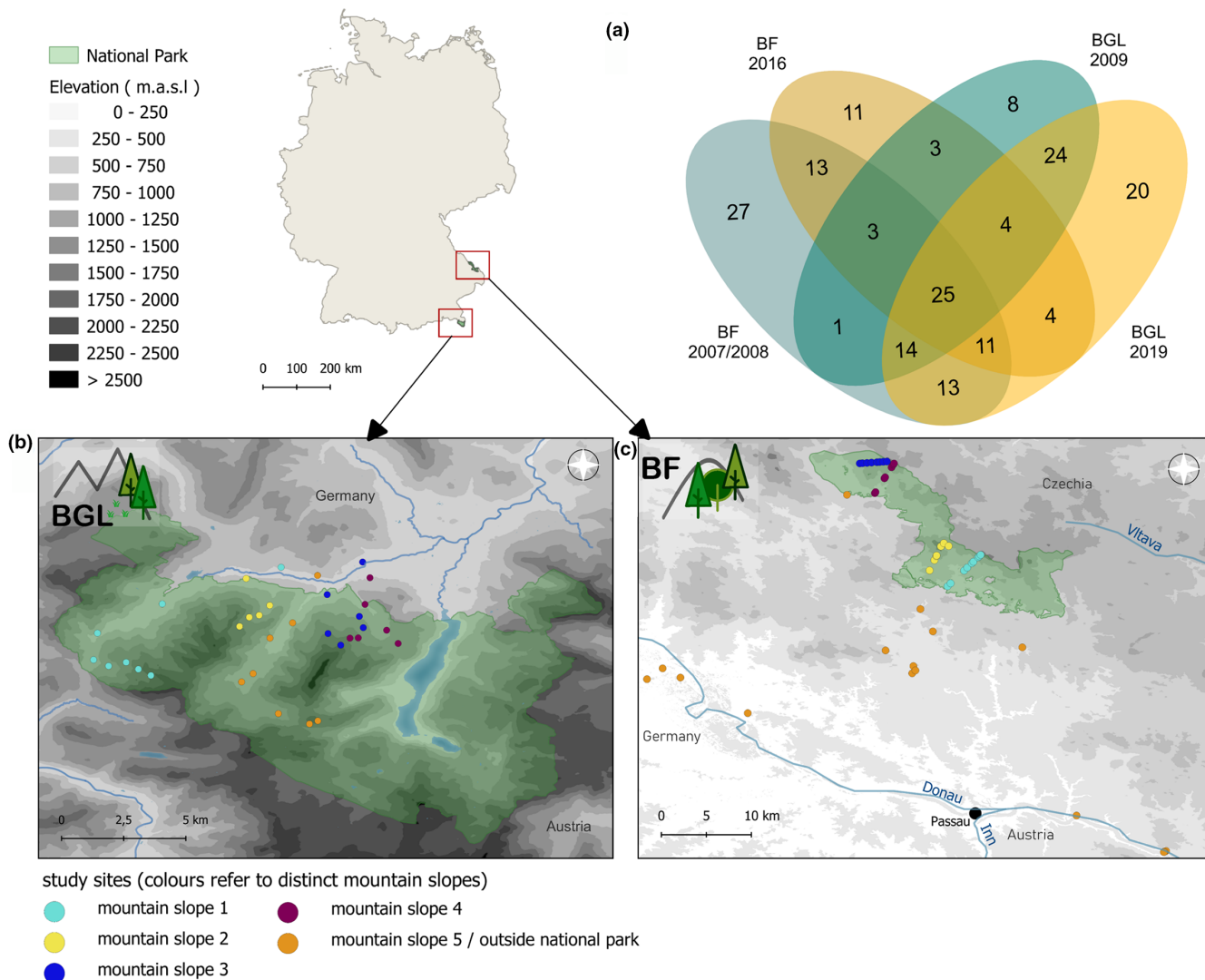


FIGURE 1 Study regions and sampled bee species pool. Study sites were located in two regions: (b) Berchtesgaden (BGL) and (c) the Bavarian Forest (BF). Elevation level is indicated in shades (at 250m intervals), with darker shades signalling increasing elevation. The National Park area within each region is represented in green. Each point is a sampling site, coloured according to distinct mountain slopes in each sampling region. In the Bavarian Forest, sites outside the National Park (orange) were not assigned to specific mountain slopes. Overlap in species numbers among the two study regions and between sampling years (a).

community mean of body size, we averaged the body sizes of all individuals recorded per site and year. We also calculated unweighted mean body size by averaging the body size of each present species irrespective of abundance. To investigate how abundance changes of differently sized bees shaped the abundance-weighted community mean of body size, we grouped bee species into four different size classes and examined how the relative proportion of body size classes in the bee community of a given elevational belt changes between years. For details, for example a list of species per size class, see Appendix S3.

2.5 | Statistical analyses

As sampling methods differed significantly between regions, we never combined data sets but conducted all statistical analyses separately per region.

2.6 | Temperature patterns in space and time

We examined mean annual temperature change between years along the elevational gradient by fitting linear model (Berchtesgaden) and linear mixed-effects models (lmer) (Bavarian Forest) with elevation, year and the interaction (elevation × year) as fixed effects (Section S1.3 in Appendix S1 for details on model selection). Different model types were necessary, because only in the Bavarian Forest site characteristics such as exposure and slope were considered when predicting temperature data (Section S1.2 in Appendix S1).

2.7 | Bee abundance and species richness patterns in space and time

In both regions, we calculated species richness and abundance per site and year over all sampling replicates by summarizing the

number of species or observations. We excluded *Apis mellifera* from the data set before analyses as its abundance strongly depends on beekeeper activity rather than on abiotic or biotic factors. We did so, after exploring and ruling out potential negative competitive effects of *A. mellifera* on wild bees (see Appendix S4 for respective analyses).

We calculated wild bee abundance, observed number of species (referred to as species richness) and estimated species richness (referred to as Chao1) using the “vegan” package (Oksanen et al., 2020). We then used generalized linear mixed-effects models (“glmer”—lme4 package) to test whether wild bee abundance, species richness and Chao1 differed between years and along the elevational gradient. For this purpose, all models were fitted with year, elevation and elevation: year interaction. Site was included as a random effect to control for multiple measurements at the same site. In Berchtesgaden we used the “poisson” data family for abundance and species richness and a negative binomial model for the Chao1 data to account for overdispersion. In the Bavarian Forest, we run a negative binomial model for all response variables to account for overdispersion. Using the “emtrend” function, we tested for the trends of elevation patterns within years.

2.8 | Drivers of bee species richness

We used piecewise structural equation models (SEM; “piecewiseSEM” package; Lefcheck, 2016) to separate the effects of temperature, flower cover (or canopy cover, respectively) and bee abundance on bee richness. In Berchtesgaden, we considered both mean annual temperature and temperature during sampling, as sampling success during relatively short transect walks may strongly depend on pollinator activity, which correlates with temperature during sampling (Classen et al., 2015). In the Bavarian Forest, we only considered mean annual temperature, because passive traps were active for several days and thus less affected by temperature fluctuations during sampling. As elevation, year and (in Berchtesgaden) management (extensively managed vs. unmanaged) may alter flower cover, bee abundance and bee richness, we included these variables in the models.

Details on model structure and model selection are given in Appendix S5.

We based our a priori model (= full model before model selection; Figure 3a,b) on the following assumptions.

1. Temperature-occurrence-hypothesis

Mean annual temperature is shaped by elevation and year and filters bee species directly, for example by their climatic niche, with less species tolerating cooler than warmer conditions (Hoiss et al., 2012). Furthermore, warmer mean annual temperature allows the establishment of larger populations (Frazier et al., 2006; Savage et al., 2004), which have a higher detectability during sampling, indirectly translating into higher richness.

2. Temperature-activity-hypothesis

Temperature during sampling is only partly explained by elevation and year, and influences bee richness indirectly, by increasing insect activity (measured as a higher insect abundance).

3. Resource-availability-hypothesis

High amounts of resources can sustain larger populations, and/or decrease competition and enable more species to coexist (Araújo et al., 2010; Classen et al., 2015; Roulston & Goodell, 2011). We, therefore, expected that higher resource availability affects bee species richness both directly and indirectly (via abundances).

2.9 | Range shifts

We examined elevational shifts of bee communities between years with two different approaches:

1. Range shifts based on mean species range shift

In the first approach (Figure 4), we asked whether species, on average, shifted their abundance-weighted mean elevational distribution along the elevational gradient. Mean elevational distributions were calculated per year and species and analysed with linear mixed-effects models, in which year was included as fixed factor and species as a random effect. We also tested which species significantly shifted their mean distribution along the elevational gradient. To do so, we first fitted a linear model with the elevation of recorded bee individuals as response variable and year and species as interacting explanatory variables. To account for repeated measurements of species on the same study sites, we then conducted a pairwise year comparison per species in the post hoc test. The pairwise yearly comparison per species was carried out with the function “emmeans.” In this first approach, we only included species that were detected in both sampling years and had a minimum abundance of 12 individuals in total. The minimum abundance threshold of 12 resulted in intermediate shift rates compared with a smaller or larger abundance threshold and was thus assumed to be representative (Figure S6.1 in Appendix S6).

2. Range shifts based on community similarity range shifts

Upslope shifts may not be restricted to single species but could be detected in many co-occurring species, potentially resulting in an upslope shift of substantial parts of the bee community. In the second approach (Figure 5), we tested for such community shifts by comparing the bee community compositions of each study site from the earlier sampling year, with the community compositions of each site from the later sampling year. Specifically, we created a dissimilarity matrix based on Bray–Curtis distances and identified “sites-pairs” with the most similar species composition between years. Site-pairs were then

assigned to their specific elevations, allowing us to test with a one-sample t-test whether, on average, the overall community in the study area had shifted in elevation. To investigate whether bee community shifts are driven predominantly by abundance changes in abundant species or by shifts of many species, we compared this analysis with an analysis applied to presence/absence species-site matrices.

2.10 | Predicted range shifts vs. measured range shifts

We investigated whether bee community shifts along the elevational gradient mirror the changes in temperature between and across years. We used the temperature lapse rate along the elevational gradient and the change of temperature between and across years to calculate expected range shifts and compared them with observed shifts (Section S1.4 in Appendix S1 for details on calculation).

2.11 | Body size shifts at community level

We analysed body size distribution along the elevational gradient and between years with generalized additive models (GAMs), which allow for the detection of both linear and non-linear relationships (Wood, 2017; Appendix S3 for details).

All analyses were performed using the software R (version 4.0.5). Unless otherwise stated, model fit testing was performed using the Dharma package (Hartig, 2021). The dredge function from the MuMin package was used for model selection (i.e. interaction vs. additive) (Barton, 2020) based on the Akaike information criterion corrected for small sampling sizes (AICc) (Burnham & Anderson, 2004). Bee pictograms used in figures are obtained from <http://phylopic.org/>. For licence see Appendix S9.

3 | RESULTS

3.1 | Temperature patterns in space and time

In Berchtesgaden, mean annual temperature decreased by about 0.44°C per 100m gain in elevation. In the sampling year 2019, it was on average 0.9°C warmer than in 2009, with an average increase of 1.43°C in this time period. In the Bavarian Forest, mean annual temperature decreased by 0.49°C with 100m gain in elevation. Mean annual temperature was 0.1°C colder in the sampling year 2016 than in 2007/2008 but increased on average by 0.69°C in this period (see Sections S1.3 and S1.4 in Appendix S1 for details on calculation and statistic tables).

3.2 | Bee abundance and species richness patterns in space and time

We observed a total of 1909 individuals from 82 bee species in Berchtesgaden in 2009 and 2336 individuals from 115 species in

2019. Sixty-seven species sampled in 2009 were resampled in 2019. In the Bavarian Forest, we recorded in total 1782 wild bee individuals from 107 species in 2007/2008 and 1477 individuals from 74 species in 2016. Fifty-four species sampled in 2007/2008 were resampled in 2016. The two regions shared 78 species across all samplings (Figure 1a).

In Berchtesgaden, wild bee abundance, observed species richness and estimated species richness (Chao1) were higher in 2019 and decreased with increasing elevation in both years (Figure 2a,c,e; Table 1). The abundance increase was greater from an elevation of about 1200m.a.s.l than at lower elevations (indicated by the interaction year:alt). In the Bavarian Forest, elevational and between-year patterns were generally less consistent: while wild bee abundances and observed species richness declined with increasing elevation in the earlier sampling (2007/2008), they tended to increase along elevation in 2016 (Figure 2b,d; Table 1). The estimated species richness (Chao1) did not differ between sampling events and decreased with increasing elevation in both sampling events (Figure 2f; Table 1).

3.3 | Drivers of bee species richness

All three hypotheses contributed at least partly to the explanation of bee species richness variation in space and time. In line with the *temperature-occurrence-hypothesis*, in Berchtesgaden, we detected higher bee abundances under warmer mean annual temperature, which resulted in the detection of more species (Figure 3a). Mean annual temperature itself was mainly explained by elevation, but also varied between years, with 2019 being warmer than 2009. Temperature during sampling contributed to the explanation of bee richness (= *temperature-activity-hypothesis*), but in comparison with the mean annual temperature effect, both its direct and indirect, abundance-mediated impact on richness was weak. As predicted by the *resource-availability-hypothesis*, a high cover of floral resources, which was mainly found in warm and extensively managed grasslands, supported a higher bee richness by increasing bee abundances. A direct effect of resource availability on species richness was not detected. The best piecewise SEM explained 64% of the total variance in species richness.

Also, in the Bavarian Forest, mean annual temperature was a strong predictor of bee richness, affecting it both directly and indirectly via abundances (*temperature-occurrence-hypothesis*; Figure 3b). Mean annual temperature was almost exclusively explained by elevations. The second year of observation was only slightly cooler than the first year. Canopy cover, which we interpret as a proxy for resource availability, was lower in high elevations but did not differ between years (Appendix S7). With denser canopy cover, we observe lower species richness. The supported piecewise SEM explained 82% of the total variance in species richness.

Drivers of bee richness were confirmed in both regions, when modelling Chao1 instead of observed species richness, suggesting that our results are not biased by sampling effects (see Section S5.2 in Appendix S5 for Chao1 model).

TABLE 1 Abundance (Abu) and species richness (observed [SR] and estimated [Chao1]) in space (along elevation gradients = ele) and time (between sampling years = years).

| Region | χ^2 | p-Value | R^2 (cond) | R^2 (marg) | Year | Ele.trend | Lower CL | Upper CL |
|-----------------------------|----------|--------------|--------------|--------------|-----------|-----------|----------------|----------------|
| BGL | | | | | | | | |
| Abundance | | | | | | | | |
| Abu ~ year + ele + year*ele | | | .93 | .34 | | | | |
| Year | 42.91 | 5.73E-11*** | | | 2009 | -0.0007 | -0.0011 | -0.0004 |
| Ele | 13.70 | 2.148E-04*** | | | 2019 | -0.0005 | -0.0008 | -0.0002 |
| Year:ele | 7.81 | .005** | | | | | | |
| Species richness | | | | | | | | |
| SR ~ year + ele | | | .59 | .35 | | | | |
| Year | 12.09 | .001*** | | | | | | |
| Ele | 19.34 | 1.09E-05*** | | | | | | |
| Chao1 | | | | | | | | |
| Chao1 ~ year + ele | | | .51 | .23 | | | | |
| Year | 5.20 | .023* | | | | | | |
| Ele | 10.71 | .001** | | | | | | |
| BF | | | | | | | | |
| Abundance | | | | | | | | |
| Abu ~ year + ele + year*ele | | | .58 | .13 | | | | |
| Year | 2.03 | .155 | | | 2007/2008 | -0.0014 | -0.0023 | -0.0004 |
| Ele | 0.48 | .488 | | | 2016 | 0.0007 | -0.0002 | 0.0016 |
| Year:ele | 16.56 | 4.73E-05*** | | | | | | |
| Species richness | | | | | | | | |
| SR ~ year + ele + year*ele | | | .42 | .15 | | | | |
| Year | 0.39 | .532 | | | 2007/2008 | -0.0011 | -0.0017 | -0.0005 |
| Ele | 7.71 | .005** | | | 2016 | -0.0002 | -0.0008 | 0.0003 |
| Year:ele | 6.24 | .012* | | | | | | |
| Chao1 | | | | | | | | |
| Chao1 ~ year + ele | | | .30 | .14 | | | | |
| Year | 0.07 | .792 | | | | | | |
| Ele | 11.02 | 9.015E-04*** | | | | | | |

Note: We used generalized linear mixed-effects models and performed type II Wald chi-square tests. All models included site as a random term. For elevational effects within years, estimated trend (ele.trend) and confidence intervals (lower CL/upper CL) are presented and highlighted in bold if significant. Conditional (cond) and marginal (marg) coefficients of determination (R^2) are given for the full model. Significance levels are presented * $p < .05$; ** $p < .01$; *** $p < .001$.

3.4 | Detection of mean species range shifts

In Berchtesgaden, the abundance-weighted elevational mean of bee species shifted on average 85 ± 29.8 m upslope in one decade (lmer: $F = 8.22$, $df = 29$, $p = .008$) (Figure 4a). When testing each species separately, eight of the 30 species considered shifted upwards, including seven bumble bee species (see Table S6.2 in Appendix S6 for pairwise yearly comparison per species).

With a given temperature lapse rate of $\sim 0.44^\circ\text{C}$ per 100m gain in elevation in Berchtesgaden, the observed overall shift across

species (85 ± 29.8 m) lagged behind the range of shift rates expected from the mean temperature increase within the sampling period (2009–2019; 1.43°C correspond to 325m) and expected from the absolute temperature difference between the years 2009 and 2019 ($\Delta T 0.9^\circ\text{C}$ correspond to 204 m); (see Section S1.4 in Appendix S1 for calculations of expected shifts).

In the Bavarian Forest, bee species shifted on average 77.14 ± 23.3 m upslope (lmer: $F = 11.011$, $df = 27$, $p = .003$), which is in the same range of the average upslope shift as in Berchtesgaden (Figure 4b). Eight of 28 considered species shifted upslope, including

seven bumble bee species (see Table S6.2 in Appendix S6 for pairwise yearly comparison per species).

With a given temperature lapse rate of $\sim 0.49^\circ\text{C}$ per 100 m gain in elevation in the Bavarian Forest, the observed overall shift across species (77.14 ± 23.3 m) lagged behind the range shift expected from the mean temperature increase within the sampling period (2007/2008–2016) respectively (0.62°C correspond to 126.7 m) and exceeded the expected shift rates derived from the absolute temperature difference between the years 2007/2008 and 2016 ($\Delta T -0.1^\circ\text{C}$ correspond to -20.4 m; see Section S1.4 in Appendix S1 for calculations of expected shifts).

3.5 | Detection of range shifts on a community level

In the approach based on community similarities, upslope shifts in Berchtesgaden were detectable at a community level: on average, the species composition of bee communities sampled at a given site

in 2019 was similar to the composition of bee communities sampled at a site 117 m lower in 2009 (one-sample-t-test: $t = 3.46$, $df = 32$, $p = .002$; Figure 5a,c). Importantly, community shifts were driven by abundance shifts, as no upwards shifts were detected in presence/absence data only (one-sample-t-test: $t = 1.57$, $df = 32$, $p = .127$).

In the Bavarian Forest, upslope shifts of bees were not detected on a community level (Figure 5b,d) either when considering bee abundances (one-sample-t-test: $t = 0.17$, $df = 46$, $p\text{-value} = .862$) or when analysing species presence/absence data (one-sample-t-test: $t = 0.51$, $df = 46$, $p\text{-value} = .611$).

3.6 | Body size shifts at community level

The abundance-weighted mean body size of bee communities increased with elevation in 2009 in Berchtesgaden, suggesting an overall decrease in body size with increasing temperature over time. Indeed, mean body size was lower in 2019 than in 2009 across the entire elevational gradient. The size difference between years

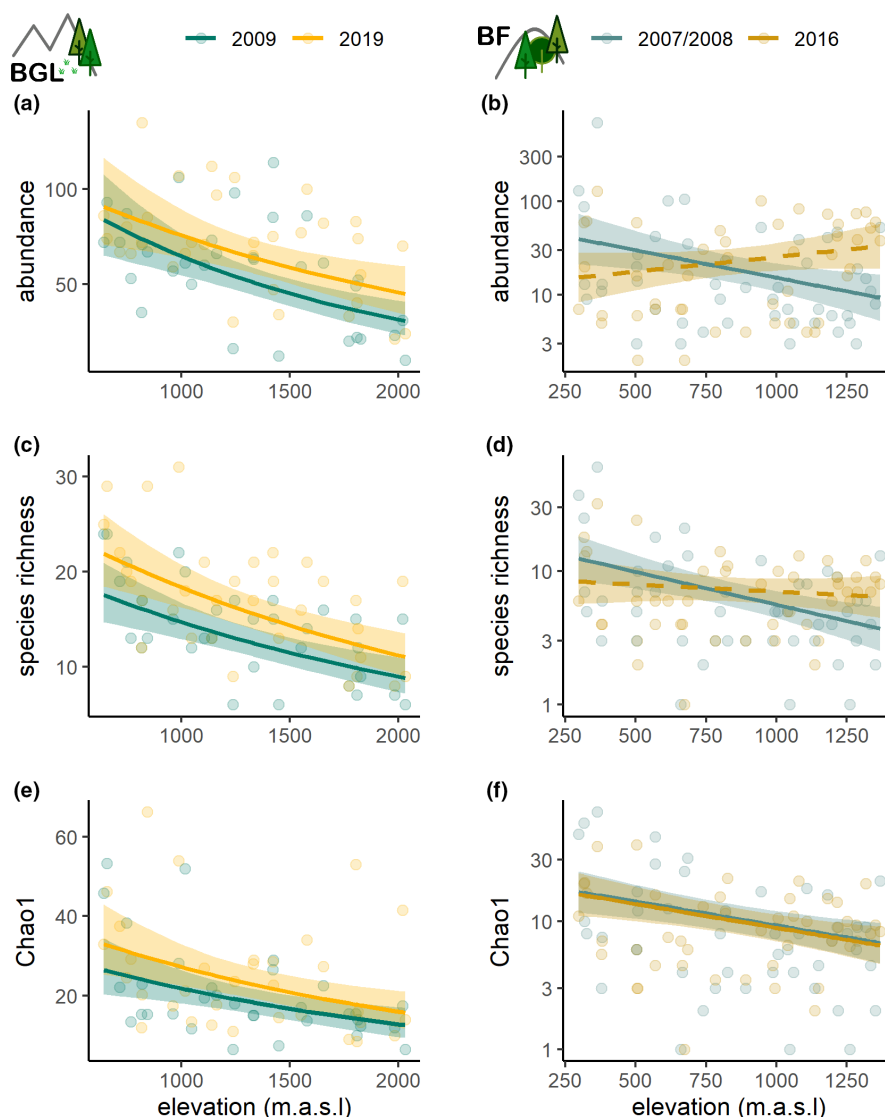


FIGURE 2 Change of wild bee abundance (a, b), observed species richness (c, d) and estimated species richness (Chao1) (e, f) in space (along elevational gradients) and time (between sampling years) in two different regions (left: Berchtesgaden = BGL; right: Bavarian Forest = BF). Species abundance (a) and species richness (c, e) declined with elevation in BGL and were higher in the later (warmer) sampling year (2019) than in the earlier (cooler) sampling year (2009). In the Bavarian Forest, bee abundance (b) and species richness (d, f) decreased with increasing elevation only in the earlier sampling (2007/2008). In the later sampling (2016), no significant elevational pattern was detected (dashed lines) in species abundance and observed species richness. Note that in the Bavarian Forest all y-axes are log-scaled for better representation.

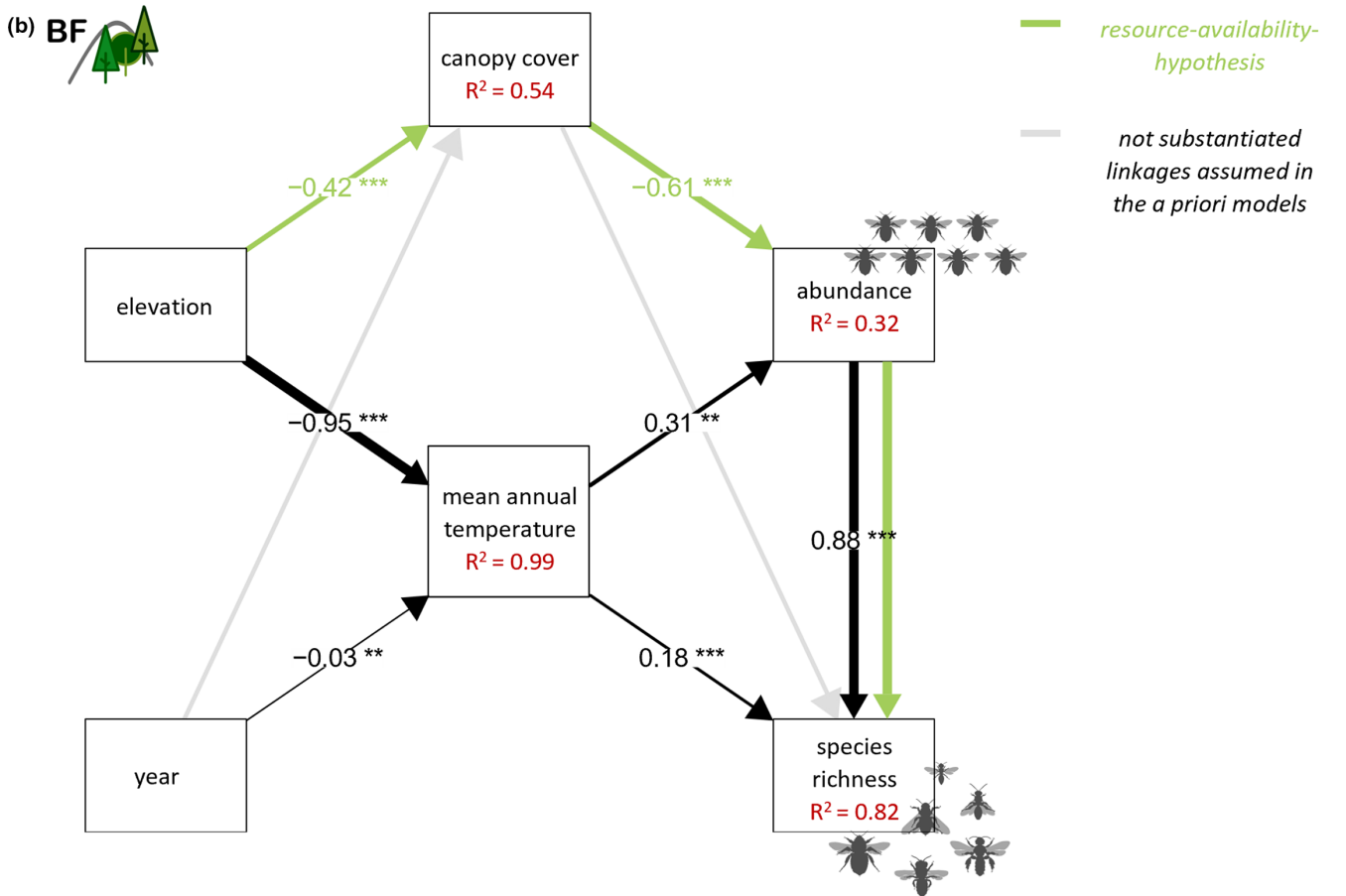
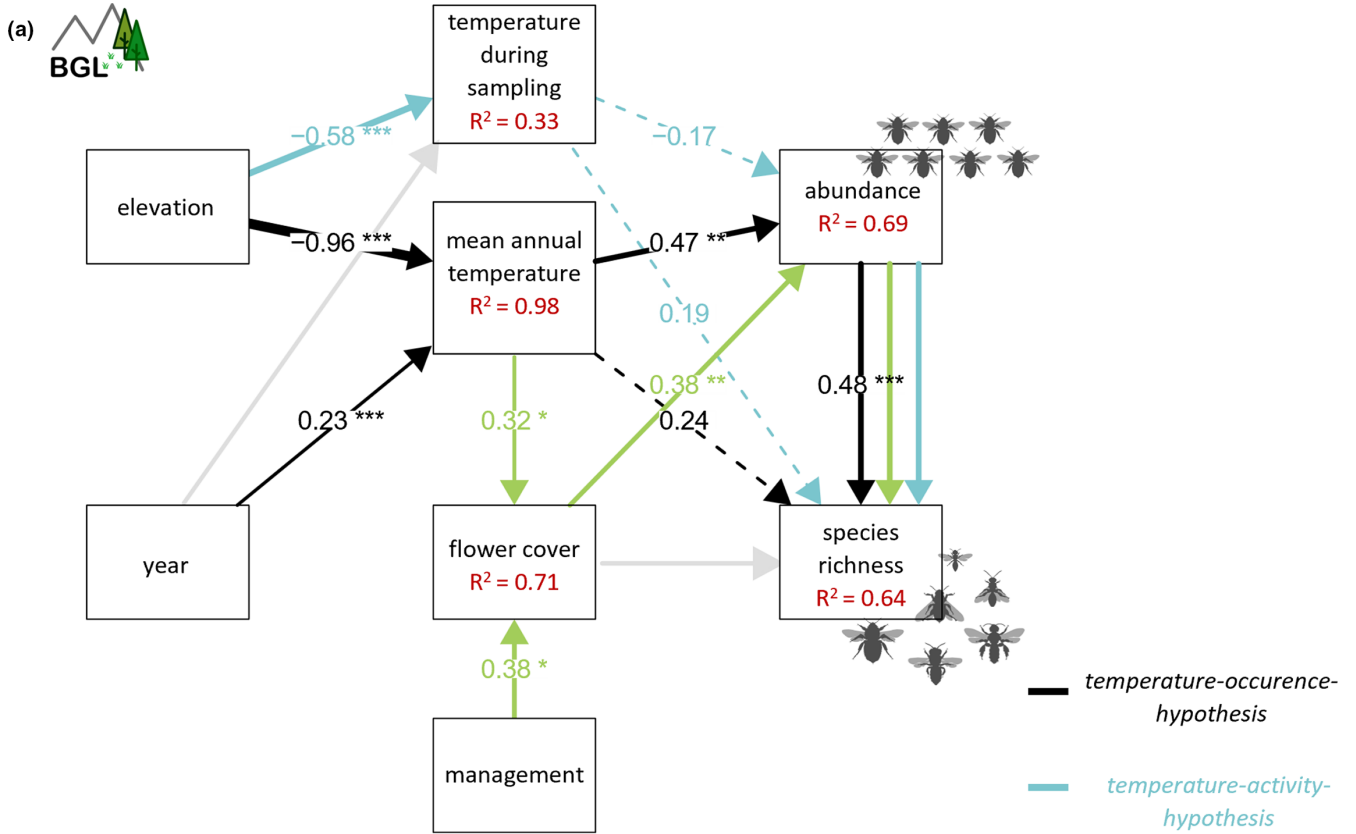
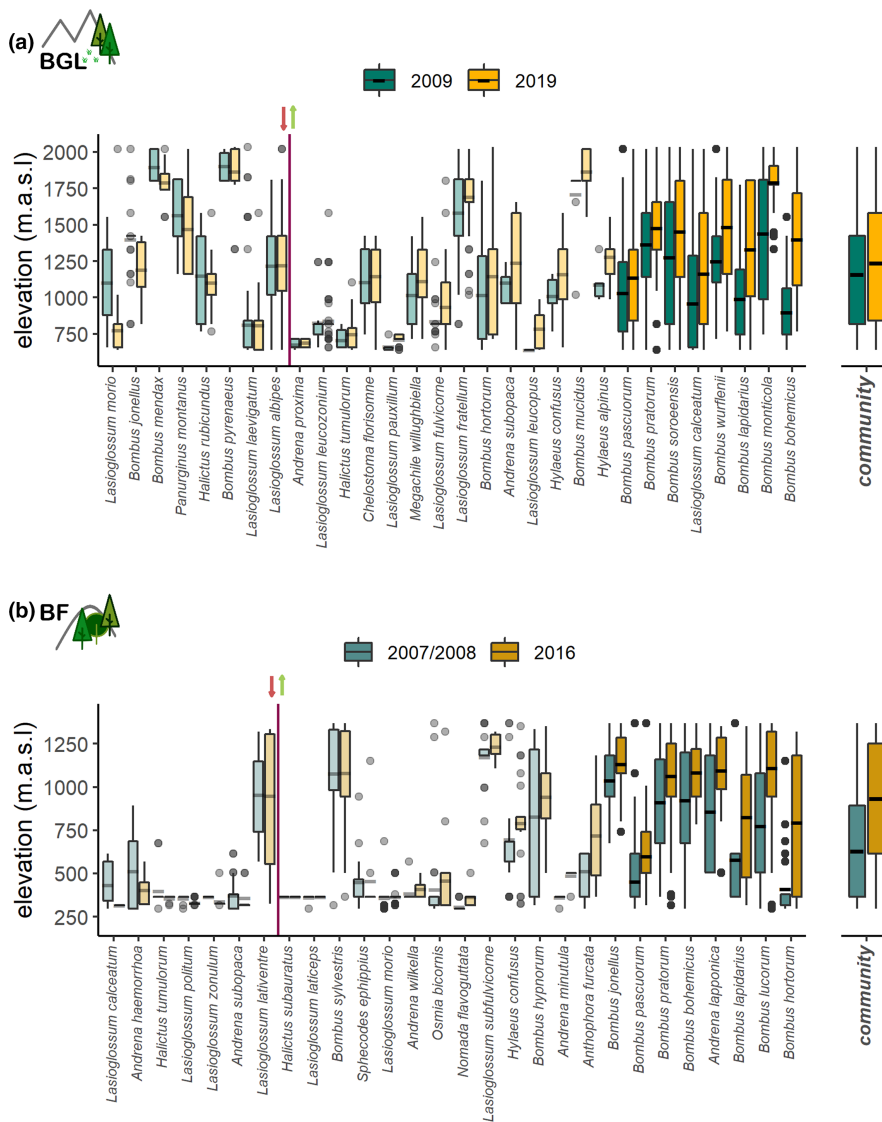


FIGURE 3 Direct and indirect drivers of bee species richness along two independent elevational gradients. Both in Berchtesgaden (BGL) (a) and in the Bavarian Forest (BF) (b) mean annual temperature was the strongest direct and indirect (via bee abundance) driver of bee species richness. Different colours depict different expected linkages between predictor variables and bee communities details on the linkage hypotheses are given in the method section (statistical analyses). In the Bavarian Forest, canopy cover was predominantly taken as a surrogate for floral resource availability, assuming fewer floral resources with denser canopy cover. Light grey arrows indicate the linkages assumed in the a priori models, but not substantiated in the model selection process. Note that the arrow from elevation to mean annual temperature is predefined due to the modelling of the temperature data. Numbers and stars represent standardized path coefficients and the respective significance levels (* $p < .05$, ** $p < .01$, *** $p < .001$). Marginal-significant relationships are presented in dotted lines. Arrow thickness represents effect strengths. The relative amount of explained variance (R^2) is given for all response variables.

FIGURE 4 Mean species range shifts in space (along elevation gradients) and time (between sampling years). (a) In Berchtesgaden (BGL), the abundance-weighted mean elevation of bee species shifted on average 85 ± 29.8 m upslope in one decade when testing each species separately, upslope shifts were statistically significant in eight out of 30 considered (bright colour = significant; pale colour = nonsignificant). (b) In the Bavarian Forest (BF), bee species shifted on average 77.14 ± 23.3 m upslope. Eight of 28 considered species significantly shifted upslope. Red vertical lines separate downslope shifts (left) from upslope shifts (right). Note, that, here, boxplots are presented with the mean.



decreased in higher elevations (Figure 6a; Table 2). The body size decline in 2019 was caused by an increase in small-bodied species (reflected in the species-weighted mean, which showed the same trend) and by an increase in the relative abundance of small-bodied species in 2019 (Appendix S3). In the Bavarian Forest, mean body size only increased up to mid-elevations (Figure 6b; Table 2). The effect that communities become smaller over time was not detected.

4 | DISCUSSION

In this study, we show that the responses of wild bee communities to temperature changes are detectable in a single decade. Observed temporal responses were often, but not always, in line with expectations from theory and community patterns along spatial temperature gradients (i.e. mountain slopes). Meanwhile, structural and

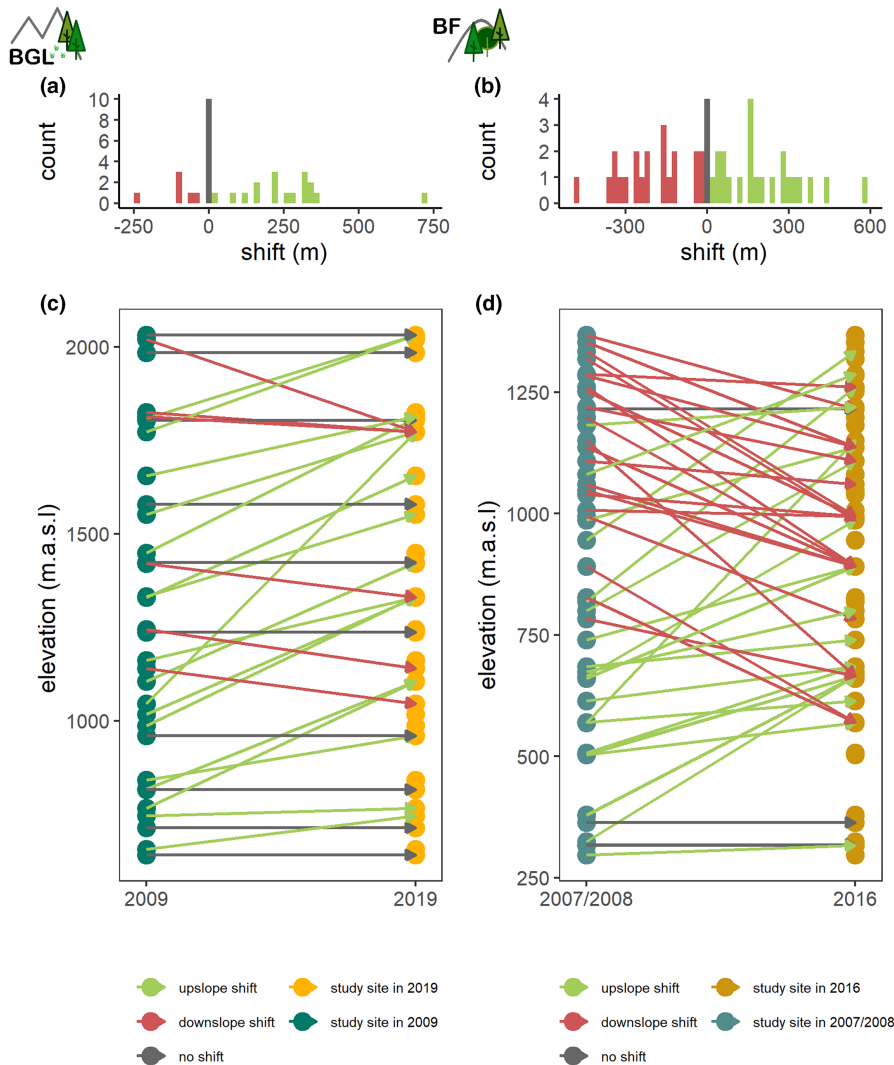


FIGURE 5 Bee community shifts based on site similarity quantified by pairwise bray-Curtis distances between earlier and later sampling events. Small histograms display the distribution of the shift strength (a, c). Green and yellow dots represent study sites in the early and late year, respectively. The most similar sites between years are connected with arrows. Colours indicate the direction of detected shifts per site (grey = no shift; red = downslope shift, green = upslope shift). (b) In Berchtesgaden (BGL), the species composition of bee communities caught on a certain study site in 2019, resembled the composition of bee communities detected on a, on average, 117 m deeper study site in 2009 (d) community upslope shift was not detected in the Bavarian Forest (BF).

microclimate diversity in forests seems to counteract and/or buffer wild bee species responses to temperature.

4.1 | Patterns and drivers of bee species richness

In Berchtesgaden, where the second sampling year was warmer than the first, abundance and species richness were elevated in the warmer year, meeting the expectation from theory and space-for-time substitution. We identified mean annual temperature as the strongest predictor of species abundance and richness, supporting the *temperature-occurrence-hypothesis*. This implies that increases in temperature due to climate change can result in a diversification of temperature limited temperate communities—at least initially. As most of the detected species belonged to the known species pool in this region, the increase in observed species richness is likely driven by increases in abundance in rarer species, leading to higher detection rates (Voith et al., 2021 but see Hopfenmüller, 2014 for *Halictus scabiosae*). Higher floral resource availability supported larger numbers of bees but was a weaker predictor than temperature,

consistent with other studies (Classen et al., 2015). However, as disruptions in precipitation and snowmelt under climate change may strongly influence floral resource availability (Litaor et al., 2008; Winkler et al., 2018), we expect that initial increases in floral resources due to warmer temperatures may ultimately give way decreases in floral resources due to drought (Phillips et al., 2018).

In the Bavarian Forest, the systematic increase in species richness was not observed. The strong negative effect of canopy cover on bee richness might contribute to the less consistent patterns observed in the Bavarian Forest. At lower elevations, the predicted increase in abundance and observed species richness under temperature increases over a decade might have been obscured by a temperature buffering effect of denser forests (due to higher canopy cover) (De Frenne et al., 2019). By contrast, the more open forests in the upper part of the gradient limit temperature buffering capacity. This may directly (via temperature) and indirectly (via temperature-dependent resource availability) increase bee abundance. Such influences cannot be inferred conclusively in our study, but we underscore the potential importance of canopy cover as source of additional variance between sites.

TABLE 2 Abundance-weighted mean body size in space (along elevation gradients) and time (between sampling years).

| Region | Model | Family | R-sq. (adj.) | ED (%) | n | Parametric coefficients | | | Approximate significance smooth terms | | | | | |
|--------|------------------|--------------|--------------|--------|----|-------------------------|------------|---------|---------------------------------------|--------------|-----------------|---------|-------|-------------|
| | | | | | | Estimate | Std. error | t Value | Pr(> z) | edf | F | p-Value | | |
| BGL | Elevation: year | Quasipoisson | .73 | 83.70 | 66 | Year | -0.06 | 0.01 | -4.26 | 1.260E-05*** | s(ele);year2009 | 1.00 | 5.80 | .021* |
| | | | | | | | | | | | s(ele);year2019 | 1.00 | 23.5 | 2.04E-05*** |
| BF | Elevation + year | Gaussian | .49 | 58.80 | 94 | Year | 0.31 | 0.16 | 1.48 | 0.142 | s(ele) | 2.70 | 14.69 | <2e-16*** |

Note: Abundance-weighted mean body size changes along space (elevation = ele) and time (year) were analysed using generalized-additive-models. Site was included as a random effect. Based on AICc comparison, either the interaction model (elevation:year) or the additive model (elevation + year) is presented, together with data family, adjusted R², explained deviance (ED) and sample-size (n). Effective degrees of freedom (edf) for model smooth terms are given. Significance levels are presented *p < .05; **p < .01; ***p < .001.

4.2 | Mean species range and community shifts to higher elevations

We detected similar shifts in mean elevational species ranges in two study regions (Figure 4). Community responses of both gradients point in the same direction—uphill—which is expected under climate change and has already been observed in many other organisms, including bumble bees (Chen et al., 2011; Kerr et al., 2015; Marshall et al., 2020; Pyke et al., 2016).

Average species range shifts in Berchtesgaden lag behind expected shifts from temperature change alone, suggesting that even mobile bee species may not track their temperature niche perfectly (Figure 4a and Section S1.4 in Appendix S1). This might be caused by dispersal limitations, but it is also possible that species from temperate regions that are accustomed to seasonal temperature fluctuations may not need to follow their temperature niche exactly (Freeman et al., 2021). In both regions, the genus *Bombus* exhibited the most pronounced upslope shifts, mirroring previous studies of mountain bumble bee communities (Kerr et al., 2015; Marshall et al., 2020; Ploquin et al., 2013; Pyke et al., 2016). But considering the shorter time period observed in our study (9–10 years), our observed shifts (~77 m per decade) are much higher than previously reported shifts (e.g. 17 m per decade reported in Marshall et al., 2020, analysing a data set spanning 115 years). This may reflect the accelerated temperature increase in recent years, but it might also be driven by the method how range shifts are investigated: our approach, which considers the mean elevation of a species based on empirically assessed abundance data, is expected to be much more sensitive than the estimation of range shifts based on upper or lower range limits (Kerr et al., 2015) or range shifts which include standardized abundance data due to different/or unknown sampling intensity (Chen et al., 2009; Marshall et al., 2020; see Section S6.3 in Appendix S6 for analyses of our data with standardized abundances between years).

In Berchtesgaden, upward shifts occurred also at the community level, when including bee abundances in analyses (Figure 5c). The finding that large parts of the communities are shifting (rather than only single species) is noteworthy and suggests that at least some existing interspecific interactions can persist within the same trophic level, while changing in space. In the Bavarian Forest, community shifts were not detectable. Instead, communities shift in contrasting directions in the lower and the higher part of the gradient (Figure 5d). The combination of 2 years as early sampling event, the greater geographic distance between sites compared to Berchtesgaden, and canopy cover as further source of community variation may cause higher species abundance fluctuations in the Bavarian Forest, which might explain such non-systematic response.

4.3 | Body size shifts at community level

In Berchtesgaden, mean community body size declined in the warmer year, consistent with the predictions derived from theory

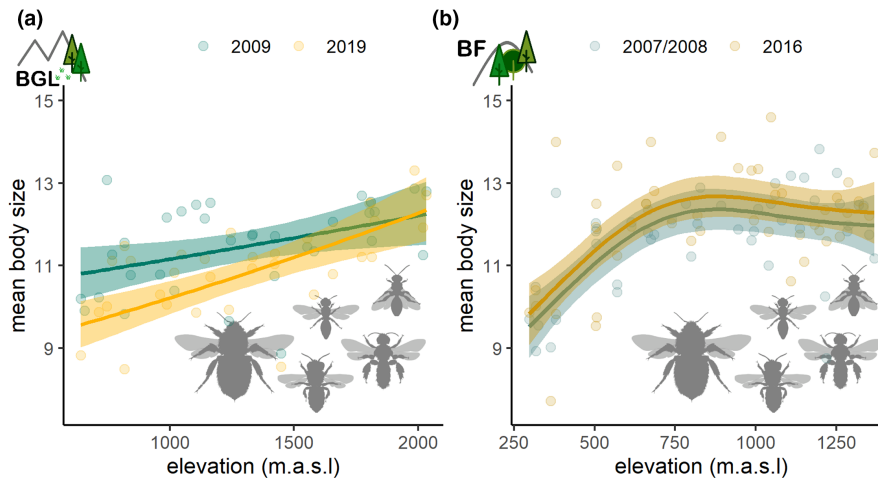


FIGURE 6 Change in the abundance-weighted mean community body size of bees in space (along elevation gradients) and time (between sampling years). Size patterns were analysed with generalized-additive models. (a) In Berchtesgaden (BGL), mean community body size increased with elevation and was smaller in the later sampling (2019) compared with the earlier sampling (2009). (b) In the Bavarian Forest (BF), mean community body size increased with elevation but did not differ between the earlier sampling (2007/2008) and the later sampling (2016).

and the observation that along spatial temperature gradients, body size declines with increasing temperature (Figure 6a). The reduction in community body size over a relatively short time period is in line with a recent study, which studied bee community response to climate variation in eight consecutive years (Pardee et al., 2022). Body size declines can also be observed over longer time scales up to 140 years (Bartomeus et al., 2013; Nooten & Rehan, 2020). In our study, the decrease in mean community body size was caused by an increase in relative abundance of smaller species. Therefore, in the warmer year, potential pollination benefits for plants depending on smaller pollinators can be expected. One might think that, in turn, the decline in the relative abundance of larger body sizes would reflect the general decline of cold-adapted bumble bees, and with this the decline of the most efficient pollinators in the community (Gorenflo et al., 2017; Willmer et al., 2017). However, in this study, bumble bee species were present in medium, large and very large size classes (Appendix S3). Interestingly, the absolute abundances of bumble bees at low and medium elevations remained constant (i.e. medium-sized bumble bees persisted in the warmer year; Appendix S8). Thus, it is likely that pollination services by these efficient pollinators remained stable. Whether pollination efficiency by bumble bee remains stable in the future will depend on the responses of bumble bees to warming temperatures. A variety of adaptive and plastic responses, that might allow the cold-evolved genus *Bombus* to handle increasing temperatures are conceivable, from gene expression to behavioural adaptation (Brenzinger et al., 2022; Maebe et al., 2021). However, given the current global decline in abundance and range of most *Bombus* species (Arbetman et al., 2017; Marshall et al., 2020; Suzuki-Ohno et al., 2020), pursuing the climatic niche appears to be the more rapid and likely response of this genus. Such a response could disrupt pollination services for plant communities in areas from which bumble bees emigrate.

In the Bavarian Forest, where changes in temperature between sampling events were minor, no decrease in average body size was observed for the whole bee community (Figure 6b). Contrasting body size (and also species richness) responses between regions might indicate that some of the reported community responses in Berchtesgaden are potentially reversible responses to a warmer sampling year. Indeed, our two-year comparisons does not have the same persuasive power as continuous observations of species communities over longer periods of time. We cannot conclusively separate systematic responses to climate change from patterns caused by annual population fluctuations (McCain et al., 2016; Stuble et al., 2021). However, stochastic annual population fluctuations are more likely to result in neutral, nondirected patterns. Here, we demonstrate that in an open grassland habitat with no confounding canopy effects, basically all considered community responses are in line with the predictions from spatial temperature gradients—supporting that temperature is the direct (or indirect) driver of these responses. Even if the responses might be reversible in cooler years, warmer years are predicted to occur more often in the nearest future, which on a long term should shape communities in the reported directions.

5 | CONCLUSION

We conclude that in well-protected temperate regions, alpine wild bee communities can be expected to diversify at least partly due to climate-niche-tracking uphill shifts and an abundance increase of small-bodied species. Even if the reported diversification and species range shifts could also be partially reversible annual effects, they are expected to be indicative for the future, because warmer years will become more frequent. Our study also provides evidence that the spatial patterns of wild bee communities along temperature

gradients are partly informative to predict wild bee responses to a temperature change in time, supporting space-for-time substitutions as common method in climate change research. In addition, we highlight the value of accurately assessed abundance data, as they allow the sensitive detection of rapid community responses in very short time frames. Future studies of mountain pollinators should focus more on the total bee community, rather than concentrating on bumble bees only, as understudied non-*Bombus* pollinators are likely to gain in importance.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.80gb5mkt1>.

PEER REVIEW

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REFERENCES

- Araújo, V., Araújo, A. P., & Antonini, Y. (2010). Impact of resource availability on bee diversity. *Sociobiology*, *56*, 163–176.
- Arbetman, M. P., Gleiser, G., Morales, C. L., Williams, P., & Aizen, M. A. (2017). Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), 20170204. <https://doi.org/10.1098/rspb.2017.0204>

- Arroyo, M. T. K., Armesto, J. J., & Primack, R. B. (1985). Community studies in pollination ecology in the high temperate Andes of central Chile II. Effect of temperature on visitation rates and pollination possibilities. *Plant Systematics and Evolution*, *149*(3–4), 187–203. <https://doi.org/10.1007/BF00983305>
- Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D. L., Hedtke, S. M., & Winfree, R. (2013). Historical changes in north-eastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences*, *110*(12), 4656–4660. <https://doi.org/10.1073/pnas.1218503110>
- Barton, K. (2020). *MuMIn: Multi-model inference*. <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>
- Bässler, C., Förster, B., Moning, C., & Müller, J. (2009). *The BIOKLIM Project: Biodiversity Research between Climate Change and Wilding in a temperate montane forest – The conceptual framework*. 14.
- Bässler, C., Hothorn, T., Brandl, R., & Müller, J. (2013). Insects overshoot the expected upslope shift caused by climate warming. *PLoS One*, *8*(6), e65842. <https://doi.org/10.1371/journal.pone.0065842>
- Bässler, C., Seifert, L., & Müller, J. (2015). The BIOKLIM project in the National Park Bavarian Forest: Lessons from a biodiversity survey. *Silva Gabreta*, *21*, 81–93.
- Belmaker, J., & Jetz, W. (2015). Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters*, *18*(6), 563–571. <https://doi.org/10.1111/ele.12438>
- Brenzinger, K., Maihoff, F., Peters, M. K., Schimmer, L., Bischler, T., & Classen, A. (2022). Temperature and livestock grazing trigger transcriptome responses in bumblebees along an elevational gradient. *iScience*, *25*(10), 105175. <https://doi.org/10.1016/j.isci.2022.105175>
- Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, *41*(1), 8–22. <https://doi.org/10.1111/jbi.12228>
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*(2), 261–304. <https://doi.org/10.1177/0049124104268644>
- Cerrato, C., Rocchia, E., Brunetti, M., Bionda, R., Bassano, B., Provenzale, A., Bonelli, S., & Viterbi, R. (2019). Butterfly distribution along altitudinal gradients: Temporal changes over a short time period. *Nature Conservation*, *34*, 91–118. <https://doi.org/10.3897/natureconservation.34.30728>
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026. <https://doi.org/10.1126/science.1206432>
- Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., Hill, J. K., & Thomas, C. D. (2009). Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences*, *106*(5), 1479–1483. <https://doi.org/10.1073/pnas.0809320106>
- Classen, A., Peters, M. K., Kindeketa, W. J., Appelhans, T., Eardley, C. D., Gikungu, M. W., Hemp, A., Nauss, T., & Steffan-Dewenter, I. (2015). Temperature versus resource constraints: Which factors determine bee diversity on Mount Kilimanjaro, Tanzania?: Bee species richness on Mt Kilimanjaro. *Global Ecology and Biogeography*, *24*(6), 642–652. <https://doi.org/10.1111/geb.12286>
- Corbet, S. A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., & Smith, K. (1993). Temperature and the pollinating activity of social bees. *Ecological Entomology*, *18*(1), 17–30. <https://doi.org/10.1111/j.1365-2311.1993.tb01075.x>
- Danforth, B. N. (1999). Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1432), 1985–1994. <https://doi.org/10.1098/rspb.1999.0876>
- De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J.

- (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5), 744–749. <https://doi.org/10.1038/s41559-019-0842-1>
- Escobedo-Kenefic, N., Landaverde-González, P., Theodorou, P., Cardona, E., Dardón, M. J., Martínez, O., & Domínguez, C. A. (2020). Disentangling the effects of local resources, landscape heterogeneity and climatic seasonality on bee diversity and plant-pollinator networks in tropical highlands. *Oecologia*, 194(3), 333–344. <https://doi.org/10.1007/s00442-020-04715-8>
- Feeley, K. J., Rehm, E. M., & Machovina, B. (2012). Perspective: The responses of tropical forest species to global climate change: Acclimate, adapt, migrate, or go extinct? *Frontiers of Biogeography*, 4(2), 69–84. <https://doi.org/10.21425/F5FBG12621>
- Frazier, M. R., Huey, R. B., & Berrigan, D. (2006). Thermodynamics constrains the evolution of insect population growth rates: “warmer is better”. *The American Naturalist*, 168(4), 512–520. <https://doi.org/10.1086/506977>
- Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V., & Fitzpatrick, J. W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences*, 115(47), 11982–11987. <https://doi.org/10.1073/pnas.1804224115>
- Freeman, B. G., Song, Y., Feeley, K. J., & Zhu, K. (2021). Montane species track rising temperatures better in the tropics than in the temperate zone. *Ecology Letters*, 24(8), 1697–1708. <https://doi.org/10.1111/ele.13762>
- Gérard, M., Vanderplanck, M., Franzen, M., Kuhlmann, M., Potts, S. G., Rasmont, P., Schweiger, O., & Michez, D. (2018). Patterns of size variation in bees at a continental scale: Does Bergmann's rule apply? *Oikos*, 127(8), 1095–1103. <https://doi.org/10.1111/oik.05260>
- Gorenflo, A., Diekötter, T., Van Kleunen, M., Wolters, V., & Jauker, F. (2017). Contrasting pollination efficiency and effectiveness among flower visitors of *Malva sylvestris*, *Borago officinalis* and *Onobrychis vicifolia*. *Journal of Pollination Ecology*, 21, 62–70. <https://doi.org/10.26786/1920-7603>
- Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *Proceedings of the National Academy of Sciences*, 118(2), e2002543117. <https://doi.org/10.1073/pnas.2002543117>
- Hartig, F. (2021). *DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. <https://CRAN.R-project.org/package=DHARMA>
- Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, 470(7335), 479–485. <https://doi.org/10.1038/nature09670>
- Hofmann, M. M., Zohner, C. M., & Renner, S. S. (2019). Narrow habitat breadth and late-summer emergence increases extinction vulnerability in central European bees. *Proceedings of the Royal Society B: Biological Sciences*, 286(1898), 20190316. <https://doi.org/10.1098/rspb.2019.0316>
- Hoiss, B., Krauss, J., Potts, S. G., Roberts, S., & Steffan-Dewenter, I. (2012). Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4447–4456. <https://doi.org/10.1098/rspb.2012.1581>
- Hopfenmüller, S. (2014). Folgt die Efeu-Seidenbiene *Colletes hederæ* Schmidt & Westrich, 1993 dem Ausbreitungsweg der Furchenbiene *Halictus scabiosæ* (Rossi, 1790) in Bayern? (Hymenoptera: Apoidea). *Nachrichtenblatt der Bayerischen Entomologen*, 63, 2–7.
- Hurlbert, A. H., & Stegen, J. C. (2014). When should species richness be energy limited, and how would we know? *Ecology Letters*, 17(4), 401–413. <https://doi.org/10.1111/ele.12240>
- Hutchinson, G. E. (1978). *Introduction to population ecology*. Yale University Press.
- Kenna, D., Pawar, S., & Gill, R. J. (2021). Thermal flight performance reveals impact of warming on bumblebee foraging potential. *Functional Ecology*, 35(11), 2508–2522. <https://doi.org/10.1111/1365-2435.13887>
- 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., & Pantoja, A. (2015). Climate change impacts on bumblebees converge across continents. *Science*, 349(6244), 177–180. <https://doi.org/10.1126/science.aaa7031>
- Klotz, S., Kühn, I., Durka, W., & Briemle, G. (2002). *BIOLFLOR: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland* (Vol. 38). Bundesamt für Naturschutz.
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1768–1771. <https://doi.org/10.1126/science.1156831>
- Lindström, Å., Green, M., Paulson, G., Smith, H. G., & Devictor, V. (2013). Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography*, 36(3), 313–322. <https://doi.org/10.1111/j.1600-0587.2012.07799.x>
- Litaor, M. I., Williams, M., & Seastedt, T. R. (2008). Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot ridge, Colorado. *Journal of Geophysical Research: Biogeosciences*, 113(G2), G02008. <https://doi.org/10.1029/2007JG000419>
- Maebe, K., Hart, A. F., Marshall, L., Vandamme, P., Vereecken, N. J., Michez, D., & Smagghe, G. (2021). Bumblebee resilience to climate change, through plastic and adaptive responses. *Global Change Biology*, 27(18), 4223–4237. <https://doi.org/10.1111/gcb.15751>
- Marshall, L., Perdijk, F., Dendoncker, N., Kunin, W., Roberts, S., & Biesmeijer, J. C. (2020). Bumblebees moving up: Shifts in elevation ranges in the Pyrenees over 115 years. *Proceedings of the Royal Society B: Biological Sciences*, 287(1938), 20202201. <https://doi.org/10.1098/rspb.2020.2201>
- Mayr, A. V., Peters, M. K., Eardley, C. D., Renner, M. E., Röder, J., & Steffan-Dewenter, I. (2020). Climate and food resources shape species richness and trophic interactions of cavity-nesting hymenoptera. *Journal of Biogeography*, 47(4), 854–865. <https://doi.org/10.1111/jbi.13753>
- McCain, C., Szweczyk, T., & Bracy Knight, K. (2016). Population variability complicates the accurate detection of climate change responses. *Global Change Biology*, 22(6), 2081–2093. <https://doi.org/10.1111/gcb.13211>
- McCain, C. M., & Garfinkel, C. F. (2021). Climate change and elevational range shifts in insects. *Current Opinion in Insect Science*, 47, 111–118. <https://doi.org/10.1016/j.cois.2021.06.003>
- Menéndez, R., González-Megías, A., Jay-Robert, P., & Marquéz-Ferrando, R. (2014). Climate change and elevational range shifts: Evidence from dung beetles in two European mountain ranges: Climate change and elevational range shifts of dung beetles. *Global Ecology and Biogeography*, 23(6), 646–657. <https://doi.org/10.1111/gcb.12142>
- Minckley, R. L., & Radke, W. R. (2021). Extreme species density of bees (Apiformes, hymenoptera) in the warm deserts of North America. *Journal of Hymenoptera Research*, 82, 317–345. <https://doi.org/10.3897/jhr.82.60895>
- Nooten, S. S., & Rehan, S. M. (2020). Historical changes in bumble bee body size and range shift of declining species. *Biodiversity and Conservation*, 29(2), 451–467. <https://doi.org/10.1007/s10531-019-01893-7>

- Noroozi, J., Talebi, A., Doostmohammadi, M., Rumpf, S. B., Linder, H. P., & Schneeweiss, G. M. (2018). Hotspots within a global biodiversity hotspot—Areas of endemism are associated with high mountain ranges. *Scientific Reports*, 8(1), 10345. <https://doi.org/10.1038/s41598-018-28504-9>
- O'Grady, J. J., Reed, D. H., Brook, B. W., & Frankham, R. (2004). What are the best correlates of predicted extinction risk? *Biological Conservation*, 118(4), 513–520. <https://doi.org/10.1016/j.biocon.2003.10.002>
- Oksanen, J., Blanchet, G. F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G., Solymos, P., Stevens, H. H., Szoecs, E., & Wagner, H. (2020). *Vegan: Community ecology package*. <https://CRAN.R-project.org/package=vegan>
- Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C.-D., & Ascher, J. S. (2021). Global patterns and drivers of bee distribution. *Current Biology*, 31(3), 451–458.e4. <https://doi.org/10.1016/j.cub.2020.10.053>
- Osorio-Canadas, S., Flores-Hernández, N., Sánchez-Ortiz, T., & Valiente-Banuet, A. (2021). Changes in the structure and composition of the 'Mexical' scrubland bee community along an elevational gradient. *PLoS One*, 16(7), e0254072. <https://doi.org/10.1371/journal.pone.0254072>
- Pardee, G. L., Griffin, S. R., Stenkovski, M., Harrison, T., Portman, Z. M., Kazenel, M. R., Lynn, J. S., Inouye, D. W., & Irwin, R. E. (2022). Life-history traits predict responses of wild bees to climate variation. *Proceedings of the Royal Society B: Biological Sciences*, 289(1973), 20212697. <https://doi.org/10.1098/rspb.2021.2697>
- Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., ... Mountain Research Initiative EDW Working Group. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5(5), 424–430. <https://doi.org/10.1038/nclimate2563>
- Perillo, L. N., Neves, F. D. S., Antonini, Y., & Martins, R. P. (2017). Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient. *PLoS One*, 12(7), e0182054. <https://doi.org/10.1371/journal.pone.0182054>
- Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Feger, S. W., Frederiksen, S. B., Gebert, F., Haas, M., Helbig-Bonitz, M., Hemp, C., Kindeketa, W. J., Mwangomo, E., Ngeresa, C., Otte, I., Röder, J., Rutten, G., ... Steffan-Dewenter, I. (2016). Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications*, 7(1), 1. <https://doi.org/10.1038/ncomms13736>
- Peters, M. K., Peisker, J., Steffan-Dewenter, I., & Hoiss, B. (2016). Morphological traits are linked to the cold performance and distribution of bees along elevational gradients. *Journal of Biogeography*, 43(10), 2040–2049. <https://doi.org/10.1111/jbi.12768>
- Phillips, B. B., Shaw, R. F., Holland, M. J., Fry, E. L., Bardgett, R. D., Bullock, J. M., & Osborne, J. L. (2018). Drought reduces floral resources for pollinators. *Global Change Biology*, 24(7), 3226–3235. <https://doi.org/10.1111/gcb.14130>
- Ploquin, E. F., Herrera, J. M., & Obeso, J. R. (2013). Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. *Oecologia*, 173(4), 1649–1660. <https://doi.org/10.1007/s00442-013-2731-7>
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Princé, K., & Zuckerberg, B. (2015). Climate change in our backyards: The reshuffling of North America's winter bird communities. *Global Change Biology*, 21(2), 572–585. <https://doi.org/10.1111/gcb.12740>
- Pyke, G. H., Thomson, J. D., Inouye, D. W., & Miller, T. J. (2016). Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. *Ecosphere*, 7(3), e01267. <https://doi.org/10.1002/ecs2.1267>
- Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B., Holt, B. G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R. J., & Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, 365, 1108–1113. <https://doi.org/10.1126/science.aax0149>
- Rhoades, P. R., Davis, T. S., Tinkham, W. T., & Hoffman, C. M. (2018). Effects of seasonality, forest structure, and understory plant richness on bee community assemblage in a southern Rocky Mountain mixed conifer forest. *Annals of the Entomological Society of America*, 111(5), 278–284. <https://doi.org/10.1093/aesa/say021>
- Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, 56(1), 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>
- Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). Effects of body size and temperature on population growth. *The American Naturalist*, 163(3), 429–441. <https://doi.org/10.1086/381872>
- Stuble, K. L., Bewick, S., Fisher, M., Forister, M. L., Harrison, S. P., Shapiro, A. M., Latimer, A. M., & Fox, L. R. (2021). The promise and the perils of resurveying to understand global change impacts. *Ecological Monographs*, 91(2), e01435. <https://doi.org/10.1002/ecm.1435>
- Suzuki-Ohno, Y., Yokoyama, J., Nakashizuka, T., & Kawata, M. (2020). Estimating possible bumblebee range shifts in response to climate and land cover changes. *Scientific Reports*, 10(1), 19622. <https://doi.org/10.1038/s41598-020-76164-5>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427(6970), 145–148. <https://doi.org/10.1038/nature02121>
- Trew, B. T., & Maclean, I. M. D. (2021). Vulnerability of global biodiversity hotspots to climate change. *Global Ecology and Biogeography*, 30(4), 768–783. <https://doi.org/10.1111/geb.13272>
- Voith, J., Doczkal, D., Dubitzky, A., Hopfenmüller, S., Mandery, K., Scheuchl, E., Schuberth, J., & Weber, K. (2021). *Rote Liste und Gesamtartenliste Bayern - Bienen - Hymenoptera, Anthophila*. 41.
- Westrich, P. (2019). *Die Wildbienen Deutschlands* (2nd ed.). Eugen Ulmer.
- Willmer, P. G., Cunnold, H., & Ballantyne, G. (2017). Insights from measuring pollen deposition: Quantifying the pre-eminence of bees as flower visitors and effective pollinators. *Arthropod-Plant Interactions*, 11(3), 411–425. <https://doi.org/10.1007/s11829-017-9528-2>
- Wilson, R. J., Gutiérrez, D., Gutiérrez, J., & Monserrat, V. J. (2007). An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, 13(9), 1873–1887. <https://doi.org/10.1111/j.1365-2486.2007.01418.x>
- Winkler, D. E., Butz, R. J., Germino, M. J., Reinhardt, K., & Kueppers, L. M. (2018). Snowmelt timing regulates community composition, phenology, and physiological performance of alpine plants. *Frontiers in Plant Science*, 9, 1140. <https://doi.org/10.3389/fpls.2018.01140>
- Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). CRC Press/Taylor & Francis Group.
- Zografou, K., Kati, V., Grill, A., Wilson, R. J., Tzirkalli, E., Pamperis, L. N., & Halley, J. M. (2014). Signals of climate change in butterfly communities in a Mediterranean protected area. *PLoS One*, 9(1), e87245. <https://doi.org/10.1371/journal.pone.0087245>

BIOSKETCH

Fabienne Maihoff studies insect communities along environmental gradients structured by macroecological processes. She is particularly interested in the ecological and evolutionary forces that shape insects functional and phylogenetic diversity.

Author contributions: A.C. and F.M. conceived the idea and developed the concept of the study. F.M. conducted the field work in 2019 in BGL, compiled the data and conducted statistical analyses in an exchange of ideas with A.C. and J.K. J.K. and F.M. collected flowering plant data and organized field work in BGL in 2019. B.H. selected the sites in BGL and provided data and comparative material from 2009. N.F., C.S.E. and C.B. collected and prepared raw data in B.F. C.B. and J.M. created the study design of the elevational gradient in B.F. S.H., J.N., C.S.E. and F.M. determined and verified specimens. F.M. wrote the first draft of the manuscript, while all authors contributed to the final version.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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