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Research article

To the top or into the dark? Relationships between elevational and canopy cover distribution shifts in mountain forests

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Numerous studies have reported that observed species shifts in mountain areas lag behind expectations under current warming trends, however, the mechanisms remain poorly understood. One important mechanism might be microclimatic heterogeneity causing migration of species to cooler conditions under closed forest canopies, but evidence is scarce. We here compared the distributions of 710 species (11 taxonomic groups including fungi, plants, and animals) along an elevation gradient (287–1419 m a.s.l.) in a temperate low mountain range between 2006–2008 and 2016–2017 to address this open question. We characterized each species' distribution (peak and breadth) based on their abundance along two environmental gradients: elevation and canopy cover. We then analysed changes in species' distribution peaks, asking whether shifts in canopy distribution and initial distribution characteristics explain variation in elevational distribution shifts. Across all taxa, the mean shift in elevational distribution peak was + 35.3 m (i.e. upslope). Species' baseline distribution peaks were strong predictors of elevational distribution shifts with stronger upslope shifts in low-elevation and open-forest species. Even though we observed considerable variation in the responses among species, canopy distribution shifts had a significant negative effect on elevational distribution shifts overall and in six taxonomic groups. We suggest that this is related to cooler microclimatic conditions under closed compared to open forest canopies. Shifts to closed-canopy forests may thus partly compensate for elevational distribution shifts, highlighting the conservation value of heterogeneous landscapes featuring microclimatic refugia. Yet, it is likely that other mechanisms, such as habitat limitation, are also at play. Future studies need to quantify the potential of microclimatic refugia under accelerating forest dynamics, considering the interplay of canopy cover and other factors driving microclimate, and to illuminate the complex climate change response mechanisms among species and taxonomic groups.

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Keywords: canopy distribution, climate change, elevational distribution, forest, macro- versus microclimate, species distribution shifts

Introduction

Anthropogenic warming is posing novel challenges to ecosystems and species that fail to adapt may face extinction (Urban 2015, Román-Palacios and Wiens 2020). Adaptive responses to climate change can be manifold, including physiological (Jamieson et al. 2012), phenological (Vitasse et al. 2021), or behavioural adaptations (Levy et al. 2019). Alternatively, organisms may track suitable climates with range shifts following shifting isotherms (Parmesan 2006, Lenoir and Svenning 2015, Chauvier-Mendes et al. 2024).

Shifts in species' ranges in response to warming temperatures have been documented for a multitude of taxonomic groups both along latitudinal (i.e. poleward shifts; Parmesan and Yohe 2003, Hickling et al. 2006) and elevational gradients (i.e. upslope shifts; Freeman et al. 2018, Vitasse et al. 2021). However, observed shifts vary strongly in direction and magnitude (Tingley et al. 2012, Freeman et al. 2018) and often deviate from expectations under the observed warming trends. For example, it has been shown that species lag behind experienced warming (climatic debt) (Devictor et al. 2012, Ash et al. 2017, Alexander et al. 2018) or even move in the opposite direction – that is, towards tropical latitudes or lower elevations (Lenoir et al. 2010). Previously discussed explanations for inconsistencies between observed and predicted range shifts include limited dispersal capacities (Schloss et al. 2012) or limitation by drivers other than temperature, such as precipitation (Tingley et al. 2012) or human pressures (Elsen et al. 2020).

Microclimatic heterogeneity within zones of similar macroclimate offers another potential explanation for lagging range shifts (Scherrer and Körner 2011). Microclimate describes the local climatic conditions on a spatial scale that is meaningful to describe the conditions an organism experiences, compared to larger-scale macroclimatic conditions (Bramer et al. 2018, Zellweger et al. 2020, Haesen et al. 2023). For instance, vegetation cover can create strong differences in microclimate with lower temperatures and more humid conditions in closed forests compared to open habitats in summer and milder temperatures in winter, a phenomenon termed microclimatic buffering (De Frenne et al. 2019, De Frenne et al. 2021). Canopy cover affects multiple physical and meteorological components of microclimatic conditions, such as evaporation (Meeussen et al. 2021) or wind speed (De Frenne et al. 2021), and previous studies have shown that it can even surpass topographical features (e.g. slope and northness) as predictor of microclimatic temperatures during the summer months (Greiser et al. 2018, Meeussen et al. 2021, Vandewiele et al. 2023). Buffering of warm temperature extremes under forest canopies can mitigate community thermophilization (Zellweger et al. 2020) and reduces impacts of macroclimatic warming, so that species inhabiting the forest floor are less likely to exceed their physiological upper thermal tolerance limits under continued global warming (Pintanel et al. 2019, Wei et al. 2024). Tracking the isotherm by moving to closed-forest habitats may thus be an alternative climate tracking mechanism modulating shifts in species distributions like upslope range shifts (Scheffers et al. 2014, Frey et al. 2016, Reiner et al. 2021). Several studies investigating elevational range shifts have accounted for microclimatic differences related to topographical features (Meineri and Hylander 2017, Lembrechts et al. 2018, Feldmeier et al. 2020). Yet, we currently lack understanding of whether and how canopy cover affects elevational range shifts.

To assess how forest canopy cover modulates elevational range shifts, we compared species abundance distributions along an elevational gradient (287–1419 m a.s.l.) in the low mountain range Bohemian Forest, Germany, during two surveys. Our study covered > 700 species from eleven taxonomic groups including plants, fungi, and animals, since climate-induced range shifts vary strongly between taxa (Bässler et al. 2013, Vitasse et al. 2021). The study area is characterized by a mosaic of open- and closed-canopy forests up to the highest elevations. We avoided factors that may confound species' elevational responses, as the area is characterized by a high moisture availability (i.e. species are not limited by water stress) and very little human intervention, allowing for unconstrained dispersal within the landscape (Bässler et al. 2013, Müller et al. 2020). First, we assessed changes in abundance distributions along the elevational and canopy gradient based on abundance-weighted means and standard deviations (distribution peak and breadth, respectively) and explored raw shifts in distribution peaks. If species are migrating in response to warming, we expect them to move their distribution peak upslope (macroclimatic temperature tracking) or towards denser forests (indicative for microclimatic temperature tracking). Second, to test our main question whether the observed macroclimatic response (i.e. shift in elevational distribution peak) of species can be explained by distribution shifts towards denser or less dense forests, we tested the relationship between shifts in species' elevational and canopy distribution peaks, while accounting for baseline elevational and canopy distribution peaks and breadths. If moving towards denser forests is an alternative climate-tracking mechanism that can alter species' responses at the elevational dimension, we expect a negative relationship between elevational and canopy distribution shifts.

Material and methods

Study area

The study was conducted in the Bohemian Forest in south-eastern Germany, a temperate low mountain range with moderately steep, mainly south-west facing slopes. The area is geologically homogeneous and long phases of erosion and weathering have rounded the elevated land forms, resulting in a low topographic complexity (Bässler et al. 2008). Annual precipitation ranges from 690 mm at low to 1890 mm at high elevations; mean annual temperature ranges from up to 10.0°C at low elevations to 3.0°C at high elevations (means from 1980 to 2015; Klöcking 2018). The region features remnants of old-growth forests and heterogeneous forest habitats due to a history of variable disturbances. Forest management within the national park was ceased upon foundation (1970) in the core zone and is limited to a minimum in the management zone.

We arranged 95 study plots between 650 and 1419 m a.s.l. along four transects within the Bavarian Forest National Park. To expand the gradient towards lower elevations, 38 study plots with similar forest structures were set up at elevations between 287 and 650 m a.s.l. outside the national park (Bässler et al. 2015), resulting in a total of 133 study plots (Supporting information).

Biodiversity data

Biodiversity data included wood-inhabiting fungi, lichens, mosses, vascular plants, land molluscs (hereafter, 'snails'), arthropods, and birds. Within the arthropod groups, we grouped true bugs/cicadas and bees/wasps/hoverflies. Data were collected with standard taxon-specific methods in two surveys (Bässler et al. 2008, Bässler et al. 2015) during the growing season over several years (first survey: 2006–2008, second survey 2016–2017). For details, see Supporting information as well as Bässler et al. (2008, 2015).

For data comparability between both surveys, we used only data from matching sampling months and from the set of plots that were surveyed in both periods (Friess et al. 2018). We kept only observations identified to species level, and species that were recorded on at least three study plots during both surveys, to ensure we had sufficient data from both periods to derive species-specific responses over time (compare Mangels et al. 2017; 1085 out of a total of 2716 species).

Environmental data

The elevation of each study plot was extracted from a digital terrain model from 2017 (resolution = 50 m; Bavarian Agency for Digitisation, High-Speed Internet and Surveying) (Bässler et al. 2008).

Macroclimatic temperatures at each plot were predicted by Klöcking (2018), who used 35 years of data from 211 locations throughout the larger region around our study area to interpolate meteorological conditions at our study plots based on topographical features. We averaged predicted daily temperatures to mean annual temperatures per plot for the years 1980–2017. The mean annual temperature across plots was 6.5°C during the first survey (reference year: 2006) and 6.8°C during the second survey (reference year: 2016). To extract long- and short-term trends in mean annual temperatures, we fitted linear mixed effects models using the *lme()* function from the 'nlme' package (ver. 3.1-163; Pinheiro and Bates 2000, Pinheiro et al. 2023). In the first model, we included year as predictor and plot as a random effect to account for repeated sampling across plots. We additionally included a correlation term using the 'nlme' *corAR1()* function to account for temporal autocorrelation. The second model included elevation as predictor and year as a random effect to account for repeated sampling across years.

Each plot's canopy cover was estimated in the field as the area shaded by horizontal projection (in %) on a circular base area of 0.02 ha (radius = 8 m) for three tree height classes (≤ 5 m: lower layer, > 5–15 m: mid-layer, > 15 m: upper layer) (Bässler et al. 2008, Hilmers et al. 2018a). Our canopy cover metric included the mid- and upper tree layer, based on the assumption that the lower tree layer contributes only marginally to temperature buffering (Jucker et al. 2018). We combined the two layers into one metric ($cover_{tot}$) using the probabilistic view of Fischer (2015) that accounts for the overlap of different layers i and can take values between 0 and 1. We then multiplied by 100 to express canopy cover as a percentage rather than a portion:

$$\mathrm{cover}_{\mathrm{tot}} = \left(1 - \prod_{i} 1 - \mathrm{cover}_{i}\right) \times 100$$

Canopy cover and elevation were negatively correlated (r = −0.37 in survey 1 and −0.41 in survey 2) due to lower canopy cover in high-elevation spruce forests (Supporting information). However, we observed this correlation at elevations above 1100 m a.s.l. only (r = −0.06 in survey 1 and −0.03 in survey 2 after removing plots with elevations ≥ 1100 m a.s.l.) and accounted for it in the data analysis (section: Statistical analyses). The mean canopy cover across plots declined by 5.6 ± 29 percentage points between the two surveys due to natural disturbances that reduced the canopy cover on almost half (48%) of the plots, whereas canopy cover increased over time on 44% of the plots (Supporting information).

We here use canopy cover as a proxy for microclimate (Supporting information) since in situ microclimate data from our study plots were not available for the considered time period. We are aware that canopy cover is a strongly simplified proxy for microclimate that does not account for other factors contributing to microclimatic conditions, such as canopy height (Jucker et al. 2018, Kašpar et al. 2021) or local water balance (Davis et al. 2019, Greiser et al. 2024). Further, previous studies have reported non-linear effects of canopy on microclimatic conditions, which saturate with increasing canopy cover (Zellweger et al. 2019) or height (Jucker et al. 2018). Therefore, we complemented the microclimatic context of our study plots by modelling microclimatic mean temperature offsets at each study plot and during both surveys based on the mechanistic 'microclimc' microclimate model by Maclean and Klinges (2021) (Supporting information). However, this modelling approach was subject to several assumptions and we lacked ground truthing data to evaluate the modelled microclimatic temperatures. We thus used the microclimate model as an add-on analysis, while keeping canopy cover as surrogate in our main analyses.

Characterization of species' abundance distributions and distribution shifts

We characterized species distributions (which we assumed to follow a Gaussian distribution) based on their abundance along two axes – namely the elevational and canopy cover gradient. We determined a species' distribution peak and breadth along the elevational or canopy cover gradient as the abundance-weighted mean (AWM) and abundance-weighted standard deviation (AWSD), respectively, in each survey (Kühsel and Blüthgen 2015, Chisté et al. 2016). We considered this more robust and conservative than potential alternatives, such as using the median or unweighted mean as distribution peak or the difference between minimum and maximum values as distribution breadth (Maggini et al. 2011, Kühsel and Blüthgen 2015). We obtained the effective shift in a species' distribution as the difference between its AWMs in the second survey and the first survey – in other words, we here define 'distribution shift' as the shift in a species' distribution peak (= abundance-weighted mean) along an environmental gradient.

We used null-models to predict the expected distribution shift (i.e. the expected shift if a species has no habitat preference in either of the two surveys and is thus randomly distributed across study plots) (Chisté et al. 2018). We took the original abundance values of a given species during a given survey and distributed them randomly across the surveyed plots. Then, we calculated the resulting AWM. The set of surveyed plots depended on the collection method of the considered species – for example, if a species was sampled via Malaise traps, we only chose from those plots where a Malaise trap was installed. We repeated this 10 000 times for each survey and then took the difference between each pair of values (survey 2–survey 1). The mean of the resulting 10 000 values represents the expected distribution shift arising from changes in the sampled gradient (e.g. through changes in canopy cover over time), even if the species remained at the same study plots. By comparing the observed AWM with each of the 10 000 null model values, we obtained a p-value ($\alpha = 0.05$) as the proportion of the observed values that were larger than the null model values. This p-value indicates whether a species significantly (i.e. spatially) shifted its distribution peak while accounting for stochasticity and changes over time in environmental conditions. See Supporting information for the model steps and relevant equations.

We applied the same approach to modelled microclimatic temperatures to characterize species' abundance distributions along the microclimatic gradient (Supporting information). We conducted the distribution characterization in R 4.3.2 (www.r-project.org) using a custom function (scripts are provided in the data repository available with this manuscript) drawing on the 'tidyverse' package (ver. 2.0.0; Wickham et al. 2019). Data preparation mainly used the 'tidyverse' and 'vegan' (ver. 2.6.2; Oksanen et al. 2022) packages.

Statistical analyses

The study's extent was limited both at the lower and the upper end of the elevation gradient and we could not cover species' full distributions beyond the study sites. To avoid potential biases in our results due to species near regional range limits, we excluded species with baseline elevational distribution peaks (i.e. their elevational distribution peaks during the first survey) closer than one elevational distribution breadth (species-specific) to the lowest or highest available elevation, as these species may have truncated distributions at the low or high extremes of the elevation gradient (compare Freeman et al. 2018, Rumpf et al. 2019). Moreover, we found strong declines in canopy cover values at elevations above 1100 m a.s.l. (Supporting information). To avoid confounding effects and to ensure each species could theoretically find the full range of possible canopy cover values (from 0 to 100%) throughout the whole elevational gradient considered, we also excluded species with a baseline elevational distribution peak above 1100 m a.s.l. Filtering helped us to address three statistical caveats in our data: 1) It ensured that observed effects of canopy distribution shifts on elevational distribution shifts were independent of the correlation between elevation and canopy cover. 2) It reduced the impact of extreme values for baseline elevational distribution peaks, thus counteracting regression to the mean (Barnett et al. 2005). 3) Excluding species close to the upper end of the elevational gradient took into account that these species have less available space to migrate upslope in pyramid-shaped mountain ranges like our study area (Elsen and Tingley 2015). The final set of species contained 710 species, with baseline elevational distribution peaks between 295.6 and 943.6 m a.s.l. An analysis of a set of 983 species including those with baseline elevational distribution peaks > 1100 m a.s.l. yielded very similar results, which can be reproduced with the scripts provided in the data repository (note that the latter set of species included the taxonomic group of ferns, which we excluded from our main analysis due to an insufficient sample size of $n = 5$ after filtering).

We explored species' responses by comparing the percentages of significant changes in elevational and canopy distribution peaks. Then, to test whether elevational distribution shifts were modulated by canopy distribution shifts, we used linear regression with the elevational distribution shift as response variable and the canopy distribution shift as predictor. To account for potential differences in responses depending on species' baseline distribution characteristics, we included species' baseline elevational and canopy distribution peaks and breadths (Pounds et al. 2006). As our predictor variable was normally distributed, our model used a Gaussian distribution family.

We z-transformed ($\text{mean} = 0$, $\text{SD} = 1$) all predictors to allow for direct comparisons of their effects. We fitted one overall model and eleven separate models for each taxonomic group to account for diverging sample sizes. We included taxonomic group as a random intercept in the overall model to account for uneven sample sizes. We fitted all models in R 4.3.2 (www.r-project.org) using the *lm()* function for single taxonomic groups and the *lmer()* function for the mixed-effects model ('lme4' package, ver. 1.1.25; Bates et al. 2015 with 'lmerTest' ver. 3.1.3; Kuznetsova et al. 2017). We extracted the adjusted R^2 values from the model summaries for the linear models and the conditional and marginal R^2 using the *r.squaredGLMM()* function from the 'MuMIn' package (ver. 1.47.5; Barton 2023) for the mixed model. We obtained square sums for each predictor using the *anova()* function and determined the percentage of explained variance as the proportion of the predictor's square sums divided by the sum of the model's explained plus residual square sums.

We compared estimated versus observed density curves and examined patterns in model residuals for each predictor. We checked for collinearity among predictors via pairwise Pearson correlations and the variance inflation factor (VIF) (Chatterjee and Simonoff 2013, Dormann et al. 2013, James et al. 2013) using the *vif()* function ('car' package, ver. 3.0-10; Fox and Weisberg 2019). Most predictors showed weak pairwise correlations (maximum pairwise correlation for the overall model: r = 0.57 between baseline elevational distribution peak and breadth; Supporting information). However, we observed moderate collinearity ($2.0 < \text{VIF} < 4.0$) in lichens, snails, true bugs/cicadas, and bees/wasps/hoverflies; and high collinearity ($4.0 < \text{VIF} < 8.0$) in springtails and birds. To assess potential related issues with statistical inference, we visually checked raw versus predicted effects of all tested predictors. We found a high agreement and are thus confident that we can safely interpret our models. Additionally, the QQ and residual plots we generated using the 'DHARMa' package (ver. 0.4.6; Hartig 2022) indicated no severe violations of model assumptions.

Results

Changes in macroclimatic temperatures in space and time

Across all plots, mean annual macroclimatic temperatures increased by +0.047°C per year between 2006 and 2017, exceeding the long-term average (1980–2017) of +0.042°C per year (Fig. 1A). The mean long-term adiabatic lapse rate was −4.49°C per 1000 m elevational gain (Fig. 1B). Under a constant adiabatic lapse rate, the macroclimatic warming trend of +0.042°C/year (+0.047°C/year) translates into an upslope shift of 102.9 m (115.1 m) between 2006 and 2017 to track the macroclimatic isotherm.

Exploration of species responses

We found elevational distribution shifts in both directions, i.e. upslope and downslope. While the proportions of significant shifts varied between taxonomic groups, we observed considerable within-group variation, both in the direction and magnitude of responses along both gradients (Fig. 2). The mean elevational distribution shift was positive (overall mean: +35.3 m) indicating upslope shifts; however, with a standard deviation of 143.6 m (Supporting information). Out of 710 analysed species, the effective elevational distribution shift was positive for 412 species (58.0%) and negative for 298 species (42.0%). We found that 45 species (6.3% of the total) showed significant upslope shifts and 22 species (3.1% of the total) showed significant downslope shifts in their elevational distribution peaks. Thus, although only few elevational distribution shifts were significant, our results indicate a prevalence of upslope distribution shifts.

The overall mean canopy distribution shift was −7.9% (SD = 15.8%), and thus slightly more negative than the overall decline of canopy cover between the two surveys (−5.6 ± 29 percentage points). The effective canopy distribution

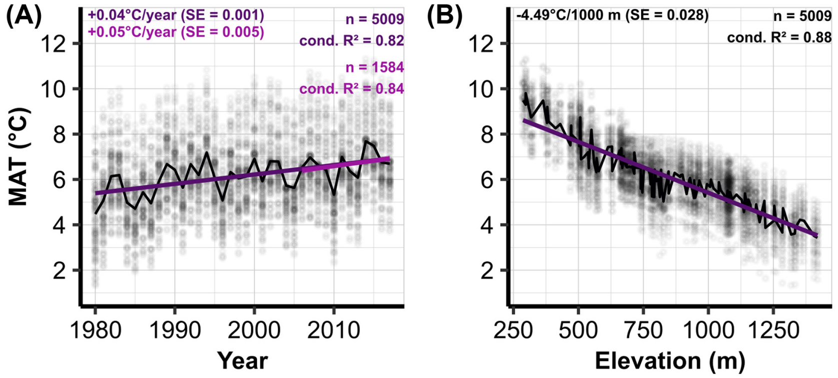
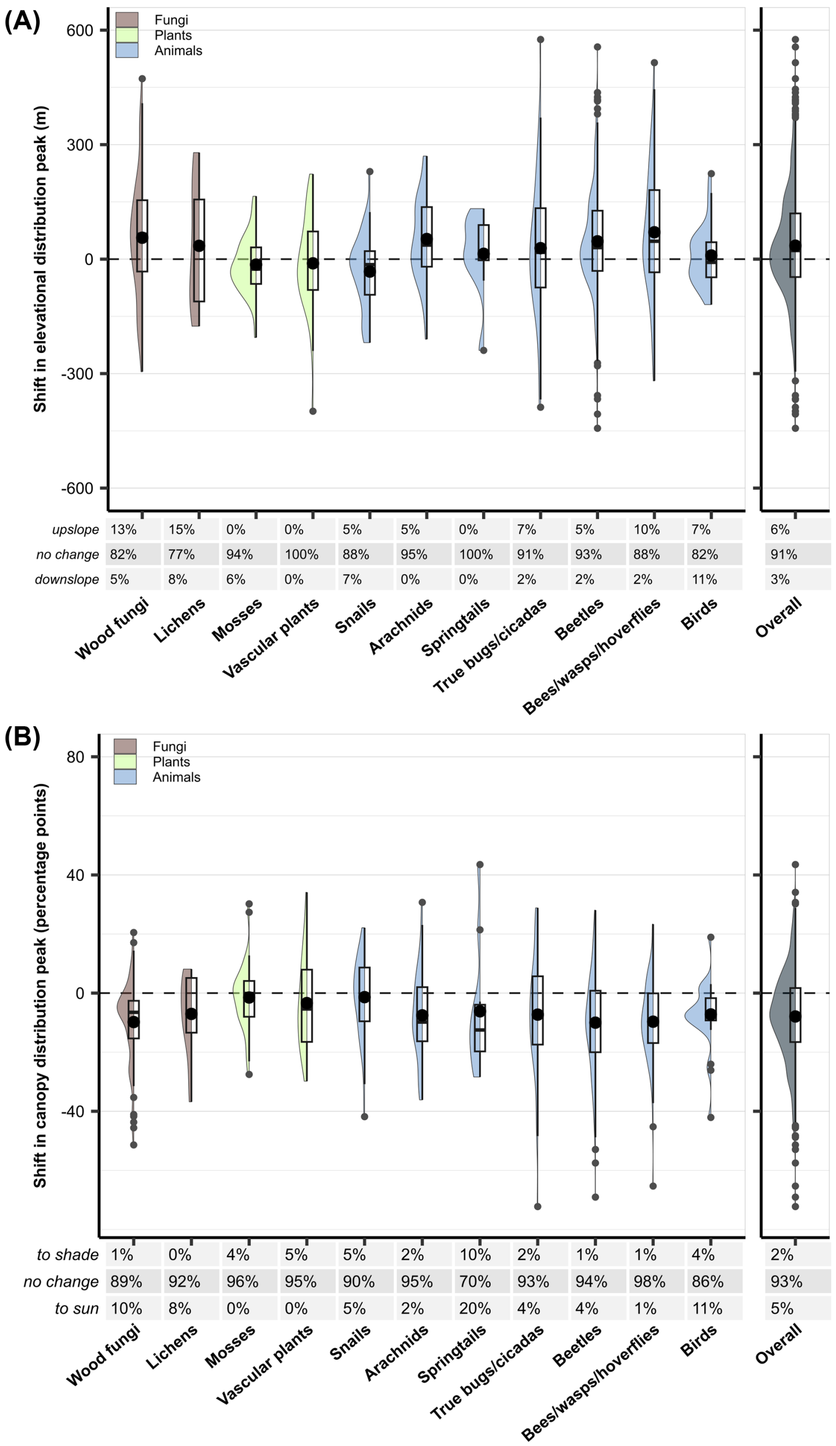


Figure 1. (A) Observed trend in mean annual temperature over time from 1980 to 2017. Points depict the values for each study plot extracted from the macroclimate model by Klöcking (2018) (see *Environmental data* for details) and the black line depicts mean annual temperatures across plots. The darker and lighter purple lines depict the long-term (starting in 1980) and short short-term (starting in 2006) linear trends, respectively. (B) Observed adiabatic lapse rate across the years 1980-2017. Points depict the values for each study plot extracted from the macroclimate model and the black line depicts mean annual temperatures across years. The purple line depicts the long-term adiabatic lapse rate in our study area predicted by a linear mixed-effects model (see *Environmental data* for details).



	Wood fungi	Lichens	Mosses	Vascular plants	Snails	Arachnids	Springtails	True bugs/cicadas	Beetles	Bees/wasps/hoverflies	Birds	Overall
upslope	13%	15%	0%	0%	5%	5%	0%	7%	5%	10%	7%	6%
no change	82%	77%	94%	100%	88%	95%	100%	91%	93%	88%	82%	91%
downslope	5%	8%	6%	0%	7%	0%	0%	2%	2%	2%	11%	3%

	Wood fungi	Lichens	Mosses	Vascular plants	Snails	Arachnids	Springtails	True bugs/cicadas	Beetles	Bees/wasps/hoverflies	Birds	Overall
to shade	1%	0%	4%	5%	5%	2%	10%	2%	1%	1%	4%	2%
no change	89%	92%	96%	95%	90%	95%	70%	93%	94%	98%	86%	93%
to sun	10%	8%	0%	0%	5%	2%	20%	4%	4%	1%	11%	5%

Figure 2. Observed shifts in (A) elevational and (B) canopy distribution peaks per taxonomic group (left panels) and overall (right panels). Numbers in the tables indicate the percentage of species within each response category (considering only significant changes) out of all analysed species in the respective group. Fill colour represents the kingdom to which each group belongs. Points within the boxplots depict the mean value within each group.

shift was positive for 213 species (30.0%) and negative for 497 species (70.0%). Analysis revealed that 32 species (4.5%) significantly shifted their canopy distribution to less dense forests and 16 species (2.3%) significantly shifted their canopy distribution to denser forests. The prevalence of negative shifts in canopy distribution peaks indicates that a majority of species shifted towards more open forests – but, again, with few significant shifts.

The mechanistic microclimate model yielded a mean increase of +0.60°C (SD = 0.73°C) in species' distribution peaks along the microclimatic temperature gradient, indicating species experienced warmer microclimatic temperatures during the second compared to the first survey (Supporting information).

Relationship between elevational and canopy distribution shifts

Our models revealed a consistent negative relationship between elevational and canopy distribution shifts overall (Fig. 3), and for six taxonomic groups (Fig. 4, Supporting information). Canopy distribution shifts accounted for 5.8% (wood fungi) to 25.7% (birds) of explained variance in elevational distribution shifts, and were the predictor explaining the largest portion of explained variance in the overall model in vascular plants, true bugs/cicadas, beetles, and birds (Table 1, Supporting information). This indicates that species shifting their distributions to denser forest canopies were shifting upslope less strongly compared to species that did not shift towards denser forests.

Based on modelled microclimatic conditions, we found a negative correlation between elevational distribution shifts and shifts in distribution peaks along the microclimatic buffering gradient, suggesting downslope-shifting species shifted to habitats with a stronger microclimatic buffer and vice versa (Supporting information). Distribution shifts towards habitats with stronger microclimatic buffering prevailed in general and were particularly common in species that remained at a similar elevation during both surveys (inset in Fig. 3, Supporting information).

Effects of baseline elevational and canopy distribution characteristics on elevational distribution shifts

Baseline elevational distribution peak had a consistent negative effect on elevational distribution shifts in the overall model, as well as in four taxonomic groups (excluding groups where the effect was marginally significant), explaining between 1.9% (beetles) and 12.7% (mosses) of observed variance (Supporting information). Similarly, baseline canopy distribution peak had a significant negative effect on elevational distribution shifts in the overall model and in three taxonomic groups, explaining between 5.1% (overall) and 19.0% (bees/wasps/hoverflies) of observed variance. This indicates that species initially inhabiting low elevations or less dense forests experienced stronger upslope shifts than species initially inhabiting higher elevations or denser forests. In contrast, baseline elevational and canopy distribution breadth only had minor effects on elevational distribution shifts, except for snails and mosses.

Discussion

We here used resurvey data along gradients of elevation and forest canopy cover to examine shifts in species' distributions along the elevational and canopy cover gradient during circa one decade to test whether distribution shifts to denser forests can compensate for lags in elevational distribution shifts. While species-specific responses were highly variable, we found a negative relationship between elevational and canopy distribution shifts across taxa. Our add-on analyses

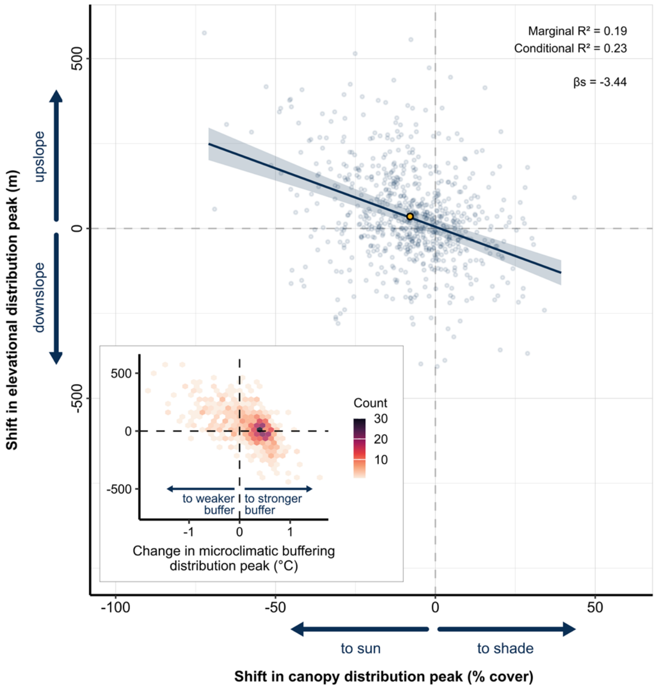


Figure 3. Overall trend of the shift in elevational distribution peak versus shift in canopy distribution peak. Blue points depict the observed values and the orange point depicts the group mean. The vertical dashed line divides shifts in canopy distribution peak towards forests with lower (left of the line) or higher canopy cover (right of the line). The horizontal dashed line divides downslope (below the line) and upslope (above the line) shifts in elevational distribution peak. The regression line depicts the marginal effect of shift in canopy distribution peak, the ribbon depicts the corresponding 95% confidence interval (see *Statistical analyses*). Marginal and conditional R^2 values refer to the overall multivariate model. βs gives the standardized slope (= the effect per one unit change in canopy cover), which we determined by dividing the model estimate (= the effect per 1 SD change in canopy cover) by the predictor's standard deviation. The inset depicts the raw 2D-density distribution of species-specific changes in the elevational versus microclimatic buffering distribution peak (based on modelled microclimatic temperatures, see *Supporting information*). Macroclimatic buffering was defined as -1 (Tmicro-Tmacro), i.e., the reversed microclimatic offset. Thus, for changes in microclimatic buffering distribution peak, positive values indicate shifts to more strongly buffered habitats, while negative values indicate shifts to less strongly buffered habitats. The vertical dashed line thus divides shifts to habitats with a weaker (left of the line) or stronger (right of the line) microclimatic buffering capacity. The horizontal dashed line divides downslope (below the line) and upslope (above the line) shifts in elevational distribution peak. Fill color depicts how often observed values lay within each hexagon. Note that the inset merely serves as supporting information and does not show any tested results.

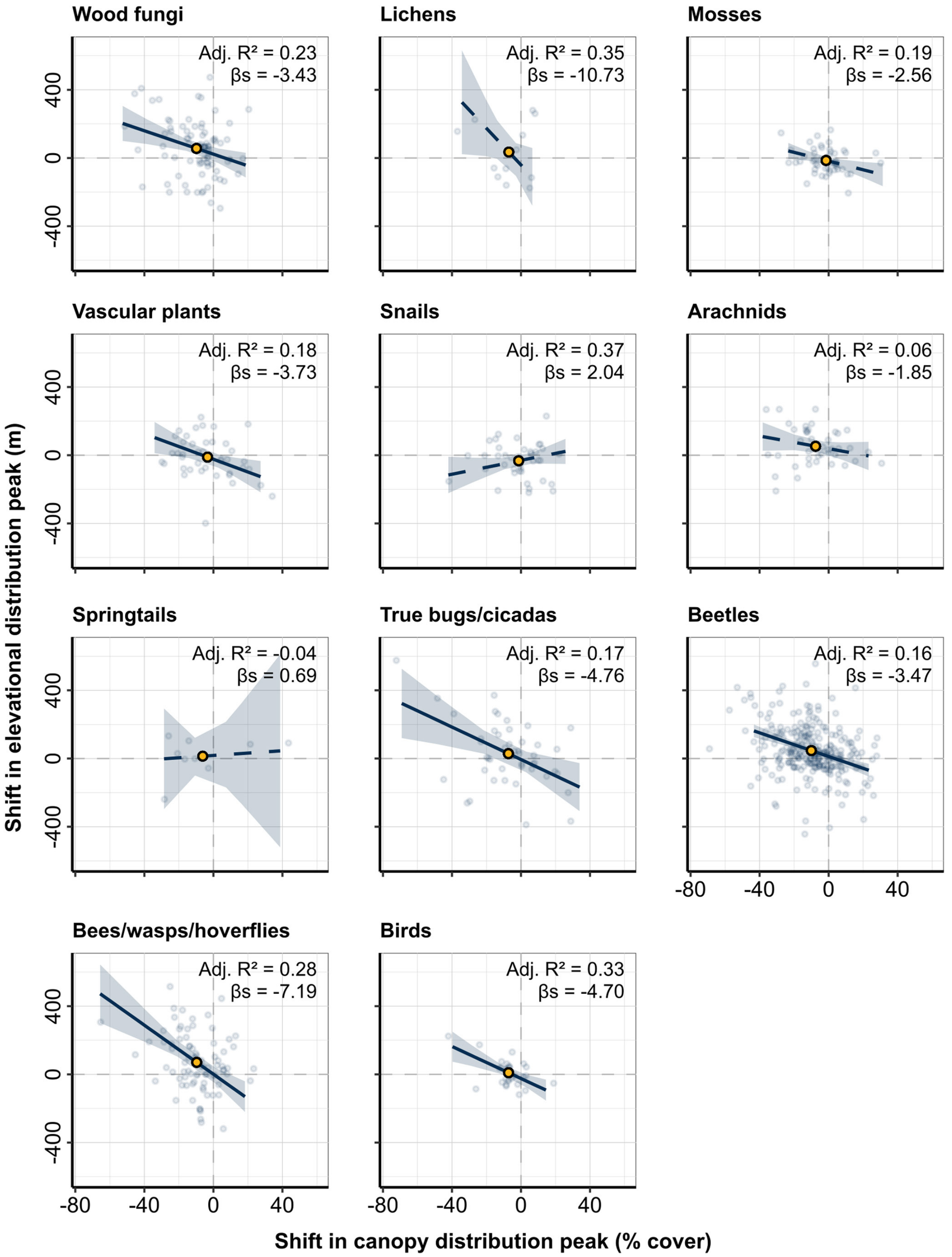


Figure 4. Taxon-specific trends of the shift in elevational distribution peak versus shift in canopy distribution peak. Blue points depict the observed values, orange points depict the group mean. The vertical dashed line divides shifts in canopy distribution peak towards forests with lower (left of the line) or higher canopy cover (right of the line). The horizontal dashed line divides downslope (below the line) and upslope (above the line) shifts in elevational distribution peak. The regression lines indicate the marginal effect of shift in canopy distribution peak and are solid for significant ($\alpha = 0.05$) and dashed for non-significant effects (see *Statistical analyses*). Ribbons indicate the corresponding 95% confidence intervals. Adjusted R^2 values refer to the taxon-specific multivariate models. To allow for comparisons of effect sizes among taxa, βs gives the standardized slope (= the effect per one unit change in canopy cover), which we determined by dividing the estimate yielded in each model (= the effect per 1 SD change in canopy cover) by the predictor's standard deviation in each model.

Table 1. Direction of predictor effects on the shift in elevational distribution peak. Significant p-values for the models per se are printed in bold. Positive effects are indicated with upward-pointing arrows, negative effects with downward-pointing arrows. Significance levels of each predictor (based on ANOVA) are indicated with asterisks (< 0.001: ***; 0.01–0.001: **; 0.01–0.05: *); marginal significance (0.05–0.1) is indicated with a dot. For (marginally) significant effects, the percentage of explained variance is indicated (i.e. the proportion of explained sum of squares of each predictor divided by the total explained sum of squares). We drew our significance level at $\alpha = 0.05$, thus, while marginally significant effects were indicated here, we did not consider them significant in a stricter sense. Likewise, since the model p-value for lichens, arachnids, and springtails was > 0.05, we did not consider any effects significant, despite predictor p-values < 0.05. Non-significant effects are indicated in grey. The provided R^2 values refer to the conditional (overall model) and adjusted (taxa-specific models) R^2 values.

Taxonomic group	R^2	Model p-value	Shift in canopy distribution peak	Baseline elevational distribution peak	Baseline elevational distribution breadth	Baseline canopy distribution peak	Baseline canopy distribution breadth
Overall	**0.23**	**< 0.001**	↓*** 11.78%	↓*** 2.92%	↑	↓*** 5.12%	↑
Wood fungi	**0.23**	**< 0.001**	↓* 5.81%	↓*** 11.58%	↓	↓** 7.61%	↑
Lichens	0.35	0.154	↓	↓	↓	↑	↑
Mosses	**0.19**	**0.012**	↓. 4.99%	↓** 12.71%	↓	↓	↑* 7.03%
Vascular plants	**0.18**	**0.031**	↓* 8.67%	↓. 6.07%	↑. 6.26%	↓. 6.99%	↓
Snails	**0.37**	**0.001**	↑	↑	↓*** 23.60%	↑	↑** 18.20%
Arachnids	0.06	0.217	↓	↓	↑	↓	↑
Springtails	-0.04	0.540	↑	↓	↑	↓	↓
True bugs/cicadas	**0.17**	**0.026**	↓** 18.28%	↓	↑	↓	↓
Beetles	**0.16**	**< 0.001**	↓*** 8.48%	↓* 1.90%	↓	↓*** 6.95%	↓
Bees/wasps/hoverflies	**0.28**	**< 0.001**	↓** 7.00%	↓* 5.57%	↑	↓*** 19.01%	↓
Birds	**0.33**	**0.015**	↓** 25.65%	↓. 10.12%	↓	↓. 7.93%	↓

based on modelled microclimatic conditions generally support the hypothesis that this may be related to microclimatic conditions. Therefore, we suggest that shifts to denser forests can modulate elevational distribution shifts and might thus offer an alternative temperature tracking mechanism. However, species' responses were highly variable and weaker than expected based on the macroclimatic temperature increase. Finally, we found that elevational distribution shifts were strongly correlated with initial distribution peaks, with elevational distribution shifts decreasing in magnitude with increasing initial elevational and canopy distribution peak.

The role of canopy cover explaining a lagging elevational response

Overall, we observed a mean upslope shift of elevational distribution peaks, confirming a tendency for upslope elevational distribution shifts that is expected for species experiencing warming (Freeman et al. 2018, Vitasse et al. 2021). However, only a few of the elevational distribution shifts were significant and the overall mean shift was weaker than expected, lagging behind the estimated elevational shift required to track the macroclimatic temperature in the region (section: Changes in macroclimatic temperatures in space and time). This is in line with previous studies reporting lagging upslope shifts and related macroclimatic debts (Ash et al. 2017, Alexander et al. 2018).

We found support that distribution shifts along the canopy axis could at least partly compensate for the observed macroclimatic debt. The negative relationship between elevational and canopy distribution shifts overall, and for most taxonomic groups, suggests that species moving to closed-canopy forests move upslope less strongly than species that remain in (or move to) more open forests. Furthermore, our add-on analysis based on modelled microclimatic temperatures at the plots indicates that a majority of species shifted their distributions towards habitats with a stronger microclimatic buffering capacity, and patterns for distribution shifts along the microclimatic gradient were largely in line with our findings for canopy distribution shifts (Supporting information). Thus, the observed patterns support our hypothesis that shifts to closed-canopy forests are related with an increased microclimatic buffering capacity. Our results conform with previous views that closed-canopy forests can serve as microclimatic refugia for species lagging behind elevational isotherm shifts (Scheffers et al. 2014, Frey et al. 2016) and highlight the importance of microclimatically heterogenous landscapes to safeguard biodiversity under a changing macroclimate (Kemppinen et al. 2024).

However, both canopy cover as a rough microclimate proxy as well as the microclimate modelling come with some uncertainties, which we discuss in detail in the next section.

Limitations and alternative mechanisms affecting species responses

1. Habitat requirements beyond microclimate. Changes in forest canopy cover are accompanied with changes in

resource availability and structural habitat conditions that may limit the ability of some organisms to shift to more closed canopy forests, causing them to persist. Many primary producers, for instance, are restricted to open-canopy forests since they require high light availability, many herbivorous insects depend on plant species occurring only in open forests, and birds breeding in the understory need specific breeding structures (Zellweger et al. 2017, Hilmers et al. 2018a, Jähnig et al. 2018, Hanberry et al. 2020). At the same time, species that persist in less suitable habitats in relation to temperature might be characterized by a high climatic plasticity (Campana et al. 2022) or respond with a time lag (Alexander et al. 2018). Further, while we mainly considered canopy cover as a proxy for microclimatic temperature in our study, it represents more and different dimensions of microclimate (e.g. moisture availability) as potential important habitat factors (Davis et al. 2019, De Lombaerde et al. 2022).

2. Availability of closed canopy habitats in the landscape. We observed a slightly negative overall mean shift in canopy distribution peak (−7.9%). This is surprising as one might assume that, on average, species should move to denser forests in response to warming macroclimatic conditions (Scheffers et al. 2014, Frey et al. 2016). The observed response might be explained by the mean decline in canopy cover at our plots (−5.6% points) during the study due to forest disturbances. As a result, for example, immobile species that remained at the same plots throughout the whole study period (i.e. species characterized by plasticity) would have experienced a negative canopy distribution shift. However, even among significant canopy distribution shifts (i.e. true spatial shifts), shifts to less dense forests were more numerous. This may be due to a reduced availability of dense forests after an overall decline of the forest canopy in the study area. It is thus possible that a limitation of available habitat space prevents a complete climatic tracking by shifting the canopy distribution peak. At the same time, we observed a mean shift towards habitats with a stronger microclimatic buffer, which seems contradictory to the canopy finding. We can only speculate about the reasons. One explanation might be that canopy decrease in our study area is mainly related to selective die-off of spruce trees due to bark beetle infestation (Hilmers et al. 2018b). These stands are often characterized by a predominance of beech, admixed with spruce. Therefore, the selective removal of spruce might shift the tree species composition towards beech with some canopy loss in the upper tree layer. However, if beech forests cause stronger microclimate cooling than spruce forests as suggested by Vandewiele et al. (2023), enhanced microclimatic cooling due to changes in tree species composition might overcompensate for the effects of canopy loss. In addition, at a relatively high level of canopy cover, canopy loss may not lead to pronounced decreases in microclimatic buffering capacity due to a potential non-linear and saturating relationship of increasing canopy cover with microclimatic buffering (Zellweger et al. 2019).
3. Coarse-scale estimation of microclimatic temperature. We could not account for fine-scale or temporal microclimatic variability – that is, within plots or along the vertical position within the canopy (Montejo-Kovacevich et al. 2020, De Frenne et al. 2021, Maclean and Klinges 2021). For example, small-bodied animals may find a variety of microhabitats with suitable microclimatic regimes within a few metres or even centimetres at our study plots (Potter et al. 2013, Pincebourde and Woods 2020), which our fixed spatial scale of 0.02 ha for canopy cover cannot represent. Thus, species may find a thermally suitable habitat in colder spots within a structurally complex three-dimensional environment, which could result in a high plasticity towards changes in macroclimatic conditions. This might also be an explanation for the low number of significant spatial distribution shifts in our data.
4. Additional uncertainties of microclimate estimation. Our spatial resolution and a lack of landscape-scale data prevented us from accounting for potential edge effects that may modify the microclimatic buffering capacity of forests (Didham and Lawton 1999, Schmidt et al. 2017). Moreover, other vegetation parameters besides canopy cover, such as canopy height (Jucker et al. 2018, Kašpar et al. 2021) and the tree species composition (Meeussen et al. 2021, Vandewiele et al. 2023) have been shown to affect microclimatic conditions. Further, topographical factors (i.e. slope or aspect) can be important predictors for the variation in microclimate conditions (Bramer et al. 2018, Jucker et al. 2018). Finally, although microclimatic summer temperatures are typically lower under closed canopies compared to open habitats (Greiser et al. 2018, De Frenne et al. 2019, Zellweger et al. 2019), under certain circumstances and during the night or winter months, temperatures can also be higher under closed canopies (Zellweger et al. 2019, De Frenne et al. 2021, Vandewiele et al. 2023).

Taken together, our results suggest that microclimatic buffering may be one driver of canopy distribution shifts towards closed forests, yet further factors are likely at play. Our data do not allow for disentangling these different mechanisms that determine whether organisms shift to more closed canopies or not. Future research should thus focus on quantifying the effects of other factors and drivers of microclimate, and on disentangling underlying mechanisms when quantifying or interpreting elevational distribution shifts of species.

Variation in species-specific responses

The large variation in species-specific responses superimposed differences between taxonomic groups. We found distribution shifts of different magnitudes and in both directions, both along the elevational and canopy cover gradient. At the same time, the model fits (R^2, Table 1, Fig. 4) and slopes (β_s, Fig. 4) of the elevational–canopy distribution shift relationships indicated no strong differences between taxonomic groups representing different lifestyles (i.e. ecto- versus endotherm or sessile versus mobile taxa). Still, the reasons for the observed lag of response in our study might differ between species with different life-history traits. For example, long-lived and sessile organisms may respond to climatic changes with a time lag, temporarily remaining at sites that are no longer suitable (Jackson and Sax 2010, Dullinger et al. 2012). For mobile and short-lived species, the comparably cold temperatures in 2016 (the larger part of our second biodiversity survey) may partly explain our observations. While species distributions likely change over longer time spans, species abundances can be highly responsive to inter-annual climatic variation (Maihoff et al. 2023, Müller et al. 2023). Since species abundances formed the basis of our distribution characterization, this may have partly reversed distribution shift trends during this year.

Species responses depend on species' baseline niche optimum

Species' elevational distribution shifts decreased with increasing baseline elevational distribution peak. Negative effects of species' initial elevational preference have been found previously (Rumpf et al. 2019, Mamantov et al. 2021, Zu et al. 2023) and potential explanations include less available area for upslope shifts with increasing elevation (Körner 2004, Elsen and Tingley 2015) or higher temperature plasticity of species living at higher elevations (Mamantov et al. 2021, Zu et al. 2023).

The negative effect of baseline canopy distribution peak on elevational distribution shifts in our models indicates that species with a preference for open habitats were more likely to respond to macroclimatic changes with elevational shifts rather than shifts to denser forests. As discussed above, habitat requirements related to resource availability and structures may be limiting for some organisms. Indeed, we found strong effects of baseline canopy distribution peak for wood fungi, which strongly depend on suitable dead wood substrates resulting from canopy disturbance (Bässler et al. 2010, Parajuli and Markwith 2023), and for bees, wasps, and hoverflies, which strongly depend on a vital herb layer (Hanula et al. 2016).

Implications for conservation

From a conservation perspective, our findings indicate that canopy distribution shifts may not fully offset macroclimatic warming in the long run. A tendency towards positive shifts of species' distribution peaks along the modelled microclimatic temperature gradient suggested that species tended to experience warmer microclimatic temperatures during the second compared to the first survey (Supporting information). Shifting to denser forest habitats may also not be a suitable mechanism for species requiring resources or habitat structures that are only available in open habitats. On the other hand, due to potential non-linear effects of canopy cover on microclimatic buffering (Zellweger et al. 2019), forest species that initially preferred closed-canopy habitats may only experience a minor microclimatic difference when shifting to even denser forests, so that this mechanism may not help them to track their climatic niche under continued global warming.

Moreover, it remains unclear how continued macroclimatic warming will change microclimatic buffering in forests in the future (De Frenne et al. 2021). Forest dynamics are expected to accelerate under global warming (Thom et al. 2022), with more frequent disturbances opening forest canopies (Cudmore et al. 2010, Seidl et al. 2017). These dynamics are likely to jeopardize the capacity of forests to buffer ambient temperatures (Lenoir et al. 2017, Thom et al. 2020), decreasing the degree to which microclimatic refugia can compensate for elevational distribution shifts (Serra-Diaz et al. 2015, Guo et al. 2018). As temperatures continue to increase, accumulating macroclimatic debts may result in extinction events – even long after the climatic requirements of a species are no longer met (Dullinger et al. 2012, Urban 2015) – as it is unlikely that persisting species are able to evolutionarily adapt to novel conditions at a sufficient rate (Quintero and Wiens 2013; but see Chevalier et al. 2024).

Conclusions

We here provide empirical support that shifts in species' canopy distribution towards forests with a higher canopy cover are related to less pronounced shifts in species' elevational distribution. Patterns in species distributions along modelled microclimatic gradients suggested that this relationship may be driven by microclimatic temperature. Thus, it is likely that distribution shifts to denser forests might provide an alternative temperature tracking mechanism. Yet, our data indicate incomplete climatic tracking, suggesting this mechanism may not suffice to offset macroclimatic debts. We revealed a high variation in responses within and across taxa that precludes generalizations and complicates predictions about future species assemblages. Future studies would benefit from including in situ microclimate data and temperature variability at different spatial resolutions and thus providing a better quantitative understanding of microclimate buffering in forests, especially with climate change leading to substantially altered forest canopy dynamics.

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Author contributions

Lisa Samira Geres: Conceptualization (equal); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Nico Blüthgen**: Formal analysis (supporting); Methodology (equal); Software (equal); Writing – review and editing (supporting). **Jörg Müller**: Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Writing – review and editing (supporting). **Linda Seifert**: Data curation (equal); Project administration (equal). **Sebastian Seibold**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Supervision (equal); Visualization (supporting); Writing – review and editing (lead). **Claus Bässler**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Supervision (equal); Visualization (supporting); Writing – review and editing (lead).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4j0zpc8k1 (Geres et al. 2024).

Supporting information

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

References

Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J. and Pellissier, L. 2018. Lags in the response of mountain plant communities to climate change. – Global Chang. Biol. 24: 563–579.

Ash, J. D., Givnish, T. J. and Waller, D. M. 2017. Tracking lags in historical plant species' shifts in relation to regional climate change. – Global Chang. Biol. 23: 1305–1315.

Barnett, A. G., van der Pols, J. C. and Dobson, A. J. 2005. Regression to the mean: what it is and how to deal with it. – Int. J. Epidemiol. 34: 215–220.

Barton, K. 2023. MuMIn: Multi-Model Inference. R package version 1.47.5. – https://CRAN.R-project.org/package=MuMIn.

Bässler, C., Förster, B., Moning, C. and Müller, J. 2008. The BIOKLIM project: Biodiversity research between climate change and wilding in a temperate montane forest – The conceptual framework. – Waldökologie, Landschaftsforschung und Naturschutz, 7, pp. 21–33.

Bässler, C., Müller, J., Dziock, F. and Brandl, R. 2010. Effects of resource availability and climate on the diversity of wood-decaying fungi. – J. Ecol. 98: 822–832.

Bässler, C., Hothorn, T., Brandl, R. and Müller, J. 2013. Insects overshoot the expected upslope shift caused by climate warming. – PLoS One 8: e65842.

Bässler, C. et al. 2015. The BIOKLIM Project in the National Park Bavarian forest: lessons from a biodiversity survey. – Silva Gabreta 21: 81–93.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., De Frenne, P., Hemming, D., Hill, R. A., Kearney, M. R., Körner, C., Korstjens, A. H., Lenoir, J., Maclean, I. M. D., Marsh, C. D., Morecroft, M. D., Ohlemüller, R., Slater, H. D., Suggitt, A. J., Zellweger, F. and Gillingham, P. K. 2018. Advances in monitoring and modelling climate at ecologically relevant scales. – Adv. Ecol. Res. 58: 101–161.

Campana, J. L. M., Raffard, A., Chaine, A. S., Huet, M., Legrand, D. and Jacob, S. 2022. Dispersal plasticity driven by variation in fitness across species and environmental gradients. – Ecol. Lett. 25: 2410–2421.

Chatterjee, S. and Simonoff, J. S. 2013. Handbook of regression analysis. – Wiley.

Chauvier-Mendes, Y., Pollock, L. J., Verburg, P. H., Karger, D. N., Pellissier, L., Lavergne, S., Zimmermann, N. E. and Thuiller, W. 2024. Transnational conservation to anticipate future plant shifts in Europe. – Nat. Ecol. Evol. 8: 454–466.

Chevalier, M., Broennimann, O. and Guisan, A. 2024. Climate change may reveal currently unavailable parts of species' ecological niches. – Nat. Ecol. Evol. 8: 1298–1310.

Chisté, M. N., Mody, K., Gossner, M. M., Simons, N. K., Köhler, G., Weisser, W. W. and Blüthgen, N. 2016. Losers, winners, and opportunists: how grassland land-use intensity affects orthopteran communities. – Ecosphere 7: 372.

Chisté, M. N., Mody, K., Kunz, G., Gunczy, J. and Blüthgen, N. 2018. Intensive land use drives small-scale homogenization of plant- and leafhopper communities and promotes generalists. – Oecologia 186: 529–540.

Cudmore, T. J., Björklund, N., Carroll, A. L. and Staffan Lindgren, B. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. – J. Appl. Ecol. 47: 1036–1043.

Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E. and Abatzoglou, J. T. 2019. Microclimatic buffering in forests of the future: the role of local water balance. – Ecography 42: 1–11.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K. and Lenoir, J. 2019. Global buffering of temperatures under forest canopies. – Nat. Ecol. Evol. 3: 744–749.

De Frenne, P. et al. 2021. Forest microclimates and climate change: importance, drivers and future research agenda. – Global Chang. Biol. 27: 2279–2297.

De Lombaerde, E. et al. 2022. Maintaining forest cover to enhance temperature buffering under future climate change. – Sci. Total Environ. 810: 151338.

Devictor, V. et al. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. – Nat. Clim. Chang. 2: 121–124.

Didham, R. K. and Lawton, J. H. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments 1. – Biotropica 31: 17–30.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.

Dullinger, S. et al. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. – Nat. Clim. Chang. 2: 619–622.

Elsen, P. R. and Tingley, M. W. 2015. Global mountain topography and the fate of montane species under climate change. – Nat. Clim. Chang. 5: 772–776.

Elsen, P. R., Monahan, W. B. and Merenlender, A. M. 2020. Topography and human pressure in mountain ranges alter expected species responses to climate change. – Nat. Commun. 11: 1974.

Feldmeier, S., Schmidt, B. R., Zimmermann, N. E., Veith, M., Ficetola, G. F. and Lötters, S. 2020. Shifting aspect or elevation? The climate change response of ectotherms in a complex mountain topography. – Divers. Distrib. 26: 1483–1495.

Fischer, H. S. 2015. On the combination of species cover values from different vegetation layers. – Appl. Veg. Sci. 18: 169–170.

Fox, J. and Weisberg, S. 2019. An R Companion to applied regression, 3rd edn. – Sage.

Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M. and Hargreaves, A. L. 2018. Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. – Global Ecol. Biogeogr. 27: 1268–1276.

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A. and Betts, M. G. 2016. Spatial models reveal the microclimatic buffering capacity of old-growth forests. – Sci. Adv. 2: e1501392.

Friess, N. et al. 2018. Biodiversity along an elevational gradient of the Bohemian Forest – the BIOKLIM project. – Silva Gabreta 24: 149–160.

Geres, L., Bluthgen, N., Muller, J., Seifert, L., Seibold, S. and Bässler, C. 2024. Data from: To the top or into the dark? Relationships between elevational and canopy cover distribution shifts in mountain forests. – Dryad Digital Repository, https://doi.org/10.5061/dryad.4j0zpc8k1.

Greiser, C., Meineri, E., Luoto, M., Ehrlén, J. and Hylander, K. 2018. Monthly microclimate models in a managed boreal forest landscape. – Agric. For. Meteorol. 250–251: 147–158.

Greiser, C., Hederová, L., Vico, G., Wild, J., Macek, M. and Kopecký, M. 2024. Higher soil moisture increases microclimate temperature buffering in temperate broadleaf forests. – Agric. For. Meteorol. 345: 109828.

Guo, F., Lenoir, J. and Bonebrake, T. C. 2018. Land-use change interacts with climate to determine elevational species redistribution. – Nat. Commun. 9: 1315.

Haesen, S., Lenoir, J., Gril, E., De Frenne, P., Lembrechts, J. J., Kopecký, M., Macek, M., Man, M., Wild, J. and Van Meerbeek, K. 2023. Microclimate reveals the true thermal niche of forest plant species. – Ecol. Lett. 26: 2043–2055.

Hanberry, B. B., Bragg, D. C. and Alexander, H. D. 2020. Open forest ecosystems: an excluded state. – For. Ecol. Manage. 472: 118256.

Hanula, J. L., Ulyshen, M. D. and Horn, S. 2016. Conserving pollinators in North American forests: a review. – Nat. Areas J. 36: 427–439.

Hartig, F. 2022. Dharma: residual diagnostics for hierarchical (multi-level/mixed) regression models. – https://CRAN.R-project.org/package=DHARMa.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R. and Thomas, C. D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. – Global Change Biol. 12: 450–455.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R. and Müller, J. 2018a. Biodiversity along temperate forest succession. – J. Appl. Ecol. 55: 2756–2766.

Hilmers, T. et al. 2018b. Changes in forest structure in the Bavarian Forest National Park – an evaluation after 10 years of the BIOKLIM-Project. – Silva Gabreta 24: 161–170.

Jackson, S. T. and Sax, D. F. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. – Trends Ecol. Evol. 25: 153–160.

Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A. and Chamberlain, D. 2018. The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. – J. Ornithol. 159: 747–759.

James, G. et al. 2013. An introduction to statistical learning. – Springer.

Jamieson, M. A., Trowbridge, A. M., Raffa, K. F. and Lindroth, R. L. 2012. Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. – Plant Physiol. 160: 1719–1727.

Jucker, T., Hardwick, S. R., Both, S., Elias, D. M. O., Ewers, R. M., Milodowski, D. T., Swinfield, T. and Coomes, D. A. 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. – Global Chang. Biol. 24: 5243–5258.

Kašpar, V., Hederová, L., Macek, M., Müllerová, J., Prošek, J., Surový, P., Wild, J. and Kopecký, M. 2021. Temperature buffering in temperate forests: comparing microclimate models based on ground measurements with active and passive remote sensing. – Remote Sens. Environ. 263: 112522.

Kemppinen, J. et al. 2024. Microclimate, an important part of ecology and biogeography. – Global Ecol. Biogeogr. 33: e13834.

Klöcking, B. 2018. Simulation of meteorological conditions in the Bohemian forest. – Silva Gabreta, pp. 69–84.

Körner, C. 2004. Mountain biodiversity, its causes and function. – AMBIO: A Journal of the Human Environment, 33: 11–17.

Kühsel, S. and Blüthgen, N. 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. – Nat. Commun. 6: 7989.

Kuznetsova, A., Brockhoff, P. B. and Christensen, R. H. B. 2017. lmerTest package: tests in linear mixed effects models. – J. Stat. Softw. 82: 1–26.

Lembrechts, J. J., Lenoir, J., Nuñez, M. A., Pauchard, A., Geron, C., Bussé, G., Milbau, A. and Nijs, I. 2018. Microclimate variability in alpine ecosystems as stepping stones for non-native plant establishment above their current elevational limit. – Ecography 41: 900–909.

Lenoir, J. and Svenning, J.-C. 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. – Ecography 38: 15–28.

Lenoir, J. et al. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. – Ecography 146: 138.

Lenoir, J., Hattab, T. and Pierre, G. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. – Ecography 40: 253–266.

Levy, O., Dayan, T., Porter, W. P. and Kronfeld-Schor, N. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? – Ecol. Monogr. 89: e01334.

Maclean, I. M. and Klinges, D. H. 2021. Microclimc: a mechanistic model of above, below and within-canopy microclimate. – Ecol. Modell. 451: 109567.

Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L. and Zbinden, N. 2011. Are Swiss birds tracking climate change? – Ecol. Modell. 222: 21–32.

Maihoff, F., Friess, N., Hoiss, B., Schmid-Egger, C., Kerner, J., Neumayer, J., Hopfenmüller, S., Bässler, C., Müller, J. and Classen, A. 2023. Smaller, more diverse and on the way to the top: rapid community shifts of montane wild bees within an extraordinary hot decade. – Divers. Distrib. 29: 272–288.

Mamantov, M. A., Gibson-Reinemer, D. K., Linck, E. B. and Sheldon, K. S. 2021. Climate-driven range shifts of montane species vary with elevation. – Global Ecol. Biogeogr. 30: 784–794.

Mangels, J., Fiedler, K., Schneider, F. D. and Blüthgen, N. 2017. Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. – Biodivers. Conserv. 26: 3385–3405.

Meeussen, C. et al. 2021. Microclimatic edge-to-interior gradients of European deciduous forests. – Agric. For. Meteorol. 311: 108699.

Meineri, E. and Hylander, K. 2017. Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. – Ecography 40: 1003–1013.

Montejo-Kovacevich, G., Martin, S. H., Meier, J. I., Bacquet, C. N., Monllor, M., Jiggins, C. D. and Nadeau, N. J. 2020. Microclimate buffering and thermal tolerance across elevations in a tropical butterfly. – J. Exp. Biol. 223.

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiß, I., Baldrian, P., Tláskal, V. and Thorn, S. 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. – Oikos 129: 1579–1588.

Müller, J. et al. 2023. Weather explains the decline and rise of insect biomass over 34 years. – Nature 628: 1–6.

Oksanen, J. et al. 2022. vegan: community ecology package. R package version 2.6-4, https://CRAN.R-project.org/package=vegan.

Parajuli, R. and Markwith, S. H. 2023. Quantity is foremost but quality matters: a global meta-analysis of correlations of dead wood volume and biodiversity in forest ecosystems. – Biol. Conserv. 283: 110100.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annu. Rev. Ecol. Evol. Syst. 37: 637–669.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.

Pincebourde, S. and Woods, H. A. 2020. There is plenty of room at the bottom: microclimates drive insect vulnerability to climate change. – Curr. Opin. Insect Sci. 41: 63–70.

Pinheiro, J. and Bates, D. 2000. Mixed-effects models in S and S-PLUS. – Springer.

Pinheiro, J. et al. 2023. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-163, https://CRAN.R-project.org/package=nlme.

Pintanel, P., Tejedo, M., Ron, S. R., Llorente, G. A. and Merino-Viteri, A. 2019. Elevational and microclimatic drivers of thermal tolerance in Andean *Pristimantis* frogs. – J. Biogeogr. 46: 1664–1675.

Potter, K. A., Arthur Woods, H. and Pincebourde, S. 2013. Microclimatic challenges in global change biology. – Global Chang. Biol. 19: 2932–2939.

Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R., Ron, S. R.; Sánchez-Azofeifa, G. A., Still, C. J., Young, B. E. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. – Nature 439: 161–167.

Quintero, I. and Wiens, J. J. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. – Ecol. Lett. 16: 1095–1103.

Reiner, R., Zedrosser, A., Zeiler, H., Hackländer, K. and Corlatti, L. 2021. Forests buffer the climate-induced decline of body mass in a mountain herbivore. – Global Chang. Biol. 27: 3741–3752.

Román-Palacios, C. and Wiens, J. J. 2020. Recent responses to climate change reveal the drivers of species extinction and survival. – Proc. Natl. Acad. Sci. USA. 117: 4211–4217.

Rumpf, S. B., Hülber, K., Zimmermann, N. E. and Dullinger, S. 2019. Elevational rear edges shifted at least as much as leading edges over the last century. – Global Ecol. Biogeogr. 28: 533–543.

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E. and Evans, T. A. 2014. Microhabitats reduce animal's exposure to climate extremes. – Global Chang. Biol. 20: 495–503.

Scherrer, D. and Körner, C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. – J. Biogeogr. 38: 406–416.

Schloss, C. A., Nuñez, T. A. and Lawler, J. J. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. – Proc. Natl Acad. Sci. USA 109: 8606–8611.

Schmidt, M., Jochheim, H., Kersebaum, K. C., Lischeid, G. and Nendel, C. 2017. Gradients of microclimate, carbon and nitrogen in transition zones of fragmented landscapes – a review. – Agric. For. Meteorol. 232: 659–671.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A. and Reyer, C. P. O. 2017. Forest disturbances under climate change. – Nat. Clim. Chang. 7: 395–402.

Serra-Diaz, J. M., Scheller, R. M., Syphard, A. D. and Franklin, J. 2015. Disturbance and climate microrefugia mediate tree range shifts during climate change. – Landscape Ecol. 30: 1039–1053.

Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J. and Seidl, R. 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. – Agric. For. Meteorol. 291: 108066.

Thom, D., Rammer, W., Laux, P., Smiatek, G., Kunstmann, H., Seibold, S. and Seidl, R. 2022. Will forest dynamics continue to accelerate throughout the 21st century in the northern Alps? – Global Chang. Biol. 28: 3260–3274.

Tingley, M. W., Koo, M. S., Moritz, C., Rush, A. C. and Beissinger, S. R. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. – Global Change Biol. 18: 3279–3290.

Urban, M. C. 2015. Accelerating extinction risk from climate change. – Science 348: 571–573.

Vandewiele, M., Geres, L., Lotz, A., Mandl, L., Richter, T., Seibold, S., Seidl, R. and Senf, C. 2023. Mapping spatial microclimate patterns in mountain forests from LiDAR. – Agric. For. Meteorol. 341: 109662.

Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat, C., Rebetez, M., Rixen, C., Strebel, N., Schmidt, B. R., Wipf, S., Wohlgemuth, T., Yoccoz, N. G. and Lenoir, J. 2021. Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. – Biol. Rev. Camb. Philos. Soc. 96: 1816–1835.

Wei, L., Sanczuk, P., De Pauw, K., Caron, M. M., Selvi, F., Hedwall, P. O., Brunet, J., Cousins, S. A. O., Plue, J., Spicher, F., Gasperini, C., Iacopetti, G., Orczewska, A., Uria-Diez, J., Lenoir, J., Vangansbeke, P. and De Frenne, P. 2024. Using warming tolerances to predict understory plant responses to climate change. – Global Chang. Biol. 30: e17064.

Wickham, H. et al. 2019. Welcome to the Tidyverse. – J. Open Source Softw. 4: 1686.

Zellweger, F., Roth, T., Bugmann, H. and Bollmann, K. 2017. Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. – Global Ecol. Biogeogr. 26: 898–906.

Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet, J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K. and De Frenne, P. 2019. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. – Global Ecol. Biogeogr. 28: 1774–1786.

Zellweger, F. et al. 2020. Forest microclimate dynamics drive plant responses to warming. – Science 368: 772–775.

Zu, K., Lenoir, J., Fang, J., Tang, Z., Shen, Z., Ji, C., Zheng, C., Luo, A., Song, W., Zimmermann, N. E., Pellissier, L. and Wang, Z. 2023. Elevational shift in seed plant distributions in China's mountains over the last 70 years. – Global Ecol. Biogeogr. 32: 1098–1112.