Contrasting thermophilization among forests, grasslands and alpine summits

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Climate warming is shifting biological communities, with warmth-demanding species being favoured at the expense of cold-adapted species in a process referred to as thermophilization[1–4]. Because biodiversity responses often lag behind climate warming, climatic debts are accumulating in many ecosystems across the world[5–7]. Although we might expect that thermophilization and climatic debts will vary among habitats, standardized quantification across ecosystems is lacking. Here we analysed multidecadal data from 6,067 resurveyed vegetation plots over 12–78 years in forests, grasslands and on alpine summits across Europe. We demonstrate that forest understory and grassland plant communities experienced positive thermophilization, although not significantly different from zero. By contrast, alpine summit vegetation showed much stronger (up to five times) and significant thermophilization. Thermophilization was driven largely by increases in warmth-demanding species in grasslands, by declines in cold-adapted species on alpine summits and by both processes in forests. Significant climatic debts have accumulated in forests and alpine summits, but less so in grasslands, with debts positively correlated with macroclimate temperature changes. Our findings uncover divergent thermophilization trajectories and increasing climatic debts across ecosystems. Moreover, we highlight the mechanisms that enable some communities to track climate change more closely than others and provide a basis for projecting future shifts in plant communities under accelerating climate warming.

Global climate change is having substantial impacts on biodiversity[8–10]. Range shifts are being observed in many species and ecosystem types as species track their thermal requirements[11–14]. As a result, directional shifts in community composition at the expense of cold-adapted species and in favour of warmth-demanding species (referred to as thermophilization) are increasingly evident in terrestrial and aquatic plant and animal communities[1–4,15,16]. For example, significant thermophilization of vegetation has been documented across alpine summits and grasslands in Europe[3,17], and in plant communities of temperate and tropical forests despite the buffering effects of forest canopies[1,18–20]. However, in many biological communities, thermophilization proceeds more slowly than contemporary warming[13,18,21,22], which results in a climatic debt in community composition[2,5,6,15,23].

Climatic debts reflect the inherent life-history and ecophysiological characteristics of species, such as limited dispersal and establishment capacity and long lifespan[7,24,25]. However, they may also arise from the buffering effects of microclimatic processes or interactions with other global change drivers[1,18,23,26]. Apparent debts may also be shaped by adaptive shifts in climatic niches of species, although such processes are generally slow[7]. Microclimates in non-forest ecosystems, such as alpine summits and grasslands, are mainly shaped by topography and vegetation feedbacks on snow cover, solar radiation, air mixing and evapotranspiration[27–30]. By contrast, in forests, the tree canopy structure largely governs microclimatic conditions and thermal buffering[1,18], although topography is also important[31]. As such, the magnitude of thermophilization might appreciably differ among ecosystems. However, comparing studies of thermophilization rates is difficult, as they often use disparate methodologies to quantify thermal niches and climatic debts (for example, as a result of different sources, resolutions, seasons and base periods of climate data). Thermophilization rates in response to climate change may differ across ecosystems[4]. However, we lack consistent large-scale, multitaxa and long-term comparisons of thermophilization rates and climatic debt magnitudes among vegetation types based on a consistent methodology. Here to address this knowledge gap, we use vegetation resurveys with a consistent methodology to answer two key questions: (1) how thermophilization rates and climatic debts differ among different ecosystem types; and (2) how these differences are related to variation in local climate warming across contrasting ecosystems.

We report cross-biome thermophilization for Europe's temperate forests, grasslands and alpine summits. These ecosystems represent widespread and ecologically distinct vegetation types with contrasting structures and microclimates relevant to responses of species to climate change. We compiled plant occurrence data for 1,919 species from 6,067 resurveyed vegetation plots (Fig. 1). In each plot, we quantified the thermophilization rate of the plant community[1,18] using a consistent methodology (Methods). In total, 4,372, 1,209 and 486 plots from forests, grasslands and alpine summits, respectively, were analysed, with sampling intervals (baseline to resurveys) of 12–78 years (median of 42 years), 16–78 (median of 35 years) and 12–15 (median of 14 years), respectively (Extended Data Table 1 and Extended Data Fig. 1a). We used these data to estimate rates of thermophilization and climatic debt (°C per decade) for each plot using an established method that relies on the thermal affinities of species inferred from their geographical

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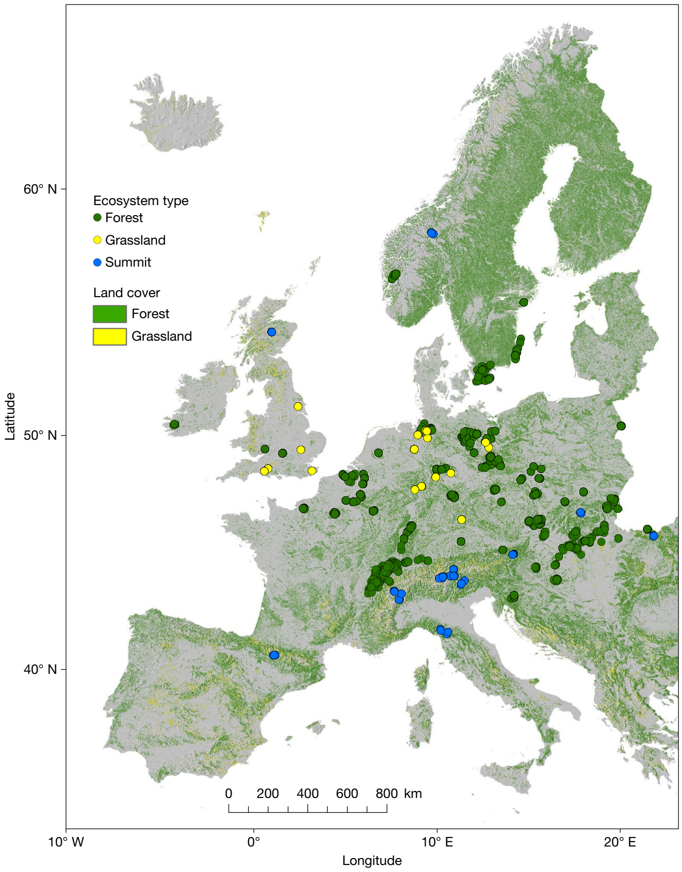

Fig. 1 | Distribution of the 6,067 resurveyed quasi-permanent and permanent plots in forests, grasslands and alpine summits across Europe. Forest cover (green) and grassland cover (yellow) are based on CORINE Land Cover 2018 data[50]. Elevation data (grey) are from the NASA Jet Propulsion Laboratory[51].

distributions relative to long-term climate data[1,18,32]. To further disentangle the mechanisms that underlie thermophilization, we separately calculated changes in the 5th and 95th percentiles of the floristic temperature distribution to represent declines in cold-adapted species compared with increases in warmth-demanding species, respectively[1].

First, we estimated thermophilization rates using plant abundance data (excluding rare species with range sizes fewer than 1,000 grid cells at 20 × 20 km resolution; Methods), which mainly reflect changes in species dominance and community reordering. We found positive, although not significantly different from zero, rates of overall thermophilization in forests (0.03 °C per decade, 95% credible interval (CI) of −0.02–0.07) and grasslands (0.03 °C per decade, 95% CI of −0.06–0.11). By contrast, the overall thermophilization rate on alpine summits was much higher and significantly different from zero at 0.12 °C per decade (95% CI of 0.05–0.19) (Fig. 2a). When estimated using plant presence/absence data, which are more sensitive to species turnover, including rare or transient species, similar results were found. The thermophilization rate on alpine summits was five times higher than in forests and grasslands (see the section ‘Sensitivity analysis’ in the Methods and Extended Data Fig. 2a). When assessed using abundance data and excluding rare species, thermophilization in grasslands was driven largely by an increase in warmth-demanding species (0.08 °C per decade, 95% CI of −0.03–0.19). In forests, thermophilization reflected both declines in cold-adapted species (0.04, 95% CI of −0.01–0.09 °C per decade) and increases in warmth-demanding species (0.03, 95% CI of −0.03–0.09 °C per decade). On alpine summits, however, we found a significant decrease in cold-adapted species (0.26 °C per decade, 95% CI of 0.18–0.34) and a decrease in warmth-demanding species (−0.16 °C per decade, 95% CI of −0.25 to −0.06). These trends did not show marked changes when rare species and/or when vegetation presence/absence data were included in the assessment (see the section ‘Sensitivity analysis’ in the Methods and Extended Data Fig. 2b).

Our second analysis involved calculations of climatic debts by subtracting thermophilization rates from local rates of climate change[2,24]. These climatic debts were mostly positive (ranging from 0.13 to 0.34 °C per decade across ecosystem types; Fig. 2b and Extended Data Fig. 2), which indicated that thermophilization lags behind macroclimate changes. The magnitude of these lags did not strongly depend on whether they were estimated from declines in cold-adapted species, increases in warmth-demanding species or overall thermophilization rates. Climatic debts were generally highest in forests, followed by alpine summits and were lowest in grasslands. Thermophilization rates were weakly correlated with rates of increase in temperature regardless of the ecosystem type. Conversely, climatic debts strongly covaried with rates of temperature change across all ecosystem types (Fig. 3).

The overall rates of thermophilization on alpine summits were generally higher (up to five times) than those in forests and grasslands. The divergence in thermophilization rates among ecosystem types may be partially attributed to differences in plant lifespans, with communities composed of shorter-lived plants potentially responding more rapidly to climate warming[33,34]. However, currently available lifespan datasets (for example, from the TRY Plant Trait Database[35]) are still limited in taxonomic coverage and resolution. This limitation is especially relevant for ecosystems such as alpine summits and forests, where many plant species are perennials and have multidecadal to centuries-long lifespans, which prevented us from quantitatively testing this hypothesis. The high thermophilization observed on alpine summits may predominantly result from topographical compression of thermal belts, which creates strong spatial gradients in microclimate and species composition such that even small shifts in species distribution can lead to marked community-level changes in thermal affinity[36]. In the alpine summit dataset, however, we did not detect significant relationships between thermophilization rates and variables that reflect rugged topography, such as the terrain ruggedness index (TRI) or slope (Extended Data Fig. 3a). This result is probably due to the fact that summit-level coordinates in our database and mid-scale topographical metrics did not capture the fine-scale microhabitats that more strongly shape community responses, especially in alpine environments. Nevertheless, thermophilization was lowest on north-facing slopes (Extended Data Fig. 3b). This finding supports the hypothesis that microhabitats are generated by topographical gradients and emphasize the role of slope exposition to sun radiation in shaping thermophilization patterns of treeless alpine vegetation.

Our results further suggest that thermophilization of the understory plants in forests is driven by both declines in cold-adapted species and increases in warmth-demanding species, which is expected with warming. By contrast, only increases in warmth-demanding species contributed to overall thermophilization in grasslands. Unlike forests, grasslands lack tree canopy buffering, and grassland plant communities experience hotter maximum daily temperatures than forest understoreys. Together with higher species turnover and recruitment rates, this factor could have favoured warmth-demanding taxa more as temperatures rise[37], which results in thermophilization being driven mainly by increases in warmth-demanding species. For alpine summits, however, our results suggest a simultaneous decline in both cold-adapted and warmth-demanding species, which could potentially be linked to recurring severe drought during the survey periods[38,39], although it may reflect additionally distinct ecological pressures. Cold-adapted species may decline or be lost because of substantial climate warming and habitat contraction[40,41]. Conversely, the decline in warmth-demanding species may result from reduced persistence after colonization, which may be due to environmental stress or biotic interactions[42]. Despite declines in both types of species, net thermophilization can still result from stronger declines in cold-adapted species

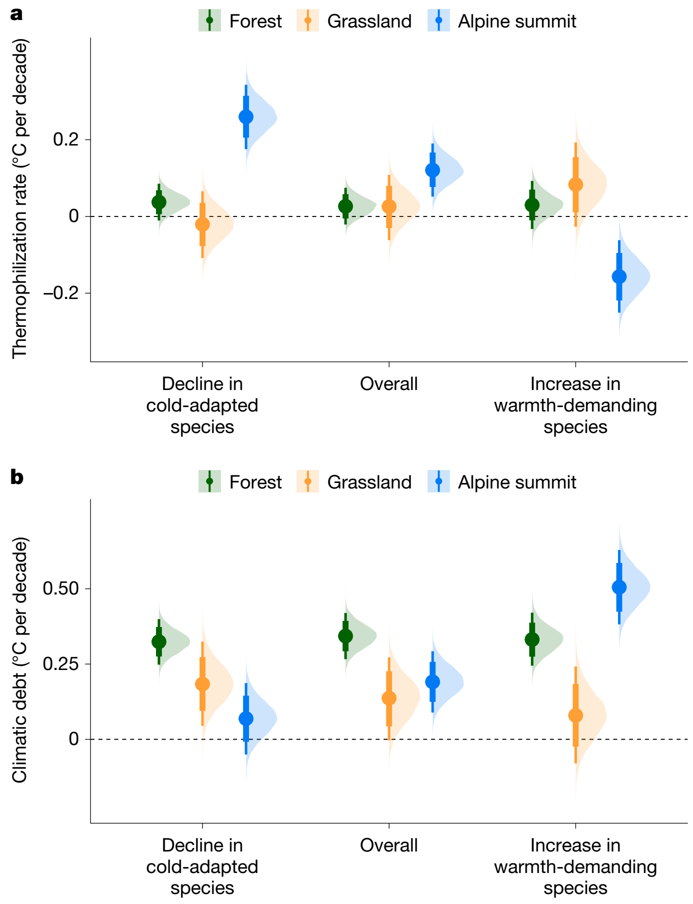

Fig. 2 | Vegetation thermophilization rates and climatic debts in forests, grasslands and alpine summits. **a**, Vegetation thermophilization rates quantified as declines in cold-adapted species (5th percentile shift), overall (median shift) and increases in warmth-demanding species (95th percentile shift). **b**, Climatic debts (°C per decade) calculated according to climate change rates and vegetation thermophilization rates of declines in cold-adapted species, overall and increases in warmth-demanding species. Thermophilization rates and climatic debts were estimated using plant abundance data that excluded rare species. Circles represent means ($n = 4{,}372$ plots, 1,209 plots and 457 plots for forests, grasslands and alpine summits, respectively) with 80% (thick line) and 95% (thin line) CIs and posterior distributions obtained from Bayesian mixed-effects models.

than warmth-demanding species (Fig. 2 and Extended Data Fig. 2) and from compositional shifts that favour warmth-demanding species through both topography-facilitated colonization and differential persistence[43]. By partitioning thermophilization into the effects of gains, losses and abundance shifts of persisting species, we found that abundance shifts, along with losses, were the primary drivers of thermophilization on alpine summits (see the section 'Sensitivity analysis' in the Methods and Extended Data Fig. 4a). Our results also confirmed that thermophilization is jointly driven by losses in cold-adapted species and gains in warmth-demanding species in forests and largely by gains in warmth-demanding species in grasslands.

Substantial climatic debts existed in all the types of ecosystems studied here. Climatic debts in forests were substantial and generally higher than those in alpine summits and grasslands. This difference is probably because tree canopies provide microclimatic buffering of climate warming, which is not captured by the macroclimate data used to assess global climate warming[23,44] (and in our study). Moreover, forest plant life-history traits (for example, long lifespan) probably impede their ability to rapidly adapt to changing conditions, thereby delaying their response to and increasing their climatic debt[6,45]. The lower climatic debt in grasslands indicates that shifts in grassland plant communities are more closely tracking climate warming[37], especially for warmth-demanding species that showed limited climatic debts. We also quantified the thermal suitability of the background climate for plant communities and assessed the extent to which species at the plot level were exposed to climatic conditions beyond their thermal tolerance ranges (see the section 'Sensitivity analysis' in the Methods for details). We found significant declines in the probability density of thermal suitability in forests and marginal declines in grasslands, but not on alpine summits (Extended Data Fig. 5a). The proportion of mismatched species significantly increased in forests but not in grasslands or alpine summits (Extended Data Fig. 5b). These results show that thermal mismatch progresses unevenly across ecosystems and that comparing the difference between changes in climate and floristic temperature may have overestimated climatic debts in grasslands and alpine summits. Notably, disturbance levels among ecosystems could also contribute to these differences. Although we were unable to assess this parameter with the current data, it represents a significant direction for future research. Together, these results highlight the ecosystem-specific responses of vegetation to climate warming.

Our results also showed that climatic debts increase with the amount of temperature change, which suggests that rapid climate change increases the risk of species reshuffling and ecosystem disruptions[5,7]. This outcome highlights the urgency of proactive strategies to mitigate and adapt to future climate change. As physical and biological drivers of microclimate are substantially different in forests, grasslands and alpine summits[46], future research should quantify how climatic debt scales with different rates of warming in each of these contrasting ecosystems. In addition to climate warming, other globally changing factors, such as droughts, nitrogen and sulfur deposition, land-use change and elevated CO_2, may interact with or modulate thermophilization patterns[14,47]. Part of the thermophilization signal we detected might be due to niche axes that are correlated with, but not causally linked to, temperature. Multifactor assessments, including other global environmental changes, are therefore needed to more precisely predict the responses of plant communities and inform more integrative conservation strategies.

In summary, we uncovered that thermophilization rates vary significantly among major terrestrial ecosystem types—forests, grasslands and alpine summits—in Europe. Thermophilization is driven largely by increases in warmth-demanding species in grasslands, by decreases in cold-adapted species and increases in warmth-demanding species in forests, and by decreases in cold-adapted species and abundance shifts of persisting species on alpine summits. Although time lags between climate warming and changes in the composition of plant communities have previously been noted[6,7,12,18,48,49], we demonstrated that climate change has generated contrasting shifts in plant communities among different ecosystem types. These contrasting patterns suggest that there is asynchronous reorganization among ecosystems, which reflect differences in exposure, biotic resistance and response lags. Notably, ecosystems with accumulating climatic debts are likely to face increased risks of ecological mismatches, functional instability and local species extirpations. Given rapid rates of climate change, climate lags will probably persist over many decades even if the climatic debt must ultimately be paid off. The differing thermophilization rates among ecosystems also highlight the importance of comparing several ecosystems when assessing the impacts of global change on biodiversity, as such quantification can enable forecasting of the duration of biodiversity changes that will continue even if climate warming stabilizes. Our findings provide a basis for projecting community change with accelerating climate change, which will facilitate the development of targeted management strategies, such as assisted migration in forests, adaptive grazing practices in grasslands and conservation of cold-adapted species, to enhance ecosystem resilience and mitigate biodiversity loss under ongoing climate change.

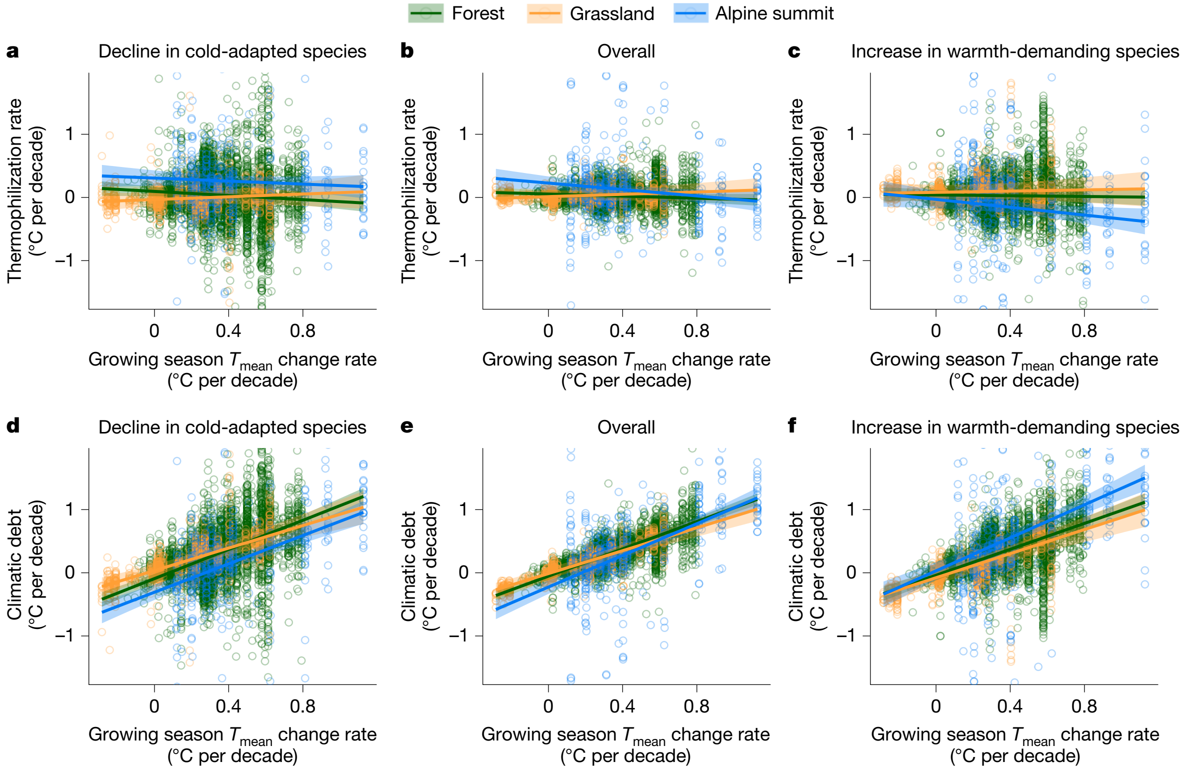

Fig. 3 | Relationships between vegetation thermophilization rates and climatic debt and the growing season mean temperature change rate in forests, grasslands and alpine summits. a–c, Relationships between the growing season mean temperature (T_{mean}) change rate (°C per decade) and the thermophilization rate (°C per decade) quantified as declines in cold-adapted species (5th percentile shift) (**a**), overall (median shift) (**b**) and increases in warmth-demanding species (95th percentile shift) (**c**). **d–f**, Relationships between the growing season T_{mean} change rate (°C per decade) and climatic debt (°C per decade) calculated according to the thermophilization rate quantified as declines in cold-adapted species (**d**), overall (**e**) and increases in warmth-demanding species (**f**). Thermophilization rates and climatic debts were estimated using plant abundance data that excluded rare species. Each circle represents a plot (n = 4,372, 1,209 and 457 for forests, grasslands and alpine summits, respectively). Lines are fits from Bayesian mixed-effect models, and shaded areas denote 95% CIs.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-025-09622-7.

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Methods

Databases and vegetation resurveys

We used data from three databases, and each database is a collation of vegetation resurvey data for a certain ecosystem type in Europe (Fig. 1 and Extended Data Table 1). Data for forests were obtained from the forestREplot database (v.2.3; www.forestreplot.ugent.be) with 4,372 plots from 76 sampling sites. The forestREplot is a resurveyed vegetation plot network that focuses on all vascular plants in the understory community (<1 m height, including tree seedlings) across temperate forests in Europe[52], as they represent on average the most important plant biodiversity compartment in forests[53]. All plots are located in natural (never cleared for other land uses than forests according to the oldest available sources such as historical maps, typically at least 150–300 years[54]) or semi-natural forests according to a published definition[55]. Grasslands were represented by 1,209 resurveyed vegetation plots from 22 sites that are situated in semi-natural grasslands, which is defined as unploughed mown or grazed areas with limited fertilization[56], from the GRACE database[57]. Data for alpine summits were from the Global Observation Research Initiative in Alpine environments (GLORIA, https://gloria.ac.at), with 486 plots in natural vegetation with a complete list of vascular plant species from 64 sites[58]. In each site, plant communities were surveyed across permanent (that is, plots were permanently marked in the field) or quasi-permanent (that is, plots were not permanently marked but have known coordinates or clear indications on physical maps for later accurate relocation)[59] plots at two time points, namely the baseline survey and resurvey. Between the two surveys, there was no major change in land use such as clearcutting, replanting, conversion to agricultural land or urbanization, among others. Moreover, at least at the plot level, the same methodology was used in both surveys, such as the number and size of plots and cover-abundance scale (for more details, see refs. 52,57,58). The time spans between the baseline survey and resurvey ranged between 12 and 78 years with a median of 42 years. Specific lengths of the study period per ecosystem type are provided in Extended Data Table 1. The median number of plots per site was 42.5 and 39 in forest and grassland surveys, respectively, and the median size of plots was 200 and 25 m^2 in forest and grassland surveys, respectively[60]. Alpine summits were always resurveyed in 8 spatial sections that together covered the entire area from the highest summit point to the contour line 10 m in elevation below this point, and the median summit area was around 300 m^2. A complete list of vascular plant species was recorded for all plots in each ecosystem type. Species abundance was recorded as the percentage cover in forest and grassland plots, and as an ordinal scale from one (very rare) to eight (dominant) in summit plots[58]. The ordinal abundance scores were standardized for each plot and survey time to a continuous 0–100 scale via min–max transformation and was subsequently converted to relative abundances, thereby rendering them directly comparable to percentage cover estimates. Vegetation surveys were generally carried out during the peak of the vegetation season (May–August), and plots with a year difference between the baseline survey and resurvey less than 10 years were excluded in our study.

Temperature data

To determine the rate of temperature change between the baseline survey and resurvey, we used monthly mean temperature data to obtain mean growing season (April–September) temperatures, given that this period broadly corresponds to the peak of plant physiological activity, although on alpine summits, this period is shorter (June–August), thereby better reflecting the climatic condition that drives species turnover and community dynamics[1,3,61,62]. We used the data of CRU TS (v.4.07), which provides updated gridded climate datasets at a spatial resolution of 0.5° (around 50 km at the equator) since 1901, based on monthly observations at meteorological stations across the land areas of the world. This dataset was selected because of its temporal depth and consistency, which enabled robust estimation of temperature change over the full period between the baseline survey and resurvey (from 1931 to 2020). For each plot across the ecosystem types, we calculated the climatic temperature change rate (expressed in °C per decade) between the baseline survey and the resurvey as the difference between the mean growing season temperature during the 5 years preceding the baseline survey and the 5 years preceding the resurvey, divided by the time span between the baseline survey and the resurvey[1,3,18]. The resulting distributions of mean growing season temperature change rates are presented in Extended Data Fig. 1b.

Thermophilization

To calculate thermophilization rates, we followed established and widely used methods in the literature based on thermal niche and distribution range data of species[1,3,6,15,18,20,63]. First, we extracted gridded long-term (1970–2000) climatic data on monthly mean temperatures of the growing season (April–September) from WorldClim (v.2) as a raster file with 10 arcmin resolution (about 20 × 20 km)[64]. Then, to obtain distribution data of the species, we estimated species range sizes as the area of occupancy (AOO)[65] using point occurrence records in the Global Biodiversity Information Facility (GBIF, www.gbif.org)[66]. We retained records from 1930 onwards to ensure full temporal coverage of the distributions of species across the baseline survey and resurvey intervals, the earliest of which began in 1931 (Extended Data Table 1). To minimize spatial sampling bias, occurrences were aggregated to 20 × 20 km resolution, and the AOO was calculated on the basis of the number of unique occupied grid cells per species, thereby not only avoiding overrepresentation of well-sampled areas but also aligning with the resolution of the climate data used. Records with missing or erroneous coordinates, high spatial uncertainty (>10 km) or flagged as outliers were removed using standard data-cleaning procedures. After filtering, a total of 1,919 species (85.8%) out of the 2,237 species identified to the species level included in our study across ecosystem types were matched and retained. This GBIF-derived range sizes for plant species in Europe has been found to correlate strongly with expert-drawn range maps and can therefore provide good relative estimates of the distributions of species[60,67]. Next, to estimate the realized thermal niches of species, defined as the climatic niche space that is genuinely occupied by a species[66], we set the study area extent to all European land between 15° W and 60° E and 25° N and 75° N, with grid cells of 20 × 20 km. For each species, we randomly sampled 1,000 grid cells, with replacement, within the range size represented by the AOO[18,32]. To generate consistent data series for all species (1,000 values), we used random sampling with replacement instead of a random sample or all grid cells, which allowed species with small distribution ranges (that is, <1,000 grid cells) to be included under the same sampling scheme and ensured comparability of climatic niche estimates across species. However, because rare species (defined here as species with range sizes smaller than 1,000 grid cells, which accounted for 36.4% of the total species pool; Extended Data Fig. 1c) are less frequently encountered, sampling efforts may not consistently detect them and therefore lead to potential underestimation or overestimation of their actual contribution to thermophilization of vegetation communities. We therefore first estimated the thermophilization rate and climatic debt only with species with AOO ≥ 1,000 grid cells and then reran the analyses with all the species included in our database to check whether the exclusion of rare species biased our results (see the section 'Sensitivity analysis' below).

We calculated the floristic temperature (T_{plant}, °C) for each plot by using the thermal niches of all species present during each survey (baseline survey and resurvey). To account for the variability and uncertainty in the thermal preferences and niche widths of species, we generated a distribution of plot-level floristic temperatures at each survey by resampling 1,000 times from the thermal niches of species (that is, from the 1,000 grid cells), with weights defined by species abundance, following a previously described method[68]. Then, we estimated the overall thermophilization rate for each plot as the difference between the median of the floristic temperature distribution of the resurvey minus the baseline survey (ΔT_{plant}), divided by the time span (Δt, in decades) between the two survey periods. Given that thermophilization represents a slow ecological response to climate warming, we therefore used decadal rates (°C per decade) in this study to better reflect long-term trends and reduce sensitivity to interannual variability. A positive value therefore reflects an overall temporal increase of floristic temperature in °C per decade.

To further evaluate the contribution of declines in cold-adapted species and increases in warmth-demanding species to the overall thermophilization rate, we quantified shifts in the left (5th percentile) and right (95th percentile) tails of the plot-level distribution of floristic temperatures per survey period, respectively[1]. A positive value in the left versus right tail shift indicates thermophilization due to a decline in relatively cold-adapted species versus an increase of the frequency of more warmth-demanding species, respectively. As we were specifically interested in this per-plot thermophilization, it is important to note that this calculation of shifts in the cold-adapted versus warmth-demanding species is a per-plot relative quantification based on the left and right tail of floristic temperature distribution shifts per plot[1]. As a result, a cold-adapted species in a plot in a warm site can be a warmth-demanding species in a plot in a colder site. Finally, as a sensitivity analysis, we also converted all vegetation data into presence/absence data and recalculated thermophilization rates and climatic debt (see the section 'Sensitivity analyses' below).

Climatic debt

Climatic debt is defined as the degree to which the rates of compositional changes in vegetation are lagging behind the rates of climate warming. The climatic debt per plot between the baseline survey and resurvey was calculated as $(\Delta T_{\text{clim}}/\Delta t) - (\Delta T_{\text{plant}}/\Delta t)$ (following refs. 2,24), where ΔT_{clim} and ΔT_{plant} are changes in the actual mean climate temperature of the growing season and floristic temperature (the median, 5th and 95th percentile of the distribution of floristic temperatures) between the baseline survey and resurvey, respectively. A large climatic debt implies a large mismatch between the dynamics of plant communities and climate change[7], which indicates that a relatively large number of species are occurring under suboptimal thermal conditions. Positive or negative climatic debts indicate that the response rates of plant communities are slower or faster, respectively, than climate warming rates.

Statistical analyses

We used Bayesian mixed-effects models with the brms package (v.2.22.0)[69] in R (v.4.4.2) for all the statistical analyses and the 95% CI to determine statistical clarity[70]. We adopted a Gaussian regression model with an identity link to evaluate whether thermophilization rates and climatic debts (°C per decade) were significantly different from zero in each type of ecosystem by fitting ecosystem type as a fixed-effect factor and 'site' as a random-effect term. The suitability of Gaussian assumption was evaluated using quantile–quantile plots of the response variables, which indicated approximate normality (Extended Data Fig. 6). Also, to account for the potential impacts of regression to the mean effects[71], we included the mean climate temperature of the growing season at the baseline survey ($T_{\text{clim baseline}}$) as a covariate, given the detected significant linear relationship between $T_{\text{clim baseline}}$ and temperature change rate (Extended Data Fig. 7a). This approach helped separate baseline effects from true temporal trends. We also fitted plot size as a fixed-effects factor in the model, which was specified as the following formula (model 1):

Thermophilization rate or climatic debt ~ ecosystem type + plot size + $T_{\text{clim baseline}}$ + (1|site).

Then, to assess the relationship between actual climatic temperature change rate and the thermophilization rate or climatic debt based on vegetation surveys across ecosystem types, we fitted the interaction of actual climatic temperature change rate and ecosystem type as fixed-effects factors (model 2):

Thermophilization rate or climatic debt ~ ΔT_{clim} × ecosystem type + plot size + $T_{\text{clim baseline}}$ + (1|site).

For each model, we fitted 4 chains of 8,000 iterations, excluding the first 2,000 iterations as the warm-up in each chain. We used the Gelman–Rubin statistic ($\widehat{R} < 1.01$) to ensure model convergence, and all the models in our analyses converged. Data visualization was performed using the ggh4x package (v.0.3.1).

Sensitivity analyses

Thermophilization was primarily estimated using abundance-weighted data, which emphasize shifts in community structure by giving more weight to dominant species. This approach provides insights into changes in ecological dominance and potential functional consequences. However, it may also underrepresent the role of rare or newly colonizing species, which can be important indicators of climate-driven species turnover and bias the results because of methodological and observer differences in abundance measurement. To address these limitations and to assess the robustness of our findings, we therefore converted all abundance data into robust presence/absence data following previous studies[1,18] and reran the analyses for estimations of thermophilization rate and climatic debt. This complementary approach captured changes in species composition regardless of abundance, which enabled a more comprehensive assessment of community thermal shifts. The rationale for performing this analysis is that the time intervals between the baseline surveys and resurveys were mostly sufficiently long (all >10 years) to allow for species replacements due to colonization and extinction. We found similar results of thermophilization rate and climatic debt generated from vegetation abundance-weighted and presence/absence data (Extended Data Fig. 2).

Rare species with small range sizes are often ecological outliers with distinct habitat requirements and thermal tolerances, and their presence may therefore disproportionately influence the calculation of average thermal preferences of plant community[72]. Also, rare species are less likely to be consistently detected across sampling events owing to their low abundance, and this variability in detection can introduce noise in the data, which makes it difficult to accurately assess trends in species composition over time[73]. We therefore excluded rare species with AOO < 1,000 grid cells in our analyses. However, rare species themselves are important components of the vegetation community and can be important indicators of climate-driven species turnover. Therefore, to test whether the exclusion of rare species in our analyses may affect estimations of thermophilization rate and climatic debt, we reran such analyses by including all the species in our dataset. The results showed that the inclusion of rare species did not affect the overall patterns of thermophilization rates and climatic debts across all ecosystems (Extended Data Fig. 2b), which indicated that the observed patterns are not an artefact of sampling bias towards rare taxa and reflect consistent community-level responses to climate warming.

In our study, we classified cold-adapted species and warmth-demanding species on the basis of the lower and upper 5% percentiles of the floristic temperature distribution. Although this approach focused on species at the thermal distribution margins, it may also result in relatively small groups that are sensitive to outliers or sampling variation. To evaluate whether our results were disproportionately influenced by these few extreme cases, we conducted a sensitivity analysis using the lower and upper 20% percentiles of the floristic temperature distribution to define cold-adapted and warmth-demanding species, respectively. The results were consistent with our original findings, showing similar patterns in the direction of thermophilization responses across ecosystems (Extended Data Fig. 7b). However, the magnitude of the effects was slightly attenuated, as expected, owing to the inclusion of species closer to the median of floristic temperature distribution.

These results confirm that our conclusions are robust to the choice of quantile thresholds used to define thermal adaptation.

As a supplementary analysis for the method used to quantify the contributions of shifts in cold-adapted versus warmth-demanding species to thermophilization, we further partitioned the observed changes in community-weighted, at the plot level, mean temperature (ΔT_{CWM}, °C) into three additive components, namely, species gains, species losses and abundance shifts of persisting species[40,74]. This framework enabled us to attribute community-level floristic temperature change into different forms of species turnover and reassembly. A gains effect was defined as the average thermal niche of species that were newly recorded in the resurvey but absent from the baseline survey minus the baseline T_{CWM}. The losses effect was calculated as the baseline T_{CWM} minus the mean thermal niche of species that disappeared between the baseline survey and resurvey. The gains effect describes the directional impact of the arrival of novel species, and the losses effect reflects the impact of species loss on thermal restructuring. The abundance shifts effect was quantified as the ΔT_{CWM} between the two surveys using only the set of species identified in both baseline surveys and resurveys, weighted by their relative abundances in each survey, which captures compositional shifts among persisting species that contribute to warming or cooling, independent of species turnover. For each plot, we estimated gains and losses effects using the median of species-specific thermal niche distribution as the respective mean thermal difference relative to the baseline T_{CWM}. The abundance shift effect was estimated as the change in T_{CWM} over time based only on the subset of shared species in both surveys. The sum of the three effects produced a total estimate (estimated ΔT_{CWM}), which was then compared with the observed ΔT_{CWM} to assess the explanatory power of mechanism. We also estimated the relative contribution of each mechanism by dividing the absolute value of its effect by the sum of the absolute values of all three effects, and the contributions were then expressed as percentages to facilitate comparison among mechanisms. We identified the dominant mechanism for each plot as the one with the largest percentage contribution. The results revealed significant linear relationships between estimated and observed ΔT_{CWM} across ecosystems, with R^2 values ranging from 0.23 to 0.53 (Extended Data Fig. 4b), which indicated that the three mechanisms collectively provide a reasonable explanation for the observed thermophilization patterns. Building on this, the results further suggested that gains and losses were the dominant contributors to thermophilization of understory vegetation in forests, losses played the primary role in grasslands, whereas losses and abundance shifts of persisting species were the major contributor on alpine summits (Extended Data Fig. 4a). These results highlight the fact that the relative importance of gains, losses and abundance shifts in driving thermophilization is ecosystem-dependent and reflect distinct community dynamics and responses to climate warming across ecosystems.

Despite the widespread use of the climatic debt metric by comparing ΔT_{clim} and $\Delta T_{\mathrm{plant}}$, it could neglect the variation in the thermal niche space in a community because one can obtain a climate debt but the background observed climate of the resurvey remains in the thermal niche space of all species in a community. Therefore, to test the robustness of the climatic debt results in our study, we further quantified the thermal suitability of background climate for plant communities and assessed the extent to which species in each community, at the plot level, were exposed to background climatic conditions beyond their thermal tolerance ranges. Specifically, for thermal niche suitability, we estimated the probability density of floristic temperature distribution (that is, T_{plant}) at the observed climatic temperature (that is, T_{clim}) for each plot and survey time. T_{plant} distribution values were generated using the 1,000 resampled values of species-specific thermal niches and abundance data, as described above. Then, for each value of the distribution, we computed a kernel density estimate and extracted the probability density at the corresponding T_{clim} value using linear interpolation. The change in probability density between the baseline survey and resurvey indicates whether the local climate has become more or less aligned with the realized thermal niche of the community, and a decline in density suggests an increasing mismatch between climate and community thermal preferences. The results showed significant and marginal declines in the probability density at T_{clim} from the baseline survey to resurvey in forests and grasslands, respectively (Extended Data Fig. 5a), which indicated an increasing climatic mismatch. However, no change in the probability density at T_{clim} was detected on alpine summits.

Furthermore, to estimate the proportion of thermally mismatched species, we derived 2.5th and 97.5th percentiles of the thermal niche distribution for each species. For each plot and survey time, we identified all recorded species and classified each as 'thermally mismatched' if the background T_{clim} fell outside its thermal niche bounds (that is, between the 2.5th and 97.5th percentiles of thermal niche distribution). We then calculated the proportion of mismatched species per plot as the number of mismatched species divided by the total number of species present, and estimated the change between the resurvey and baseline survey. This metric therefore captures the prevalence of species experiencing thermal stress relative to their historical niche distribution. We found that the proportion of mismatched species showed a significant increase in forests, but not in grasslands or on alpine summits (Extended Data Fig. 5b). These results suggest that thermal mismatch is progressing unevenly across ecosystems. In forests, the observed increase in mismatched species, together with declining probability density, indicates that climatic conditions are moving away from the realized thermal preferences of the plant community. By contrast, the lack of detectable change in grasslands and summits may reflect either reduced climatic displacement relative to forests or species assemblages with broader thermal affinities. Overall, these results suggest that comparing the difference in ΔT_{clim} and $\Delta T_{\mathrm{plant}}$ may have overestimated climatic debts in grasslands and alpine summits. The data also refine our understanding of climate debt by highlighting both directional responses and ecosystem-specific characteristics in tracking climate change.

Alpine summits are characterized by rugged topographic gradients that generate strong microclimatic heterogeneity, which may have strong impacts on vegetation thermophilization[36]. To assess the potential impacts of alpine summit topography on thermophilization, we derived TRI and slope data from a 30-m resolution digital elevation model using the terrain function from the terra R package (v.1.8.29) and extracted snow cover data from CHELSA (v.2.1) with a resolution of 30 arcsec (around 1 km)[75]. We found that neither TRI nor slope showed significant relationships with thermophilization rates (Extended Data Fig. 3a), which may be because in our database, only summit-level coordinates were available, and metrics such as TRI fail to capture the fine-scale microclimate that more strongly influence community responses. However, the thermophilization rate was significantly lower in north-facing slopes compared with south-facing slopes, and the snow cover change rate was lowest on northern aspects (Extended Data Fig. 3b). These findings indicate that microclimatic habitats, generated by rugged topographic gradients and slope aspect, could be a key mechanism in shaping thermophilization patterns on alpine summits.

To further evaluate whether the use of 20 × 20 km temperature data would bias the estimation of thermophilization rates on alpine summits, given that data at such a resolution may not adequately capture the fine-scale thermal conditions experienced by alpine plants, we extracted the climatic data of monthly mean temperature of the growing season from WorldClim (v.2) as a raster file with 30 arcsec resolution (about 1 × 1 km)[64] and re-estimated thermophilization rates on alpine summits using the same method and compared the results with those estimated using 20 × 20 km resolution temperature data. The results showed that the two sets of estimates were strongly correlated

(Extended Data Fig. 8a), and only a small difference was found between the thermophilization rates of the 95th percentile as estimated using Bayesian mixed-effects models (Extended Data Fig. 8b). Nevertheless, this difference will not affect the interpretation of the overall patterns of thermophilization on alpine summits, which demonstrated a high degree of consistency between the estimation of thermophilization derived from fine-resolution and coarse-resolution climate data, which indicates that the use of the 20 × 20 km resolution data remains appropriate and our core conclusions are robust to the choice of climate data resolution.

To evaluate whether spatial autocorrelation might bias the ecosystem effects on thermophilization rates, we incorporated a spatial Gaussian process (GP) term into our Bayesian mixed-effects models (model 3)[76]:

Thermophilization rate ~ ecosystem type + plot size + $T_{\text{clim baseline}}$ + GP(longitude, latitude) + (1|site).

We then compared the posterior distributions of the fixed-effect estimates for ecosystem type between the spatial and non-spatial model specifications. The results showed a high degree of consistency, with substantial overlap in the 95% CIs (Extended Data Fig. 8c). This strong agreement between the models indicates that spatial autocorrelation did not influence the estimated ecosystem effects, which is probably because the random intercept for 'site' captured most of the large-scale spatial structure. Given the robustness of the estimates and for the sake of model parsimony, we present the results from the simpler, non-spatial models.

Sources of uncertainty

Although we document general patterns of vegetation thermophilization and climatic debts here, uncertainties remain, which reflect inherent limitations in the data. First, declines and increases in species abundance may reflect sampling variation (for example, shifts in plant locations or inexact placement of quasi-permanent plots) rather than actual community changes between baseline surveys and resurveys, and the inclusion of quasi-permanent plots may therefore influence the overall patterns of vegetation response to warming. In our study, all the plots on alpine summits are permanent, whereas most of the plots are quasi-permanent in forests and grasslands. Regardless of their formal designation, all plots were located again using high-precision GPS coordinates or clearly documented map references, which ensured accurate resurveys across time. Although metadata did not always distinguish between permanent and quasi-permanent plots, the accuracy of finding the same location was closely comparable across plot types. Importantly, we restricted our inferences to averages across plots and at the community level rather than focusing on results from individual plots. Hence, small relocation errors only added some uncertainty to results rather than introducing any systematic bias in the magnitude or direction of effects at the community level (thermophilization). Moreover, many plants move over time, which means that even permanent plots that were exactly found at the correct location show shifts in composition and abundance. Our key conclusions are robust to these sources of noise as supported by a previous study[77] using a subset of the forest plots in our dataset. That study showed that the impact of relocation errors is limited when focusing on overall temporal changes in vegetation communities[77]. As such, the inclusion of both types of plots does not introduce systematic bias or influence the observed ecosystem-level patterns[77,78].

Second, although our study provides a unique opportunity to compare vegetation responses to climate warming across ecosystems using harmonized plot-level resurveys and standardized climate metrics, we acknowledge that full methodological standardization is not possible. The underlying datasets were originally collected by different monitoring networks using different survey protocols, plot sizes and time intervals. These differences may introduce some uncertainty into cross-ecosystem comparisons. Nevertheless, by applying consistent analytical methods and filtering to include only plots with comparable abundance data, we minimized potential bias and ensured the robustness of our main conclusions.

Third, another source of uncertainty may stem from the variation in time intervals between the baseline survey and resurvey across plots (Extended Data Fig. 1a). Some plots span multiple decades and are therefore more likely to capture clear climatic changes, whereas others have shorter intervals with potentially weaker climate signals. This temporal heterogeneity, which also differs among ecosystems, may influence the observed rates of thermophilization. Although such variation is inherent in resurvey-based studies and reflects logistical and historical constraints, it represents an important consideration when interpreting the strength and consistency of observed patterns.

Last, the distribution of our plots was skewed towards Northern and Central Europe, with comparatively fewer sites in Southern Europe (Fig. 1). Although the dataset still covers a broad range of European climatic and ecological gradients and is therefore suitable for continental-scale analysis, this spatial imbalance would still represent a source of uncertainty. Future research should aim to increase plot coverage in underrepresented southern regions of Europe to ensure more robust and spatially comprehensive assessments of thermophilization patterns.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The raw data used in this study are available at Figshare (https://doi.org/10.6084/m9.figshare.28368743.v5)[79]. Vegetation survey data include the forestREplot database (v.2.3; https://forestreplot.ugent.be) for forests, the GRACE database (https://doi.org/10.1111/jvs.12727)[57] for grasslands and the GLORIA database (https://gloria.ac.at) for alpine summits. Other publicly available datasets used in the study include climate data from CRU TS (v.4.07; https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.07) and WorldClim (v.2; https://rmets.onlinelibrary.wiley.com/doi/10.1002/joc.5086)[64], topography data from the R package elevatr (https://cran.r-project.org/web/packages/elevatr), species occurrence records from GBIF (https://doi.org/10.15468/dl.hffjcf) and snow cover data from CHELSA-bioclim (v.2.1; https://chelsa-climate.org).

Code availability

The R code used in this study is available at Figshare (https://doi.org/10.6084/m9.figshare.28368743.v5)[79].

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Author contributions K.Y. and P.D.F. conceived, designed and supervised the project. P. Vangansbeke, I.H.M.-S., D.M.W., K.V., M.B.-R., L.B., I.R.S., A.D.B., R.H., C.A., E.B., T.B., A.B.-S., J.-L.B.-A., J. Bennie, I.B., V.B., J. Brunet, J.M.B., H.V.C., M. Carbognani, M. Chudomelová, D.C.-K., P.D.T., G.N.D., G.D., J.D., M.D., T. Dirnböck, T. Durak, O.E., B.E., B.J.G., T.H., M.H., P.H., U.J., B.J., R.K., J.K., M.K., T.K., A.L., J.L., M. Macek, M. Malicki, F. Máliš, O.M., F. Mitchell, T.N., T.A.N., M.N., A.C.N., L.N., L.O., A.O., S.O., A.O.-A., J.d.O., H.P., G.P., P.P., R.P., M.P., C. Randin, K.R., C. Rixen, F.H.S., W.S., J.Š., A.S.-S., T.S., K.Ś., B.T., J.-P.T., T.-M.U., T.V., M.V., P. Vergeer, O.V., L.V., P. Vittoz, M.W., S.W. and P.D.F. are the members of the data-related working groups and/or contributed data. K.Y., P. Vangansbeke, F.W., S.Z. and P.D.F. performed the statistical analyses. K.Y. developed the manuscript, with contributions and editing from all co-authors.

Competing interests The authors declare no competing interests.

Additional information

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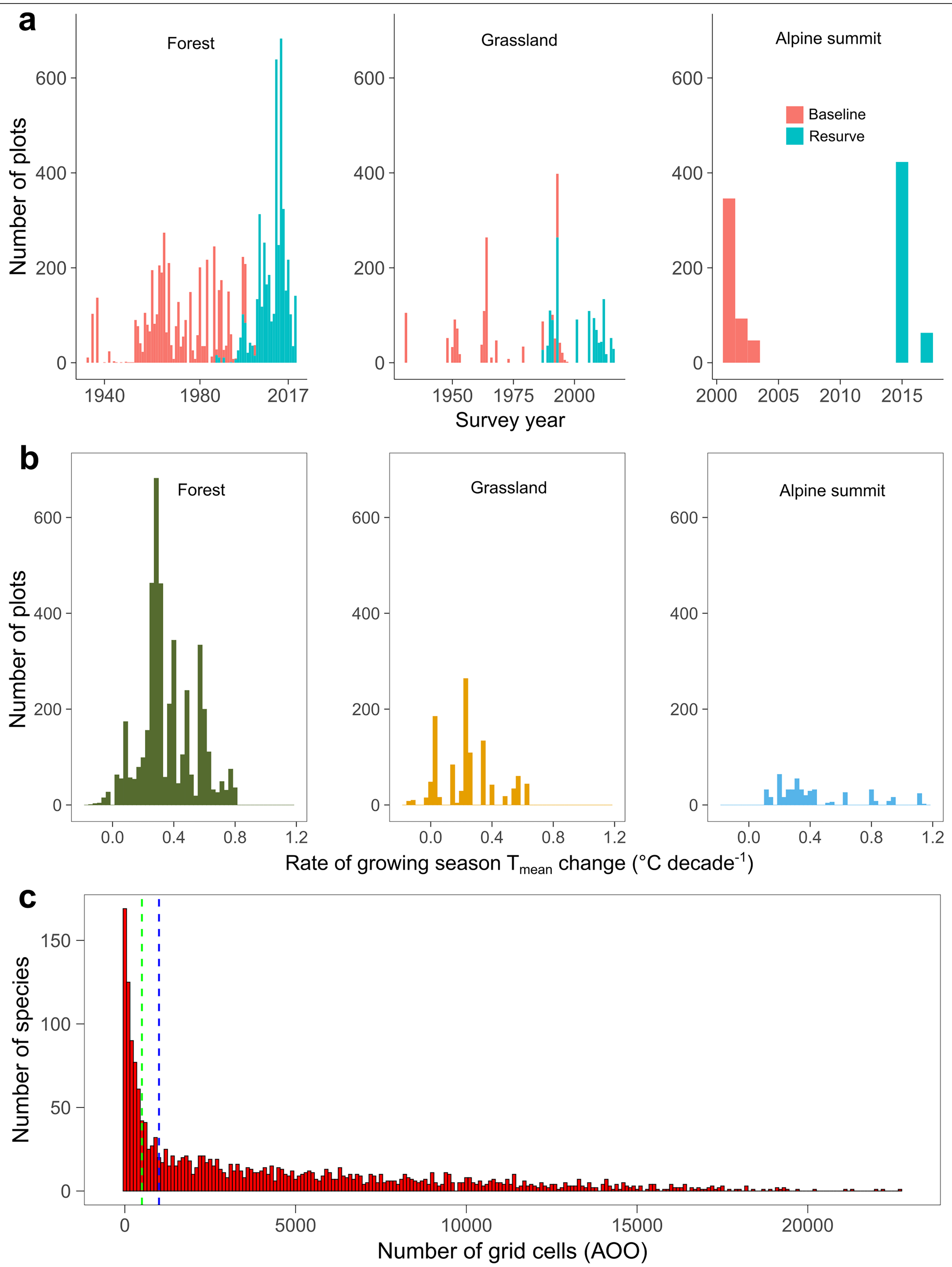
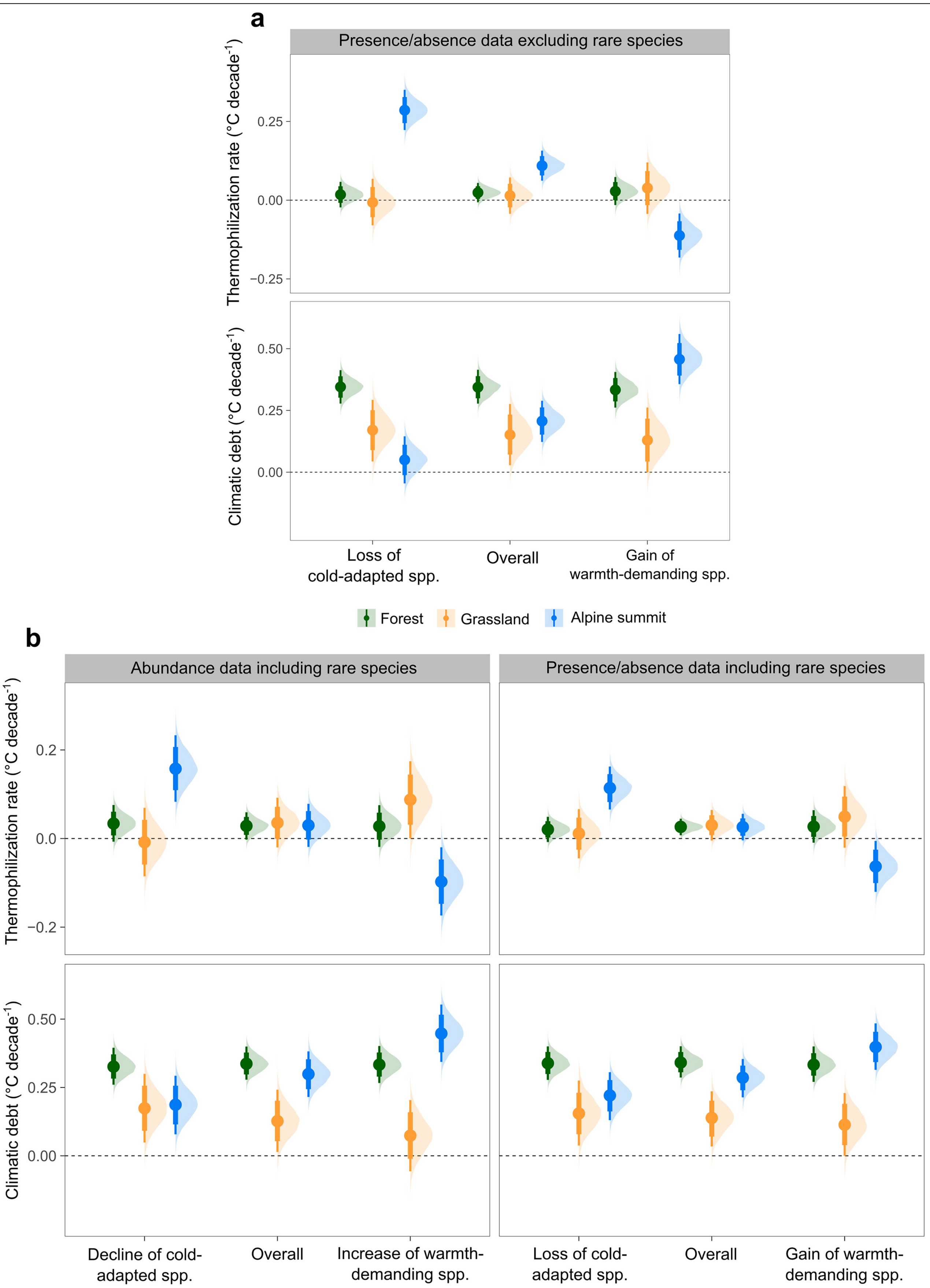


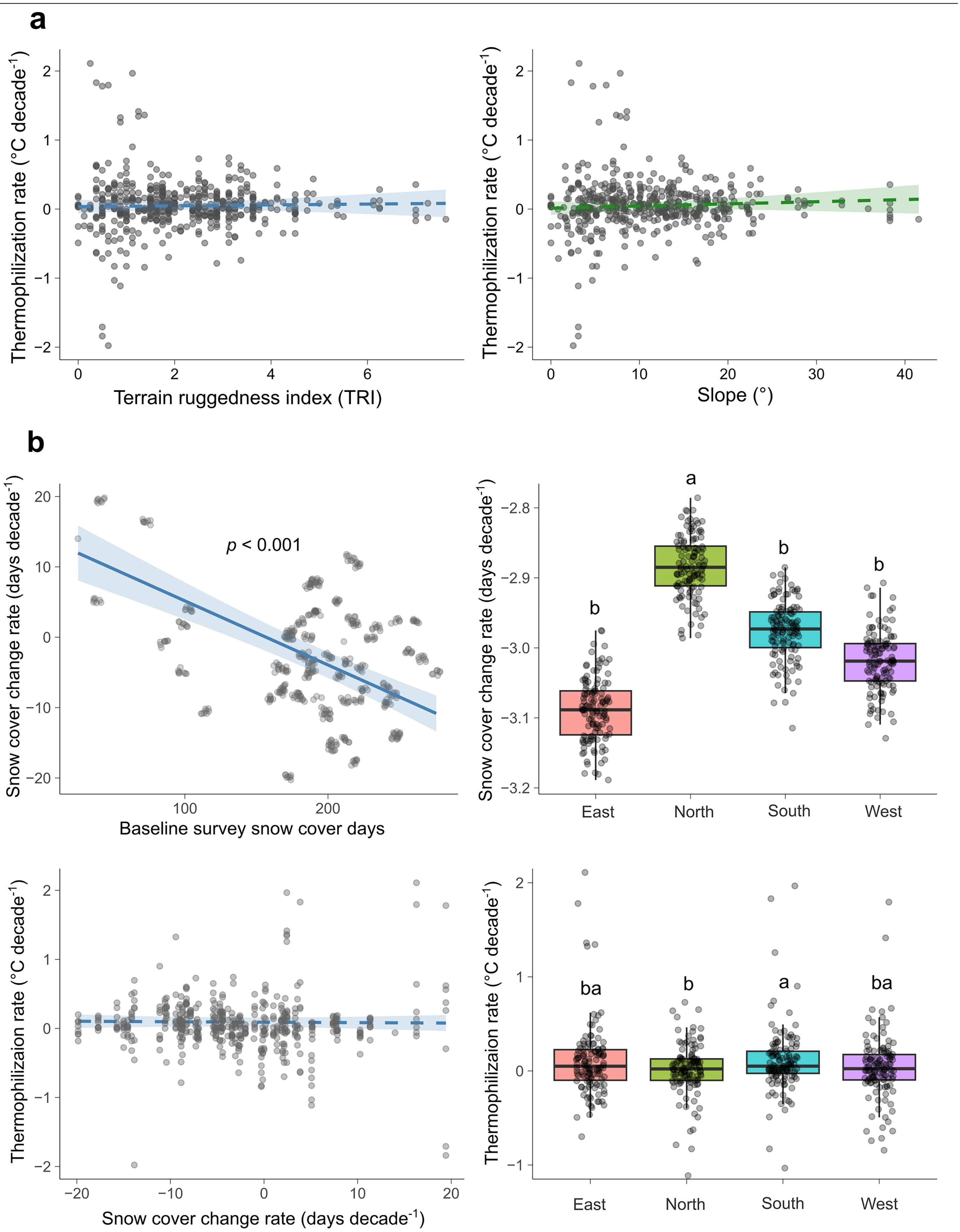
Extended Data Fig. 1 | See next page for caption.

Extended Data Fig. 1 | Frequency distributions of data for survey plots, climate, and plant species. **a**, Frequency distribution of plot at baseline and resurvey years in forest, grasslands, and alpine summits. **b**, Frequency distribution of growing season (April to September) mean temperature (T_{mean}) change rate across the duration of plant surveys in forests, grassland, and alpine summits. The rate of T_{mean} change for each plot was calculated as the difference between the average mean temperature during the 5 years preceding the baseline survey and the resurvey, divided by the time interval between the two surveys. The medians of the growing season T_{mean} change rate across forests, grasslands, and alpine summits were 0.31, 0.22, and 0.31 °C per decade, respectively. **c**, Frequency distribution of the number of grid cells representing species range sizes quantified by area of occupancy (AOO). Across the species pool in our study, 36.4% of the species have AOO < 1000, among which 77.5% of the species have AOO < 500. The green and blue dashed line indicate an AOO of 500 and 1000, respectively.



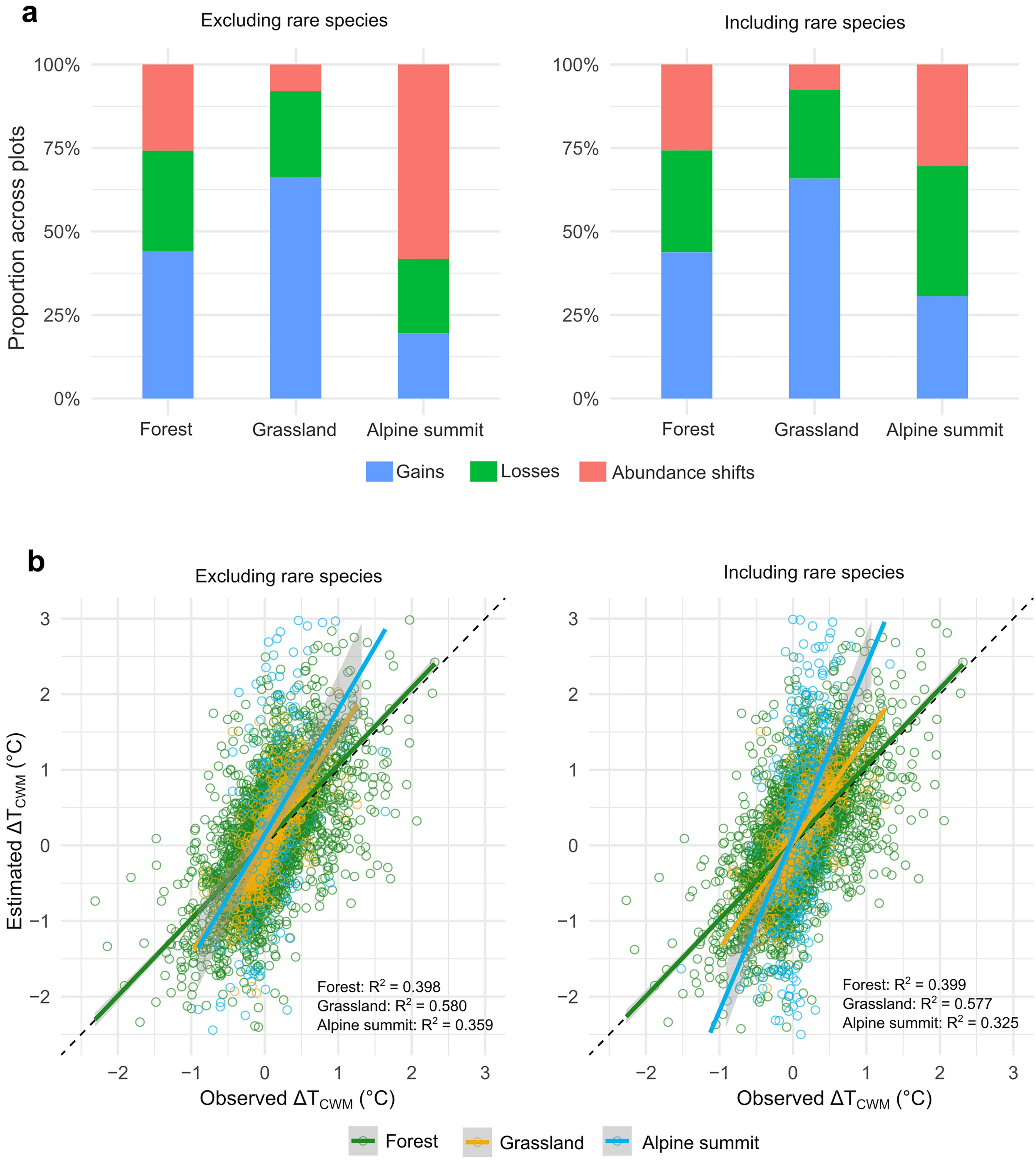
Extended Data Fig. 2 | See next page for caption.

Extended Data Fig. 2 | Vegetation thermophilization rate and climatic debts (°C per decade) in forests, grasslands, and alpine summits estimated using different datasets. a, Vegetation thermophilization rate and climatic debt quantified as the loss of cold-adapted species (5th percentile shift), overall (median shift), and gain of warmth-demanding species (95th percentile shift) using plant presence/absence data excluding rare species. Circles represent means (*n* = 4372, 1209, and 457 plots for forests, grasslands, and alpine summits, respectively) with 80% (thick line) and 95% (thin line) credible intervals (CIs) and posterior distributions obtained from Bayesian mixed-effects models. These results are similar with those estimated using plant abundance data excluding rare species in Fig. 2. **b**, Vegetation thermophilization rate and climatic debt quantified as the decline/loss of cold-adapted species (5th percentile shift), overall (median shift), and increase/gain of warmth-demanding species (95th percentile shift) using plant abundance and presence/absence data including rare species. Circles represent means (*n* = 4372, 1209, and 486 plots for forests, grasslands, and alpine summits, respectively) with 80% (thick line) and 95% (thin line) CIs and posterior distributions obtained from Bayesian mixed-effects models. The overall patterns for thermophilization rate and climatic debt are in line with those estimated using plant data excluding rare species.

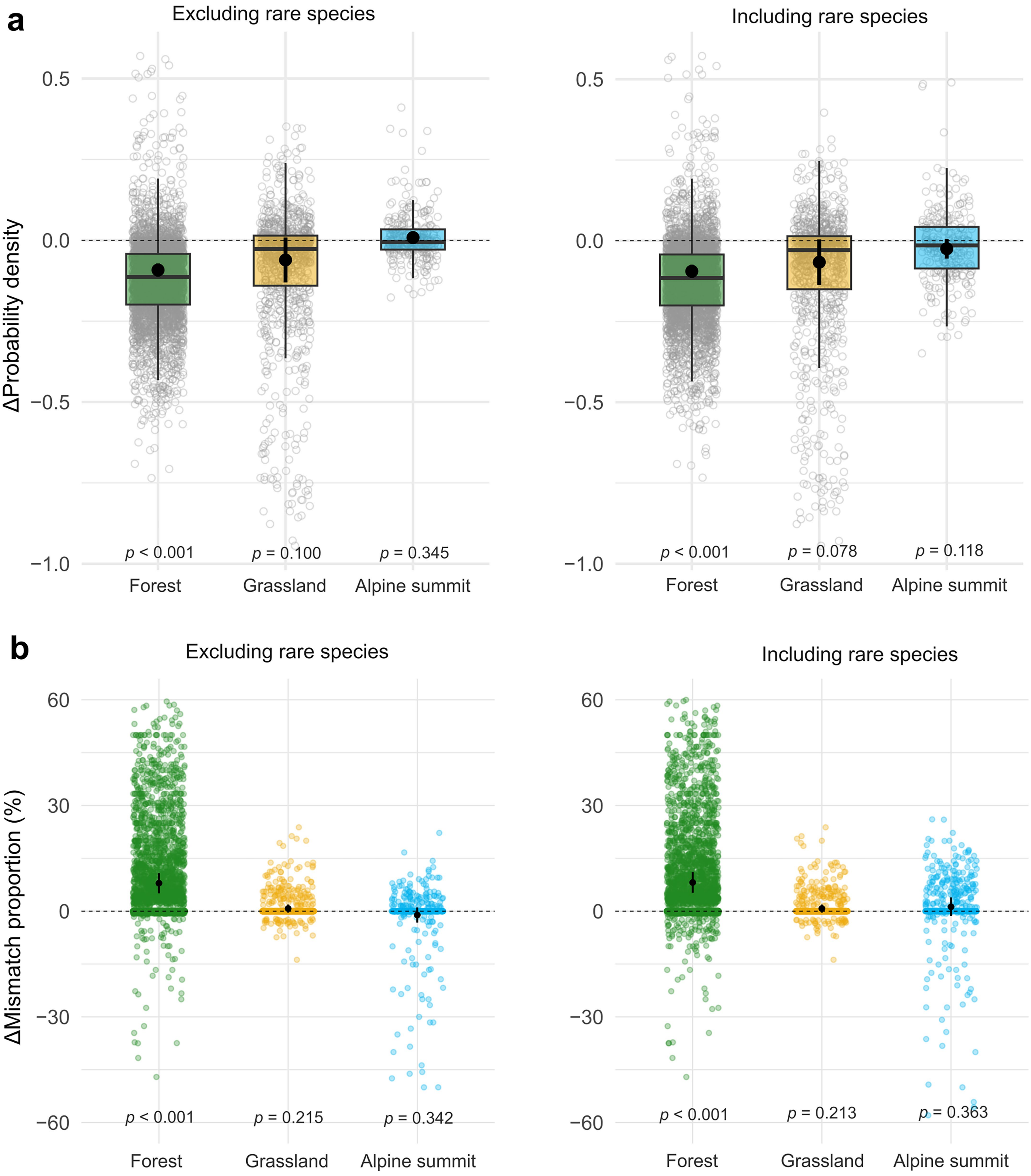


Extended Data Fig. 3 | See next page for caption.

Extended Data Fig. 3 | Impacts of topography, snow cover and slope aspect on vegetation thermophilization rates on alpine summits. a, Relationships between thermophilization rates and terrain ruggedness index (TRI) and slope. Each point represents a plot ($n = 457$), and shaded bands around fitted lines indicate 95% confidence intervals (CIs) from linear mixed-effects models with "site" as a random effect. Thermophilization rates were calculated using the median of the floristic temperature distributions that were estimated with vegetation abundance data excluding rare species. TRI and slope were derived from a 30-meter resolution digital elevation model (DEM) using the *terrain* function from the *terra* R package. **b**, Impacts of snow cover days and slope aspect on vegetation thermophilization rate. Thermophilization rates were estimated using vegetation abundance data excluding rare species, and data for snow cover were extracted from CHELSA version 2.1 (30 arc-sec resolution, around1 km). Box plots show the median (centre line), the 25th and 75th percentiles (bounds of box), and the minimum and maximum values (whiskers). Each point represents a plot ($n = 457$), and a slight jitter was applied to the points to better visualize overlap, where applicable. Snow cover change rate was calculated as the difference in mean snow cover days between the five years preceding the baseline survey and the five years preceding the resurvey, divided by the time span (in decades) between the baseline and resurvey surveys. Statistical differences were assessed using linear mixed-effects models with "site" as a random effect. Different lowercase letters denote significant differences among slope aspects, based on Tukey's post-hoc tests (two-sided, adjusted for multiple comparisons at $p < 0.05$). Shaded bands around fitted lines indicate 95% CIs from the linear mixed-effects models.

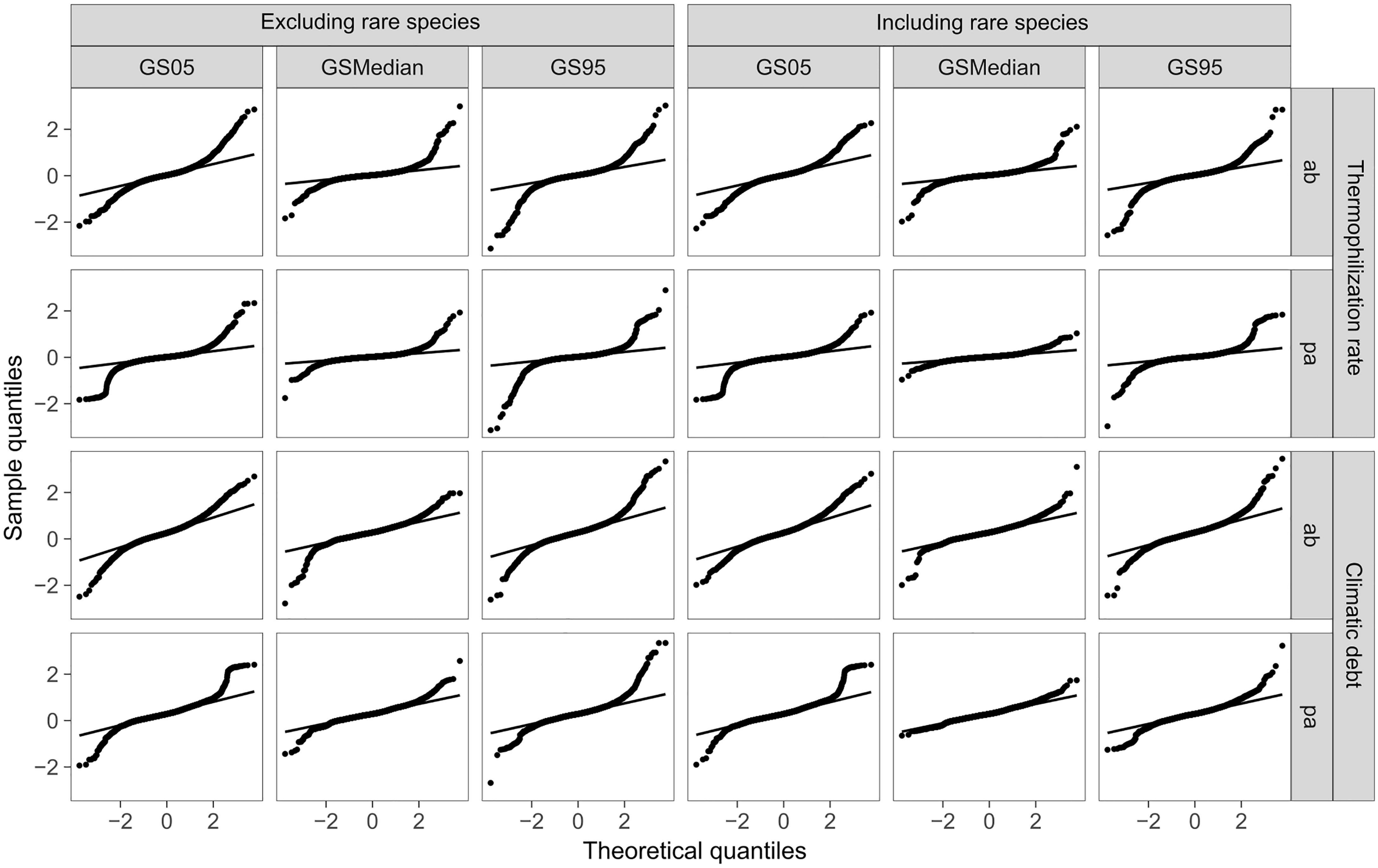


Extended Data Fig. 4 | Thermophilization explained by the mechanisms of species gains, losses, or abundance shifts in different ecosystems. **a**, Proportions of plots in which thermophilization was primarily driven by mechanisms of species gains, losses, or abundance shifts. The dominant mechanism was identified for each plot as the one contributing the most (in absolute terms) to the observed shift in community thermal affinity. These results indicate that thermophilization was mainly driven by mechanisms of gains in grasslands, gains and losses in forests, and losses and abundance shifts on alpine summits. **b**, Relationship between observed versus estimated community-weighted mean temperature (ΔT_{CWM}) for different ecosystem types without or with rare species. The sum of gains, losses, and abundance shifts of persisting species was used to estimate ΔT_{CWM} per plot and compared with the observed ΔT_{CWM}. Each point represents a plot (n = 4372, 1209, and 457 for forests, grasslands, and alpine summits, respectively), coloured by ecosystem type. Solid lines represent linear regression per ecosystem with 95% confidence intervals, and the dashed line denotes the 1:1 relationship. The significant linear relationships between estimated and observed ΔT_{CWM} indicate that the three mechanisms collectively provide a reasonable explanation for observed thermophilization patterns.

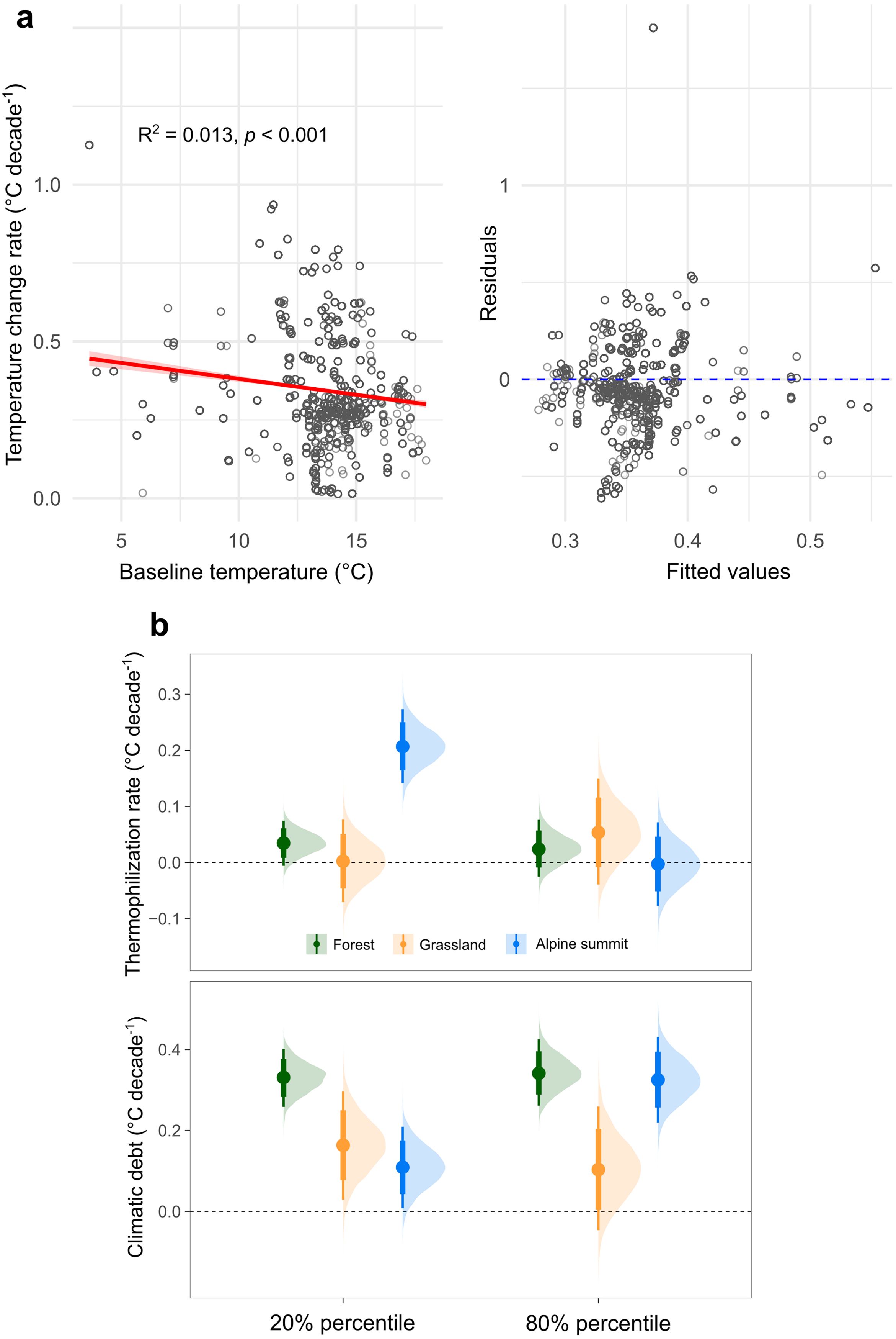


Extended Data Fig. 5 | See next page for caption.

Extended Data Fig. 5 | Changes in the probability density of species thermal suitability and the proportion of thermally mismatched species in different ecosystems. **a**, Changes in the probability density of thermal suitability under local climate (T_{clim}) inferred from plot-level floristic temperature (T_{plant}) distributions. Boxplots showing changes in probability density of T_{plant} between baseline survey and resurvey (Δ = resurvey – baseline survey), with the centre line indicating the median, the box representing the 25th and 75th percentiles, and the whiskers showing the minimum and maximum values. These results show that the probability density at T_{clim} significantly and marginally decreased from baseline to resurvey in forest and grassland ecosystems, respectively, suggesting increasing climatic mismatch. **b**, Changes in the proportion of thermally mismatched species (Δ = resurvey – baseline survey). Mismatch is defined as background macroclimate falling outside of the 2.5–97.5% range of a species' thermal distribution. These results suggest that the proportion of mismatched species significantly increased in forests, but not in grasslands or on alpine summits. In both panels **a** and **b**, each point represents a plot (*n* = 4372, 1209, and 457 for forests, grasslands, and alpine summits, respectively), and the black circles with error bars indicate means with 95% confidence intervals estimated using linear mixed-effects models with "site" as a random-effects factor, and the *p* values indicate whether change differs significantly from zero (linear mixed-effects models; two-sided).

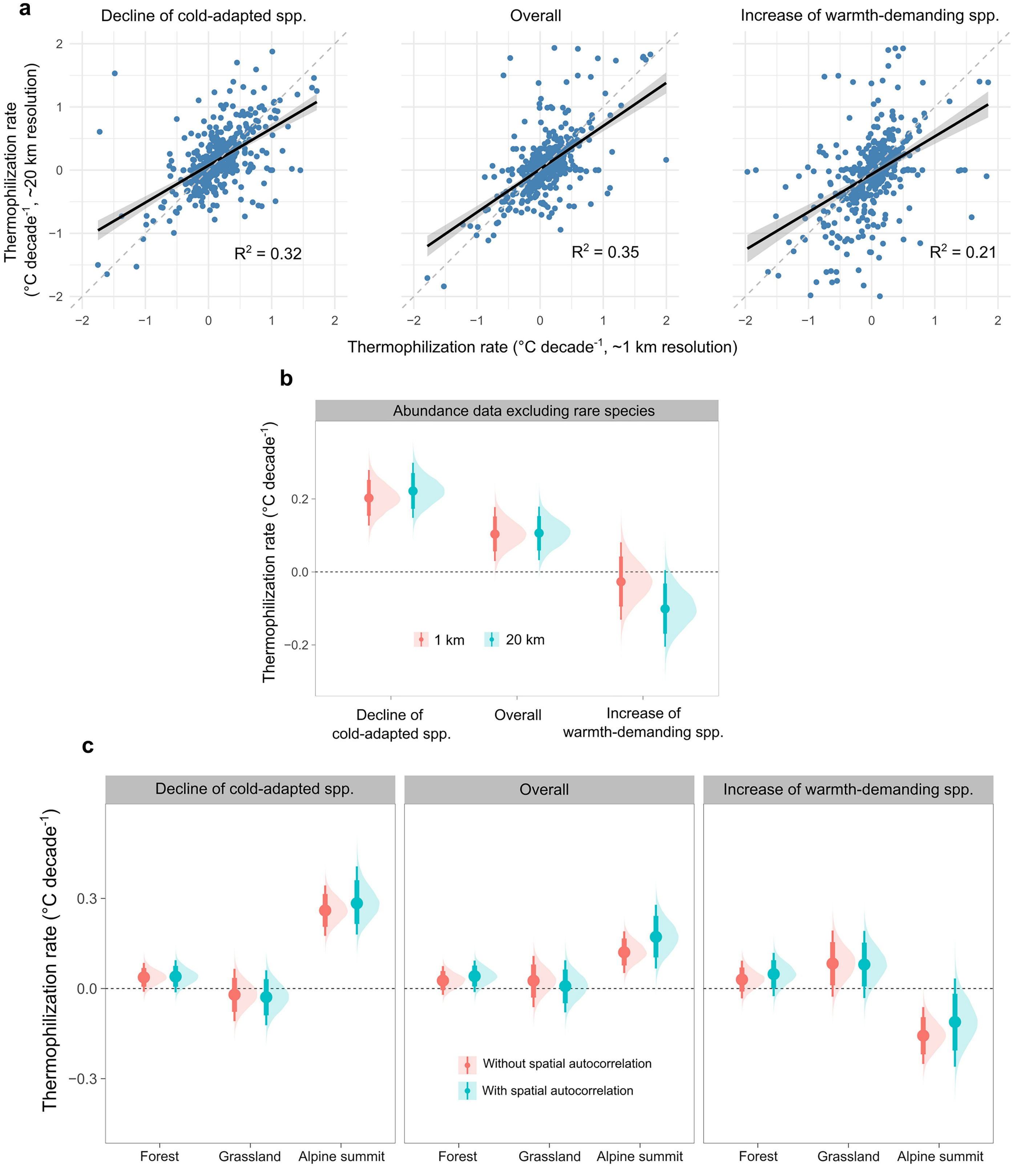


Extended Data Fig. 6 | Quantile-quantile (QQ) plots of vegetation thermophilization rates and climatic debts (°C per decade). Each plot ($n = 6038$ and 6067 for estimations excluding and including rare species, respectively) compares the sample quantiles of the observed data with the theoretical quantiles of a normal distribution. The degree of alignment with the 1:1 reference line indicates how well each variable approximates normality, informing the suitability of linear modelling assumptions. GS05, GSMedian, and GS95 indicate the 5th, median, and 95th percentiles of the floristic temperature distribution estimated using mean growing season temperature, respectively, and ab and pa indicate the abundance and presence/absence vegetation data, respectively. These plots show an approximately linear relationship between theoretical and observed quantiles, indicating the deviations from normality were minimal and not severe enough to invalidate the Gaussian assumption.



Extended Data Fig. 7 | See next page for caption.

Extended Data Fig. 7 | Climate warming patterns and vegetation thermophilization rate/climatic debt. a, Relationship between baseline temperature and temperature change rate of the growing season across ecosystems and the associated residual plot. Each point represents a plot (*n* = 6038), with the red line indicating the linear regression fit and the shaded red area showing the 95% confidence interval around the fitted relationship. These visual and statistical diagnostics suggest that a linear baseline temperature term provides a reasonable adjustment in the estimation of thermophilization rate and climatic debt, with no strong evidence that a more complex or non-linear formulation is necessary in our analysis. **b**, Vegetation thermophilization rates and climatic debts (°C per decade) in different ecosystems as estimated using the 20% and 80% percentiles of the floristic temperature distribution. Thermophilization rate and climatic data were estimated using vegetation abundance data excluding rare species. Circles represent means (*n* = 4372, 1209, and 457 plots for forests, grasslands, and alpine summits, respectively) with 80% (thick line) and 95% (thin line) credible intervals and posterior distributions obtained from Bayesian mixed-effects models.



Extended Data Fig. 8 | See next page for caption.

Extended Data Fig. 8 | Impacts of climate data resolution and spatial autocorrelation on vegetation thermophilization. **a**, Relationship between thermophilization rates estimated using fine (30 arc-sec, around 1 × 1 km) and coarse (10 arc-min, around 20 × 20 km) resolution climate data. Each point represents a plot (*n* = 457). The dashed lines represent the 1:1 relationship, while solid black lines show the fitted linear regression, with shaded bands indicating the 95% confidence interval around the fitted relationship. **b**, Overall thermophilziation rates estimated from Bayesian mixed-effects models using fine and coarse resolution climate data. Circles represent means (*n* = 457 plots) with 80% (thick line) and 95% (thin line) credible intervals (CIs) and posterior distributions obtained from Bayesian mixed-effects models. Thermophilization rates were quantified as the declines of cold-adapted species (5th percentile shift), overall (median), and increases of warmth-demanding species (95th percentile shift) using vegetation abundance data excluding rare species. **c**, Comparison of estimated thermophilization rates (°C per decade) with and without accounting for spatial autocorrelation using a Gaussian Process (GP). Circles represent means (*n* = 4372, 1209, and 457 plots for forests, grasslands, and alpine summits, respectively) with 80% (thick line) and 95% (thin line) CIs and posterior distributions obtained from Bayesian mixed-effects models. Thermophilization rates were quantified as the declines of cold-adapted species (5th percentile shift), overall (median), and increases of warmth-demanding species (95th percentile shift) using vegetation abundance data excluding rare species. The overlapping 95% CIs across models suggests that spatial autocorrelation does not confound the observed ecosystem differences in thermophilization, and that the ecosystem effects are robust to spatial structure.

Extended Data Table 1 | Detailed information on the databases of forests, grasslands, and alpine summits used in this study

Ecosystem	Database	Number of plots	Number of sites	Earliest year of baseline survey	Latest year of resurvey	Range of intercensal time span (year)	Website	Key Reference
Forest	forestREplot	4372	76	1933	2020	12–78	forestreplot.ugent.be	Verheyen et al., 2012[80]
Grassland	GRACE	1209	22	1931	2016	16–78		Diekmann et al., 2019[57]
Alpine summit	GLORIA	486	64	2001	2017	12–15	gloria.ac.at	Pauli et al., 2015[58]

Key references: 57,58,80.

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n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
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☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software or code was used in the collection of community composition data.
Data analysis	All the statistical analyses were conducted using R version 4.4.2. Vegetation thermophilization rate and climatic debt were estimated using Bayesian mixed-effects models with the brms package (version 2.22.0). The elevatr package (version 0.99.1) and terra package (version 1.8.29) were used to extract and process topography data, and the ggh4x package (version 0.3.1) to generate figures. No custom code was developed in this study.

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- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Raw data used in this study are available at figshare (https://doi.org/10.6084/m9.figshare.28368743.v5). Vegetation survey data include the forestREplot database version 2.3 (www.forestreplot.ugent.be) for forests, the GRACE database (https://doi.org/10.1111/jvs.12727) for grasslands, and the GLORIA database (https://gloria.ac.at) for alpine summits. Other publicly available datasets used in the study include climate data from CRU TS version 4.07 (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.07) and WorldClim v.2 (https://rmets.onlinelibrary.wiley.com/doi/10.1002/joc.5086), topography data from the R package elevatr (https://cran.r-project.org/web/packages/elevatr), species occurrence records from GBIF (https://doi.org/10.15468/dl.hffjcf), and snow cover data from CHELSA-bioclim version 2.1 (https://chelsa-climate.org).

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	not applicable.
Reporting on race, ethnicity, or other socially relevant groupings	not applicable.
Population characteristics	not applicable.
Recruitment	not applicable.
Ethics oversight	not applicable.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study analyzed multidecadal data from (quasi-)permanent plots resurveyed over 12–78 years in forests, grasslands, and alpine summits across Europe, aiming to evaluate if thermophilization and climatic debts of plants vary among these contrasting habitats.
Research sample	We focused on vascular plant species in forest understory layer and in grasslands and alpine summits across Europe. Data used in this study were from three available databases, the forestREplot database version 2.3 (www.forestreplot.ugent.be) for forests, the GRACE database for grasslands, and the GLORIA (https://gloria.ac.at) database for alpine summits. Details about the databases are available in the following references: 1. Verheyen, K. et al. Combining biodiversity resurveys across regions to advance global change research. BioScience 67, 73-83 (2017). 2. Diekmann, M. et al. Patterns of long-term vegetation change vary between different types of semi-natural grasslands in Western and Central Europe. Journal of Vegetation Science 30, 187-202 (2019). 3. Pauli, H., Gottfried, M., Lamprecht, A., Niessner, S., Rumpf, S.B. & Winkler, M. et al. (2015). The GLORIA field manual-standard Multi-Summit approach, supplementary methods and extra approaches. Vienna: GLORIA-Coordination, Austrian Academy of Sciences & University of Natural Resources and Life Sciences. ISBN: 978-92-79-45694-7.
Sampling strategy	We included the available plant community composition data, and sample size was thus not predetermined but rather a maximum possible based on available data.
Data collection	Data was collected by many different people at diverse locations across Europe (see author contribution statement).
Timing and spatial scale	Plant community composition data were collected between 1933 and 2020 at 76 sites in forests, between 1931 and 2016 at 22 sites, and between 2001 and 2017 at 64 sites across Europe.
Data exclusions	To make sure the plant communities have enough time to respond to climate warming, we only used data with a time period between baseline survey and resurvey no less than 10 years.
Reproducibility	This study was not experimental, but the large number of sampling sites for all three ecosystems across Europe ensures good spatial replication.
Randomization	This study is non-experimental; therefore, samples were not randomly assigned to experimental groups.

Blinding	Vegetation surveys were not carried out with the goal of documenting community composition change over time, and thus bias in data collection is unlikely.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Field conditions varied by ecosystem types and sites. Site climate conditions varied across sites and sampling time. Information about temperature changes is shown in the Methods section of the study.
Location	Plant composition data were collected from forests, grasslands, and alpine summits across Europe, the distribution of plots is shown in Figure 1.
Access & import/export	The appropriate data collection permits, which varied among different sites and countries, were obtained whenever necessary.
Disturbance	Vegetation sampling was non-destructive.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern
☐	☒	Plants

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
☒	☐	Public health
☒	☐	National security
☒	☐	Crops and/or livestock
☒	☐	Ecosystems
☒	☐	Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No | Yes
☒ ☐ Demonstrate how to render a vaccine ineffective
☒ ☐ Confer resistance to therapeutically useful antibiotics or antiviral agents
☒ ☐ Enhance the virulence of a pathogen or render a nonpathogen virulent
☒ ☐ Increase transmissibility of a pathogen
☒ ☐ Alter the host range of a pathogen
☒ ☐ Enable evasion of diagnostic/detection modalities
☒ ☐ Enable the weaponization of a biological agent or toxin
☒ ☐ Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	not applicable.
Novel plant genotypes	not applicable.
Authentication	not applicable.