

Alpine plant thermophilisation is driven by shrubs, snow and microclimates

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Abstract

Shrubification (i.e., increasing shrub abundance) and thermophilisation (i.e., increasing dominance of warmth-demanding species) are among the most widely documented imprints of climate change on mountain ecosystems. Still, it remains insufficiently quantified how increasing shrub cover alters the near-ground microclimate and snow duration, and in turn, how this interacts with the climate-change responses of alpine plant communities. To this end, we leveraged 21 years of vegetation resampling data and soil temperature time-series from 576 permanent plots positioned on European mountaintops and covering the treeline ecotone up to the middle alpine belt. Snow duration decreased faster in plots with stronger macroclimate warming, which in turn led to a rise in minimum soil temperatures of 0.28 °C per decade across all plots. Overall thermophilisation rates were higher in sheltered habitats with snow accumulation, while habitats with higher shrub cover showed faster loss of cold-adapted species. Further research is needed to disentangle the joint effects of shrubs, snow and microclimates, yielding more accurate projections of climate-induced plant community reshuffling in alpine habitats.

Keywords

Alpine biome, climate change, European mountaintop flora, GLORIA network, microclimate, plant community turnover, shrubification, vegetation resampling

1. Main text

1.1. Introduction

The alpine belt of Europe's mountain ranges, being situated above the upper limit of tree growth, consists of a mosaic of grasslands and heathlands interspersed with rocks (outcrops, cliffs, screes) and wet habitats (lakes, streams, wetlands) (Körner and Spehn 2019, Rahbek et al. 2019a,b). Alpine ecosystems disproportionally contribute to the overall vascular plant diversity of the continent (Väre et al. 2003) and support high levels of endemism relative to lower elevations (Körner 2004, Marder et al. 2025). Their proximity to the treeline also implies a strong influx of lowland species that benefit from warming and move upwards under climate change (Rumpf et al. 2018, Rumpf et al. 2019a, Iseli et al. 2023, Barros et al. 2025). Mountaintops across Europe have been regarded for decades as symbols of climate-driven shifts in species distributions (Pauli et al. 2012, Steinbauer et al. 2018), provoking the “elevator-to-extinction” hypothesis with upslope displacements, and ultimately, mountaintop extirpations (Urban 2018, Chen et al. 2025).

Thermophilisation, that is, the increasing dominance of warmth-demanding species at the expense of cold-adapted species, occurs across European mountain flora as more species become established at higher elevations (Gottfried et al. 2012, Hausharter et al. 2026, Yue et al. 2026). This has led to local extinctions of

small, light-demanding, and slow-growing cold-adapted mountain species, which are replaced by taller, more vigorous, and thermophilic generalists that colonize from lower elevations (Steinbauer et al. 2018, Nomoto et al. 2024, Wessely et al. 2026). Yet, many community responses are lagging behind climate warming, leading to a disequilibrium referred to as “climate debts” (Dullinger et al. 2012, Rumpf et al. 2019b, Nomoto and Alexander 2021). Such debts may manifest themselves in the apparent resistance of mountain floras to climate change, which is likely caused by demographic inertia as well as a complex suite of interacting abiotic and biotic drivers (Alexander et al. 2018, Nomoto and Alexander 2021).

Perhaps one of the most important factors driving climate debts in mountain flora are the existence of microclimates caused by topographic complexity and associated variation in snow dynamics, vegetation and soil properties (Bramer et al. 2018, Körner and Hiltbrunner 2021, von Büren and Hiltbrunner 2022, Körner and Hiltbrunner 2026). Mountain plants have evolved to withstand the climatically demanding conditions of high-elevation habitats, and typically occur in small, dense growth-forms close to the ground where they are decoupled from the free-air temperature (Körner and Hiltbrunner 2021, Körner 2024). The near-surface microclimate, or soil thermal regime, is thus crucial to alpine plant life and persistence as well as the many ecosystem functions and processes associated with them (Niittynen et al. 2020, Kemppinen et al. 2021).

Mountain microclimates vary across space and time (Kemppinen et al. 2021a, von Oppen et al. 2022, Marta et al. 2023), among others due to the increasing shrub abundance and biomass across mountain ecosystems (Myers-Smith et al. 2011, García Criado et al. 2025a, Vanneste et al. 2026a). Shrubification is especially apparent in the low to middle alpine belt of Europe where warming temperatures and abandonment of livestock grazing are driving the expansion of woody species (Pajunen et al. 2012, Ameztegui et al. 2016, Mekkonen et al. 2021, Vanneste et al. 2026a, Verdonen et al. 2026). Shrubs are often the tallest plants occupying these ecosystems, where they can form dense thickets with closed canopies that modify the micro-environment experienced by low-stature alpine vegetation (Myers-Smith et al. 2011, Marsman et al. 2020, Kemppinen et al. 2021b, Domine et al. 2022, Domine et al. 2023).

Shrubs impact near-ground microclimates in complex ways, mostly through shading and evaporative cooling during the growing season, and in winter, by trapping and accumulating snow between their branches resulting in local soil warming under the thicker, insulating snowpacks (Myers-Smith et al. 2011, Vowles and Björk 2019). Conversely, shrubs can also act as thermal bridges fostering heat loss from the ground during autumn and winter, but heat gain and earlier snowmelt in spring (Domine et al. 2022, Domine et al. 2023). In addition, shrubs can also alter the structure and density of the snowpack (see, e.g., Lathrop et al. 2025) with more intricate and unexpected consequences for the soil thermal regime as well as the herbaceous vegetation (Niittynen et al. 2018, Niittynen 2020).

Here, we present the first continental-scale study on the impact of shrubification on snow and soil microclimate dynamics in alpine ecosystems, and how this in turn interacts with the climate-change response

of the alpine plant communities (cf. Vanneste et al. 2026b) by using Europe's most extensive and long-term monitoring network of mountain floras, GLORIA (Global Observational Research Initiative in Alpine environments; <https://gloria.ac.at>). We merged vegetation resampling data from 576 permanent plots of 1 m² located from the treeline ecotone up to the middle alpine belt of Europe's major mountain ranges with two decades of soil temperature time-series (**Fig. 1, Extended Data Fig. 1, Fig. S1, Table S1**). This allowed us to assess how changes in snow cover duration and microclimate owing to shrubification have impacted the response of alpine plant communities to macroclimate warming over the past 21 years.

We expected that **(1)** given their generally higher stature, shrubs are more coupled to macroclimate (free-air temperature) warming. In contrast, the herbaceous communities growing close to the ground are decoupled from macroclimate and more related to microclimate (soil) temperature changes, **(2)** shrubs alter the surface albedo and snow cover duration, thus leading to a sustained rise in soil temperatures, and **(3)** unlike direct macroclimatic warming, these microclimatic changes are more likely to drive near-ground plant community shifts by speeding up thermophilisation rates and decreasing climate debts in heavily encroached alpine communities (**Fig. S2**). The treeline ecotone and low to middle alpine belt of Europe is a hotspot of shrubification, warming air temperatures, and changing snow patterns, hence providing an ideal natural testing ground for the proposed hypotheses (Weides et al. 2026, Vanneste et al. 2026b).

1.2. Results and discussion

Cascading effects: macroclimate warming reduces snow duration, which speeds up microclimate warming

Snow cover duration decreased at an average rate of 6.52 days per decade in the 1-m² plots (95% CI = 3.28 – 9.75 days per decade), despite increasing shrub cover with an average rate of 3.01% per decade (95% CI = 1.71 – 4.31% per decade). The decline in snow duration was primarily reinforced in sites with stronger macroclimate warming. We found a decrease of 13.4 snow days per extra °C of increasing minimum ambient temperatures (**Extended Data Fig. 2-3**), confirming earlier findings (Rumpf et al. 2022, Choler et al. 2025). Higher rock cover, however, tended to dampen the decline in snow cover. Rocky areas, often occurring along ridges, typically support greater microhabitat variation and thus more complex patterns of changes in snowmelt. Late in winter, however, large rocks also absorb and conduct heat from solar radiation more effectively, leading to faster snowmelt and reduced local snow persistence (Zeidler et al. 2025).

Stronger declines in snow cover duration were, in turn, positively associated with faster soil warming (**Extended Data Fig. 2-3**), likely due to changes in surface albedo and a prolonged growing season (as indicated by the significant increase in growing-degree days > 0 °C; **Fig. S3**). Across all plots, annual soil temperature minima increased by 0.28 °C per decade (95% CI = 0.19 – 0.36 °C per decade), but plots with warmer baseline soil minima did not increase as much (**Extended Data Fig. 2-3**). In contrast, plots with stable or even increasing snow duration over time showed more stable, or even cooling, soil minima.

Stable snow cover is often found in sheltered locations where snow drift is trapped, accumulates during winter, and remains present until late spring or even early summer (Björk et al. 2007, Huelber et al. 2011, Körner 2024). Indeed, plots with stable snow duration also had warmer baseline soil temperature minima (**Extended Data Fig. 2-3**), likely due to the insulating effect of a thick winter snowpack. Plots with a cooling microclimate but stable snow duration, on the other hand, could hint on altered snow composition, density or depth, and thus changes in the snowpack's thermal properties (Domine et al. 2022, Rumpf et al. 2022, Roussel et al. 2024, Choler et al. 2025). For instance, more frequent rain-on-snow events under climate warming create ice layers within the snowpack, thereby reducing its insulative capacity (Serreze et al. 2021).

Amplified thermophilisation in more stable microclimates

The herbaceous vegetation unexpectedly showed greater thermophilisation rates in plots with more stable soil temperature minima over time (**Fig. 2a-c, Fig. 3a**). Assuming these plots are located in sheltered sites with high snow accumulation, their resident community is composed of mat-forming species typical for late-lying snow, e.g., *Sibbaldia procumbens* interspersed with lichens, liverworts and mosses (Körner et al. 2003). This low-growing vegetation is more prone to invasion from, and competition by, opportunistic lowland species (Matteodo et al. 2016, Morgan and Walker 2023, Choler et al. 2024). Matteodo et al. (2016), for instance, reported an increasing frequency of tall thermophilous graminoids such as *Nardus stricta* in locations with late-lying snow during the past decades in the Swiss Alps. Sites with snow accumulation sometimes also harbour high densities of shrub species (e.g., *Vaccinium vitis-idaea*) that depend on the insulating effect of snow for protection against extreme winter temperatures and frost damage (Körner et al. 2003). These shrub layers could act as a mediator for thermophilisation by providing more benign microclimate conditions and facilitating colonization by warmth-demanding species (Schweiger et al. 2015).

Alternatively, stable or increasing snow cover duration could also be associated with altered snow distribution in dense patches of shrubby vegetation. Contrary to our hypotheses, however, both snow cover duration and soil microclimate seemed to be largely independent of shrub cover in our plots (**Extended Data Fig. 2-3**). The expected indirect relationships between shrubs, snow cover duration, and soil microclimate were thus absent from our dataset. Neither could we detect how these pathways proceeded into thermophilisation patterns of the herbaceous alpine vegetation. Overall, the complex impacts of shrubs on snow duration and soil microclimate need further investigation, given that shrubs also alter snow density and shrub branches tend to act as thermal bridges fostering heat loss from the ground in winter but heat gain in spring, thus leading to trade-off effects (see Domine et al. 2022, Domine et al. 2023).

Shrub-dominated sites lose their cold-adapted flora faster

Despite the lack of obvious interactive responses between shrubs, snow, microclimate and vegetation responses, we observed a clear decline in cold-adapted species across plots with higher baseline shrub cover (**Fig. 3a-b**). Most likely, shrubs outcompete many of the low-growing alpine specialists for light and nutrients,

while thick litter layers below deciduous shrubs such as *Betula nana* also inhibit emergence of short-statured, herbaceous species (Vanneste et al. 2017, Zehnder et al. 2020, García Criado et al. 2025b). Evergreen dwarf-shrubs are, however, also driving the shrubification and greening trend on European mountains (Bråthen et al. 2010, Vanneste et al. 2026a), with species such as the allelopathic *Empetrum nigrum* inhibiting seedling establishment and suppressing herbaceous plant growth in alpine grasslands (Tuomi et al. 2024, Bråthen et al. 2024, Maliniemi et al. 2025).

Vegetation thermophilisation rates also responded positively to macroclimate warming (**Fig. 3a-c**). Warmer free-air temperatures are likely to alleviate climatic constraints, fostering the establishment and expansion of warmth-demanding species that come from lower elevations (Steinbauer et al. 2022, Wessely et al. 2026). Hence, we would also have expected stronger thermophilisation rates close to the treeline due to the influx of warmth-demanding species from the nearby montane belt (i.e., similar to the “borealisation” trend observed across the southern Arctic; García Criado et al. 2025a,b), while the opposite was observed (**Fig. 3a-c, Extended Data Fig. 4**). Higher grazing intensity in low alpine belt could have attenuated climate-induced community reshuffling by selective browsing on newly arriving, warm-adapted species with traits related to higher palatability (e.g., greater stature and leaf area, higher leaf nutrient levels, etc.; Dostálek et al. 2020). While the GLORIA summits were originally selected in areas where grazing activities by, e.g., livestock are minimal or absent (Pauli et al. 2015), some of the lower mountaintops in our dataset are still regularly visited by cattle, sheep, or semi-domestic reindeers in the Scandes.

Still, more synthesising insights from long-term herbivore exclusion experiments across European mountain regions are needed to confirm this hypothesis (Saccone et al. 2014, Mayer and Erschbamer 2017, Petit Bon et al. 2020, Marsman et al. 2020, Kaufmann et al. 2021, Yan et al. 2026). Alternatively, Hausharter et al. (2026) showed that, even though fewer species are available for colonization further from the treeline, the variation in thermal niches of the species that are already present tends to be higher as well as the proportion of cold specialists, and thus potential loser species, resulting in more opportunities for community reshuffling.

Climate debts are mostly caused by limited space and substrate

Climate debts, calculated as the difference between macro- or microclimate warming and vegetation thermophilisation, were generally low in our plots and, on average, not clearly different from zero – except for macroclimate debts in warmth-demanding species and microclimate debts in cold-adapted species (**Fig. 2d-f, Fig. S4**). The herbaceous communities observed across European summits thus seem to be in equilibrium or closely following rising ambient air and soil temperatures. Previous research from mountain environments in Europe and elsewhere have documented considerable climate debts in alpine plant populations and communities owing to the inherent life-history or eco-physiological characteristics of species (e.g., longevity, clonal growth and limited dispersal capacity) as well as the buffering effects of

topographically heterogeneous alpine landscapes (Dullinger et al. 2012, Rumpf et al. 2019a,b, Nomoto and Alexander 2021).

Larger macroclimate debts were detected in plots with higher rock cover and less bare soil (**Fig. S5**). Rock cover represents a physical barrier for upward-moving species' establishment, while topographic complexity in rocky terrain provides microrefugia for cold-adapted specialists to persist (Körner and Hiltbrunner 2026). At even higher elevations, i.e., beyond the alpine grassland line, upward species movements into the rock-dominated nival belt will thus likely be slowed down by limited space for colonization and slow soil formation (Vrábel et al. 2026). Lack of suitable substrate, moisture and nutrients are likely key limiting factors inhibiting upslope plant migration induced by climate change (see also Liu et al. 2026, Vanneste 2026). Macroclimate debts also tended to decrease further away from the treeline (**Fig. S5**), which is in line with our previous conjecture that grazing close to the treeline is likely to selectively remove warmth-demanding colonizers thereby halting thermophilisation rates in the herbaceous communities.

Microclimate debts appeared to be overall independent of site characteristics, but responded significantly to the rate of soil warming (**Fig. 3e**). For cold-adapted species, however, the thermal mismatch seemed to be lower in plots with longer snow persistence and stable or decreasing soil temperature minima (**Fig. 3e**). The latter supports the conjecture that sheltered locations with high snow accumulation and more stable soil temperature regimes can be hotspots of plant community reshuffling.

Synthesis and implications for future research

Accounting for baseline vegetation conditions is essential for understanding and interpreting rates of vegetation change. For example, shrub cover change was not consistently linked to macroclimatic warming, but depended strongly on the initial abundance of shrubs within plots (**Extended Data Fig. 2-3**). The magnitude of shrubification was lower where shrub cover was already high, likely because of limited space and inter-specific competition between shrub species and populations already present. A similar pattern emerged for vegetation thermophilisation. Herbaceous communities initially composed of more warmth-demanding species exhibited lower rates of further thermophilisation, and vice versa (**Extended Data Fig. 5**). Our findings underpin that ecological responses to climate change are strongly contingent on the baseline vegetation as this determines the amount of ecological and functional niche space available for change and therefore shapes the magnitude of vegetation responses.

Notably, part of the observed thermophilisation signal may also be related to other niche axes that covary with, and are not causally linked to, temperature; including other snow parameters or soil texture, water and nutrients. Multifactorial experiments that manipulate, e.g., moisture, snow, and soil temperature changes in tandem could provide a deeper understanding and more precise projections of plant community responses in above-treeline ecosystems. We simplified topographic complexity as plot-level rock cover. However, future studies could explore the role of microtopography in shaping vegetation thermophilisation patterns

using high-resolution remote sensing techniques such as drones and airborne laser scanning. Besides topography, we did not account for other surface features and processes related to, for instance, hydrological, geological or geomorphological heterogeneity in mountain terrains (i.e., *geodiversity*; le Roux et al. 2013a,b, le Roux and Luoto 2014, Kemppinen et al. 2022, Salminen et al. 2023). These factors could further explain the observed variation in thermophilisation rates and climate debts.

In summary, we uncovered clear direct relationships between shrub cover and the decline of cold-adapted species, and between macroclimate warming and gain of warmth-demanding species. Together, these direct mechanisms prevailed in driving overall thermophilisation rates and community reorganization on the European alpine summits. The observed thermophilisation rates proceeded differently depending on the rate of soil warming or local site conditions, being attenuated in rock-covered terrain but amplified in habitats located in depressions or leeward positions, where snow accumulates, offering large amounts of unfilled niche space. The hierarchical approach adopted here provides mechanistic insights that suggest causal pathways into plant community assembly above the treeline, and unveils asynchronous reshuffling across different alpine habitat types.

Even though time lags between climate warming and compositional changes in herbaceous communities are far from uncommon in mountain environments (Rumpf et al. 2019, Chen et al. 2025, Yue et al. 2026), we demonstrate that plant communities in the treeline ecotone and lower alpine belt of Europe are shifting fast and already tracking climate warming over just two decades. Given the contemporary acceleration in climate warming rates, our approach supports future projections of plant community trajectories above the treeline. This, in turn, informs urgently needed management strategies, such as ex-situ conservation of cold-adapted species or reintroduction of traditional livestock grazing practices to counteract shrubification as well as competition-driven replacements by taller and acquisitive thermophilic species. In particular, the widespread shrubification and thermophilisation trends in herbaceous communities detected here across a broad set of European mountaintops, could hint at increased risk of biotic homogenization, disruption of ecosystem functioning and food webs, and local species extirpations (see Vanneste et al. 2024, Wessley et al. 2026), making it not only timely but also imperative to enhance mountain ecosystem resilience and mitigate future biodiversity loss under contemporary climate change.

2. Methods

2.1. Study area and setup

Data on percentage cover of all vascular plant species were gathered from a wide array of permanent plots, spread across Europe's major mountain regions. These plots are part of the GLORIA network, i.e., a global and long-term monitoring program devoted to studying the impact of climate change on our planet's mountaintop flora. Here, we used a subset of the European GLORIA dataset with eighteen different mountain sites (**Fig. 1a**). Each mountain site consisted of four summits spread across an elevational gradient from

subalpine grasslands near the treeline up to the uppermost limit of vascular plant life (or the highest vegetation zone available). A standardized setup of permanent plots was used to monitor vegetation and microclimate dynamics on the mountain summits, according to the protocol by Pauli et al. (2015). Each summit contained sixteen plots of 1 m², arranged in four quadrat clusters of 3 m × 3 m, of which only the four outer quadrats were surveyed. The quadrat clusters were always positioned in the major cardinal directions (North, East, South, West) at five elevational meters below the highest summit point. In this study, we only focused on the two lowest summits in each site, given that the lower to middle alpine vegetation belt is most strongly affected by shrub cover dynamics. The lowest summit was always located in the treeline ecotone or lower alpine belt with relatively continuous vegetation cover, while the second summit was situated further from the treeline in the middle alpine belt where vegetation cover has become more sparse and interspersed by rocks and scree (**Extended Data Fig. 1**). In total, this resulted in a dataset of 36 mountain summits with 576 permanent plots (see **Table S1** for a complete list of summits).

2.2. Shrubification

Species-level data on the occurrence and abundance (i.e., visual estimation of plant cover relative to the entire plot area) of all vascular plants were collected from the 576 plots at least twice over the past two decades (average sampling interval between baseline survey and last resurvey = 20.5 ± 0.9 years). First, we distinguished between shrubs and herbaceous (i.e., non-woody) species using the plant functional type classification by Plants of the World Online (POWO; <https://powo.science.kew.org>, considering both categories 'shrub' and 'subshrub' as shrubs). In total, 66 different shrub species were identified including 22 deciduous and 44 evergreen species (see Vanneste et al. 2026a for a complete shrub species list). The total shrub cover was calculated per plot as the sum of covers of all individual shrub species (in %). Next, the rate of shrub cover change (i.e., the shrubification trend) was determined as the difference in total shrub cover between the last resurvey and the baseline survey divided by the respective time interval, and recalculated to % change per decade.

2.3. Thermophilisation rate and climate debt

For all herbaceous (i.e., non-shrub) plant species per plot, the species-specific temperature niche was extracted from Yue et al. (2026). In this recent study, temperature niches were based on a combination of species geographical distribution ranges and gridded climate data. Species range sizes were estimated based on point occurrence records and the area of occupancy across Europe in the Global Biodiversity Information Facility (GBIF; www.gbif.org). Raw GBIF records were first aggregated to 20 km × 20 km grid cells and the area of occupancy was then computed as the total number of uniquely occupied grid cells of each species separately, hence minimizing bias due to overrepresentation of well-sampled locations. The species occurrences were then matched to the mean annual temperature grid (BIO1) of WorldClim v.2 with 20 km × 20 km resolution to quantify the realized thermal niche by species (i.e., climatic niche that can potentially be

occupied by a focal species across Europe). Next, to allow consistent estimates of thermal niches across species, also for species with very small distribution ranges, Yue et al. adopted a random sampling with replacement approach based on 1000 values with the median of these random samples representing the standardized species' climatic niche estimate.

For each plot, the community temperature index (CTI) was then calculated as the average temperature niche of all observed herbaceous species in the baseline survey and final resurvey, respectively (thus excluding species abundances). The thermophilisation rate was then quantified by the difference in CTI between the final resurvey and baseline survey divided by the temporal interval between the two survey timepoints (Δt). Because alpine plant populations and communities are known to respond slowly to changes in their environment owing to species longevity, clonal growth, demographic inertia, etc., the obtained thermophilisation rates were always recalculated to decadal rates ($^{\circ}\text{C}$ per decade), thus minimizing the effect of interannual variability and account for long-term trends. Positive values thus reflect overall increase in CTI, and thus an increase in dominance of warmth-demanding species and/or decline in cold-adapted species.

In addition to overall thermophilisation rates (i.e., temporal shift in mean CTI), the rate of change in 5th and 95th percentile of CTI was calculated to represent the communities' decline in cold-adapted species and gain in warmth-demanding species, respectively. This approach relying on the quantification of left and right tails of the plot-level species thermal niche distributions has been adopted previously by De Frenne et al. (2013), Zellweger et al. (2020) and Yue et al. (2026), and has been proven a robust method to assess thermophilisation due to a decline in relativity of cold-adapted species vs. an increase in frequency or abundance of warmth-demanding species. Note that is a per-plot relative quantification in the shift of cold-adapted vs. warmth-demanding species, and that the same species can be assessed as cold-adapted inside a plot in a warm site but as warmth-demanding inside a plot in a colder site. Plots with less than three herbaceous species were omitted from these calculations to avoid bias in the distribution-based (i.e., 5th and 95th percentile) variables.

Macro- and microclimate debts between baseline survey and last resurvey were calculated as the difference between the rate of air and soil temperature change, respectively, and the thermophilisation rates of the herbaceous vegetation (i.e., mean, 5th percentile and 95th percentile of CTI, and recalculated to $^{\circ}\text{C}$ per decade) (following Bertrand et al. 2016). Climate debts represent the thermal mismatch between plant communities and their surroundings, and thus the degree to which the rates of vegetation compositional changes are lagging behind the velocity of macro- or microclimate warming. Positive and negative values indicate that plant communities are responding slower or faster, respectively, than would be expected from the rates of climatic change. Finally, in addition to using presence/absence data for calculating thermophilisation rates and climate debts, we also used species relative abundances and presented the results in the section **Sensitivity analyses**.

2.4. Macroclimate, soil microclimate and snow

Gridded air temperature data were extracted from the online E-OBS database (<https://climate.copernicus.eu>, resolution approximately 10 km). We collected daily minimum, mean and maximum values between 2001 and 2022, and subsequently corrected those for the different summits' elevations based on daily lapse rate values and the elevational difference between the summits and the corresponding grid cells. The latter was extracted from the E-OBS digital elevation model. Daily minimum, mean and maximum values were then aggregated to the annual mean, minimum and maximum temperature, while the rate of macroclimate change was quantified as the regression slope between the annual temperature statistics and respective years and recalculated to °C change per decade.

Soil microclimate data were collected from each summit using miniature data loggers (GEOprecision M-Log5, <https://geoprecision.com>) which were buried at 10 cm below the soil surface and recorded the temperature at an hourly interval during the period 2001-2022. Data loggers were always positioned in the middle square of each 3 m × 3 m quadrat cluster (that is, four dataloggers per summit), and the soil temperature measurements were considered representative for the four outer squares used as vegetation plots. In total, 144 data loggers were deployed across the 36 studied mountain summits. For each logger, daily minimum and maximum values were calculated as the 5th and 95th percentile of the hourly values, respectively (hence avoiding extreme values). The daily mean temperature was then quantified as the average of the minimum and maximum temperature. Daily minimum, mean and maximum values were again aggregated to annual mean, minimum and maximum temperatures, while the rate of soil temperature change was quantified as the regression slope between the annual temperature statistics and respective years and recalculated to °C change per decade. However, given that some temperature records were incomplete due to battery failures or erratic measurements, we set a threshold of 80% of daily values to be available for calculating annual averages and at least three years separated across a 10-year period to be available for calculating a regression slope.

Snow cover duration was quantified based on the microclimate soil data records as the total number of snow cover days per year. A day was considered as snow-covered when the maximum temperature did not exceed 0.5 °C and the daily temperature range was below 2 °C (Man et al. 2023). The rate of change in snow cover duration was quantified as the regression slope between the annual total snow cover days and the respective years and recalculated to °C change per decade. At least three years separated across a 10-year period had to be available for calculating a regression slope.

2.5. Covariates

In addition to shrub cover, snow duration and soil microclimate dynamics, we quantified four environmental covariates that also play an important role in shaping thermophilisation rates and climate debts of the herbaceous communities. First, rock cover (i.e., visually estimated relative to the plot area) was used as proxy

for topographic complexity of the alpine terrain as well as a physical barrier for the establishment of newly-colonization species. Second, bare ground cover (i.e., also visually estimated relative to the plot area) was used as a proxy for potentially available habitat thus facilitating species colonisations. Third, the elevational distance of each plot to the nearest treeline was calculated based on visually estimated treeline position estimation by local site managers. The rationale here is that plots closer to the treeline are expected to receive a higher influx of lowland species that move upslope from outside the montane forest belt. Fourth, the amount of radiation received by mountain slopes of different aspects was estimated by computing the Heat Load Index (HLI). HLI values range between 0 (least) and 1 (most incoming solar radiation), and depend on the latitudinal position, aspect and steepness of the plots. It is a proxy for daily mean temperature amplification related to relief, i.e., topographic features most exposed to sunlight, as well as slope orientation with respect to the warmest period of the day (south and west slopes in the northern hemisphere) (Borderieux et al. 2025).

2.6. Data analyses

First, density plots were created for the rate of shrub cover change, change in snow duration, soil temperature (i.e., microclimate) change, thermophilisation and microclimate debt in the plot-level herbaceous plant communities. Both mean and 95% confidence intervals (CI) were calculated for each variable. If the 95% CI in the density plots did not contain zero, the rate of change over time was considered as statistically clear. Next, a mixed-effect modelling approach was used to assess the relationships between shrub cover change, change in snow duration, soil microclimate change, and vegetation thermophilisation and microclimate debts. Specifically, we designed a hierarchical framework mirroring our four main hypotheses, in which the both response variable and predictors of the first model were used as predictors in the second model, which then feed together in the third model, etc. (Eq. 1-6).

$$\frac{\Delta \text{shrub cover}}{\Delta t} \sim \frac{\Delta T_{\text{macro}_{\min}}}{\Delta t} + \text{baseline shrub cover} \quad (\text{Eq. 1})$$

$$\frac{\Delta \text{snow duration}}{\Delta t} \sim \frac{\Delta T_{\text{macro}_{\min}}}{\Delta t} + \frac{\Delta \text{shrub cover}}{\Delta t} + \text{baseline shrub cover} + \text{baseline snow duration} \quad (\text{Eq. 2})$$

$$\frac{\Delta T_{\text{micro}_{\min}}}{\Delta t} \sim \frac{\Delta T_{\text{macro}_{\min}}}{\Delta t} + \frac{\Delta \text{shrub cover}}{\Delta t} + \frac{\Delta \text{snow duration}}{\Delta t} + \text{baseline shrub cover} + \text{baseline snow duration} + \text{baseline } T_{\text{micro}_{\min}} \quad (\text{Eq. 3})$$

$$\frac{\Delta CTI}{\Delta t} \sim \frac{\Delta T_{\text{macro}_{\min}}}{\Delta t} + \frac{\Delta \text{shrub cover}}{\Delta t} + \frac{\Delta T_{\text{micro}_{\min}}}{\Delta t} + \frac{\Delta \text{snow duration}}{\Delta t} + \text{baseline shrub cover} + \text{baseline snow duration} + \text{baseline } T_{\text{micro}_{\min}} + \text{baseline CTI} \quad (\text{Eq. 4})$$

$$CD_{\text{macro}_{\min}} \sim \frac{\Delta T_{\text{macro}_{\min}}}{\Delta t} + \frac{\Delta \text{shrub cover}}{\Delta t} + \frac{\Delta T_{\text{micro}_{\min}}}{\Delta t} + \frac{\Delta \text{snow duration}}{\Delta t} + \text{baseline shrub cover} + \text{baseline snow duration} + \text{baseline } T_{\text{micro}_{\min}} + \text{baseline CTI} \quad (\text{Eq. 5})$$

$$CD_{\text{micro}_{\min}} \sim \frac{\Delta T_{\text{macro}_{\min}}}{\Delta t} + \frac{\Delta \text{shrub cover}}{\Delta t} + \frac{\Delta T_{\text{micro}_{\min}}}{\Delta t} + \frac{\Delta \text{snow duration}}{\Delta t} + \text{baseline shrub cover} + \text{baseline snow duration} + \text{baseline } T_{\text{micro}_{\min}} + \text{baseline CTI} \quad (\text{Eq. 6})$$

For each model, the baseline conditions (e.g., baseline shrub cover, baseline snow cover duration, etc.) were used as additional predictors to account for regression toward the mean. All models also included plot-level rock cover, bare ground cover, distance to the treeline, and HLI as covariates. Finally, all models included summit nested within mountain site as random intercept to account for the hierarchical setup of the plot network as well as potential spatial autocorrelation in plant communities located on the same summit or within the same mountain site (**Table S2-S7**). Multicollinearity among predictors was checked for all models using variance inflation factors (VIFs always < 4). Model assumptions were evaluated with density curves and residual plots but transformations were not deemed necessary.

Relationships were considered as statistically significant when the 95% CIs of model estimates did not overlap with zero. All analyses were performed in the statistical programming software R version 4.4.1 (R Core Team 2025). We used the packages *dplyr* (Wickham et al. 2023) for data manipulation, *lme4* (Bates et al. 2015) and *broom.mixed* (Bolker and Robinson 2022) for model building, and *ggplot2* (Wickham 2016) and *patchwork* (Pedersen 2024) for visualisation.

2.7. Sensitivity analyses

In this study, we specifically decided to focus on daily minimum temperatures given its biological relevance in mountain systems (i.e., key limiting factor to plant growth) and because annual minimum temperatures emerged as the best climatic predictor of alpine plant species distributions according to Chytrý et al. (2026). However, because macro- and microclimate temperature can be represented by a wide variety of summary statistics each with different biological meaning (Körner and Hiltbrunner 2018), we reran our analyses using annual mean and maximum temperatures as well as freezing (FDD; thermal sums below 0 °C) and thawing degree days (TDD; thermal sums above 0 °C; similar to growing degree days > 0 °C). The results showed relatively similar temporal patterns in these additional temperature metrics, as well as in their relationships to the calculated thermophilisation rates and climate debts (see **Fig. S6-S13**). Hence, these additional analyses underpin the robustness of our conclusions to the choice of temperature statistic used to define macro- and microclimate conditions.

Second, we here estimated thermophilisation rates using the presence/absence-based community-average thermal niches, thus neglecting species relative abundances. This approach was specifically chosen to give additional weight to rare or newly colonizing species, given that they can play disproportionate roles in climate-driven community dynamics. Moreover, species abundance recordings over time can suffer from observer bias when different observers with varying experience are used throughout the resurveys, and hence presence/absence data may allow for a more comprehensive and standardized assessment of community shifts. Including abundance-weighted data, however, puts more emphasis on community structural shifts by giving more weight to dominant species and therefore relates more strongly to larger scale changes in ecosystem functioning. To assess the robustness of our findings, we performed an additional

analysis by recalculating thermophilisation rates and climate debts using community-weighted average thermal preference based on species relative abundances. The results were consistent with our original findings, showing similar patterns in thermophilisation rates and climate debts generated from species abundance data compared to presence/absences (**Fig. S14-S17**).

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4.

5. Figure legends

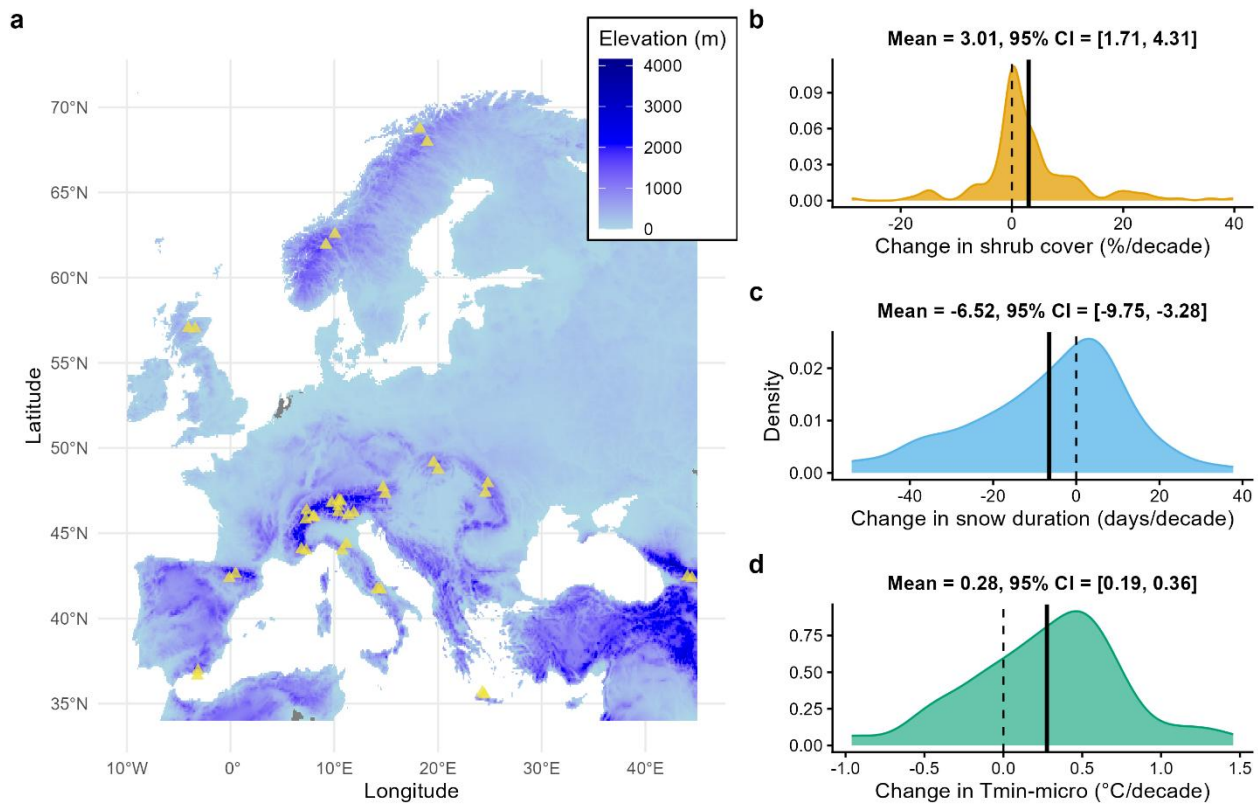


Fig. 1. Distribution of the 36 alpine summits containing 576 permanent plots of 1 m², as well as the plot-level changes in shrub cover, snow duration, soil microclimate and vegetation thermophilisation rate. (a) The 36 sampled mountaintops (yellow triangles) are part of eighteen different mountain regions spread across a 3600-km latitudinal and a 3000-km longitudinal gradient in Europe. The background map shows the E-OBS digital elevation model (<https://climate.copernicus.eu>), while the position of the triangles was slightly jittered to avoid overlap between the summits' locations. The summits are part of the GLORIA (Global Observational Research Initiative in Alpine environments; <https://gloria.ac.at>) initiative, which is currently the largest monitoring network of mountain floras and their microclimates worldwide. In each of the eighteen mountain sites two mountaintops were selected, one in the treeline ecotone to low alpine belt and one in the middle alpine belt. The lower summits are mostly covered by continuous alpine heath and grasslands, whereas the summits in the middle alpine belt, vegetation is dominated by herbaceous species interspersed with rocks and scree. Each summit contained sixteen vegetation plots of 1-m², which were permanently marked to facilitate relocation (see Pauli et al. 2015). The plots were always arranged in four quadrat clusters of 3 m × 3 m, positioned at the 5-m contour line below the summit and in every cardinal direction. Of these clusters, the outer squares were surveyed for the occurrence and abundance of all vascular plant species at least twice between 2001 and 2022 (average sampling interval of 7 years across all summits). In the middle square of each cluster, a microclimate data logger (GEOprecision M-Log5, <https://geoprecision.com>) was buried 10 cm below the soil surface, recording the temperature at an hourly interval during the period 2001-2022. In total, 576 vegetation plots were monitored and 144 microclimate time-series were collected over a period of more than two decades. Across these plots, (b) shows the distribution for the rate of shrub cover change (in % per decade), (c) the rate of change in snow cover duration (in number of days per decade), and (d) the rate of change in minimum soil temperature (in °C per decade). The y-axis in the density plots represents the estimated probability density with the area under each curve summing to 1. At any point, the height of the curve reflects the relative likelihood of the respective variables taking that value. The dashed line in (b-d) shows the zero-change line, whereas the solid black line depicts the average rate of change for each focal variable.

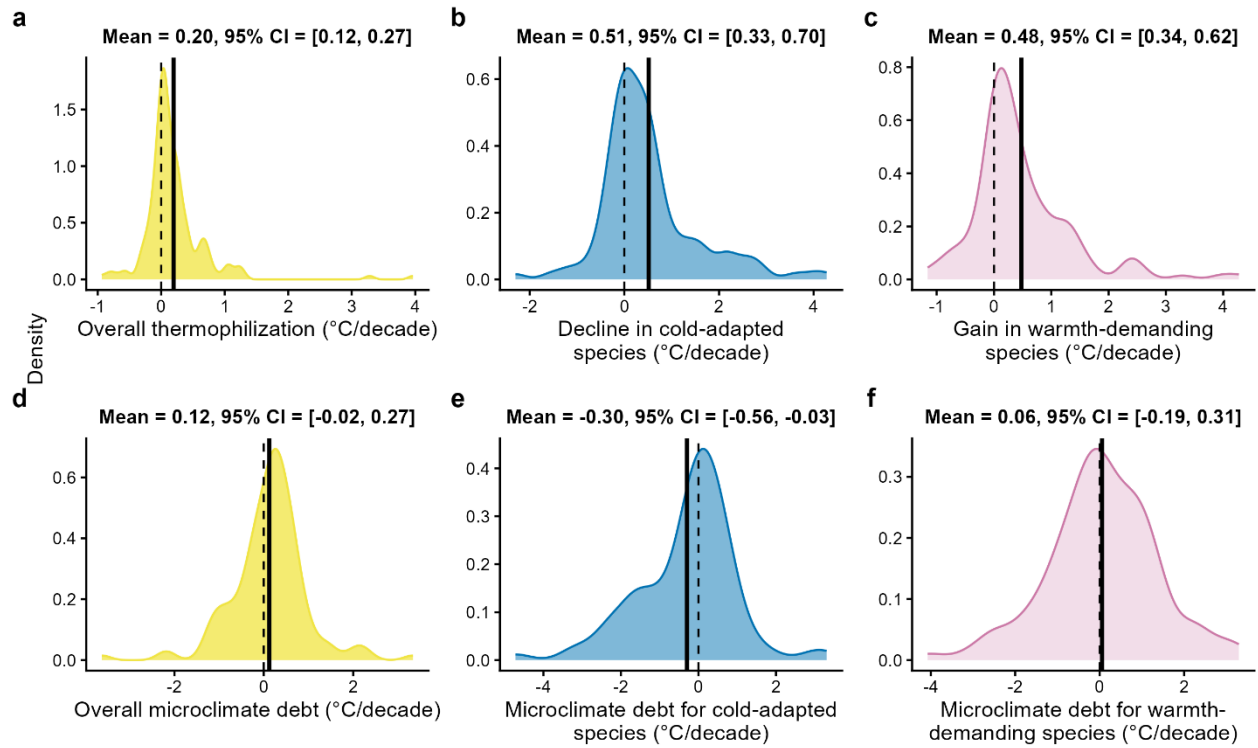


Fig. 2. Density plots for the thermophilisation rates and microclimate debts in the herbaceous vegetation across the European alpine summits. Thermophilisation rates (in °C per decade) were quantified as the rate of change in mean community temperature index (CTI, i.e., overall thermophilisation; **a**), the 5th percentile of the CTI (i.e., decline in cold-adapted species; **b**) and the 95th percentile of the CTI (i.e., gain in warmth-demanding species; **c**) for the herbaceous vegetation per 1-m² plot. CTI values were calculated as the average temperature niche of all species per plot. Species temperature niches were extracted from Yue et al. (2026) and are based on a combination of the species' geographical distributions and gridded climate data. (**d-f**) Microclimate debts (in °C per decade) were calculated as the difference between the rate of soil (i.e., annual minimum) temperature change, on the one hand, and the thermophilisation rates of the herbaceous vegetation (i.e., mean, 5th percentile and 95th percentile of CTI), on the other hand. The y-axis in the density plots represents the estimated probability density with the area under each curve summing to 1. At any point, the height of the curve reflects the relative likelihood of the respective variables taking that value. The dashed lines show the zero-change line, whereas the solid black lines depict the average rate of change for each focal variable.

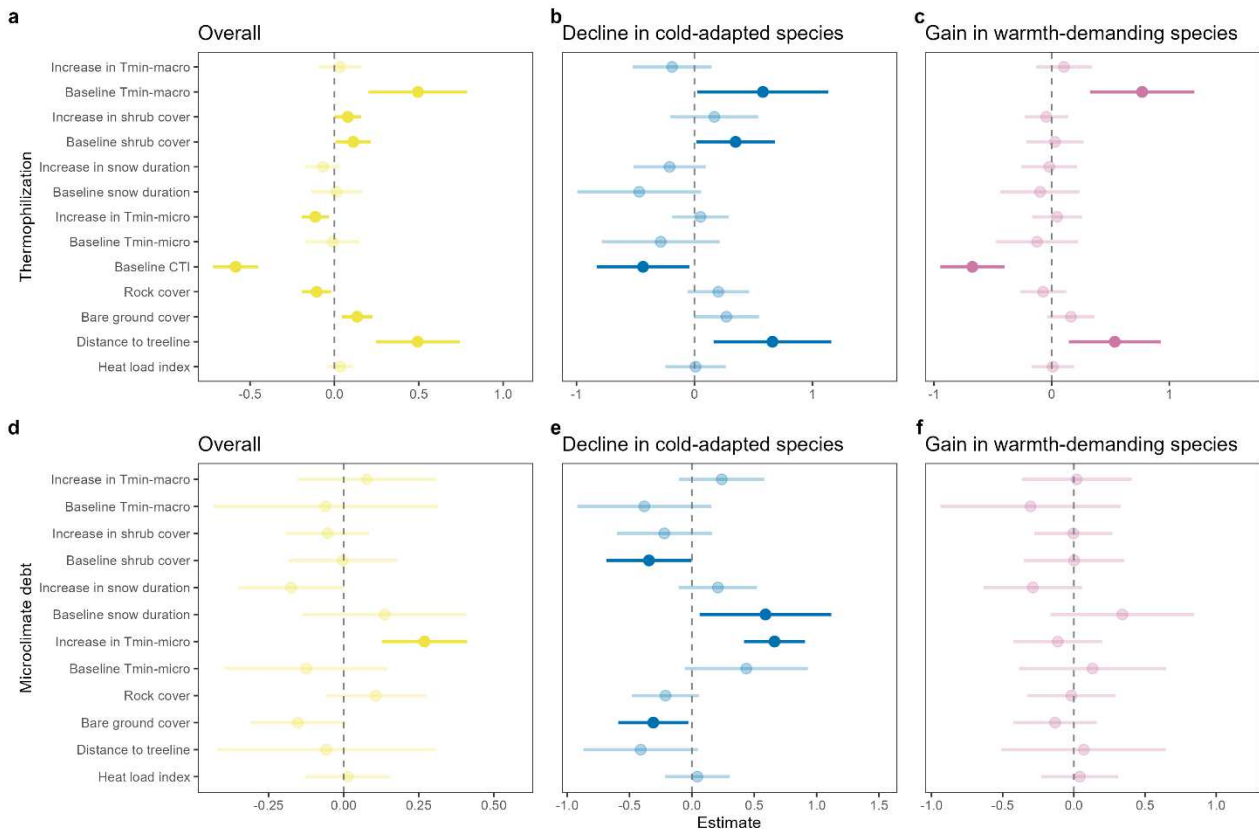


Fig. 3. Thermophilisation rates and microclimate debts in the herbaceous plant communities on the European alpine summits modelled as function of macroclimate change, shrub cover change, change in snow duration and soil microclimate change. Thermophilisation was quantified as the rate of change in mean community temperature index (CTI, i.e., overall thermophilisation; **a**), the 5th percentile of the community temperature index (i.e., decline in cold-adapted species; **b**) and the 95th percentile of the community temperature index (i.e., gain in warmth-demanding species; **c**). (**d-f**) Microclimate debts (in °C per decade) were calculated as the difference between the rate of soil (i.e., annual minimum) temperature change, on the one hand, and the thermophilisation rates of the herbaceous vegetation, on the other hand. Main predictor variables in the linear-mixed effect models were: the rate of shrub cover change, the rate of change in snow duration and the rate of soil temperature change. For each model, the baseline conditions (e.g., baseline shrub cover, baseline snow cover duration, etc.) were used as additional predictors to account for regression toward the mean. All models also included plot-level rock cover (i.e., proxy for topographical complexity), plot-level bare ground cover (i.e., amount of colonization space), distance of summit to the treeline (i.e., proximity to colonization source of more warmth-demanding species), and heat load index (HLI, i.e., proxy for the amount of radiation a mountain slope receives and calculated based on latitude, aspect and steepness) as covariates. Dots depict mean model estimates and error bars the 95% confidence intervals (CIs) of linear mixed-effect models. Bright colours indicate statistically clear effects (i.e., 95% CIs not including zero), while faded colours depict the absence of statistically clear effects. The dashed line shows the zero-effect line.

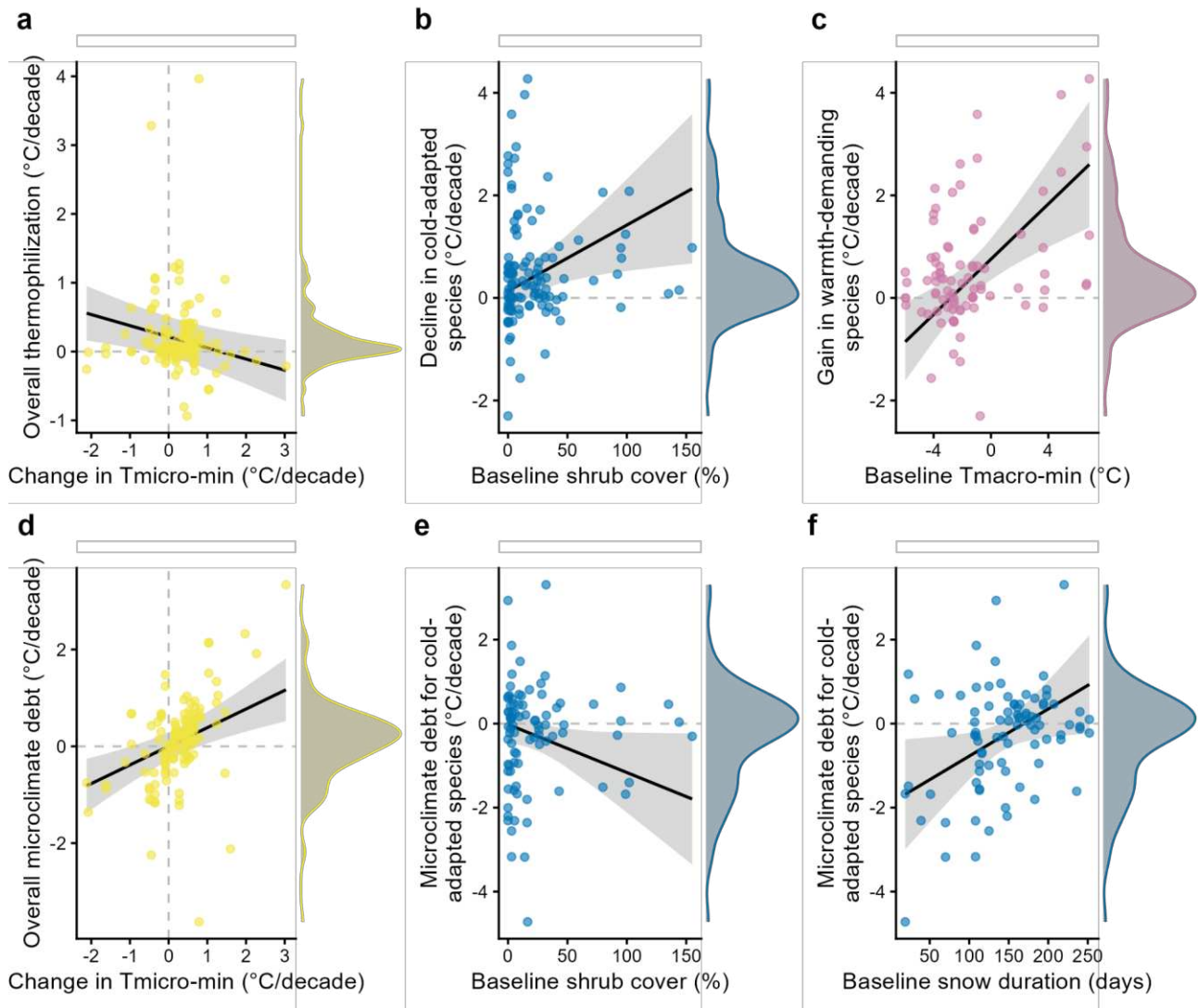
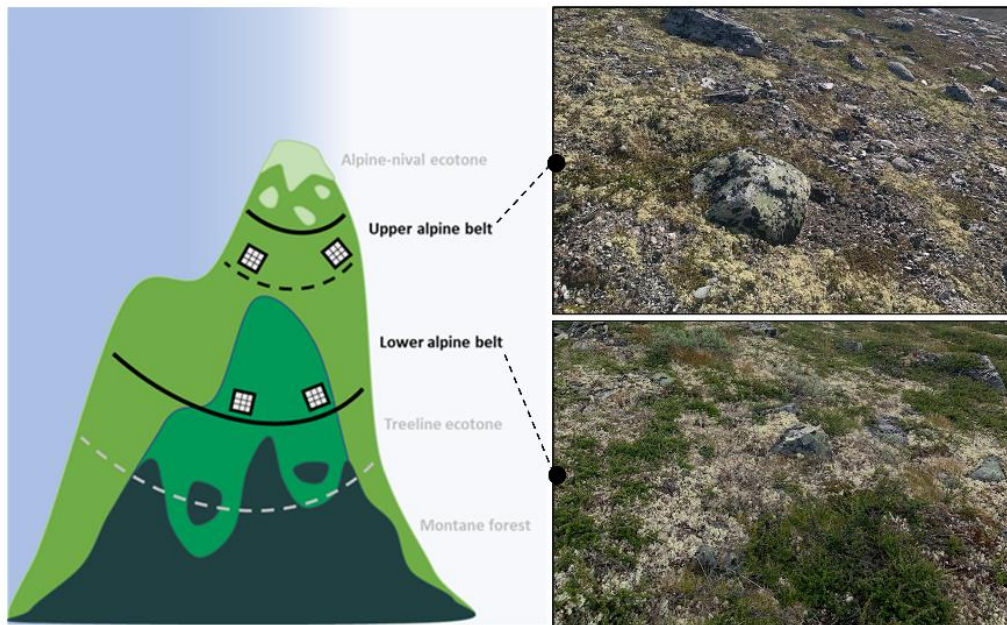


Fig. 4. Relationships between the thermophilisation rates and microclimate debts in the herbaceous plant communities on the European alpine summits, on the one hand, and macroclimate change, shrub cover change, change in snow duration and soil temperature change, on the other hand. Thermophilisation was quantified as the rate of change in mean community temperature index (CTI, i.e., overall thermophilisation; **a**), the 5th percentile of the community temperature index (i.e., decline in cold-adapted species; **b**) and the 95th percentile of the community temperature index (i.e., gain in warmth-demanding species; **c**). (**d-f**) Microclimate debts (in °C per decade) were calculated as the difference between the rate of soil (i.e., annual minimum) temperature change, on the one hand, and the thermophilisation rates of the herbaceous vegetation, on the other hand. Main predictor variables in the linear-mixed effect models were: the rate of shrub cover change, the rate of change in snow duration and the rate of soil temperature change. For each model, the baseline conditions (e.g., baseline shrub cover, baseline snow cover duration, etc.) were used as additional predictors to account for regression toward the mean. All models also included plot-level rock cover (i.e., proxy for topographical complexity), plot-level bare ground cover (i.e., amount of colonization space), distance of summit to the treeline (i.e., proximity to colonization source of more warmth-demanding species), and heat load index (HLI, i.e., proxy for the amount of radiation a mountain slope receives and calculated based on latitude, aspect and steepness) as covariates. Lines and shaded ribbons depict model predictions and 95% confidence intervals (CIs) for linear mixed-effect models, while dots with fading to avoid overlap show the actual data points. The axes are always rescaled according to the original data to facilitate interpretation of the graphs. The dashed grey lines depict the zero-change lines. In **b-e**, the number of observations (sample size) reduced towards high shrub cover resulting in greater uncertainties, because plots with very few species (often in plots with a dense shrub layer) — and thus imbalanced CTI distributions — were omitted from the analyses.

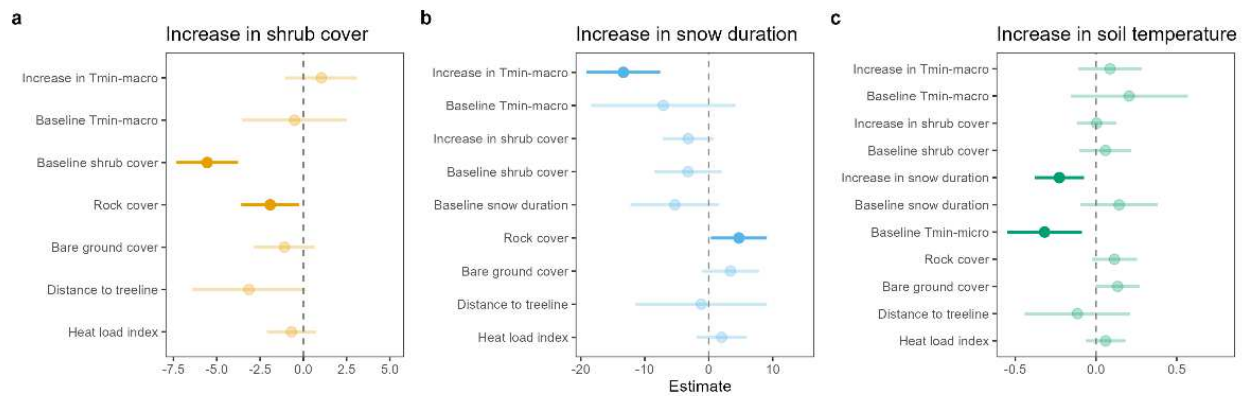
6. Data Availability Section

The raw data used in this study is available upon request at the GLORIA coordination office (gloria.office@boku.ac.at), while a derivative of the data including plot-level and species-level shrub cover shifts as well as all code necessary to reproduce the analyses and figures are available on Github (<https://github.com/to-vanneste/GLORIA-shrubification.git>) and Figshare with unique identifier (DOI) [10.6084/m9.figshare.31398462](https://doi.org/10.6084/m9.figshare.31398462).

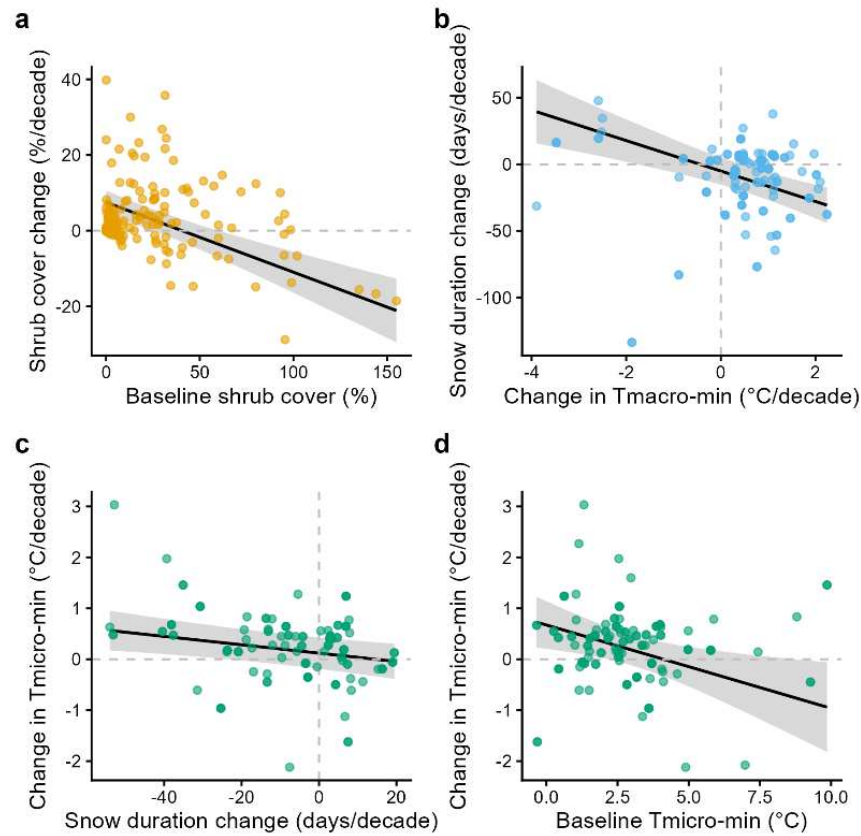
7. Extended data



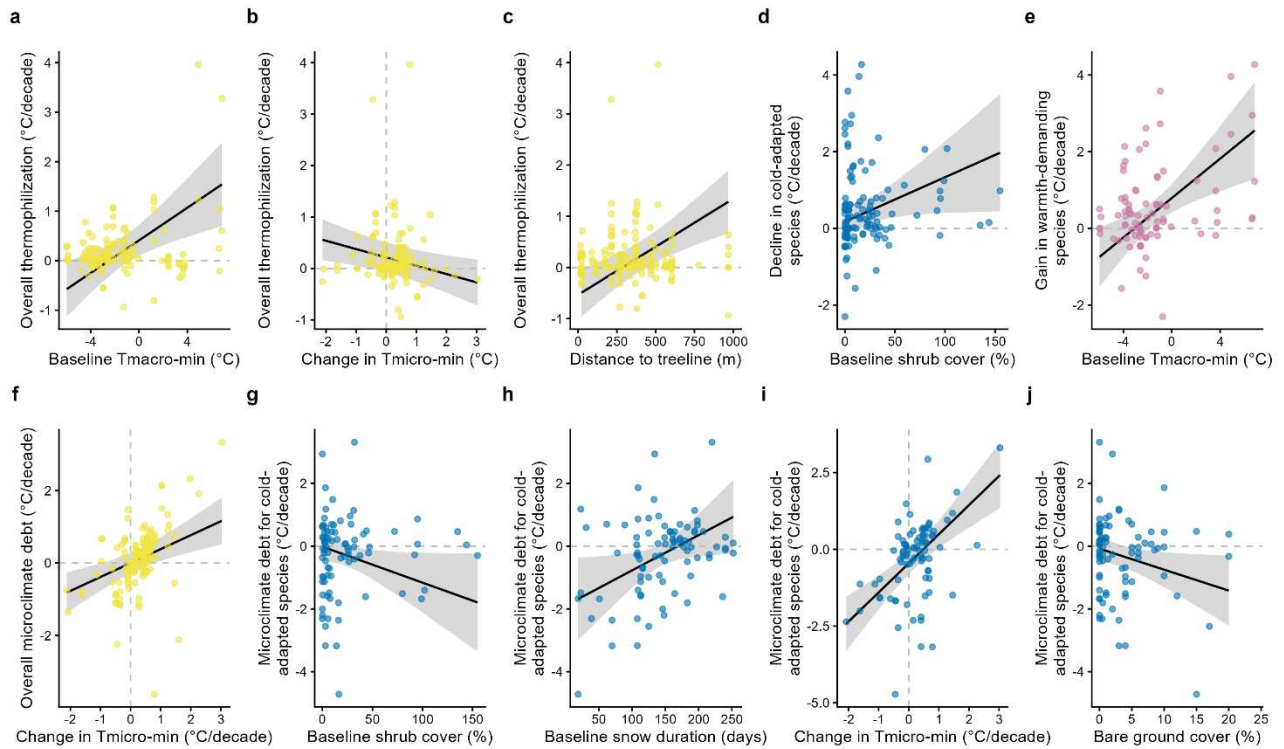
Extended Data Fig. 1. Setup of the mountain sites and 1-m² permanent plots. Each mountain site is part of the GLORIA network and consists of two summits, i.e., one summit in the lower alpine vegetation belt close to the treeline and one summit in the upper alpine belt close to the alpine-nival ecotone. The vegetation on the lower summit is mostly continuous with large patches of shrubs and dwarf shrubs, graminoid tussocks and small forbs interspersed by lichen mats and bryophytes. The vegetation on the higher summit is much sparser with large patches of scree, rocks and boulders, and some open ground. The small grids on the summits represent the 3 m × 3 m quadrat clusters of which the four corner quadrats are used for vegetation surveys on the middle quadrat for soil temperature monitoring.



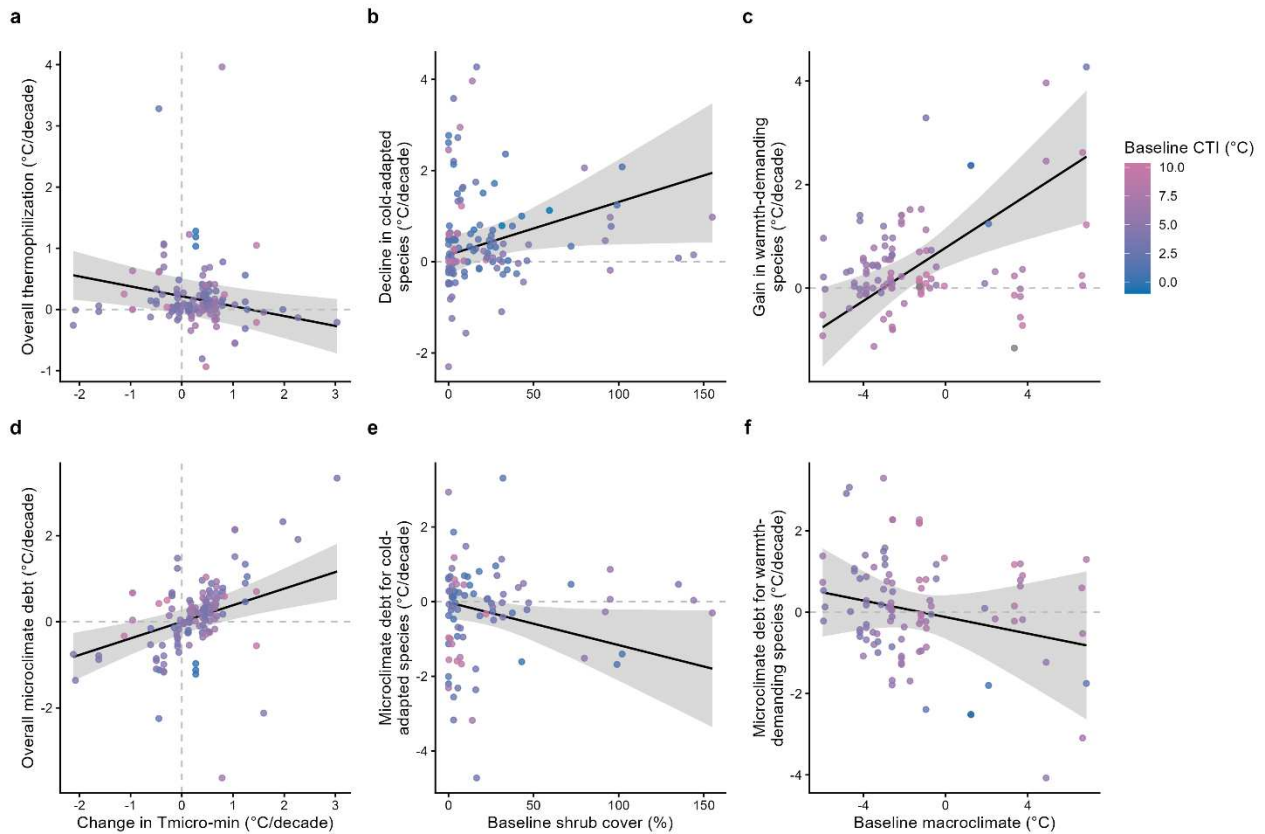
Extended data Fig. 2. Rate of change in shrub cover, snow cover duration and soil microclimate on the alpine summits between 2001 and 2022. The first model (a) predicts the rate of shrub cover change in the 1-m² plots based on the rate of change in the annual minimum air temperature (i.e., macroclimate), the second model (b) predicts the rate of change in snow cover duration based on the rate of change in shrub cover and minimum macroclimate temperature and, and the third model (c) predicts the rate of change in minimum soil temperature (i.e., microclimate) change based on the rate of shrub cover, minimum macroclimate temperature and snow cover duration. All models also included plot-level rock cover (i.e., proxy for topographical complexity), plot-level bare ground cover (i.e., amount of colonization space), distance of summit to the treeline (i.e., proximity to colonization source of more warmth-demanding species), and heat load index (HLI, i.e., proxy for the amount of radiation a mountain slope receives and calculated based on latitude, aspect and steepness) as covariates. Dots depict mean model estimates and error bars the 95% confidence intervals (CIs) of linear mixed-effect models. Bright colours indicate statistically clear effects (i.e., 95% CIs not including zero), while faded colours depict the absence of statistically clear effects. The dashed line shows the zero-effect line. Positive effect sizes indicate an increase in shrub cover, snow duration and soil temperature, and vice versa.



Extended data Fig. 3. Relationships between the rate of air temperature (i.e., macroclimate) change, rate of shrub cover change, rate of change in snow duration, and rate of soil temperature (i.e., microclimate) change on the alpine summits. For each model, the baseline conditions (e.g., baseline shrub cover, baseline snow cover duration, etc.) were used as additional predictors to account for regression toward the mean. Lines and shaded ribbons depict model predictions and 95% confidence intervals (CIs) for linear mixed-effect models, while dots with fading to avoid overlap show the actual data points. The axes are always rescaled according to the original data to facilitate interpretation of the graphs. The dashed grey lines depict the zero-change lines. Scatterplot **(a)** shows the negative relationship between the rate of shrub cover change and the baseline shrub cover (measured at the start of the surveys). Plots with a higher initial shrub cover thus tended to experience proportionally lower change over time. Scatterplot **(b)** depicts the negative relationship between the rate of change in snow duration and the rate of macroclimate change. Plots with stronger macroclimate warming (i.e., faster rising minimum air temperatures) were thus also more likely to experience faster declines in the length of the snow-covered period. Scatterplots **(c-d)** show the negative relationships between the rate of microclimate temperature change, on the one hand, and respectively the rate of change in snow cover duration and the baseline microclimate temperature, on the other hand. In other words, soils in plots with initially cooler soil temperature minima or with a strong decrease in the length of the snow-covered period were overall experiencing stronger warming over time.



Extended data Fig. 4. Extended figure showing relationships between the thermophilisation rates and microclimate debts in the herbaceous plant communities on the European alpine summits, on the one hand, and macroclimate change, shrub cover change, change in snow duration and soil temperature change, on the other hand. Thermophilisation was quantified as the rate of change in mean community temperature index (CTI, i.e., overall thermophilisation; **a-c**), the 5th percentile of the community temperature index (i.e., decline in cold-adapted species; **d**) and the 95th percentile of the community temperature index (i.e., gain in warmth-demanding species; **e**). (**f-j**) Microclimate debts (in °C per decade) were calculated as the difference between the rate of soil (i.e., annual minimum) temperature change, on the one hand, and the thermophilisation rates of the herbaceous vegetation, on the other hand. Main predictor variables in the linear-mixed effect models were: the rate of shrub cover change, the rate of change in snow duration and the rate of soil temperature change. For each model, the baseline conditions (e.g., baseline shrub cover, baseline snow cover duration, etc.) were used as additional predictors to account for regression toward the mean. All models also included plot-level rock cover (i.e., proxy for topographical complexity), plot-level bare ground cover (i.e., amount of colonization space), distance of summit to the treeline (i.e., proximity to colonization source of more warmth-demanding species), and heat load index (HLI, i.e., proxy for the amount of radiation a mountain slope receives and calculated based on latitude, aspect and steepness) as covariates. Lines and shaded ribbons depict model predictions and 95% confidence intervals (CIs) for linear mixed-effect models, while dots with fading to avoid overlap show the actual data points. The axes are always rescaled according the original data to facilitate interpretation of the graphs. The dashed grey lines depict the zero-change lines.



Extended data Fig. 5. Extended figure showing the relationships between the thermophilisation rates and microclimate debts in the herbaceous plant communities on the European alpine summits, on the one hand, and macroclimate change, shrub cover change, change in snow duration and soil temperature change, on the other hand. Thermophilisation was quantified as the rate of change in mean community temperature index (CTI, i.e., overall thermophilisation; **a**), the 5th percentile of the community temperature index (i.e., decline in cold-adapted species; **b**) and the 95th percentile of the community temperature index (i.e., gain in warmth-demanding species; **c**). (**d-f**) Microclimate debts (in °C per decade) were calculated as the difference between the rate of soil (i.e., annual minimum) temperature change, on the one hand, and the thermophilisation rates of the herbaceous vegetation, on the other hand. Main predictor variables in the linear-mixed effect models were: the rate of shrub cover change, the rate of change in snow duration and the rate of soil temperature change. For each model, the baseline conditions (e.g., baseline shrub cover, baseline snow cover duration, etc.) were used as additional predictors to account for regression toward the mean. All models also included plot-level rock cover (i.e., proxy for topographical complexity), plot-level bare ground cover (i.e., amount of colonization space), distance of summit to the treeline (i.e., proximity to colonization source of more warmth-demanding species), and heat load index (HLI, i.e., proxy for the amount of radiation a mountain slope receives and calculated based on latitude, aspect and steepness) as covariates. Lines and shaded ribbons depict model predictions and 95% confidence intervals (CIs) for linear mixed-effect models, while dots show the actual data points coloured according to the baseline CTI (blue – low CTI, red – high CTI). The axes are always rescaled according to the original data to facilitate interpretation of the graphs. The dashed grey lines depict the zero-change lines.

Supplementary Files

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