

Shrub-induced microclimate buffering on European alpine summits

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Abstract

Alpine microclimates vary tremendously across space and time, and changes in vegetation cover can be an important driver of this fine-scale thermal heterogeneity. While European alpine summits have experienced significant shrubification over the past few decades, the influence of these widespread processes on the ground-level microclimate has been poorly studied. Here we quantified the magnitude of temperature coupling between soil and gridded free-air conditions on 34 European alpine summits using 136 time-series comprising 747,847 daily temperature records and spanning a 21-year sampling period. The magnitude of coupling amounted to 0.303 (95% CI = 0.299–0.307) and 0.353 (95% CI = 0.348–0.358) for minimum and maximum temperatures, respectively. Overall, this indicates a buffering of soil microclimates on the alpine summits, which was more pronounced on north-facing slopes and during spring and winter due to snow presence. Higher shrub cover resulted in a non-linear decrease of the magnitude of temperature coupling, and this buffering effect was stronger in deciduous than in evergreen shrubs. Not only shrubs but also lichens and bryophytes contributed to microclimate buffering, albeit the effect was highly season-dependant. Future studies will benefit from including the mediating effect of shrubs on microclimate modulations when predicting mountain biodiversity or ecosystem responses to a warming climate.

Introduction

Open, treeless alpine environments across Europe are currently experiencing strong rates of shrubification and greening, that is, increasing shrub and vascular plant cover over time (Rumpf et al. 2022, Choler et al. 2024, De Toma et al. 2025, Vanneste et al. 2026). Both warming temperatures under contemporary climate change and the abandonment of century-old grazing practices in Europe are the most likely culprits (Ameztegui et al. 2016, Vanneste et al. 2026, Elmendorf and García Criado 2026). Shrubs are typically the tallest plant functional types in alpine ecosystems, and increases in their abundance could have far-reaching consequences for the climate change itself (i.e., positive feedback loop on climate amplification) as well as local biodiversity, ecosystem functioning and local livelihoods (Myers-Smith et al. 2011, Pecl et al. 2017, Mekonnen et al. 2021).

Through the formation of contiguous canopies (albeit not much taller than 50 cm) or dense carpets on the soil surface, shrubs capture a large proportion of the incoming shortwave radiation, thus outcompeting many of the lower-statured and light-demanding alpine grassland and meadow specialists, including lichen species (Vanneste et al. 2017, Angers-Blondin et al. 2018, Pierce et al. 2019). On top of that, many shrubs have acquisitive traits or produce thick, sometimes allelopathic, litter layers that inhibit the emergence and survival of most stress-tolerant alpine plant species (Opedal et al. 2021, Rosbakh et al. 2025). Hence, shrubification of alpine habitats is often associated with local plant diversity loss and biotic homogenisation (Pierce et al. 2019, Bråthen et al. 2024, García Criado et al. 2025). Besides affecting plant diversity, shrubs also strongly impact soil respiration, nutrient cycling and the carbon balance in alpine ecosystems (Elmendorf et al. 2012, Vowles and Björk 2019, Mekonnen et al. 2021) – but the effect differs considerably between tall deciduous shrubs with fast-decomposing leaf

litter (e.g., *Salix* sp. *Betula* sp. and *Alnus* sp.) and evergreen (often *Ericaceae*) dwarf shrubs with recalcitrant leaves (Vowles and Björk 2019, Vanneste et al. 2026). Through their darker canopy, shrubs also lower the surface albedo, and thus, thereby altering the surface energy balance, snowmelt timing and permafrost thawing in alpine environments (Sturm et al. 2005, Myers-Smith and Hik 2013). In spring, for instance, the dark branches of tall shrubs that protrude the snowpack may advance the onset of snow snowmelt, and thus, alter plant phenology, carbon uptake and result in overall greening (reviewed by Mekonnen et al. 2021).

Last but not least, shrubs can also affect the thermal environment, or microclimate, below their canopy (Myers-Smith et al. 2011, Kemppinen et al. 2021, Domine et al. 2022). This is particularly important, because shrubs can act as mediators on microclimate modulations and subsequently alter the aforementioned ecosystem processes. In winter, for example, shrub branches are known to trap snowdrift and locally accumulate snow, resulting in a thicker and more insulating snowpack (Sturm et al. 2005, Grünberg et al. 2020). Less than a meter of snow is amply sufficient to decouple the soil microclimate from the free-air temperature, and keep the soil at about 0 °C thereby stimulating soil mineralization and litter decomposition rates, and nutrient supplies that benefit plants later during the growing season (Körner et al. 2019, Vowles and Björk 2019). But this buffering of temperature extremes is not systematic under shrubs, and in some cases the reverse may be observed: microclimate amplification. Indeed, there is now rising evidence that, particularly in low-growing shrubs, frozen branches can act as thermal bridges through the snowpack, fostering heat loss and thus soil cooling in autumn and winter. In spring, this effect is reversed when branches absorb shortwave radiation and transfer heat to the soil (Domine et al. 2022, Domine et al. 2023). In late spring and summer, however, shrub canopies also provide shade, creating locally buffered and cooler microclimates (Marsman et al. 2020, Kemppinen et al. 2021) – albeit taller deciduous shrubs are likely more effective at summer cooling than evergreen dwarf shrubs with generally lower albedo (see conceptual diagram in **Fig. 1**).

Overall, the effect of shrubs on alpine microclimates is complex and multifaceted, and the trade-offs between microclimate buffering and amplification in different functional types and across different seasons remains poorly understood for alpine ecosystems. Here, we leverage the European GLORIA network (Global Observational Research Initiative in Alpine environments; gloria.ac.at) by combining data on deciduous and evergreen shrub cover from 544 vegetation plots resampled across 34 summits between 2001-2022 paired with a network of 136 microclimate data loggers recording hourly soil temperature since 2001. Vegetation plots and data loggers were always distributed across the four cardinal directions (north, east, south, west; henceforth “aspects”) of the 34 studied mountain summits spread from the treeline ecotone to the middle alpine belt of Europe’s major mountain ranges (**Fig. 2a**, **Table S1**). For each aspect per summit and season per year, we calculated the magnitude of coupling (i.e., the slope coefficient of a generalised additive model) between soil temperature (microclimate) and gridded free-air temperature records (macroclimate) following Gril et al. (2023). Next, we assessed to what extent the magnitude of temperature coupling related to the plot-level deciduous and evergreen shrub cover as well as other local site characteristics (i.e., rock and bare ground cover, vascular plant, lichen and bryophyte cover, azimuth angle and slope). Finally, for aspect per summit and season per year,

we also quantified the temporal shift in the magnitude of temperature coupling between 2001-2022, and related this to the surface type dynamics (i.e., changes in the cover of shrubs, rocks, bare ground, vascular plants, lichens and bryophytes).

Results and discussion

Stronger microclimate buffering in spring and winter

Across all time-series, the magnitude of coupling between microclimate and macroclimate conditions for minimum and maximum temperatures amounted to respectively 0.303 (95% CI = -0.011 – 0.731) and 0.353 (95% CI = -0.013 – 0.870), indicating an overall buffering of soil microclimates relative to free-air temperatures. Overall, the buffering effect was stronger on north-facing mountain slopes compared to other aspects, and more pronounced in spring and winter compared to autumn and summer (**Extended data Fig. 1, Table S2**). North-facing aspects receive less direct solar radiation and retain their snow cover generally longer compared to the other mountain aspects, which likely results in the observed stronger decoupling between soil and air temperatures. Likewise, in winter and early spring, the presence of a thick snowpack buffers the soil from cold temperature extremes, while vegetation cover in summer and autumn provides soil cooling through shading or evapotranspiration (albeit with a smaller effect size compared to the winter warming effect of snow cover).

Both deciduous and evergreen shrubs effectively buffer alpine microclimates

Second, we found that the magnitude of coupling for both minimum and maximum temperatures was positively related to the plot-level rock cover, bare ground cover (only for $T_{\max}$) and the azimuth angle of the sampled mountainsides, whereas a negative effect was found for plot-level deciduous shrub cover, evergreen shrub cover (albeit only marginally significant for $T_{\min}$) and slope angle of the mountainsides (**Fig. 3a-b, Fig. 4a-d, Extended data Fig. 2 and Table S3-S4**). The effect of the different site characteristics on the magnitude of coupling clearly varied between seasons (**Fig. 4a-d, Extended data Fig. 2 and Table S3-S4**). For instance, the magnitude of coupling decreased sharply with increasing deciduous shrub cover in summer and autumn, whereas the effect was less pronounced in winter and spring (**Fig. 4a, c**). Moreover, the effect of deciduous shrub cover on the magnitude of coupling was markedly stronger than for evergreen shrub cover, and this discrepancy among functional types was especially clear in summer and winter (**Fig. 4a-d and Table S3-S4**).

Low-albedo rocks and open ground without the sheltering effect of vegetation cover result in stronger heat transfer to the soil, especially during the snow-free season. Shrubs, on the other hand, can temper soil temperature extremes through summer shading or winter snow trapping, but this buffering effect is more effective in tall deciduous shrub species with greater leaf area such as *Salix philicifolia* or *S. lanata* compared to low-growing, mat-forming evergreens such as *Empetrum nigrum* (Vowles and Björk 2019). In autumn after leaf shedding, this buffering effect underneath deciduous shrubs is of course strongly diminished, while in spring thermal bridging and heat conduction through snow-protruding branches can

also partly offset the snow-insulation effect (Domine et al. 2023, Domine et al. 2025). Besides shrub cover, the presence of snow is thus a crucial factor shaping the soil microclimate, as shown by the clear difference between snow and snow-free days (**Extended data Fig. 3**).

Cryptogams can also be effective microclimate buffers

Not only shrubs and snow but also the lichen and bryophyte cover significantly affected the magnitude of coupling on the sampled summits, thus enhancing microclimate buffering, albeit the direction of the effects differed among seasons (**Fig 3c-d, Fig. 5a-f**). Lichens only demonstrated a buffering effect in summer and autumn, while they increased the coupling during spring and winter. Lichens often form extensive mats on dry mountain slopes where they insulate the soil against temperature extremes, while also providing evaporative cooling and thermal inertia after rainfall interception, and decoupling soil from air temperatures (Asplund and Wardle 2007, Ellis et al. 2021). Moreover, many of the more common lichen species in the alpine vegetation belt (e.g., of the genera *Cladonia* sp. or *Flavocetraria* sp.) reflect a large proportion of the incoming shortwave solar radiation through high albedo, thereby reducing heat transfer to the soil during the snow-free season (Mallen-Cooper et al. 2021 and **Extended Data Fig. 5a, c**). Conversely, during the snow-covered season, lichens usually have insufficient moisture and tend to dry out completely below the snowpack, thereby losing their buffering effect on soil microclimates (Ellis et al. 2021 and **Extended data Fig. 5b, d**). Bryophytes increased the magnitude of coupling during autumn, likely because their darker-toned surface becomes exposed after leaf shedding of deciduous shrub species.

Stable magnitude of coupling over time despite strong shrubification trends

Across the 21-year sampling period, we found no significant trend in the magnitude of the coupling for minimum and maximum temperatures (**Extended data Fig.4**). For maximum temperatures, increasing bare ground cover significantly increased the magnitude of coupling over time, suggesting a decrease in the buffering effect (Estimate = 0.008, 95% CI = 0.003 – 0.012). Increasing deciduous (Estimate = -0.009, 95% CI = -0.014 – -0.004) and evergreen shrub cover (Estimate = -0.008, 95% CI = -0.013 – -0.002) as well as lichen (Estimate = -0.010, 95% CI = -0.016 – -0.005) and bryophyte cover (Estimate = -0.009, 95% CI = -0.016 – -0.003), on the other hand, significantly reduced the magnitude of coupling in maximum temperatures, thus enhancing buffering of the warm extremes (see **Table S5**). Rising shrub cover in alpine ecosystems often outcompetes cryptogams for light (Vanneste et al. 2017, Hagenberg et al. 2022 and **Extended data Fig. 6**), potentially leading to a trade-off effect in the magnitude of buffering, and thus also the lack of a significant trend over time.

Implications and future research avenues

In sum, our findings highlight the strong spatial and temporal heterogeneity in the coupling between soil and free-air temperatures in the European alpine zone. Given alpine microclimates' key role in shaping biodiversity patterns, community assembly, ecosystem functioning, and climate-change responses (Körner and Hiltbrunner 2021, Körner and Hiltbrunner 2026), our study provides an interesting new look

into the spatiotemporal dynamics of these processes under widespread global-change drivers such as shrubification and climate warming. Not only herbaceous plant communities, but also other organism groups living underneath or in the vicinity of shrubs are affected by their buffering effect, including arthropod abundance, pollinator visitation, and soil microorganisms (e.g., Donhauser and Frey 2018, Ohler et al. 2020). These are, in turn, also linked to other ecosystem processes, such as soil respiration, decomposition and nutrient cycling, and are ultimately also part of biotic interactions and food webs (Donhauser and Frey 2018, Manlick et al. 2024). Moreover, shrub-induced microclimates may interact with organism responses to climate change, for instance, by accelerating thermophilisation and borealisation rates through microclimate amelioration (Schweiger et al. 2015, Vanneste et al. preprint). Through summer cooling shrubs can buffer indigenous communities from climate extremes, but at the same time, by providing more benign microclimates, they can also act as stepping-stones or “nurse plants” for more competitive, resource-acquisitive thermophilic species that move upwards and colonize alpine grasslands from lower elevations (e.g., montane forest belt). Unravelling the intricate links between climate change, shrubification, microclimates, organism responses and ecosystem processes should therefore be the focus of future climate-impact research in alpine environments.

Materials and Methods

2.1. Study area and setup

Time series on percentage cover of all vascular plant species were gathered from 17 mountain sites spread across Europe's major mountain regions, following a standardized setup of permanent vegetation plots used to monitor vegetation compositional dynamics on the mountain summits (Pauli et al. 2015). Time series were extracted from a subset of permanent vegetation plots that are part of the European GLORIA network (Global Observational Research Initiative in Alpine environments; gloria.ac.at), i.e., currently the largest long-term vegetation resampling program worldwide with the goal to assess climate-change impacts on mountaintop flora. Here, we focused on a total of 34 summits nested within the 17 mountain sites, such that each mountain site has two paired summits (one located in the lower alpine vegetation zone close to the treeline and one in the lower to middle alpine belt; **Fig. 1a**). All 34 mountain summits typically consist of species-rich alpine grasslands, meadows and pastures, and have been strongly affected by shrub cover dynamics in recent decades (Vanneste et al. 2026). Each summit comprised sixteen plots of 1 m², arranged in four quadrat-shaped clusters of 3 m × 3 m each, of which only the four outer quadrats were surveyed. The quadrat clusters were always positioned in the four cardinal directions (north, east, south, west) at five elevational meters below the highest summit point. This resulted in a dataset encompassing 544 permanent plots in total, which were all resurveyed at least twice between 2001 and 2022 (see **Table S1** for a complete list of summits).

2.2. Shrub cover and other surface types

Species-level data on the occurrence and abundance (i.e., visual estimation of plant cover relative to the plot area) of all vascular plant species were collected from the 544 permanent plots over the past two

decades (average sampling interval between the baseline survey and last resurvey = 20.5 ± 0.9 years; see **Table S1**). We differentiated shrubs from herbaceous (i.e., non-woody) species using the plant functional type classification by Plants of the World Online (POWO; powo.science.kew.org, considering both categories 'shrub' and 'subshrub' as shrubs). In total, we identified 66 different shrub species including 22 deciduous and 44 evergreen species (see Vanneste et al. 2026 for a full shrub species list). For each of the 544 plots, the total deciduous (95% CI = 0 – 44 %) and evergreen shrub cover (95% CI = 0 – 88 %) was then calculated per plot as the sum of covers of all individual deciduous and evergreen species, respectively. Total shrub cover values could exceed 100% due to species overlaps. In addition to shrub cover, we also collected information on the total rock cover (permanent large rocks or bedrock; 95% CI = 0 – 55 %), bare ground cover (95% CI = 0 – 13 %), total vascular plant cover (95% CI = 6 – 99 %), lichen cover (95% CI = 0 – 39 %) and bryophyte cover (95% CI = 0 – 6 %) as well as the azimuth angle (i.e., angle between the plot and the reference direction, here north; in degrees) and slope angle (measured with a clinometer; in degrees) of the sampled plots.

2.3. Macroclimate and microclimate

Gridded ambient-air temperature (i.e., atmospheric conditions or “macroclimate”) data were extracted from the online E-OBS reanalysis database (climate.copernicus.eu, resolution approximately 10 km). We collected daily minimum, mean and maximum values between 2001 and 2022, and corrected these for the respective summits' elevations based on daily lapse rate values (also extracted from E-OBS climate database) and the elevational difference between the summits and the corresponding grid cells, extracted from the corresponding E-OBS digital elevation model.

Soil temperature (microclimate) data were collected from each summit using miniature data loggers (GeoPrecision M-Log5, geoprecision.com) was buried at 10 cm below the soil surface, recording the temperature at an hourly interval between 2001 and 2022. Data loggers were always positioned in the middle quadrat of each 3 m × 3 m quadrat-shaped cluster (that is, four data loggers per summit). These soil temperature measurements were always considered representative for the four outer squares used as vegetation plots. In total, 136 data loggers were deployed across the 34 studied mountain summits. For each logger, daily minimum, mean and maximum values were calculated from the hourly records. Measurement errors, such as sensors left at room temperature instead of deployed in the field, were checked visually by plotting time-series, and were removed prior to summary statistics' calculations. In total, 747.847 daily minimum, mean and maximum temperature values were used across the 34 summits and across the 21-year sampling period. In this study, we decided to focus on the buffering or amplification of temperature extremes, i.e., daily minimum and maximum values, whereas results for the daily mean temperature statistic were reported in the **Supplementary information Table S2** and **Fig S1-S3**.

2.4. Data analyses

First, for each of the 34 summits independently, we estimated the magnitude of the temperature (i.e., either for daily minimum or maximum values) coupling between microclimate and macroclimate (i.e.,

buffering vs. amplifying modulations over time) using a generalized additive model (GAM) with smoothing splines to account for non-linearity in the relationship (owing to the snow-insulating effect) and for cyclicity in the multiyear datasets (owing to recurring seasonal patterns between years). For each summit, the fitted GAM included the in-situ minimum (or maximum) soil temperatures as the response variable, aspect (i.e., a factor variable with four levels: north, east, south, west) as a fixed effect, a cubic regression spline (*cr*) on year (assuming a non-linear relationship in soil temperatures over time), a cubic regression spline (*cr*) on the gridded free-air minimum (or maximum) temperature (assuming a non-linear relationship between soil and free-air temperatures), an interaction term between the free-air temperature smoother and aspect (assuming a different coupling depending on aspect position), a tensor interaction term (*ti*) between the two smoothers (year and gridded free-air temperatures) and a cyclic smoother (*cc*) on day of the year (DOY; to correctly link the last Julian days of the ending year with the early Julian days of the subsequent starting year). The GAM models were fitted using restricted maximum likelihood estimation (REML), including a temporal autocorrelation structure on DOY, and with a Gaussian error distribution for continuous temperature data (see **Eq. 1**):

$$\begin{aligned}
 T_{\text{micro}} \sim & \text{aspect} + \\
 & s(\text{year}, \text{bs} = "cr", k = 5) + \\
 & s(T_{\text{macro}}, \text{bs} = "cr", k = 5) \\
 & s(T_{\text{macro}}, \text{bs} = "cr", k = 5, \text{by} = \text{aspect}) + \\
 & ti(T_{\text{macro}}, \text{year}) + \\
 & s(\text{DOY}, \text{bs} = "cc", k = 10) \text{ (Eq. 1)}
 \end{aligned}$$

From this GAM model, we extracted the estimated model coefficients for T_{macro} , separately for each aspect per summit and for each sampling year per aspect. This procedure was repeated for each of the four seasons per sampling year, resulting in a total of $n = 12524$ estimates for the magnitude of the coupling (i.e., buffering vs. amplifying modulations).

Next, we fitted hierarchal (mixed-effect) linear models (LMM) with REML to assess the relationship between the magnitude of the coupling (the response variable, $n = 12524$) for minimum and maximum temperatures and a corresponding set of local site characteristics (plot-level cover of rock, bare ground, deciduous shrubs and evergreen shrubs as well as azimuth angle and slope of the sampled mountainside; as predictors). Multicollinearity among predictors was checked by computing the variance inflation factors ($VIF < 3$). The mixed-effect models also included summit nested within region and year as two separated random intercept terms. For each separate predictor, we also fitted a GAM with REML including a smoother term on the different site characteristics and an interaction with season, to also model potential non-linear relationships. Furthermore, we ran separate GAMs with the vascular plant, lichen and bryophyte cover as predictors for the magnitude of coupling for minimum and maximum

temperatures. These separate models could only be run with a subset of the data ($n = 12252$) for which lichen and bryophyte cover was consistently recorded over the 21-year sampling period. All percentage cover data was ln-transformed to conform better normality.

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 % confidence intervals (CI) of model estimates did not overlap with zero, and marginally significant when the 80 % 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 2026) using the packages *dplyr* (Wickham et al. 2023) for data manipulation, *lme4* (Bates et al. 2015), *broom.mixed* (Bolker and Robinson 2022) and *mgcv* (Wood 2017) for model building, and *ggplot2* (Wickham 2016) and *patchwork* (Pedersen 2024) for data visualisation.

Declarations

6. Data availability statement

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. Acknowledgements

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Figures

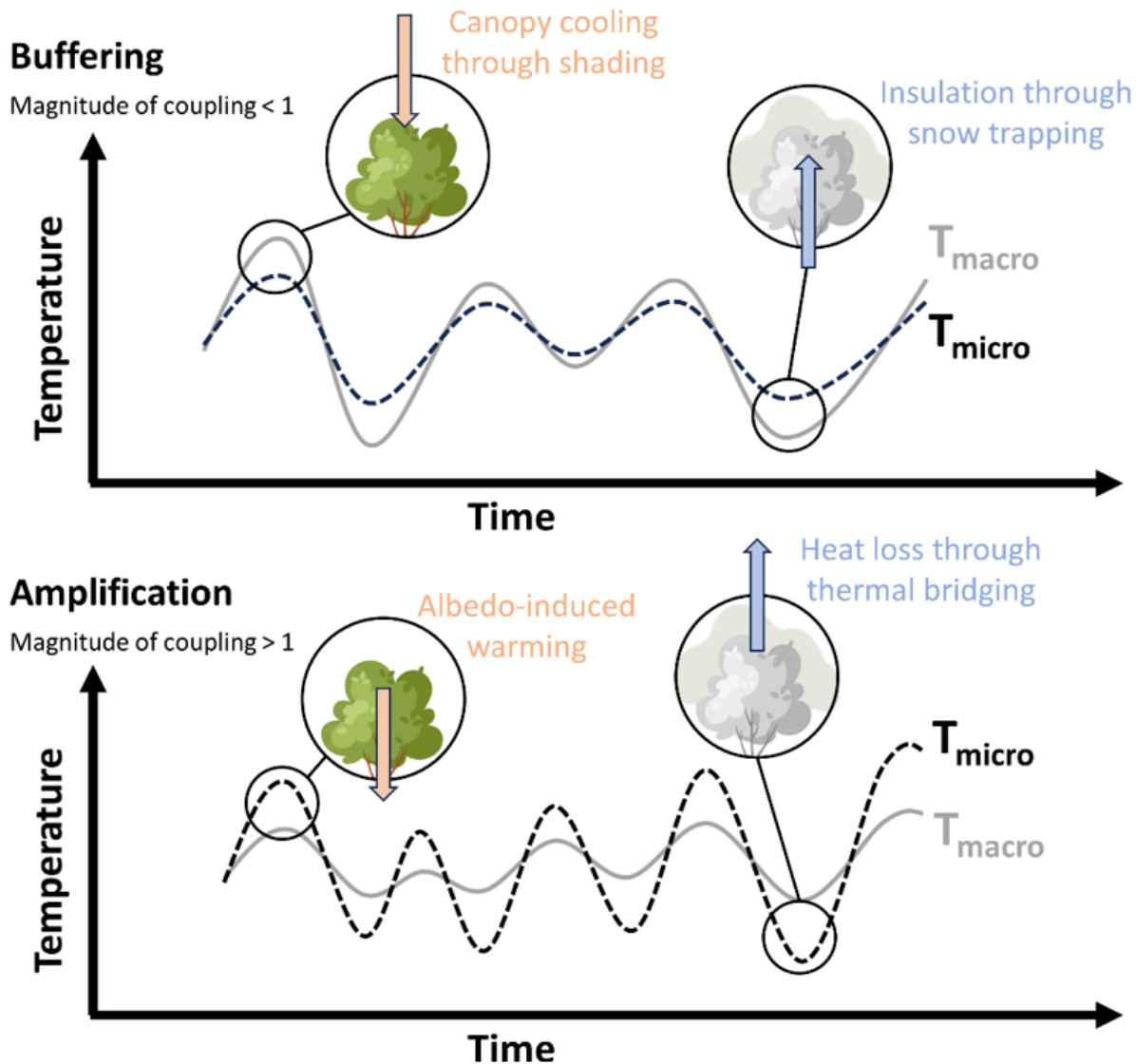


Figure 1

Conceptual diagram of different scenarios of buffering vs. amplification of soil temperatures (microclimate) relative to free-air temperatures (macroclimate) underneath shrub canopy cover. In late spring and summer, shrub canopies (particularly in tall deciduous species with large leaf area) provide cooling through shading and evapotranspiration (Kempainen et al. 2021), while in winter and early spring shrub branches trap snowdrift and locally increase snow depths resulting in more insulated (warmer) soils (Sturm et al. 2005). During summer, however, dark-toned shrub canopies with low albedo absorb more solar radiation which may result in locally amplified soil warming (Mekonnen et al. 2021), while in winter shrub branches sometimes act as thermal bridges fostering increased heat loss from the soil (Domine et al. 2022).

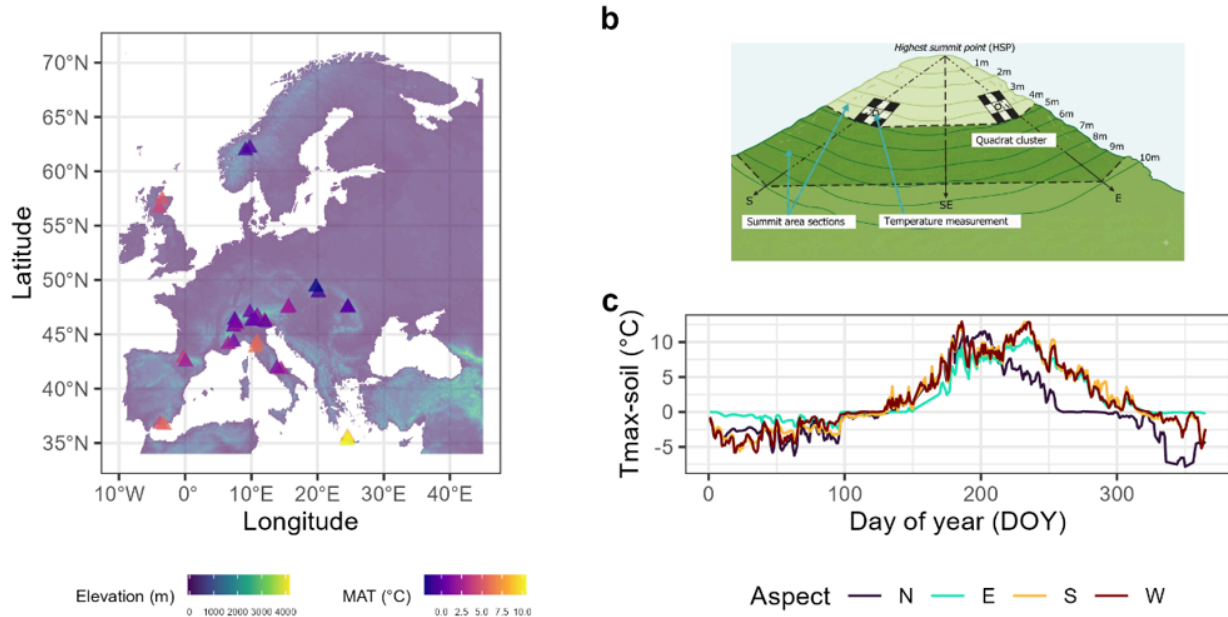


Figure 2

Geographic distribution of the sampled mountain summits and their mean annual temperature (MAT, corrected for elevation), as well as the magnitude of coupling between soil microclimate and gridded macroclimate data across the different summit aspects and seasons. (a) The 34 sampled mountaintops (triangles) are part of seventeen different mountain sites spread across a 3600-km latitudinal and a 3000-km longitudinal gradient in Europe. The background map depicts the E-OBS digital elevation model (climate.copernicus.eu), while the position of the triangles was slightly jittered to avoid overlap between the summit locations. The summits are part of the GLORIA initiative (Global Observational Research Initiative in Alpine environments; gloria.ac.at), i.e., the largest monitoring network of mountain floras and their microclimates worldwide. Each of the seventeen mountain sites consists of two summits, one in the lower zone of the alpine vegetation belt (in the treeline ecotone) and one in the upper alpine zone (close to the alpine-nival ecotone). The lower summits are composed of continuous alpine grasslands, while the upper summits are dominated by large vegetation patches interspersed with rocks and scree. **(b)** Each summit consisted of sixteen permanently marked vegetation plots of 1-m² (see Pauli et al. 2015). These plots were 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 (north, east, south, west; i.e., aspects). 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, geoprecision.com) was installed at 10 cm below the soil surface, recording the temperature at an hourly interval during the 21-year sampling period. In total, 544 vegetation plots were sampled and 136 microclimate time-series were collected. **(c)** Maximum soil temperatures measured at 10 cm below the

soil surface on the GLORIA summit, Vesle Armodshøkollen in central Norway (62°15'40.5"N, 9°39'55.4"E, 1161 m a.s.l. – see picture), on the different aspects of the summit. The time series for the northern aspect clearly showcases a prolonged period of snow cover with stable near-zero soil temperatures.

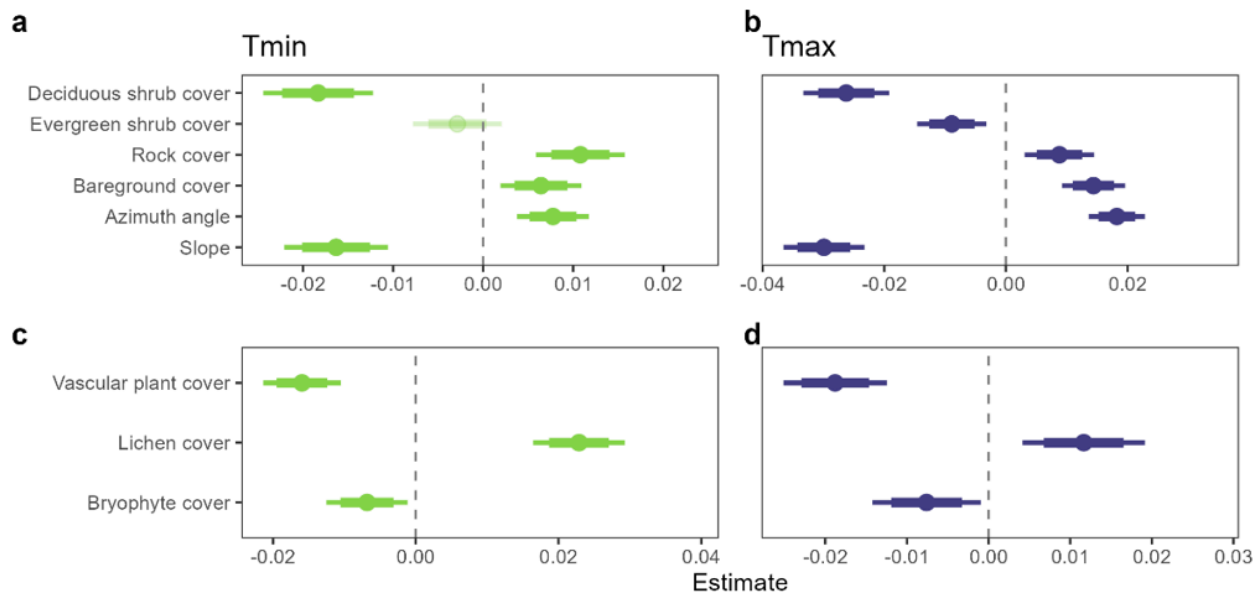


Figure 3

Relationships between magnitude of coupling between in-situ soil temperatures and gridded free-air temperatures, on the one hand, and site characteristics including deciduous and evergreen shrub cover on the mountain summits, on the other hand. Model estimates $\pm 80\%$ (thick lines) and 95% (thin lines) confidence intervals (CI) for mixed-effect modelling framework relating the magnitude of buffering between soil microclimates and gridded macroclimates for daily minimum temperatures (**a, c**) and daily maximum temperatures (**b, d**) to a set of site characteristics (rock cover, bare ground cover, deciduous shrub cover, evergreen shrub cover, azimuth angle and slope angle as well as total vascular plant, lichen and bryophyte cover) for the 544 resampled plots and 136 soil temperature time-series. The magnitude of coupling was estimated as the slope coefficient of the relationship between daily minimum or maximum soil temperatures (microclimate), on the one hand, and the gridded free-air temperatures (macroclimate), on the other hand, for each of the mountain aspects and seasons across the 136 time-series. Bright colours indicate statistically significant (i.e., 95% CIs not including zero) or marginally significant effects (i.e., 80% CIs not including zero), while faded colours depict the absence of statistically significant effects. The dashed line shows the zero-effect line.

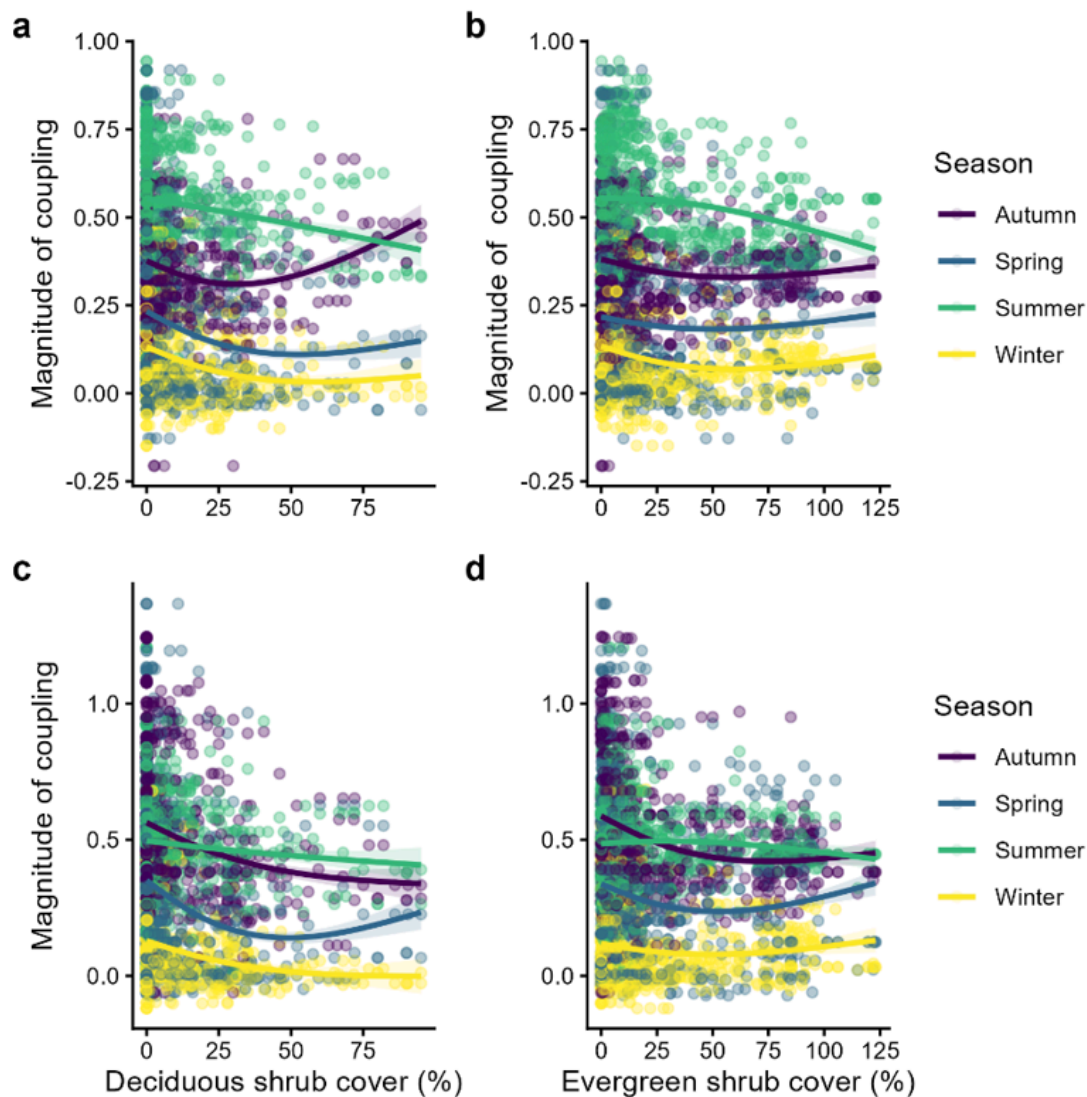


Figure 4

Relationships between magnitude of coupling between in-situ soil temperatures and gridded free-air temperatures, on the one hand, and site characteristics including deciduous and evergreen shrub cover on the mountain summits, on the other hand. Non-linear relationships between the magnitude of coupling for minimum and maximum temperatures and the plot-level deciduous and evergreen shrub cover are depicted in **b-c** and **e-f**, respectively, across the different seasons and using generalised additive modelling (GAMs). The faded dots represent the raw data points (coloured per season), lines the different GAMs (coloured per season) and shaded areas the 95% confidence intervals. The magnitude of coupling was estimated as the slope coefficient of the relationship between daily minimum or maximum soil temperatures (microclimate) and the corresponding gridded free-air temperatures (macroclimate) for each of the mountain aspects and seasons across the 136 time-series.

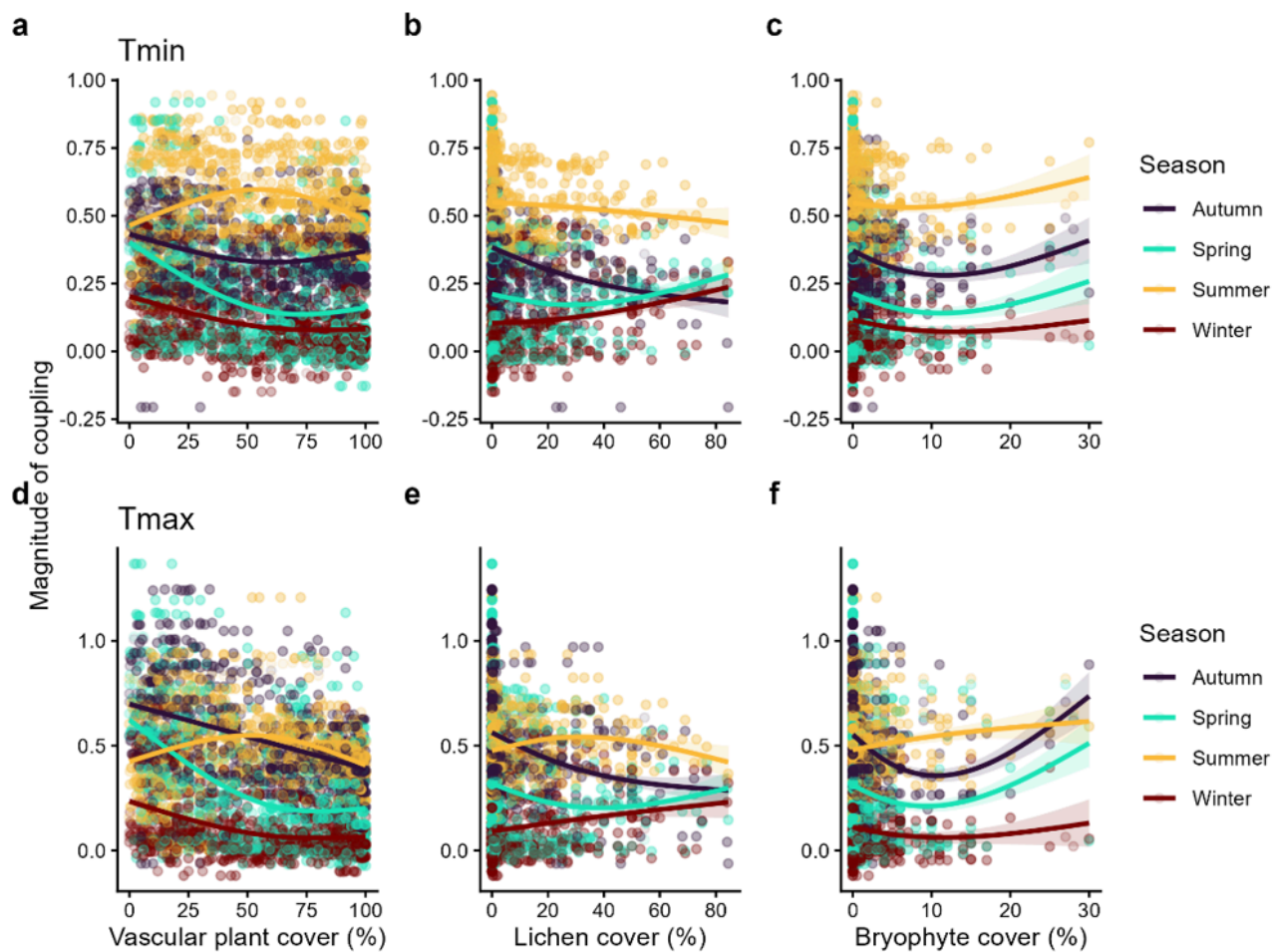


Figure 5

Relationships between the magnitude of coupling between in-situ soil temperatures and gridded free-air temperatures, on the one hand, and vascular plant, lichen and bryophyte cover on the mountain summits, on the other hand. Non-linear relationships between the magnitude of coupling and the plot-level vascular plant, lichen and bryophyte cover for minimum and maximum temperatures are depicted in **a-c** and **d-f**, respectively, across the different seasons and using generalised additive modelling (GAMs). The faded dots represent the raw data points (coloured per season), lines the different GAMs (coloured per season) and shaded areas the 95% confidence intervals. The magnitude of coupling was estimated as the slope coefficient of the relationship between daily minimum or maximum soil temperatures (microclimate) and the corresponding gridded free-air temperatures (macroclimate) for each of the mountain aspects and seasons across the 136 time-series.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Extendeddata.docx](#)