TITLE

Spatiotemporal patterns of microclimatic buffering in relict alpine communities.

RUNNING TITLE

Spatiotemporal buffering.

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ABSTRACT

**Questions**: In alpine landscapes, topography creates a mosaic of microclimatic niches that might prevent climate-driven extinctions, but the magnitude of this buffering is largely unknown. Using relict alpine communities as a model system, we ask (1) how soil climatic factors are comparable at temporal and spatial scales, and (2) how such microclimatic variation influences local extinctions and species composition.

**Location**: Picos de Europa National Park, northern Spain.

**Methods**: We resurveyed permanent plots in four alpine sites after a 10-year record of soil temperatures (temporal survey). We then sampled the variation in species composition and microclimatic temperatures in 80 plots around the permanent plots (spatial survey). We evaluated differences in microclimate between the temporal and the spatial surveys, evaluating the observed trends in species cover, and predicting local extinctions under extreme microclimatic scenarios.

**Results**: We found a trend of temperature warming with stronger effects on (micro-ridge) fellfields rather than on (micro-valley) snowbeds. Microclimatic variation was wider in space than in time, with narrow temperature variation in snowbeds and extreme low temperatures in fellfields. Species composition was mainly influenced by growing degree days (GDD) and freezing degree days (FDD), both related with snow cover duration. A total of 16 species (out of 86) showed significant responses to microclimatic variation. The highest number of local extinctions were predicted for a hot-freezing scenario, followed by cold- freezing, hot-snowy and cold-snowy scenarios.

**Conclusions**: Our results support that microclimatic buffering can compensate climate warming. However, a continuous reduction of snow cover will result in a tipping point beyond which the buffer effect will not be effective, leading to community homogenization. This process may have been started in relict alpine communities where species from snowy microclimates are being outcompeted by species adapted to below-zero winter temperatures, rather than by warm-demanding species as predicted by thermophilization.

KEYWORDS

Alpine vegetation, Climate warming, Microclimate, Temporal change, Topography, Thermophilization, Microrefugia, Snow cover

# 1. Introduction

The Anthropocene has impacted alpine biodiversity through multiple factors (Schickhoff et al. 2022). Besides direct human impacts such as land degradation and grazing, contemporary climate warming has been hypothesized as a major driver of change (Pauli et al. 2012) and a likely cause of extinctions (Jiménez-Alfaro et al. 2016) and community homogenization (Britton et al. 2009) in alpine communities. Global warming is expected to affect high-mountain ecosystems by increasing soil temperatures and drought periods to reach tipping points with impact on plant persistence and regeneration (Lu et al. 2022). The resulting trends observed in long-term vegetation monitoring indicate changes in species composition across temperate and Mediterranean mountains (Pauli et al., 2012, Nicklas et al., 2021). These trends have been described as a process of thermophilization, or the replacement of high-elevation (cryophilic) species by low-elevation (thermophilic) species in alpine communities (Gottfried et al. 2012). Thermophilization is expected to be the result of changes in soil bioclimatic drivers of plant life, such as the duration of snow cover, the length of the growing season (growing degree days, GDD), and the period of below-zero temperatures (freezing degree days, FDD) (Choler 2018).

Current evidence supports the thermophilization hypothesis of compositional change with increasing trends of generalist species in cold regions (Steinbauer et al., 2018) and decreasing trends of high-mountain specialists in relatively warmer regions (Jiménez-Alfaro et al. 2014a, Steinbauer et al., 2020). However, the concept of massive climate-driven extinctions of alpine plants has been challenged by the realization that microscale heterogeneity allows plant populations to persist in alpine landscapes (Scherrer & Körner 2011). According to this view, alpine microclimatic variation along topographic gradients provide a wide spectrum of niches, enough to buffer macroclimatic trends (Opedal et al. 2015, Körner & Hiltbrunner 2021). Thanks to this buffering, global warming would mainly result in local species shifts and a re-organization of communities (or species shuffling), rather than local extinctions (Opedal et al. 2015), supporting the hypothesis that regional alpine species pools remained relatively stable through the climatic changes of the Holocene (Jiménez-Alfaro et al. 2021a). Nevertheless, the potential impact of climatic trends on local extinctions is difficult to predict because many alpine species are long-lived and highly resilient to environmental variation (Doak & Morris 2010), with delayed population responses via extinction debts (Dullinger et al. 2012) and meta-community dynamics (Graae et al. 2018).

The importance of microclimatic buffering for preventing local extinctions of alpine plants will depend on the extension and topographic complexity of alpine areas (Malanson et al. 2023), which may differ widely among regions (Testolin et al. 2020). A correct assessment of the role of microclimatic buffering will require a local evaluation of the temporal and spatial variation of the bioclimatic drivers related to thermophilization, and their effects on local community gradients (Graae et al. 2018). Unfortunately, there is a general lack of studies addressing how topographical niches may compensate climate warming in alpine landscapes and specific regions. This information is necessary to complement long-term monitoring initiatives mainly focused on mountain summits, like e.g., the Global Observation Research Initiative in Alpine Environments (Pauli et al. 2015). A necessary strategy for understanding the role of microclimatic buffering is to analyze its effect on marginal alpine regions, where alpine communities have been subjected to climatic warming for longer times than in non-marginal alpine regions. Relict alpine communities are typically confined to reduced areas after postglacial contractions, and they are highly influenced by relatively warmer temperatures and geographic isolation (Jiménez-Alfaro et al. 2021a). Evaluating microscale bioclimatic drivers in relict communities may allow us to understand species responses to potential microrefugia and to predict the tipping points beyond which alpine communities may suffer irreversible changes in species composition, including local plant extinctions.

In this study, we evaluate the spatiotemporal patterns of soil microclimate in relict alpine plant communities of northern Spain, combining a long-term monitoring of permanent vegetation plots with a detailed topographical survey. Our first aim is to evaluate the temporal trend in microclimate over the last decade in different sites across the topographical gradient, and how temporal variation relates to the spatial variation in surrounding areas as potential buffering niches. Like in other mountains of Europe, we expect an increase in annual mean temperature with effects on related microclimatic drivers. In agreement with topographic buffering, we also expect a high spatial variation in microclimate to accommodate the temporal variation observed in the permanent plots. Our second aim is to investigate how the observed spatiotemporal variation of microclimate influences local communities. In agreement with thermophilization, we expect an increase of warm-demanding species (winners) and a decrease in the relative cover of cold-adapted species (losers). We further expect that changes in species composition will depend on the responses of individual species to specific soil microclimatic drivers. Measuring these responses will allow us to predict the potential changes in relict alpine communities under local microclimatic scenarios.

**2. Methods**

## 2.1 Field sampling

The study was conducted in the central calcareous massif of the Picos de Europa National Park, in northern Spain, where alpine vegetation occurs above 1900 m a.s.l. (Fig. 1A). The study system is an isolated mountain massif with a rocky landscape of glacial origin that has a heterogeneous topography on limestone and dolomitic substrates with karstic geomorphology. The diversity of local alpine communities is regulated by topographic gradients with a known influence on the relative abundance of species with Eurosiberian, Mediterranean or endemic origin (Jiménez-Alfaro et al., 2014b). These species co-exist in two relict vegetation types associated to specific topographic settings and plant functional types: Mediterranean-like stripped habitats mostly occupying micro-ridges (hereafter ‘fellfields’) and Eurosiberian alpine-like communities occupying micro-valleys (hereafter ‘snowbeds’) (García-Gutiérrez et al. 2018). Grazing impact in the study system is limited to wild populations of the Cantabrian chamois (*Rupicapra pyrenaica parva*). Plant species nomenclature follows Jiménez-Alfaro et al. (2021b).

In summer 2008, we established a long-term ecological research program for monitoring soil climate and vegetation with four study sites placed along a North-South gradient (Fig. 1B) that include representative communities of both fellfield and snowbed vegetation. In each of the four sites, we buried a temperature logger (M-Log5W, GeoPrecision, Ettlingen, Germany; accuracy: +/- 0.1 ºC at 0 ºC, resolution: 0.01 ºC, records each hour) at 5 cm depth in a homogeneous vegetation patch. We sampled in each site two permanent plots of 1 m2, separated 1 m from the logger. In each permanent plot, we identified species composition of vascular plants and estimated relative cover in %. Within each plot, we recorded species frequency using a grid template of 100 cells of 10 cm x 10 cm, following the methodology of GLORIA (Pauli et al. 2015). Loggers were replaced by new ones when needed, recording a continuous temperature series from 1 Jan 2009 to 31 Dec 2018. In summer 2019, we re-surveyed the permanent plots to detect changes in species presence and frequency. The vegetation data from the 8 permanent plots, together with the soil temperatures recorded for 10 years, represent the ‘temporal survey’.

In summer 2018, we conducted an additional study to measure the spatial variation of microclimate and plant communities around the four sites sampled in the temporal survey. Using the long-term temperature logger of each site as the central point, we additionally placed 20 iButtons (Thermochron, iButton, Newbury, UK; accuracy: +/- 0.5 ºC from -10 ºC to +65 ºC, resolution: 0.5 ºC, records every 4 hours) in 20 plots of 1 m2 separated 10 m from each other along the cardinal directions (Fig. 1C). The recording period for the iButtons went from 1 Oct 2018 to 31 Aug 2019 (330 days). For each one of the 20 plots per site, we identified all vascular plants and estimated their relative cover in %. The iButton climatic data and the related compositional data of the 80 plots recorded in the four sites represent the ‘spatial survey’.

*2.2. Soil bioclimatic indices*

We used microclimatic data of the temporal and spatial surveys to calculate soil bioclimatic indices. For comparison, we homogenized the data of the temporal survey at four-hour intervals, keeping the same 330 calendar days covered by the spatial survey. In total, we obtained 40 data points for the temporal survey (four sites x 10 years) and 80 for the spatial survey (four sites x 20 plots). We calculated bioclimatic indices based on standard variables used by WorldClim (Fick & Hijmans 2017), together with other variables with a relevant function on alpine topographic gradients. The selected variables were: (1) bio1 = annual mean temperature; (2) bio2 = mean diurnal range, i.e. the mean of the monthly differences between maximum and minimum temperatures; (3) bio7 = temperature annual range; i.e. the difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month; (4) snow = the number of days of snow cover, when soil temperature is around 0 ºC, calculated for the period in which the maximum temperature was < 0.5 ºC and the minimum temperature was > -0.5 ºC; (5) FDD = freezing degree days, i.e. the sum of daily mean temperatures for days in which the mean temperature was below 0 ºC (Choler 2018); and (6) GDD = growing degree days, i.e. the sum of daily mean temperatures for days in which the soil mean temperature at five cm deep was above 5 ºC (Körner 2021). For FDD, we transformed the values from negative to positive, so higher values represent more freezing. To identify the main gradients of microclimatic variability at both temporal and spatial scales, we conducted a principal component analysis (PCA) with the full set of bioclimatic indices.

*2.3 Data analyses*

All analyses were conducted with R (R Core Team, 2021). The code and data are available at GitHub (see Data Availability Statement).

We first analyzed the variation of microclimate in the temporal and spatial surveys. To identify the temporal trends in soil temperature, we decomposed the hourly temperature logs into seasonal, trend and irregular components using the function *stl* in R. We also compared the spatial and temporal variation in soil temperatures to assess the potential of the topographic variation for microclimatic buffering. For this, we (a) calculated the density plots of temperature records in each survey and (b) calculated and compared, for each survey and site, the difference between the maximum and minimum values recorded for all the bioclimatic indices (i.e., in different years for the temporal survey vs. in different plots for the spatial survey).

Secondly, we analyzed the responses of the study communities to microclimate. We used non-metric multidimensional scaling (NMDS) with environmental fitting (Oksanen et al. 2019) to assess the variation in species composition in relation with the bioclimatic variables. For this, we used the plots of the spatial survey because they represent the largest available data set of the study system in the same temporal range. We removed from the NMDS two plots that had fallen on rocks and had no vascular plant species, thus analyzing a total number of 78 plots. To identify temporal trends in the composition of the study communities, we calculated the percentage change in species frequency in 10 x 10 cm cells between the 2009 initial sampling and the 2018 resurvey. We excluded five annual species (*Euphrasia salisburgensis*, *Gentiana nivalis*, *Herniaria glabra*, *Iberis carnosa*, and *Sedum atratum*) from the analysis because they were subjected to uncertainties in field detection. To assess the responses of individual species to soil climate, we used the data of the temporal survey to construct four scenarios of climate change using the most extreme values recorded in the 10 years (2009 - 2018). The scenarios were based on the main axes of variation in the system, as interpreted by PCA and NMDS ordination of the climatic and vegetation data. We then used Generalized Linear Models (GLMs, binomial family) to predict the probability of occurrence for each species and scenario, considering that a probability of 0 in a scenario would mean the extinction of the species, but also evaluating probabilities between 0 and 5% as a pseudoextinction. The predictions were computed for each plot (n = 78) as a response to the plot’s values of GDD and FDD. From the 81 species recorded in the spatial surveys, we modeled 36 with at least 10 occurrences. We kept the models in which at least one of the bioclimatic indices had a significant effect size (p < 0.05) and for which the value of McFadden’s pseudo R2 was higher than 0.15 – since McFadden’s pseudo R2 tends to have lower values than R2 in ordinary least squares regression, values between 0.2 and 0.4 represent good fit (McFadden 1979).

**3. Results**

## 3.1. Vegetation and bioclimatic data

Across the temporal and spatial surveys, we recorded 86 taxa of vascular plants, representing 38% of the local habitat species pool (Jiménez-Alfaro et al. 2014c). Of these, 48 species were found in the temporal survey and 81 in the spatial survey (species richness per plot varied from 8 to 18, mean = 13.6). In the temporal survey (2 visits x 2 plots x 4 sites, n = 16) we recorded 42 species in 2009 and 47 in 2018. In the spatial survey, the average species richness per 1 m2 plot was 13, with the richest plot having 25 species and the poorest two species. The most frequent recorded species in the two surveys were *Thymus praecox* subsp. *ligusticus* (83 occurrences), *Anthyllis vulneraria* (73), *Koeleria vallesiana* (59), *Minuartia verna* (55) and *Helianthemum canum* (52).

After 10 years of soil temperature monitoring (**Fig. 2A**), two of the sites (Los Cazadores and Los Boches) showed a consistent pattern of continuous snow cover during winter (i.e., snowbed conditions reflected by winter temperature records around 0 ºC). In contrast, the two other sites (Ḥou Sin Tierri and Hoyo Sin Tierra) showed repeated freezing temperatures during winter (i.e., fellfield conditions). Such differences were associated with contrasting conditions of annual temperature, GDD and FDD among the four sites (mean values in **Table 1**) and were consistent with the topographic setting observed in each site. In general, the highest yearly values of GDD and FDD were associated with the lowest number of days with snow cover **(Supplementary Fig. S1**). In the spatial surveys, soil temperatures showed high within-year variation among the 20 plots sampled in each site, for both snowbed and fellfield conditions (**Fig. 2B**). The length of snow cover ranged from 0 days under snow (with freezing temperatures during most of the winter) to 8 months (with a maximum of 234 days, from November to early July). The annual temperature range (bio7) varied from 17.8 ºC to 30.3 ºC, and the diurnal range (bio2) from 1.6 ºC to 5.5 ºC. The absolute maximum was 33 ºC, the absolute minimum -12 ºC. FDD ranged from 0 ºC to 206 ºC and GDD from 517 ºC to 1,612 ºC.

The first PCA axis of the climatic data (**Supplementary Fig. S2**) explained 49% of the variance and represented a gradient of thermality mixed with seasonality: it ordered plots from low to high values of growing degree days (GDD), annual mean temperature (bio1), diurnal thermal range (bio2) and annual thermal range (bio7). The second PCA axis explained 24 % of the variance and represented a gradient of freezing intensity: it ordered plots from high to low values of freezing degree days (FDD). The third PCA axis explained 15 % of the variance and mainly represented a gradient of snow cover, although snow cover was also negatively correlated with FDD along the second PCA axis.

## 3.2. Temporal vs. spatial microclimatic variation

The soil temperature data obtained by the dataloggers for the period 1 Jan 2009 – 31 Dec 2018 showed a steady increase during the ten-year period, but also high interannual variation (**Fig. 3A**). The increase was most noticeable in the two fellfield sites, and less pronounced in the coldest of the two snowbed sites (i.e., Los Boches).

The soil temperatures recorded during the two surveys showed higher variation in the spatial than in the temporal survey (**Fig. 3B**). A pattern emerged when comparing the snowbed and fellfield sites: in the snowbeds (Los Cazadores and Los Boches) the range of temperature values recorded in the spatial survey was larger than that of the temporal survey in both the hot and cold extremes; whereas in the fellfields (Hou sin Tierri and Hoyo Sin Tierra) the whole range of values of the temporal survey was displaced towards colder values compared to the spatial survey. When comparing the bioclimatic indices, the range of values was also larger in the spatial than in the temporal survey, except for FDD; however, the differences were only significant for bio2 and snow cover length (**Supplementary** **Table S1**).

*3.3. Community responses*

Along the temporal survey we detected a similar number of increasing (winners) and decreasing (losers) species, but the winners showed stronger changes in frequency (**Fig. 4**). Two species were not found again (*Agrostis schleicheri*, *Galium pyrenaicum*) and other eight species were recorded for the first time during the resurvey (*Arenaria purpurascens*, *Lotus corniculatus*, *Potentilla crantzii*, *Sedum album*, *Sedum atratum*, *Seseli montanum*, *Silene ciliata*, and *Solidago virgaurea*). Excluding annual species and species that occurred in less than ten 10 x 10 cm cells in 2009, the species with the highest decrease in frequency from 2009 to 2018 were *Armeria cantabrica*, *Poa alpina*, *Salix breviserrata*, *Jurinea humilis* and *Ranunculus parnassiifolius* subsp. *favargeri*. In contrast, the species with the highest increases were *Minuartia verna*, *Helianthemum apenninum* subsp. *urrielense*, *Arenaria moehringioides*, *Saxifraga conifera* and *Silene acaulis*.

In the NMDS ordination of plant composition (**Fig. 1D**) we found significant environmental fitting with the first and second axes for growing degree days (GDD, R2 = 0.783, *P* < 0.001) and freezing degree days (FDD, R2 = 0.3348, *P* < 0.001) but not for snow cover duration (Snow, R2 = 0.06, *P* = 0.099). Nevertheless, the association of snow cover with GDD and FDD reflected four major combinations of climatic drivers of plant composition: hot & snowy, cold & snowy, hot & freezing and cold & freezing (**Fig. 1D**). We therefore created four plausible scenarios corresponding to the maximum and minimum values recorded during the 10 years of monitoring: hot & snowy (max GDD = 2795 ºC, min FDD = 0 ºC), hot & freezing (max GDD = 2795 ºC, max FDD = 247 ºC), cold & snowy (min GDD = 1150 ºC, min FDD = 0 ºC) and cold & freezing (min GDD = 1150 ºC, max FDD = 246 ºC). Model predictions based on these scenarios were computed for 16 species for which at least one of the bioclimatic indices had a significant effect (**Table 3**). While some species showed survival only in the snowy (e.g., *Alchemilla catalaunica*) or the freezing (e.g., *Galium pyrenaicum*) scenarios, others would likely go extinct in any scenario (e.g., *Festuca glacialis*) and others can potentially thrive in all four scenarios (e.g., *Helianthemum canum*). When considering a zero probability of occurrence (extinction), the hot & freezing scenario produced the highest number of predicted extinctions (8 species), while the cold & snowy scenario produced the lowest (1 species). The other two scenarios (cold & freezing and hot & snowy) provided predictions for 5 and 6 species respectively (**Fig. 5A**). When using a 0-5% threshold of probability of occurrence (quasi-extinction), the differences among scenarios were reduced, but keeping the highest and lowest extinctions in the hot freezing and cold snowy scenarios, respectively (**Fig. 5B**).

**4. Discussion**

*4.1 Spatiotemporal microclimatic buffering*

Our results confirm the expectation of a 10-year warming in relict alpine vegetation of southern Europe, in agreement with the general trends observed in other mountains (Gottfried et al. 2012). However, we also found that, within the same alpine landscape, the rate of warming differed between topographically protected sites (snowbeds) and exposed ridges (fellfields), with the latter showing a more noticeable increase in temperatures. Despite the wide interannual variation in temperature observed along the 10 years of microclimate monitoring, the study sites were relatively consistent in their patterns of winter snow cover, suggesting that snowbed sites prevent macroclimatic warming effects, thus contributing to microclimatic buffering. Interestingly, FDD and GDD represented the main axis of microclimatic variation, supporting the importance of both variables in driving temperature-related effects on alpine plant life (Choler 2018). Both variables seem to be the direct drivers of microclimatic variation in the study area, at least partially influenced by the length of snow cover as a major indirect driver of ecological conditions. The lack of a stronger effect of snow cover in local bioclimatic patterns may be explained by the microclimatic protection of topographical valleys even in snow-free periods, as indicated by the lower temperature variation found in the two snowbed sites. In contrast, the fellfield sites are more exposed to dominant winds, resulting in wider microclimatic ranges with the lowest minimum values of temperature during the coldest years.

In agreement with our expectations, we also found that the microclimatic variation in a one-year spatial survey was wider than the temporal macroclimatic trend found during the 10 years of monitoring. Initially, this result supports the microclimatic buffering hypothesis, whereby climatic changes in any given microsite can be buffered by nearby microsites with different conditions (Scherrer & Körner 2011). Nevertheless, during some years the fellfield sites were subjected to spells of extreme freezing temperatures that were not mirrored in the surrounding plots during the one year of spatial monitoring. Since these sites are not topographically protected during most of the winter, they are sensitive to unusual events of extreme low temperatures, which are more likely to occur within longer time periods (Walsh & Patterson 2022). Increasing days with freezing temperatures and no snow protection is associated to frost damage on roots and leaves, limiting the survival of species that need the protective cover of snow (Körner 2021). In contrast, soils in snowbed sites maintain warmer (close to 0 ºC) temperatures in winter and cooler (< 25 ºC) temperatures in summer. Our results indicate that the buffer effect of microsites with topographical protection (eventually with longer snow cover) is consistent across years and seasons, thus suggesting that they may provide microrefugia for species with low tolerance to fellfield conditions (i.e., hot summers and freezing winters). However, the spatial distribution of these microrefugia is scattered across the study system, with a dominance of fellfield rather than snowbed vegetation (Jiménez-Alfaro et al. 2014c). Local dominance of exposed micro-sites explains the observed similarities of FDD between the temporal and the spatial surveys in circular areas of 50 m radius, pointing to the relict status of local snowbeds. A key remaining question is whether future changes in the local climatic conditions will reach a tipping point beyond which the snowy end of the microclimate gradient will be lost. It is also essential to explore how microtopographic gradients correspond with local patterns in soil humidity, a factor which has been identified as one of the main drivers of diversity patterns (Moeslund et al. 2013, Mazalla et al. 2022) and alpine vegetation (Körner 2021).

*4.2 Microclimatic effects on alpine communities*

Our resurvey after 10 years of monitoring showed slight changes in species cover, but with remarkable patterns in winners and losers. In accordance with the warming trend, we found a reduction in the cover of species associated with colder and snowy conditions, like *Armeria cantabrica*, *Salix breviserrata* and *Poa alpina*, similarly to the results found in other regions (Schöb et al. 2009; Jiménez-Alfaro et al. 2014a). According to the description of local vegetation (Jiménez-Alfaro et al. 2014c), the winners were not especially associated with warmer conditions, but they are high-mountain specialists linked to snow-free microsites with winter freezing temperatures (i.e., fellfields). In addition to these species, the set of new species recorded in the resurvey were in most cases opportunists with preferences for fellfield rather than snowbed habitats, agreeing with the trends of increasing generalist species in temperate European mountains (Steinbauer et al. 2018). These results partially support the hypothesis of a thermophilization of community composition correlating with a warming climate, suggesting complex microclimatic effects beyond a mere increase of warm-demanding species. Moreover, the majority of dominant species recorded in the 78 plots are linked to relatively warm and freezing conditions (e.g. *Thymus praecox, Anthyllis vulneraria, Koeleria vallesiana*) confirming the local rarity of snowbed vegetation types reported by local vegetation maps. We also note that many of the recorded species are widely distributed in the study area and have no preference for specific microclimatic conditions, suggesting high tolerance to microclimatic heterogeneity. This may be explained by the adaptation of the local species pool to the wide spectrum of local conditions, especially considering the relatively low area of the local alpine system. The Holocene adaptation of these species to local microclimatic variation may have resulted in a local homogenization of plant communities, which is one of the expected and already observed effects of climate change on biodiversity (Matteodo et al. 2016, Verma et al. 2023). The simplification of relict communities was defined by Braun-Blanquet (1932) as a “fragmentary” effect that results in low-diversity communities which has been also identified in mountain mire communities (Jiménez-Alfaro et al. 2012). According to this view, the loss of micro-sites with snow and topographic protection will reduce the cover of plant specialists, leading to a general homogenization of alpine communities (Britton et al. 2009), a process that could have started during the Holocene, and eventually incremented during the Anthropocene.

Our models for individual species indicate that 16 out of 86 species show significant responses to microclimatic conditions, indicating that only a small portion of the local species pool would noticeably respond to extreme climatic conditions. Some species showed extinction risks in more than one scenario, generally reflecting their ecological preferences along one side of the microclimatic gradient. Predicted responses to extreme microclimatic scenarios further suggest that the most sensitive species are those adapted to cold and/or snowy conditions. Accordingly, a hot & freezing scenario, with loss of snow protection would result in local extinctions of alpine species with a clear requirement for snowy microclimates (e.g., *Erigeron alpinus*, *Alchemila catalaunica*), but also wide-niche species reaching the relatively deeper soils created by snowbeds (e.g., *Lotus corniculatus, Scilla verna*). In contrast, the scenario with the lowest risk of local extinction will be that of cold and snowy conditions, although this would imply a likely decrease of species with a preference for Mediterranean-like high-mountain conditions, like *Galium pyrenaicum*. Interestingly, two species (*Arabis alpina* and *Festuca glacialis*) show high probability of extinction in all scenarios, suggesting that even when considering microclimatic buffering, these species are likely under an extinction debt (Dullinger et al. 2012). Although evaluating the local extinction risk of the study species will require different approaches (e.g., population genetics), our results suggest that the most sensitive species to climate change will be those adapted to the coldest and snowiest side of the microclimatic gradient. This supports that microrefugia for the rarest species of the local pool are found in the conditions that were more frequent during past coldest periods, confirming their character as relict communities.

**5. Conclusions**

This study supports the expectation of microclimatic buffering along topographic gradients, but also highlights that the buffer effect depends on spatiotemporal variation in the alpine landscape. We found that thermal gradients in alpine landscapes are more complex than changes in annual mean temperature, as a possible explanation of the general disconnect between regional climatic models and local scale data (Giorgi et al. 2009). Specifically, we confirmed that bioclimatic indices like GDD and FDD are major microclimatic drivers in alpine communities, with strong connections to local patterns of snow cover and topographic refugia. The influence of these drivers was highly informative in relict alpine communities subjected to long-term periods of natural and anthropogenic climate warming. Our results from either vegetation resurveys or local modeling indicate an increase in species with tolerance to winter freezing at the expense of species from snow-protected microsites. The reduction of snow-protected microsites will eventually result in the simplification of microclimatic gradients and the homogenization of local communities, increasing extinction risks of relict species from snowy sites. Although these patterns agree with the thermophilization process, our study also shows that species replacement is favoring cold-adapted species with ecological preferences for snow-free microsites. These predictions highlight the need for further monitoring bioclimatic drivers and snow patterns, ideally complemented with the assistance of temporal series of satellite images, together with physiological, genetic and demographic approaches. It will be also necessary to identify critical plant life stages responding to microclimatic conditions, since only a few studies have tackled this question in adult plant survival, seed dispersal and persistence (Auffret et al. 2023), germination (Shimono & Kudo 2005) or seedling survival (Rosbakh et al. 2022, Gya et al. 2023). Such studies will be especially informative in alpine relict communities reduced to small alpine areas, which are more likely to experience local extinctions (Körner & Hiltbrunner 2021). In these systems, major tipping points are likely depending on the spatiotemporal variation of snow cover and its effect on the topographical buffering of bioclimatic variables.

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AUTHOR CONTRIBUTIONS

B.J.-A. led the research and the manuscript editing. E.F.P. conducted the data analyses. Both B.J.-A. and E.F.P. contributed equally to the manuscript. C.E.A. contributed to data analysis and manuscript writing. B.J.-A., CM and E.F.P. conducted the fieldwork.

# DATA AVAILABILITY

The original data, R code for the analysis and creation of the manuscript can be accessed at the GitHub repository <https://github.com/efernandezpascual/picos>. A version of the repository is deposited in Zenodo.

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**Table 1.** Bioclimatic description of the study sites. Soil temperatures were obtained at -5 cm, recorded at 1-hour interval hour in the central plots of four alpine sites in the Picos de Europa National Park, Spain. Mean values correspond to the whole period of the temporal survey, from 1 Jan 2009 to 31 Dec 2018.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Los Cazadores | Los Boches | Ḥou Sin Tierri | Hoyo Sin Tierra |
| Habitat | Snowbed | Snowbed | Fellfield | Fellfield |
| Elevation (m asl) | 2130 | 2140 | 1990 | 1950 |
| Mean annual temperature (bio1, ºC) | 6 | 4.3 | 5.5 | 6.9 |
| Diurnal thermal range (bio2, ºC) | 3.3 | 2.4 | 3.5 | 3.2 |
| Annual thermal range (bio7, ºC) | 20.9 | 19.3 | 22.3 | 23.8 |
| Absolute min temperature (ºC) | -2.8 | -4.1 | -12.0 | -9.9 |
| Absolute max temperature (ºC) | 27.1 | 24.9 | 27.0 | 27.4 |
| Annual growing degree days (ºC) | 2064 | 1538 | 1999 | 2454 |
| Annual freezing degree days (ºC) | 3.0 | 25.6 | 89.2 | 99.7 |
| Annual snow cover (days) | 129 | 193 | 100 | 71 |
| Growing season length (days) | 168.5 | 132.7 | 173.6 | 196.1 |
| Range growing season (days) | 135 – 203 | 103 – 158 | 149 – 200 | 161 - 228 |
| Mean annual temperature during growing season period (bio1, ºC) | 11.7 | 11.1 | 10.2 | 11.9 |
| Mean diurnal thermal range during growing season period (bio2, ºC) | 6.5 | 6.0 | 6.2 | 5.0 |

**Table 2.** Results ofGLM models computed for the occurrence of 16 species in response to growing degree days (GDD) and freezing degree days (FDD) values recorded in 80 1m2 plots sampled in alpine vegetation of the Picos de Europa National Park, Spain (spatial survey). The last four columns show the probability of occurrence of each species under extreme scenarios of FDD and GDD based on the values recorded in 10 years of microclimatic monitoring (temporal survey).

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Taxon | GDD estimate | GDD p | FDD estimate | FDD p | rho2 | Cold & Freezing | Cold & Snowy | Hot & Freezing | Hot & Snowy |
| Alchemilla catalaunica | 0 | 0.181 | -0.06 | 0.035 | 0.2 | 0 | 39 | 0 | 93 |
| Androsace villosa | 0.01 | <0.001 | -0.01 | 0.438 | 0.45 | 37 | 70 | 100 | 100 |
| Arabis alpina | -0.01 | 0.003 | -0.01 | 0.355 | 0.22 | 1 | 5 | 0 | 0 |
| Arenaria grandiflora | 0 | 0.004 | -0.01 | 0.243 | 0.17 | 2 | 10 | 0 | 0 |
| Arenaria moehringioides | -0.01 | 0.001 | 0.01 | 0.035 | 0.36 | 11 | 1 | 0 | 0 |
| Armeria cantabrica | -0.01 | <0.001 | -0.01 | 0.021 | 0.39 | 1 | 24 | 0 | 0 |
| Carex sempervirens | 0 | 0.004 | -0.02 | 0.007 | 0.19 | 6 | 79 | 91 | 100 |
| Erigeron alpinus | 0 | 0.972 | -0.06 | 0.033 | 0.19 | 0 | 34 | 0 | 36 |
| Euphrasia salisburgensis | 0 | 0.116 | 0.03 | <0.001 | 0.32 | 98 | 6 | 100 | 84 |
| Festuca glacialis | -0.02 | <0.001 | 0.01 | 0.467 | 0.65 | 0 | 0 | 0 | 0 |
| Festuca hystrix | 0.01 | <0.001 | 0 | 0.685 | 0.28 | 20 | 35 | 100 | 100 |
| Galium pyrenaicum | 0 | 0.938 | 0.03 | <0.001 | 0.37 | 95 | 2 | 96 | 3 |
| Helianthemum canum | 0.01 | <0.001 | 0 | 0.427 | 0.39 | 59 | 81 | 100 | 100 |
| Iberis carnosa | 0 | 0.018 | 0.02 | <0.001 | 0.28 | 83 | 3 | 1 | 0 |
| Lotus corniculatus | 0 | 0.035 | -0.04 | 0.049 | 0.19 | 0 | 39 | 0 | 99 |
| Scilla verna | 0 | 0.004 | -0.05 | 0.033 | 0.28 | 0 | 46 | 2 | 100 |

**Figure 1.** Study system. (A) Location of the Picos de Europa National Park (purple star) in northern Spain. (B) The four study sites (purple circles) placed in a North-South gradient in the central calcareous massif: 1) Los Cazadores; 2) Ḥou Sin Tierri; 3) Los Boches; and 4) Hoyo Sin Tierra. (C) Sampling design in one of the sites, showing the central plot of the temporal survey and the additional 20 plots of the spatial survey. (D) Non-Metric Dimensional Scaling (NMDS) of species composition for the 78 1 m2 plots sampled in the spatial survey, where points represent the 20 plots of each site (sites scores). Species abbreviations are shown in **Supplementary Table S2**.

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**Figure 2.** Soil temperature logs recorded at -5 cm in the alpine system of the Picos de Europa National Park, Spain. (A) Temperatures recorded every hour in the temporal survey plots of the four sites from 1 Jan 2009 to 31 Dec 2018. (B) Soil temperatures recorded every 4 hours in the 20 plots x 4 sites of the spatial survey (each color being a plot) from 1 Oct 2018 to 31 Aug 2019.

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**Figure 3.** (A) Temporal trends in soil temperature. Shaded smooth lines indicate the trend component in the soil temperature time series from 1 Jan 2009 to 31 Dec 2018 (temporal survey). The dark red line is the slope of a linear regression fitted to the temperature trends. (B) Spatial vs. temporal variation in soil temperature. Actual values and density plots of the values recorded during the spatial survey (4 sites x 20 plots, in red) and the temporal survey (4 sites x 10 years, in blue) in alpine soils of the Picos de Europa National Park (Spain).

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**Figure 4.** Plant species losers and winners observed in the temporal survey conducted on alpine relict communities of the Picos de Europa National Park (Spain). Each bar shows the percentage change of species frequency in 10 x 10 cm cells across 2 plots and 4 study sites, between 2009 and the resurvey of 2018. The numbers next to each species indicate the number of 10 x 10 cm cells in which each species was present in 2009.

**A graph showing different plants and flowers

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**Figure 5.** Number of predicted extinctions (A) and quasi-extinctions (B) resulting from GLM models computed for 16 species with significant responses to local microclimatic gradients in relict communities of the Picos de Europa National Park, Spain. Microclimatic scenarios were based on the maximum and minimum values of growing degree days (GDD) and freezing degree days (FDD) recorded in the alpine soils during the 10 years of the temporal survey. The values of individual GLM models and predicted probability of occurrence for each species are shown in **Table 3**.

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