




## RESEARCH ARTICLE

# Spatiotemporal patterns of microclimatic buffering in relict alpine communities

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## Abstract

**Questions:** In alpine landscapes, topography creates a mosaic of microclimatic niches that might prevent local extinctions, but the influence of this spatial heterogeneity on plant communities is largely unknown. Here we ask (1) how soil microclimatic variation is comparable at temporal and spatial scales, and (2) how such variation influences species composition and local extinctions in relict alpine communities.

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

**Methods:** We resurveyed permanent plots in four alpine sites following the recording of soil temperatures (temporal survey) for 10 years. We then sampled the spatial variation in species composition and microclimatic temperatures in 80 plots around the permanent plots (spatial survey). We evaluated the variation of six microclimatic indices between the temporal and the spatial surveys, and calculated the temporal trends observed in species cover. We finally predicted local extinction rates under microclimatic scenarios based on the observed microclimate–community relations.

**Results:** Despite high interannual variation, we found a 10-year trend of temperature warming on (microridge) fellfields and (microvalley) snowbeds. Microclimatic variation was larger in space than in time, with little temperature variation in snowbeds and extreme low temperatures recorded in fellfields. Species composition was mainly influenced by growing degree days (GDD) and freezing degree days (FDD), which were both related to snow cover duration. Plant cover of 16 species (out of 36 frequent species) showed significant responses to microclimatic variation. Local extinctions were mainly predicted under relatively hotter and more freezing conditions.

**Conclusions:** Our results support the idea that microclimatic spatial heterogeneity can reduce the negative influence of climate change on alpine plant communities. However, a continuous reduction of snow cover will result in a tipping point beyond which the buffer effect of this spatial heterogeneity will not be effective in protected microsites, leading to community homogenization. This process may have started in relict alpine communities where species from snowy microclimates are being outcompeted by species adapted to below-zero winter temperatures.

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## KEYWORDS

alpine vegetation, climate warming, microclimate, microrefugia, snow cover, temporal change, thermophilization, topography

## 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 is 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. Specifically, 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 local 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 the effects of global warming on microclimate conditions, that is, the climatic conditions experienced by plants on the scale of their main organs. In alpine soils, the most relevant microclimatic factors have been related to 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 of plant communities with increasing abundance of generalist species in cold regions (Steinbauer et al., 2018) and decreasing abundance of high-mountain specialists in relatively warm 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 idea that microscale heterogeneity allows plant populations to persist in alpine landscapes (Scherrer & Körner, 2011). According to this view, microclimatic variation along alpine topographic gradients provides a wide spectrum of local temperature and moisture conditions, generating contrasting microclimates over short spatial extents (Opedal et al., 2015; Körner & Hiltbrunner, 2021). Consequently, global warming would result in local species range shifts and community re-organization (species shuffling), rather than in local extinctions (Opedal et al., 2015). This would also support the hypothesis that regional alpine species pools remained relatively stable through the deep-time climatic changes of the Holocene (Jiménez-Alfaro et al., 2021a). Nevertheless, the potential impact of climate change on local extinctions is difficult to predict because many alpine species are long-lived and 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 potential of microclimatic heterogeneity to prevent local extinctions of alpine plants under global warming, or microclimatic buffering (Suggitt et al., 2018), will depend on the extent and topographic complexity of alpine areas (Malanson et al., 2023), which may differ among regions (Testolin et al., 2020). Assessing the role of microclimatic buffering requires investigating the temporal and spatial variation of the bioclimatic drivers that are related to thermophilization, and their effects on local plant communities (Graae et al., 2018). Yet, it is insufficiently understood how the influence of topography on microclimates may compensate climate warming in alpine landscapes. This information is necessary to complement long-term monitoring initiatives mainly focused on mountain summits, like, for example, the GLORIA initiative (Global Observation Research Initiative in Alpine Environments, Pauli et al., 2015). A useful strategy for understanding the processes associated with microclimatic buffering is to analyse its effect on marginal alpine regions, where alpine communities have been subjected to climatic thresholds not yet reached in other (non-marginal) regions. In southern Europe, 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 these communities may allow us to understand how species rely on microrefugia and to predict the tipping points beyond which alpine communities may suffer irreversible changes in species composition.

In this study, we evaluate the spatiotemporal patterns of soil microclimatic conditions in relict alpine plant communities of northern Spain, combining a long-term monitoring of vegetation plots with a detailed topographical survey. Our first aim is to evaluate the temporal trends in local snow cover, temperature and related variables (GDD, FDD) over the last decade in the studied alpine topographical gradient. We also ask how temporal variation relates to the spatial variation in soil microclimate in the global and regional context of climate warming. In line with the assumption of microclimatic buffering, we expect a high spatial variation in microclimate to accommodate the temporal variation observed in permanent plots. Our second aim is to investigate how the observed spatiotemporal variation of microclimate influences local plant communities. In agreement with the concept of community thermophilization, we expect an increase of warm-adapted species (winners) and a decrease in the relative cover of cold-adapted species (losers). These patterns would imply predictable changes in community composition that depend on the responses of individual species to microclimatic variation. Measuring these responses will allow us to predict extinction risk of cold-adapted species under different scenarios of soil temperature, freezing and snowbed conditions. Such information is necessary to contextualize the effect of climate warming on relict alpine

communities at their marginal distribution, and to anticipate future scenarios in other alpine regions.

## 2 | METHODS

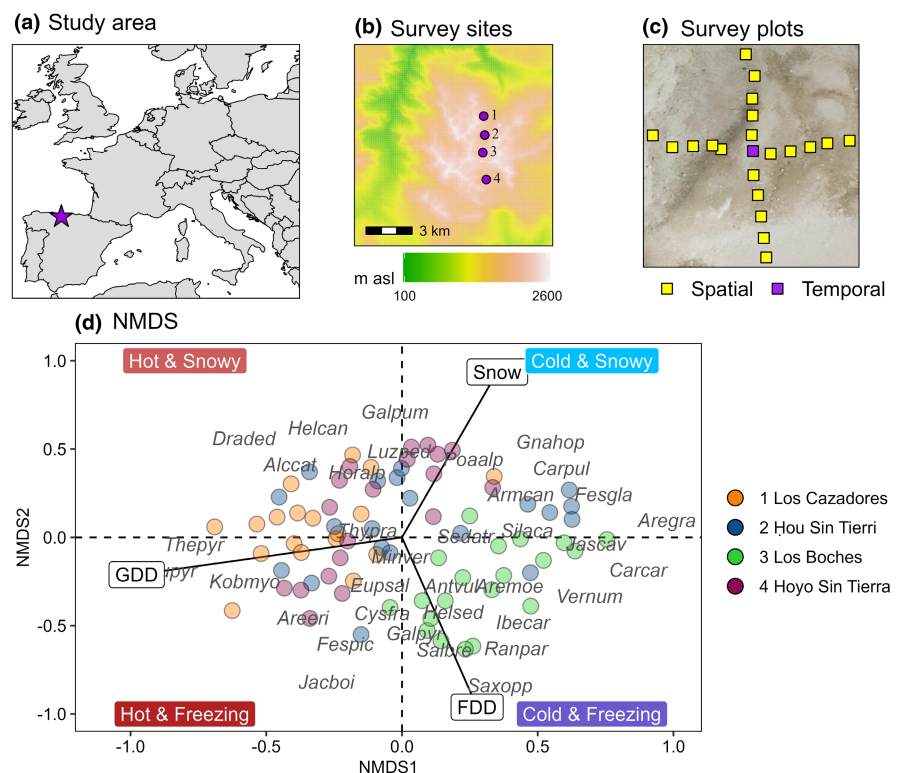
### 2.1 | Field sampling

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. (Figure 1a). The study system is an isolated mountain massif with a rocky landscape of glacial origin and a rough topography on limestone and dolomitic substrates with karstic geomorphology. The diversity of local alpine communities is regulated by topographic gradients influencing the relative abundance of species with Eurosiberian, Mediterranean or endemic distribution (Jiménez-Alfaro et al., 2014b). These species co-exist in two broad vegetation types associated with specific topographic settings and plant functional types: Mediterranean-like stripped habitats mostly occupying microridges—hereafter ‘fellfields’, mostly dominated by *Galium pyrenaicum*, *Jasione cavanillesii* and *Silene ciliata*; while Eurosiberian alpine-like communities occupy microvalleys—hereafter ‘snowbeds’ dominated by *Carex sempervirens*, *Alchemilla catalaunica* and *Plantago alpina* (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 the summer of 2008, we established a long-term ecological research programme for monitoring soil microclimate and

vegetation in four study sites placed along a North–South gradient (Figure 1b), including 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:  $\pm 0.1$  at  $0^\circ\text{C}$ , resolution:  $0.01^\circ\text{C}$ , records each hour) at 5 cm depth in a homogeneous vegetation patch. In each site, we sampled two permanent plots of  $1\text{ m}^2$  marked with permanent steel sticks and separated 1 m from the logger. We identified species composition of vascular plants and estimated relative cover in percent. Within each plot, we also recorded species frequency using a grid template of 100 cells of  $10\text{ cm} \times 10\text{ cm}$ , following the methodology of GLORIA (Pauli et al., 2015). Loggers were replaced by new ones when needed, recording a continuous temperature time series from 1 January 2009 to 31 December 2018. In summer 2019, we resurveyed the permanent plots to detect changes in species presence and frequency. All surveys were conducted at the peak of the vegetation season. The vegetation data from the eight permanent plots, together with the temperatures recorded for 10 years, represent the ‘temporal survey’.

In the summer of 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:  $\pm 0.5^\circ\text{C}$  from  $-10^\circ\text{C}$  to  $+65^\circ\text{C}$ , resolution:  $0.5^\circ\text{C}$ , records every four hours) in the centre of 20 plots of  $1\text{ m}^2$  separated 10 m from each other along the four cardinal directions (Figure 1c). The recording period for the iButtons went from 1 October 2018 to 31 August 2019 (330 days). For each of the 20 plots per site, we identified all



**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 along a North–South gradient in the central calcareous massif: (1) Los Cazadores; (2) Hou Sin Tierra; (3) Los Boches; and (4) Hoyo Sin Tierra. (c) Sampling design for each site, showing the central plot of the temporal survey and the 20 plots sampled in the spatial survey. (d) Non-metric multidimensional scaling (NMDS) of species composition for the  $1\text{ m}^2$  plots sampled in the spatial survey ( $N=78$ ), showing the 20 plots for each site (sites scores). Species abbreviations are shown in Appendix S4.

vascular plants and estimated their relative cover in percent. The iButon 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 purposes, 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  $\times$  10 years) and 80 for the spatial survey (four sites  $\times$  20 plots). We calculated bioclimatic indices at 5 cm deep based on standard variables used by WorldClim (Fick & Hijmans, 2017), together with other variables having a relevant impact on alpine topographic gradients. The selected variables were: (1) bio1, the annual mean temperature; (2) bio2, the mean diurnal range, that is, the mean of the monthly differences between maximum and minimum temperatures; (3) bio7, the temperature annual range; that is, 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°C, calculated for the period in which the maximum temperature was below 0.5°C and the minimum temperature was higher than -0.5°C. This range agrees with the maximum daily variation of less than 2°C suggested by Teubner et al. (2015) and with the visual inspection of temperature series in dates with field observations in the study area; (5) FDD, freezing degree days, that is, the sum of daily mean temperatures for days in which the mean temperature was below 0°C (Choler, 2018); and (6) GDD, growing degree days, that is, the sum of daily mean temperatures for days in which the soil mean temperature was above 5°C (Körner, 2021). For FDD, we transformed the values from negative to positive, so higher values represent more freezing conditions. 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 <https://zenodo.org/doi/10.5281/zenodo.10587703>.

We first analysed 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 the seasonal component (the mean), the trend (loss-smoothed values without the seasonal component) and the remaining component (the residuals from the seasonal plus trend fit) using the function 'st' in R (Cleveland et al., 1990). Since we lack a reference period for estimating climatic trends, we calculated the mean temperature change in each site as the mean of interannual variation in mean annual temperature ( $n=9$  between-year

intervals). We also compared the spatial and temporal variation in soil temperatures to assess the spatiotemporal variation in microclimate. For this, we (a) calculated the density plots of temperature records in each survey and (b) calculated, 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 versus in different plots for the spatial survey). Although the data loggers differed in accuracy (0.1°C vs. 0.5°C), the magnitude of the temperature values was large enough to ensure comparability.

Secondly, we analysed the responses of the studied communities to microclimate. We used non-metric multidimensional scaling (NMDS) with environmental fitting in the *vegan* R package (Oksanen et al., 2019) to assess the variation in species composition in relation to the bioclimatic variables. 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 on rocks that had no vascular plant species, thus analysing a total of 78 plots. To identify temporal trends in the composition of the study communities, we calculated the percentage change of species frequency in 10 cm  $\times$  10 cm cells between the 2009 initial sampling and the 2018 resurvey. We excluded five annual species from the analysis (*Euphrasia salisburgensis*, *Gentiana nivalis*, *Herniaria glabra*, *Iberis carnosa* and *Sedum atratum*) because they were subjected to uncertainties in field detection.

Finally, we modelled the distribution of individual species to predict local extinctions in response to microclimatic conditions. We used the data of the temporal survey to construct four scenarios based on the most extreme values recorded in the 10 years of monitoring (2009–2018). The scenarios were based on the main axes of variation as interpreted by PCA and NMDS ordinations of the climatic and vegetation data (see Section 3). We used generalized linear models (GLMs, binomial family) to predict the probability of occurrence for each species and scenario, considering that a probability of zero would mean the extinction of the species, but also evaluating probabilities between 0 and 5% as pseudo-extinctions. 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 only modelled 36 species 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- $R^2$  was higher than 0.15—since McFadden's pseudo- $R^2$  tends to have lower values than  $R^2$  in ordinary least-squares regression, values between 0.2 and 0.4 represent good fit (McFadden, 1977).

## 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). In the temporal survey (two visits  $\times$  two plots  $\times$  four sites,  $n=16$ ) we recorded 42 species in 2009

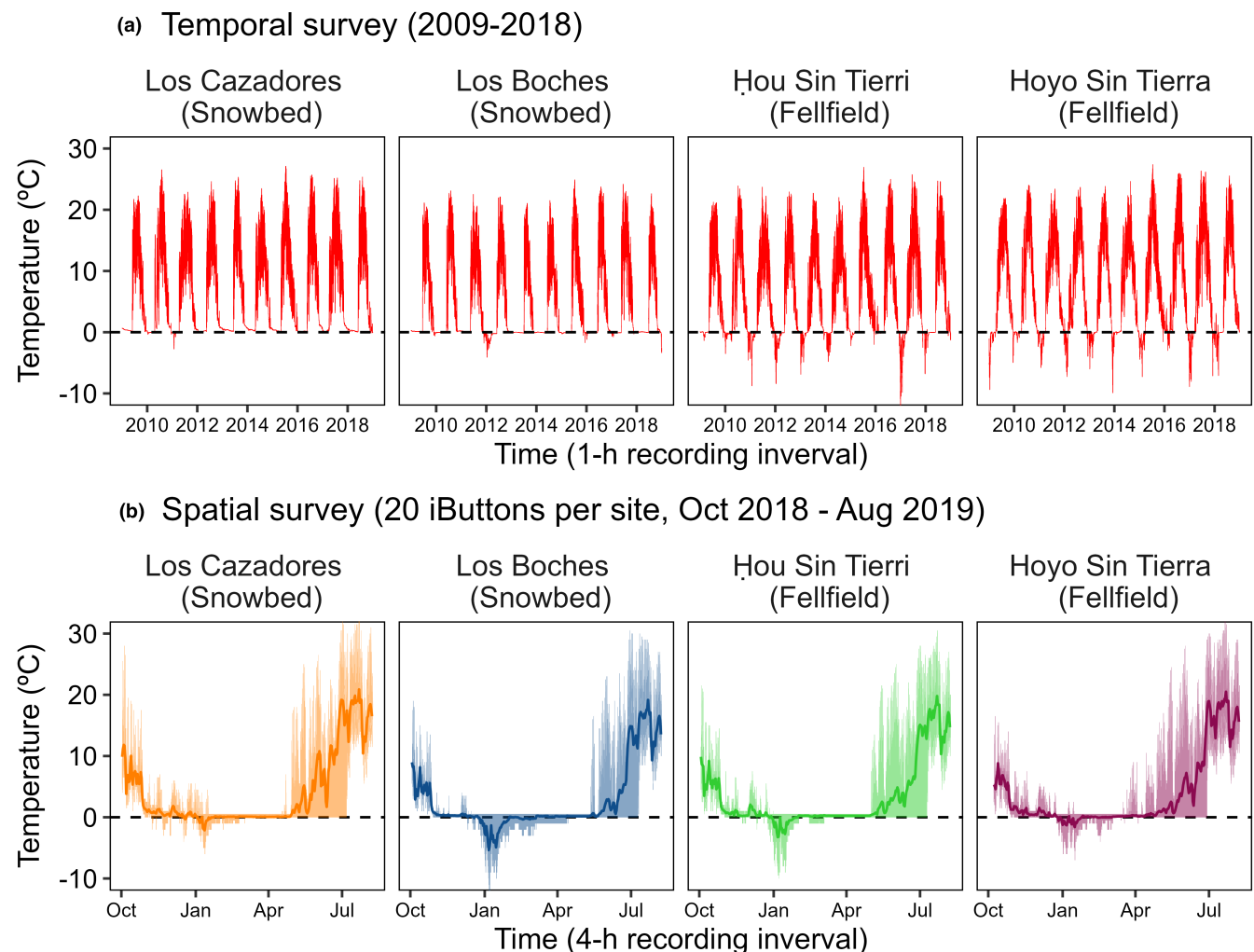


and 45 in 2018. Species richness varied from eight to 18 (mean species per plot = 13.6). In the spatial survey (78 plots), we found a total of 80 species, with the richest plot having 25 species and the poorest having two species (mean species per plot = 13.2). The most frequently recorded species in the two surveys were *Thymus praecox* subsp. *ligusticus* (75 plots), *Anthyllis vulneraria* (66), *Koeleria vallesiana* (53), *Minuartia verna* (49) and *Helianthemum canum* (44).

After 10 years of soil temperature monitoring (Figure 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°C). In contrast, the two other sites (Hou 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). In general, the highest yearly values of GDD and FDD were associated with the lowest number of days with snow cover (Appendix 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 sites (Figure 2b). In all cases, we found plots within the same site corresponding to either snowbed or fellfield conditions, irrespective of the central (temporal) plot. The length of snow cover ranged from zero days under snow (with freezing temperatures during most of the winter) to eight months (with a maximum of 234 days, from November to early July). The annual temperature range (bio7) varied from 17.8°C to 30.3°C, and the diurnal range (bio2) from 1.6°C to 5.5°C. The absolute maximum was 33°C and the absolute minimum was -12°C. FDD ranged from 0 to 206°C and GDD ranged from 517 to 1612°C.

The first PCA axis of the climatic data (Appendix S2) explained 49% of the variance and represented a gradient of temperature variation: it ordered plots from low to high values of 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 FDD. The third PCA axis



**FIGURE 2** Soil temperature logs recorded at -5 cm in alpine soils of Picos de Europa National Park, Spain. (a) Temperatures recorded every hour in four study sites from 1 Jan 2009 to 31 Dec 2018 in the temporal survey. (b) Soil temperatures recorded every four hours in 20 plots around the same four sites from 1 Oct 2018 to 31 Aug 2019 in the spatial survey. The thicker line represents the daily mean temperature for the 20 loggers and the thinner lines show the values of 20 individual loggers per site.



	Los Cazadores	Los Boches	Hou Sin Tierri	Hoyo Sin Tierra
Habitat	Snowbed	Snowbed	Fellfield	Fellfield
Elevation (m a.s.l.)	2130	2140	1990	1950
Absolute min. temperature (°C)	-2.8	-4.1	-12.0	-9.9
Absolute max. temperature (°C)	27.1	24.9	27.0	27.4
Mean annual temperature (bio1, °C)	6±0.5	4.3±0.5	5.5±0.3	6.9±0.5
Diurnal thermal range (bio2, °C)	3.3±0.4	2.4±0.3	3.5±0.4	3.2±0.5
Annual thermal range (bio7, °C)	20.9±1.8	19.3±1.6	22.3±2.4	23.8±2.5
Annual growing degree days (GDD, °C)	2064±195	1538±202	1999±133	2454±193
Annual freezing degree days (FDD, °C)	3.0±6.8	25.6±27.3	89.2±68.9	99.7±56.5
Annual snow cover (days)	129±26	193±26	100±33	71±30
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, °C)	11.7±0.8	11.1±0.7	10.2±0.9	11.9±0.8
Mean diurnal thermal range during growing season period (bio2, °C)	6.5±0.7	6.0±0.6	6.2±0.8	5.0±0.7

Note: The data were obtained from temperature loggers buried at -5 cm in the soil, with values recorded at one-hour intervals. Mean values and standard deviation ( $\pm$ ) correspond to the whole period of the temporal survey, from 1 Jan 2009 to 31 Dec 2018.

explained 15% of the variance, mainly representing a gradient of snow cover length, which was also negatively correlated with FDD along the second PCA axis.

### 3.2 | Temporal versus spatial microclimatic variation

The soil temperature data obtained from the dataloggers for the period 1 January 2009–31 December 2018 showed a general increase during the 10-year period. However, this trend was linked with high interannual variation (Figure 3a), and the mean temperature change was negative in two of the study sites due to the influence of the coldest years. The increase trend was most noticeable in Hoyo Sin Tierra (fellfield, slope estimate  $2.31e-9$ , standard error [SE]= $1.48e-11$ ; mean temperature change,  $0.0047^\circ\text{C}$ ), which is also the warmest site; followed by Cazadores (snowbed,  $1.52e-9$ , SE= $1.67e-11$ ; mean change,  $0.0038^\circ\text{C}$ ); Hou Sin Tierri (fellfield,  $1.17e-9$ , SE= $1.19e-11$ ; mean change,  $-0.0259^\circ\text{C}$ ); and Los Boches (snowbed,  $7.45e-10$ , SE= $1.86e-11$ ; mean change,  $-0.0414^\circ\text{C}$ ), which is the coldest and snowiest site.

Soil temperatures recorded during the two surveys showed higher variation in the spatial than in the temporal survey (Figure 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

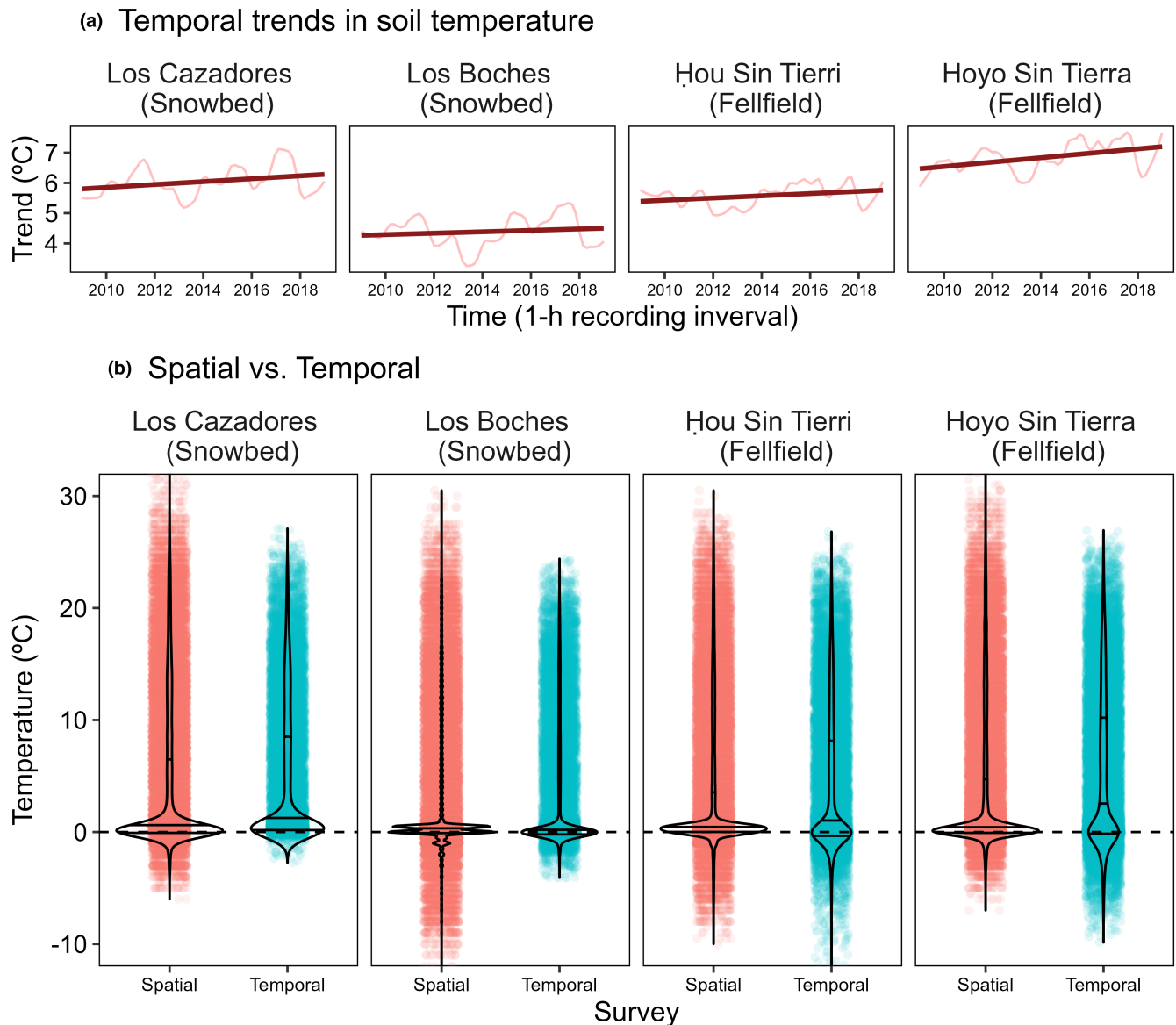
TABLE 1 Microclimatic description of four study sites monitored in alpine communities of the Picos de Europa National Park, Spain.

for FDD; however, the differences were only significant for diurnal thermal range (bio2) and snow cover length (Appendix S3).

### 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 (Figure 4). Two species were not found again (*Agrostis schleicheri*, *Galium pyrenaicum*) and 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 cm  $\times$  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 parnassifolius* subsp. *favargerii*. 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 community composition (Figure 1d) we found significant environmental fitting with GDD (first axis,  $R^2=0.78$ ,  $p<0.001$ ) and FDD (FDD,  $R^2=0.33$ ,  $p<0.001$ ) but not for snow cover duration (snow,  $R^2=0.06$ ,  $p=0.09$ ). The association of snow cover with GDD and FDD revealed four major combinations of climatic drivers of plant composition: hot-and-snowy; cold-and-snowy; hot-and-freezing and cold-and-freezing (Figure 1d). We therefore created four plausible scenarios corresponding to the maximum and minimum values recorded during the 10years of monitoring: hot-and-snowy (max. GDD= $2795^\circ\text{C}$ , min. FDD= $0^\circ\text{C}$ ),



**FIGURE 3** Microclimatic variation recorded in alpine soils of the Picos de Europa National Park, Spain. (a) Temporal trends in soil temperature, where 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 versus temporal variation in soil temperature. Actual values and density plots of the values recorded during the spatial survey (data for one year across 20 plots  $\times$  four sites, in red) and the temporal survey (data for 10 years in four sites, in teal).

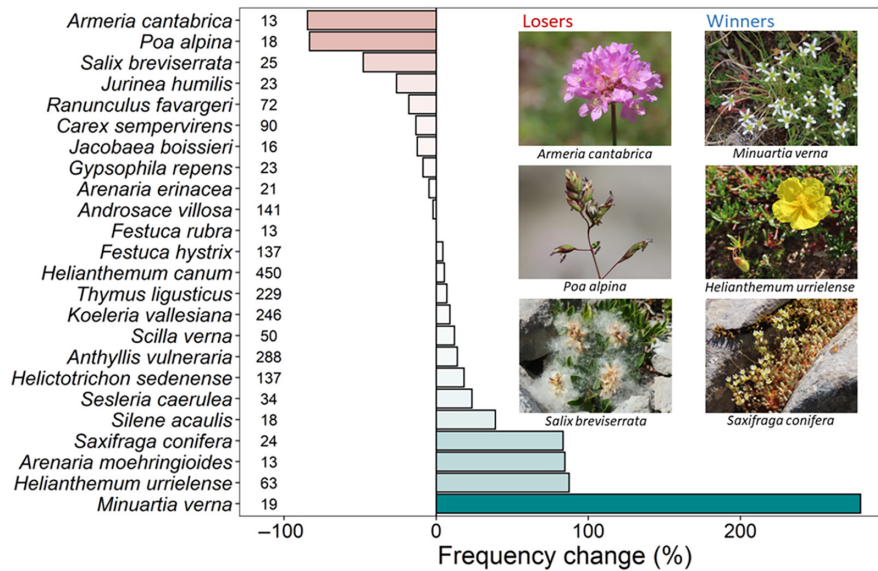
hot-and-freezing (max. GDD=2795°C, max. FDD=247°C), cold-and-snowy (min. GDD=1150°C, min. FDD=0°C) and cold-and-freezing (min. GDD=1150°C, max. FDD=246°C). Model predictions based on these scenarios were computed for 16 species for which at least one of the bioclimatic indices had a significant effect (Table 2). While some species showed no extinction 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-and-freezing scenario produced the highest number of predicted extinctions (eight species), while the cold-and-snowy scenario produced the lowest number of predicted extinctions (one species). The other two scenarios

(cold-and-freezing and hot-and-snowy) predicted extinctions for five and six species, respectively (Figure 5a). When using a 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 (Figure 5b).

## 4 | DISCUSSION

### 4.1 | Spatiotemporal microclimatic variation

We found a wide interannual variation in temperature over 10 years of microclimate monitoring, with relatively colder and warmer years



**FIGURE 4** Plant species with decreasing (losers) and increasing (winners) trends in frequency observed on alpine relict communities of the Picos de Europa National Park, Spain. Each bar shows the percentage change of species frequency in 10 cm × 10 cm cells across eight permanent plots (2 × 4 sites) between year 2009 and a resurvey in 2018. The numbers next to each species indicate the number of 10 cm × 10 cm cells in which each species was present in the first survey.

**TABLE 2** Results of generalized linear models (GLMs) computed for modeling the occurrence of 16 species in response to growing degree days (GDD) and freezing degree days (FDD) values recorded in 1-m<sup>2</sup> plots (N = 78) sampled in alpine communities of the Picos de Europa National Park, Spain (spatial survey).

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

Note: 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).

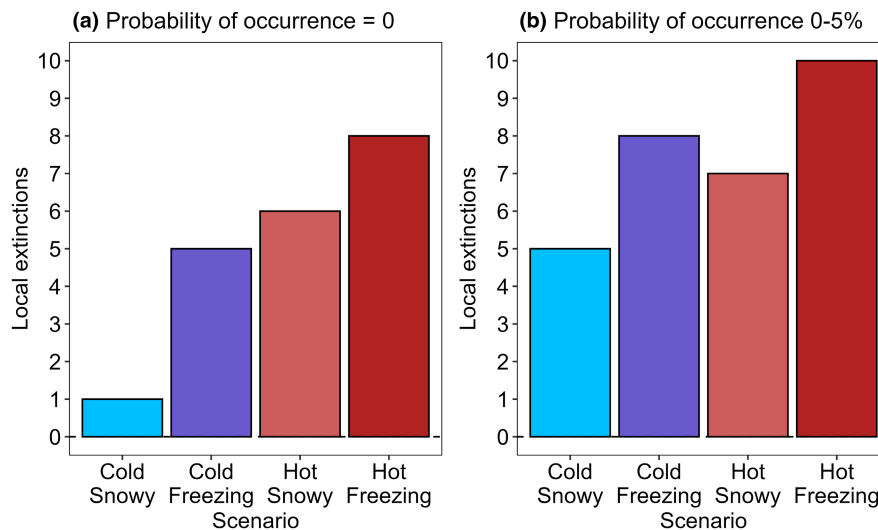
affecting similarly all the study sites. Despite this variation, the length of winter snow cover was relatively consistent in all sites, suggesting that the microclimatic protection of snowbeds was maintained also in the warmest years. Similarly, a recent study in the Alps found relatively few changes in alpine snow cover during the last 40 years, where the main impact of global warming resulted in a general increase in productivity (Rumpf et al., 2022). Our results also confirm the expectation of contemporary warming in relict alpine communities, in agreement with the general trends observed in other European regions (Gottfried et al., 2012). The rate of warming

differed among sites, with the most and least noticeable increases detected in a fellfield and a snowbed site, respectively. Although these results support spatial heterogeneity of microclimate between protected sites (snowbeds) and exposed ridges (fellfields), it is difficult to evaluate whether the warming observed in 10 years responds to macroclimatic trends or is caused by interannual variation in soil temperatures.

We also found that FDD and GDD explain the main axes of microclimatic variation, supporting the importance of both variables in explaining temperature-related effects on alpine plant life



**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 for 10 years. The values of individual generalized linear models (GLMs) and species probabilities are shown in Table 2.



(Choler, 2018). These variables are also partially influenced by the length of snow cover, which had a relatively minor effect on local bioclimatic patterns. This suggests that snow cover is mainly an indirect driver of local microclimate in the study area, modulating FDD and GDD along topographical gradients. Such an effect may be explained by the microclimatic protection of topographical valleys in snow-free periods, as indicated by the low temperature variation found in the two snowbed sites. In contrast, the fellfield sites are more exposed to dominant winds, resulting in wider microclimatic ranges and low minimum values of temperature during the coldest years. These findings indicate that microclimatic gradients are mostly influenced by the topographical setting of the alpine landscape, and complementary by the distribution and length of snow cover. In our relict alpine system, FDD and GDD seem to play a relevant role also because the Picos de Europa massif is subjected to high solar radiation, given the relatively low latitude (43°N) in the context of other alpine regions.

In agreement with our expectations, we found that the microclimatic variation in a one-year spatial survey (in 78 loggers) was wider than the temporal trend found during the 10 years of monitoring (in four loggers). Initially, this supports the idea that microclimatic changes in any given site can be compensated by nearby sites with different conditions (Scherrer & Körner, 2011). Nevertheless, during the coldest years the fellfield sites were subjected to spells of extreme freezing temperatures that were not mirrored in the surrounding plots during one year of spatial monitoring. Since the fellfield 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 without snow protection is associated with 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°C) temperatures in winter and cooler (<25°C) temperatures in summer. Since the microsites with topographical protection (longer

snow cover) were relatively consistent across years and seasons, they may provide microrefugia for species with low tolerance to fellfield conditions (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 communities (Jiménez-Alfaro et al., 2014c). The local dominance of exposed microsites explains the observed similarities of FDD between the temporal and the spatial surveys in circular areas of 50m radius (Appendix S3), 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 coldest and snowy end of the microclimate gradient will be lost. It is also essential to explore how the temperature and snow gradients correspond with local patterns in soil moisture, as one of the main drivers of diversity in cold-adapted grasslands (Moeslund et al., 2013; Körner, 2021; Mazalla et al., 2022).

## 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 a 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* (Jiménez-Alfaro et al., 2014a), similarly to the results found in the European Alps (Schöb et al., 2009). The winners were not especially associated with warmer conditions, but they are considered high-mountain specialists linked to snow-free microsites and winter freezing temperatures, that is, fellfields (Jiménez-Alfaro et al., 2014c). Moreover, the set of new species recorded in the resurvey were in most cases generalists with preferences for fellfield rather than snowbed habitats, in line with the trends of increase of generalist species observed in temperate European mountains (Steinbauer et al., 2018). These results partially support the hypothesis of community thermophilization correlating



with a warming climate, but also suggest further microclimatic effects (e.g., increasing freezing in winter) beyond a mere increase of warm-demanding species. Although not measured in this study, the increase of summer drought associated with increasing summer temperature and soil freezing may also lead to shifts in plant biomass allocation from shoots to roots, and the extirpation of drought-sensitive species (Möhl et al., 2023).

The most frequent species recorded in the 78 plots of the spatial survey are linked to relatively warm and freezing (fellfield) conditions (e.g. *Thymus praecox*, *Anthyllis vulneraria*, *Koeleria vallesiana*) confirming the rarity of snowbed communities reported in local vegetation maps (Bueno & Fernández Prieto, 2013). We also note that at least 20 out of 36 frequent species are widely distributed in the study area and may tolerate the whole gradient of microclimatic conditions. This may be explained by the past adaptation of the regional species pool to the local spectrum of niches, especially considering the relatively low area of the alpine system. The postglacial, warming-driven reorganization of these species to local microclimatic conditions 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 also been identified in mountain mires (Jiménez-Alfaro et al., 2012). According to this view, the continuous loss of microsites with long snow cover will reduce the abundance of plant specialists, leading to a progressive homogenization of alpine communities (Britton et al., 2009). This long-term process could have resulted in the decline of alpine species with narrow ecological niches, leading to past and future local extinctions.

Our models indicate that 16 out of 36 frequent species are linked to specific microclimatic conditions. 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-and-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*, *Alchemilla 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 extinctions 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 (e.g., *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 currently under an extinction debt (Dullinger et al., 2012). Although our models are realistic in the magnitude of the tested microclimatic factors, we did not consider interannual variation or plant biological resilience and thus they are mainly informative to compare the ecological factors with the highest impact in species' occurrences. Under this assumption, our results suggest that the most sensitive species to local climate change will

be those adapted to the coldest and snowiest side of the microclimatic gradient.

## 5 | CONCLUSIONS

This study supports the existence of microclimatic gradients that may lead to microclimatic buffering in relict alpine communities under global warming. However, our results also highlight that thermal gradients are more complex than changes in mean annual temperature, supporting the general disconnect between global climatic models and local-scale data (Giorgi et al., 2009). We also confirmed that bioclimatic indices like GDD and FDD are major microclimatic drivers in alpine communities, with strong connections with topographic refugia and local patterns of snow cover. Our results from either vegetation resurveys or local modelling agree with the thermophilization process, but also indicate an increase in species with tolerance to winter freezing at the expense of species from snow-protected microsites. If the predictions of decreasing snow precipitation are correct (Lastrada et al., 2021), the reduction of snow-protected microsites will eventually result in the simplification of microclimatic gradients and the homogenization of local plant communities. This would increase the extinction risk of species adapted to topographically protected sites, reducing the effect of microclimatic buffering. These predictions highlight the need for long-term monitoring of microclimate and snow patterns, ideally complemented with the assistance of time 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 likely depend on the spatiotemporal variation of snow cover and its effect on thermal thresholds and moisture conditions along topographical gradients.

## AUTHOR CONTRIBUTIONS

Borja Jiménez-Alfaro led the research and the manuscript writing. Eduardo Fernández-Pascual conducted the data analyses. Both Borja Jiménez-Alfaro and Eduardo Fernández-Pascual contributed equally to the manuscript. Clara Espinosa Del Alba contributed to data analysis and manuscript writing. Borja Jiménez-Alfaro, Corrado Marcenò and Eduardo Fernández-Pascual conducted the fieldwork.

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## CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The original data and 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, <https://zenodo.org/doi/10.5281/zenodo.10587703>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Annual values of growing degree days (GDD), freezing degree days (FDD) and snow cover duration (snow) averaged from soil climatic data recorded during 10 years in four alpine sites of the Picos de Europa National Park (Spain).

**Appendix S2.** Principal Component Analysis of the variation in soil bioclimatic indices.

**Appendix S3.** Mean values and standard error for soil bioclimatic indices calculated from the spatial and temporal surveys (N=84) conducted in four alpine sites of the Picos de Europa National Park, Spain.

**Appendix S4.** Species registered during the temporal and spatial surveys in 84 vegetation plots sampled in the Picos de Europa National Park, Spain, with their corresponding abbreviations and scores obtained from the Non-metric Multidimensional (Distance) Scaling (NMDS) (Figure 1D).

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