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TITLE

Spatiotemporal microclimatic variation highlights the importance of snow microrefugia in relict alpine communities.

RUNNING TITLE

Alpine microclimatic buffering can save species from local extinction.

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ABSTRACT

**Questions**: In alpine landscapes, topography creates a mosaic of microclimatic niches that might prevent climate-driven extinctions under climate warming, but the magnitude of this buffering is largely unknown. We ask (1) how microclimatic factors influencing relict alpine communities are comparable at temporal and spatial scales, and (2) how microclimatic scenarios may affect local extinctions and species composition.

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

**Methods**: We resurveyed 8 permanent plots in four alpine sites after a 10-year record of soil microclimate temperatures (temporal survey). We then sampled the variation in species composition and registered microclimate temperatures in 80 plots around the permanent plots (spatial survey). We evaluated differences in microclimate and species composition between the temporal and the spatial surveys, comparing the observed trends in species cover with predictions of local extinctions calculated for extreme microclimatic scenarios.

**Results**: We found a temporal trend of temperature warming coupled with slight changes in the cover of species with winners and losers along a microclimatic gradient from fellfields to snowbeds. Temporal changes of growing degree days in the permanent plots were less variable than spatial heterogeneity, but freezing degree days and snow cover varied equally in time and space. A total of 16 species (out of 86) showed significant responses to microclimate. A hot-freezing microclimatic scenario had the highest predicted number of local extinctions, followed by cold- freezing, hot-snowy and cold-snowy scenarios.

**Conclusions**: Our results support that spatial microclimatic heterogeneity can compensate current trends in climate warming. However, resurveys suggest that species needing snowy microclimates are being outcompeted by species adapted to below-zero winter temperatures. Several years with a drastic reduction of snow cover may reach a tipping point beyond which the buffer effect of topography will not be effective. It is necessary to implement monitoring systems based on remote sensing of snow patterns and sampling vulnerable population genetics of relict species for ex-situ conservation purposes.

KEYWORDS

Alpine vegetation, Climate warming, Microclimate, Temporal change, Topography

# 1. Introduction

The Anthropocene has impacted the biodiversity of alpine vegetation 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) in alpine plant communities. Global warming is expected to affect high-mountain habitats by increasing soil temperatures and drought reaching tipping points that will impact plant communities (Lu et al. 2022). At local scales, the observed trends in long-term vegetation from temperate and Mediterranean mountain summits indicate changes in species composition (Pauli et al., 2012, Nicklas et al., 2021) coupled with recent thermofilization, i.e., the continuous increase in soil temperatures (Gottfried et al. 2012). Thermofilization is expected to influence direct climatic drivers of alpine communities, such as snow cover duration, or the photosynthetic (growing degree days, GDD) and below-zero (freezing degree days, FDD) time periods accumulated along the year (Choler 2018).

As mentioned, current evidence is mainly related to changes in species composition, with increasing trends of generalist species in cold regions (Steinbauer et al., 2018) and decreasing trends of alpine specialists in relatively warm temperate regions (Jiménez-Alfaro, Gavilán, et al. 2014a, Steinbauer et al., 2020). The impact of these 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 effects of populations via extinction debts (Dullinger et al. 2012) and meta-community dynamics (Graae et al. 2018). During the last decade, the view of massive climate-driven extinctions of alpine plants under global warming has been challenged by the idea that microscale heterogeneity allows plant populations to persist in alpine landscapes (Scherrer, D. and Körner 2011). This idea relies on the microclimatic variation of alpine microhabitats along local topographic gradients, providing a wide spectrum of niches to buffer local climates from macroclimatic trends (Opedal et al. 2015, Körner & Hiltbrunner 2021). According to this view, climate warming will result in local species shifts and a re-organization of communities (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. 2021). Nevertheless, the extent of alpine systems to microclimatic buffering under global warming is regionally contingent and strongly dependent on the geographic extent of alpine areas (Malanson et al. 2023). Evaluating the temporal and spatial variation of these bioclimatic indices is crucial for understanding the extent of climatic buffering and its potential effect in local alpine communities (Graae et al. 2018). However, there is a general lack of studies addressing how topographical niches may compensate climate warming under regional specific conditions. To this aim, the study of relict alpine communities in southern Europe may provide a useful framework to anticipate the effects of climate warming in northern temperate alpine systems. In southern Europe, relict alpine communities are mostly distributed in reduced areas because of postglacial contractions (Jiménez-Alfaro et al. 2021), but had a wider distribution in the past (Jiménez-Alfaro et al. 2012). Evaluating microscale drivers in these communities may allow us to understand species responses to potential microrefugia and predict the conditions beyond which these ecosystems may lose current plant diversity.

In this study, we evaluate the spatiotemporal patterns of microclimate in relict alpine communities of northern Spain. We combine a long-term vegetation monitoring of permanent plots and 10 years of soil climatic data with a compositional survey assessing spatial microclimatic patterns in an alpine refugia massif. Our first aim is to evaluate how the temporal trend in microclimate changed over the last decade in different sites across the topographical gradients, and how this variation relates to the spatial microclimatic variation in surrounding areas as potential buffering niches. Like other mountains of Europe, we expect an increasing temporal trend in temperature annual means. In agreement with topographic buffering, we further hypothesize that high spatial variation in microclimate may accommodate the temporal variation observed in focal permanent plots. Our second aim is to assess how the observed spatiotemporal variation in microclimate influences local communities. In the case of thermofilization trends, we expect warm-demanding species to increase relative cover (winners) and a decrease in cold adapted species (losers) in plant communities, and we further hypothesize that changes in species composition will depend on the responses of individual species to specific microclimatic scenarios. Predictions of species performance under these scenarios will allow us to assess changes in local communities under climate change.

**2. Methods**

## 2.1 Data collection

The study was conducted in the central calcareous massif of the Picos de Europa National Park (**Fig. 1A**), northern Spain, where alpine vegetation occurs between 1900 and 2400 m a.s.l. with a local species pool of 230 plant species (Jiménez-Alfaro et al., 2014b). The system is an isolated mountain massif with a rocky landscape of glacial origin, supporting a heterogeneous topography on limestone substrates with karstic geomorphology. The diversity of local alpine communities is regulated by mesotopographic gradients, influencing relative abundance of species with Eurosiberian, Mediterranean or endemic origin. In 2008, we established a long-term ecological research program for monitoring soil climate and vegetation, including four study sites along a North-South gradient (**Fig. 1B**). These sites reflect variation in local climatic gradients along the two major vegetation types described in the study area: Mediterranean-like stripped habitats (fellfields) and Eurosiberian alpine-like communities (snowbeds) (García-Gutiérrez et al. 2018).

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 relatively homogeneous vegetation patch. In 2008, we first established and surveyed plant communities in two permanent plots of 1 m2 separated 1 m from the logger, identifying species composition of vascular plants and estimating relative cover in %. Within each plot, we sampled species frequency using a grid template of 100 cells of 10 cm x 10 cm following the methodology of the Global Observation Research Initiative in Alpine Environments, GLORIA (Pauli et al. 2015). Loggers were replaced by new ones when needed, recording a continuous temperature series from 1 Jan 2008 to 31 Dec 2018. In 2019, we re-surveyed the permanent plots to detect changes in species presence and frequency. The data from the 8 permanent plots, together with the soil temperature collected for 10 years, represent the ‘temporal survey’.

In 2018, we visited the study sites 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 spatial reference, we additionally placed 20 iButtons (Thermochron, iButton, Newbury, UK; accuracy: +/- 0.5 ºC from -10 ºC to +65 ºC, resolution: 0.5 ºC, records each 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 compositional data of the 80 plots recorded in the four sites represent the ‘spatial survey’.

*2.3. Data analyses*

We used microclimatic data of the temporal and spatial surveys to calculate 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 effect on alpine topographic gradients: snow cover, growing degree days and freezing degree days. The final 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 temperature is around 0 ºC, based on those days in which the maximum temperature was < 0.5 ºC and the minimum temperature was > -0.5 ºC; (5) 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); and (6) 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). For FDD, we transformed the values from negative to positive, so higher values equal more freezing, making interpretation more straightforward. We then conducted a principal component analysis (PCA) of the bioclimatic indices to identify the main gradients of microclimatic variability at both temporal and spatial scales.

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 (R Core Team 2021). 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 values 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.

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 (**Fig. 1D**). 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 species recorded, thus analyzing a total number of 78 plots. To identify the temporal trends in the study communities, we calculated the percentage change in species frequency in 10 x 10 cm cells between the 2009 initial sampling and the 2019 resurvey. We excluded five annual species from the analysis because they are subjected to uncertainties in field detection between years.

To assess the probability of species extinctions in different microclimatic scenarios, 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 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. 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 (McFadden 1974) 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 very good fit (McFadden 1979). All analyses in this article were conducted with R (R Core Team, 2021). The code and data are available at GitHub (see Data Availability Statement).

**3. Results**

## 3.1. Microclimatic variation

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 reflected by temperatures below 0ºC). Such differences were associated with contrasting conditions of annual temperature, GDD and FDD along the four sites (mean values in **Table 1**). Using annual means from the temporal monitoring we could observe complementary trends between FDD and snow cover **(Supplementary Fig. S1**). Soil temperatures from the spatial survey also showed variation between snowbed and fellfield conditions among the 20 plots sampled in each site (**Fig. 2B**). From the spatial survey across the whole system, the length of snow cover across plots 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 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. GDD ranged from 517 ºC to 1,612 ºC and FDD from 0 ºC to 206 ºC.

The first PCA axis of the climatic data (**Supplementary Fig. S2**) explained 49 % of the variance and represented a gradient of thermicity 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.

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 (Ḥou Sin Tierri, Hoyo Sin Tierra), and less pronounced in the snowbed and coldest site (Los Boches). The soil temperatures recorded during the temporal and spatial surveys showed comparable patterns (**Fig. 3B**). However, a pattern emerged when comparing the snowbed permanent plots (Los Cazadores, Los Boches) with the fellfield permanent plots (Ḥou Sin Tierri, Hoyo Sin Tierra): in the snowbeds, the range of temperature values from the spatial survey was larger than that of the temporal survey; whereas in the fellfields the spatial surroundings did never reach values as cold as those recorded during the ten years in the temporal survey. The range and frequency of values of the bioclimatic indices obtained in the spatial survey was generally larger than the values obtained during ten years of temporal survey except for FDD, however differences were only significant for Bio2 and snow (see **Table 2** for more details).

*3.2. Species composition*

Across the temporal and spatial surveys, we recorded 86 taxa of vascular plants, representing 38% of the local species pool known in the study system (Jiménez-Alfaro, Alonso Felpete, et al. 2014b). Of these, 81 species were found in the spatial survey and 48 in the temporal 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 2019. 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 were *Thymus praecox* subsp. *ligusticus* (83 occurrences), *Anthyllis vulneraria* (73), *Koeleria vallesiana* (59), *Minuartia verna* (55) and *Helianthemum canum* (52).

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 in the plots (*Arenaria purpurascens*, *Lotus corniculatus*, *Potentilla crantzii*, *Sedum album*, *Sedum atratum*, *Seseli montanum*, *Silene ciliata*, *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 2019 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 computed for the 78 plots of the spatial survey, we identified four major climatic conditions: Hot & Snowy, Cold & Snowy, Hot & Freezing and Cold & Freezing (**Fig. 1D**). These conditions were related to the environmental fitting of growing degree days (GDD, p < 0.001, R2 = 0.783), freezing degree days (FDD, p < 0.001, R2 = 0.3348) and snow length (Snow, p = 0.099, R2 = 0.06) to the first and second NMDS axes. According to this, we established four plausible scenarios corresponding to the maximum and minimum values recorded during the 10 years of monitoring: hot and snowy (max GDD = 2795 ºC, min FDD = 0 ºC), hot and freezing (max GDD = 2795 ºC, max FDD = 247 ºC), cold and snowy (min GDD = 1150 ºC, min FDD = 0 ºC) and cold and freezing (min GDD = 1150 ºC, max FDD = 246 ºC). The occurrence models for these scenarios were computed for 16 species for which at least one of the bioclimatic indices had a significant effect size and the value of McFadden’s pseudo R2 was higher than 0.15. The predictions (**Table 3**) show that some species might survive only in the snowy scenarios (e.g., *Alchemilla catalaunica*) or in the freezing scenarios (e.g., *Galium pyrenaicum*). Interestingly some will likely go extinct in any scenario (e.g., *Festuca glacialis*) while other can potentially thrive in all scenarios (e.g., *Helianthemum canum*). When considering a 0 % chance of occurrence, 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**). However, if we consider a 0 - 5 % chance of occurrence, the four possible scenarios get more similar values of local extinctions (**Fig. 5B**).

**4. Discussion**

This study investigates microclimatic spatiotemporal patterns of alpine communities, thus covering key research questions for understanding climate change on alpine ecology (Körner & Hiltbrunner 2021). In agreement with the thermofilization observed in European mountains (Gottfried et al. 2012), we confirmed the expectation of a warming trend during the 10 years of climate monitoring in our study area in southern Europe. Despite this general trend, we also found that the intensity of warming and the temporal variation of microscale bioclimatic variables differed between topographically protected sites (snowbeds) and exposed ridges (fellfields), with the latest showing a more noticeable increase. Thus, our results suggest that thermofilization is differently associated with snow cover and microclimatic effects across topographical gradients. We also observed wide interannual variation suggesting that compensatory processes might take place in the region. The influence of FDD on microclimatic variation was orthogonal with GDD, further supporting the importance of both variables in driving temperature-related effects on alpine communities (Choler 2018). Accordingly, species composition in our area was first characterized by a heat-related gradient from warm to cold conditions, and a second gradient from snowy to freezing microsites. These results support that the main effect of thermofilization on local communities will depend on the specific responses of the constituent species to multiple microclimatic gradients driven by GDD, FDD and snow cover. Since the study area is occupied by relict alpine communities, accounting their resilience to climate change will depend on species-specific life-history traits and the spatial (Opedal et al. 2015) and temporal variation of the microclimatic conditions along local topographical variation that could potentially buffer those climatic variations.

We found that microclimatic variation in a one-year spatial survey was wider than the variation found during the 10 years of monitoring in the four temporal surveys specially for snowbed sites (Los Boches and Los Cazadores). This supports our hypothesis that microclimatic changes detected in the permanent plots during the monitoring project can be buffered by nearby microsites with different conditions. Nevertheless, the fellfield sites were subjected to periods of extreme cold that were not mirrored in the surrounding plots during the year of spatial monitoring. Since these sites are not protected by snow during most of winter, they are sensitive to unusual events of extreme low temperatures, which are more likely to occur within longer time periods (Walsh & Patterson 2022). The increase of 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 effect 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 long snow cover is consistent across years and seasons, thus suggesting that they may provide microrefugia for species with sensitivity to fellfield conditions represented by hot summers and freezing winters. The spatial distribution of these microrefugia is scattered along the study system, with contrasting climatic changes in distances within 50 meters. A key remaining question is whether future changes in the local climatic conditions will reach a tipping point by which the snowy side of the microclimate gradient will be lost, and the potential effect of these changes in the local communities. Such effect might be also influenced by local patterns in soil humidity which has been identified as one of the main drivers in diversity patterns (Moeslund et al. 2013, Mazalla et al. 2022) and in alpine systems, specific soil conditions develop a particular vegetation types (Körner 2021); however, the role of soil humidity in alpine systems needs to be furtherly explored and quantified. Another key question is identifying the critical life stage in alpine plant communities where microclimate conditions more restrictively drive community composition. To date only few studies have tackled this question testing effects of microclimate in adult plant survival, germination (Shimono & Kudo 2005), seedling survival (Rosbakh et al. 2022, Gya et al. 2023) or dispersal in time (Auffret et al. 2023) and space capacities.

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 considerable reduction in the cover of species associated with colder and snowy conditions, like *Armeria cantabrica, Salix breviserrata* and *Poa alpina* supporting the results found by Schöb et al. (2009) and Jiménez-Alfaro, Gavilán, et al. (2014). However, the winners were not especially represented by species associated with warmer conditions, although some of them are linked to relatively less snowy conditions, like *Helianthemum urrielense* and *Saxifraga conifera*. This barely confirms our hypothesis of warm-demanding species increasing abundance with a warming climate, rather suggesting that microclimatic conditions are more complex than thermofilization. The set of new species recorded in the resurvey are in most cases opportunists with preferences for fellfield rather than snowbed habitats, supporting the trend of increasing generalist species found by Steinbauer et al. (2018). The most dominant species recorded in the 78 plots are mostly positively linked to relatively warmer and freezing conditions (e.g., *Thymus praecox*, *Anthyllis vulneraria,* *Koeleria valesiana*) confirming the relative rarity of snowbed vegetation types reported by local vegetation maps (Jiménez-Alfaro & Bueno 2010). Nevertheless, most species are widely distributed in the study area and have no preference for specific microclimatic conditions suggesting high tolerance to environmental conditions suggesting wide niche. This may be explained by the local history of the study system, which has been subjected to continuous postglacial warming in a relatively reduced area (REF?). During the Holocene, extinctions of marginal populations and local adaptation of remaining species to local microclimatic variation may have resulted in a homogenization of local 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 already suggested by Braun-Blanquet (1932) as a fragmentary effect that has been also identified in mire communities from southern Europe (Jiménez-Alfaro et al. 2012).

We also found that 16 out of 86 species had significant responses to microclimatic conditions, indicating that only a small portion of the local species pool would noticeably respond to extreme climatic conditions. The predicted responses of these species to new scenarios suggest that most of them are adapted to cold and/or snowy conditions. Accordingly, a scenario of continuous hot freezing (not snowy) conditions will result in local extinctions of alpine species with a clear requirement for snowy microclimates (e.g., *Erigeron alpinus,* *Alchemila catalaunica*), but also lowland 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 like *Galium pyrenaicum*... Interestingly, two species (*Arabis alpina* and *Festuca glacialis*) show high probability of extinction in all scenarios, suggesting that even with the spatial buffering, current warming trend will result in the loss of local populations, even maybe already in extinction debt (Dullinger et al. 2012). In the stud, 69% of the species with significant responses to microclimate showed high extinction risks with either cold freezing or hot snowy microclimates. These species reflect individual preferences for intermediate conditions within the study system, which is likely related to the topographical variation in elevation and aspect. According to these responses, some species showed extinction risks in more than one scenario, generally reflecting their ecological preferences along one specific gradient. For example, *Alchemilla catalaunica* and *Erigeron alpinus* showed high extinction probability under freezing conditions irrespective of temperature, reflecting their major dependence on snow microhabitats.

**5. Conclusions**

This study demonstrates how microclimatic variation changes along temporal and spatial scales in alpine communities, supporting the general expectation of microclimatic buffer along topographic gradients. We found that thermal gradients in alpine landscapes are more complex than temporal changes in annual mean temperature, explaining the general disconnect between local scale and regional climatic models (Giorgi et al. 2009). The topographic buffer of microclimate is therefore dependent on the local abundance of different microhabitats and the expected trends of climate change at local scales. Our results on vegetation resurveys and species responses are congruent in highlighting an increment in species with tolerance of winter microclimatic freezing at the expense of species from snow protected microsites. The buffer effect of snowy microhabitat will therefore depend on the future trends of snow precipitation within and between years, determining the relative abundance of different microhabitat acting like microrefugia. The study system is dominated by species with wide ecological niches, likely because of long-term adaptations to climate fluctuations and long interglacial periods under dry and cold conditions. The species with narrower niches are mainly associated with cold and snowy conditions, indicating that microrefugia are mostly found on the most “alpine” conditions, i.e., those that were more frequent during glacial periods. It is thus expected that several years with a drastic reduction of snow cover may reach a tipping point beyond which the buffer effect of topography will not be effective. The reduction of snow-protected microsites eventually will result in the simplification of local gradients and the homogenization of local communities, increasing extinction risks of relict alpine species from snowy sites. The consecution of local extinctions and community homogenization will result in novel communities beyond the re-organization of local communities that likely occurred in response to natural climatic oscillations during postglacial periods. Further monitoring of snow patterns will be basic with the support of temporal series of satellite images at high spatial resolution (between 1 and 20 m), ideally linking that information with local species and microclimatic data and will be especially needed in mountains with a narrow alpine belt because they are more likely to local extinctions (Körner & Hiltbrunner 2021). Since mountain regions are subjected to different climatic conditions across gradients of humidity and seasonality (Testolin et al. 2020), the direction of these changes, and the species susceptible of local extinctions, may also differ across regions. This makes necessary to implement complementary monitoring systems based on population genetic diversity or demographic trends, to assess contemporary changes on relict alpine communities.

# 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 record of the repository is deposited in Zenodo.

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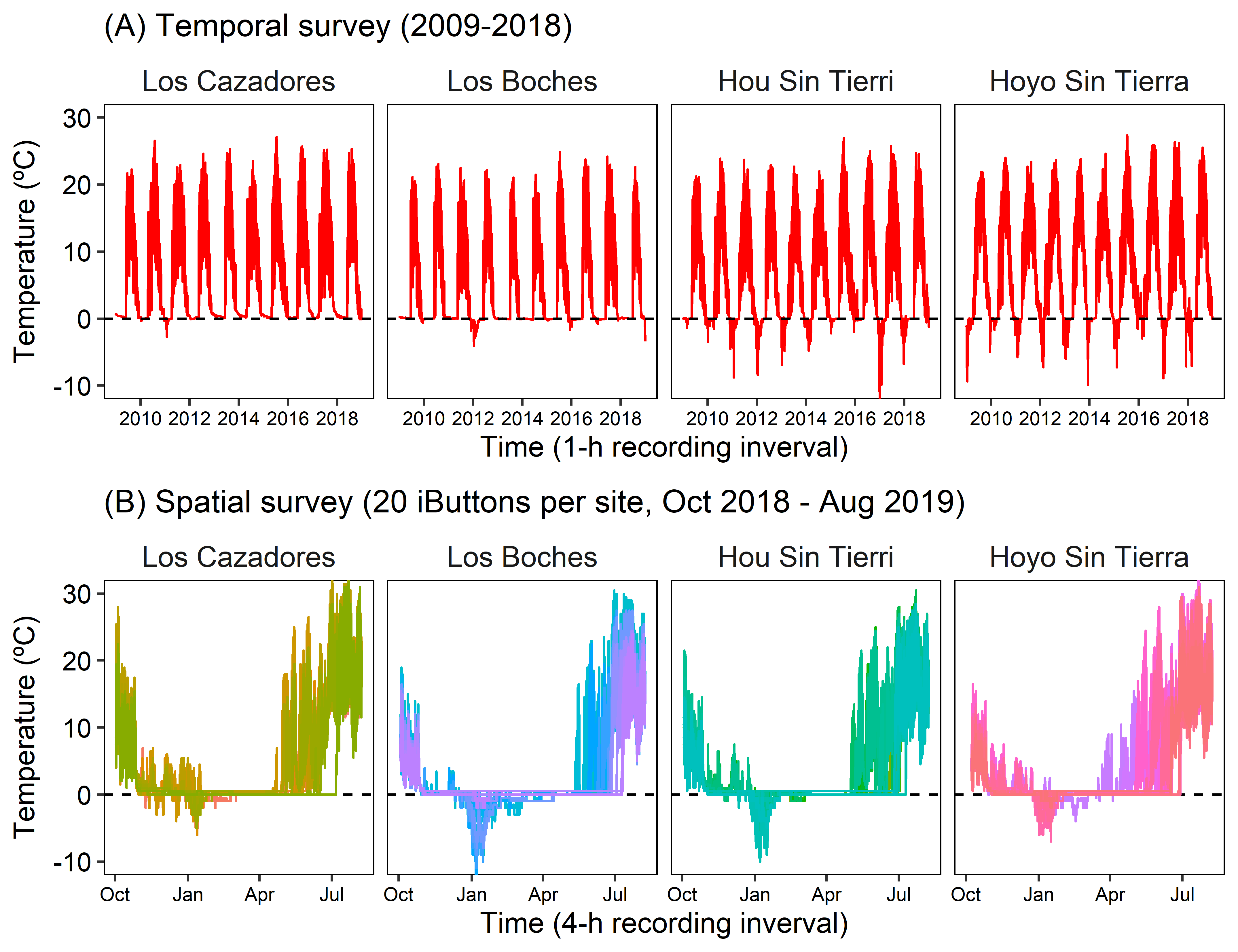
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**Figure 1.** Study system. (A) Situation of the study area (purple star) in Western Europe. (B) Four study sites (purple circles) placed in a North-South gradient in the central massif of Picos de Europa National Park. Site names are Los Cazadores (1); Ḥou Sin Tierri (2); Los Boches (3); Hoyo Sin Tierra (4). (C) Sampling design in one of the sites, showing the central plot (purple square) for the temporal survey and the additional plots (yellow squares) for the spatial survey. (D) Non-Metric Dimensional Scaling (NMDS) of the variation in species composition for 78 1 m2 plots sampled in the spatial survey, points represent the 20 plots of each site (sites scores) and species abbreviated names are situated in the graph according to species scores. See species abbreviations in **Supplementary Table S4**.

**Interfaz de usuario gráfica

Descripción generada automáticamente**

**Figure 2.** Soil temperature logs. (A) Soil temperatures at -5 cm, recorded every hour in the central temporal survey plots of the 4 sites for the period 1 Jan 2009 – 31 Dec 2018. (B) Soil temperatures at -5 cm, recorded every 4 hours in the 20 spatial survey plots (each color being a plot) of the 4 sites for the period 1 Oct 2018 to 31 Aug 2019.



**Figure 3.** (A) Temporal trends in soil temperature. Shaded red lines indicate the trend component in the soil temperature time series for the period 1 Jan 2009 – 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 temporal survey (4 sites x 10 year in blue) and the spatial survey (4 sites x 20 plots in red) of alpine soils in the Picos de Europa National Park (Spain).

Gráfico

Descripción generada automáticamente con confianza media

**Figure 4.** Winners and losers in the temporal survey of vegetation. Each bar shows the percentage change of species frequency in 10 x 10 cm cells across 2 plots x 4 study sites, between the initial sampling of 2009 and the resurvey of 2019. The numbers next to the species indicate the number of 10 x 10 cm cells in which each species was present in 2009.

**Gráfico

Descripción generada automáticamente con confianza media**

**Figure 5.** Number of species extinctions per microclimatic scenario. 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. Species extinctions were estimated as the probability of occurrence (A) equal to zero and (B) < 5 % according to the predictions of GLMs fitted with the GDD and FDD values recorded in the spatial survey (see **Table 3**).

Gráfico, Gráfico de barras

Descripción generada automáticamente

**Table 1.** Bioclimatic description of the study sites. Soil temperatures at -5 cm, recorded every hour in the central temporal survey plots of 4 alpine sites of Picos de Europa National Park, Spain mean values for the period 1 Jan 2009 – 31 Dec 2018. This table includes all records of the temporal survey, not only the records homogenized for comparison with the spatial survey (see methods).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | 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.** Mean values and standard error for all bioclimatic indices calculated from spatial and temporal surveys across our four sites. Differences tested with one sided paired t-test.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Bioclimatic index | Spatial mean ± SE | Temporal mean ± SE | T | Df | p-value |
| Bio1 | 2.38 ± 0.537 | 1.95 ±0.26 | 1.13 | 3 | 0.1702 |
| Bio2 | 3.16 ± 0.139 | 1.22 ± 0.26 | 12.70 | 3 | < 0.005 |
| Bio7 | 8.99 ± 2.07 | 7.95 ± 1.99 | 0.765 | 3 | 0.2499 |
| Snow | 202 ± 22.4 | 88.2 ± 7.76 | 13 | 3 | < 0.005 |
| GDD | 752 ± 104 | 647 ± 110 | 1.01 | 3 | 0.1934 |
| FDD | 121 ± 62 | 134 ± 86.4 | -0.29 | 3 | 0.6047 |

**Table 2.** Occurrence models for 16 species in four microclimatic scenarios 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. Species extinctions were estimated as the probability of occurrence in two different thresholds: equal to 0 or < 5 according to the predictions of GLMs fitted with the GDD and FDD values recorded in the spatial survey. Columns 'Cold & Freezing' to 'Hot & Snowy' show the probability of occurrence of each species in each scenario.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 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 |

**Supplementary material**

**Fig. S1.** Annual values of GDD, FDD and snow cover calculated from the temporal data soil climatic data across all 4 study sites.

**Gráfico, Histograma

Descripción generada automáticamente**

**Fig. S2.** Principal Component Analysis of the variation in soil bioclimatic indices. Data includes the temporal survey (triangles, 4 sites x 10 years) and the spatial survey (squares, 4 sites x 20 plots) of alpine soils in the Picos de Europa National Park (Spain). Bioclimatic variables include the annual mean temperature (bio1), the diurnal thermal range (bio2), the annual thermal range (bio7), the length of snow cover (Snow), the growing degree days (GDD) and the freezing degree days (FDD).

Mapa

Descripción generada automáticamente

Table S3. Bioclimatic indices correlation with Principal Component Analysis axis

|  |  |  |
| --- | --- | --- |
| Bioclimatic indices | Axis 1 | Axis 2 |
| Mean anual temperatura (bio1, ºC) | 0.7830687 | 0.5959156 |
| Diurnal thermal range (bio2, ºC) | 0.8349018 | -0.0926131 |
| Annual termal range (bio7, ºC) | 0.6808243 | -0.4809319 |
| Annual snow cover (days) | -0.530218 | 0.3384176 |
| Annual freezing degree days (FDD, ºC) | 0.4075113 | -0.6954813 |
| Annual growing degree days (GDD, ºC) | 0.832887 | 0.481412 |

Table S4. Species registered during spatial survey, their corresponding abbreviations and scores used in NMDS (**Fig 1D**).

|  |  |  |  |
| --- | --- | --- | --- |
| Species | Abbreviation | NMDS 1 | NMDS 2 |
| *Agrostis schleicheri* | Agrsch | -0.22626249 | -0.32865479 |
| *Alchemilla catalaunica* | Alccat | -0.24786943 | 0.44510949 |
| *Androsace villosa* | Andvil | -0.56092072 | -0.13187965 |
| *Anemone pavoniana* | Anepav | -0.30701826 | -0.00645525 |
| *Anthyllis vulneraria* | Antvul | 0.09275869 | -0.19304245 |
| *Arabis alpina* | Araalp | 0.24387917 | 0.3089445 |
| *Arenaria erinacea* | Areeri | -0.40324069 | -0.37136211 |
| *Arenaria grandiflora* | Aregra | 0.57040639 | 0.03229533 |
| *Arenaria moehringioides* | Aremoe | 0.37818069 | -0.18958146 |
| *Arenaria purpurascens* | Arepur | -0.29890923 | -0.05363037 |
| *Armeria cantabrica* | Armcan | 0.55688866 | 0.12081685 |
| *Botrychium lunaria* | Botlun | 0.23467495 | 0.33913668 |
| *Carduus carlinoides* | Carcar | 0.66358154 | -0.17465052 |
| *Carex ornithopoda* | Carorn | 0.37664498 | 0.13271975 |
| *Carex pulicaris* | Carpul | 0.58957326 | 0.25104494 |
| *Carex sempervirens* | Carsem | -0.38531771 | 0.22600719 |
| *Cystopteris fragilis* | Cysfra | -0.14760722 | -0.35747592 |
| *Dethawia splendens subsp. cantabrica* | Detspl | -0.40297643 | 0.07236984 |
| *Draba dedeana* | Draded | -0.43467822 | 0.49376216 |
| *Erigeron alpinus* | Erialp | 0.10832918 | 0.22171564 |
| *Eryngium bourgatii* | Erybou | -0.18389075 | 0.21969489 |
| *Euphorbia pyrenaica* | Euppyr | -0.41246197 | -0.09036552 |
| *Euphrasia salisburgensis* | Eupsal | -0.22463362 | -0.34160941 |
| *Festuca glacialis* | Fesgla | 0.70335011 | 0.10426121 |
| *Festuca gr. rubra* | Fesrub | -0.07073091 | 0.39051504 |
| *Festuca hystrix* | Feshys | -0.39802784 | -0.24144864 |
| *Festuca picoeuropeana* | Fespic | -0.24077199 | -0.37138493 |
| *Galium pumilum* | Galpum | 0.05775293 | 0.62816766 |
| *Galium pyrenaicum* | Galpyr | 0.07784597 | -0.62731841 |
| *Genista legionensis* | Genleg | -0.59950319 | -0.08017966 |
| *Gentiana nivalis* | Genniv | 0.14433934 | 0.08736727 |
| *Gentiana verna* | Genver | -0.37209895 | 0.08123781 |
| *Gentianella campestris* | Gencam | -0.29402477 | 0.03083168 |
| *Gnaphalium hoppeanum* | Gnahop | 0.36306039 | 0.37459588 |
| *Gypsophila repens* | Gyprep | -0.41713995 | -0.18485794 |
| *Helianthemum apenninum subsp. cantabricum* | Helcan | -0.24673604 | 0.53550255 |
| *Helianthemum apenninum subsp. urrielense* | Helurr | 0.245896 | 0.20158793 |
| *Helianthemum canum* | Helcan | -0.36110367 | -0.14829857 |
| *Helictotrichon sedenense* | Helsed | 0.11271417 | -0.36558285 |
| *Herniaria glabra* | Hergla | 0.24357241 | 0.27885013 |
| *Hippocrepis comosa* | Hipcom | -0.28729515 | 0.32971575 |
| *Hornungia alpina* | Horalp | -0.13351775 | 0.47141159 |
| *Iberis carnosa* | Ibecar | 0.46144181 | -0.36236435 |
| *Jacobaea boissieri* | Jacboi | -0.1924265 | -0.73282049 |
| *Jasione cavanillesii* | Jascav | 0.57937134 | -0.1176246 |
| *Jurinea humilis* | Jurhum | -0.49422318 | 0.11829457 |
| *Kobresia myosuroides* | Kobmyo | -0.44449408 | -0.33052187 |
| *Koeleria vallesiana* | Koeval | -0.17264968 | 0.28080103 |
| *Linaria alpina* | Linalp | 0.37222351 | 0.12164061 |
| *Lotus corniculatus* | Lotcor | -0.25730487 | 0.270113 |
| *Luzula pediformis* | Luzped | 0.06005125 | 0.54201188 |
| *Minuartia verna* | Minver | -0.14282894 | -0.18459774 |
| *Oxytropis neglecta* | Oxyneg | -0.21519678 | -0.09516628 |
| *Paronychia kapela subsp. serpyllifolia* | Parkap | -0.36367437 | 0.03166732 |
| *Pedicularis pyrenaica* | Pedpyr | -0.46045857 | -0.0387913 |
| *Phyteuma orbiculare* | Phyorb | -0.53012903 | 0.19782045 |
| *Pilosella officinarum* | Piloff | -0.33275803 | 0.05725185 |
| *Plantago alpina* | Plaalp | -0.07503951 | 0.30626518 |
| *Poa alpina* | Poaalp | 0.17499679 | 0.52416381 |
| *Potentilla crantzii* | Potcra | -0.24968586 | 0.28787799 |
| *Ranunculus carinthiacus* | Rancar | 0.08426838 | 0.40420889 |
| *Ranunculus parnassiifolius subsp. favargeri* | Ranpar | 0.25504086 | -0.48631208 |
| *Salix breviserrata* | Salbre | 0.2215869 | -0.67289038 |
| *Saxifraga conifera* | Saxcon | -0.06149894 | 0.23007927 |
| *Saxifraga oppositifolia* | Saxopp | 0.26347407 | -0.75611155 |
| *Saxifraga paniculata* | Saxpan | 0.17472814 | 0.20689849 |
| *Scilla verna* | Sciver | -0.31485349 | 0.24837992 |
| *Sedum album* | Sedalb | -0.01947289 | 0.36454999 |
| *Sedum atratum* | Sedatr | 0.3383434 | -0.09301587 |
| *Sempervivum vicentei* | Semvic | -0.32351823 | 0.15798158 |
| *Silene acaulis* | Silaca | 0.54757546 | -0.05851618 |
| *Silene ciliata* | Silcil | 0.3222897 | 0.1622936 |
| *Teucrium pyrenaicum* | Teupyr | -0.65936597 | -0.12521348 |
| *Thesium pyrenaicum* | Thepyr | -0.62590247 | 0.03910524 |
| *Thymus praecox subsp. ligusticus* | Thypra | 0.01181457 | 0.11542884 |
| *Veronica nummularia* | Vernum | 0.50973766 | -0.24495923 |
| *Viola rupestris* | Viorup | -0.2901378 | 0.21205072 |