Alpine Botany
https://doi.org/10.1007/s00035-022-00283-0

ORIGINAL ARTICLE

Mesoscale refugia for European alpine grasslands based on climatic envelopes

George P. Malanson[1] · Riccardo Testolin[2,3,4] · Elizabeth R. Pansing[1] · Borja Jiménez-Alfaro[5]

Received: 16 November 2021 / Accepted: 1 May 2022

Abstract
Refugia will be important to the response of alpine vegetation to climate change. Potential refugia exist at multiple scales, including a range-wide mesoscale. The climates of alpine grasslands of 23 mountain ranges of southern and central Europe were evaluated to assess whether each range would support potential refugia in projected future climates. The mean temperature the warmest month and quarter with the precipitation of the warmest quarter, derived from gridded global climate data at ~ 1 km resolution, were examined range-wide and for areas identified as alpine grassland to identify limits within each range. The overlap of current grassland climate and future range-wide climates, the latter calculated using regional projections from three global models with three socioeconomic driving scenarios, were assessed as potential refugia. Among the nine projections, three had none of the current grassland climates in any of the 23 ranges by 2100, while two retained more than 20% in more than half of the ranges. Most of the potential mesoscale refugia were in the Alps. Micro-refugia and warmer and drier fundamental climatic niches for alpine grassland species could mitigate these bleak results, but otherwise they are extremely threatened.

Keywords Climatic niche · Climate envelope · Grasslands · Micro-refugia · Refugia · Scale

Introduction

Climate change is expected to alter plant community structure and diversity because of their species climatic niches, spatial isolation, and limited potential for dispersal (e.g., Alatalo et al. 2020; Sklenar et al. 2021). These changes are ongoing across Europe (e.g., Steinbauer et al. 2020). Engler et al. (2011) projected alpine species losses of > 50%, with notable variation among mountain ranges, and Rubel et al. (2017), using projected Köppen-Geiger climate zones, reported elimination of alpine vegetation and most montane coniferous forest as a worst-case scenario for 2100. Barredo et al. (2020) found potential losses of alpine habitat in European mountains ranging from 44% to nearly 100% with 1.5–3 °C warming scenarios in regional climate simulations. A potential for mitigation of the worst effects of ongoing warming exists in climatic refugia (e.g., Graae et al. 2018). We assess whether alpine grasslands in southern and central Europe (SACEU) have range-wide climatic limits and if future climates might exceed them.

Refugia are central to understanding the response of alpine vegetation to climate change. Refugia are locations, currently occupied or not, where species can exist during periods when the climate differs from that at present (e.g., Holderegger and Thiel-Egenter 2009; Ashcroft 2010; Keppel et al. 2012). Thus, for alpine vegetation, refugia at the Last Glacial Maximum (LGM) may have been more extensive than present ranges (e.g., Testolin et al. 2021), while projections for the future are that alpine vegetation area will be reduced (e.g., Gentili et al. 2015).

✉ George P. Malanson
george-malanson@uiowa.edu

1 Department of Geographical and Sustainability Sciences, University of Iowa, Iowa City, IA 52242, USA

2 BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, Via Irnerio 42, 40126 Bologna, Italy

3 Department of Biological, Geological and Environmental Sciences, Centro Interuniversitario per la Biodiversità Vegetale Big Data-Plant Data, Alma Mater Studiorum University of Bologna, Via Irnerio 42, 40126 Bologna, Italy

4 LifeWatch, Lecce, Italy

5 Research Unit of Biodiversity (CSIC/UO/PA), University of Oviedo, 33600 Mieres, Spain

Refugia are multiscale, occurring at macro-, meso-, and micro- (or crypto-) scales, but alpine habitats manifest as distinct zones on this gradient because of their spatial separation (e.g., among vs. within mountain ranges). Macroscale alpine refugia would be on different, currently unoccupied mountain ranges, and alpine vegetation, which generally has limited dispersal capacities (Morgan and Venn 2017), would face the problem of whether dispersal distances are sufficient to match climate velocities. Thus, we do not address macroscale refugia here. Mesoscale alpine refugia are constrained to exist within a macroclimate such that major topographic differences within a mountain range can create meso-climates beyond the current climatic envelope of a given vegetation (or the niche dimensions of a species). The most likely future mesoscale refugia for alpine vegetation would exist at higher elevations—if other factors such as soil are suitable. Current mesoscale patterns of alpine vegetation also include slope aspect and exposure (Winkler et al. 2016; Liberati et al. 2019). Micro-refugia, on the other hand, could persist within meso-climates where topography can buffer some climate change (Dobrowski 2011; Mosblech et al. 2011; Patsiou et al. 2014; Niskanen et al. 2017; Graae et al. 2018; Körner and Hiltbrunner 2021). For example, geomorphic features can create temperature inversions (Lundquist et al. 2007; Patsiou et al., 2017) and heterogeneity in temperature even within a single slope (Scherrer and Körner 2011; Garcia et al. 2020), and the now-cooler sites could be micro-refugia for species now in warmer ones. New glacial forelands could also provide micro-refugia (Gentili et al. 2015). However, potential micro-refugia may not function as such if the mesoscale climate changes sufficiently, and because these are micro, they are unlikely to sustain all current plant species over a longer term.

We examine the bioclimates and the potential for mesoscale refugia for alpine grasslands in SACEU. We focused on alpine grasslands because they are the most extensive vegetation occurring above climatic treeline (Testolin et al. 2020). Our purposes are, first, to determine whether the alpine grasslands of 23 mountain range in SACEU have climatic limits at a range-wide extent that parallel the findings of Bürli et al. (2021) for European summit vegetation (a growing-season soil temperature of 4.9 °C or a growing-season length of 85 days marked the upper elevation), and second, to determine whether these alpine grasslands would have potential mesoscale climatic refugia within the same range in a warmer and drier future, given that isolation from past refugia has affected patterns of diversity (Jiménez-Alfaro et al. 2021). We assess the vulnerability of alpine grasslands to climate change using the observed climatic envelope (analogous to the realized climatic niche of a species) for each mountain range with projections of three climate models for three socioeconomic scenarios. It has long been known that observations of the realized niche may be inadequate for understanding responses to climate change (e.g., Malanson et al. 1992), and as part of our first objective we assess this issue. We ask:

- Are high- or low-temperature boundaries, parallel to those reported by Bürli et al. (2021), evident for lower resolution climatic data at a greater extent, and if so, does it change with precipitation?
- Do alpine grasslands have mesoscale (within the same range) climatic refugia in a warmer and drier future, and how limited are they?

Methods

Study regions and data

We investigated patterns in the 23 mountain ranges in southern and central Europe studied by Jiménez-Alfaro et al. (2021) (Fig. 1) with detailed explanation in their first appendix (https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fgeb.13274&file=geb13274-sup-0001-AppendixS1.pdf). After delineating the treeline for each range based on local records, they identified alpine grasslands by excluding tree-covered, wetland, rocky substrate, and successional vegetation using the normalized difference vegetation index (NDVI) derived from Landsat data as explained in Testolin et al. (2020; see http://www.ecography.org/sites/ecography.org/files/appendix/ecog-05012.pdf).

For current climates, we extracted 19 bioclimatic variables from CHELSA V2.1, 1979–2017 (Karger et al. 2017, 2021; 1979–2013; see https://chelsa-climate.org/wp-admin/download-page/CHELSA_tech_specification.pdf) for the 30-arcsecond cells (c. 1 × 1 km) of the entire 23 ranges (72,328 cells) and the alpine grassland cells (49,085 cells) (Fig. 1). CHELSA data are an accurate interpolation of climate variables, with correspondence to independent station data having $R^2 > 0.90$ for temperature (Morales-Barbero and Vega-Álvarez 2019). Temperature variables are for 2 m above the surface.

For future climates, we used CHELSA's compilation of CMIP6 ISIMIP3 model projections. We selected three models, as prioritized by the ISIMIP3 protocol, and the three scenarios for future climate forcing:

Models:
M1: GFDL-ESM4
M2: UKESM1-0-LL
M3: MPI-ESM1-2-HR
Scenarios:
S1: SSP1-RCP2.6
S2: SSP3-RCP7.0
S3: SSP5-RCP8.5

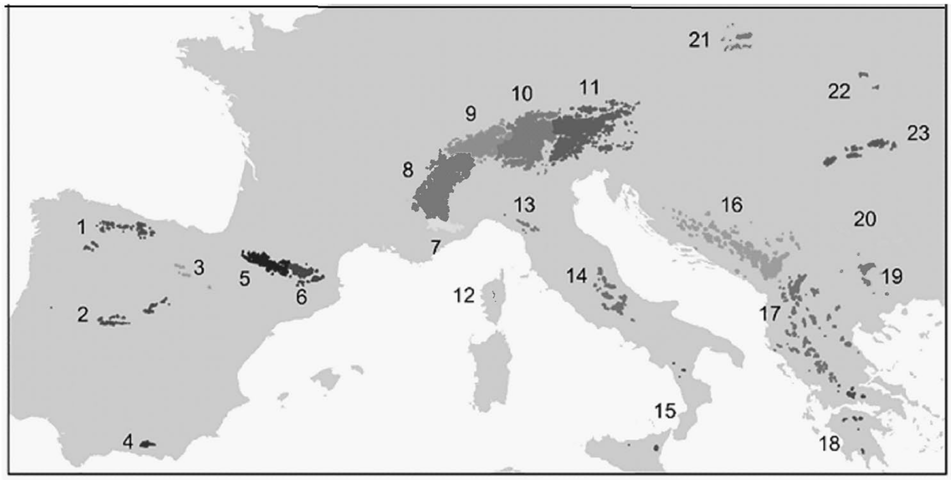

Fig. 1 The location, areas, grassland areas, and their proportion of the alpine habitats in the 23 ranges of southern and central Europe. The delineation of these regions was described in detail by Jiménez-Alfaro et al. (2021) (https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fgeb.13274&file=geb13274-sup-0001-AppendixS1.pdf). The regions were based on identification of local treeline and the treeline elevation, and the relevant sources were provided in that document

Legend	Region	Area	Grassland	Proportion
1	Cantabrian	423	317	0.749
2	Central System	522	486	0.931
3	N Iberian	50	49	0.980
4	Baetic System	324	114	0.352
5	W Pyrenees	2255	1671	0.741
6	E Pyrenees	1387	1334	0.962
7	Maritime Alps	1638	1361	0.831
8	W Alps	16156	9670	0.599
9	WC Alps	7998	4559	0.570
10	EC Alps	16566	11218	0.677
11	E Alps	11236	8090	0.720
12	Corsica	58	18	0.310
13	N Apennines	64	9	0.141
14	C Apennines	928	815	0.878
15	S Apennines	128	32	0.250
16	Dinarides	6397	4357	0.681
17	Scardo-Pindic	2524	2077	0.823
18	S Hellenides	206	196	0.951
19	Rhodope-Rila	1173	1121	0.956
20	Balkan range	256	154	0.602
21	W Carpathians	911	485	0.532
22	E Carpathians	41	36	0.878
23	S Carpathians	1017	927	0.912

Of the socioeconomic scenarios, S1 is optimistic in terms of reduction in CO_2 emissions while S3 assumes increases in both populations and the use of coal. The bioclimatic variables for the nine combinations of models and scenarios were extracted for all cells and the grassland cells in the 23 regions.

Temperature boundaries

We examined the mean temperatures of the warmest month and warmest quarter with the mean precipitation of the warmest quarter (CHELSA does not include the precipitation of the warmest month, and because of soil water storage, the quarterly data are more relevant; the precipitation of the wettest month can be in different seasons and so would not have the same biological meaning). These three variables should be relevant to physiological processes during the growing season, as mean temperature of the warmest month can better represent the effects of extremes while mean temperature of the warmest quarter represents the growing season. Also, these two temperature variables are well-correlated with their mean annual and cold season counterparts. Summer temperatures and precipitation have been shown to influence alpine grasslands (Wang et al. 2013; Marchin et al. 2018,), and they are expected to change with global warming (Coppola et al. 2021; Pichelli et al. 2021). Mean temperatures of the warmest month and warmest quarter should be correlated with the soil temperatures reported by Bürli et al. (2021), given that the temperatures reported by Scherrer and Korner (2011) for soil surfaces and at 3 cm depth bracketed 2 m air temperatures and tracked the daily change in radiation (differences in soil and air temperatures vary seasonally and geographically, but patterns are consistent within biomes; Lembrechts et al. 2022).

We plotted mean precipitation of the warmest quarter vs the mean temperatures of the warmest month and warmest quarter for the grassland cells over the range-wide cells to determine whether any upper or lower boundaries were evident for any variable, i.e., if the climate range of the grassland cells was exceeded by non-grasslands in the same mountain range. Visual inspection of the plots revealed that the patterns for those with the mean temperatures of the warmest month and warmest quarter were virtually identical (Online Resources 1 and 2), and we further examined the latter. For temperature, we defined a lower boundary for mean temperature of the warmest quarter if the 5th percentile of the temperature distribution of the grassland points was > 0.25 °C higher than the same percentile for all points in the range. We similarly looked for an upper limit (95th percentile), which would inform thinking on the realized envelope for these alpine grasslands, and we visually examined the plots for any evidence of interaction between temperature limit and precipitation (no boundaries were evident for precipitation alone).

Mesoscale refugia

For our second question, we constructed climatic envelopes for each of the 23 ranges using principal components analysis (PCA) using PC-ORD v.7 (McCune and Mefford 2016) with a correlation-based cross-products matrix. We used this diverse climate envelope for this question because climate change may be more complex than would be represented by WMT or WQT and WQP alone as seen in preliminary analyses. Of the 19 CHELSA bioclimatic variables, we excluded eleven:

- Wet and dry season temperature and precipitation (4) because they can use different seasons for different locations;
- The monthly variables (4), which are highly correlated with the corresponding quarterly variables; and
- Daily and annual ranges and isothermality (3), which are correlated with temperature seasonality but do not have a corresponding precipitation variable.

We retained mean annual temperature and precipitation, mean temperature and precipitation of the warmest and coldest quarters, and temperature and precipitation seasonality (MAT, MAP, WQT, WQP, CQT, CQP, TSY, PSY). Mean annual temperature and precipitation capture broad differences; mean temperature and precipitation of the warmest quarter emphasize the growing season; mean temperature and precipitation of the coldest quarter include the effects of snow; and seasonality of temperature and precipitation reflect continentality and the mid-latitude vs. Mediterranean climates.

For each of the 23 ranges, present + future climate envelopes were created using the current data with each of the nine future climate model scenarios in 207 separate PCAs (PC-ORD v.7). Thus, each future envelope is independent of the other modeled futures for the calculation of present and future overlap. The significance of the eigenvectors was assessed by comparison of the variance captured relative to 1000 randomizations of the same climatic data. The climatic variables most represented by the eigenvectors were identified by examining the correlation coefficient between scores for rows in the main matrix and the climate variables (computationally equivalent to the eigenvector scaled to its standard deviation).

To assess the likelihood of future mesoscale refugia, we visually examined and counted the incidence of cells falling within future grassland climates. For each mountain range, we plotted the scores of the first two eigenvectors for the future range-wide PCAs with those of the current grassland

PCAs. We counted the visual incidence of the future range-wide cells falling within the envelopes of the current grassland cells and calculated the proportion of the total range. For ranges with many overlapping points, we divided areas of overlap of the two PCA dimensions in a spreadsheet and counted the points in the subsections.

For the set of simulations for each range, we noted the highest proportion, the mean proportion (although the distribution is not normal the mean can be used for simple comparisons), and the number of zeroes (i.e., cases where no area was within the envelope in future). We examined these three indicators in relation to the location of the ranges, their areas, elevation range from treeline to the highest peak, and selected climatic variables {mean, maximum, minimum, and range of mean temperature of the warmest month and quarter and precipitation of the warmest quarter) including a climatic envelope size based on the distribution of the points for the two dimensions of a PCA for all 72,328 points together, to which we applied the shoelace algorithm using 5–15 points to define a bounding polygon. We calculated a General Linear Model for each with a stepwise procedure using a threshold alpha of 0.01 to enter.

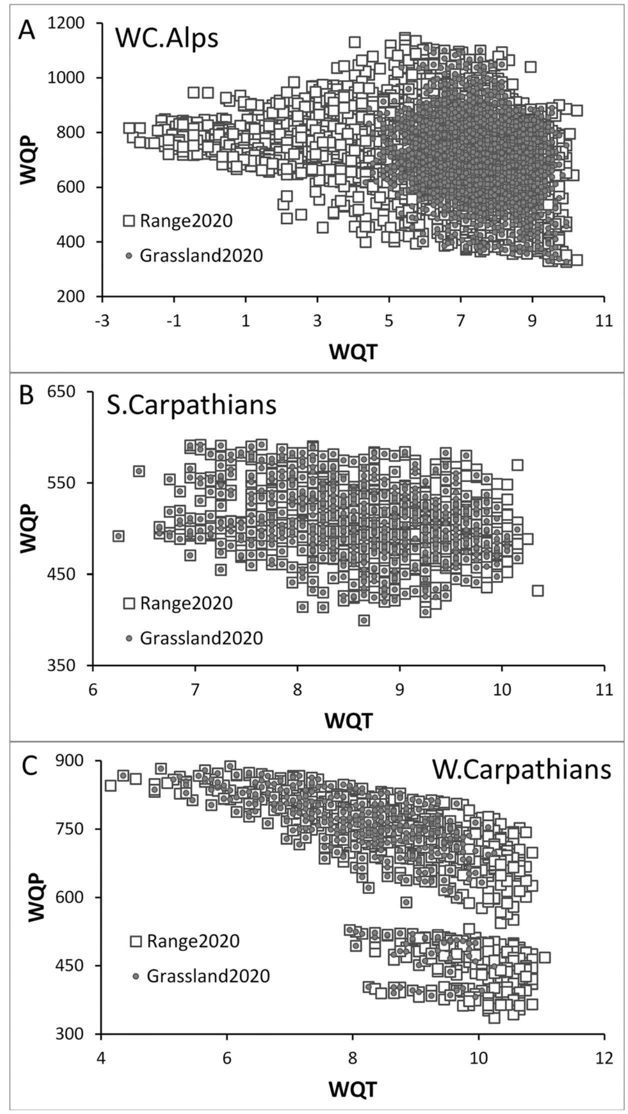

Fig. 2 Examples of the patterns of precipitation and temperature variables warm quarter precipitation, WQP) and warm quarter temperature, WQT) illustrate cold-, neither, and warm limits of the alpine grasslands. Similar figures for plots of WQP and WQT and WQP and warmest month temperature (WMT) for all mountain ranges are in Online Resources 1 and 2

Results

Description

The 23 ranges exhibit a substantial breadth of the three growing-season variables examined (Online Resource 3, Table SI1). Values of mean temperature of the warmest month and quarter and precipitation of the warmest quarter of individual geographic cells that comprise each range (the 30-arcseconds or c. 1 × 1 km cells of CHELSA) ranged 0.75–22.15 °C, − 5.85–17.55 °C and 37.50–1199.9 mm, respectively. The Alps, with a greater span of elevation, have the greatest breadth in temperatures. The drier ranges have a narrow span of precipitation of the warmest quarter. Furthermore, many ranges have fewer cells (i.e., less area due to pyramidal topography) at lower temperatures and a resulting triangular distribution (e.g., Fig. 2A, C).

Temperature boundaries

A lower-temperature boundary is evident—counting a difference > 0.25 °C—in tens of the ranges, or 50% after excluding three ranges with few records (Table 1, Fig. 2, and Online Resource 1). The average low limit of WQT is 5.99 °C. In 11 ranges with sufficient area, alpine grasslands occur within pixels that reach the coldest summer temperatures, which average 9.2 °C WQT, with a minimum of 5.99 °C (W. Carpathians; absolute lowest 4.15 °C). At the highest levels of summer precipitation, e.g., ≥ 1000 mm in the E. Alps, the cold limit is 1–2 °C higher than the limit for most grassland cells; Online Resource 1). A high-temperature boundary is seen only in the W. Carpathians at 9.75 °C. However, there are several ranges where grasslands persist at the highest observed temperatures, e.g., at > 14 °C in the geographically distant Central System and Dinarides.

Table 1 Potential summer low and high temperature limit (°C) for alpine grasslands observed in relation to the range-wide temperatures of the 23 ranges based on the 5th and 95th percentiles, respectively, of the distributions (e.g., Fig. 2 and Online Resource 1)

	Low WQT limit (5th quantile)	High WQT limit (95th quantile)	
	Grassland/range	Grassland/range	Comment
Baetic	12.56/10.46	14.40/14.35	Cold limit, but high
Balkans	9.27/8.92	11.45/11.85	Cold limit
C. Apennines	8.72/8.75	12.95/13.05	
Cantabrians	9.23/8.46	11.57/11.55	Cold limit
Central	12.55/12.35	14.95/14.95	
Corsica*	9.12/9.04	10.88/11.27	
Dinarides	10.65/10.45	13.95/14.05	
E. Alps	5.5/4.15	9.45/9.65	Cold limit, 6° where wetter
E. Carpathians*	7.55/7.53	8.98/8.95	
E. Pyrenees	7.45/7.28	10.25/10.25	
EC. Alps	5.45/3.55	9.45/9.45	Cold limit, 5.7° where wetter
Mar.Alps	7.75/7.25	10.45/10.45	Cold limit
N. Apennines*	10.95/10.95	12.21/12.54	
N. Iberian*	11.33/11.34	12.71/12.71	
Rhodope-Rila	8.05/8.05	11.15/11.25	
S. Apennines	11.66/7.42	14.10/14.10	Cold limit, but high
S. Carpathians	7.25/7.25	9.75/9.87	
S. Hellenides	10.45/10.45	13.55/13.65	
Scardo-Pindhic	9.45/9.45	13.55/13.55	
W. Alps	6.15/2.65	10.05/10.05	Cold limit, 6.3° where wetter
W. Carpathians	5.95/6.30	9.75/10.65	Warm limit
W. Pyrenees	7.55/6.75	10.25/10.25	Cold limit
WC. Alps	5.65/2.65	9.15/9.05	Cold limit, 6.3° where wetter

No limit is evident where the values are within 0.5°. Unusual cold limits or those with possible interactions with precipitation are mentioned in comments

*Ranges with < 50 grassland observations

Mesoscale refugia

PCAs

Two eigenvectors were significant in 70% of the 207 PCAs, and three were in the other 30%. The significant eigenvectors extracted an average of 90% of the variance in the climate data (Online Resource 3, Table SI2). The first eigenvector was most highly correlated with both temperature and precipitation variables but in opposite directions, which indicated a gradient from warm, dry to cold, wet conditions (Online Resource 3, Table SI3). In those cases, the second eigenvector was usually most correlated with precipitation seasonality. In some cases, with three significant eigenvectors, the order of correlations was temperature, precipitation, precipitation seasonality.

Climatic envelopes

Among the 207 regions × model × scenario cases, 44 were instances where the proportion of the range that sustained grassland habitat in future was > 20% (Table 2, Figs. 3, 4 and Online Resources 4 and 5); 21 of these were in the four regions of the high Alps. Of these, nearly the entire current grassland climate envelope was still within the future climate envelope of the range in eight instances: the GFDL and MPI models with the SSP1 (most optimistic) scenario. Of the 163 cases with < 20% potential mesoscale refugia, 102 had no remaining grassland climate. Fifty of these were with the SSP5 scenario of most extreme change. The change in the climatic envelopes was primarily toward warmer, drier conditions as indicated by a shift of points to the right in most graphs (the direction of the gradient can be reversed and the figures in Online Resource 4 can be linked to Online Resource 3 Table SI3). By region, the Alps consistently harbored the most potential refugia, while Corsica and the East Carpathians, the smallest ranges, harbored none. Preliminary analyses of climatic envelopes defined by temperature and precipitation of the warmest quarter had generally similar results with temperature being the important driver of the difference in extant alpine grassland climates (Online Resources 1 and 2).

Table 2 The proportions of the future ranges that lie within the current climatic envelopes of the alpine grasslands on each of the 23 mountain ranges

Range	M1S1	M1S2	M1S3	M2S1	M2S2	M2S3	M3S1	M3S2	M3S3
Baetic	0.40	0.00	0.01	0.07	0.00	0.00	0.08	0.07	0.00
Balkan	0.05	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00
C. Apennines	0.29	0.09	0.02	0.02	0.00	0.00	0.23	0.08	0.06
Cantabrian	0.30	0.03	0.01	0.07	0.00	0.00	0.90	0.15	0.11
Central	0.18	0.00	0.00	0.02	0.00	0.00	0.36	0.00	0.00
Corsica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dinarides	0.58	0.06	0.01	0.07	0.00	0.00	0.38	0.04	0.01
E. Alps	0.77	0.25	0.09	0.27	0.00	0.00	0.70	0.30	0.09
E. Carpathian	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E. Pyrenees	0.32	0.00	0.00	0.01	0.00	0.00	0.66	0.00	0.00
EC. Alps	0.67	0.29	0.19	0.36	0.00	0.00	0.68	0.53	0.11
Mar. Alps	0.76	0.00	0.00	0.03	0.00	0.00	0.77	0.02	0.00
N. Apennines	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
N. Iberian	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00
Rhodope-Rila	0.19	0.00	0.00	0.02	0.00	0.00	0.48	0.00	0.00
S. Apennines	0.11	0.00	0.00	0.00	0.00	0.00	0.59	0.30	0.00
S. Carpathian	0.21	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
S. Hellenides	0.08	0.00	0.00	0.01	0.00	0.00	0.64	0.00	0.00
Scardo-Pindic	0.72	0.29	0.11	0.52	0.02	0.00	0.79	0.12	0.03
W. Alps	0.55	0.23	0.00	0.34	0.01	0.00	0.60	0.46	0.11
W. Carpathian	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
W. Pyrenees	0.43	0.05	0.02	0.09	0.00	0.00	0.65	0.03	0.00
WC. Alps	0.57	0.56	0.23	0.54	0.00	0.00	0.57	0.57	0.07
Minimum	0	0	0	0	0	0	0	0	0
Median	0.29	0	0	0.02	0	0	0.48	0.02	0
Maximum	0.77	0.56	0.23	0.54	0.02	0	0.9	0.57	0.11

Results are rounded to the nearest 5% to recognize imprecision in estimating superposition with hundreds of points. M#S# refer to the model–scenario combinations

The proportions of the alpine regions that remained within the grassland climatic envelopes in future scenarios have one geographic pattern: a greater area of potential mesoscale refugia in the Alps (Online Resource 5). In general linear models with a stepwise procedure, only the log of the area of the climate envelope in PCA space, which was correlated with actual range area, was a significant predictor of any of the three indicators (Table 3). However, the relationship may be heteroscedastic: the potential for refugia is consistently high with the greater breadth of climates in the Alps but varies among the model/scenario combinations if the climate envelope areas are small (Fig. 5).

Model comparisons

Because of the many zeroes and high skew in the proportion of the climate of the ranges that remained within the climatic envelope of their current grasslands, the differences among models and scenarios are best assessed by inspection of the column totals in Table 2. The MPI model projects slightly less loss of alpine grassland climate than the GFDL model, but the UK model has the greatest changes. The greatest differences among the models are with the optimistic SS1 scenario but these narrow in the SSP3 conditions and all three models approach complete loss of alpine grassland climate with the SSP5 scenario.

Discussion

The climates of the alpine habitats of the 23 mountain ranges of SACEU are not uniform. Highest monthly and quarterly temperatures among all points varied by over 20 K, and summer precipitation by over 1100 mm, with coefficients of variation of 0.33 and 0.37, respectively. Variability within ranges was less, but still exceeded 10 K in both temperatures variables four ranges and spanned > 800 mm of summer precipitation in seven.

Alpine grasslands occupy the full range of warm-season temperatures within 10 of the 23 ranges of SACEU and close to the full range on others. The exceptions for temperature are primarily in the Alps, where colder temperatures

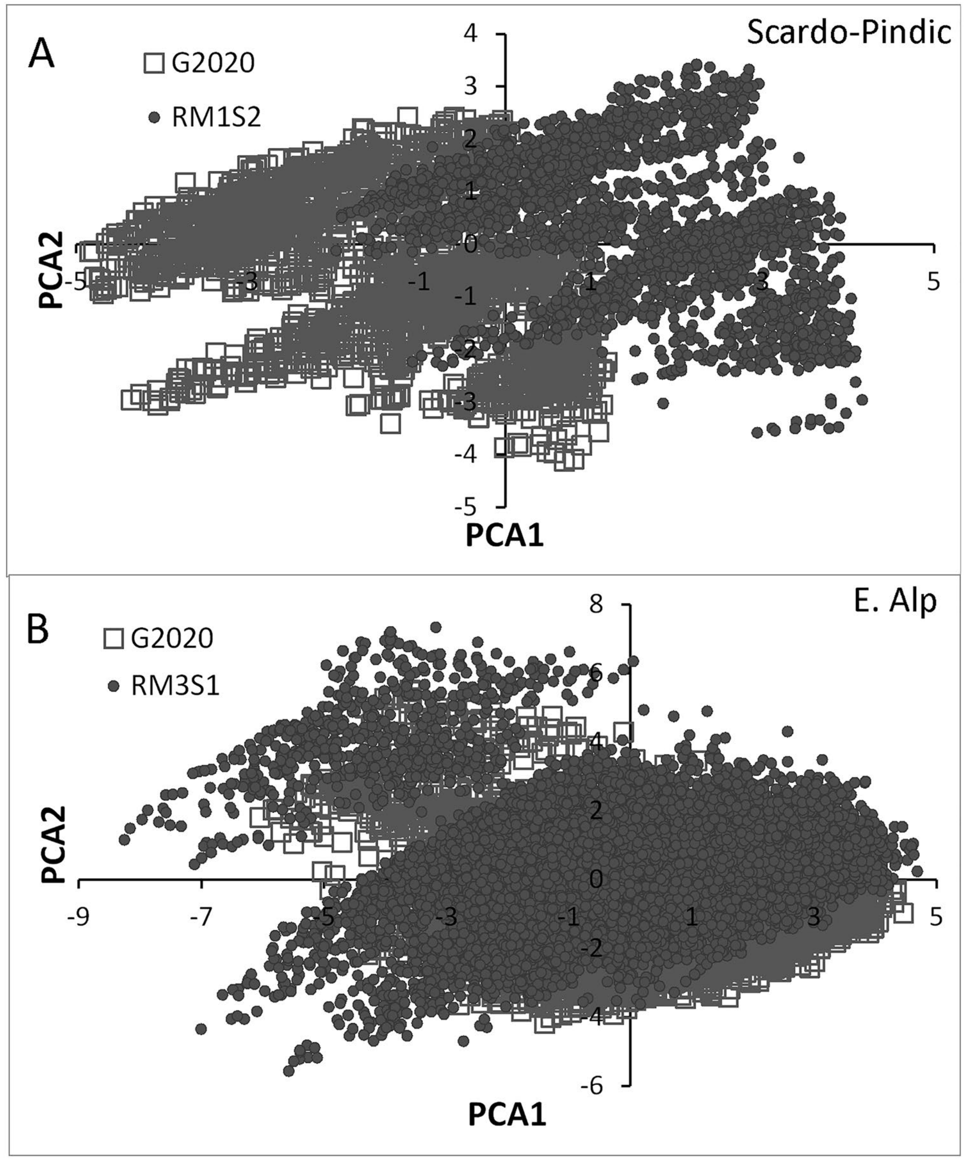

Fig. 3 Examples of the relationship of the current grassland climatic envelopes (G2020) to future projections for the range-wide envelopes from selected model-climate scenarios (here, the GFDL model and the optimistic SSP1 scenario for the Scardo-Pindic and the MPI model and pessimistic SSP5 scenario for the eastern Alps). Similar plots of all model-scenario combinations for all ranges with an overlap of > 5% of the range-wide points are in Online Resource 4

at higher elevations probably exclude grassland vegetation (cf. Bürli et al. 2021). The mean summer cold limit, where evident, is 8.1 °C with a coefficient of variation of 0.32 (excluding the Baetic System and the S. Apennines, where the mean and CV are 7.27 and 0.22 and we expect the > 11 °C limits may be confounded by a factor other than climate). Lack of evidence for a warm-limit indicates that the high-temperature boundary is likely determined by competition with trees, which may in turn be locally determined by land use. Alpine grasslands also occupy the full range of the summer precipitation envelope, and potential interactions between precipitation and temperature suggest that high precipitation may raise the cold limit. This pattern of interaction holds for the combination of mean annual and mean winter temperature and precipitation, not shown here, and so the limit for grasslands could also be related to snow depth and its effect on soil temperatures and growing-season length (Choler 2018; Vorkauf et al. 2021).

The model and scenario results parallel those of earlier studies (Rubel et al. 2017; Barredo et al. 2020). Here, the details of the climatic envelopes of alpine grasslands are revealed. The potential for refugia at mesoscale is limited. It depends on the breadth of the current climate and species niches (cf. Engler et al. 2011; Lynn et al. 2021). To support even minimal climatic refugia at this scale, ranges must have a wider range of current climates than the predicted amount of change. Most ranges do not have the breadth of current climate greater than the change predicted even in the moderate scenario; those that do are within the Alps, which have more area at higher elevation than current grasslands in other ranges. While these areas meet our definition of climatic mesoscale refugia, they include places without soil,

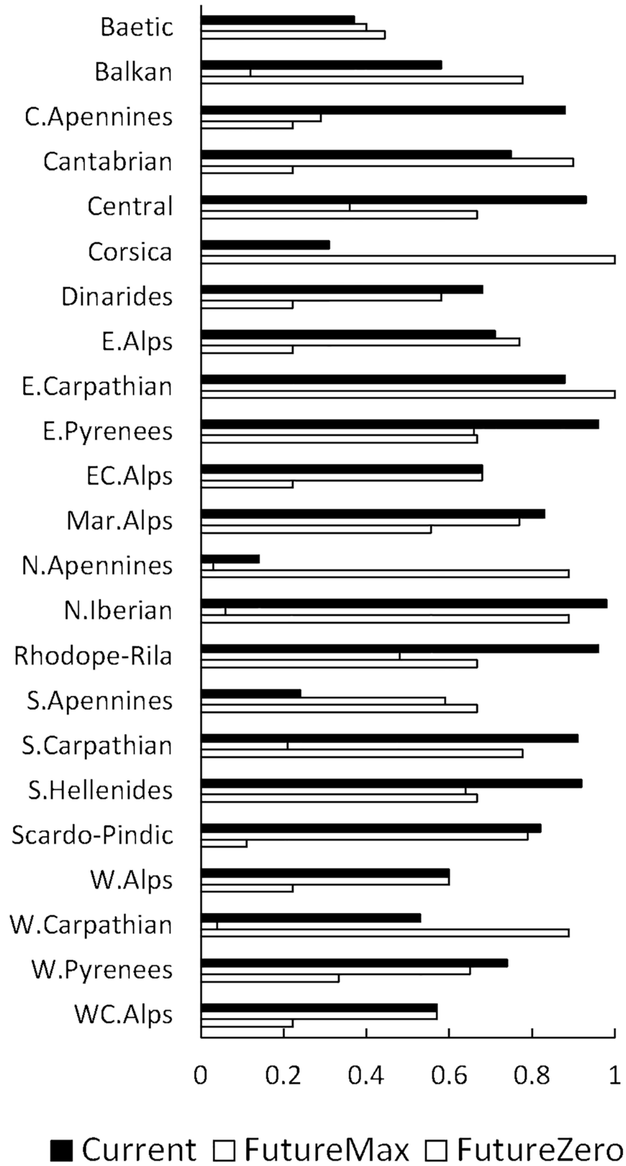

Fig. 4 The potential for refugia among the nine model and scenario combinations for each of the 23 ranges as indicated by the current, and future maximum proportions of range area within the current grassland climate envelope and the number of future instances with none (summary of rows Table 2)

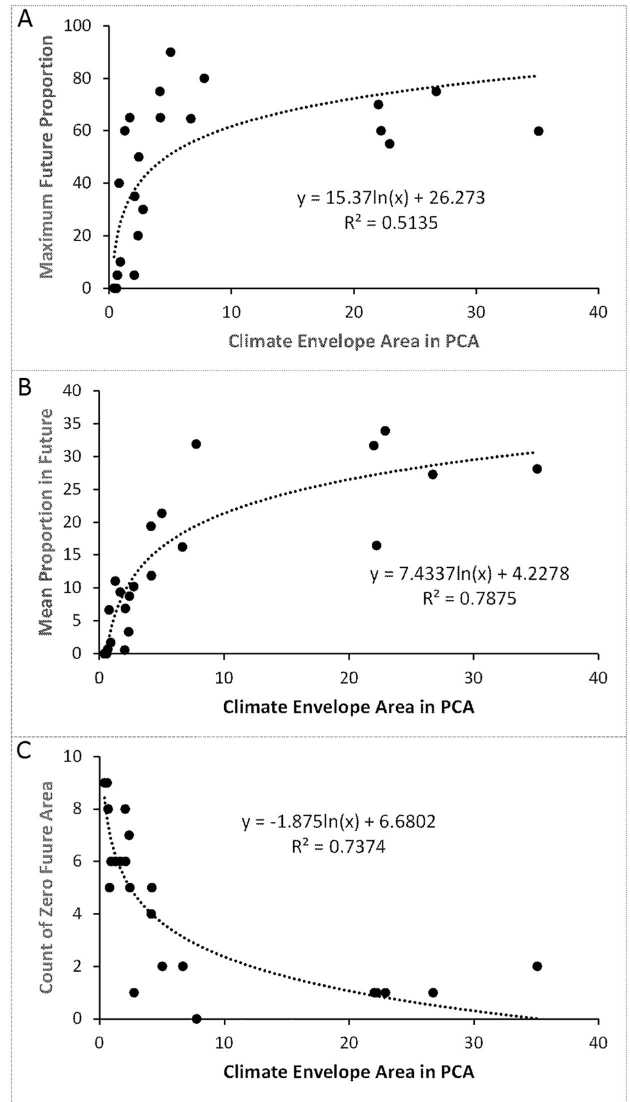

Fig. 5 Relationships of maximum (**A**) and mean (**B**) proportions of range area and the number of future instances with zero area within the current grassland climate envelope

Table 3 GLM results for indicators of the mesoscale refugia in the nine model and scenario combinations for each range

Maximum proportion = 26.27 + 35.39 logCEA	R^2 = 51.35
Mean proportion = 4.23 + 17.12 logCEA	R^2 = 78.75
Count of zeroes = 6.68 – 4.32 logCEA	R^2 = 73.74

Only the log of the climate envelope area (CEA), calculated from the distribution of points in PCA space defined by the first two eigenvectors, was significant; however, this variable was correlated with the log of the area of the range (r = 0.95)

including glaciers. Indeed, where the proportion of the range that could support grassland does not change in the more optimistic scenario, additional niche limitations should be evaluated. Even these areas lose all grassland climates in the most extreme model and scenario combination (M2S3: UKESM1 with SSP5). Where more potential refugia relative to the breadth of current climate exist (i.e., the Cantabrian and Scardo-Pindic ranges), the changes projected some model-scenario combinations are small (e.g., M1S1: GFDL with SSP1).

Although the climates of the 23 mountain ranges of SACEU provide little potential for mesoscale refugia for their alpine grasslands in a warmer, drier future, micro-refugia exist where topography can buffer some climate change (e.g., Mosblech et al. 2011; Patsiou et al. 2014), which can be more complex than represented at 1-km resolution (e.g., Lundquist and Cayan 2007; Patsiou et al. 2017). Microsites on single slopes can have a range of surface temperatures greater than 10 °C (Scherrer and Körner 2011), but, given that the variation at 2 m is less, many fewer would still be within the temperature niche of their local grassland species with the changes projected. Furthermore, the current variation does not necessarily imply that any areas will remain stable or maintain such temperature difference with further mesoscale warming.

Our analysis is limited to the patterns of the realized climatic envelopes of the alpine grasslands and the fundamental envelopes could be broader in the direction of increased productivity, i.e., higher temperatures, on the climatic gradients (Pellisier et al. 2013). Thus, additional refugia could exist if some grassland species can persist in warmer, drier conditions than observed. The future realized envelopes will depend on the realized treeline ecotone. Although fundamentally responsive to temperature (Körner 2021), this limit for alpine grasslands will be driven by the regeneration niches of its species as determined by biotic and other abiotic factors (Malanson et al. 2019). Lags in treeline response in dry conditions could reduce some potential losses of alpine grassland area. While the combination of cooler microsites and broader tolerance of higher temperatures could lessen the impact of climate change, both would still be constrained by mesoscale climate.

While micro-refugia will be important for future biodiversity, the area of alpine grasslands would be reduced. The species–area relationship—the most consistent pattern in biogeography—portends significant local losses of species after a period of extinction debt (Malanson 2008). Given unknown thresholds in the buffering capacity of microsites and the climatic niche breadth of individual species, the amount and timing of extinction debt will make projections from current distributions and trends uncertain (cf. Malanson et al. 2019). The future of alpine grasslands in SACEU will also depend on the dynamics of other montane vegetation with intersecting climatic envelopes. The resistance of alpine vegetation proposed by Körner and Hiltbrunner (2021) could be limited in extent, and micro-refugia may not prevent significant losses of biodiversity in alpine grasslands in a warmer, drier future (recognizing time lags; e.g., Windmaisser and Reisch 2013).

The potential for refugia to mitigate the impact of climate change should recognize their multiscale context. Micro-refugia can be effective only up to the point where their ability to buffer climate changes is exceeded by mesoscale change. Where mesoscale limits are exceeded, the geography of macroscale refugia and the extent and abiotic and biotic conditions of micro-refugia may become relevant. Our results illustrate the need for more precise spatial metrics at greater extents and are relevant to the location of conservation measures (cf. Balantic et al. 2021; Carroll and Ray 2021).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00035-022-00283-0.

Acknowledgements This research was supported by: US NSF award 1853665 to GPM and by the following grants to BJ-A: Gobierno del Principado de Asturias IDI/2018/000151, Agencia Nacional de Investigación e Innovación AEI/10.13039/501100011033, and Clarín COFUND ACB17-26.

Author contributions GPM defined the project, based on discussions with ERP, and analyzed the data. RT organized the climate data based on location definitions worked out with BJ-A. All authors participated in writing the paper at multiple stages.

Data availability All data used herein are publicly available from the CHELSA repository at https://chelsa-climate.org/.

Declarations

Conflict of interest The authors declare no conflicts of interest.

References

Alatalo J, Erfanian MB, Molau U, Chen S, Bai Y, Jägerbrand A (2020) Changes in plant composition and diversity in an Alpine heath and meadow after 18 years of experimental warming. Alp Bot. https://doi.org/10.1007/s00035-021-00272-9

Ashcroft MB (2010) Identifying refugia from climate change. J Biogeogr 37:1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Balantic C, Adams A, Gross S, Mazur R, Sawyer S, Tucker J, Vernon M, Mengelt C, Morales J, Thorne JH, Brown TM, Athearn N, Morelli TL (2021) Toward climate change refugia conservation at an ecoregion scale. Conserv Sci Pract 3:e497. https://doi.org/10.1111/csp2.497

Barredo JL, Mauri A, Caudullo G (2020) Alpine tundra contraction under future warming scenarios in Europe. Atmosphere 11:698

Bürli S, Theurillat JP, Winkler M, Lamprecht A, Pauli H, Rixen C, Steinbauer K, Wipf S, Abdaladze O, Andrews C, Barancok P, Benito-Alonso JL, Carranza ML, Dick J, Erschbamer B, Ghosn D, Gigauri K, Kazakis G, Mallaun M, Michelsen O, Moiseev D, Moiseev P, Molau U, Mesa JM, di Cella UM, Nadeem I, Nagy L, Nicklas L, Palaj A, Pedersen B, Petey M, Puscas M, Rossi G, Stanisci A, Tomaselli M, Unterluggauer P, Ursu TM, Villar L, Vittoz P (2021) A common soil temperature threshold for the upper limit of alpine grasslands in European mountains. Alp Bot 131:41–52. https://doi.org/10.1007/s00035-021-00250-1

Carroll C, Ray JC (2021) Maximizing the effectiveness of national commitments to protected area expansion for conserving biodiversity and ecosystem carbon under climate change. Glob Change Biol 27:3395–3414. https://doi.org/10.1111/gcb.15645

Choler P (2018) Winter soil temperature dependence of alpine plant distribution: implications for anticipating vegetation changes under a warming climate. Perspect Plant Ecol Evol Syst 30:6–15. https://doi.org/10.1016/j.ppees.2017.11.002

Coppola E, Nogherotto R, Ciarlo JM, Giorgi F, van Meijgaard E, Kadygrov N, Iles C, Corre L, Sandstad M, Somot S, Nabat P, Vautard

R, Levavasseur G, Schwingshackl C, Sillmann J, Kjellstrom E, Nikulin G, Aalbers E, Lenderink G, Christensen OB, Boberg F, Sorland SL, Demory ME, Bulow K, Teichmann C, Warrach-Sagi K, Wulfmeyer V (2021) Assessment of the European climate projections as simulated by the large EURO-CORDEX regional and global climate model ensemble. J Geophys Res Atmo 126:e2019JD032356. https://doi.org/10.1029/2019JD032356

Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. Glob Change Biol 17:1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, Araujo MB, Pearman PB, Le Lay G, Piedallu C, Albert CH, Choler P, Coldea G, De Lamo X, Dirnbock T, Gegout JC, Gomez-Garcia D, Grytnes JA, Heegaard E, Hoistad F, Nogues-Bravo D, Normand S, Puscas M, Sebastia MT, Stanisci A, Theurillat JP, Trivedi MR, Vittoz P, Guisan A (2011) 21st century climate change threatens mountain flora unequally across Europe. Glob Change Biol 17:2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

García MB, Domingo D, Pizarro M, Font X, Gómez D, Ehrlén J (2020) Rocky habitats as microclimatic refuges for biodiversity. A close-up thermal approach. Environ Exp Bot 170:103886. https://doi.org/10.1016/j.envexpbot.2019.103886

Gentili R, Baroni C, Caccianiga M, Armiraglio S, Ghiani A, Citterio S (2015) Potential warm-stage microrefugia for alpine plants: feedback between geomorphological and biological processes. Ecol Complex 21:87–99. https://doi.org/10.1016/j.ecocom.2014.11.006

Graae BJ, Vandvik V, Armbruster WS, Eiserhardt WL, Svenning JC, Hylander K, Ehrlén J, Speed JD, Klanderud K, Bråthen KA, Milbau A, Opedal OH, Alsos IG, Ejrnaes R, Bruun HH, Birks HJB, Westergaard KB, Birks HH, Lenoir J (2018) Stay or go–how topographic complexity influences alpine plant population and community responses to climate change. Perspect Plant Ecol Evol Syst 30:41–50. https://doi.org/10.1016/j.ppees.2017.09.008

Holderegger R, Thiel-Egenter C (2009) A discussion of different types of glacial refugia used in mountain biogeography and phylogeography. J Biogeogr 36:476–480. https://doi.org/10.1111/j.1365-2699.2008.02027.x

Jiménez-Alfaro B, Abdulhak S, Attorre F, Bergamini A, Carranza ML, Chiarucci A, Ćušterevska R, Dullinger S, Gavilán RG, Giusso del Galdo G, Kuzmanović N, Laiolo P, Loidi J, Malanson GP, Marcenó C, Milanović D, Pansing ER, Roces-Díaz JV, Ruprecht E, Šibik J, Stanisci A, Testolin R, Theurillat J-P, Vassilev K, Willner W, Winkler M (2021) Postglacial determinants of regional species pools in alpine grasslands. Glob Ecol Biogeogr 30:1101–1115. https://doi.org/10.1111/geb.13274

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Sci Data 4:170122. https://doi.org/10.1038/sdata.2017.122

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2021) Climatologies at high resolution for the earth's land surface areas. EnviDat. https://doi.org/10.16904/envidat.228.v2.1

Keppel G, Wardell-Johnson GW (2012) Refugia: keys to climate change management. Glob Change Biol 18:2389–2391. https://doi.org/10.1111/j.1365-2486.2012.02729.x

Körner C (2021) The cold range limit of trees. Trends Ecol Evol 36:979–989

Körner C, Hiltbrunner E (2021) Why is the alpine flora comparatively robust against climatic warming? Diversity 13:383. https://doi.org/10.3390/d13080383

Lamprecht JJ et al (2022) Global maps of soil temperature. Glob Change Biol 28:3110–3144. https://doi.org/10.1111/gcb.16060

Liberati L, Messerli S, Matteodo M, Vittoz P (2019) Contrasting impacts of climate change on the vegetation of windy ridges and snowbeds in the Swiss Alps. Alp Bot 129:95–105. https://doi.org/10.1007/s00035-019-00223-5

Lundquist JD, Cayan DR (2007) Surface temperature patterns in complex terrain: daily variations and long-term change in the central Sierra Nevada. Calif J Geophys Res 112:D11124. https://doi.org/10.1029/2006JD007561

Lynn JS, Klanderud K, Telford RJ, Goldberg DE, Vandvik V (2021) Macroecological context predicts species' responses to climate warming. Glob Change Biol 27:2088–2101. https://doi.org/10.1111/gcb.15532

Malanson GP (2008) Extinction debt: origins, developments, and applications of a biogeographic trope. Prog Phys Geogr 32:277–291. https://doi.org/10.1177/0309133308096028

Malanson GP, Westman WE, Yan Y-L (1992) Realized versus fundamental niche functions in a model of chaparral response to climatic change. Ecol Model 64:261–277. https://doi.org/10.1016/0304-3800(92)90026-B

Malanson GP, Resler LM, Butler DR, Fagre DB (2019) Mountain plant communities: uncertain sentinels? Prog Phys Geogr 43:521–543. https://doi.org/10.1177/0309133319843873

Marchin RM, McHugh I, Simpson RR, Ingram LJ, Balas DS, Evans BJ, Adams MA (2018) Productivity of an Australian mountain grassland is limited by temperature and dryness despite long growing seasons. Agric Meteor 256:116–124. https://doi.org/10.1016/j.agrformet.2018.02.030

McCune B, Mefford MJ (2016) PC-ORD: multivariate analysis of ecological data, Version 7. MjM Software Design, Gleneden Beach, OR, USA

Morales-Barbero J, Vega-Álvarez J (2019) Input mattersmatter: bioclimatic consistency to map more reliable species distribution models. Methods Ecol Evol 10:212–224. https://doi.org/10.1111/2041-210X.13124

Morgan JW, Venn SE (2017) Alpine plant species have limited capacity for long-distance seed dispersal. Plant Ecol 218:813–819. https://doi.org/10.1007/s11258-017-0731-0

Mosblech NAS, Bush MB, van Woesik R (2011) On metapopulations and microrefugia: palaeoecological insights. J Biogeogr 38:419–429. https://doi.org/10.1111/j.1365-2699.2010.02436.x

Niskanen AKJ, Heikkinen RK, Mod HK, Vare H, Luoto M (2017) Improving forecasts of arctic-alpine refugia persistence with landscape-scale variables. Geografiska Annaler 99:2–14. https://doi.org/10.1080/04353676.2016.1256746

Patsiou TS, Conti E, Zimmermann NE, Theodoridis S, Randin CF (2014) Topo-climatic microrefugia explain the persistence of a rare endemic plant in the Alps during the last 21 millennia. Glob Change Biol 20:2286–2300. https://doi.org/10.1111/gcb.12515

Patsiou TS, Conti E, Theodoridis S, Randin CF (2017) The contribution of cold air pooling to the distribution of a rare and endemic plant of the Alps. Plant Ecolog Divers 10:29–42. https://doi.org/10.1080/17550874.2017.1302997

Pellissier L, Bråthen KA, Vittoz P, Yoccoz NG, Dubuis A, Meier ES, Zimmermann NE, Randin CF, Thuiller W, Garraud L, Van Es J, Guisan A (2013) Thermal niches are more conserved at cold than warm limits in arctic-alpine plant species. Glob Ecol Biogeogr 22:933–941. https://doi.org/10.1111/geb.12057

Pichelli E, Coppola E, Sobolowski S, Ban N, Giorgi F, Stocchi P, Alias A, Belušić D, Berthou S, Caillaud C, Cardoso RM,·Chan S, Christensen OB, Dobler A, de Vries H, Goergen K, Kendon EJ, Keuler K, Lenderink G, Lorenz T, Mishra AN, Panitz H-J, Schär C, Soares PMM, Truhetz H, Vergara-Temprado J (2021) The first multi-model ensemble of regional climate simulations at kilometer-scale resolution part 2: historical and future simulations of precipitation. Clim Dyn 56:3581–3602. https://doi.org/10.1007/s00382-021-05657-4

Rubel F, Brugger K, Haslinger K, Auer I (2017) The climate of the European Alps: shift of very high resolution Köppen-Geiger climate zones 1800–2100. Meteor z 26:115–125. https://doi.org/10.1127/metz/2016/0816

Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J Biogeogr 38:406–416. https://doi.org/10.1111/j.1365-2699.2010.02407.x

Sklenář P, Romoleroux K, Muriel P, Jaramillo R, Bernardi A, Diazgranados M, Moret P (2021) Distribution changes in páramo plants from the equatorial high Andes in response to increasing temperature and humidity variation since 1880. Alp Bot 131:201–212. https://doi.org/10.1007/s00035-021-00270-x

Steinbauer K, Lamprecht A, Semenchuk P, Winkler M, Pauli H (2020) Dieback and expansions: species-specific responses during 20 years of amplified warming in the high Alps. Alp Bot 130:1–11. https://doi.org/10.1007/s00035-019-00230-6

Testolin R, Attorre F, Jiménez-Alfaro B (2020) Global distribution and bioclimatic characterization of alpine biomes. Ecography 43:779–788. https://doi.org/10.1111/ecog.05012

Testolin R, Attorre F, Borchardt P, Brand RF, Bruelheide H, Chytry M, De Sanctis M, Dolezal J, Finckh M, Haider S, Hemp A, Jandt U, Kessler M, Korolyuk AY, Lenoir J, Makunina N, Malanson GP, Montesinos-Tubee DB, Noroozi J, Nowak A, Peet RK, Peyre G, Sabatini FM, Sibik J, Sklenar P, Sylvester SP, Vassilev K, Virtanen R, Willner W, Wiser SK, Zibzeev EG, Jimenez-Alfaro B (2021) Global patterns and drivers of alpine plant species richness. Glob Ecol Biogeogr 30:1218–1231. https://doi.org/10.1111/geb.13297

Vorkauf M, Kahmen A, Körner C, Hiltbrunner E (2021) Flowering phenology in alpine grassland strongly responds to shifts in snowmelt but weakly to summer drought. Alp Bot 131:73–88. https://doi.org/10.1111/10.1007/s00035-021-00252-z

Wang Z, Luo T, Li R, Tang Y, Du M (2013) Causes for the unimodal pattern of biomass and productivity in alpine grasslands along a large altitudinal gradient in semi-arid regions. J Veg Sci 24:189–201. https://doi.org/10.1111/j.1654-1103.2012.01442.x

Windmaißer T, Reisch C (2013) Long-term study of an alpine grassland: local constancy in times of global change. Alp Bot 123:1–6. https://doi.org/10.1007/s00035-013-0112-9

Winkler M, Lamprecht A, Steinbauer K, Hulber K, Theurillat J-P, Breiner F, Choler P, Ertl S, Giron AG, Rossi G, Vittoz P, Akhalkatsi M, Bay C, Alonso JLB, Bergstrom T, Carranza ML, Corcket E, Dick J, Erschbamer B, Calzado RF, Fosaa AM, Gavilan RG, Ghosn D, Gigauri K, Huber D, Kanka R, Kazakis G, Klipp M, Kollar J, Kudernatsch T, Larsson P, Mallaun M, Michelsen O, Moiseev P, Moiseev D, Molau U, Mesa JM, di Cella UM, Nagy L, Petey M, Puscas M, Rixen C, Stanisci A, Suen M, Syverhuset AO, Tomaselli M, Unterluggauer P, Ursu T, Villar L, Gottfried M, Pauli H (2016) The rich sides of mountain summits—a pan-European view on aspect preferences of alpine plants. J Biogeogr 43:2261–2273. https://doi.org/10.1111/jbi.12835