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VEGETATION SURVEY

Living on the edge: Plant diversity in the Iberian chionophilous vegetation

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Abstract

Aims: Chionophilous vegetation (i.e. snowbed vegetation and chionophilous grasslands) hosts relict arctic–alpine species, among which snowbed specialists, that find their southernmost limit in the Iberian Peninsula, where they are especially threatened by climate change. Our aims were to identify the main Iberian chionophilous vegetation groups, and analyse their plant diversity patterns and their role as refugia for snowbed glacial relicts, as well as that of Iberian high-mountain regions.

Location: Iberian high mountains.

Methods: We used the *beta-flexible* clustering method to classify 1002 vegetation relevés of Iberian chionophilous vegetation, and computed species Indicator Values and frequencies for the resulting groups. We performed a Detrended Correspondence Analysis (DCA) ordination of the relevés, and fitted six climatic variables to reveal the main ecological gradients. We constructed rarefaction curves to compare species richness between vegetation groups and between mountain regions.

Results: We obtained eight vegetation groups, four consisting of snowbed vegetation and four of chionophilous grasslands. All but one group were present in the Pyrenees, where snowbed specialist richness was the highest. In southern and central Iberian ranges, snowbed vegetation was extremely scarce, and the main vegetation group corresponded to cryoromediterranean grasslands, where both species and specialist richness were the lowest. Snowbed and northern Iberian grassland groups accounted for similar high specialist richness, although specialists were infrequent and scarce at relevé level in these grasslands.

Conclusions: Despite the set of specialised species that thrive in snowbeds, many of them are also present but scarce in northern Iberian chionophilous grasslands. In a future scenario with a high reduction of snow cover duration, which may entail the disappearance of many snowbed vegetation patches, northern Iberian chionophilous grasslands may act as terminal refugia for snowbed specialists. Nevertheless, specialists are very threatened in central and southern Iberian ranges, where snowbed vegetation is infrequent and chionophilous grasslands provide almost no shelter to them.

KEYWORDS
Cantabrian Range, Central System, chionophilous grasslands, glacial relicts, Iberian high mountain, Pyrenees, Sierra Nevada, snowbed specialists, snowbed vegetation, species richness

1 | INTRODUCTION

During Pleistocene interglacial periods, southern European mountain ranges acted as refugia for arctic and alpine species (Gentili et al., 2015a), which could more easily migrate to higher elevations rather than to higher latitudes (Médail & Diadema, 2009). There, the topographical heterogeneity provided them microrefugia in specific landforms such as scree slopes or snowbeds (Gentili et al., 2015b), among others. Because of their isolation, many of these species underwent speciation events, whilst others survived as peripheral populations (Gentili et al., 2015b), contributing to the current high diversity and degree of endemicity of southern European mountains (Nagy & Grabherr, 2009).

Likewise, major Iberian mountain ranges, with their scattered distribution throughout the Iberian Peninsula, offered multiple isolated refugia during the Pleistocene (Hewitt, 2001; Gómez & Lunt, 2007). At present, the coexistence in these mountains of arctic–alpine species belonging to different source floras (Comes & Kadereit, 2003) and a high number of endemics (Aedo et al., 2017), results in a relatively high proportion of rare species (Miranda et al., 2022) and in the highest species richness within the Iberian Peninsula (Aedo et al., 2017).

The rough and variable topography of alpine landscapes results in a high environmental heterogeneity over short distances and an irregular distribution of snow, which is the main abiotic factor driving the distribution of arctic and alpine species in high mountains (Körner, 2003). The snowiest areas, where snow melts from late spring to mid- or late summer, hold particular species and vegetation types, also called chionophilous. Among them, the most dependent on a long-lasting snow cover is snowbed vegetation, which is distributed in scattered small patches at wind-sheltered places where snow accumulates due to wind redistribution or to an irregular topography. In snowbeds, the deep and long-lasting snow cover avoids winter and spring below-zero temperatures, and maintains soil moisture during the short growing season (Björk & Molau, 2007). Nevertheless, the brevity of the growing period is limiting for most species from the regional floristic pool, and only a certain number of specialists, most of them with arctic or alpine distribution, can thrive there (Schöb et al., 2009). At wind-protected landforms where snowmelt occurs earlier in summer or in late spring and which are larger and more frequent in the landscape than snowbed patches, environmental conditions are more favourable for chionophilous grasslands (Braun-Blanquet, 1948), constraining the presence of snowbed species and vegetation.

Nowadays, climatic conditions in Iberian high mountains are shifting towards warmer temperatures, fewer snow precipitation, and a redistribution of monthly rainfall (Morán-Tejeda et al., 2013), leading to a reduction of snowpack duration (López-Moreno et al., 2009; Pérez-Palazón et al., 2015). These climatic variations are the main cause of change in species composition in high mountains (Sanz-Elorza et al., 2003; Pauli et al., 2012), and entail a serious threat for the relict snowbed specialists confined to the Iberian mountains' snowiest patches.

It remains unclear if snowbed patches will be affected with the same intensity as other alpine landforms, as macroclimatic and snow-predictive models do not consider this small-scale environmental heterogeneity. In any case, the longer growing season resulting from a reduced snowpack may allow species from surrounding chionophilous grasslands, more competitive than snowbed specialists (Heegaard & Vandvik, 2004; Schöb et al., 2008), to colonize snowbed vegetation patches and outcompete specialists (Illa et al., 2019). Thus, in a near future, Iberian snowbed vegetation is doomed to experience a reduction of its distribution area, or even to disappear, because of its replacement by neighbouring chionophilous grasslands. But at the species level, the fate of snowbed specialists remains an open question. Whether they will survive as isolated populations within a grassland-dominated landscape, or they will go extinct, is still unknown.

Although high-mountain vegetation has been widely studied in the Iberian Peninsula (e.g. Braun-Blanquet, 1948; Quézel, 1953; Rivas-Martínez, 1963; Nava, 1988), a detailed analysis focusing specifically on chionophilous vegetation (i.e. snowbed vegetation and chionophilous grasslands) is missing. Taking into consideration that a significant number of arctic–alpine species find their southernmost distribution limit in Iberian high mountains, and that the snowiest patches host a number of glacial relicts, namely snowbed specialists, it is relevant to identify the mountain regions and vegetation types that nowadays represent a refugium for these species, since they may be the most vulnerable to climate change.

In this work, based on all the available relevés of Iberian chionophilous vegetation, we aimed to identify and characterize the main Iberian chionophilous vegetation groups to: (i) analyse the role of Iberian high mountains as refugia for them; (ii) explore their contribution, and that of Iberian high-mountain regions, to species richness; and (iii) assess their role as refugia for snowbed specialists in the current context of climate change.

2 | METHODS

2.1 | Nomenclature

The scientific nomenclature of vegetation units follows Rivas-Martínez et al. (2001). The scientific nomenclature of plant taxa follows the WFO (World Flora Online), last accessed on 9 February 2020.

2.2 | Study area

We included the main Iberian high-mountain ranges reaching the alpine belt, including here both the cryorotemperate belt (Pyrenees, Cantabrian Range) and the cryoromediterranean belt (Central System, Sierra Nevada, Figure 1). We excluded the Iberian System because of its reduced area at high elevations, from where no data on the target vegetation types is available. As for the alpine belt, we

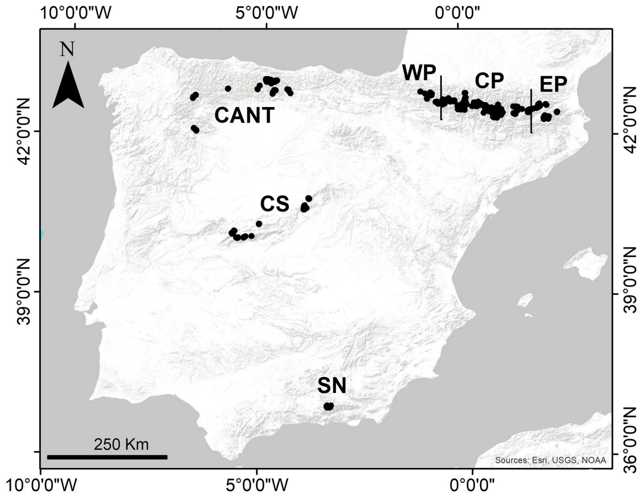


FIGURE 1 Distribution of the relevés of chionophilous vegetation in the Iberian high-mountain regions (including the French Pyrenees): CANT, Cantabrian Range; WP, Western Pyrenees; CP, Central Pyrenees; EP, Eastern Pyrenees; CS, Central System; and SN, Sierra Nevada.

consider the areas above 2200 m a.s.l. on northern slopes and above 2400 m a.s.l. on southern slopes (Ninot et al., 2007; Sánchez-Mata et al., 2017) in all the mountain ranges except the Sierra Nevada, where we consider the areas above 2800 and 3000 m a.s.l., respectively (Molero & Marfil, 2017). However, alpine vegetation can thrive at lower elevations in favourable locations, from approximately 2000 m a.s.l. upwards in central and northern Iberian mountains, and from 2700 m a.s.l. upwards in the Sierra Nevada (Gavilán et al., 2017).

The Pyrenees, with a length of 430 km, represent the natural division between the Iberian Peninsula and the rest of Europe, and between temperate and Mediterranean bioclimates. They are divided in this study into three main bioclimatic regions. The Western Pyrenees are limited in the west by the Atlantic Ocean, which provides an oceanic climate, and in the east by the Somport pass (42°47′39.6″ N 0°31′38.3″ W). Elevation increases gently from W to E, and reaches its maximum at Peña Llerga (2670 m a.s.l.). The central parts of the range hold the highest average elevation, with a large number of peaks exceeding 3000 m a.s.l. (the highest peak is Aneto, with 3403 m a.s.l.). There, northern slopes experience an oceanic climate, whereas southern slopes receive the continental influence of the Iberian Peninsula. In the Eastern Pyrenees, from Envalira pass (42°32′21.9″ N 1°43′25.8″ E) to the Mediterranean Sea, mean elevation remains uniformly high (Pic du Carlit, 2921 m a.s.l., is the highest peak) up to a sudden decrease near its easternmost point. Climate is oceanic with a high Mediterranean influence. Geological substrates in the Pyrenees are mainly siliceous (Loidi, 2017), but there are important limestone massifs (e.g. Ordesa and Monte Perdido) and outcrops throughout the range.

The Cantabrian Range (including the southwestern Montes de León) is located at the northern edge of the Iberian Peninsula, following a W–E direction (and a SW–NE direction at its southwestern edge) for 480 km. The highest peak reaches 2650 m a.s.l. (Torre Cerredo), and limestone rocks are predominant in the eastern half of the range, whereas siliceous substrate dominates in the western half (Loidi, 2017). The vicinity to the Cantabrian Sea keeps climate on the northern slopes damp and cool, whereas the southern slopes take much less rain and lie under a Mediterranean climatic influence (Nava, 1988).

The Central System occupies a central position within the Iberian Peninsula, where the main mountain ranges (mainly Guadarrama and Gredos) account for ca. 200 km following first a W–E, and then a SW–NE direction. The highest elevation is reached in Almanzor (2590 m a.s.l.), and siliceous bedrock is prevailing (Loidi, 2017). Central areas of the range (i.e. Guadarrama) endure continental climatic conditions, whereas eastwards and westwards there is a significant increase in precipitation (Sánchez-Mata et al., 2017).

Sierra Nevada is the southernmost major Iberian mountain range, with a main axis of 94 km following a W–E direction within the Baetic ranges. The highest peak reaches 3478 m a.s.l. (Mulhacén), and geological substrates are mainly siliceous (Loidi, 2017). The low latitude and top elevation confer harsh weather conditions, where extreme winter cold is suddenly followed by intense summer drought.

2.3 | Vegetation data

We first established the list of vegetation units considered as chionophilous in the Iberian context, i.e. snowbed vegetation and chionophilous grasslands (Appendix S1). Based on the synthesis of Rivas-Martínez (2011), Iberian snowbed vegetation is included in the phytosociological alliances *Salicion herbaceae* and *Mucizonion sedoidis* (calcifuge snowbed vegetation) and *Arabidion caeruleae* (calcicole snowbed vegetation). We also considered as a particular snowbed vegetation type the wet screes with long-lasting snow cover from the alliance *Saxifragion praetermissae*. Concerning Iberian chionophilous grasslands, we additionally relied on the original descriptions and on the bibliography of the main Iberian mountain ranges to select 15 phytosociological associations, included in the calcifuge grassland alliances *Campanulo herminii-Nardion strictae*, *Festucion supinae*, *Nardion strictae* and *Plantaginion nivalis*, and in the calcicole alliances *Armerion cantabricae* and *Primulion intricatae*.

Then, we gathered all the floristic relevés belonging to the selected vegetation units available at the SIVIM database (www.sivim.info/, database in Spanish; Font et al., 2012), last accessed 20 April 2018, consisting of a total number of 1144 relevés. Based on the list of snowbed specialists (Appendix S2) from Rivas-Martínez (2011), we also obtained those relevés not assigned to any phytosociological unit but containing one or more snowbed specialist species. These relevés were supervised individually in order to strictly select vegetation from snowbeds and chionophilous grasslands, resulting in a number of 436. Finally, we included 245 of our own unpublished relevés, sampled between 2004 and 2007 mainly in Aigüestortes and Estany de Sant Maurici National Park (Central Pyrenees, 42°33′36″ N 0°54′36″ E). At this point, the database consisted of

1825 relevés, dating from 1948 to 2014. With the aim to include the lowest elevational limit of chionophilous vegetation, we retained the relevés from 2600 m a.s.l. upwards in the Sierra Nevada, and from 1900 m a.s.l. upwards in the other mountain ranges, resulting in 1498 relevés. Then, we excluded the relevés without information about the area sampled, as well as those with areas smaller than 1 m^2 or larger than 50 m^2. At this point, the database contained 1419 relevés.

The relevés were accurately georeferenced with a precision of 100 m when possible using the online map viewers Iberpix 4 (https://www.ign.es/iberpix/visor) for the Iberian Peninsula, and Géoportail (https://www.geoportail.gouv.fr/) for the French Pyrenees, both last accessed 30 April 2018. Relevés with low georeferencing accuracy (lower than 1000 m) were excluded. In order to reduce the over-sampling effect of some areas and homogenize the data, we performed a stratified resampling to the data matrix. For each alliance and UTM square of 1 km × 1 km, we kept three times the number of equivalents of order one (i.e., the number of different communities; Jost, 2007). After this stratification, the final number of relevés retained for the analyses was 1002, which were heterogeneously distributed among mountain regions: from 645 in the Central Pyrenees to around 40 in the Western Pyrenees and Sierra Nevada, with the remaining regions including around 100 relevés each.

2.4 | Species data

We standardised the taxonomy using the WFO taxonomic reference source using the TNRS online tool (https://tnrs.biendata.org/, Boyle et al., 2013). We accepted all the names and synonyms with a match score of 1, and revised individually the rest at the WFO website (http://www.worldfloraonline.org/). We removed cryptogams from the relevés, as they are irregularly recorded among the original sources, as well as hybrids. We then merged infraspecific taxa into species level, and grouped taxonomically problematic taxa into aggregates as narrow as possible: for example, *Alchemilla* gr. *alpina*, *Festuca* gr. *rubra* or *Thymus* gr. *serpyllum*. Once filtered, our matrix included 525 taxa of vascular plants, hereafter referred to as species.

2.5 | Environmental data

We used the geographical coordinates of each relevé to extract the estimated monthly value of mean temperature and mean annual precipitation cumulate from different sources depending on the mountain range. For the Pyrenees, we used the available 30-m resolution Pyrenean Digital Climate Atlas (Batalla et al., 2018); for the Central System we used the 180-m resolution Iberian Digital Climate Atlas (Ninyerola et al., 2005); and for the Cantabrian Range and Sierra Nevada we used unpublished data with 30 m resolution provided by the same authors.

With these data we calculated summer (June, July and August) mean and mean maximum temperatures; summer precipitation cumulate; summer potential evapotranspiration (summer PET) following Thornthwaite (1948); summer mediterraneity index following Rivas-Martínez (1983); and an approximate value of snowiness considering winter–spring (December to April) precipitation cumulate.

Finally, we classified the relevés depending on the bedrock type (siliceous or calcareous). When this information was not found within the relevés' environmental information, we obtained it from digital geological cartographic sources at scale 1:50,000 (Magna 50 2nd series, http://mapas.igme.es/Servicios/default.aspx#IGME_MAGNA_50; Mapa Geològic Comarcal de Catalunya 1:50,000, https://www.icgc.cat/Administracio-i-empresa/Serveis/Geoinformacio-en-linia-Geoserveis/WMS-Geoindex/WMS-Cartografia-geologica#MG50M; Mapa Geològic d'Andorra 1/50,000, https://www.iea.ad/mapa-geologic-1-50-000; Carte géologique 1/50,000 vecteur harmonisée (BRGM), https://infoterre.brgm.fr/page/geoservices-ogc).

2.6 | Statistical analyses

All statistical analyses were performed with the free software R, version 3.6.1 (R Core Team, 2021).

First, we transformed the Braun-Blanquet cover–abundance scale of the relevé species to the combined scale (Van der Maarel, 1979), and computed the Bray–Curtis dissimilarity matrix of the vegetation data with the 'vegdist' function from the *vegan* package (Oksanen et al., 2021). Then, we used this matrix to classify the relevés into groups with the *beta-flexible* hierarchical clustering (beta parameter set to −0.25). To do so, we used the 'agnes' function with the 'flexible' method from the *cluster* package (Maechler et al., 2021). We pruned the classification dendrogram from two to 15 clusters with the 'cutree' function. We chose the best partition, which consisted of eight groups, based on the average Silhouette Width Criterion (Rousseeuw, 1987) with the 'silhouette' function from the afore-mentioned *cluster* package. Then, to measure the association between species and vegetation groups, we computed the species' Indicator Values (*IndVal*, Dufrêne & Legendre, 1997) accounting for the different group sizes, with the 'strassoc' function from the *indicspecies* package (de Cáceres & Legendre, 2009).

Taking into consideration the high disparity in the number of relevés of the different vegetation groups and mountain ranges, we used sample-based rarefaction curves (Gotelli & Colwell, 2001) to compare group and region species richness and snowbed specialists richness as a function of sampling effort. Thus, comparisons were based on equal sample sizes, corresponding to the number of relevés of the smallest group, that is, 71 relevés for vegetation groups and 36 relevés for mountain regions. For that purpose, we used the 'specaccum' function from the *vegan* package (Oksanen et al., 2021).

Finally, we ordinated the vegetation relevés with a Detrended Correspondence Analysis (DCA), and fitted all climatic variables mentioned above to reveal the main climatic determinants. We used the functions 'decorana' and 'envfit', respectively, also from the afore-mentioned *vegan* package.

3 | RESULTS

3.1 | Vegetation groups

Based on the average silhouette width, the best partition of chionophilous vegetation in the Iberian Peninsula was that of eight groups: four consisting of snowbeds and four composed by grasslands:

Group 1 - Iberian calcifuge hemicryptophyte snowbeds are found in all Iberian high-mountain regions (Figure 2), mainly on siliceous bedrock (more than 95% of the relevés). Only snowbed specialists have high to very high frequencies (Table 1) and significant *IndVal* (Appendix S3), among which *Gnaphalium supinum*, *Cardamine bellidifolia* (subsp. *alpina*, see Appendix S2), *Veronica alpina* or *Sedum candolleanum*.

Group 2 - Pyrenean calcifuge *Salix herbacea* snowbeds are present in the Central and Eastern Pyrenees (Figure 2), mainly on siliceous bedrock (more than 70% of the relevés) but always on acidic soils (Braun-Blanquet, 1948). The snowbed creeping chamaephyte *Salix herbacea* is present in all the relevés (Table 1), and is the most indicative species (Appendix S3). While other snowbed specialists such as *Gnaphalium supinum*, *Sibbaldia procumbens*, *Sedum alpestre* or *Veronica alpina* have high *IndVal* and frequencies, some grassland species such as *Carex curvula*, *Agrostis rupestris*, *Primula integrifolia* or *Scorzoneroides pyrenaica* are also very frequent and have relatively high *IndVal* (Table 1, Appendix S3).

Group 3 - Pyrenean calcicole *Salix* snowbeds are strictly found in the Central and Eastern Pyrenees (Figure 2), always on calcareous bedrock. Calcicole snowbed creeping chamaephytes of the *Salix* genus (*Salix retusa*, *Salix reticulata*) and *Carex parviflora* are very frequent (Table 1) and have significant *IndVal* (Appendix S3), while other snowbed specialists are also very frequent (*Salix herbacea*, *Veronica aphylla* or *Ranunculus alpestris*). Some grassland species such as *Kobresia myosuroides*, *Festuca glacialis*, *Helictotrichon sedenense* or *Gentiana verna* have also significant *IndVal* and high frequencies in this group (Appendix S3).

Group 4 - Iberian snowbed-related scree vegetation spread throughout the Pyrenean–Cantabrian ranges mainly on calcareous bedrock (81% of the relevés), although there are two relevés in the Sierra Nevada (Figure 2). Although this group is composed mainly of scree specialists such as *Pritzelago alpina*, *Doronicum grandiflorum* or *Crepis pygmaea*, the snowbed specialist *Saxifraga praetermissa* is the most frequent and indicative species (Appendix S3), and most of the snowbed specialists are present in the relevés, some of them with relatively high frequencies (e.g. *Epilobium anagallidifolium*, *Veronica alpina* or *Ranunculus alpestris*; Table 1). We have thus considered this vegetation group as a particular case within snowbed groups.

Group 5 - Pyrenean calcifuge *Carex curvula* grasslands are located exclusively in the Central Pyrenees (Figure 2), mainly on siliceous bedrock (85% of the relevés). A set of grassland species such as *Carex curvula*, *Gentiana* gr. *acaulis*, *Scorzoneroides pyrenaica* or *Oreochloa blanka* have significant high *IndVal* and frequencies (Appendix S3), but some snowbed specialists also appear frequently (e.g. *Sibbaldia procumbens*, *Sedum alpestre* or *Gnaphalium supinum*; Table 1).

Group 6 - Northern Iberian calcifuge *Nardus stricta* grasslands are distributed across the Pyrenean and Cantabrian ranges, mainly on siliceous bedrock (75% of the relevés), and include four relevés in the Central System (Figure 2). *Nardus stricta* has the highest frequency and *IndVal*, but other grassland species such as *Trifolium*

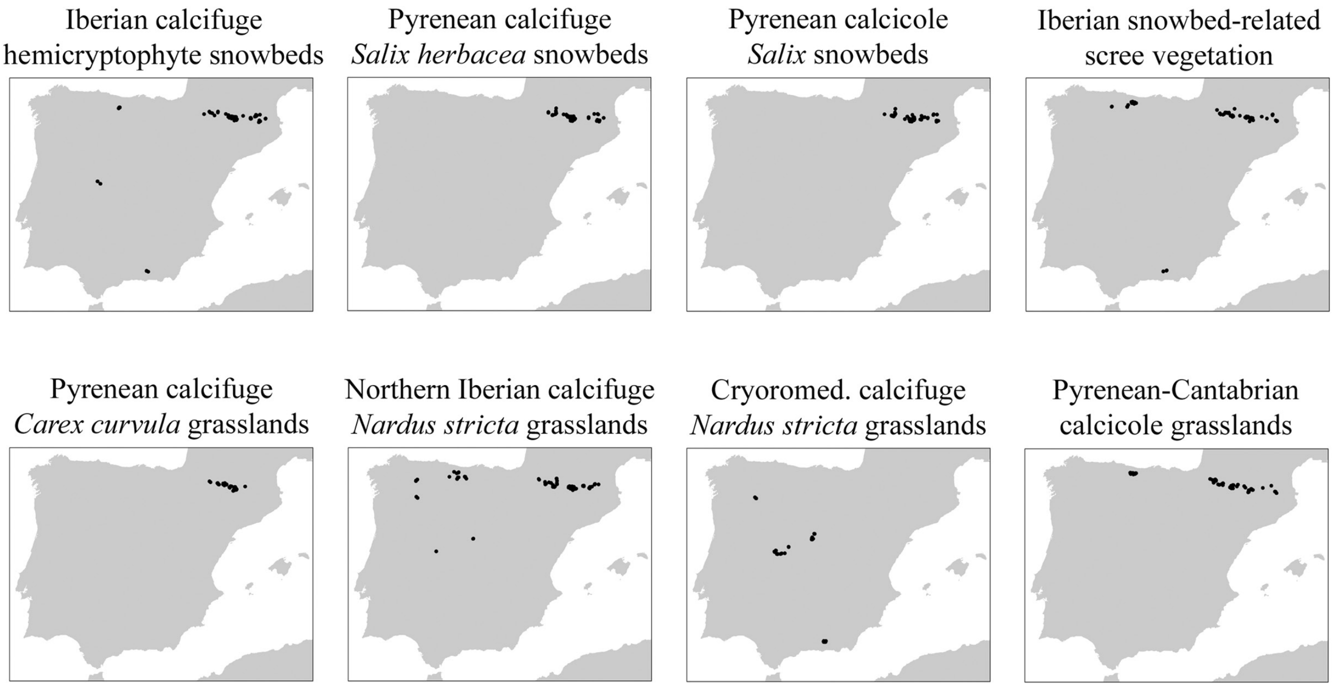


FIGURE 2 Distribution of the relevés assigned to each vegetation group in the Iberian Peninsula.

TABLE 1 Frequencies (in percentage) of snowbed specialists within the relevés of each vegetation group.

	Iberian calcifuge hemicryptophyte snowbeds	Pyrenean calcifuge Salix herbacea snowbeds	Pyrenean calcicole Salix snowbeds	Iberian snowbed-related scree vegetation	Pyrenean calcifuge Carex curvula grasslands	Northern Iberian calcifuge Nardus stricta grasslands	Cryromediter-raneancalcifuge Nardus stricta grasslands	Pyrenean-Cantabrian calcicole grasslands
Alchemilla fissa	13.9	12.0	5.1	4.3	2.8	4.2	–	1.5
Alchemilla pentaphyllea	–	–	–	–	–	3.4	–	–
Arenaria biflora	35.9	9.8	–	–	–	14.4	–	1.5
Cardamine bellidifolia alpina	71.3	28.3	0.9	2.9	4.2	25.4	–	0.7
Carex foetida	1.3	1.1	–	0.7	–	–	–	0.7
Carex lachenalii	0.4	–	–	–	–	–	–	–
Carex parviflora	1.3	21.7	64.1	9.4	5.6	–	–	27.2
Carex pyrenaica	63.7	39.1	3.4	0.7	15.5	45.8	–	5.1
Cerastium cerastoides	34.1	19.6	1.7	9.4	–	9.3	1.9	0.7
Epilobium anagallidifolium	34.1	3.3	0.9	42.4	–	1.7	–	0.7
Gnaphalium hoppeanum	–	1.1	5.1	12.2	–	–	–	10.3
Gnaphalium supinum	95.1	85.9	23.1	13.7	28.2	52.5	6.6	7.4
Lepidium hirtum stylatum	1.8	–	–	–	–	–	6.6	–
Luzula alpino-pilosa	47.5	25.0	–	4.3	12.7	2.5	–	–
Poa minor	–	–	–	7.9	–	–	–	0.7
Potentilla brauneana	0.4	3.3	10.3	–	2.8	2.5	–	11.8
Ranunculus alpestris	0.4	19.6	41.0	32.4	1.4	4.2	–	6.6
Salix herbacea	7.6	100.0	53.8	2.2	12.7	4.2	–	2.9
Salix reticulata	–	5.4	53.0	1.4	–	0.8	–	2.2
Salix retusa	–	–	53.0	3.6	1.4	0.8	–	1.5
Saxifraga androsacea	–	2.2	10.3	3.6	–	–	–	–
Saxifraga praetermissa	0.4	3.3	3.4	71.9	–	–	–	1.5
Sedum alpestre	42.2	43.5	2.6	5.0	39.4	7.6	–	–
Sedum candolleanum	68.6	12.0	–	0.7	–	8.5	20.8	–
Sibbaldia procumbens	43.0	63.0	14.5	3.6	49.3	17.8	0.9	7.4
Veronica alpina	71.8	51.1	9.4	32.4	11.3	11.0	1.9	5.1
Veronica aphylla	–	5.4	35.0	7.9	1.4	0.8	–	9.6

Note: Values higher than 25% are shaded light grey.

alpinum, *Plantago alpina* or *Meum athamanticum* also have high and significant values (Appendix S3). Many snowbed specialists appear in the group, among which *Carex pyrenaica* and *Gnaphalium supinum* are present in about half of the relevés (Table 1).

Group 7 - Cryoromediterranean calcifuge *Nardus stricta* grasslands are spread throughout central and southern Iberian ranges, and reach the southwestern edge of the Cantabrian Range (Figure 2), always on siliceous bedrock. Significant *IndVal* correspond exclusively to grassland species such as *Nardus stricta* — also indicative of the previous group, *Festuca iberica* or *Campanula herminii* (Appendix S3). Among snowbed specialists, *Lepidium hirtum* (subsp. *stylatum*, see Appendix S2) and *Sedum candolleanum* are the only species with relatively high *IndVal*, although only the latter is quite frequent in the relevés (Table 1). Other snowbed specialists are missing or very scarce.

Group 8 - Pyrenean–Cantabrian calcicole grasslands spread throughout the calcareous regions in the Pyrenees and the Cantabrian Range (Figure 2). A large number of grassland species have significant *IndVal* and high frequencies (e.g. *Festuca* gr. *rubra*, *Trifolium thalii*, *Erigeron alpinus*; Appendix S3), and three snowbed specialists also have relatively high values (*Carex parviflora*, *Potentilla brauneana* and *Gnaphalium hoppeanum*). Other snowbed specialists are uncommon or very uncommon (Table 1).

3.2 | Environmental variables

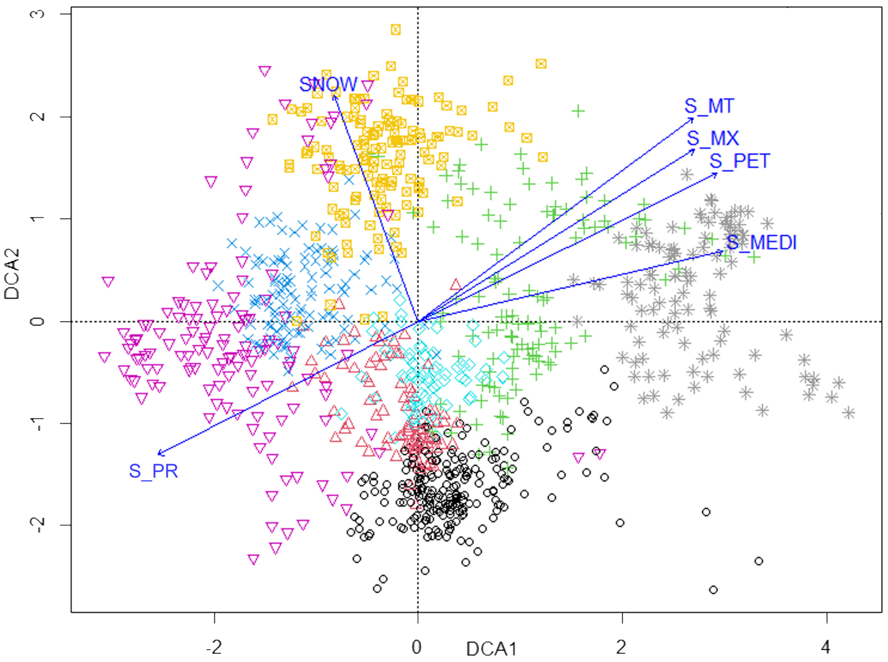
The DCA showed an increasing gradient of mediterraneity along axis 1 (Figure 3). The relevés corresponding to the group of cryoromediterranean *Nardus stricta* grasslands were clearly isolated from the rest of groups at the positive extreme of axis 1, where summer mean temperature and PET were the highest, and summer precipitation the lowest (Appendix S4). The four snowbed groups were at the opposite extreme, together with Pyrenean *Carex curvula* grasslands. The second axis of the DCA related to winter snow precipitation, which pointed towards the calcicole vegetation groups, located in the top-left quadrant. The angle bisectors of the two main DCA axes separated snowbed and grassland groups on the one hand, and calcifuge and calcicole vegetation groups on the other (Figure 3).

Eastern and Central Pyrenean relevés showed practically overlapping cluster centroids (Figure 3), indicating strong floristic similarity, close to the intersection point between the two DCA axes. These two regions had the lowest values of summer temperatures and PET, and the highest values of summer precipitation (Appendix S4). The centroids of Cantabrian and Western Pyrenean relevés were close to each other at the top-left DCA quadrant, characterized by the highest winter–spring precipitation (or snow). The relevés from the Central System and the Sierra Nevada were located at the positive extreme of the first DCA axis, where the highest values of summer mediterraneity and the lowest summer precipitation occurred in the Sierra Nevada, and the highest PET in the Central System (Appendix S4).

3.3 | Species richness

Total species pool was highest in the Pyrenean–Cantabrian calcicole grasslands ($n = 297$), and lowest in hemicryptophyte calcifuge snowbeds ($n = 97$, Appendix S5). These two vegetation groups also

(a) Ordination of relevés within vegetation groups



(b) Dispersion of relevés within mountain regions

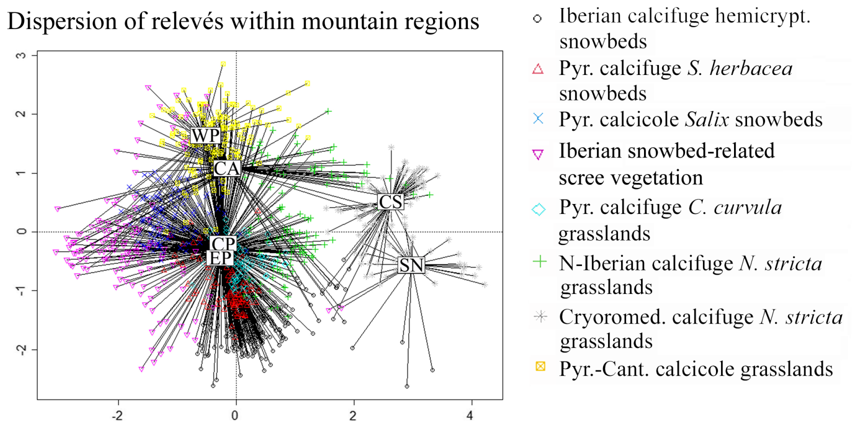


FIGURE 3 Distribution within the two first axes of the Detrended Correspondence Analysis (DCA) of the relevés (a) classified into chionophilous vegetation groups, with fitted environmental variables, and (b) in relation to the centroid of each mountain region. Eigenvalues of the DCA1 and DCA2 axes: 0.624 and 0.605, respectively. Environmental variables: S_MED, Summer Mediterraneity Index; S_MT, Summer Average Mean Temperature; S_MX, Summer Mean Maximum Temperature; SNOW, Precipitation from December to April; S_PET, Summer Potential Evapotranspiration; S_PR, Summer Precipitation. Mountain regions: CA, Cantabrian Range; WP, Western Pyrenees; CP, Central Pyrenees; EP, Eastern Pyrenees; CS, Central System; SN, Sierra Nevada.

showed the most contrasted species richness according to sample-based rarefaction curves (Figure 4), with 246 ± 8.3 and 94.9 ± 5.7 species, respectively.

At plot level, the richest relevés were those from Pyrenean–Cantabrian calcicole grasslands with 22.9 ± 5.7 species (Figure 5a, Appendix S5), whereas cryoromediterranean calcifuge *Nardus stricta* grasslands and snowbed-related scree vegetation had the lowest values (10.8 ± 4.2 and 11.5 ± 4.2, respectively). Total specialist species pool was around 20 in all snowbed groups, as well as in northern Iberian calcifuge *Nardus stricta* grasslands and in Pyrenean–Cantabrian calcicole grasslands. At plot level, hemicryptophyte and *Salix herbacea* calcifuge snowbeds were the richer (Figure 5a, Appendix S5). Cryoromediterranean *Nardus stricta* grasslands had the lowest values in all cases.

Speaking of geography, the Central Pyrenees accounted for the highest species pool ($n = 328$), whereas species richness according to sample-based rarefaction curves, and species richness at plot level were the highest in the Western Pyrenees (187.9 ± 4.1 and 20.5 ± 7.1, respectively; Figure 5b, Figure 6).

The smallest species pool was for the Sierra Nevada ($n = 85$), whereas the lowest species richness and at plot level were in thec Central System (78.0 ± 4.0 and 9.9 ± 2.9, respectively). Concerning snowbed specialists, the Central Pyrenees had the highest values in all cases ($n = 25$, 21.2 ± 1.2 and 4.6 ± 2.6), closely followed by the Eastern Pyrenees, whereas the lowest values were in all cases in the Central System, closely followed by the Sierra Nevada (Figure 5b, Figure 6, Appendix S5).

4 | DISCUSSION

4.1 | Iberian high mountains as refugia for chionophilous vegetation

The Pyrenees stand as one of the main southwestern European glacial refugia (Gentili et al., 2015a; Schmitt, 2017, etc.), and the main Iberian refugium for snowbed specialists, particularly its central and eastern regions. Their proximity to the Alps and the French Central Massif (about 350 and 250 km, respectively) likely allowed for a higher immigration of arctic–alpine species — and snowbed specialists — than in the other and more isolated Iberian high mountains (Loidi et al., 2015). Some of these arctic–alpine species currently find their southwesternmost distribution limit in the Pyrenees, where they shape strictly Pyrenean chionophilous vegetation groups within the Iberian context such as calcifuge and calcicole *Salix* snowbeds, or *Carex curvula* grasslands, also present in other European alpine regions (Mucina et al., 2016). However, the intermediate geographical situation of the Pyrenees between the Alps and the other Iberian high mountains, results in the presence of a high number of species from different source floras (Comes & Kadereit, 2003; Loidi et al., 2015), which at present confer the highest species richness to the Pyrenees, not only at species level but also when considering the number of chionophilous vegetation groups. Indeed, the Pyrenees show floristic connections to the other Iberian high mountains, stronger or weaker depending on the length of the migratory routes during the Pleistocene (Loidi et al., 2015; Jiménez-Alfaro et al., 2021), which result in shared vegetation groups (i.e. snowbed-related scree vegetation, calcifuge hemicryptophyte snowbeds, and northern Iberian calcifuge *Nardus stricta* and calcicole grasslands). Despite the clear floristic relationship between the Pyrenees and the Cantabrian Range, which is higher than to any other Iberian high-mountain ranges (Jiménez-Alfaro et al., 2021), the absence of some snowbed groups in the Cantabrian Range and the intermediate number of snowbed specialists in the Cantabrian relevés are indicators of a certain degree of biogeographic isolation (Schmitt, 2017; Jiménez-Alfaro et al., 2021). These indicators highlight the more relict situation of chionophilous vegetation there, and particularly snowbed vegetation, when compared to the Pyrenees. It is interesting to note here the high floristic affinity between the Cantabrian Range and the Western Pyrenees (Figure 3), concerning not only the richness of snowbed specialists, but also the lack of the same vegetation groups. Their similar elevations and their oceanic climate, together with their geographical proximity, could explain their similarity (Jiménez-Alfaro et al., 2021), although the steep slopes of Western Pyrenean rarefaction curves (Figure 4) suggest that this region could provide higher species and specialist richness if more sampling effort was performed there.

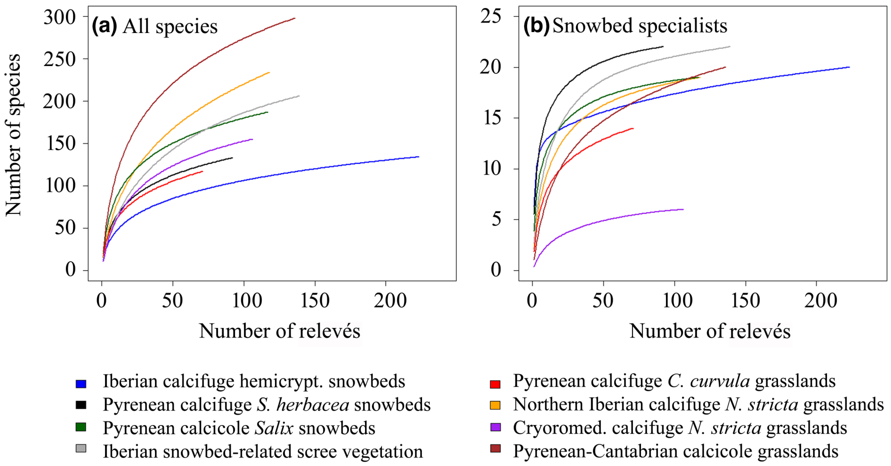


FIGURE 4 Rarefaction curves of (a) all plant species, and (b) snowbed specialists by vegetation group.

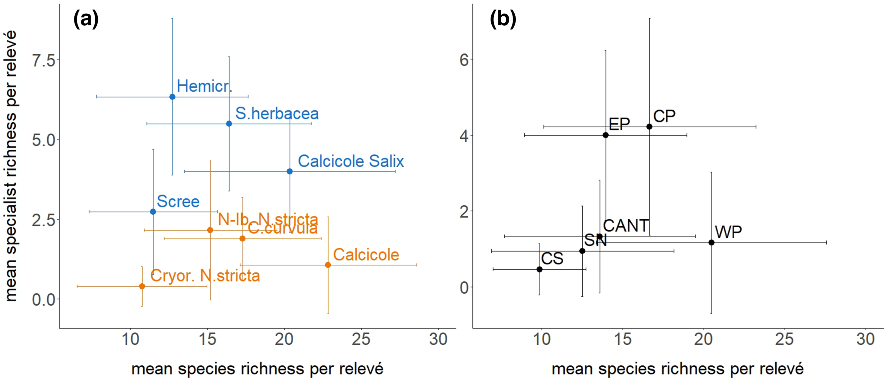


FIGURE 5 Relation of the mean species richness and the mean snowbed specialist richness per relevé for (a) each vegetation group, and (b) each mountain region. Standard deviations are represented for both means. Snowbed groups are represented in blue, grassland groups in orange. Mountain regions: CANT, Cantabrian Range; WP, Western Pyrenees; CP, Central Pyrenees; EP, Eastern Pyrenees; CS, Central System; and SN, Sierra Nevada.

In the central and southern Iberian ranges, the low number of snowbed specialists and the residual occurrence of snowbed vegetation evidence the magnitude of their geographic isolation, and highlight an extremely relict situation for these species and vegetation types. There, the scarce and scattered snowiest areas are mainly occupied by cryoromediterranean *Nardus stricta* grasslands, the unique vegetation group not found in the Pyrenees. Indeed, the isolation of these ranges, together with the high summer mediterraneity and PET and the low summer precipitation, not only limit the diversity of cold-adapted species (Loidi et al., 2015), and particularly, snowbed specialists, but also translate to the low floristic affinity with northern Iberian high mountains (Figure 3; Jiménez-Alfaro et al., 2021). Moreover, their geographic isolation and current climatic conditions result in low overall species richness within the Iberian chionophilous context, counterbalanced to some extent by a high endemicity, especially in the Sierra Nevada (Blanca et al., 1998; Kropf et al., 2006; Loidi et al., 2015).

4.2 | Contrasting species richness among chionophilous vegetation groups

Snowbed groups hosted a high specialist richness not only at group level but also at plot level, as their presence and abundance rely on a long-lasting snow cover (Björk & Molau, 2007), which is the highest in snowbeds. That high specialist richness was not paired, however, with a high overall species richness, and snowbed groups accounted for intermediate to low values, evidencing the constraining conditions for plant growth imposed by a long duration of snow cover (Körner, 2003). However, Pyrenean *Carex curvula* grasslands and cryoromediterranean *Nardus stricta* grasslands also accounted for very low species richness. Thus, the reported negative relation between snow cover duration and species richness (Virtanen et al., 2003; Schöb et al., 2009) is not clearly evidenced within the context of Iberian chionophilous vegetation. We may attribute these low values in the mentioned grassland groups to the environmental extremes where they both occur (Vonlanthen et al., 2006). On the one hand, *Carex curvula* grasslands endure similar environmental conditions to snowbed groups, resulting in a relatively high floristic similarity to them and also in a low species richness. On the other hand, cryoromediterranean grasslands provide an environmental limit related to summer drought, which constrains the occurrence of cold-adapted flora (Loidi et al., 2015; Jiménez-Alfaro et al., 2021) mainly in the Central System and Sierra Nevada, and translates not only to a reduced snowbed specialist species pool, but also to low overall species richness.

The milder climatic conditions found in northern Iberian *Nardus stricta* grasslands and in Pyrenean–Cantabrian calcicole grasslands may result in their highest species pool sizes (Virtanen et al., 2003; Vonlanthen et al., 2006). Moreover, these two grassland groups host overall an unexpectedly high number of snowbed specialists, although only a few are relatively frequent (e.g. *Carex parviflora*, *Carex pyrenaica* or *Gnaphalium supinum*). Nevertheless, at plot level the number of specialists is very low or they are even absent, evidencing the less favourable conditions for them in these grasslands, probably related to a combination of environmental constraints and competitive interactions with grassland species. However, microtopographic heterogeneity in the larger areas occupied by chionophilous grasslands — when compared to snowbed vegetation patches — may provide scattered favourable microhabitats for snowbed specialists (Schöb et al., 2008), translating to that high specialist richness at group level.

4.3 | Chionophilous grasslands: A terminal refuge for snowbed specialists?

In the current context of climate change, a reduction of snowbed specialists has already been reported throughout Europe at their lower elevational limits (Klanderud & Birks, 2003) or along the snowmelt gradient (Matteodo et al., 2016), together with an expansion of grassland species in snowbeds (Illa et al., 2019; Palaj & Kollár, 2019). Indeed, dominant or frequent alpine species in some chionophilous grasslands such as *Nardus stricta*, *Poa alpina* or *Scorzoneroides pyrenaica*, have increased their frequency in Pyrenean snowbed vegetation patches over the last years (Illa et al., 2019). These species, which have an active clonal growth and occur with relatively high frequencies in some Iberian snowbed groups (Appendix S3), may easily outcompete the mostly tiny snowbed specialists once established into a snowbed vegetation patch. However, despite the lower competitive ability of snowbed specialists (Schöb et al., 2008), our data showed that many of them persist in the northern Iberian chionophilous grasslands, and some of them with relatively high frequencies (e.g. *Gnaphalium supinum*, *Sibbaldia procumbens*, *Carex pyrenaica*). Consequently, although

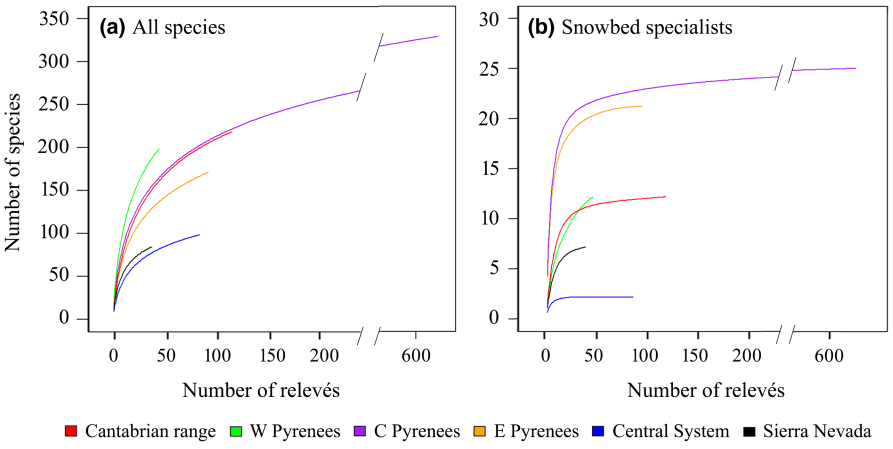


FIGURE 6 Rarefaction curves of (a) all plant species, and (b) snowbed specialists by Iberian high-mountain regions.

the observed decreasing trend of snowpack accumulation (Morán-Tejeda et al., 2013) may favour the colonisation of snowbed communities by grassland species, even entailing the disappearance of many snowbed vegetation patches, we suggest that Pyrenean and Cantabrian chionophilous grasslands may represent a terminal refuge for many snowbed specialists in the short or medium term. This is in line with the predictions of Schöb et al. (2009) for snowbed species in the Alps, who suggest that with an increase of the length of the growing season, the set of dominant specialists may become less abundant but may coexist with grassland species, whereas the set of non-dominant specialists highly dependent on a long-lasting snow cover will almost disappear. In this sense, we highlight the high sensitiveness of some snowbed species currently very scarce or absent in northern Iberian chionophilous grassland groups, such as *Alchemilla pentaphyllea*, *Alchemilla fissa*, *Saxifraga androsacea* or *Saxifraga praetermissa*, which may be the most affected by climate change.

In cryoromediterranean grasslands, however, the situation of snowbed specialists is critical, as except for vthe relatively frequent Iberian endemic *Sedum candolleanum*, only a much reduced number of specialists occurs there occasionally. Actually, in central and southern Iberian ranges these species are almost exclusively restricted to the scarce snowbed vegetation patches, the unique environments where they find suitable conditions to survive. Taking into consideration the predicted snowfall reduction during the next decades (Pérez-Palazón et al., 2018), and that noticeable effects of climate change have already been reported in alpine grasslands of the Central System (Jiménez-Alfaro et al., 2014), we consider that local extinctions are likely to occur in the short term, and may be more frequent as temperatures kees rising and snowpack duration shortens.

Not only snowbed specialists, but also species from chionophilous grasslands may be affected by climate change. However, the contrasted sets of species shaping northern and southern Iberian grasslands, currently adapted to different environmental conditions, may respond differently to changing climate. Then, the previously suggested role of northern Iberian grasslands as refuge for snowbed specialists should be handled with caution, depending on how their composition and structure are more or less affected in the near future.

5 | CONCLUSIONS

The Pyrenees, and especially the Central and the Eastern Pyrenees, represent the main glacial refugia for snowbed communities and specialists within Iberian high-mountain regions, as they hold their maximum richness and frequency, and host all snowbed groups and almost all the groups of chionophilous grasslands. Snowbed groups, mostly restricted to northern Iberian mountains, are characterized by their higher number and frequency of specialists compared to chionophilous grasslands, especially at plot level. However, the long snowpack duration restricts species richness in snowbeds, resulting in poor vegetation types rich in specialists. Not only snowbeds, but also grassland groups enduring harsher environmental conditions in terms of longer snow cover duration and colder temperatures (i.e. Pyrenean *Carex curvula* grasslands), or higher summer mediterraneity and PET (i.e. cryoromediterranean *Nardus stricta* grasslands), have low values of species richness. Indeed, in those Iberian high-mountain regions with higher summer drought (Sierra Nevada and the Central System), snowbed vegetation is nearly absent and hosts species-poor communities with a particularly reduced pool of snowbed glacial relicts, which mostly occur at very low frequencies.

Under the current context of climate change, southern European snowbed vegetation patches are expected to be colonized to some extent by grassland species or even disappear. However, the fact that Pyrenean and Cantabrian chionophilous grassland groups host a large number of snowbed specialists, some of them at high frequencies, lets us suggest that they may act as terminal refuge for these glacial relicts, where they may persist at least in the short–medium term. On the contrary, we highlight the sensitiveness of these species in central and southern Iberian ranges, where the reduction or the disappearance of snowbed vegetation patches may lead to local extinctions, as cryoromediterranean *Nardus stricta* grasslands would not provide shelter to them.

Given this situation, we stress the necessity to assess the current status of chionophilous vegetation in the Iberian Peninsula, taking into consideration that many of the relevés used for the analyses date from the last half of the 20th century. Indeed, an accurate resampling of the existing relevés would be necessary, which in addition would demonstrate the magnitude of the changes in species composition that have occurred during the last decades, as reported in other mountain ranges for similar periods of time (e.g., Matteodo et al., 2016; Palaj & Kollár, 2019).

AUTHOR CONTRIBUTIONS

Estela Illa and Aaron Pérez-Haase conceived of the idea; Estela Illa, Rainer Brufau and Xavier Font gathered the relevés; Estela Illa and Rainer Brufau processed data; Estela Illa, Aaron Pérez-Haase and Rainer Brufau performed the statistical analyses; Estela Illa, Aaron Pérez-Haase and Rainer Brufau wrote the manuscript; all authors discussed the manuscript.

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DATA AVAILABILITY STATEMENT

Among the 1002 relevés used for the analyses, those extracted from the SIVIM database are available in Appendix S6. The remaining 208 unpublished relevés, and the code used, are available upon request.

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SUPPORTING INFORMATION

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

Appendix S1. List of alliances and associations selected.

Appendix S2. List of snowbed specialists.

Appendix S3. Indicator values and frequency of the species in the vegetation groups.

Appendix S4. Environmental variables.

Appendix S5. Species richness values of vegetation groups and mountain regions.

Appendix S6. Table with the publicly available relevés used in the analyses, extracted from the SIVIM database (794 relevés), in csv format.

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