


Living at the limit in the Pyrenees: Peripheral and endemic plants are rare but underrepresented in protection lists

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Abstract

Aim: Mountains shelter high biological diversity and constitute both important barriers and confluence areas for species. They often contain species whose populations occur at their range limit (peripheral species), which according to the “Centre-Periphery” hypothesis (CPH) are expected to occur in marginal environments, exhibit low abundance and consequently high vulnerability. Our study investigates this hypothesis for the flora of the Pyrenees, a biogeographical crossroads containing a large proportion of the total European plant diversity.

Location: Pyrenees.

Methods: We determined whether more than 2600 native plant species were endemic to the Pyrenees or found at the centre or periphery of their whole distribution range within the mountain chain. We then compared the ecological preferences, local and regional abundance, and conservation status among central, peripheral and endemic species.

Results: A quarter of the flora was found at its geographic range limit within the Pyrenees. Endemic and peripheral species were more likely to be soil specialists in alpine grasslands and rocks, and exhibited smaller regional ranges than central species, but their local abundance did not tend to differ. Peripheral species at their southern range edge were more widespread regionally than at their northern range edge. Peripheral taxa were more prevalent in the Pyrenean red list of threatened species (55%) compared to national and regional protection lists (40% and 31%, respectively).

Main conclusions: Peripheral species contribute substantially to the diversity of the Pyrenean flora. They follow the predictions of the CPH given their occurrence in scarce habitats, their low regional abundance and their high vulnerability according to the Pyrenean red list, although they tend to show similar local abundances as other species and are infrequent in protection lists. Integrative and cross-border assessments of the ecology and rarity of mountain floras provide better estimates of their vulnerability and ensure more efficient prioritization of their conservation.

KEYWORDS

abundance, centre-periphery hypothesis, conservation status, endemic, habitat, mediterranean, range margins, rarity, red list, widespread

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1 | INTRODUCTION

Ongoing global change is having unprecedented consequences on biodiversity (Corlett, 2015; Pereira et al., 2012), and conservation biologists often focus on assessing and forecasting biodiversity loss to prioritize areas and species for urgent preservation due to limited resources (Pelletier et al., 2018). In this context, determining the relationship between local species extinction risk or vulnerability and both intrinsic (e.g. demographic characteristics such as small population size) and extrinsic factors (e.g. deterministic human-induced drivers) is of high value for more effective conservation planning (Darbyshire et al., 2017; Wilson et al., 2005).

Comprehensive cross-species studies often highlight an important association between extinction risk and different measures of rarity. For instance, species with larger geographic ranges have been shown to persist for longer periods (Harnik et al., 2012; Purvis et al., 2000), extinct species have often been observed to be formerly endemic (Fontaine et al., 2007), and small-sized populations have been associated with lower probabilities of survival (Matthies et al., 2004). However, most species are rare and only a few are widespread, especially across plants (Enquist et al., 2019), which makes it difficult for conservationists to identify the most vulnerable taxa and then to prioritize conservation actions accordingly. Moreover, rarity can be measured at different scales and using different metrics, such as species geographic range size that reflects the extent of occurrence across space, or the number or density of individuals found at a given place (i.e. local abundance) (Rabinowitz, 1981). These different forms of rarity may not systematically covary across species (e.g. both species with large and small geographic ranges can exhibit either high or low local abundance (Boulangeat et al., 2012; Lesica et al., 2006; Mills & Schwartz, 2005), and their contribution to extinction risk can differ depending on the organism and region considered (Harnik et al., 2012). Given the wide range of threats that species and populations can face, identifying groups of species exhibiting different forms of rarity is particularly relevant when assessing vulnerability and setting conservation priorities across large and diverse areas (Kunin & Gaston, 2012; Rabinowitz, 1981).

Species can also be impacted differently by global change depending on the habitat, bioregion or elevation zone that they inhabit (Leidner & Neel, 2011; Pauli et al., 2012). Mountain regions are particularly sensitive, as evidenced for example by the accelerated changes in plant richness observed in Europe over the last decades as a consequence of global warming (Gottfried et al., 2012; Steinbauer et al., 2018). Range limits of many low-elevation plant species of the Alps have shifted upslope faster than high elevation species, posing a competitive threat to the latter (Rumpf et al., 2018). Land use change has also a major impact on the persistence of biodiversity (Newbold et al., 2015). For example, a study conducted in southern France spanning more than a hundred years highlighted that local persistence of rare species was related to topography and land use, and that Eurosiberian rare species exhibited higher extinction rates than endemics and other rare Mediterranean species (Lavergne et al., 2005a, 2005b). Thus, accounting not only for species rarity,

but also for the possibility that extrinsic factors such as climate or land cover change could affect populations differentially across habitats is paramount to assess species vulnerability.

Because species are distributed across diverse and distinct geographic and ecological gradients, their populations will experience a variety of evolutionary and ecological constraints, and threats. The “centre-periphery” hypothesis (CPH) proposes that environmental conditions become progressively harsher from the centre towards the periphery of species ranges and that, consequently, their abundance follows the same decreasing pattern (Brown, 1984; Hengeveld & Haecck, 1982). The assumed lower habitat suitability and higher isolation in peripheral populations are subsequently predicted to reduce their overall performance (Pironon et al., 2017; Sexton et al., 2009). Within plant communities, species occurring at their limit of distribution (hereafter, “peripheral species”) are also expected to exhibit lower demographic performance and be more vulnerable compared to species closer to their range centre (“central species”) (Gotelli & Simberloff, 1987). However, many empirical studies contested the predictions of the CPH (Dallas et al., 2017; Pironon et al., 2017; Santini et al., 2018, but see Osorio-Olvera et al., 2020), and others emphasized the need to consider the specificities of different margins of a given species range, such as the rear- versus leading-edges (Hampe & Petit, 2005; Rumpf et al., 2019) or geographical versus ecological versus historical peripheries (Pironon et al., 2015). Moreover, local extinctions have not always been shown to be more frequent at the edge of species ranges (Boakes et al., 2018; Channell & Lomolino, 2000), which shows the complexity of forecasting peripheral species’ vulnerability. Even though the CPH has been extensively investigated across populations of given species (Pironon et al., 2017), little is known about the environmental and demographic characteristics, and conservation status, of species found at their distribution limit within vast territories, which is crucial for assessing the vulnerability of entire floras.

The Pyrenees is one of the largest and highest European mountain chains, containing about 3600 autochthonous vascular plant species (Gómez et al., 2017) (about one third of the total European flora according to Tutin et al. 1964-1980; or one fourth according to other recent estimations: <https://biodiversity.europa.eu/topics/species/vascular-plants>). Such biodiversity arises as a result of the combination of historical events, complex topography and particular geographical location at the crossing of two biomes (Mediterranean forests, woodlands and scrub, and temperate broadleaf and mixed forests; Figure 1). This biogeographical crossroads shelters not only endemic taxa but also many peripheral populations of more widespread species, including the southern-most populations of Boreoalpine and Eurosiberian species, and the northern-most populations of many Mediterranean species (Figure 1; Abeli et al., 2018; Gómez et al., 2017). The Pyrenees are also among the most impacted regions by ongoing climate and land use changes in Europe (Engler et al., 2011; Lasanta-Martínez et al., 2005; Pauli et al., 2012; Steinbauer et al., 2018). Given global change may affect peripheral populations disproportionately (Hampe & Petit, 2005), it is critical to assess their potential vulnerability in order to preserve

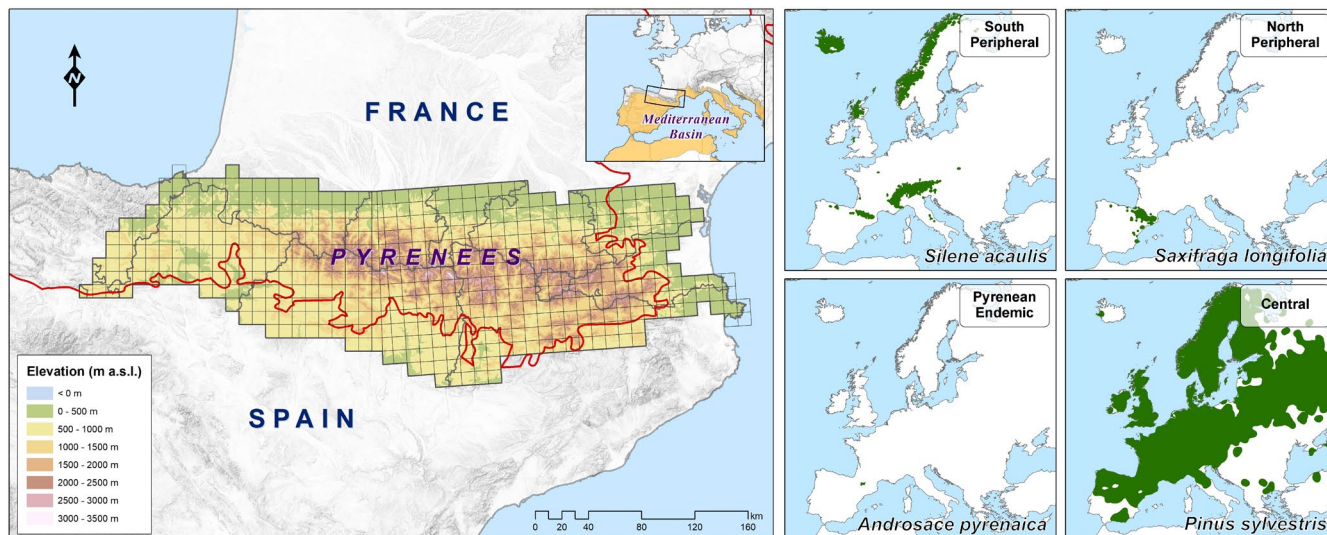


FIGURE 1 The Pyrenean mountain range, a biogeographical crossroads for central, peripheral and endemic species. The left panel represents the study area divided by 10 km × 10 km grid cells. The red line represents the boundary between two biomes according to Dinerstein et al. (2017). The right panel provides examples of distribution of central, peripheral and endemic species of the Pyrenees. Central species are found beyond both the northern and southern sides of the Pyrenees. Peripheral species do not extend latitudinally beyond one of the sides of the Pyrenees. Endemic species do not extend beyond either side of the Pyrenees. We also distinguished southern peripheral species (i.e. species not occurring at lower latitudes than the Pyrenees) from northern peripheral species (i.e. species not found at higher latitudes)

plant diversity, especially in biogeographical crossroads such as the Pyrenees (Spector, 2002).

Following the predictions of the CPH, we tested whether peripheral species of the Pyrenees are found in marginal habitat conditions, exhibit low abundance and thus are of higher priority for conservation. We first compared environmental preferences and abundance across three groups of plant species: (i) species found beyond both the northern and southern sides of the Pyrenees (i.e. central species), (ii) species that do not extend latitudinally beyond one of the sides (i.e. peripheral species) and (iii) species that do not extend beyond either side (i.e. endemics) (see examples in Figure 1). Considering that future climate change will presumably impact species differently at different range margins (Hampe & Petit, 2005; Rumpf et al., 2019), we also compared patterns between peripheral species not occurring at lower latitudes than the Pyrenees (i.e. southern-peripheral species; hereafter SP) and those not found at higher latitudes (i.e. northern-peripheral species; hereafter NP). Finally, we tested whether peripheral and endemic species are more prevalent within lists of priority species for conservation at different spatial and administrative scales, and discussed their importance for the preservation of the Pyrenean flora.

2 | METHODS

2.1 | Study area

The Pyrenean mountains constitute a natural border between Spain and France, where two large biomes converge (Figure 1). They extend for 50,000 km² along a 430 km West-to-East axis with a

North-to-South width ranging from 50 to 100 km. The territory presents a highly contrasting relief with more than 200 peaks reaching altitudes higher than 3000 m.a.s.l. The climate is very diverse due to the topography and the influence of the Atlantic Ocean in the West, and Mediterranean Sea in the East. The history of the mountain range is complex: it starts with the compression of the European and African plates, and results in three current sectors differentiated in terms of climate, topography, geology and vegetation (see details in Gómez, García, et al., 2017).

2.2 | Study species

All species records presented in this study, as well as their regional abundance estimates and ecological preferences were collected via a European project involving more than 35 scientists from 12 academic institutions of all French, Spanish and Andorran Pyrenean regions: the Atlas of the Flora of the Pyrenees (hereafter, FLORAPYR; <http://www.atlasflorapyrenaea.eu>). FLORAPYR divides the study area into 519 UTM grid cells of 10 km x 10 km (~50,000 km²; Figure 1) and compiles approximately 2,000,000 occurrence records (i.e. presence of a species within a given grid cell) for more than 4000 vascular plant taxa (see more details in Gómez, García, et al., 2017).

For this study, we first discarded all non-native plant taxa identified in the FLORAPYR database (<http://www.atlasflorapyrenaea.eu/src/taxon/index.php?idma=11>), given that recently introduced species could exhibit different geographic, ecological, and abundance patterns, and they are of low concern for conservation. Then, to reduce potential biases caused by taxonomic inflation, potential

misidentifications or incomplete knowledge of distribution, we removed taxa with taxonomic conflicts or uncertainty (e.g. apomictic taxa like the genus *Hieracium*). We also restricted our analyses to the species-level by combining data of all subspecies into their corresponding species. To focus solely on the mountain flora and avoid inclusion of coastal species, we removed species whose entire Pyrenean range was found below 500 m.a.s.l. (i.e. any species with its highest occurrence record found below this elevation). A total of 2682 species were finally used for subsequent analysis, which corresponds to about 85% of the 3170 native species occurring above 500 m of altitude.

Based on occurrence records of each species in FLORAPYR, and confirmation from the literature when necessary, we assessed whether each species was found elsewhere further North and further South of the Pyrenees (i.e. "central species"), occurred at the latitudinal limit of its distribution in the Pyrenean range (i.e. "peripheral species"), or strictly within the Pyrenees (i.e. "endemic species"). Within peripheral species, we distinguished those that are found further South of the Pyrenees (NP) from those occurring further North of the Pyrenees (SP).

Each species was also assigned to a chorological group by the FLORAPYR experts according to six categories: endemic to the Pyrenees, Arctic and Boreoalpine (i.e. species found in arctic and boreal regions at higher latitudes; hereafter "Boreoalpine"), Alpine (i.e. species present at the alpine level of other European mountains such as Sierra Nevada, Cantabrian range, Alps, Balkan or Carpathian Mountains, but absent from arctic and boreal regions), Eurosiberian (i.e. species present in temperate regions North of the Pyrenees, and not restricted to alpine and boreal regions) and Mediterranean. Species found across several chorological groups and diverse areas of the world were considered widespread.

2.3 | Ecological variables

We tested the assumption of the CPH by assessing whether peripheral species were mainly found in marginal environments such as high/low elevations, highly disturbed or undisturbed land cover types and specialized soil substrates. First, each of the 2682 species was assigned to one of four vegetation belts based on its position across the elevational gradient according to FLORAPYR, and as defined specifically for the Pyrenees by Engler et al. (2011): colline (<500 m), montane (500 m–1800 m), subalpine (1800–2300 m) or alpine (>2300 m). Contrary to species elevational range, which reflects their geographic range extent, species position along the elevational gradient is rather associated with their climatic preferences (Steinbauer et al., 2018). Habitat type was defined by the FLORAPYR experts according to six general classes: anthropic (i.e. areas that are cultivated or highly disturbed by humans), wetland, forest, shrubland, grassland and rocks. Although some species can occur in more than one category, for this study we only considered the one in which most occurrence records were found according to experts, to standardize classification across species and

minimize errors related to less common habitat classes. Species were also assigned a soil type preference according to the following four classes: saline soil specialists (gypso- and halo-phyte), acidophyte, basophyte or indifferent (i.e. soil generalists occurring on different soil types).

2.4 | Abundance

Following the predictions of the CPH, we then tested whether peripheral and endemic species of the Pyrenees had lower continental, regional and local abundance than central species. To have a broad estimate of the continental abundance of each species (hereafter "European range size"), we extracted the number of European countries that they occupy from the *Atlas Flora Europaea* (AFE; Kurtto et al., 2013). However, please note that each European country has a different extent and mountainous area, so that several species occupying many countries might indeed have relatively small range sizes, or vice-versa. Second, this estimate does not represent the total range size of each species given that some might reach non-European regions (e.g. Africa, Asia). Yet, despite the accuracy of such estimation being limited, it is the best current option available to provide a coarse estimate of the continental range size of all Pyrenean species used in this study (but see Sabatini et al., 2021 for other recent estimates).

Different measures of species regional abundance were extracted from FLORAPYR. The first regional abundance measure refers to the total number of 10 km × 10 km grid cells occupied by the species within the Pyrenees (hereafter "Grid-based abundance"). Second, each species was assigned a regional abundance value by FLORAPYR experts within each of six regions of the Pyrenees (i.e. South-West, -Central, -East and North-West, -Central, -East) according to the following rank order: (1) very rare, (2) rare, (3) scarce, (4) frequent, (5) common and (6) very common. We then averaged values across the six regions where the species was present to get a continuous measure of regional abundance (hereafter "Expert-based abundance"). Finally, we also obtained the elevational range of each species (hereafter "Elevational range") by subtracting their lowest elevation of occurrence by their highest from FLORAPYR. While the two previous indices provided regional abundance estimates across the geographical space (i.e. longitude and latitude), this measure relates to species regional abundance along the elevational dimension.

While regional abundance provides an estimate of the area covered by all populations of a given species within the Pyrenees, local abundance relates to the average size of all known populations of that same species. The latter was estimated based on expert knowledge of the authors for half of the dataset: 1398 species occurring in the South-Central part of the Pyrenees (Aragon region, Spain). Only species from this region were assessed because this is one of the richest and most intensively prospected areas of the Pyrenees, where local botanists have regularly conducted inventories of plant communities and have assembled detailed expert knowledge of population sizes for the plant species occurring there.

Each species was assigned to an average population size class out of the three following: (1) few plants or groups, estimated as less than 25–30 individuals (i.e. low abundance), (2) up to a hundred plants (i.e. medium abundance), (3) hundreds to thousands of plants (i.e. high abundance). Although plots or transects could provide finer estimates, those were not available at such large taxonomic and geographic scales. Thus, we kept our estimate consistent across species as recommended in the literature (Reisch et al., 2018) by considering a unique population size index and the expertise of botanists of the Pyrenean region.

2.5 | Conservation status

To assess whether peripheral and endemic species represent higher priorities for conservation, we reviewed the official lists of endangered and threatened plants in each Pyrenean region (Aquitaine, Midi-Pyrenees, Languedoc-Roussillon, Pyrenees-Atlantiques, Hautes-Pyrenees, Ariège and Haute-Garonne in France, and the Basque Country, Navarra, Aragon, and Catalonia in Spain) and country (France and Spain national lists). As each region and country has its own official criteria and terms to identify priority taxa for protection, we focused on the endangered and threatened categories (in risk of extinction, critically endangered, endangered, vulnerable, sensitive to habitat disturbance and strictly protected), while leaving aside categories of less concern (of special interest, rare and harvesting under authorization). Each Pyrenean species was then checked against official lists (Appendix S1) and classified as protected or not, both at national and regional levels. In addition, we assessed the conservation status and threat level of species of the Pyrenees according to the recent Pyrenean red list (https://www.opcc-ctp.org/sites/default/files/editor/florapyr_liste_rouge_fr.pdf). Contrary to regional and national lists, this red list was built by members of the FLORAPYR consortium following the classical IUCN criteria and considering the whole Pyrenean flora and territory. Because we worked at a species level and these lists can include subspecies, we considered Pyrenean species to be under protection when at least one of their subspecies was listed in the catalogue. Thus, we consider as protected those species whose Pyrenean populations are either fully (species level) or partially (at least one subspecies) catalogued.

2.6 | Analyses

We assessed central, peripheral and endemic species ecological variables using a Multiple Correspondence Analysis (MCA). The species restricted to saline soil were discarded given their low sample size. Environmental categories were transformed into dummy variables, which acted as active variables, and all species as active individuals. Categories related to species' position within the range (i.e. central, peripheral and endemic species) were then represented as supplementary variables in this environmental space. This analysis was performed using the *FactoMineR* package (Lê et al., 2008) in R [4.1.0] (R Core Team, 2021).

We then used a Principal Component Analysis (PCA) and a correlation matrix (Spearman coefficient) to analyse associations among the three measures of regional abundance (grid-based abundance, expert-based abundance, elevational range). Given that the three variables were positively correlated and well summarized by the first axis of the PCA (77% of variance explained; see Appendix S2), we considered the scores of each species on this first axis as a composite variable, later called "Regional abundance." This new variable therefore represents a comprehensive measure of occupancy in the Pyrenees along longitudinal, latitudinal and altitudinal axes, which follows recent conservation advances to integrate the altitudinal ranges of species in distribution assessments (Brooks et al., 2019; Jung et al., 2021). The PCA was performed using the *ade4* package in R (Thioulouse et al., 1997).

We compared means of regional abundance and European range size between central, peripheral and endemic species by performing Kruskal–Wallis tests and *post hoc* tests for multiple comparisons with a Holm correction using the *kruskalmc* function of the *pgirmess* package in R (Giraudeau et al., 2018). Given that the frequency of plants of different chorological groups, and the availability of their suitable habitat in the Pyrenees may vary considerably, we repeated this mean comparison for each chorological group separately.

Frequencies of central, peripheral and endemic species were compared across the Pyrenean flora, local abundance categories and conservation status using chi-square tests (*chisq.test* function in R) and the Cramer's V index as a measure of the effect size (*cramersV* function from the R package *Isr*) (Navarro, 2015).

3 | RESULTS

One fourth of the Pyrenean flora (638 out of the 2682 species analysed; 24%) was found at the edge of its geographic range in the Pyrenees, whereas only 84 species (3%) were strict Pyrenean endemics. Forty-four percent of the 638 peripheral species occurred in the Pyrenees as NP, whereas 56% were found as SP.

3.1 | Ecological variables

Grasslands exhibited the highest species richness and contained large fractions of all central (27%), peripheral (36%) and endemic species of the Pyrenees (26%; Appendix S3-4). Central species were mainly soil generalists that are common at low elevation, mainly in anthropic habitats, wetlands and forests. On the contrary, peripheral and endemic species were rather soil specialists, found at higher elevation in alpine grasslands and rocks. NP taxa contained many basophytes and were commonly found in grasslands, shrublands and rocks across the elevation gradient. SP species contained proportionally more acidophytes than NP and were more likely to be found in wetlands, grasslands, forests and rocks at higher elevation (Figure 2).

3.2 | Abundance

From the 2682 species analysed, we found that central species had a larger European range size than peripheral species (Appendix S5; Kruskal–Wallis test: $X^2 = 59.93$, $df = 2$, $p < .001$).

Central species also had a significantly higher regional abundance within the Pyrenees than peripheral (both NP and SP) and endemic ones (Figure 3; Kruskal–Wallis test: $X^2 = 269.74$, $df = 3$, $p < .001$). However, regional abundance did not differ significantly between NP, SP and endemic species. When examining the effect of species' chorological groups, we found that the pattern held: central Mediterranean, Eurosiberian, Alpine and Boreoalpine species systematically occupied more space than peripheral species of the same chorological group (Figure 4; Kruskal–Wallis test: $X^2 = 407.26$, $df = 9$, $p < .001$). Endemic species occupied as much space as peripheral species of all chorological groups, whereas widespread species exhibited the highest regional abundance together with the central Eurosiberians.

Based on the 1398 species analysed in the South-Central Pyrenees, we found that local abundance of central, peripheral (both NP and SP) and endemic species did not differ significantly (Figure 5; Chi-squared test: $X^2 = 10.10$, $df = 6$, $p = .12$, *Cramer's V* = 0.06). Local abundance did not differ between central and peripheral species across the different chorological groups (Appendix S6).

3.3 | Conservation status

Of the 2682 Pyrenean species analysed, more than a quarter (731 species; 27%) were included as endangered or threatened

in national or regional conservation lists, whereas a much more restrictive number of species was considered vulnerable, endangered or critically endangered in the integrative Pyrenean red list (45 species; 2%) (Figure 6). Twenty-three percent of the total number of central species in the flora (453 species), 37% of all peripheral species (236 species) and 54% of all endemics (45 species) were under regional or national protection. The Pyrenean, national and regional conservation lists included a higher proportion of peripherals and endemics, and a lower proportion of centrals, than the entire flora (Figure 6; Chi-squared test: $X^2 = 104.89$, $df = 6$, $p < .001$, *Cramer's V* = 0.12). However, Pyrenean countries and regions only protected a minority of peripheral species (40% and 31%, respectively), while a majority of threatened species in the Pyrenean red list were peripheral species (55%; Figure 6). A larger proportion of SP than NP species was considered of high conservation priority, much larger in the case of the integrative Pyrenean red list (Figure 6; Chi-squared test: $X^2 = 9.60$, $df = 3$, $p < .05$, *Cramer's V* = 0.10).

4 | DISCUSSION

By assessing both environmental characteristics and abundance of central, peripheral and endemic vascular plants of the Pyrenees, we provided partial support for the Centre-Periphery Hypothesis (CPH). Indeed, species living at their range limit in the Pyrenees inhabit more marginal habitats, are less abundant at large spatial scale and show high vulnerability according to the Pyrenean red list; however, they show similar abundance as central species at local scale

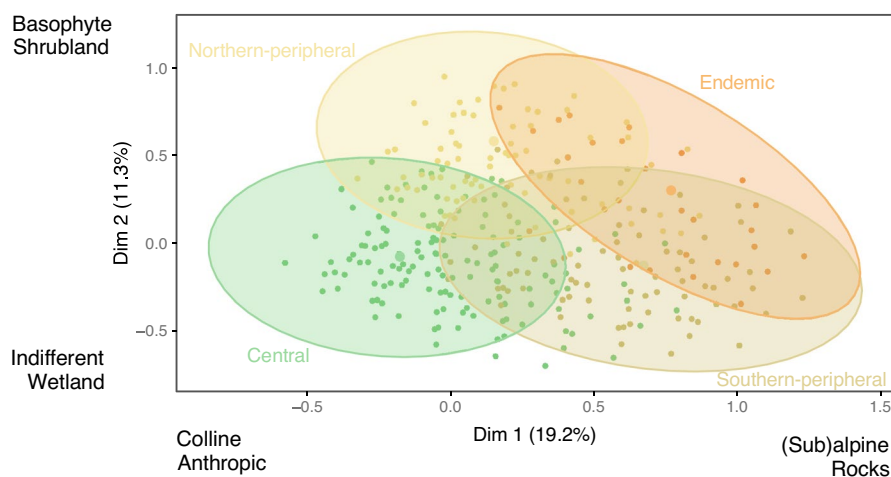


FIGURE 2 Elevation, habitat and soil preferences of central, peripheral (northern- and southern-periphery) and endemic species. A multiple correspondence analysis (MCA) was used to create an environmental space summarizing the variation in the distribution of species across four elevation zones: colline (<500 m), montane (<1800 m), subalpine (<2300 m) and alpine (>2300 m), six habitat types (i.e. habitat in which each species is most commonly found): anthropic, wetland, forest, shrubland, grassland and rocks, and three soil categories: basophytes, acidophytes and indifferent (i.e. soil generalists). One species can occur in more than one elevation zone, while it has been assigned only one habitat and soil category. The two first axes of the MCA explained 19% and 11% of the variance in the data, respectively. Variables that contributed the most to the definition of the two first MCA axes are given below the axes (see also Appendix S4 for more details about the contribution of each individual variable to the MCA axes). More details about the distribution of species across each environmental variable are given in Appendix S3

FIGURE 3 Regional abundance of central, peripheral (northern- and southern-periphery), and endemic species within the Pyrenees. Regional abundance is a composite variable made of three variables (Grid-based abundance, expert-based abundance, elevational range; see Materials and Methods for a complete description). Each bar of the boxplot represents the median, first and third quartiles, minimum and maximum values (error bars excluding outliers) of the regional abundance distribution. Different letters indicate statistically significant differences among groups (post-hoc Kruskal-Wallis multiple comparison test)

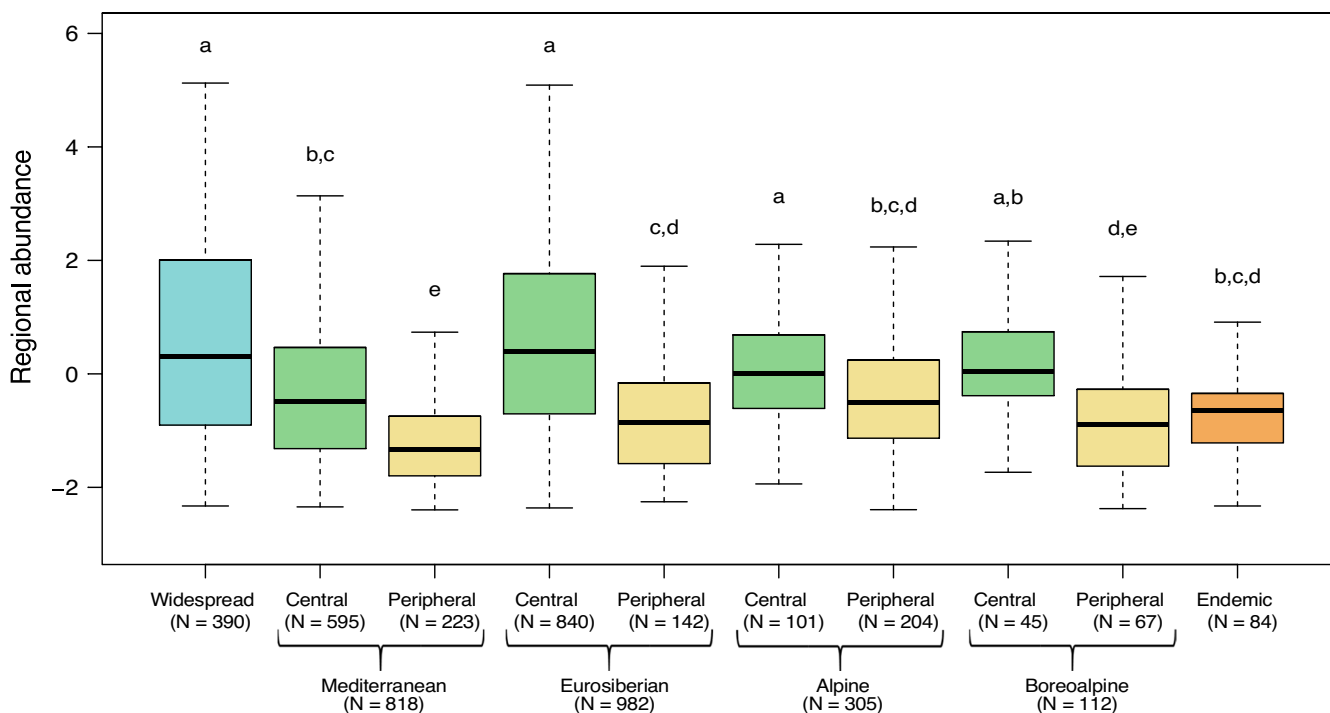
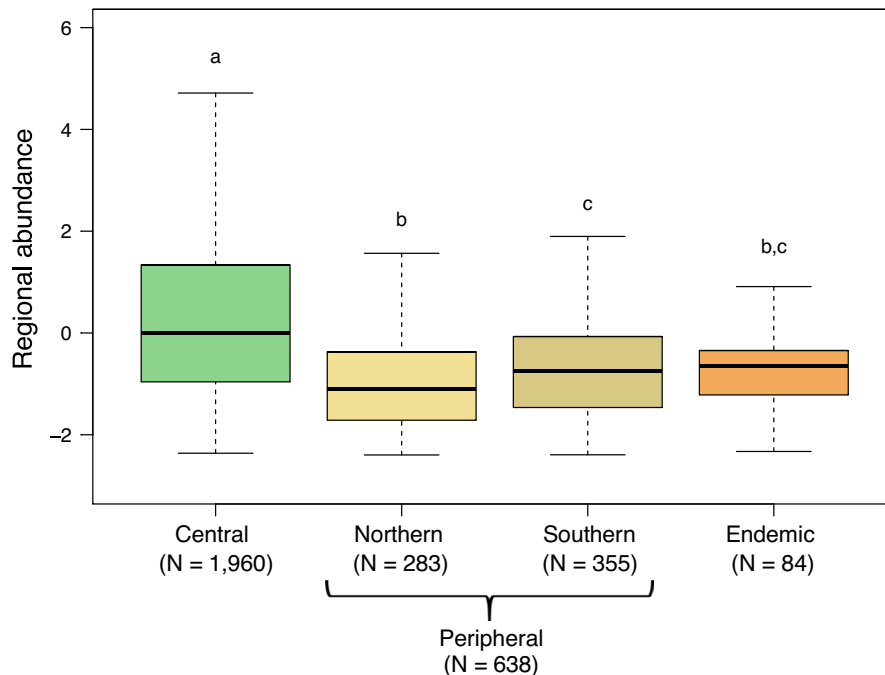


FIGURE 4 Regional abundance of central, peripheral and endemic species according to their chorology. Regional abundance is a composite variable made of three variables (Grid-based abundance, expert-based abundance, elevational range; see Materials and Methods for a complete description). Each bar of the boxplot represents the median, first and third quartiles, minimum and maximum values (error bars excluding outliers) of the regional abundance distribution. Different letters indicate statistically significant differences among groups (post-hoc Kruskal-Wallis multiple comparison test)

(population size) and are marginally threatened according to national and regional protection lists. These findings highlight strengths and limitations of the CPH as a general rule for assessing species environments, abundance and vulnerability patterns, and provide useful

information to reassess plant conservation priorities in a context of global change.

Almost one fourth of the Pyrenean flora is composed of species occurring at their range limit (i.e. peripheral species), and only 3% are

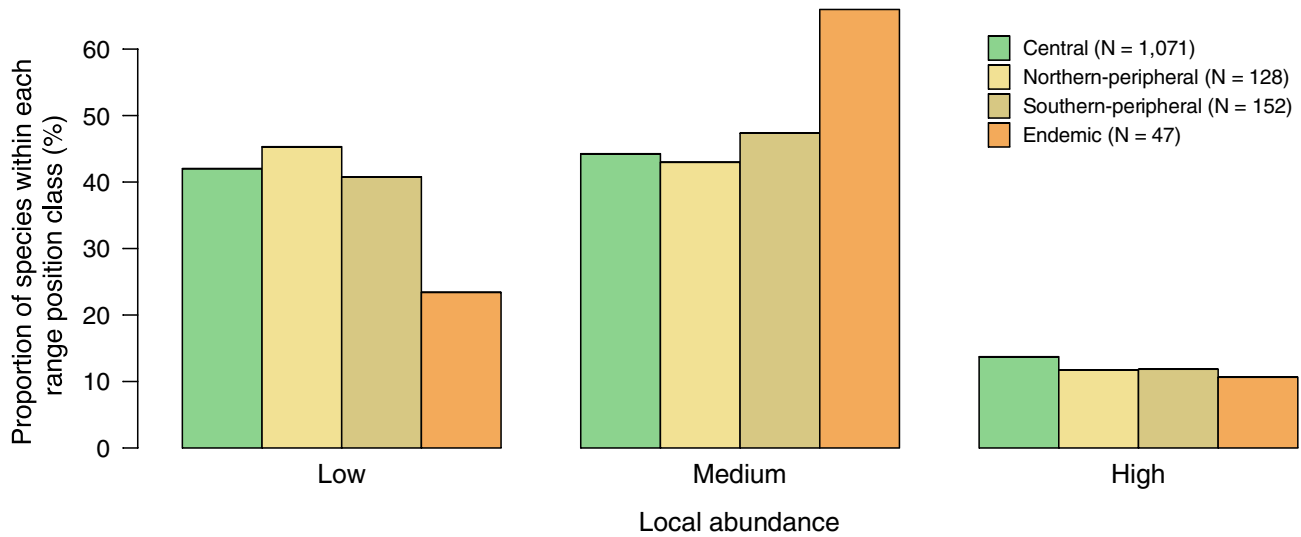


FIGURE 5 Relative proportion of central, peripheral (northern- and southern-periphery) and endemic species within three local abundance classes. Local abundance was assigned by a local expert to 1398 species occurring in the South-Central region of the Pyrenees (Aragon, Spain). No local abundance measure is available for the other species of the flora of the Pyrenees

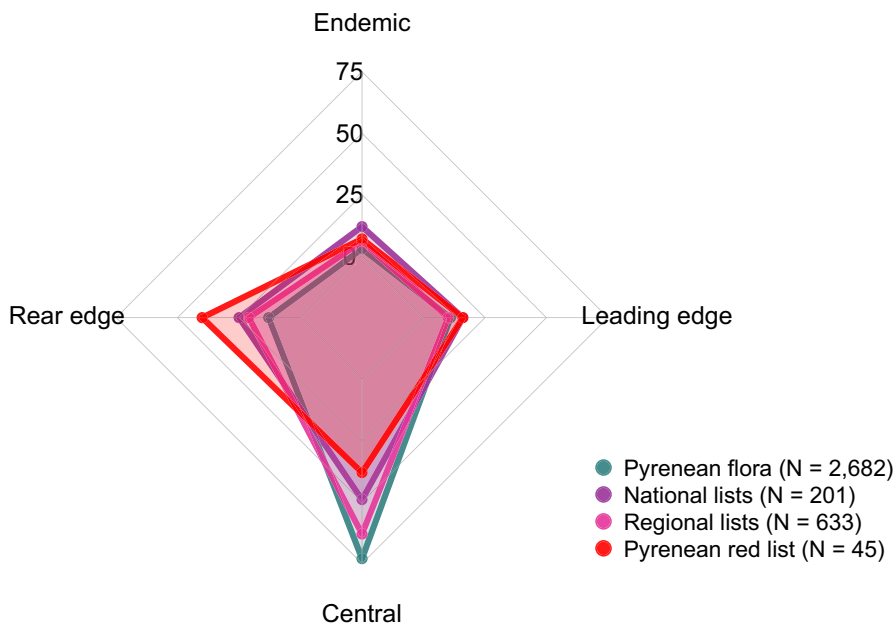


FIGURE 6 Percentage of central, peripheral (northern- and southern-periphery), and endemic species within the flora of the Pyrenees mountains, national and regional protection lists, and the Pyrenean red list

strictly restricted to this mountain range (i.e. Pyrenean endemics). These proportions support the view that peripheral species contribute significantly to the high species richness of biogeographical crossroads (Spector, 2002), and highlights the conservation value of mountains in sheltering marginal populations (Loidi et al., 2015; Tordoni et al., 2020).

Endemic species tend to occur at high elevation, on the least disturbed habitats (mostly rocks and alpine grasslands) and specific soil types. Such patterns are concordant with previous results found in nearby regions such as in the Mediterranean southern France (Lavergne et al., 2004, 2005a, 2005b) or the French Alps (Boulangeat et al., 2012). Beyond area, richness and climate, this

pattern has been attributed to increased isolation causing high speciation rates in continental mountain systems (Steinbauer et al., 2016).

Peripheral species share similar environmental characteristics (García et al., 2020). As rare plant species tend to be more specialized to particular biotic or abiotic conditions than common species (Boulangeat et al., 2012; Wamelink et al., 2014), it is not surprising that not only Pyrenean endemics, but also peripheral species, have narrower and more specialized ecological niches than central ones. Moreover, this is consistent with the main assumption of the CPH, which expects peripheral populations to inhabit mainly marginal environments (Brown, 1984).

Species occurring at their range limit in the Pyrenees exhibit lower continental and regional abundance than central ones but have similar local abundance. These results follow the predictions of the CPH at regional but not at local scale, being consistent with a previous review of the literature reporting relatively high and low support for the CPH for species regional and local abundance respectively across a wide range of studies on animals and plants found in different areas of the world (Pironon et al., 2017). Peripheral species might occur in locally favourable sites but within a generally unfavourable environmental matrix (Lennon et al., 2002; Murphy et al., 2006). Endemics, which can be considered extreme cases of peripheral species, exhibit a similar pattern of regional abundance. Both endemics and peripheral species can thus be considered regionally rare, but not locally rare. Working with seven North American endemic plants, Lesica et al. (2006) found that they were locally more common than their widespread congeners. The authors attributed the pattern to recent speciation rather than ecological mechanisms such as dispersal ability, which are expected to act at a larger geographical scale (Estrada et al., 2015). While differences in local abundance between chorological groups of plants could be explored more thoroughly through quantitative field measurements across the entire flora, causal factors of such distribution patterns remain to be explored.

The fact that regional abundance is consistently lower in peripheral than central species across chorological groups, and across NP and SP species, strongly supports that this is a robust pattern. Again, this follows previous results from Pironon et al. (2017), which found no clear differences in the degree of support of the CPH among species of different bioregions of the world, and between peripheries of low and high latitude. Moreover, SP species of the Pyrenees exhibit similar local abundance patterns to those of central and NP species. This, coupled with a higher regional abundance in SP species compared to NP species, may (i) partly explain their past persistence, and (ii) act as a buffer against future environmental disturbance (Hampe & Petit, 2005).

Engler et al. (2011) assessed the potential impact of predicted future climate change on the flora of most European mountain ranges using high-resolution species distribution models. They found that the Pyrenees (and the Eastern Austrian Alps) could be the most affected region with considerable losses of alpine and sub-alpine species by 2070–2100, and recent studies have shown that abrupt ecological disruptions could occur even earlier than that (Trisos et al., 2020). However, these predictions have not considered biological characteristics, local abundances and non-climatic environmental factors that may buffer or exacerbate the effects of climate change through species-specific responses. To target priority species for conservation, it would be necessary to consider differences among species in terms of abundance, habitat preference and other factors such as biological traits conferring resistance to different global change drivers (Hartley & Kunin, 2003; Kunin & Gaston, 2012; Rabinowitz, 1981). This may ultimately provide more insights into the potential of species to avoid demographic collapse and thrive in the future.

Because of their small geographic ranges, ecological specialization to infrequent habitats, and frequent location at high elevation, endemics are often considered as potential candidates of high concern for conservation. Our study demonstrated that peripheral species represent another important group when setting conservation priorities because of their reduced regional abundance compared to central ones, which could make them more prone to extinction (Harnik et al., 2012; Purvis et al., 2000). In addition, peripheral species may be particularly vulnerable to predicted future climate warming given their preference for high elevation areas (Engler et al., 2011; Gottfried et al., 2012; Pauli et al., 2012; Steinbauer et al., 2018). However, the fact that both groups are found mainly in habitats of low human-induced disturbance (alpine grasslands and rocks; García et al., 2020) could also make them more resistant to future global change, as observed in one of the Pyrenean areas of highest diversity: the Ordesa and Monte Perdido National Park (García et al., 2019). The slow dynamics and high stability of Pyrenean plants restricted to rocky places and natural alpine grassland communities support the idea that many endemics (and potentially several peripheral species) could be less vulnerable than expected despite their restricted distribution (García, 2003; Pardo et al., 2015).

Our results also show that NP and SP species exhibit similar regional and local abundance but slightly different environmental characteristics. Although both are frequent in grasslands, SP species are more frequent in wetlands and forests, and NP taxa in shrublands and disturbed habitats. The type of periphery may thus represent another interesting criterion for conservation policy in the context of climate change, as SP Alpine, Boreoalpine and Eurosiberian species, and particularly those inhabiting threatened habitats such as wetlands (Erwin, 2008), are the ones expected to suffer greater impacts (Engler et al., 2011; Pauli et al., 2012). The predicted future increase in temperatures may expand the availability of suitable habitat for many NP species (especially Mediterranean) within the Pyrenees or further north of this geographical barrier (Gottfried et al., 2012). Nevertheless, forest expansion due to the abandonment of traditional land use is also increasing opportunities for Eurosiberian plants at their southern limit of distribution in the Pyrenees (García et al., 2010). Thus, the combination of climate and land use changes, and species habitat preferences, is producing very complex scenarios where full sets of peripheral species can be either favoured or disadvantaged across heterogeneous landscapes (Peters et al., 2019).

Our study emphasizes the view that biogeographical crossroads might represent areas of high conservation priority (Spector, 2002) not only due to the presence of many endemics, but also for their high concentration and diversity in peripheral species. Within the Pyrenees, about half of the endemics and one third of the peripheral species are currently protected at national and regional levels, the two groups accounting for 38% of all protected plants across the Pyrenean range. Although several endemic and peripheral species (especially SP) are considered priorities for conservation, central species are still largely overrepresented. This is because regional

protection lists do not consider species global range and abundance. Interestingly, the importance of peripheral species in conservation lists became stronger when the list was set considering the whole Pyrenean range, rather than separate regional or national territories. Global assessment criteria for the entire mountain range may enable a more integrative management and a better assessment of the "regional responsibility" of each administrative region (Gauthier et al., 2010; Gómez, Lorda, et al., 2017). If managers and policy-makers were to make use of the Pyrenean red list to prioritize conservation actions, those would be targeted more towards peripheral (especially SP) species.

While the CPH is partly supported by our analyses, its predictions do not match local abundance of peripheral species in the Pyrenees. Thus, the CPH does not constitute a fully reliable predictive framework for assessing the conservation status of the flora of this biogeographical crossroads. Accounting for multiple extrinsic (environmental) and intrinsic (species-specific abundance) factors, at different scales, is key for a better understanding of the sensitivity of the flora of mountainous areas to both deterministic environmental drivers related to global change and stochastic events usually associated with rarity. Ultimately, such integrative assessment will help us to estimate current risks and improve projections of the future of biodiversity, including peripheral species, in a changing world.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

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BIOSKETCHES

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Author contribution: M.B.G. and S.P. designed the study. D.G., X.F., and M.B.G. collected the data. S.P. performed the analyses. S.P. and M.B.G. wrote the manuscript with inputs from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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