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SPATIAL DISTRIBUTION AND ENVIRONMENTAL DESCRIPTION OF THE ENDEMIC FLORA OF THE PYRENEES

Distribución espacial y rasgos ecológicos de la flora endémica de los Pirineos

P. Tejero, M.B. García y D. Gómez*

Instituto Pirenaico de Ecología (CSIC). Avda. Nuestra Señora de la Victoria, 16, 22.700-Jaca (Huesca, España).

Identificador ORCID de los autores y e-mail:
P. Tejero: http://orcid.org/0000-0001-6735-3423 E-mail: ptibarra@ipe.csic.es
M.B. García: http://orcid.org/0000-0003-4231-6006 E-mail: mariab@ipe.csic.es
D. Gómez: http://orcid.org/0000-0002-9738-8720 E-mail: dgomez@ipe.csic.es
* Autor corresponsal

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ABSTRACT: A detailed knowledge of the endemic plant species in the Pyrenees benefits both conservation policy and ecological research. Here we describe the spatial distribution patterns and floristic and ecological aspects of the updated list of Pyrenean endemisms after the on line edition of the Atlas of vascular flora of the Pyrenees. A total of 88 unambiguous endemic plant species have been recorded in the Pyrenees (excluding apomictic and other non-clear taxa), which represents the 2.4% of its total native flora. They belong to 27 families, and are geographically concentrated in the central part of the chain. Pyrenean endemics present a narrower distribution and grow at higher altitude than non-endemics, but do not present spatial distribution breaks along the mountain chain. The distribution of the endemic taxa also indicates that East-West dispersal is more limited than the North-South, despite the altitudinal barrier. Endemisms are mostly chamaephytes and are overrepresented in calcicolous rocky habitats. Overall, these results indicate that the isolation of the Pyrenees during the glacial cycles might have been moderate, and serve as a starting point for further integrative investigations.

KEYWORDS: Altitudinal distribution; spatial occupancy; abundance; chorology; life-form; habitat; naturalness.

RESUMEN: El conocimiento detallado de los endemismos pirenaicos resulta de gran utilidad en la adopción de medidas de conservación y en la investigación de patrones ecológicos de la flora. Describimos la distribución espacial y distintos aspectos florísticos y ecológicos de la lista revisada de endemismos pirenaicos tras la edición digital del "Atlas de flora vascular de los Pirineos". Las 88 especies endémicas genuinas representan el 2,4% del conjunto de la flora pirenaica, se incluyen en 27 familias taxonómicas y se concentran en la parte central de la cadena. Los endemismos estudiados presentan notables diferencias ecológicas respecto al conjunto de la flora, en términos de una distribución territorial más reducida y localización en altitudes más elevadas, pero no presentan una distribución fragmentada en el conjunto de los Pirineos. Su distribución también indica que la dispersión Este-Oeste es más limitada que la Norte-Sur, a pesar de la barrera altitudinal del eje de la cordillera. Los endemismos son mayoritariamente caméfitos y están más representados en los hábitats rocosos calizos. En conjunto, estos resultados indican que el aislamiento durante las glaciaciones puede haber sido moderado y sirven como punto de partida para futuras investigaciones.

PALABRAS CLAVE: Distribución altitudinal; abundancia; corología; forma biológica; hábitat; naturalidad.

1. Introduction

Local endemisms reflect the portion of biodiversity unique to a particular geographic area and therefore highlights its biological singularity (Good, 1947; Sainz & Moreno, 2002). Although endemic species have concentrated research effort for different scientific interest (Favarger & Siljak-Yakovlev, 1986; Segarra-Moragués & Catalán, 2008; McMullen, 2009) we want to point out two major points. First, their restricted distribution often requires priority conservation politics (Médail & Verlaque, 1997; Dirnböck *et al.,* 2011; Swenson *et al.,* 2012; Huang *et al.,* 2016) and second, they are valuable targets in evolutionary biology (Segarra-Moragués *et al.,* 2007; Ikeda & Setoguchi, 2007; Casazza *et al.,* 2008; Schönswetter & Schneeweiss, 2009; García *et al.,* 2012; Loidi *et al.,* 2015).

Evolutionary processes resulting from geographical isolation or habitat discontinuity may promote the generation of endemisms (Stebbins & Major, 1965; Sunding, 1979). There are different ecological and geographic examples that fit this basic island model in biogeography. Among them, the Northern hemisphere mountain ranges have been intensively studied (Billings & Mooney, 1968; Brochmann *et al.,* 2003; Albach *et al.,* 2006; Winkler *et al.,* 2012), particularly in Europe (Favarger, 1972; Abbot *et al.,* 1995; Schönswetter *et al.,* 2005, Schönswetter *et al.,* 2006). The repeated glaciation cycles during the quaternary have influenced dramatically present vegetation in Europe (Abbot & Brochmann, 2003; Hewitt, 2004; Birks, 2008). Both, transitions from interglacial to glacial state and from glacial to interglacial, increased connectivity between mountain ranges like Sierra Nevada, the Pyrenees, the Alps or Carpathians, which share alpine taxa (Küpfer, 1974; Tutin *et al.,* 1964-1980; Villar *et al.,* 2001 and 2003; Blanca, 2002; Aeschimann *et al.,* 2004; Vargas, 2003; Castroviejo, 1986-2015). These processes have been also documented in the Iberian Peninsula (Loidi *et al.*, 2015; Buira *et al.,* 2017). During interglacial periods, isolation of plant population in high altitudes have been predominant, triggering speciation processes that sometimes were completed before a new glacial cycle started (Rešetnik *et al.,* 2013; Roquet *et al.,* 2013; Deng *et al.,* 2015) and therefore originating endemic species.

Endemic plants in the Pyrenees have been previously investigated by Dupias (1985), Villar & García (1989), Rivas-Martínez *et al.,* (1991) or Villar *et al.,* (1994) and revised in Sainz & Moreno (2002). Recent works in the Alps (Casazza *et al.,* 2008) or the Carpatians (Kliment *et al.,* 2016) developed more detailed floristic and ecological descriptions of the endemisms of these mountains. For a valuable analysis of the Pyrenean endemisms, however, we first require clear criteria to resolve ambiguities on what an endemic taxon is. As Sainz & Moreno (2002) extensively discussed, this is not an easy task, due to the intensive taxonomical revision required, particularly at the level of subspecies or varieties. Local botanists have often concentrated a high effort in the description of local variants, which potentially led to enlarge the list of endemisms. It is illustrative the case of the endemic subspecies *Oxytropis campestris* subsp *tirolinesis* described in Schönswetter *et al.,* (2004), for which it was demonstrated no genetic differentiation from the extensively distributed subspecies.

In this paper we present a basic floristic description based on an updated and revised list of endemisms of the Pyrenean flora (Gómez *et al.,* 2016) as a step forward in the description of the biodiversity of the second most important mountain chain of Europe from a biodiversity point of view. To complete this description we also conduct a comparative analysis of the endemisms against the non-endemic flora of the Pyrenees.

2. Material and methods

Initially we recorded all taxa previously described as endemic of the Pyrenees, including species, subspecies and different apomictic microspecies. Unfortunately, not all proposed endemic taxa have been clearly resolved with unambiguous taxonomic works. For instance, deep molecular research is needed to evaluate the taxonomic entity of all varieties described in apomictic genus and the inclusion of them as endemic taxa might include considerable uncertainty and bias in the floristic and ecological descriptions and analysis here presented. For that reason we discarded microespecies or subspecies from genus such as *Achemilla, Hieracium* or *Pilosella*. We also excluded the cases in which only a subspecies of a widely distributed taxon is endemic to the Pyrenees. In this way we attempt to buffer the "overfragmentation" of taxa traditionally linked to taxonomy.

Strictly, a Pyrenean endemism is a species whose distribution area is restricted to the Pyrenees. For that reason, we excluded Pyrenean species of recently discovered punctual localities in mountain ranges far apart from the Pyrenees that have been traditionally considered endemic taxa. That is the case of *Veronica aragonensis* Stroh, recently cited by Martínez-Ortega (1999) in South Spain (La Sagra, Granada). Nevertheless, we included in our analysis subendemisms, i.e., species whose major distribution area is restricted to the Pyrenees but occur at punctual localities in peripheral areas like *Ramonda myconi* (L.) Rchb. cited by Calduch *et al.,* (2007) in the Montsiá (Tarragona) or *Saponaria caespitosa* DC. occurring in the Cantabrian Range.

After screening all Pyrenean taxa, we generated a list of endemisms matching the above mentioned criteria (Gómez *et al.,* 2016). In order to investigate the endemic taxa of the Pyrenees and based on the information recorded in the "Atlas de la Flora Vascular de los Pirineos" (http://www.atlasflorapyrenaea.org) we compiled for all species different biotic and abiotic information such as family, altitude, altitudinal range, vegetation belt, geographic distribution at 3 levels (administrative, biogeographic sector and 10x10 Km UTM grids), abundance, habitat, habitat naturalness, life form and edaphic affinity. We carried out descriptive analysis and comparisons with entire and the non-endemic Pyrenean flora based on Gómez *et al.,* (2017).

Initially, we revised the number of species, genus and families to which the Pyrenean endemisms belong and explored in which administrative regions and biogeographic sectors they are present. The geographic distribution analysis of the Pyrenean endemic taxa was carried in two ways. First we classified each species in one of the 63 possible distribution cases combining 6 sectors. In this way it is possible to explore patterns of distribution within the endemic Pyrenean taxa and to quantify the distribution break events between contiguous sectors. Besides, we plotted the total number of endemisms in each 10x10 Km UTM grid in order to visualize the areas where the endemisms concentrate.

The regional abundance scored for each taxon was tested considering both the whole Pyrenees and only those sectors where the taxon occurs. To test if the distribution of Pyrenean endemisms according to different ecological factors was significantly different from the non-endemic Pyrenean flora we performed Chi-square tests (Table 1).

3. Results

3.1. Number of taxa and classification

There are to date 88 species of vascular plants unambiguously endemic to the Pyrenees, two of them considered subendemic (*Ramonda myconi* (L.) Rchb. and *Saponaria caespitosa* DC.). The evaluation of endemic status started with about 140 potential taxa. The uncertainty of this number relies on the apomictic genera which need further taxonomic investigation and from which we recorded and excluded about 35 type species potentially endemic to the Pyrenees. Besides, another 17 subspecies included at higher taxonomic level with wider distribution were also recorded and excluded for the analysis, ending up in the above mentioned 88 endemic taxa. More than 50% of these 88 endemisms are protected in national or regional catalogues.

Among the 145 families represented in the Pyrenees only 27 (18.6%) include endemic taxa, being CARYOPHYLLACEAE (16) SAXIFRAGACEAE (8) and ASTERACEAE (8) the most represented families. These 88 species belong to a total of 57 genus, being *Saxifraga* (8) *Petrocoptis* (6) *Androsace* (4) and *Dianthus* (4) the most represented ones. There are several families with at least 10% of endemic taxa like SAXIFRAGACEAE (20.5%) and PRIMULACEAE (12.2%) among the most represented families. Some families poorly represented in the overall Pyrenean flora present a high percentage of endemic taxa within the family, as ISOETACEAE and SANTALACEAE, DIOSCOREACEAE or GESNERIACEAE.

Table 1: Summary of factors for which differences between the Pyrenean endemisms and the non-endemic flora where tested by a Chi-square test. Number of classes and their description are detailed.
Tabla 1: Resumen de los factores comparados entre la flora endémica y la del conjunto de los Pirineos. Se detalla el número de clases y su descripción.

Factor tested	N Classes	Description of the classes
Geographic extension	6	Species present in 1,2,3,4,5 or 6 sectors
10x10 Km UTM extension	6	Species present in 1-10, 11-50, 51-100, 201-350 or more 10x10 Km UTMs
Average records per UTM	8	(0-3], (3-5], (5-7], (7-9], (9-11], (11-13], (13, 15], >15
Abundance in the Pyrenees	7	Extremely rare; very rare; rare; scarce; frequent; common; very common
Abundance when present	6	Very rare; rare; scarce; frequent; common; very common
Vegetation belt	7	Basal Mediterranean; basal Atlantic; submontane; montane; subalpine; alpine; subnival
Altitudinal amplitude	6	Between 0-499 meters (500-999; 1000-1499; 1500-1999; 2000-2499; 2500-2999)
Habitat	7	Costal & salty soils; Forest; Anthropic; Shrubland; Rocky; Humid; Grassland.
Habitat naturalness	4	Very high, high, intermediate, low
Life-form	8	Epiphytes; hydrophytes, phanerophytes, nanophanerophytes, geophytes, chamaephytes, therophytes, hemicryptophytes.
Substrate affinity	3	Indifferent; acidic; basic

Compared with the entire Pyrenean flora, most of the families with endemic taxa are overrepresented as it shows figure 1. Among them CARYOPHYLLACEAE, SAXIFRAGACEAE, PRIMULACEAE, GERANIACEAE and DIOSCORIACEA clearly double their representation. Oppositely, few families are underrepresented and only POACEAE and LAMIACEAE present two times less percentage of endemic taxa than they exhibit among the entire Pyrenean flora.

3.2. *Spatial distribution*

Figure 2a shows that the administrative regions presenting higher amount of endemic taxa are Aragón with 62 (70.4% of the Pyrenean endemisms) and Catalunya with 58 (65.9%), followed by Hautes-Pyrénées with 42 (47.7%). Euskadi has only 3 (3.4%) Pyrenean endemisms, Aude 17 (19.3%), and Navarra 24 (27.2%). The percentage of Pyrenean endemisms relative to the total local flora within these regions is low and ranges from 0.2% in Euskadi to 2.3% in Haute-Pyrénées.

The distribution of endemisms according to the 6 geographic sectors reveals differences across the Pyrenees. Pyrenean endemisms have significantly more constricted distribution (Table 2) than non-endemic flora, having less representation of widely distributed taxa and more representation of taxa only distributed in 1 to 4 sectors as it is shown in figure 2b. The Southern Central sector hosts 75% of the Pyrenean endemisms (66) followed by the North Central (51) and Southern Eastern (45). In the remaining 3 sectors about 40% of the endemisms are recorded (figure 3a).

Figure 3b shows that none of the 88 endemisms present a fragmented distribution attending to the 6 biogeographic sectors. There are neither endemic taxa restricted to the entire North face nor to the South face of the mountain range. The locally restricted endemisms, present only in one sector, are concentrated in the central and eastern-south Pyrenees. Among the endemisms with wider distribution, there is a relevant differentiation between the West and the East of the Pyrenees. Western and eastern sectors only share about 15% of the ende-

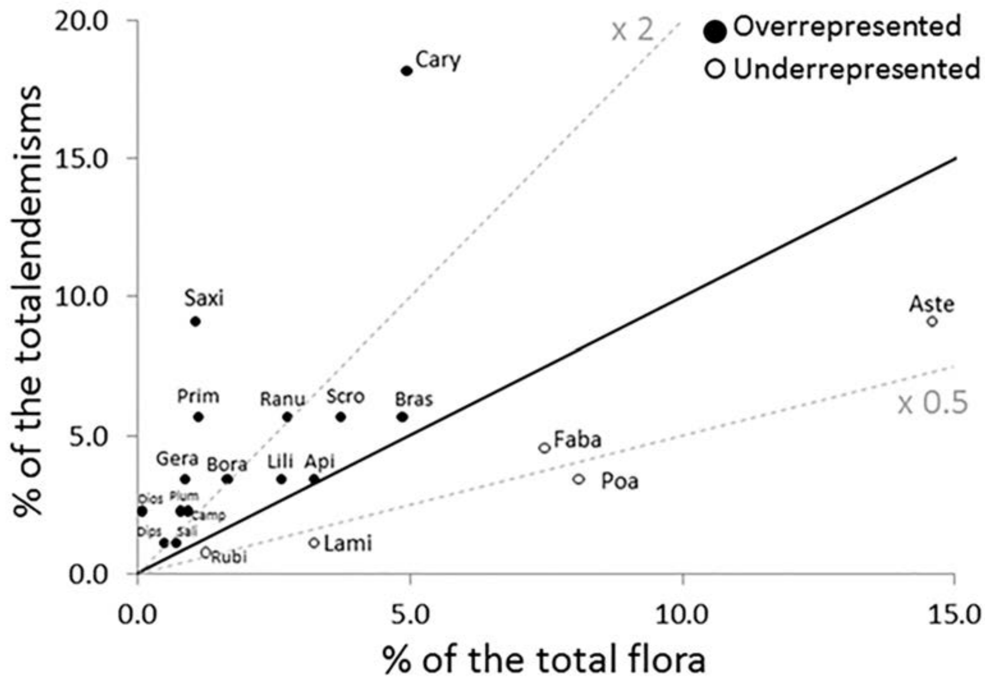

Figure 1: Families containing higher number of endemisms, with over- or under-representation of the endemic element (in %), compared to the total Pyrenean flora. The continuous line indicates an equal representation, and the dotted lines mark the two-fold over or underrepresentation. (Api: APIACEAE, Aste: ASTERACEAE, Bora: BORAGINACEAE, Bras: BRASSICACEAE, Camp: CAMPANULACEAE, Cary: CARYOPHYLLACEAE, Dips: DIPSACACEAE, Faba: FABACEAE, Gera: GERIANIACEAE, Lami: LAMIACEAE, Lili: LILIACEAE, Plum: PLUMBAGINACEAE, Poa: POACEAE, Prim: PRIMULACEAE, Ranu: RANUNCULACEAE, Sali: SALICACEAE, Saxi: SAXIFRAGACEAE, Scro: SCROPHULARIACEAE, Rubi: RUBIACEAE)

Figura 1: Relevancia de las familias con mayor número de endemismos, y su mayor o menor representación respecto al conjunto de la flora. La línea continua marca la misma representación y las líneas de puntos los dos grupos sobre o sub-representados. (Api: APIACEAE, Aste: ASTERACEAE, Bora: BORAGINACEAE, Bras: BRASSICACEAE, Camp: CAMPANULACEAE, Cary: CARYOPHYLLACEAE, Dips: DIPSACACEAE, Faba: FABACEAE, Gera: GERIANIACEAE, Lami: LAMIACEAE, Lili: LILIACEAE, Plum: PLUMBAGINACEAE, Poa: POACEAE, Prim: PRIMULACEAE, Ranu: RANUNCULACEAE, Sali: SALICACEAE, Saxi: SAXIFRAGACEAE, Scro: SCROPHULARIACEAE, Rubi: RUBIACEAE)

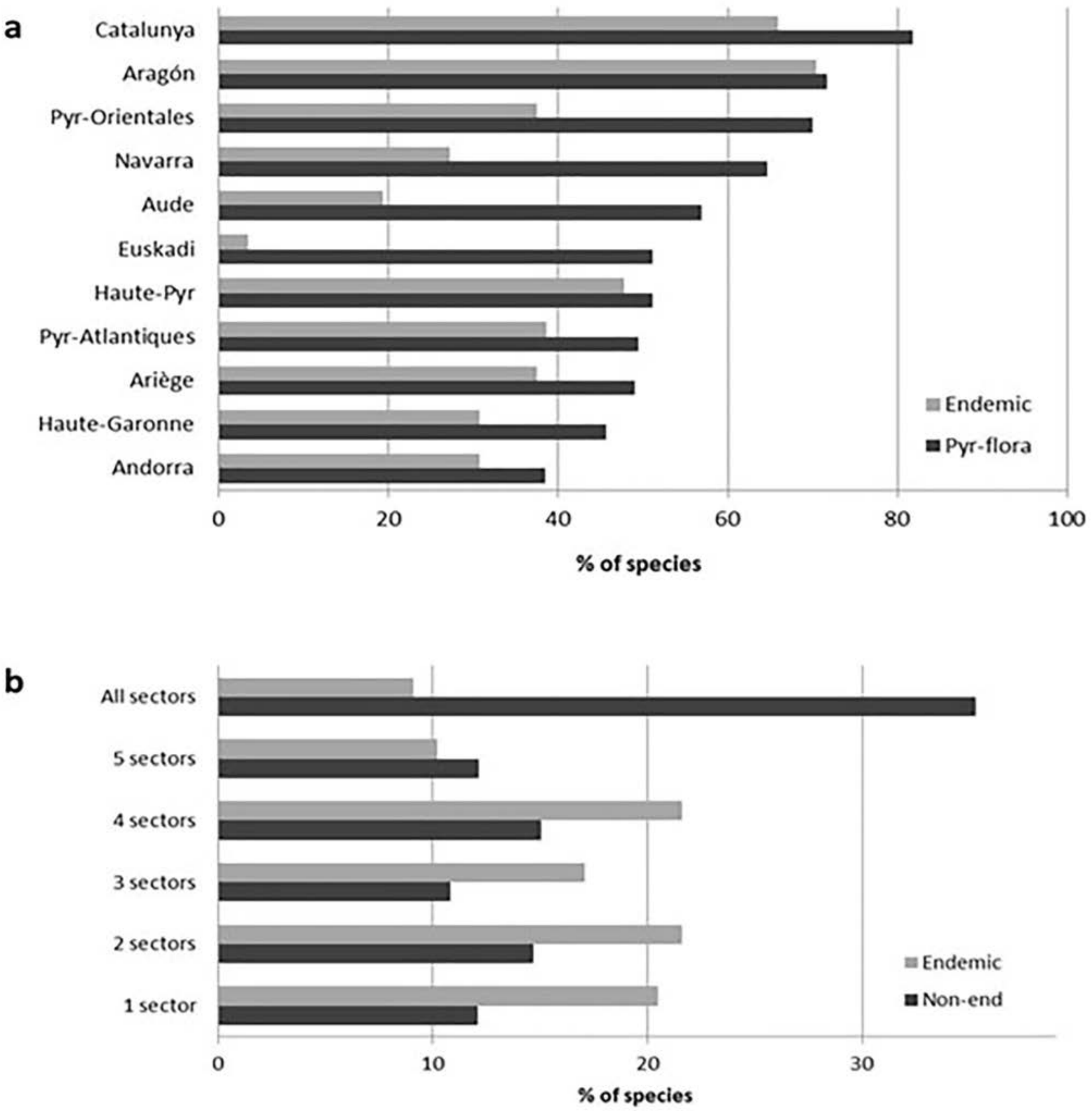

Figure 2: Geographic distribution of the Pyrenean endemisms (Endemic) and the entire flora (Pyr-flora) or the non-endemic flora of the Pyrenees (Non-end). a) Administrative division. b) Division according to biogeographic sectors.
Figura 2: Distribución geográfica de los taxones endémicos (Endemic) y no endémicos (Non-end) del Pirineo y la flora total (Pyr-flora). a) División administrativa. b) División en los sectores biogeográficos.

misms (NW with NE 16% and SW with SE 13.5%), whereas northern and southern sectors (both in the Eastern or Western Pyrenees) share one third of the total amount of endemisms. The central Pyrenees, despite presenting the highest altitudes, share more than 50% of the total endemisms between both NC and SC sectors. Figure 3c summarizes previous description showing that distribution breaks of Pyrenean endemic taxa preferably occur in a west-east gradient and it is very weak in its North-South component.

A more detailed geographical description based in 10x10 Km UTM records of the endemisms confirms that they present significantly more restricted distribution than non-endemic flora (Table 2 and Figure 4a). *Ramonda myconi* is the Pyrenean endemism recorded to have the widest geographic distribution present in 164 (30%) of the

Table 2: List of the Chi-square test performed**.** The null Hypothesis is listed, with the degrees of freedom, the significance of the p-value of the test (NS no significant, ***: p-value<0.001) and a short interpretation which is detailed in the text.
*Tabla 2: Listado de los test Chi-cuadrado con la Hipótesis nula, los grados de libertad, el valor de significación de p (NS no significativo, ***: p-value<0,001) y una breve interpretación del resultado*

Test (H0:)	df	p-value	Interpretation
The sector abundance of the Pyr-end is similar to the non-end (non-endemic)	5	***	Pyrenean endemisms have more constricted general distribution than non-endemic flora.
The 10x10 Km abundance of the Pyr-end is similar to the non-end	5	***	Pyrenean endemisms have more constricted distribution than the non-endemic flora.
The records per UTM grid of the Pyr-end is similar to the non-end	7	***	Pyrenean endemisms have more records per UTM grids than the non-endemic flora
The overall abundance of the Pyr-end is similar to the non-end	6	***	Pyrenean endemisms are less abundant in the Pyrenees than the non-endemic flora
The local abundance of the Pyr-end is similar to the non-end	5	NS	Can't refuse that Pyrenean endemisms are as abundant as the non-endemic flora where they are present
The distribution along the vegetation belts of the Pyr-end is similar to the non-end	6	***	Pyrenean endemisms are more represented at high vegetation belts than the non-endemic flora
The altitudinal amplitude of the Pyr-end is similar to the non-end	5	NS	Can´t refuse that Pyrenean endemisms have different altitudinal amplitude than the non-endemic flora.
The habitat distribution of the Pyr-end is similar to the non-end	6	***	Pyrenean endemisms concentrate in rocky habitats.
The habitat naturalness of the Pyr-end is similar to the non-end	3	***	Pyrenean endemisms are present in habitats with more naturalness.
The life-form distribution of the Pyr-end is similar to the non-end	7	***	Among Pyrenean endemisms the chamaephytes are overrepresented.
The substrate affinity of the Pyr-end is similar to the non-end	2	***	Pyrenean endemisms are more specific to the substrate than the non-endemic flora.

540 10x10 Km UTM grids. There are also other species like *Erysimum seipkae* Polatschek (159), *Salix pyrenaica* Gouan (135), *Saxifraga umbrosa* L. (124) and *Ranunculus pyrenaeus* L. (107) with more than 100 UTM occurrences, which nearly occupy the 20% of the grids. Sixty (68%) Pyrenean endemisms are recorded, to date, in less than 50 UTMs of the Pyrenees, while this percentage for the non-endemic flora is about 45%. Finally, there are 16 endemisms whose presence was recorded in less than 10 grids, and five are only recorded over a unique grid: *Borderea chouardii* Gaussen, *Erigeron cabelloi* A. Pujadas, R. García-Salmones y E. López, *Polygala vayredae* Costa, *Primula subpyrenaica* Aymerich, L. Sáez & López-Alvarado and *Seseli farrenyi* Molero & J. Pujadas.

The endemisms have significantly more records per UTM grid than the non-endemic Pyrenean flora (Table 2). While more than 2/3 of the non-endemic flora has less than 5 records per grid, about 3/4 of the endemic Pyrenean taxa have more than 5 records (figure 4b). Both *Borderea pyrenaica* (Bubani) Miégeville and *B. chouardii* Gaussen, together with *Petrocoptis pseudoviscosa* Fern. Casas and *Xatardia scabra* (Lap.) Meissner are the most intensively surveyed taxa with more than 20 records per 10x10 Km UTM on average.

Figure 5 shows the distribution of the endemisms in 10x10 Km UTM grids. The endemisms are concentrated in the boundary between the North and South Pyrenees, where the higher altitudes are reached. The decrease of Pyrenean endemisms to the West and North is abrupt. There is also a clear decrease of the endemisms to the South, but less intense. Interestingly, the Easternmost part of the Pyrenees (Andorra, Nuria-Puigmal and Orlu), still shows a high presence of endemisms.

3.3. Abundance

The endemic species, as a group, are significantly less abundant across the Pyrenees than the non-endemic flora as it is shown in figure 6a and table 2. But figure 6b and table 2 also shows that this significance blurs when testing differences in local abundance taking into account only the geographic sectors in which the species are present.

3.4. Altitudinal distribution

Figure 7a shows a clear mismatch in the altitudinal distribution between the endemic taxa and the non-endemic flora of the Pyrenees. The shapes of both distributions are similar with a maximum values of presence constantly held for a 1000 m altitudinal range, between 400 and 1400 for

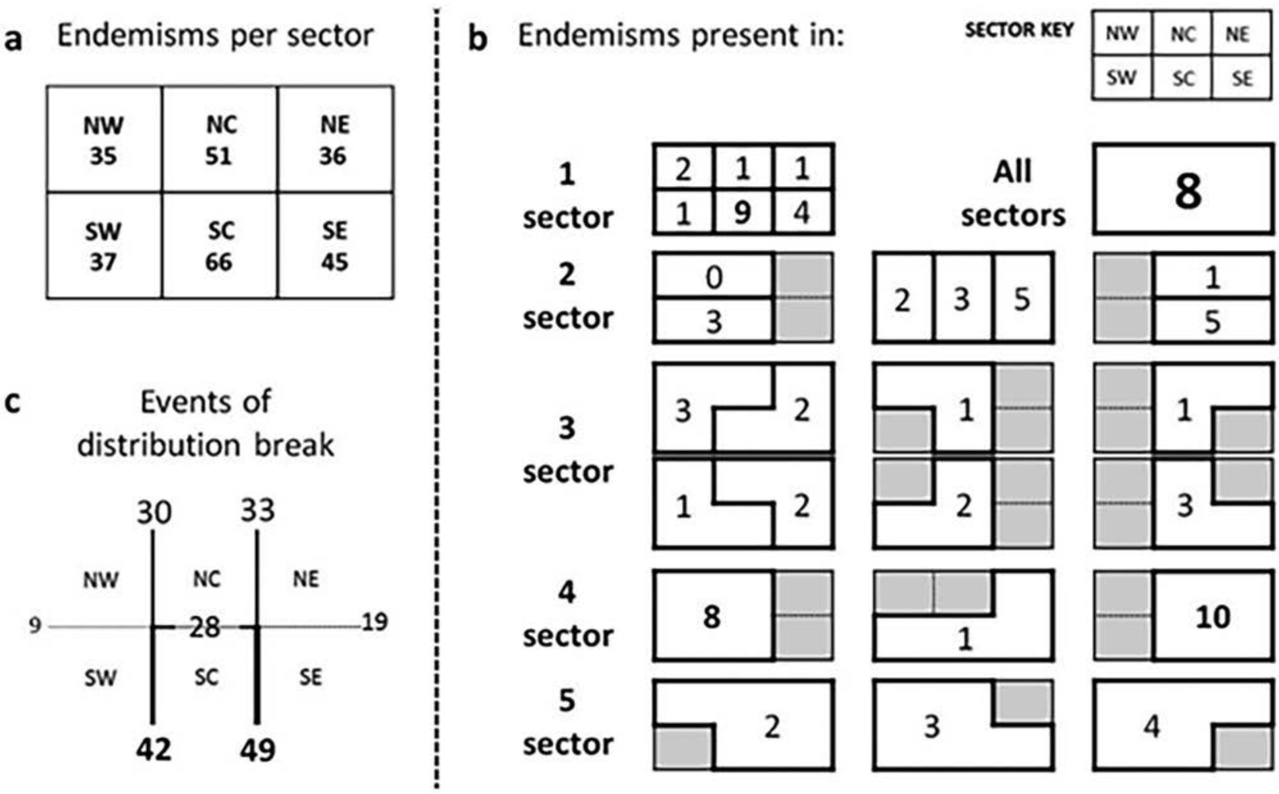

Figure 3: Geographical distribution of the Pyrenean endemisms. a) Endemisms per sector. b) Sector-distribution of the 88 endemic species. The continuous and thick lined area represents the sector-distribution, and the amount of endemisms is reported for each sector-distribution. The sector distributions no represented here present no cases. c) Distribution breaks between contiguous sectors are represented and scaled with numbers.

Figura 3: Distribución geográfica de los endemismos pirenaicos. a) endemismos en cada sector. b) distribución por sectores de los 88 taxones endémicos. La línea continua gruesa delimita las distribuciones sectoriales; se indica el número de especies en cada distribución sectorial. No se representan las distribuciones sectoriales sin endemismos. c) Las discontinuidades de distribución entre sectores contiguos están representadas con números.

the non-endemic flora and 1500 to 2500 for the Pyrenean endemisms. This shift implies that the decrease of taxa at high altitudes is more abrupt for endemisms than for the non-endemic flora. At low altitudes almost no Pyrenean endemisms are described. Previous differences remain significant attending to vegetation belts as it shows figure 7b and table 2. At montane belt the relative representation of the Pyrenean endemic flora is similar to the non-endemic flora, but at higher belt, like subalpine or alpine, the endemisms are overrepresented. At lower altitudinal belts such the submontane and the basal, the Pyrenean endemisms are strongly underrepresented.

Pyrenean endemisms present more constricted altitudinal amplitude than the non-endemics but these differences are not significant (table 2). Figure 7c shows that 75% of the endemisms range between 500 and 1500 meters of altitudinal amplitude and this value is about 60% for non-endemics.

3.5. *Analysis of environmental features*

Figure 8a and table 2 show that Pyrenean endemisms have significantly different habitat distribution than the non-endemic Pyrenean flora. More than 50% of Pyrenean endemisms concentrate at rocky habitats and secondarily about 25% of them at grasslands. All other habitats are underrepresented among the endemisms compared with the non-endemic flora. These differences in habitats also conduct to a significant more habitat naturalness among the Pyrenean endemics than among the non-endemic flora as it is shown in figure 8b and table 2. No Pyrenean endemisms are found in low naturalness habitats.

Edaphic affinity is significantly different between the endemic and the non-endemic flora of the Pyrenees, as shown in Figure 8c and Table 2: endemisms are biased towards taxa with defined substrate affinity, particularly towards calcicolous ones.

3.6. *Life-forms*

Figure 8d and Table 2 show that the life forms of the Pyrenean endemic species are significantly different from the non-endemic flora. Whereas the hemicryptophytes are largely the most represented life form among the Pyrenean non-endemic taxa, the chamaephytes are the most represent-

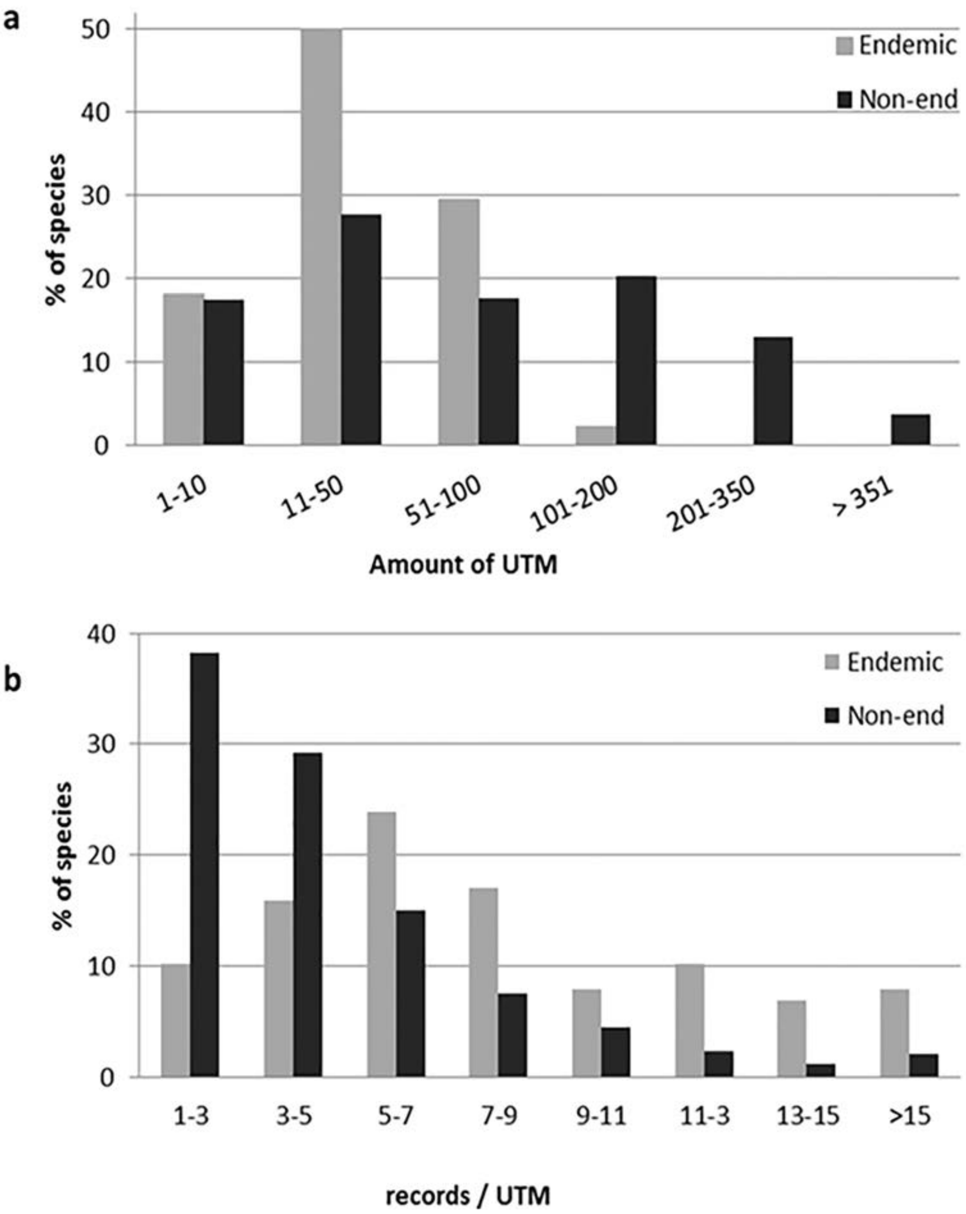

Figure 4: 10x10 Km UTM records of the Pyrenean endemisms (Endemic) and the non-endemic flora of the Pyrenees (Non-end). a) Amount of UTMs where the species are recorded b) average records per UTM grid.

Figura 4: Número de UTMs de 10x10 Km ocupados por las especies endémicas (Endemic) y no endémicas (Non-end) del Pirineo. a) Número de UTMs donde la planta está presente, b) media del número de citas por cuadrícula UTM.

ed among the endemic species, although the hemicryptophytes remain in second position. The geophytes show similar percentages for both groups and the rest of life forms are strongly diminished among the Pyrenean endemisms.

4. Discussion and conclusions

A careful and integrative revision of the Pyrenean flora reveals that this mountain range does not host a particular high frequency of endemisms, as only 2.4% of native species in the Pyrenees would be restricted to this territory. This number could increase up to 5% when taking into account all microtaxa included in apomictic genus and the endemic subspecies belonging to taxa with a wider distribution range, as already documented by Villar & García (1989). In any case, the number and percentage of endemisms in the Pyrenees contrast with the 477 endemics and subendemics –included apomictic taxa- listed in the Alps (10.8%, Aeschimann *et al.,* 2004), or the 215

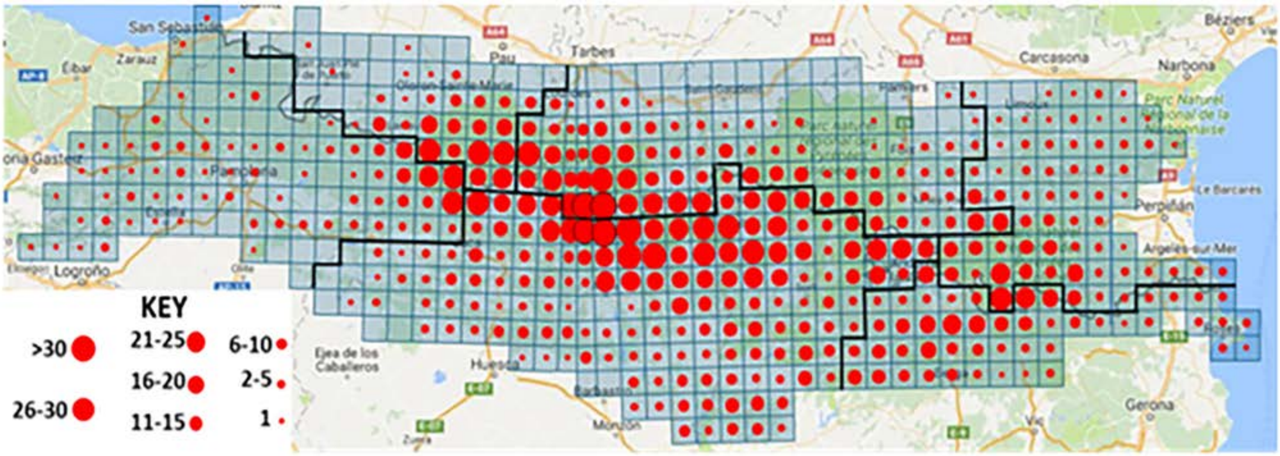

Figure 5: Number of endemisms in each 10x10km UTM grid.
Figura 5: Número de endemismos en cada cuadrícula UTM de 10x10km.

listed in the Carpatians (5,5%, Kliment *et al*., 2016), and it is more similar to the about 90 taxa-including apomictic ones— listed in the Sierra Nevada (4.2%, Blanca, 2002) and higher than the 1-2% reported for the Cantabrian Range (Jiménez-Alfaro, 2008). Nevertheless, further investigations clarifying the taxonomy of the excluded taxa may slightly increase the number of endemic taxa.

Overall, percentages of vascular endemisms in mountain areas are far below of those of oceanic islands such as Canary Islands (25%, Izquierdo *et al*., 2004), or Madagascar (over 50%, Madagascar Catalogue, 2017), but closer to 7% described in Mediterranean islands like Corsica (Médail & Verlaque, 1997) or Baleares (Govern des Illes Balears, 2012). This pattern suggests that mountain areas are not as isolated to behave as strong refuge as thought. The glacial cycles of the quaternary, which are proposed to promote speciation and radiation of different genus (Koch *et al.,* 1999; Cires & Fernández, 2015), need to be understood as a whole, taking into account glacial and interglacial cycles, which might allow or promote plant migration and therefore reduce the number of narrow distributed mountain endemisms. Buira *et al*., (2017) reported that Iberian endemisms tend to concentrate in the Northern Western mountains, but with low number of species reduced to a single mountain chain. For instance Villar *et al.,* (1994) recorded 60 vascular plants endemic to the Pyrenees and the Cantabrian mountains, a similar number to the exclusively Pyrenean endemisms. Similar results are described by Jimenez-Alfaro (2008) in the Cantabrian Range. This issue needs further investigation in order to research not only the role of the Pyrenees as a refuge during the glacial maximum, but also as a radiation center in the interglacials (Hewitt, 2004; Loidi *et al.*, 2015).

Radiation processes have been already described in the phylogeny of several genus of families like CARYOPHYLLACEAE (Oxelman *et al.,* 1997; Greenberg & Donoghue, 2001), SAXIFRAGACEA (Deng *et al.,* 2015), PRIMULACEAE (Martins *et al.,* 2003), BRASSICACEAE (Bailey *et al.,* 2006; Rešetnik *et al.,* 2013), which concentrate endemisms in the North hemisphere mountains. In the Pyrenees, endemisms are also concentrated and restricted to few genus and families, included the above mentioned, confirming that radiation processes are not random events, but are evolutionary favored in some lineages.

From an evolutionary perspective, the study of geographical distribution of the endemisms is very informative. It is remarkable that the distribution of the Pyrenean endemisms is particularly well known, as illustrated by the significantly higher number of records per UTM grid they exhibit. Although more attention has been traditionally paid to endemic taxa, our data show a significantly more constricted distribution than the non-endemic flora. Therefore, an ideal complete knowledge of the distribution of all Pyrenean taxa might only accentuate this difference. Another remarkable finding is that all Pyrenean endemisms present continuous distributions at regional scale. The more restricted area that Pyrenean endemisms occupy, however, contrasts with their abundance when present, which is similar to the non-endemic set of plants in the Pyrenees. Moreover, the endemic Pyrenean element presents wide altitudinal amplitude, which is not significantly different from the non-endemics, indicating that the endemic taxa are widely distributed where they are present. These results suggest that the perception of rarity linked to the endemisms is more related to their reduced geographic distribution than to being rare in the environments where they occur.

Our results, therefore, evidence that the distribution areas of the endemisms are locally continuous and geographically restricted within the Pyrenees, but locally abundant as the non endemic flora. These two facts suggest an effective short distance dispersal capacity (sexual and vegetative) together with a strong limitation for long distance seed dispersal of this group of taxa, which may be a clue to understand endemic distribution. Ecological factors like the seed dispersal mechanisms of these endemic taxa

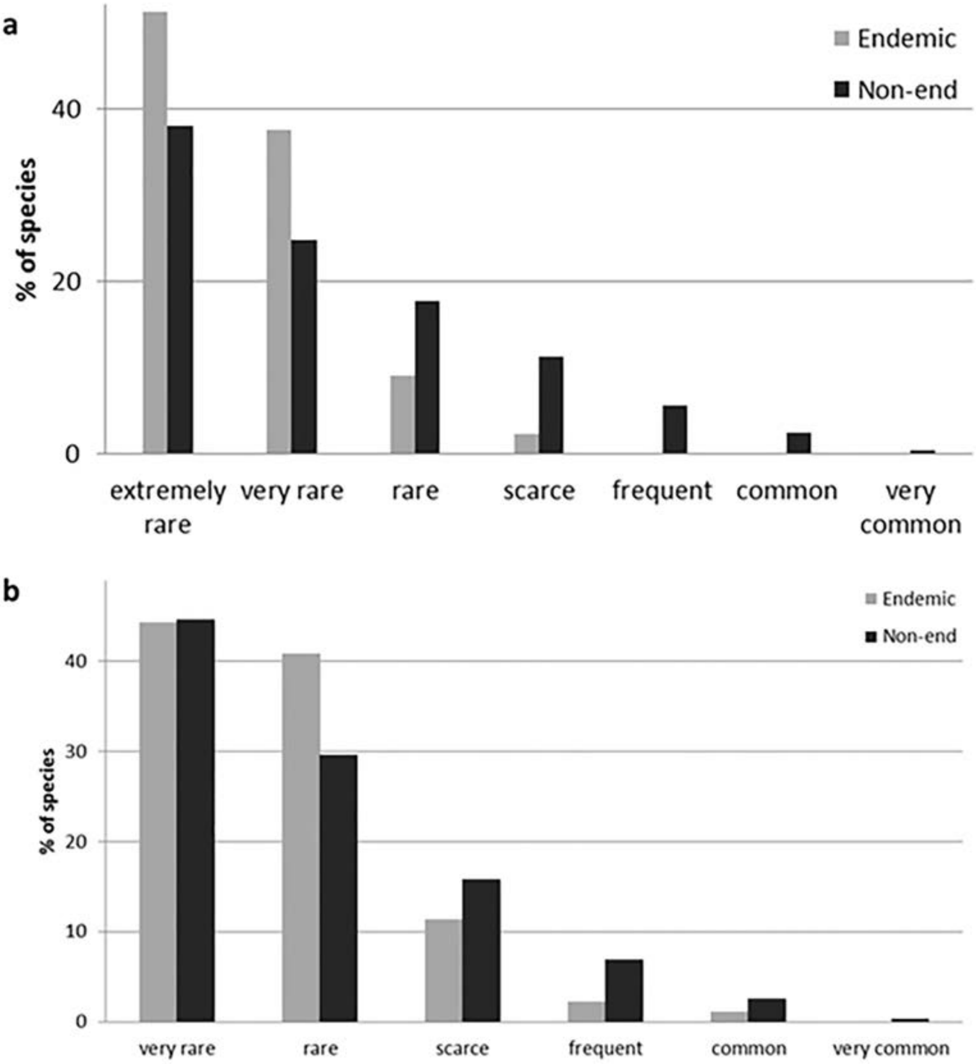

Figure 6: Abundance of the Pyrenean endemisms (Endemic) and the non-endemic flora of the Pyrenees (Non-end) a) Overall abundance in the Pyrenees. b) Abundance of taxa in the sectors in which they are present.

Figura 6: Abundancia de los taxones endemismos (Endemic) y no endémicos (Non-end) del Pirineo. a) Abundancia considerando todo el Pirineo b) Abundancia considerando únicamente el número de sectores donde están presentes las plantas.

would help to understand its aggregated distribution. On the other hand, a clear fragmentation was found in the endemic element between the western and eastern Pyrenees, as for the entire Pyrenean flora (Izard, 1985). In the western Pyrenees the Atlantic and oceanic influence is more dominant, whereas in the eastern Pyrenees the Mediterranean influence is preponderant. The central Pyrenees are indeed characterized by more continental conditions. This longitudinal climatic variation seems to limit the migration of many plant taxa across the East-West axis due to restriction or absence of suitable habitats. Oppositely, latitudinal fragmentation is diminished although the altitudinal barrier might suggest a strong North-South differentiation in the Pyrenees. It is relevant the contrast with the Alps, where the endemisms are predominant in the peripheral areas (Schoswetter *et al.,* 2005) whereas in the Pyrenees they are more abundant in the highest part of the territory.

As described previously for a fraction of the range (García & Gómez, 2007), Pyrenean endemics preferably occupy rocky habitats, and elevations of 1.300-2.500 meters. As previously discussed, it has been largely proposed that mountains promote isolation of the flora in the context of the glacial cycles of the quaternary (Brochmann *et al.,* 2003; Hewitt 2004). This could easily explain why endemisms are rare in lowlands and concentrate above the montane vegetation belt, above the 1.500 meters. These isolation processes are also habitat dependent, and rocky and grassy habitats, where the Pyrenean endemisms

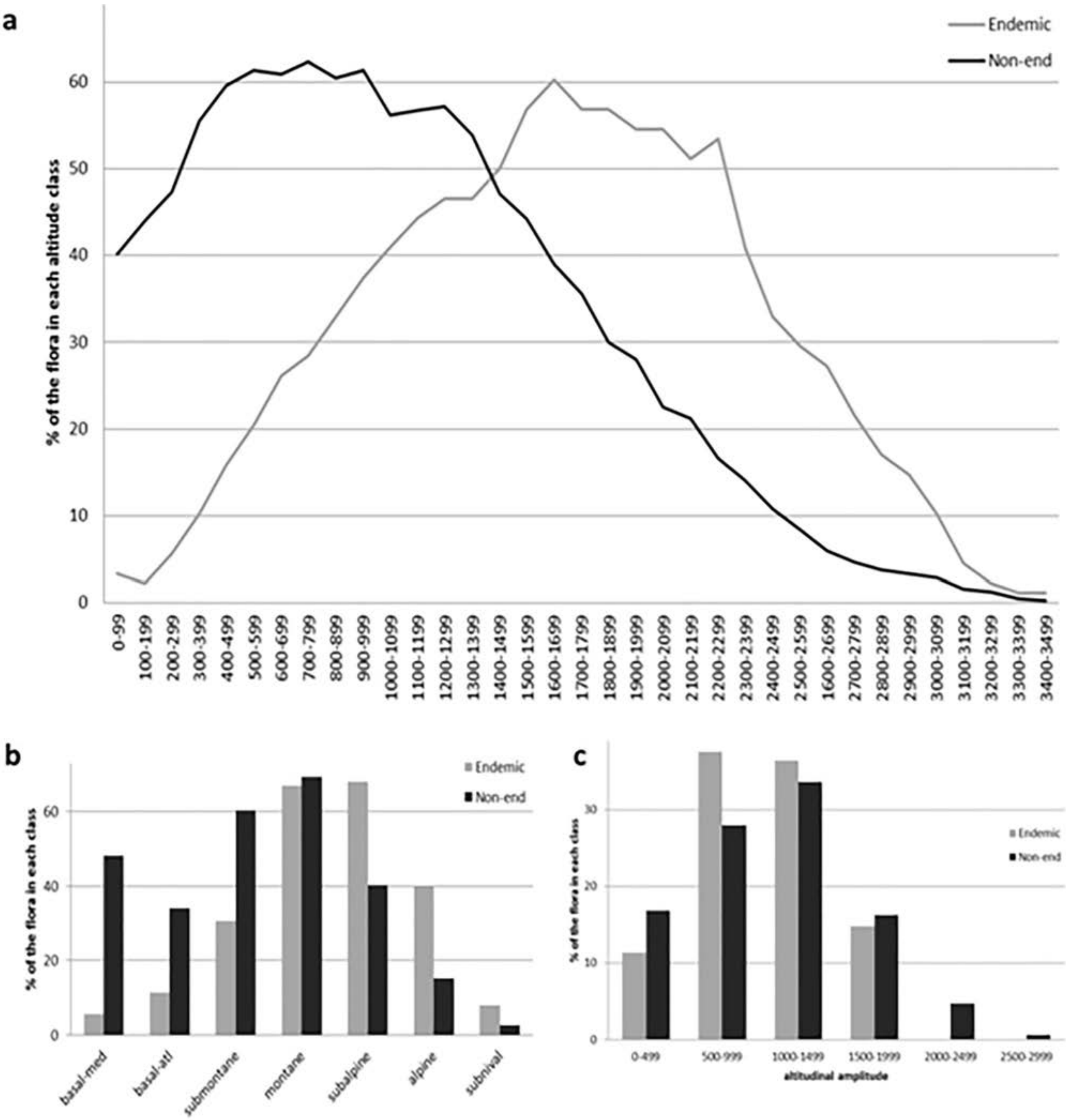

Figure *7:* Altitudinal distribution of the Pyrenean endemisms (Endemic) and the non-endemic flora of the Pyrenees (Non-end). a) % of species recorded in the 100 m altitude classes represented. b) Percentage of species recorded in each vegetation belt c) Percentage of species with documented altitudinal amplitude classified in classes of 500 m.

Figura 7: Distribución altitudinal de las especies endémicas (Endemic) y no endémicas (Non-end) del Pirineo. a) Porcentaje de especies representadas en cada intervalo de 100 m de altitud. b) Porcentaje de especies representado en cada piso de vegetación. c) Porcentaje de especies en cada clase de amplitud altitudinal de 500 m.

concentrate, have been historically among the most patchy and isolated habitats in the mountain regions (Billings, 1968).

One of the endemics, *Borderea chouardii,* has been intensively studied (García *et al.*, 2002 and 2012) because it is restricted to a single Pyrenean location in the entire world and therefore considered highly endangered. Nevertheless, there are other endemic species very restricted in distribution that might be more sensitive to local perturbations which remain poorly re-

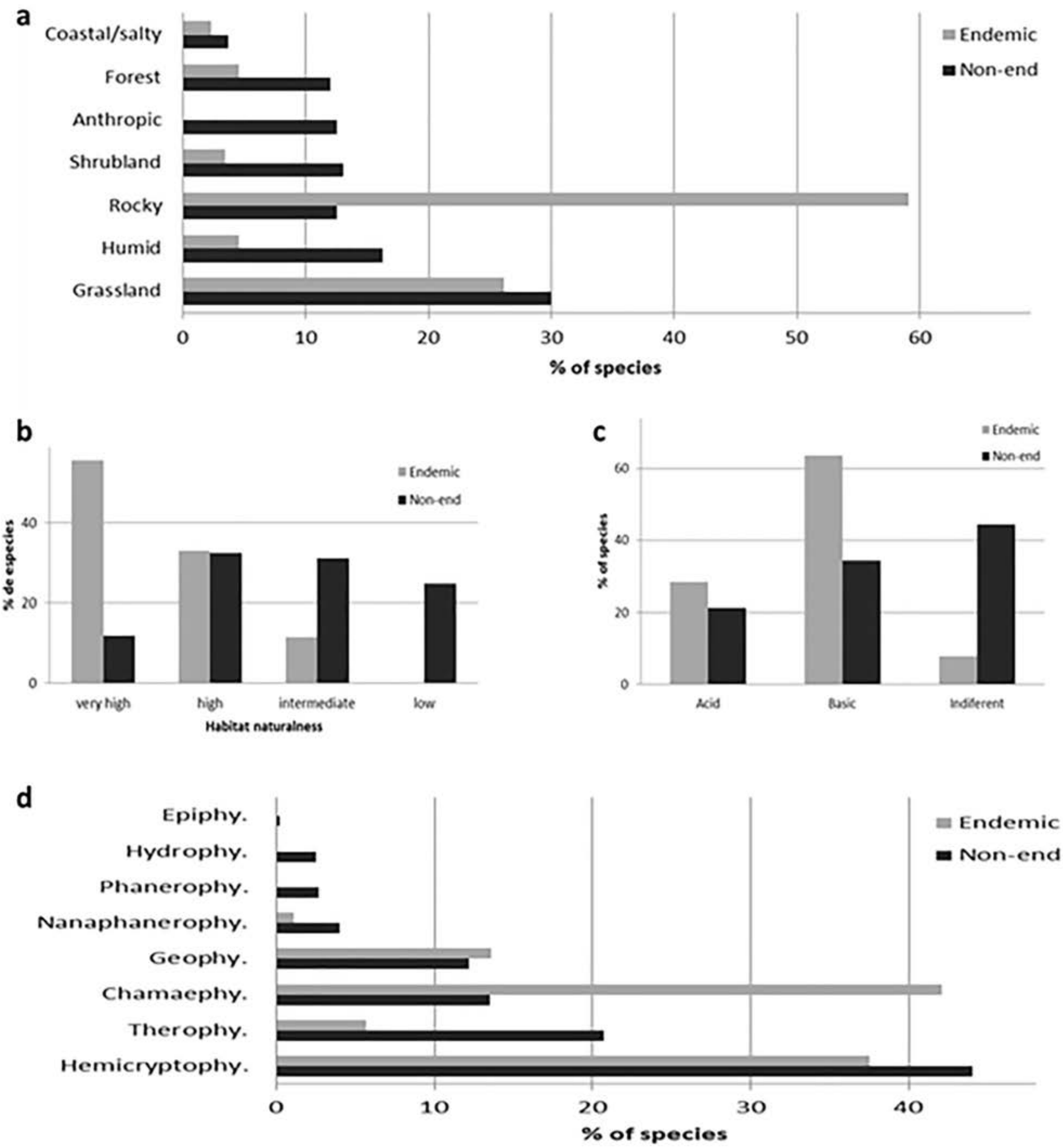

Figure 8: Comparisons among some environmental features and life-forms of the Pyrenean endemisms (Endemic) and the non-endemic flora of the Pyrenees (Non-end). a) Habitat preference b) Habitat naturalness c) substrate preference and d) Life form.
Figura 8: Diferentes comparaciones en la ecología y formas biológicas de los endemismos (Endemic) y la flora no endémica (Non-end). a) Hábitat preferencial. b) Naturalidad del hábitat. c) Preferencia edáfica. d) Forma biológica.

searched. For example, *Armeria euscadiensis*, *Erigeron cabelloi*, *Polygala vayredae*, *Primula subpyrenaica* or *Seseli farrenyi* should be investigated to describe their basic biological traits and demographic trends in order to adopt appropriate conservation strategies.

The results of the geographic distribution of endemisms have administrative implications. From a conservation perspective, the highest responsibility lies on large regions like Aragon, Catalunya or Haute-Pyrénées, which concentrate most endemisms. These regions represent most of the area of the Pyrenees. Geographically marginal and smaller regions like Euskadi, Aude and Navarra host less endemic taxa as expected by their location and size.

In summary, after a careful and integrative review of the Pyrenean flora using near 2 millions of records, the endemism rate turned out to be lower than expected and published so far, although not so different to other European mountain floras. Our results about geographical distribution patterns suggest that isolation during the glacial cycles might have not been as strong as expected either. Pyrenean endemic plants tend to be chamaephytes which concentrate in grasslands and rocky habitats, on limestone substrates at 1.200-2.500 meters of altitudes. There is a clear taxonomic bias in families and genus represented in the Pyrenean endemisms towards some alpine groups, which are also more sensitive to speciation processes in other mountain chains of the Norther Hemisphere. Further and deeper analysis, integrated with neighbour mountain chains might conduct to new understanding of the evolutionary process which led to the present flora distribution of the Pyrenees. Finally, we consider that the accurate knowledge of the Pyrenean endemic taxa distribution should help to adopt effective conservation strategies.

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