Pirineos. Revista de Ecología de Montaña
Vol. 172
Jaca, Enero-Diciembre, 2017, e027
ISSN-L: 0373-2568
doi: http://dx.doi.org/10.3989/Pirineos.2017.172002

SPATIAL DISTRIBUTION AND ENVIRONMENTAL ANALYSIS OF THE ALPINE FLORA IN THE PYRENEES

Distribución espacial y análisis ambiental de la flora alpina en los Pirineos

D. Gómez[1]*, J.V. Ferrández[1], P. Tejero[1], X. Font[2]

[1] Instituto Pirenaico de Ecología (CSIC). Avda. Nuestra Señora de la Victoria, 16. 22700 Jaca (Huesca, España).
[2] Centre de Documentació de Biodiversitat Vegetal (CeDocBiV) Baldiri Reixac, 2 08028 Barcelona.

Identificador ORCID de los autores y e-mail:
D. Gómez: http://orcid.org/0000-0002-9738-8720. E-mail: dgomez@ipe.csic.es
J.V. Ferrández: http://orcid.org/0000-0003-2618-1797. E-mail: jv_ferrandez@yahoo.es
P. Tejero: http://orcid.org/0000-0001-6735-3423. E-mail: ptibarra@ipe.csic.es
X. Font: http://orcid.org/0000-0002-7253-8905. E-mail: xfont@ub.edu
*Autor corresponsal.

Recibido: 19-04-2017. **Aceptado:** 12-06-2017. **Fecha de publicación on-line:** xx/xx/2017

Citation / Cómo citar este artículo: Gómez, D., Ferrández, J.V., Tejero, P., Font, X. (2017). Spatial distribution and environmental analysis of the alpine flora in the Pyrenees. *Pirineos, 172,* e027. doi: http://dx.doi.org/10.3989/Pirineos.2017.172002

ABSTRACT: On the basis of the digital edition of the "Atlas of the vascular flora of the Pyrenees" (www.florapyrenaea.org), the alpine flora of this mountain range is delimited in order to know its diversity and the different patterns of its spatial distribution, along with some other environmental characteristics. The Pyrenean alpine flora is made up of 645 taxa (630 species and 15 subspecies). All the administrative regions harbour more than 60% of the alpine plants, with Catalonia and Aragon reaching the highest values (around 90%). Along the altitudinal gradient, the highest plant diversity is found between 2300 and 2600 m. a. s. l., although 25% of the total alpine flora goes beyond 3000 m. On the other hand, a remarkable number of alpine plants live in the lowlands, and thus more than 300 alpine plants can be found below 1500 m. The average altitude range of the alpine plants is 1369 m, 300 m wider than that observed for the whole Pyrenean flora. Life-forms, habitat distribution and habitat naturalness of alpine plants are significantly different from those of the whole Pyrenean flora. Distribution of abundance categories also shows values of rarity significantly lower among alpine plants than for the whole flora. More than half the Pyrenean endemic plants are present in the alpine flora. High diversity and wide ecological amplitude of the alpine flora must be taken into account either when considering vulnerability of alpine plants facing "global change" or when addressing conservation policies for the whole Pyrenees from a common perspective.

KEYWORDS: Floristic diversity; spatial distribution; altitudinal distribution; chorology; life-form; habitat naturalness; rarity.

RESUMEN: La reciente edición del "Atlas digital de Flora vascular de los Pirineos" (www.florapyrenaea.org) permite delimitar la flora alpina para conocer su diversidad, su distribución espacial y algunas características ambientales. La flora alpina de los Pirineos está formada por 645 taxones (630 especies y 15 subespecies). Todas las regiones administrativas muestran más del 60% de las plantas y Cataluña y Aragón tienen la mayor representación (sobre el 90%). En el gradiente altitudinal la mayor diversidad se encuentra entre 2300 y 2500 m, pero un 25% supera los 3000 m. Por otra parte, sorprende el número de plantas alpinas que se encuentran en los niveles altitudinales más bajos: más de 300 plantas viven por debajo de los 1500 m. El rango medio altitudinal de la flora alpina es de 1369 m, 300 m más amplio que el del conjunto de la flora pirenaica. Las formas biológicas, distribución por hábitats y naturalidad de los hábitats de la flora alpina es diferente significativamente del conjunto de la flora. Las categorías de abundancia difieren también significativamente y muestran un menor grado de rareza entre las plantas alpinas que en el conjunto de la flora. Más de la mitad de los endemismos pirenaicos están presentes en la flora alpina. La alta diversidad y amplitud ecológica de la flora alpina debe ser considerada a la hora de evaluar su fragilidad frente al "cambio global" y de definir políticas de conservación desde una perspectiva común para toda la Cordillera.

PALABRAS CLAVE: Diversidad florística; distribución espacial y altitudinal; corología; formas biológicas; naturalidad de los hábitats, rareza.

1. Introduction

Alpine ecosystems are defined as those located above the timberline in the high mountains around the earth or, in a more restrictive way, in the alpine ranges grouped by a common orogeny which in Europe encompasses the Carpathians, Balkans, Alps, Pyrenees and the Cantabrian Mountains. Alpine ecosystems spread over nearly 3% of the terrestrial biomes, and they are located along a wide altitudinal range which, by varying in accordance with latitude, covers from 200-500 m. a. s. l. in sub-arctic regions to 4000 m. a. s. l. in the tropics (Körner, 1999) or to 6000 m in the Himalayas (Bliss, 1971). They are characterised by enduring large environmental restrictions, in particular those related to atmospheric and topographic traits. They differ from the "arctic tundra", although in a number of occasions both ambiences have been considered jointly as the "arctic-alpine" (Billings, 1973).

Alpine climate is characterized by its extreme temperatures with both daily and seasonal large oscillations, high amounts of snow, strong winds and intense solar radiation. These environmental factors show very noticeable gradients related to topography, resulting in a complex mosaic of topoclimates and microclimates and thus, in a remarkable number of habitats. Predominance of ragged terrain reduces soil area; besides, these soils are usually shallow and stony (Billings & Mooney, 1968; Billings, 1979; Körner, 1999).

Alpine flora brings together the plants called cryophytes, which live almost exclusively or preferably in the aforementioned environment; by covering regions so distant on our planet, we can talk about different "tundra floras" that probably evolved in the late Miocene and early Pliocene in the Central Asian highlands and in the Rocky Mountains and spread during the Pleistocene cooling (Bliss, 1971; Billings, 1974) and therefore, its current distribution range is highly linked to the latest glacial evidences and their present remnants. As for their morphology, alpine plants are mostly herbaceous with just some scant dwarf-shrub formations and very scarce, scattered short-height trees belonging to a limited group of species.

Apart from the vascular flora, the presence of mosses and especially lichens must be pointed out. They both gain importance with altitude and replace vascular plants in the most barren spots, playing the role as pioneers in colonizing high mountain areas after the ice thaw. The harsh environmental conditions aforementioned impose on plants a short growing season, soil instability and scarcity, low levels of nutrients and extreme temperatures along with a strong ultraviolet radiation. In many cases, as well, they must stand hydric limitations during the growing season, which implies a limited primary production and a very slow growth in relation to that showed by the mountain flora at lower and middle elevations. However, this deceleration in many life processes does not necessarily mean a decrease in fitness (Körner, 1999).

Enumeration and description of alpine plants has attracted the interest of botanists since long ago (Braun-Blanquet, 1954; Bliss, 1956), because their discovery has been linked to the conquest and exploration of the mountain summits (Rusell, 1878). Besides their remote location they show appealing morphologies and magnificent blooms standing out in the high-mountain stark landscape. Seen from a biological perspective, the study of alpine plants is of special interest to unravel the traits and ecophysiological responses which qualify them to thrive in special environmental conditions (Billings, 1963 & 1974; Billings & Money, 1968; Bliss, 1971; Löve & Löve, 1967a and b; Körner *et al.,* 1989; Körner, 1995 and 1999). In addition to that, these plants are suitable enough for studying biogeography (Riebesell, 1982), phenology (Inouye & Wielgolaski, 2003) and polyploidy (Bliss, 1971), as well as for tracking migration, colonization and isolation of populations by studying the variability and gene flow using molecular biology techniques (Wright, 1943; Vargas, 2003). Most recently high mountain flora has gained a renewed interest in confirming particularly fast, intense and, in some cases, irreversible changes forecast by the IPCC –Intergovernmental Panel on Climate Change– (2007) in the alpine ecosystems. Therefore they are included among the most fragile ecosystems due to the spatial limitation imposed by mountain tops, short stress tolerance (Jernelöv & Rosenberg, 1976) and their vulnerability to global change (Mitchell *et al*., 1990; McCarthy *et al.,* 2001; Gotfried *et al.,* 2012). Finally, it should be pointed out that alpine flora shows a high diversity if we bear in mind the space availability and it is considered especially well represented by plants with narrow distribution ranges, scarce populations, too small and often isolated and, therefore, with a high ecological interest and conservation value (Sáinz Ollero & Moreno Saiz, 2002).

Within the Pyrenees, alpine flora has been considered in various studies of flora and vegetation (Braun-Blanquet, 1948; Vigo, 1976; Sesé *et al.,* 1999), and different aspects of its spatial distribution, ecology (Gómez *et al.,* 1997 and 2003; Illa *et al.,* 2006) and biological traits (Illa *et al.*, 2006). However, most of these studies have a regional scope and some imprecision regarding territorial and floristic delimitation, making it difficult to accomplish a thorough analysis of distribution patterns, abundance and ecological characterization. Thus, updated and accurate data are essential to analyze flora as well as to evaluate its vulnerability and to define conservation measures facing Global Change.

Within this framework and based on the recent digital edition of the Atlas of the Vascular Plants of the Pyrenees (www.florapyrenaea.org), the objective of this study is to establish some basic figures of the Pyrenean alpine flora such as the species number and their altitudinal range, abundance and geographic and habitat distribution.

2. Material and methods

2.1. Study area

The territory of study covers the Pyrenean Mountains with the limits already explained in the introductory article of this same publication. Their total area is about 50,000 km^2 and the area of the alpine belt is of 1,973 km^2 (Figure 1), of which 949 km^2 are located in France, 881 km^2 in Spain and 143 km^2 in Andorra. Ancestral exploitation of the forests of *Pinus uncinata* Ramond ex DC., makes it difficult to discern the alpine belt lower delimitation (Camarero & Gutiérrez, 2004). Moreover, a latitudinal gradient of such boundary –which increases from the edges to the centre of the mountain range according to climate continentality and topography– together with the current recovery of woodland, also complicates the establishment of a single timberline altitude value. In most descriptions of the Pyrenean vegetation this altitudinal threshold tends to be placed between 2100 and 2450 m of altitude (Rivas-Martínez *et al.,* 1991; Ninot *et al.,* 2007). In order to simplify, we have adopted the average value of 2300 m.

The climate of the Pyrenean alpine belt is still little known because of its high variability and the scarcity of weather stations providing long-time series of records. Concerning rainfall, the longest data collection is that at the Midi de Bigorre station, located in Hautes Pyrénées (French Central Pyrenees) at 2860 m. a. s. l., with data of over more than a century. In this location average yearly precipitation between 1960 and 1990 was 1,700 mm (Rivas Martínez *et al.,* 1991), an amount that increases substantially westwards due to Atlantic influence, and which significantly decreases towards the central zone, particularly on the southern slopes of the range, with a marked continentality and Mediterranean influence (Creus, 1982; Izard, 1985). Yearly average temperatures in the alpine belt range between -1 and 3ºC, with an average decrease of 0.6ºC per 100m height (Rivas-Martínez *et al.,* 1991). Regression models of the existing data mark the 0ºC isotherm at 2726 m and, what is more determinant for the flora and vegetation, a mean durations of the vegetative period of 85 days at 2300 m, with a decrease of 11 days per 100 m of altitude and considerable fluctuations imposed by topography (Del Barrio *et al.,* 1990).

2.2. Species and variables selection

As alpine plant we have chosen those found above 2300 m. a. s. l. in at least 10% of their existing citations. Using this criterion, taxa whose presence is considered accidental have been discarded. In many cases these correspond to nitrophile plants found occasionally and adventitiously and

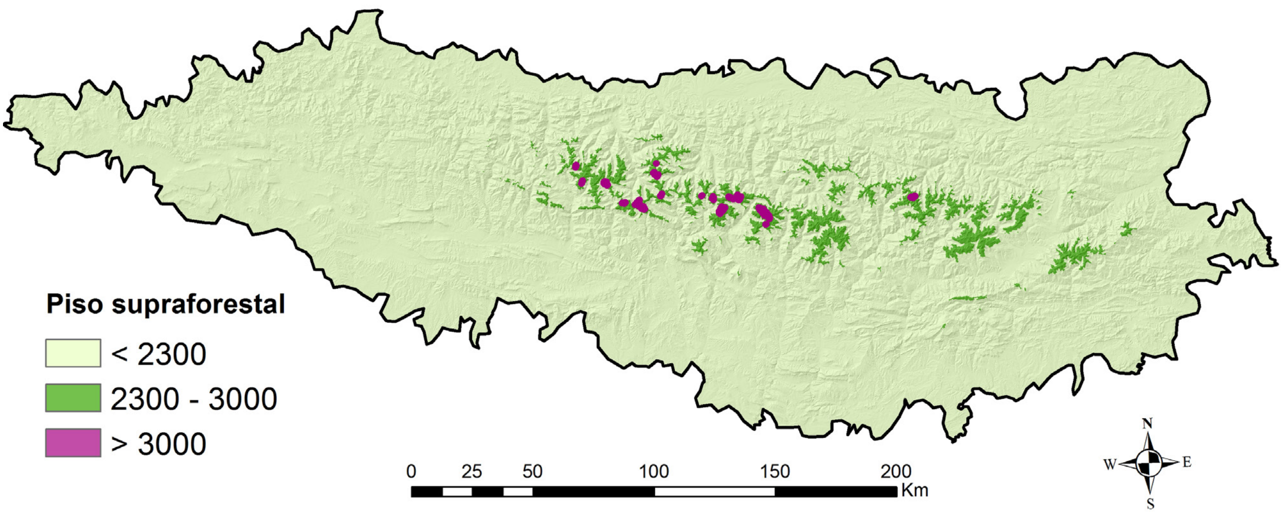

Figure 1: Map showing the delimitation of the alpine territory in the Pyrenees (above 2300 m) and the area located above 3,000 m. a. s. l.
Figura 1: Mapa con la delimitación del territorio alpino de los Pirineos y del área situada sobre los 3000 m.s.n.m.

related to the movements of herbivores or frequented mountain paths. Besides, a poor taxonomic and chorological knowledge of quite a few taxa included in apomictic genera and others with numerous microtaxa has led us to take into account just those clearly identifiable. The genera treated in this synthetic fashion have been: *Alchemilla*, *Taraxacum, Hieracium, Pilosella*, *Armeria* and *Festuca*. The selection described is based upon the data compiled in several floristic Atlas: the ones from the Pyrenees (http://www.florapyrenaea.org), Aragon (http://floragon.ipe.csic.es/index.php), Catalonia (http://biodiver.bio.ub.es/biocat/) and France (http://www.tela-botanica.org/), along with other floras and regional catalogues (Aseginolaza *et al.*, 1985; Aizpuru *et al.,* 1999; Bolós & Vigo, 1984-2001; Villar *et al.,* 1997-2001 and Lorda, 2013) and also upon the "expert-criterion" revision made by the authors.

Values of abundance and spatial distribution have been obtained from the revised maps of the Floristic Atlas of the Pyrenees and also from the number of 10x10km UTM grids. Altitudinal range has been obtained considering the lowest and highest customary altitudes of each plant. Life-forms have been classified according to Raunkiaer (1934). The vegetation belt has been assessed following (Ninot *et al.,* 2007). The chorology has been synthesized from www.florapyrenaea.org. In order to assess the abundance/rarity we have considered the average abundance assigned in www.florapyrenaea.org to each plant in each of the six geographic sectors of the territory (see Gómez *et al.,* in this issue for sector description). The following classes have been considered: "very rare", "rare", "scarce", "frequent", "common" and "very common", which have been allotted to each plant according to the number of references without considering population density. Soil affinity and chorology have been extracted from the aforementioned botanical works but simplifying the categories (Table 1) in order to standardize such information.

Habitat characterization in the alpine belt, up to three for each taxon, has been defined using the information available in herbarium citations, field notes and phytosociological filiation extracted from the bibliography and databases of the Herbarium JACA. If more than one habitat was assigned to a taxon, we chose as "priority habitat" the one in which the plant lives most frequently. The 13 habitats considered are: pastures (calcareous and siliceous), screes (calcareous and siliceous), rocky areas (cliffs calcareous and siliceous), snow beds, wetlands (springs, muddy swamp soils and mires), shrublands, megaphorbs and ruderal communities. Habitat naturalness has been evaluated considering their independence from human influence (Loidi, 1994) with four ordinal values (Table 1).

2.3. Data analysis

To test if the distribution of Pyrenean alpine flora according to different biotic and abiotic factors was significantly different from the entire flora, we performed Chi-square tests. Departing from the percentages of the entire flora we calculated the expected absolute values relative to N=645 –total alpine plant found in this study– to perform the test together with the observed values for Pyrenean alpine plants. Table 1 explains the criteria tested and the classes used. In addition to that, Spearman correlation coefficient was used to determine the relationships between the number of species per altitudinal intervals and their areas. To analyze the differences of chorology between sectors, the Kruskal-Wallis test was used.

3. Results

3.1. Number of species and taxonomic distribution

Alpine plants account for 645 taxa (630 species, of which 11 have two alpine subspecies and two, *Silene vulgaris* (Moench) Garcke and *Ranunculus parnassifolius*

Table 1: Summary of factors for which differences between the Pyrenean alpine plants and the entire flora where tested by a χ^2 test. Number of classes and their description are indicated.
Tabla 1: Resumen de las variables en que se ha analizado mediante test chi-cuadrado la flora alpina y el conjunto de la flora de Pirineos. Se detalla el número de clases y su descripción.

Factor tested	N Classes	Description of the classes
Taxonomy (major groups)	4	Pteridophytes, Gymnosperms, Dicots, Monocots
Geographic extension	6	Species present in 1,2,3,4,5 or 6 sectors
Chorology	6	Wide distribution, Alpines, Boreo-alpines, Endemics, Eurosiberians, Mediterraneans
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; Forest; Anthropic; Shrubland; Rocky; Humid; Grassland.
Habitat naturalness	4	Very high, High, Intermediate, Low
Life-form	7	Epiphytes, Hydrophytes, Phanerophytes, Geophytes, Chamaephytes, Therophytes, Hemicryptophytes.
Substrate affinity	3	Indifferent, Acidic, Basic

L., three). These represent 15% of the total native vascular flora of the Pyrenees and are integrated into 231 genera (30% of the total) and 68 families (47% of the total).

All the alpine taxa have been found in the French Pyrenees, except *Alyssum alpestre* L., *Arenaria ligericina* Lecoq & Lamotte, *Brassica repanda* (Will.) DC. subsp. *cadevallii* (Font Quer) Heywood, *Carex lachenalii* Schkuhr, *Erigeron cabelloi* A. Pujadas, R. García-Salmones y E. López, *Oxytropis lapponica* (Wahlenb.) J. Gay, *Plantago monosperma* Pourret subsp. *discolor* (Gand.) M. Laínz, *Senecio boissieri* DC., *Taraxacum aquilonare* Hand.-Mazz., *Teucrium pyrenaicum* L. subsp. *guarensis* P. Montserrat, *Tofieldia pusilla* Pers., *Veronica aragonensis* Stroh and *Woodsia pulchella* Bertol. On the southern slope (Andorra included) the only alpine taxa not found were *Dracocephalum ruyschianum* L., *Festuca prudhommei* Kerguélen & Plonka, *Hierochloe odorata* (L.) P. Beauv., *Saxifraga adscendens* L. and *Trisetum distichophyllum* (Vill.) P. Beauv.

With regard to taxonomic representation, Figure 2 shows the most abundant families in the alpine flora. Among the 15 families with the largest representation of taxa, 12 coincide with the whole of the Pyrenean flora. In the alpine belt CYPERACEAE, SCROPHULARIACEAE, RANUNCULACEAE, CAMPANULACEAE, SAXIFRAGACEAE and PRIMULACEAE show a proportion of double or even higher that of the proportion in the whole area of the Pyrenees. In contrast, COMPOSITAE, LEGUMINOSAE and APIACEAE are clearly under-represented, with frequencies of half or less of that in the whole of the Pyrenean flora. As for the taxonomic major groups, alpine flora differs significantly from the total Pyrenean flora being dicotyledonous less represented and monocotyledonous and ferns more represented (summarized in table 5).

3.2. *Territorial distribution and altitudinal range*

The regions with the highest number of alpine plants (Table 2) are Catalonia and Aragón which, after Midi-Pyrénées, have the largest areas of alpine belt. At the other end of the scale are Andorra, with just 7% of the alpine

Table 2: Area of the alpine belt and number of alpine taxa in each administrative region of the Pyrenees ordered form west to east.
Tabla 2: Área *del piso alpino y número de plantas en cada región administrativa de los Pirineos, ordenadas de oeste a este.*

	Basque Country	**Aquitaine**	**Aragón**	**Midi-Pyrénées**	**Andorra**	**Catalonia**	**Languedoc**
Area (Km^2)	0	27	452	582	143	572	196
No. taxa	344	395	489	436	423	498	418
% of alpine taxa	62,6	72,0	89,1	79,0	77,0	90,7	76,1

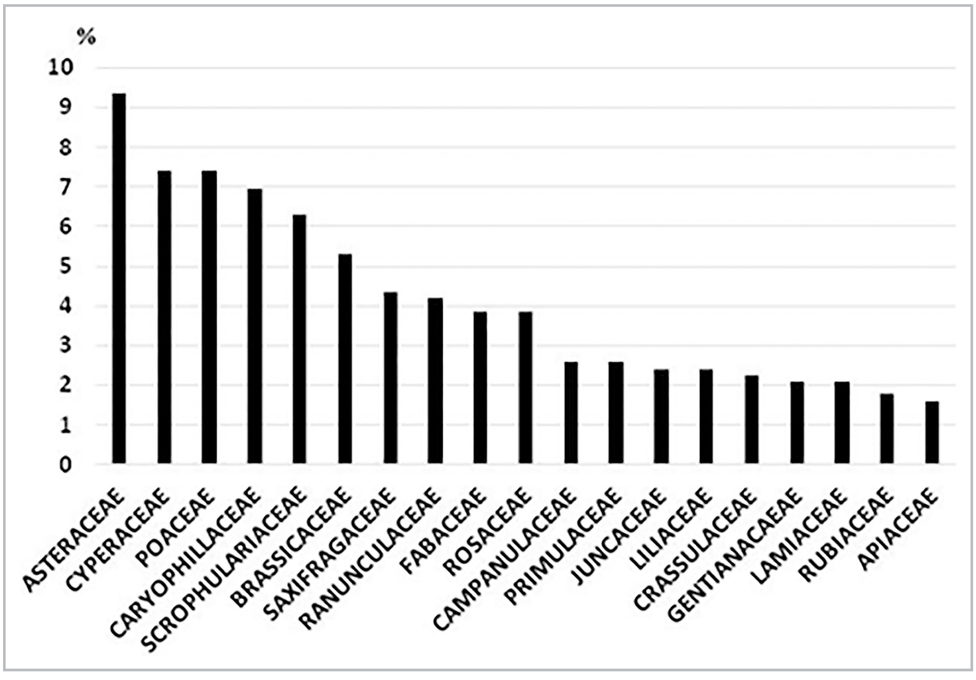

Figure 2: Taxa percentage of the 19 most abundant taxonomic families of Pyrenean alpine flora.
Figura 2: Porcentaje de taxones de las 19 familias más abundantes de la flora alpina de los Pirineos.

territory but 77% of the alpine flora, and the Basque Country, without alpine territory itself, but with more than 62% of the alpine taxa. Figure 3 show the distribution map of the alpine and boreoalpine plants in the Pyrenees with the highest concentration in the central and East sectors.

Table 3 shows the distribution of alpine taxa along the altitudinal gradient. The highest representation occurs between 2300 and 2500 m and almost a quarter of them surpass the 3000 m. A high positive and significant correlation exists between the number of taxa and the area of the different administrative regions (Rho = 0.729; p = 0.011) as well as a significant positive correlation is also found between the altitudinal stretch and the number of taxa per area (Rho = 0.614; P <0.001).

On the other hand, it is worth stressing the high presence of alpine plants recorded in the lower altitudinal strips: about 90% of alpine taxa are represented between 2000 and 2300 m and half of the alpine flora is found below 1500 m whereas 10% is beneath 500 m. At the other extreme, only 23 plants live exclusively above 2300 m, that is to say, they can be considered “strict alpines”. In addition, *Trisetum spicatum* (L.) K. Richt. subsp. *ovatipaniculatum* Hultén ex Jonsell and *Draba fladnizensis* Wulfen, live exclusively above 2600 and 2700 m respectively, while *Phyteuma globulariifolium* Sternb. & Hoppe subsp. *pedemontanum* (R.

Table 3: Area of each 100-metre altitudinal interval in the Alpine belt of the Pyrenees, number and percentage of alpine plants, percentage of the total flora and number of alpine plants per Km^2.
Tabla 3: Superficie (en Km^2), número de taxones alpinos, porcentaje de la flora alpina en cada intervalo altitudinal de 100m del piso alpino; porcentaje respecto al conjunto de la flora de Pirineos y densidad de las plantas alpinas (en nº de taxones por km^2).

Altitude	Area (km^2)	No. alpine taxa	% alpine flora	% total flora	No. alpine taxa/km^2
2300-2400	644	552	85,6	15,1	0,9
2400-2500	525	486	75,3	13,3	0,9
2500-2600	377	371	57,5	10,2	1
2600-2700	226	301	46,7	8,2	1,3
2700-2800	116	229	35,5	6,3	2
2800-2900	47	197	30,5	5,4	4,2
2900-3000	20	145	22,5	4,0	7,3
3000-3100	9,4	133	20,6	3,6	14,1
3100-3200	4,5	75	11,6	2,1	16,7
3200-3300	1,3	53	8,2	1,5	40,8
3300-3400	0,05	30	4,7	0,8	600
> 3400	<0,01	8	1,2	0,2	-

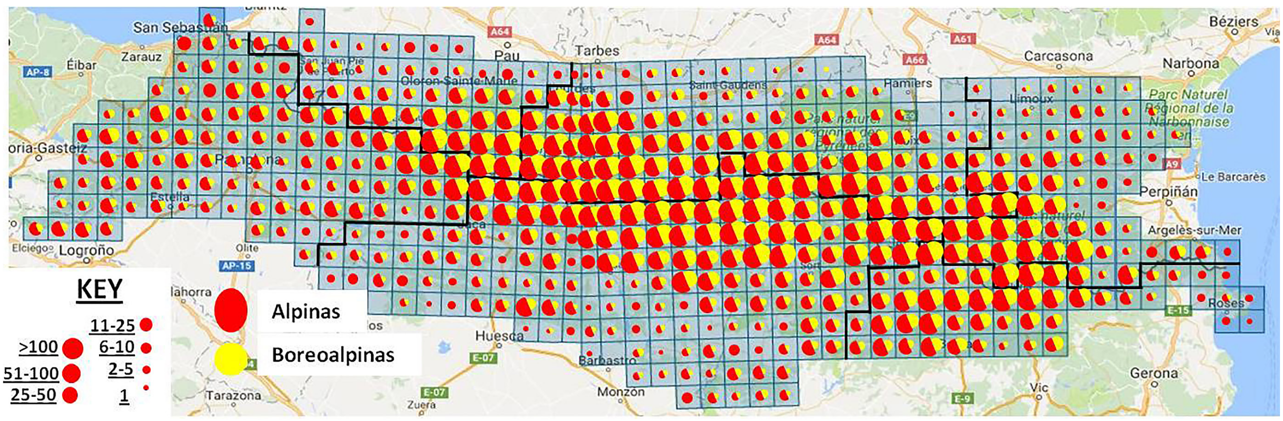

Figure 3: Distribution map of the alpine (245 taxa) and boreoalpine (91 taxa) plants in the Pyrenees. Thick dark lines delimit the 6 sector in which the Pyrenees is divided.
Figura 3: Mapa de distribución de las plantas alpinas (245 taxa) y boreoalpinas (91 taxa) en los Pirineos. Las líneas negras delimitan los 6 sectores en que se divide el Pirineo.

Schulz) Becherer, *Saxifraga adscendens* L., *S. retusa* Gouan, *Senecio boissieri* DC. and *Erigeron cabelloi* A. Pujadas, R. García-Salmones y E. López (this one recently described and therefore still with an imprecise distribution area) are to be found only above 2500 m.

Considering the different vegetation belts (Figure 4), the highest representation of alpine flora is observed both in the subalpine (almost 95%) and alpine (88%) belts, but more than 25% and 10% respectively descend into the basal and montane belts.

With regard to altitude span, it is observed that the average amplitude of the alpine flora is 1369 m versus 1035 m for the whole of the flora. About 75% of the alpine flora occurs within an altitudinal range larger than 1000 m, whereas in the whole of the flora just 54% show the same value (Figure 5). Boreoalpine plants and alpine orophytes, which are dominant in the highest zones, show an average altitudinal interval of 1150 m. Altogether, alpine plants occupy significantly larger altitudinal intervals than the whole of the flora (Table 5).

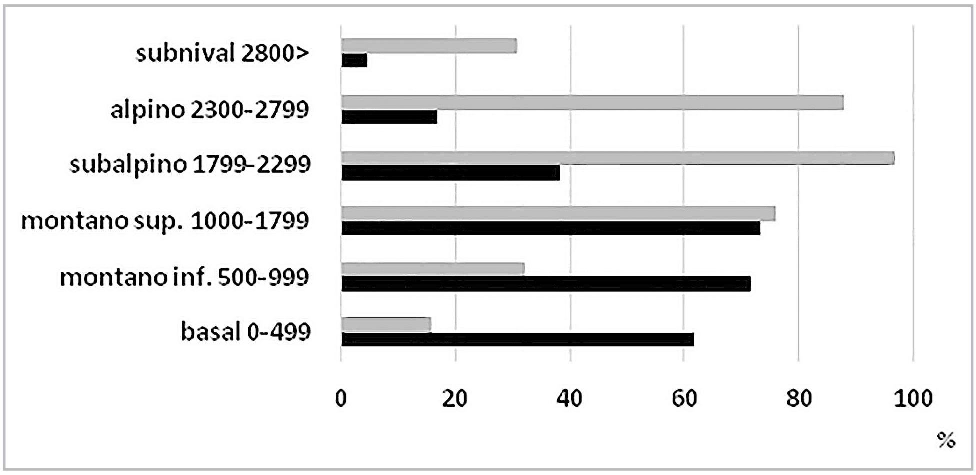

Figure 4: Percentage of alpine flora (grey) and total flora (black, or the reverse) of the Pyrenees in each vegetation belt.
Figura 4: Porcentaje de la flora alpina y del total de la flora presente en Pirineos en cada piso de vegetación.

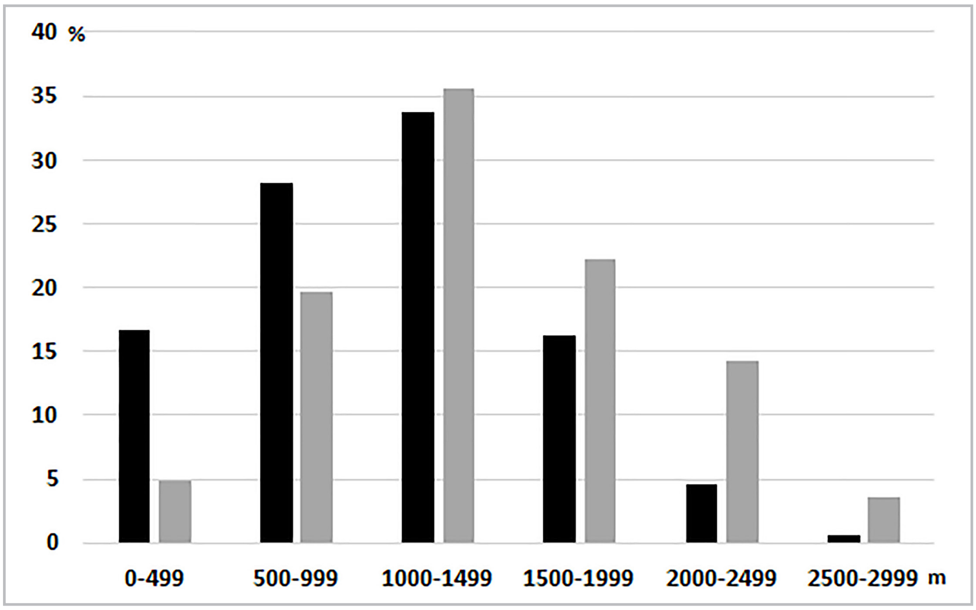

Figure 5: Percentage of plants living in each 500-metre altitudinal range. Alpine plants (in grey) and total flora (in black).
Figura 5: Porcentaje de plantas que muestran los distintos rangos altitudinales de 500 m. Plantas alpinas (columnas grises) y el total de la flora (en columnas negras).

3.3. *Chorology and distribution limits*

Figure 6 shows the distribution of the different chorological groups of the alpine flora. Boreoalpine plants and alpine orophytes represent more than 52%. One fifth of the alpine flora are Eurosiberian taxa. Among the alpine plants there are 72 Pyrenean endemisms that account for 37% of the total endemisms of the Pyrenees (considering endemic subspecies and microspecies). If only strict endemisms are considered at species level, the alpine belt harbours 48 of a total 88 endemic Pyrenean species. Hardly 4% (45 species) of the Mediterranean Pyrenean flora and 11% of the "wide distribution" Pyrenean plants are represented in the alpine belt. Altogether, the alpine flora has a distribution of chorological groups significantly different from the general flora (Table 5).

Considering their total distribution area, 237 alpine taxa have border populations in the Pyrenees: 16 correspond to the northern limit of Mediterranean plants and the rest to southern limits (52 of the 91 Boreoalpine taxa, 148 of the 246 Alpine orophytes and 21 of the 129 Eurosiberian taxa).

3.4. *Abundance and rarity in the alpine flora*

Figure 7 shows the degrees of abundance of alpine flora considering the breadth of its distribution. Proportion of very rare plants is lower in the alpine flora than in the whole of the flora. At the other extreme, frequent, common and very common plants show similar frequencies.

When looking at the distribution range of alpine plants, only 13 species are found in a single sector of the six aforementioned for the Pyrenees, 38 in two, 45 in three, 95 in four, 82 in five and 377 in all the six sectors. Considering the number of 10 x 10-kilometre grids, Table 4 shows the frequency of the alpine flora and of the whole Pyrenean flora measured by their presence in 10x10 km^2 grids. Little more than 5% of alpine plants are represented in less than 10 grids, compared to 39% of the whole flora. Nearly three quarters of them are found in more than 50 grids, while only 34% of the flora as a whole shows such a wide distribution. Altogether, the alpine flora shows a distribution in abundance classes significantly different from that of the whole flora (Table 5).

Table 4: Extension of the alpine plants (in number of 10 x 10 km grids) in comparison with the whole flora of the Pyrenees.
Tabla 4: Amplitud territorial de las plantas alpinas (en número de cuadrículas ocupadas de 10 x10 km) en comparación con el conjunto de la flora.

No. Grids	No. alpines	% alpine flora	% all flora
< 20	33	5,1	31,8
21 a 50	135	20,9	29,8
51 a 100	174	27	12,9
101 a 150	121	18,8	7,7
151 a 200	63	9,8	5,9
> 200	119	18,4	11,9

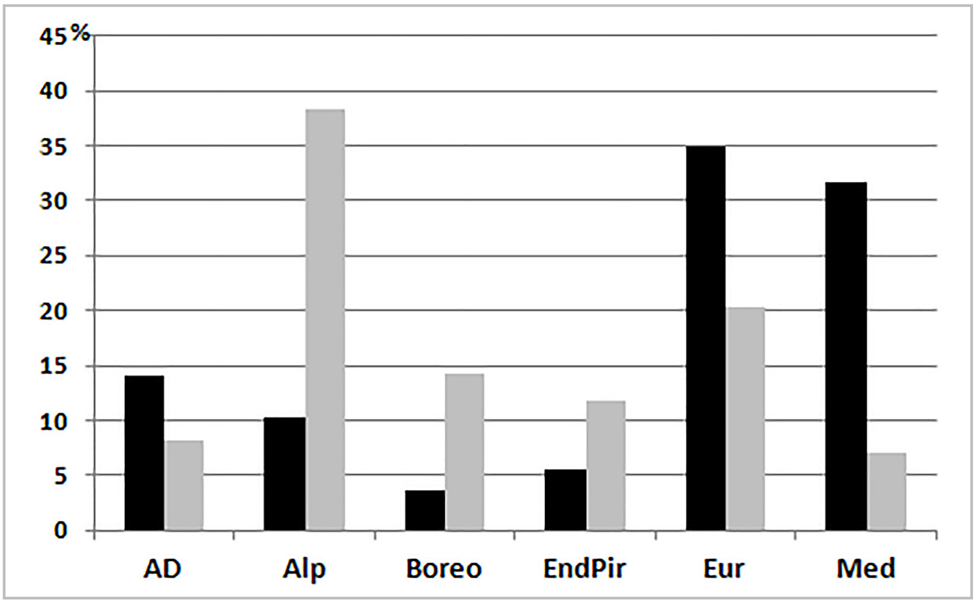

Figure 6: Chorology of the alpine plants (in grey) and of the whole flora (in black). AD: wide distribution; Alp: Alpines; Boreo: Boreoalpines; EndPyr: Pyrenean endemics Eur: Eurosiberians and Med: Mediterraneans.
Figura 6: Corología de las plantas alpinas (columnas grises) y del conjunto de la flora (columnas negras). AD: Amplia distribución; Alp: alpinas; Boreo: Boreoalpinas; EndPyr: Endémicas pirenaicas Eur: Eurosiberianas y Med: Mediterráneas.

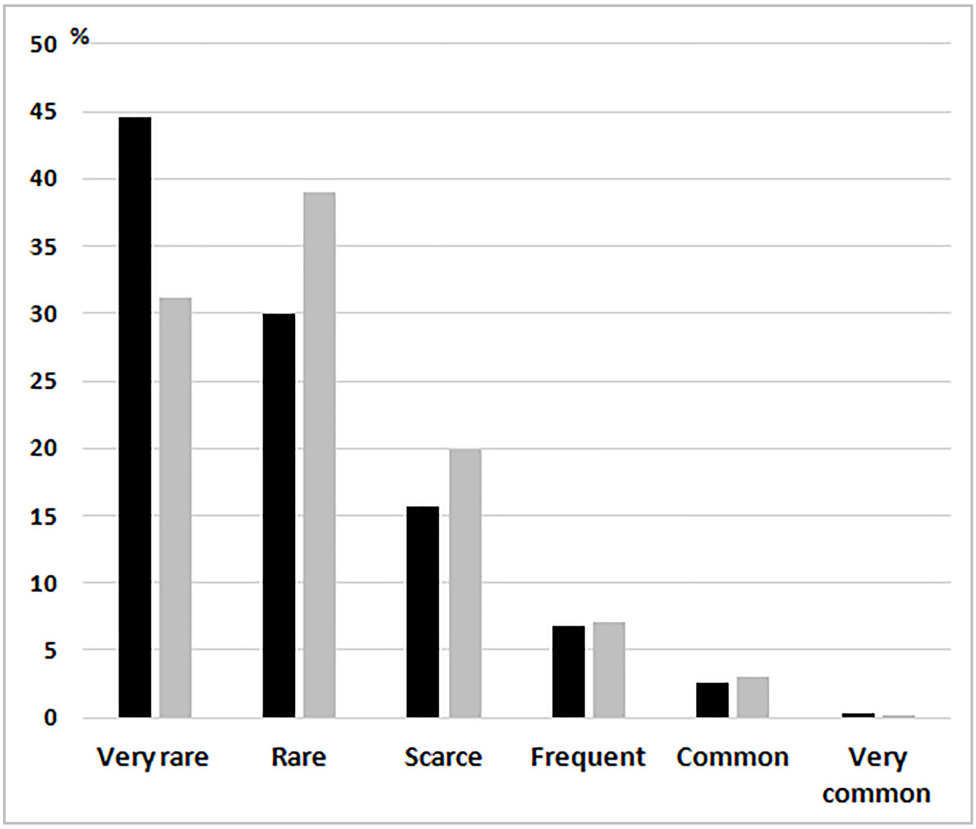

Figure 7: Percentage of the abundance degrees of the alpine flora (in grey) and of the whole flora (in black).
Figura 7: Porcentaje de las categorías de abundancia de la flora alpina (columnas grises) y del conjunto de la flora (columnas negras).

3.5. Life-forms

Alpine flora of the Pyrenees is dominated by hemicryptophytes (55.1% compared to 43.9 of the whole flora) and chamaephytes (24.3% vs 14.2%). Geophytes (12.1% vs 12.2%) and hydrophytes (2.6% vs 2.4%) show frequencies similar to those of the whole flora. Fanerophytes (2.6% vs 6%) and, above all, terophytes (2.8% vs. 20.4%) show a markedly smaller representation, with only three species (*Euphrasia alpina* Lam., *Mucizonia sedoides* (DC.) D.A. Webb and *Sedum atratum* L.) reaching 3000 m. Altogether, distribution of life forms within the alpine flora is significantly different from that of the whole flora (Table 5).

At higher altitudes, there is an increase of chamaephytes that reach 28% above 2800 m and 33% above 3000 m, at the expense of hemicryptophytes that descend, respectively, to 60% and 56% above these altitudes, and geophytes, that decrease from 7% to 5%.

3.6. Soil affinity, habitat distribution and naturalness

Edaphic affinity of the alpine plants with respect to the flora as a whole shows a similar percentage of calciphilous plants (about 35%), a notable higher presence of acidophilus plants (39.5% vs 21.4%) and a lower representation of the indifferent (25% compared to 43.5%). These differences are significantly different from that of the whole flora (Table 5).

49% of alpine flora can be found in three or more habitats, 35% in two of them and 16% in a single habitat. Habitat distribution (Figure 8), considering only the preferred environment occupied by each species, shows the predominance of alpine flora in pastures and rocky habitats (rocks and screes) compared to the whole of the Pyrenean flora; in addition, a similar representation is observed in wetlands (springs, streams and peaty soils) but in shrubland and nitrophile communities it is much smaller.

However, if all the habitats of alpine plants (up to 3) are considered, their distribution shows a smaller difference with respect to that of the total flora, with 30% of the alpine flora in pastures, 23% in ridges and rocky slopes (screes), 19% in rocky areas, 12% in wetlands, 6% in snowbeds, 5% in shrublands, 3% in megaforb communities and 2% in livestock resting areas. Finally, naturalness of the Pyrenean alpine flora shows that 85% of the taxa are characteristic of high or very high natural environments, 12% of middle naturalness habitats and 3% of the low naturalness ones.

Table 5: List of the eight X^2tests performed. The null Hypothesis is listed, with the degrees of freedom (df), the significance of the P-value of the test (***: p-value<0,001) and a quick interpretation which is detailed in the text.
Tabla 5: Lista de las ocho pruebas X^2 mencionadas en el texto. Se detalla la hipótesis nula, los grados de libertad (df), el valor de significación de P (: 0,01<p<0,05; ***: p<0,001) y una breve interpretación de los resultados.*

Test (H0:)	df	p-value	Interpretation
The taxonomic distribution of alpine flora is similar to the total flora	3	*	Pyrenean alpine plants show more monocots and ferns than the total flora.
The altitudinal range of alpine flora is similar to the total flora (Figure 5)	5	***	Pyrenean alpine plants have tighter altitudinal range than the total flora.
The chorology of alpine flora is similar to the total flora (Figure 6)	5	***	There are more alpines and endemics and less Eur. and Med. in the Pyrenean alpine flora compared to the total flora.
The abundance classes distribution of alpine flora is similar to the total flora (Figure 7)	5	***	Very rare plants are not as represented among the Pyrenean alpine plants as they are among the total flora.
The habitat distribution of the alpine flora is similar to the total flora (Figure 8)	6	***	Percentage of plants living in grasslands and rocks is higher among the Pyrenean alpine plants than the total flora.
The substrate affinity of the alpine flora is similar to the total flora	2	***	Pyrenean alpine plants show double percentage of acidophilus taxa compared to the total flora.
The life-form distribution of the alpine flora is similar to the total flora	7	***	Among Pyrenean alpine plants chamaephytes and hemicryptophytes are overrepresented.
The habitat naturalness of the alpine flora is similar to the total flora	3	***	Pyrenean alpine flora has more naturalness than the total flora.

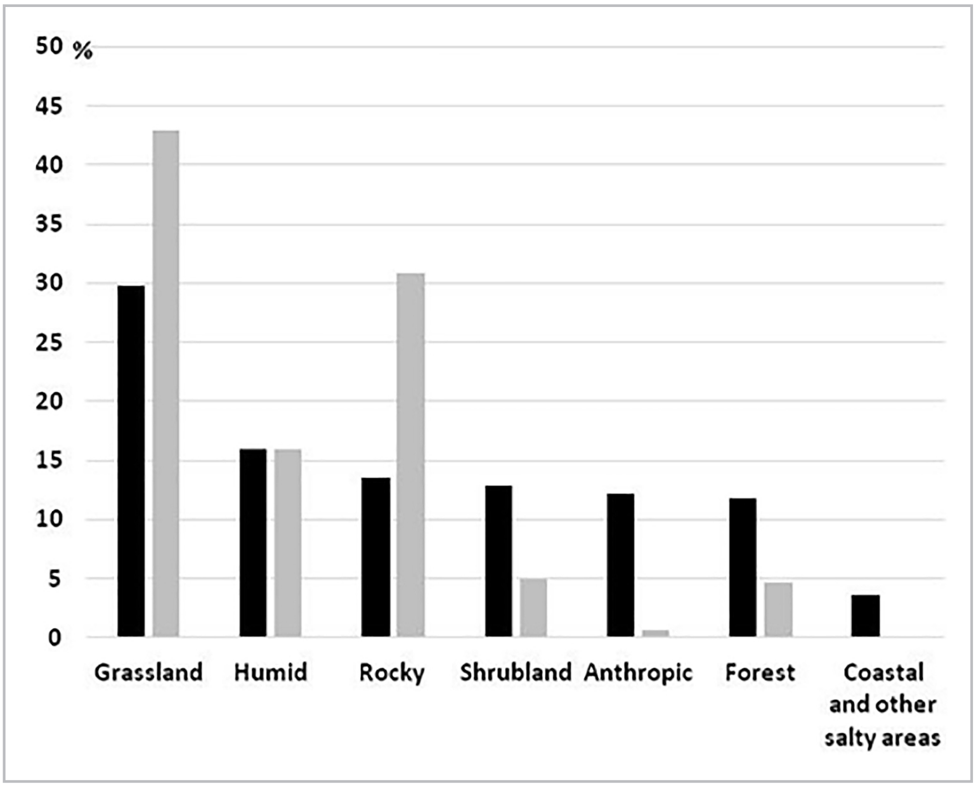

Figure 8: Habitat distribution -in percentage- of the alpine flora (in grey) and of the whole flora (in black), drawn from the preferred habitat of each plant.
Figura 8: Distribución por hábitats (en porcentaje) de la flora alpina (columnas en gris) y del total de la flora (columnas en negro), considerando el hábitat preferente de cada planta.

4. Discussion

The Pyrenean alpine flora shows a very remarkable diversity represented by 15.4% of the total Pyrenean taxa in just 3.8% of the mountain range area, and a plant density per unit of area that increases with altitude up to the summits, as previously verified at regional level (Gómez *et al.,* 1997). On a global scale, the 645 taxa living on the alpine belt of the Pyrenees, even if choosing only the alpine orophytes and boreoalpine ones, which can be considered the most genuine, constitute a very significant number compared to those in the Alps –with an area four times bigger– (Aeschimann *et al.,* 2004) and at an even larger scale, as compared to Asian or American mountain ranges, where this figure is seldom exceeded (Bliss, 1971). In addition, when assessing this diversity, the presence of abundant genotypes closely linked to high mountain environments –which have both a great ecological and economic interest and are largely to be described and characterized– should be considered (Billings, 1957).

Taxonomic representation of the whole of the Pyrenean flora in the alpine flora can be considered to be very complete, with almost half of the families present in the Pyrenees along with one third of the total genera, as compared to the floras from other regions of the world (Löve & Löve , 1967a y b).

As for its territorial distribution, alpine flora is represented in over 50% in all sectors and administrative regions of the mountain range, even in regions with no or little territorial representation of alpine belt, as it is the case of the Basque Country. Alpine flora is represented throughout the altitudinal gradient of the mountain range and it shows a great span regarding the altitude range occupied by its plants, which is larger than in the whole of the flora. This altitudinal range of more than 1000 m, translated to the climatic range of precipitations and, above all, of temperatures, comprises an annual average variation of 6ºC (Del Barrio *et al.,* 1990), the notable gradients derived from microtopography notwithstanding. The distribution breadth of many species, both at territorial and altitudinal levels, suggests checking the interpretation of summits (“nunataks”) as possible floristic shelters during the glacial ages (Villar, 1977).

As for their abundance, alpine plants do not show higher rarity than the flora as a whole, neither in their population size nor in the territorial extension they occupy in the mountain range, although when considering their global distribution area –outside of the Pyrenees–, it is indisputable the marked stenotic character of many of its species.

Regarding their chorology, we could highlight the absolute absence of xenophytes and the significant presence of Mediterranean plants in the alpine belt of the Pyrenees, especially on the southern slopes. The remarkable representation of this chorological group marks perhaps the greatest floristic contrast between both sides of the Pyrenees and can be considered one of its most notable aspects in comparison with other alpine mountain ranges, as well as an outstanding component of its remarkable diversity. On the other hand, population trends of these Mediterranean plants on the Pyrenean alpine belt can be very appropriate indicators in detecting global warming by presenting “a priori” a bigger suitability for altitudinal expansion (Grabherr *et al.,* 2010). Finally, it should be noted that more than a third of the alpine flora has its absolute distribution limit in the Pyrenees.

Life forms of the alpine flora show an increase of chamaephytes with altitude, becoming dominant in the highest peaks. In addition, a very poor representation of therophytes must be noted, as well as a little variation in the rest of the categories. This spectrum of life forms coincides with that observed on a smaller scale in different regions of the mountain range (Ferrández Palacio & Sesé Franco, 1995) and, in general, in other alpine territories of the planet (Raunkiaer, 1934; Cain, 1950; Löve & Löve, 1967).

As for their habitats, the predominance of acidophilous plants, in contrast to that of the flora as a whole, denotes extensive areas of siliceous rock (granites, schists) as well as acidification of soils on limestone substrate due to the prolonged snow-span.

The notable floristic representation of the alpine flora of the Pyrenees, which includes a large amount of the flora also present at low altitudes, together with the environmental flexibility shown by the features analyzed, makes us reconsider the aprioristic interpretation of the alpine belt as “extreme” for high mountain life. From this perspective, it is worth analyzing the diversity and biological characteristics of a flora capable of occupying these environments that are only limiting for plants that are not fit (Körner, 1999). The ecological amplitude of this flora should be taken into account when assessing the fragility of the different plants with regard to climate change and also when designing classification rates and conservation measures (Young *et al.,* 2010).

Lastly, it is necessary to underline the high ecological value of the Pyrenean alpine habitats due to their small size, exclusivity at a peninsular scale, diversity and high naturalness, a reflection of low human impact but also of high sensitivity to disturbance (Billings, 1973 and 1979) and to the effects of global warming (Engler *et al.,* 2009 and 2011) that make them a priority goal in conservation management.

Acknowledgements

The basic data of this work have been in part elaborated from the “Atlas digital de la flora vascular de los Pirineos”, funded by “Fondos FEDER de la UE”, sponsored by a POCTEFA Project of the Comunidad de Trabajo de los Pirineos (CTP) and the Observatorio Pirenaico de Cambio Climático (OPCC). The plant files have been edited by the following authors (in alphabetical order): C. Aedo, I. Aizpuru, J. Ascaso, C. Bergès, M. Domenech, O. Fernández, J.V. Ferrández, X. Font, J. Garmendia, D. Gómez, N. Ibáñez, B. Komac, F. Laigneau, M. Lorda, F. Martínez, J.M. Martínez, J. Molina, N. Montes, J.M. Montserrat, F. Muñoz, C. Navarro, N. Nualart, L. Oreja, J. Pedrol, J. Peralta, D. Pérez, C. Pladevall, J. Puente, A. Pujadas, S. Pyke, J.L. Remón, I. Soriano, J.M. Tison, L. Uriarte, P.M. Uribe-Echebarría, A. Valverde. The institutions that have taken part in the Project are: IHOBE, CSIC (Instituto Pirenaico de Ecología, Jardín Botánico e Institut Botanic), Universitat de Barcelona, Universidad Pública de Navarra, Sociedad de Ciencias Aranzadi, Conservatoire Botanique Mediterranéen, Conservatoire Botanique des Hautes Pyrénées y CENMA de Andorra. To draw maps and figures, we have been assisted by Luis Calderón and Paz Errea. The study is part of the research project PERDIVER (Fundación BBVA).

References

Aeschimann, D., Lauber, K., Moser, D.M. & Theurillat, J.P., 2004. *Flora alpina*. 3 Vol. ISBN 2-7011-3899-X (1). Paris.

Aizpuru, I., Aseginolaza, C., Uribe-Echebarría, P. M., Urrutia, P. & Zorrakin, I., 1999. *Claves ilustradas de la Flora del País Vasco y territorios limítrofes*. Publicaciones del Gobierno Vasco: 831 pp., Vitoria-Gasteiz.

Aseginolaza, C., Gómez, D., Lizaur, X., Montserrat, G., Morante, G., Salaberría, M. R., Uribe-Echebarría, P. M. & Alejandre, J. A., 1985. *Catálogo florístico de Álava, Vizcaya y Guipúzcoa*. Vitoria.

Billings, W.D., Mooney, H.A., 1968. The ecology of arctic and alpine plants. *Biological Reviews,* 43: 481–530. https://doi.org/10.1111/j.1469-185X.1968.tb00968.x

Billings, W.D., 1957. Physiologycal ecology. *Annual Review of Plant Physiology*, 8: 375-391. https://doi.org/10.1146/annurev.pp.08.060157.002111

Billings, W.D., 1963. Arctic and alpine vegetation: plant adaptation to cold summer climates. In: Ives JD, Barry RG (eds): *Arctic and alpine environments*. Methuen, pp 403-443.

Billings, W.D., 1973. Arctic and alpine vegetations: Similarities, Differences and Susceptibility to disturbance. *BioScience*, 23 (12): 697-704. https://doi.org/10.2307/1296827

Billings, W.D., 1974. Adaptations and origins of alpine plants. *Arctic and Alpine Research*, 6: 129-142. https://doi.org/10.2307/1550081

Billings, W.D., 1979. Alpine ecosystems of western North America. In: *Special Management Needs of Alpine Ecosystems* (ed: Douglas A. Johnson) Range Science Series nº 5 (Society for Range management; USDA-SEA-AR, Utah State University).

Bliss, L.C., 1956. A comparison of plant development in microenvironments of artic and alpine tundras. *Ecological Monographs,* 26: 303-337. https://doi.org/10.2307/1948544

Bliss, L.C., 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics,* 2: 405–438. https://doi.org/10.1146/annurev.es.02.110171.002201

Bolòs, O. de & Vigo, J., 1984-2001. *Flora dels Països Catalans*. 4 vols. Ed. Barcino. Barcelona.

Braun-Blanquet, J., 1948. La végétation alpine des Pyrénées Orientales. *Monografías de la Estación de Estudios Pirenaicos e Instituto Español de Edafología, Ecología y Fisiología Veg*etal, 9 : 1–306.

Braun-Blanquet, J., 1954. *La végétation alpine et nivale des Alpes françaises*. Station Internationale de Géobotanique Méditerranéenne et alpine, Montpellier, Communication No., 125: 27–96.

Cain, S.A., 1950. Life-form and phytoclimate. *The Botanical Review,* XVI (1): 1-32. https://doi.org/10.1007/BF02879783

Camarero, J.J. & Gutiérrez, E., 2004. *Climatic Change,* 63: 181-200. http://dx.doi.org/10.1023/B:CLIM.0000018507.71343.46

Creus, J., 1982: *El clima del alto Aragón occidental.* Monografías del Instituto de Estudios Pirenaicos, 109: 233 pp., Jaca.

Del Barrio, G., Creus, J. & Puigdefábregas, J., 1990. Thermal Seasonality of the High Mountain Belts of the Pyrenees. *Mountain Research and Development*, 10(3): 227-233. https://doi.org/10.2307/3673602

Engler R., Randin, C.F., Vittoz, P., Czáka, T., Beniston, M., Zimmermann, N.E. & A. Guisan, A., 2009. Predicting future distributions of mountain plants under climate change: does dispersal capacity matter?. *Ecography*, 32: 34-45. http://dx.doi.org/10.1111/j.1600-0587.2009.05789.x

Engler, R., Randin, C., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.A., Pearman, P.B., Albert, C.H., Choler Ph., De Lamo, X., Dirnböck, T., Gómez-García, D., Grytnes, J.A., Heegard, E., Høistad, F., Le Lay, G., Nogués-Bravo, D., Normand, S., Piédalu, C., Puscas, M., Sebastià, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M., Vittoz, P. & Guisan A., 2011. 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17: 2330-2341 http://dx.doi.org/10.1111/j.1365-2486.2010.02393.x

Ferrández Palacio, J.V. & Sesé Franco, J.A., 1995. *Estudio sobre la flora y vegetación del Piso alpino del Pirineo aragonés*. Informe inédito para el Instituto de Estudios Altoaragoneses, 167pags. (Huesca).

Gómez, D., Sesé, J.A., Ferrández, J.V. & Aldezábal, A., 1997. Altitudinal variation of floristic features and species richness in the Spanish Pyrenees alpine belt. In: *36th IAVS Symposium, Ser. Informes*, 40: 113–123 pp., Univ. La Laguna, Tenerife.

Gómez, D., Sesé, J.A. & Villar, L., 2003. Alpine Biodiversity in Europe, In: L. Nagy, G. Grabherr, C. Körner and DBA Thompson (eds.). *Ecological Studies* Vol. 167. Springer-Verlag, Berlin, Heidelberg.

Gottfried, M. *et al.,* 2012. Continent-wide response of mountain vegetation to climate change. *Nature Climate Change,* 2: 111-115 http://dx.doi.org/10.1038/nclimate1329

Grabherr G., Gottfried, M. & Pauli, H., 2010. Climate change impacts in Alpine environments. *Geography Compass,* 4/8: 1133-1153. https://doi.org/10.1111/j.1749-8198.2010.00356.x

Illa, E., Carrillo, E. & Ninot, J.M., 2006. Patterns of plant traits in Pyrenean alpine vegetation. *Flora- Morphology, Distribution, Functional Ecology of Plants,* 201: 528–546 https://doi.org/10.1016/j.flora.2005.10.007

Inouye, D.W. & Wielgolaski, F.E., 2003. Phenology of high altitude climates. In: *Phenology: An Integrative Environmental Science* (M.D. Schwartz, ed.) Kluwer Academic Publishers. Pages 195-214. https://doi.org/10.1007/978-94-007-0632-3_13

IPCC, 2007. *Intergovernmental Panel on Climate Change, Fourth Assessment Report, Climate Change 2007*: Syntheses Report. UNEP, Genève.

Izard, M., 1985. Le climat. In *Végétation des Pyrénées. Mémoire de la carte de la végétation de la France au 200.000* (G. Dupias). Edition CNRS. Paris.

Jernelöv, A. & Rosenberg, R., 1976. Stress tolerance of ecosystems. *Environmental Conservation,* 3: 43-46. https://doi.org/10.1017/S0376892900017732

Körner, C., 1995. Alpine plant diversity: a global survey and functional interpretations. In: Chapin, Jr., F.S., Körner, C. (Eds.), *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. Ecol. Stud. 113. Springer, Berlin. https://doi.org/10.1007/978-3-642-78966-3_4

Körner, C., 1999. *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems*. Springer, Berlin.

Körner, C., Neumayer, M., Peláez Menéndez-Riedl, S. & Smeets-Scheel, A., 1989. Functional morphology of mountain plants. *Flora,* 182: 353–383. https://doi.org/10.1016/S0367-2530(17)30426-7

Loidi, J., 1994. Phytosociology applied to nature conservation and land managemet. Applied vegetation Ecology. Proceed. 35th Symposium IAVS pp. East China Normal Univ. Press., Shanghai.

Lorda, M., 2013. *Catálogo Florístico de Navarra-Nafarroako Landare Katalogoa*. Monografías de Botánica Ibérica nº 11. J.L. Benito (Ed.).

Löve, A. & Löve, D., 1967a. Origin and evolution of the arctic and alpine floras. In: *North Atlantic Biota and their History*. Macmillan: 430 pp. New York.

Löve, A, Löve, D., 1967b. Continental drift and the origin of the artic-alpine flora. Rev. *Roum. Biol., Sér. Bot*., 12: 163-169.

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J. & White, K.S. (eds.) 2001. Climate Change 2001: The Scientific Basis. Contribution of working group I to the third Assessment Report of the Intergovernmental Panel on Climate Change, IPCC, Cambridge University Press, Cambridge. http://www.ipcc.ch/

Mitchell, J.F.B., Manabe, S., Meleshko, V. & Tokioka, T., 1990. Equilibrium climate change and its implications for the future. In: Houghton, J.T., Jenkins, G.J., Ephraums, J.J. (eds.). *Climate change, the IPCC scientific assessment*. University press, Cambridge, pp. 131-172, Cambridge.

Ninot, J.M., Carrillo, A., Font, X., Carreras, J., Ferré, A., Masalles, R.M., Soriano, I. & Vigo, J., 2007. Altitude zonation in the Pyrenees. A geobotanic interpretation. *Phytocoenologia*, 37(3-4): 371-398. https://doi.org/10.1127/0340-269X/2007/0037-0371

Raunkiaer, O., 1934. *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.

Rivas-Martínez, S., Bascones, J.C., Díaz, T.E. Fernández-González, F. & Loidi, J., 1991. Vegetación del Pirineo occidental y Navarra. *Itinera Geobotánica,* 5: 5-456.

Riebesell, J.F., 1982. Artic-alpine plants on mountain tops: Agreement with island biogeography theory. *The American Naturalist*, 119 (5): 657-674. https://doi.org/10.1086/283941

Rusell, H., 1878. *Souvenirs d'un montagnard*, Pau: Vignancour, Lalheugue.

Sáinz Ollero, H. & Moreno Saiz, J.C., 2002. Flora vascular endémica española. In: *La diversidad biológica de España* (Díaz Pineda, F., coord.). Prentice Hall.

Sesé J.A., Ferrández, J.V. & Villar, L., 1999. *La flora alpina de los Pirineos: un patrimonio singular*. Espacios naturales protegidos del Pirineo. Ecología y cartografía. Consejo de Protección de la Naturaleza de Aragón: 57-76, Huesca.

Vargas, P., 2003. Molecular evidence for multiple diversification patterns of alpine plants in Mediterranea in Europe. *Taxon*, 52: 463-476. https://doi.org/10.2307/3647446

Vigo, J., 1976. *L'Alta montanya catalana. La flora y vegetació*. Centre excursionista de Catalunya. Editorial Montblanc-Martín, 421 págs.

Villar, L., 1977. Una prueba biológica de la existencia de refugios glaciares («nunataks») en el Pirineo occidental. *Trabajos sobre Neogeno-Cuaternario*, 6: 299-303.

Villar, L., Sesé, J.A. & Ferrández, J.V., 1997-2001. *Atlas de la Flora del Pirineo Aragonés*. 2 vols. Instituto de Estudios Altoaragoneses-Consejo de Protección de la Naturaleza. Huesca y Zaragoza.

Young, B., Byers, E., Gravuer, K., Hall, K., Hammerson, G. & Redder, A., 2010. *Guidelines for Using the Nature Serve Climate Change Vulnerability Index*. NatureServe 2010, Arlington, VA (https://connect.natureserve.org/sites/default/files/documents/Guidelines_NatureServeClimateChange-VulnerabilityIndex_r2.0_Apr10.pdf accesed 25/3/2017).

Wright, S., 1943. Isolation by distance. *Genetics*, 28: 139-156.