Trends in altitudinal distribution of plant diversity in the Catalan Pyrenees

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ABSTRACT

In this paper we analyse the species richness of the entire flora and of different distributional and functional subgroups in the Catalan Pyrenees along the altitudinal gradient. We used the Pyrenean data gathered in the Biodiversity Data Bank of Catalonia, which consist on more than 300,000 citations of 2,491 species of vascular plants.

The species number in each 100 m altitude band grows from sea level to 1,000 m and decreases from there upwards, more sharply beyond 1,500 m. The medio-European species form the largest biogeographical group, whereas Alpine and Boreo-Alpine taxa form the smallest group, which nevertheless becomes very dominant towards higher altitudes. As for life forms, hemicryptophytes are generally dominant, followed by therophytes —which are concentrated at lower altitudes— and chamaephytes —which increase slightly with the altitude.

As in other neighboring mountain ranges, species richness in the Catalan Pyrenees follows an asymmetric unimodal distribution along altitude. Pyrenean particularities in the pattern of the entire flora and of the subgroups considered respond to regional physiography, bioclimate and biogeographic particularities.

Key words: biogeography, elevation gradient, endemism, life forms, species richness, vascular flora

Introduction

Understanding the mechanisms behind broad scale patterns in species diversity has been a main topic for ecologists for a long time (Lomolino 2001, Grytnes & McCain 2007). Studies of altitudinal variation in species richness represent a suggesting opportunity to test hypotheses on plant diversity (Nogués-Bravo *et al.* 2008), because there exist many independent altitudinal transects in the world. Relating these patterns to physiography and to taxonomic, functional or

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distributional plant groups provides very valuable information about species distribution, adaptation and speciation (Körner 2000, Lomolino 2001, Rahbek 2005).

Altitudinal plant diversity patterns in the Catalan Pyrenees have not been described in detail yet, although there are studies which describe the effect of altitude on vegetation patterns (Ninot *et al.*, 2007 and references therein) and on aspects of plant diversity in other Pyrenean regions (Gómez *et al.* 1997, Petit & Thompson 1999, Villar *et al.* 2001, Ninot & Ferré 2008, Nogués-Bravo *et al.* 2008).

The aim of this study is to describe the species richness patterns in vascular plants along the altitudinal gradient of the Catalan Pyrenees by using an extensive compilation of observations, which includes herbarium and literature records of the last 126 years. We also analyse the factors determining the altitudinal pattern of species richness by separating the species into taxonomic, functional and distributional groups.

Methods

THE STUDY AREA

The Catalan Pyrenees roughly correspond to the eastern half of the Iberian Pyrenees (41º53'12"-42º54'9" N, 0º35'22"-3º10'17" E), which include most of the south-facing valleys stretching from the vicinity of the highest Aneto massif to the Mediterranean coast, and also one north-facing valley (Val d'Aran) (fig. 1). This area forms an entire physiographic unit, as defined in Bolòs *et al.* (2005).

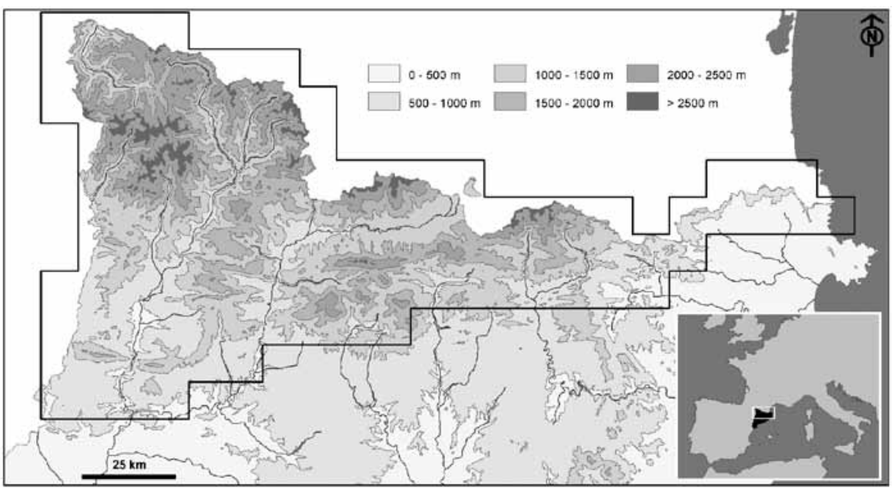

FIGURE 1. Area of study, defined by 10 x 10 km UTM squares in the Catalan Pyrenees.

However, given the size of the UTM squares used in the analyses (10 x 10 km), some surrounding areas beyond the Catalan Pyrenees have also been included (small parts of Aragón, Andorra and southern France). For simplicity reasons, we will refer our study area to as Catalan Pyrenees hereafter.

The high mountain zone (from 1,600-1,800 m a.s.l. upwards) has a typically Alpine landscape and a flora mostly composed by Boreo-Alpine and orophytic (mostly Alpine) taxa. The intermediate elevations (from 700-900 m a.s.l. to the high mountain) host a strong physiographic and bioclimatic diversification. There, the landscape ranges from typically Atlantic in the northern Val d'Aran and other oceanic areas, with prominent medio-European flora, to sub-Mediterranean —transitional between medio-European and Mediterranean— in most southern valleys. At lower altitudes vegetation is mostly Mediterranean, although including scattered medio-European vegetation units (Ninot *et al.* 2007).

Other enviromental factors influencing the local flora are the continentality gradient towards inner valleys, the phylogeographic influence of other mountain ranges (such as the Alps or the Cantabrian mountains), and the complex shifts between siliceous and carbonated substrata. Also, the human influence is especially noticeable in the lowlands, where old land use has produced generalised landscape changes, and decreases towards higher areas, still affected by extensive farming activities (Lasanta 1990).

Data sources and analysis

The data we used to quantify the richness patterns of the flora were obtained from the Biodiversity Data Bank of Catalonia (Font 2008). They correspond to plant citations from a wide scope of papers (local floras, floristic notes or phytosociological works), from personal contributions, and from herbarium records, and have been compiled during the last 20 years. Each plant citation includes the elevation and the coordinates within the UTM grid of 10 x 10 km. We selected the data belonging to any of the squares included totally or partially within the Catalan Pyrenees. We rejected some low-quality data, such as imprecise taxonomical identifications or wrong altitudinal information, and we reduced the data at species level. In that way we built a regional flora of 2,491 species, according to the taxonomy stated in Bolòs *et al.* (2005), obtained from more than 300,000 citations.

We analysed the altitudinal species richness for the entire flora, and then for different taxonomic, functional and distributional groups, as defined by Bolòs *et al.* (2005). The species richness was estimated for each 100 m altitudinal band, from sea level up to 3,404 m, which is the highest point in the Pyrenees. We used the interpolation method as an approximation to the species richness pattern, which assumes the occurrence of a given species along the interval defined by the maximum and minimum altitudes where it has been observed. This may cause an artificially humped pattern if sampling is not complete (Grytnes & Romdal 2008), but given the amount of citations we used, anomalies may be expected only at the edges of the altitudinal gradient.

The number of observations varies very much along the altitudinal gradient, with approximately 2,300 citations at the lowest interval (0-100 m), a maximum of 21,223 citations between 1,200 m and 1,300 m, and less than 200 citations above 3,000 m (fig. 2). This humped pattern is very similar to that of the area occupied by each elevational interval, although the peak maximum area is reached at around 1,000 m of altitude. Thus, it should be emphasized that the large amount of data used are relatively unbiased with respect to altitude and, since 56% of citations come from vegetation relevés, also with respect to species rarity.

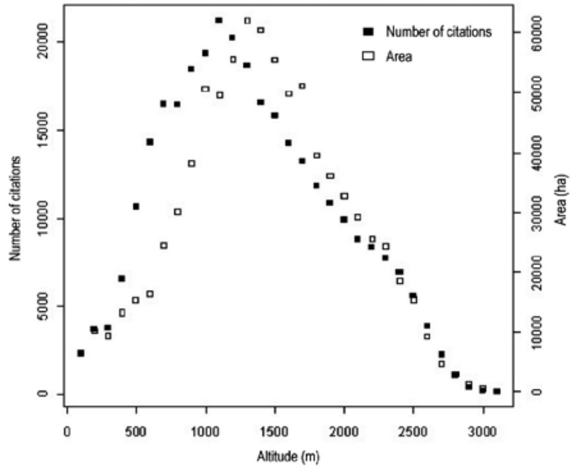

Figure 2. Number of citations and area per 100 m interval along the altitudinal gradient in the Catalan Pyrenees.

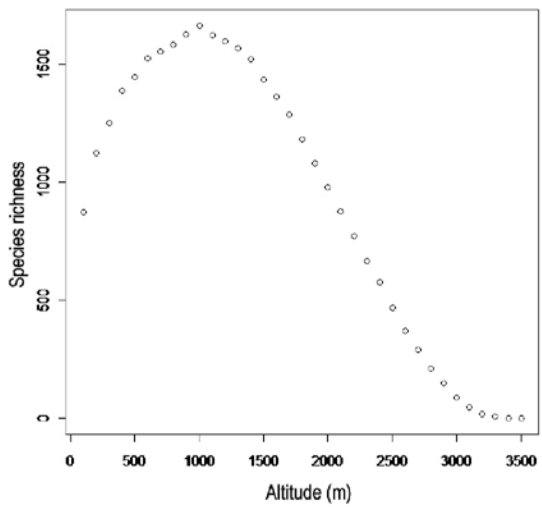

Figure 3. Altitudinal species richness pattern estimated from interpolated ranges along the altitudinal gradient in the Catalan Pyrenees.

Results and discussion

Species richness

The altitudinal species richness pattern shows a very marked humped response, with a maximum of 1,666 species of vascular plants at 1,000 m (fig. 3). There is a very fast increase from sea level to 400 m, and then a moderate increase up to 1,000 m. At higher altitude, there is a marked linear decrease of species richness from 1,400 m to 3,000 m, with an average reduction of 90 species approximately per 100 m interval.

From a taxonomical point of view, larger families such as Asteraceae, Poaceae and Fabaceae have a similar pattern to that of the whole flora (data not shown), which means that broad taxonomical groups within Spermatophyta have presumably experienced similar ecological diversification processes than the entire flora. In smaller families and in Pteridophyte the distribution may be more or less contrasting.

The unimodal pattern for the entire flora and for larger groups is a very common trend in altitudinal or latitudinal gradients (e.g. Odland & Birks 1999, Bhattarai *et al.* 2004, Hillebrand 2004, Romdal *et al.* 2005, Grau *et al.* 2007). It is also very similar to those described in the Aragón Pyrenees (Villar *et al.* 2001), where the species richness is also highest from 800 to 1,300 m a.s.l. approximately.

The maximum richness at low-intermediate elevations could be partially explained by the mid-domain effect hypothesis (Colwell *et al.* 2004), which states that mid-elevation habitats have a higher diaspore input than areas close to the end points of the elevational gradient, where most of the diaspore input comes from one direction only (Grytnes 2003). But the strong variation found in different taxonomic, functional and distributional groups analysed (see later) will indicate that climatic, spatial, biotic, historical or evolutionary factors may be also defining the diversity pattern along the elevational gradient (see Grytnes & McCain 2007).

As for climatic and physiographic factors, low and medium altitudes clearly host greater diversity of soils, outcrops, and landforms, which create a remarkable physiographic diversity. At small and medium scales, such physiographic diversity creates a high diversity of habitats and of local floristic pool (Pausas *et al.* 2003), which may in turn enhance the asymmetry of species richness along the altitudinal gradient. Also, climatic variability is stronger at low altitudes, since there is a greater variability in major climatic descriptors (annual rainfall, spring rainfall, and summer temperature; Ninyerola *et al.* 2000). Moreover, traditional anthropogenic activities such as farming and forest exploitation have created spatial heterogeneity at low and medium altitudes in the Pyrenees (Lasanta 1990), which in turn would increase habitat diversity and species richness in these areas.

Besides, a considerable proportion of medio-European plants may develop in locally humid habitats within Mediterranean lowlands, such as riverbanks or in particularly mild areas. Also, although a number of temperate species may reach the high mountain, their favourable habitats (south-facing, thermal slopes) decrease rapidly above 2,200 m.

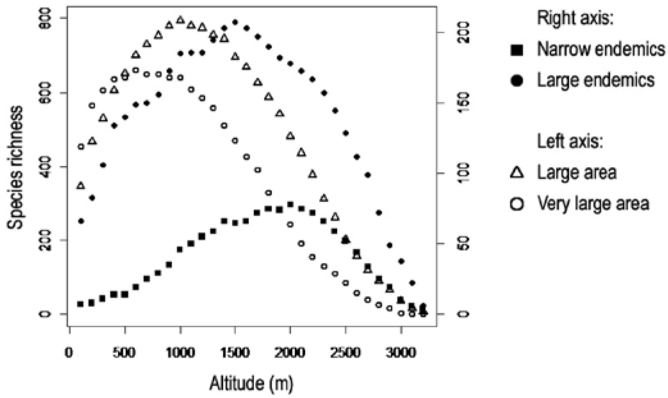

Figure 4. Species richness patterns for groups of different range size along the altitudinal gradient in the Catalan Pyrenees.

Biogeographical groups

When the flora is divided into different range size (fig. 4), we observe a very interesting pattern in the species richness. The number of endemics of small to medium range (117 sps., 5%) peaks at 2,000 m, whereas the endemics of large range (361 sps.) reach the highest richness at 1,500 m; the number of species occurring over a large area (1,163 sps.) peaks at 1,000 m, and the species of very large range (850 sps) reach their maximum at 600 m. The percentage of endemic species increases markedly with altitude, with more than 30% large range endemics and more than 10% of small range endemics above 2,600 m.

These results reinforce the hypothesis that higher degree of isolation generally creates endemism, by means of promoting isolated habitats and speciation (Vetaas & Grytnes 2002). Long-term climatic change strongly has affected vascular flora, as they facilitate hybridisation between previously isolated populations followed by polyploidisation, which may result in new species adapted to new conditions following climatic change (Stebbins 1984, Petit & Thompson 1999). Higher endemic occurrence with increasing altitude has been also stated in other mountainous ranges affected by strong glacial periods and climate changes, as in the Himalayas, in the Andes, in the Alps or in Sierra Nevada (Kessler 2000, Vetaas & Grytnes 2002, Casazza *et al.* 2005, Giménez *et al.* 2004, Grau *et al.* 2007). From a regional scale, the Catalan Pyrenees share many species with close mountain ranges such as the Alps or the Cantabrian range, which may explain that large range endemics are more abundant than small range endemics along the altitudinal gradient.

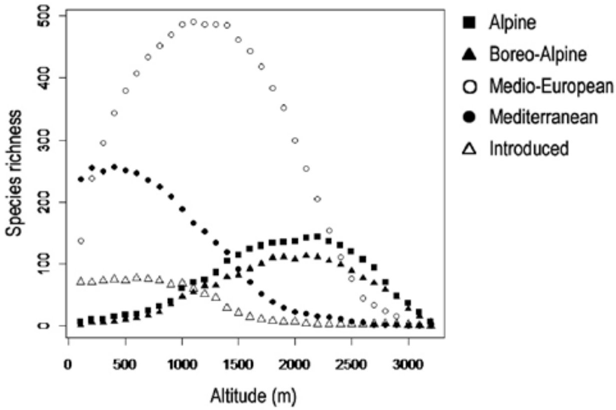

Figure 5. Species richness patterns for different biogeographical groups along the altitudinal gradient in the Catalan Pyrenees.

As for biogeographical types (fig. 5), the species classified as Alpine and Boreo-Alpine are especially abundant between 1,600 m and 2,500 m. The medio-European species are the most abundant and have the widest altitudinal range in general, and they reach their maximum between 1,000 and 1,500 m. The Mediterranean species are very common from the sea level to 600 m, and show a marked and linear decrease upwards. The introduced species form a small group, although a considerable amount is found up to 1,000 m approximately. Thus, these groups respond to the three main altitude units found in the Catalan Pyrenees: high mountain, intermediate altitudes and low altitudes (Ninot *et al.* 2007).

Functional groups

The distribution of each life form shows a humped pattern, but except for geophytes and deciduous phanerophytes, it clearly differs from that of the whole flora (fig. 6). This reinforces the hypothesis that life forms correspond to a marked adaptation to different bioclimatic areas and ecological niches (Raunkiær 1934).

Hemicryptophytes is the biggest group along the whole gradient. Their capacity to actively regenerate most of the above ground structures during the favourable vegetative period in many contrasting bioclimates makes them the most abundant group through the entire altitudinal zonation. The ability of therophytes growing under an irregular climatic seasonality or in areas affected by hard disturbance (Grime 2001) explains their high richness towards lower altitudes. Chamaephytes are very widely distributed along the altitudinal gradient and their relative importance increases at higher altitudes. The stress-tolerant

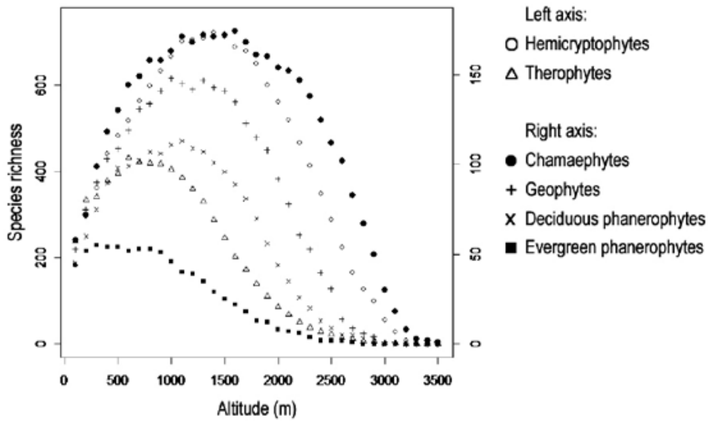

FIGURE 6. Species richness patterns for different life forms along the altitudinal gradient in the Catalan Pyrenees.

strategy dominant in this life form (Grime 2001) allows them to thrive in a wide scope of unfavourable habitats, such as rocky slopes, in the understorey of dry forests and shrubs, and in wind swept edges, which often become dominant in the higher Alpine zone.

Geophytes and deciduous phanerophytes follow the general pattern, which means that their life strategy is neutral concerning the altitude gradient, whereas evergreen phanerophytes are concentred at lower altitudes, mostly related to Mediterranean climate.

Conclusions

Species richness of vascular plants in the Catalan Pyrenees follows an asymmetric unimodal distribution, as described in other ranges, concerning the whole flora and larger subgroups. Such asymmetry may be partially explained in terms of higher physiographic heterogeneity, climatic variability, biogeographic diversity and anthropisation at lower altitudes.

The varying patterns observed in the subgroups considered (life forms, biogeographic groups, families) confirm the distinct role played of a number of environmental factors. This is more evident in smaller groups (i.e. phanerophytes, chamaephytes, Boreo-Alpine taxa, narrow endemics, small families), which reveal their adaptive strategies, or historical traits particular to the Pyrenees.

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