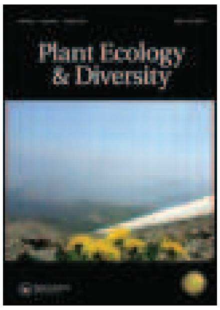

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# Altitudinal species richness patterns of vascular plants in the south-eastern Pyrenees and nearby mountains of Catalonia

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***Background:*** Studying how species richness varies with altitude has become an important part of investigations on mechanisms explaining regional-scale plant species diversity. Altitudinal diversity patterns are poorly known in the Pyrenees and elsewhere in the main mountain massifs in Catalonia (north-eastern Iberian Peninsula).
***Aim:*** We examine the altitudinal patterns of species richness in the Catalan Pyrenees and compare them with those in other mountains in Catalonia. Altitude patterns of species richness in the Pyrenees are compared for functional and taxonomic groups of vascular plants.
***Methods:*** Data on vascular plants were obtained from the Biodiversity Data Bank of Catalonia. We used rarefaction and interpolation to quantify the altitudinal diversity patterns.
***Results:*** The interpolated and rarefied richness generally peaked in the lower part of the altitudinal gradient, but with remarkable variation depending on the taxonomic or functional groups considered. Using all species, there was little variation between the different mountains, but the altitude at which richness started to decrease varied between them.
***Conclusions:*** The pronounced differences among different taxonomic groups and life-forms indicate a strong phylogenetic and adaptive signal on the altitudinal diversity pattern in the Catalan Pyrenees. The lack of regional differences within Catalonia is probably due to small differences in the intensity of climatic gradients across mountains.

**Keywords:** altitudinal gradient; endemism; interpolation; life-forms; plant species richness; Pyrenees; rarefaction

## Introduction

Understanding the mechanisms behind broad-scale patterns of species diversity has been a focus for ecologists for many years, and many hypotheses to explain the diversity patterns observed have been proposed (Willig et al. 2003). However, it is difficult to test these hypotheses experimentally on the appropriate scales (Brown 1995; Lomolino et al. 2006) or to disentangle factors that often co-vary geographically. Given that many of the main factors thought to influence broad-scale diversity patterns (e.g. temperature, precipitation, area) vary among mountains (Körner 2000; Nogués-Bravo et al. 2008; McCain 2010), a comparison of altitudinal diversity patterns between different mountains is a suitable alternative to test some hypotheses related to broad-scale diversity patterns.

Climatic factors are commonly used to explain the patterns of broad-scale species richness, as well as altitudinal diversity patterns (McCain and Grytnes 2010). Several climatic hypotheses predict different species richness patterns depending on regional climate. McCain (2007) predicts that mountains that are found in a humid climate will show a monotonically decreasing diversity with altitude, whereas mountains found in a dry climate will have a humped relationship with altitude. In contrast, the mid-domain hypothesis predicts a humped relationship with a peak at the midpoint of the domain, regardless of the climate of the region in which the mountain is found (Colwell et al. 2004). Therefore, a comparison of several mountains that vary in size and climate would contribute to our understanding of broad-scale species richness patterns.

An alternative approach is to compare the diversity patterns for different taxonomical or functional groups (Lomolino 2001; Kessler 2000). Several studies have found variations in the altitudinal diversity patterns of several taxonomic and functional groups (Grytnes et al. 2006; Grau et al. 2007). Some hypotheses suggest that there is a difference in altitudinal patterns of species diversity between taxonomic groups; e.g. hypotheses relating to species tolerance (Currie et al. 2004) or niche conservatism (Wiens et al. 2010). More general hypotheses based on climatic factors, for instance the theory of water–energy dynamics (O'Brien 1993), predict a constant relationship between different groups regardless of whether climatic factors limit the number of individuals or determine speciation rates (Currie et al. 2004). Similar patterns between functional groups should also be expected from the species-area (Rosenzweig 1995) or the mid-domain (Colwell et al. 2004) hypotheses. Comparing diversity patterns between different functional or taxonomic groups may provide a different perspective on these patterns from that provided by the comparison of mountains alone.

Here we describe and analyse the altitudinal patterns of species richness in the north-eastern Pyrenees as a whole, and also the altitudinal richness patterns in smaller areas

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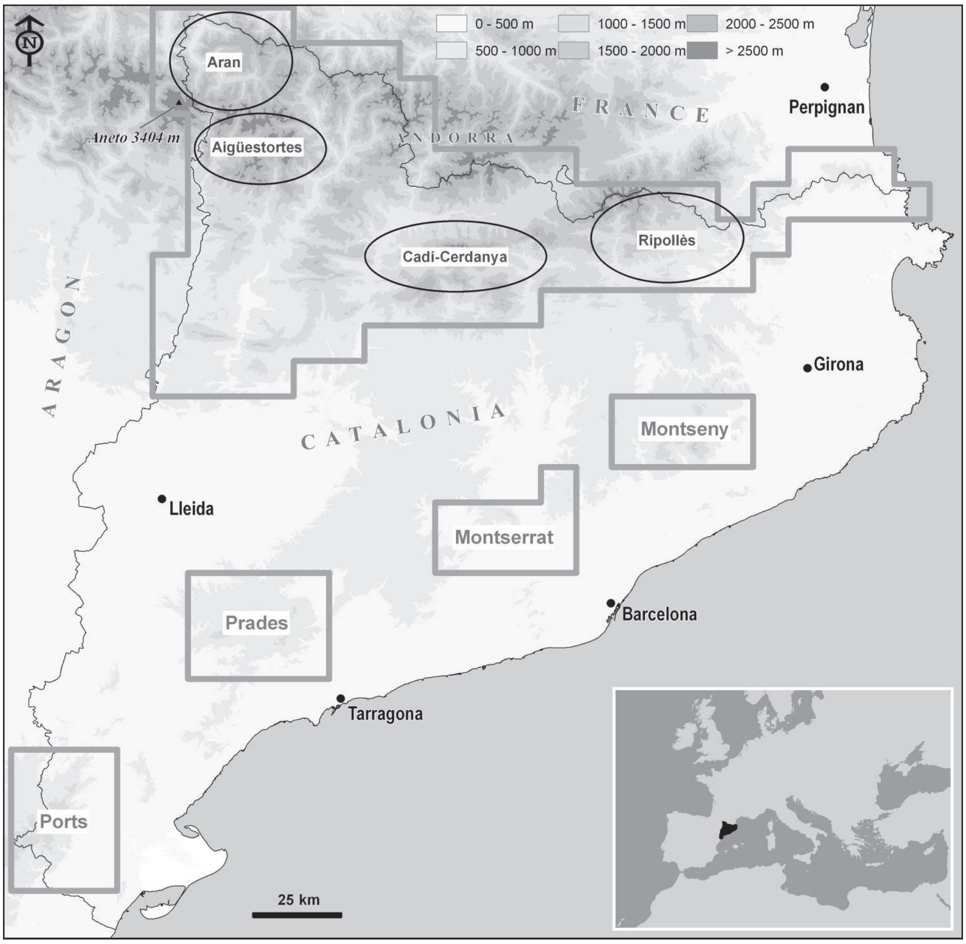

Figure 1. Map of Catalonia and location of the study areas: the north-eastern Pyrenees (the large mountain system marked in the north of the map) with the areas considered within this range and other non-Pyrenean mountains (full names of the areas studied and main features of each are in Table 1). The smaller inset indicates the location of the study region in south-western Europe.

within this range and in some adjacent non-Pyrenean mountain massifs in Catalonia (Figure 1). We also describe and compare the patterns between different functional and taxonomic groups of vascular plants in the Catalan Pyrenees. We use these analyses to discuss implications for some of the common hypotheses concerning broad-scale patterns of species diversity. To date, studies on Pyrenean vegetation have provided only a general description of the effect of altitude on vegetation patterns in some Pyrenean areas (e.g. Gómez et al. 1997; Villar et al. 1997; Petit and Thompson 1999; Villar et al. 2001; Gómez et al. 2003; Ninot et al. 2007; Ninot and Ferré 2008; Nogués-Bravo et al. 2008). Also, with regard to species richness patterns, few studies have addressed neighbouring mountain massifs. To gain insight into this issue, we describe and analyse the altitudinal patterns of vascular plant richness based on a detailed dataset of historical observations of vascular plant species from a large area in the Pyrenees and also from the main non-Pyrenean mountain massifs in Catalonia.

## Methods

### *Data sources*

The data used to quantify the richness patterns of the flora were obtained from the Biodiversity Data Bank of Catalonia (Font 2009) and correspond to plant observations from a wide range of papers (local flora, flora notes or phytosociological studies), from various personal contributions, and from herbarium records. The individual plant observations in this study also provide the altitude and UTM co-ordinates, which place each observation into 10 km × 10 km squares across the whole region. To obtain the data from the database for the studied areas, we selected the information from the UTM squares included wholly or partially within the Pyrenees in Catalonia, our main study area. Given the size of the squares used (10 km × 10 km) and to avoid unnatural boundaries, some small surrounding areas beyond the Catalan Pyrenees were also included (parts of Aragon – including the Aneto massif, the highest in the whole Pyrenees –, Andorra and southern France; Figure 1). For reasons of simplicity, we refer hereafter to our main study area as the Pyrenees.

The database contains information on observations from the entirety of Catalonia; we therefore used the data from the whole of Catalonia as well as from different geographical subsets within the Pyrenean area and also from non-Pyrenean mountain massifs (Figure 1) to quantify the altitudinal diversity patterns in these different geographical areas. More details about the study areas are summarized in Table 1 and Figure 1.

Table 1. Description of the areas studied. See Figure 1 for the location of each area. Abbreviations: Med., Mediterranean; Submed., Submediterranean; Atl., Atlantic; Hmn., High mountain; cont., continental; mar., maritime.

| Area | Physiographic unit | Area (ha) | Minimum altitude (m) | Maximum altitude (m) | Main outcrops | Bioclimates | Number of species | Number of observations |
|---|---|---|---|---|---|---|---|---|
| Catalonia | The whole of Catalonia | 32,105 | 0 | 3400 | Lime-rich, acidic, gypsum and salt rich | Med. (mar. and cont.), Submed., Atl., Hmn. | 3121 | 743,435 |
| Catalan Pyrenees (extended to the Aneto massif in Aragon) | Pyrenees | 9075 | 0 | 3400 | Lime-rich, acidic (gypsum and salt rich) | Med. (mar. and cont.), Submed., Atl., Hmn | 2649 | 385,865 |
| Aigüestortes-Estany de Sant Maurici | Western Pyrenees | 727 | 710 | 3030 | Acidic, lime-rich | (as in W Pyrenees) | 1471 | 69,530 |
| Val d'Aran | Western Pyrenees | 697 | 550 | 3400 | Acidic, lime-rich | Atl., Hmn. | 1243 | 30,064 |
| Cerdanya | Eastern Pyrenees | 900 | 450 | 2700 | Acidic, lime-rich | (as in W. Pyrenees) | 1509 | 42,895 |
| Ripollès | Eastern Pyrenees | 857 | 100 | 2900 | Lime-rich, acidic | (as in E. Pyrenees) | 1741 | 62,795 |
| Muntanyes de Prades | Pre-littoral Range | 1200 | 40 | 1200 | Lime-rich, acidic | Med. (mar.), Submed. | 1391 | 26,736 |
| Montserrat-Sant Llorenç del Munt i l'Obac | Pre-littoral Range | 900 | 35 | 1237 | Lime-rich | Med. (mar.), Submed. | 1204 | 33,671 |
| Ports de Tortosa-Beseit | Pre-littoral Range | 864 | 0 | 1450 | Lime-rich | Med. (mar.), Submed. | 1488 | 66,359 |
| Montseny | Pre-littoral Range | 800 | 50 | 1714 | Acidic, lime-rich | Med. (mar.), Submed., Atl. | 1283 | 18,423 |

Before analysis, we rejected some low-quality data, such as observations with imprecise taxonomic identification, and classified all the observations at species level, following the taxonomy by de Bolòs et al. 2005. In addition, for the Pyrenean dataset, we used the information provided in de Bolòs et al. (2005) to classify taxa into life-forms and range size. Regarding the former, we considered the following main types: therophytes, geophytes, hemicryptophytes, chamaephytes, deciduous phanerophytes and evergreen phanerophytes. Based on information in de Bolòs et al. (2005) we classified the range sizes into four categories: narrow-range endemic (Pyrenean or north-eastern Iberian Peninsula), wide-range endemic (alpine mountains – i.e. Pyrenees, Alps and related south European systems –, west Mediterranean or Iberian Peninsula), wide distribution area (Mediterranean, mid-European or boreal-alpine), and very wide distribution area (ranging from two of the previous regions to cosmopolitan). A taxonomic classification (again based on de Bolòs et al. 2005) at the family level was also made in order to analyse the richness patterns of the largest families found in the Catalan Pyrenees.

### *Biogeography and location of the study area*

Located in the north-east of the Iberian Peninsula, the Pyrenean range extends from the Mediterranean Sea to the Atlantic Ocean (Figure 1). It is a typical interzonal mountain range, with Mediterranean, Atlantic and high-mountain bioclimatic influences, which produce a great diversity of climatic and floristic characteristics (Petit and Thompson 1999).

The upper montane zone in the Pyrenean range occurs from 1600–1800 m upwards, and includes the typical subalpine forest zone, and the alpine landscapes above the treeline, located at ca. 2300 m (Batllori and Gutiérrez 2008). Most of the flora in this zone consists of boreal-alpine and orophytic (Alpine, Pyrenean or Mediterranean) taxa. The elevations from 700–900 m to the high-mountain zone correspond to a montane forest zone and have a strong physiographic and bioclimatic diversification. The landscape is typically Atlantic on the northern and western sides of the range, where the strong oceanic influence favours deciduous temperate forests and the pre-eminence of temperate montane flora. The southern and eastern sides are characterized by transitional sub-Mediterranean landscapes, where temperate and Mediterranean vegetation and flora comprise a complex patchwork subjected to local physiography. At lower altitudes, bioclimatic, floristic and landscape variability is greater between the Atlantic and Mediterranean sides (Ninot et al. 2007).

Other environmental factors that affect the local flora include the continentality of some inner valleys, the phylogeographic influence of other mountain ranges (such as the Alps and the Cantabrian and Iberian mountains) and the complex transitions between siliceous and carbonate-rich substrata (Villar et al. 2001; Ninot and Ferré 2008). In addition, the effect of human activities on the landscape and its flora is especially noticeable in the lowlands, at the bottom of the valleys, where historical land use caused noticeable changes in the ecosystem. Although some areas in the lowlands are currently intensively farmed, the area affected by such activity has decreased substantially over recent decades (Améztegui et al. 2010). This kind of human pressure also decreases with altitude, as higher areas are only partially affected by farming activities, such as livestock grazing (Lasanta 1990).

The Catalan Pyrenees are located in the eastern half of the Iberian Pyrenees (41° 53’ 12”–42° 54’ 9” N, 0° 35’ 22”–3° 10’ 17”, north-eastern Iberian Peninsula), and include most of the south-facing valleys stretching from the vicinity of the highest massif (the Aneto) to the Mediterranean coast and one north-facing valley (Val d’Aran, Occitania) (Figure 1). This area, forming an entire physiographic unit, as defined in de Bolòs et al. (2005), includes altitudes from sea level to 3404 m (a.s.l.) with very rugged and complex surfaces.

### *Data analysis*

Species richness was estimated for each 100-m altitude band for the total dataset and for the individual areas considered, from the lowest altitude in the area to the highest peak. The number of individual plant observations varied greatly along the altitudinal gradient and between areas, depending on the size of the area and on how intensively it was sampled (Table 1). In the Pyrenees, the total dataset included approximately 3320 individual observations in the lowest altitudinal interval (0–100 m), more than 28,500 observations between 1200 and 1300 m, and about 300 observations above 3000 m (Figure 2). The reason for the relatively low sampling intensity in the lower part is partly due to the focus of the collectors on higher altitudes in the Pyrenean area. The smaller area in these

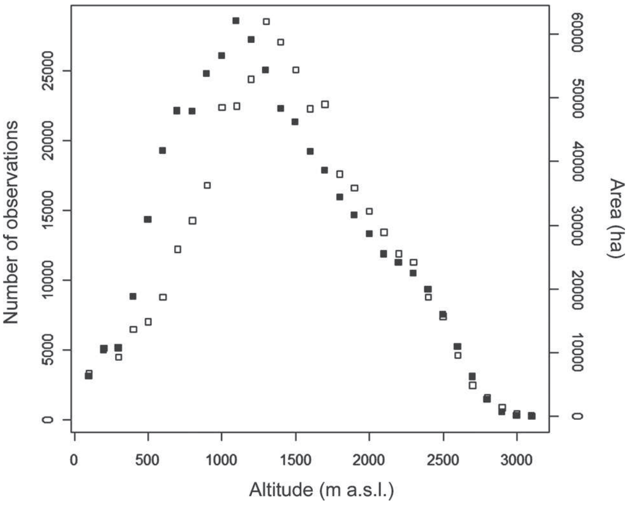

Figure 2. Number of observations (empty squares) and area in hectares (filled squares) per 100 m interval along the altitudinal gradient in the Catalan Pyrenees. The area of each altitudinal interval was obtained from a digital elevation model in raster format at a resolution of 20 m. From this model, we calculated the number of pixels for each interval and hence the total area.

lower parts is the result of the delineation of our study area, which confined low-elevation areas to foothills of mountains, with little extension into the lowlands. The species richness observed depends strongly on the number of observations for all regions. Therefore, to account for sampling effort, we estimated the species richness pattern by means of two methods, namely interpolation and rarefaction, which are commonly used to quantify these patterns along geographical gradients (Grytnes and Romdal 2008).

The large number of observations (over 385,000 individual observations in the Pyrenean dataset; Table 1) with detailed information on species distribution along the altitudinal gradient allowed us to use rarefaction to estimate richness patterns. We used this method to quantify altitudinal diversity patterns for Catalonia as a whole, for the Catalonian Pyrenees and some regions within the Pyrenees, and for some neighbouring non-Pyrenean mountain areas (Figure 3). This method accounts for sampling effort by estimating the expected species richness in a given subsample of the total number of observations randomly drawn from a large pool of individuals (Gotelli and Colwell 2001). If certain assumptions are fulfilled, this technique provides an unbiased estimation of the true distribution of species richness, i.e. an estimation of the relative species richness between intervals (Grytnes and Romdal 2008). The rarefaction method can estimate the richness pattern only for the altitude intervals that contain more than a chosen number of observations.

The number of observations was very low in large parts of the gradient for some taxonomic or functional groups. Thus, to use rarefaction to quantify and compare the patterns between groups, either a small number of observations should be used for all intervals or large parts of the gradient should be discarded. To circumvent these limitations, we used the interpolation method to compare groups and focused mainly on the central parts of the gradient.

The interpolation method uses the maximum and minimum observed elevation for all species and assumes that the individual species are present at all elevations between the extremes. This approach may cause an artificially humped pattern when sampling is incomplete (Grytnes and Vetaas 2002; Grytnes and Romdal 2008). Despite this methodological flaw, interpolation is more useful than rarefaction for comparing patterns between groups with a large variation in the number of observations, especially when focusing on the relative placement of a mid-altitude peak in species richness within the same altitudinal transect, in which sampling bias can be assumed to be equal for the different groups. Therefore, we used the interpolation method to describe the interpolated species richness pattern for Catalonia and for the Pyrenees (Figure 4) and to compare functional and taxonomic groups within the Catalonian Pyrenees (Figures 5–7).

The patterns observed in families and life-forms were compared in two steps. We first evaluated the richness pattern for each group by plotting the patterns observed together with 1000 randomly generated patterns, to assess if observed patterns deviated from what would be expected from randomness. The generated patterns were based on randomly selecting the same number of species as found in the groups from the total species pool. Deviating richness patterns were evaluated only graphically for this part. Next, we developed a more formal test to evaluate if the altitude of maximum species richness (optimum) deviated more from the overall optimum than would be expected by randomness. For this purpose we used a permutation test, in which for each permutation the same number of species

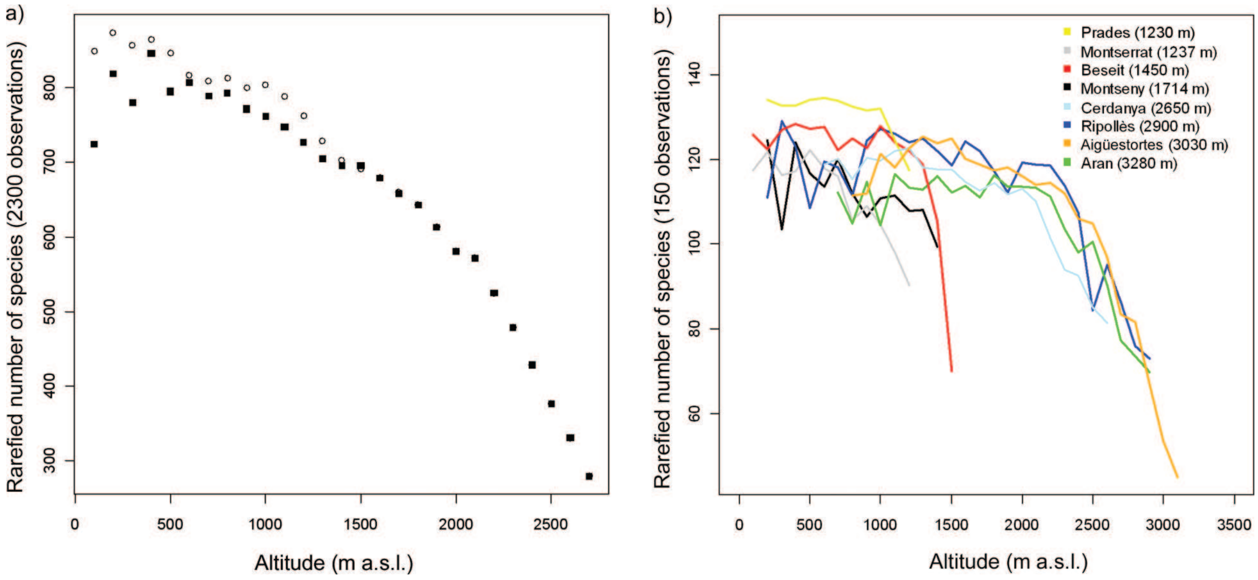

Figure 3. (a) Species richness pattern quantified by rarefaction along the altitudinal gradient in Catalonia as a whole (open circles) and the Catalan Pyrenees (filled squares); (b) Species richness pattern quantified by rarefaction along the altitudinal gradient in several mountains in Catalonia. Note that in Montseny and Val d'Aran the number of observations at the highest altitudes is below 150, which means that the rarefied pattern is truncated before the maximum altitude of these areas. See Table 1 for full names and description of the mountains and Figure S3 (supplementary material, available online) for the distribution of area along altitude in these mountains.

as found in the group analysed was drawn from the total species pool and an optimum for species richness was found for this random assemblage. This procedure was repeated 999 times and a *P*-value was derived from a one-sided test by counting the number of permutations that had a higher (or equal) optimum than that observed with a higher optimum than expected (or lower for those with a lower-than-expected optimum) (Table S1. Supplementary material available online.). A one-sided test was used instead of a two-sided test because the latter would be biased, since the deviations from the expected optimum would not be symmetrical when the observed and randomized optima are given at 100 m intervals, whereas the expected value (mean of all randomizations) can take any value. As we used a one-sided test, *P*-values below 0.025 were considered significant.

The data used in this study were derived from a mix of phytosociological relevés (56% of the observations) and floristic reports and museum specimens (44% of the observations). The data from the relevés are probably closer to a random set of samples than the museum collections, since the latter tend to have more rare species than would be found in a vegetation sampling (cf. Grytnes and Romdal 2008). However, a relative estimate of species richness between altitudes is still reliable when there is no over-collecting or under-collecting of certain groups (e.g. rare species) at certain altitudes compared with other altitudes. We have no reason to believe that such biased sampling occurred, but a comparison of the species-abundance distribution for the different altitudes was made to assess the potential impact of distinct sampling regimes (see Figures S1; see also Figure S2, which estimates the completeness of the sampling. Supplementary material available online.) (cf. Grytnes and Romdal 2008).

The analyses were performed in R version 2.10.1 (R Development Core Team 2010), using the vegan package (Oksanen et al. 2009).

## Results

The total number of species found in the whole of Catalonia was 3121, based on 743,435 individual observations (Table 1). The total number of species found in the Pyrenean area amounted to 2649, on the basis of 385,865 observations. The most commonly observed species in the Pyrenean data set was *Thymus serpyllum* (3108 observations). There were 653 species with <10 observations in the same dataset and 108 species with a single observation. The distribution of individual observations along altitude followed a humped pattern, with a maximum of 28,560 at the interval between 1200 and 1300 m and a marked decrease towards higher and lower elevations. Interestingly, the area occupied by each altitudinal interval followed a very similar pattern, although the maximum was reached at around 1000 m (Figure 2).

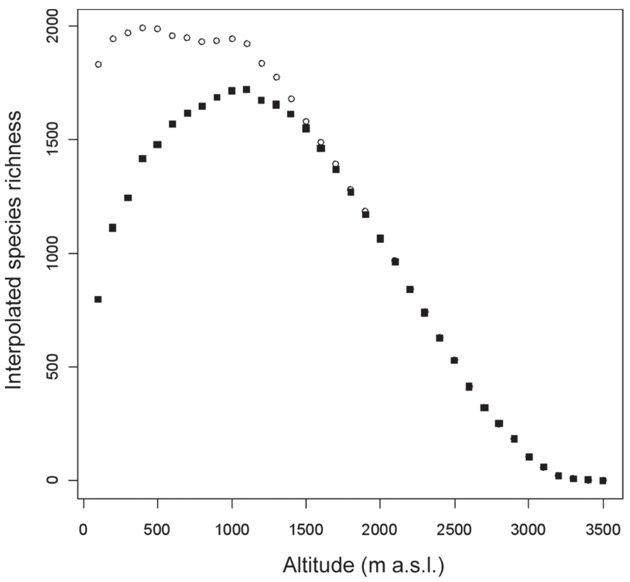

Figure 4. Species richness pattern quantified by interpolation along the altitudinal gradient in Catalonia as a whole (open circles) and the Catalan Pyrenees (filled squares).

The interpolated species richness pattern (Figure 4; Figure S2, supplementary material available online) showed an asymmetric humped pattern for the Pyrenean flora, with a maximum richness between 1000 and 1100 m, where ca. 1700 species were found (note that this method underestimates the richness at the upper and lower parts compared with the central part). The pattern observed for Catalonia as a whole indicated fairly constant species richness up to 1000 m, and then a constant decrease. The peak of maximum species richness was at 400 m, with about 2000 species.

The rarefaction made on Pyrenean data was based on 2300 observations in each altitudinal interval (Figure 3a). This allowed a reasonably detailed pattern that included most of the altitudinal range, even though we had to exclude the intervals above 2600 m, which had too few observations. The pattern was only relatively asymmetrically humped, with a marked increase in richness up to 400 m, a rather constant maximum richness up to 800 m (plateau), a moderate decrease above 1000 m and a very marked decrease above 1500 m. When comparing the richness pattern from the Catalan Pyrenees with that from Catalonia as a whole (Figure 3a), we found that the lowest parts deviated from the pattern obtained by interpolation (Figure 4) because the hump disappeared and species richness followed a monotonically decreasing trend with altitude. For the dataset for the whole of Catalonia, richness decreased moderately from the lowlands (with the exception of the lowest interval), with a steeper decrease above 1200 m. A reduction in the number of individual species observations included in the rarefaction allowed the inclusion of a larger part of the gradient in the upper part of the gradient and showed that richness continued with a steep decrease towards the maximum elevation of the Pyrenees (results not shown).

With respect to separate mountain areas in Catalonia, they showed a similar overall pattern (Figure 3b). None of the areas showed an obvious trend in species richness

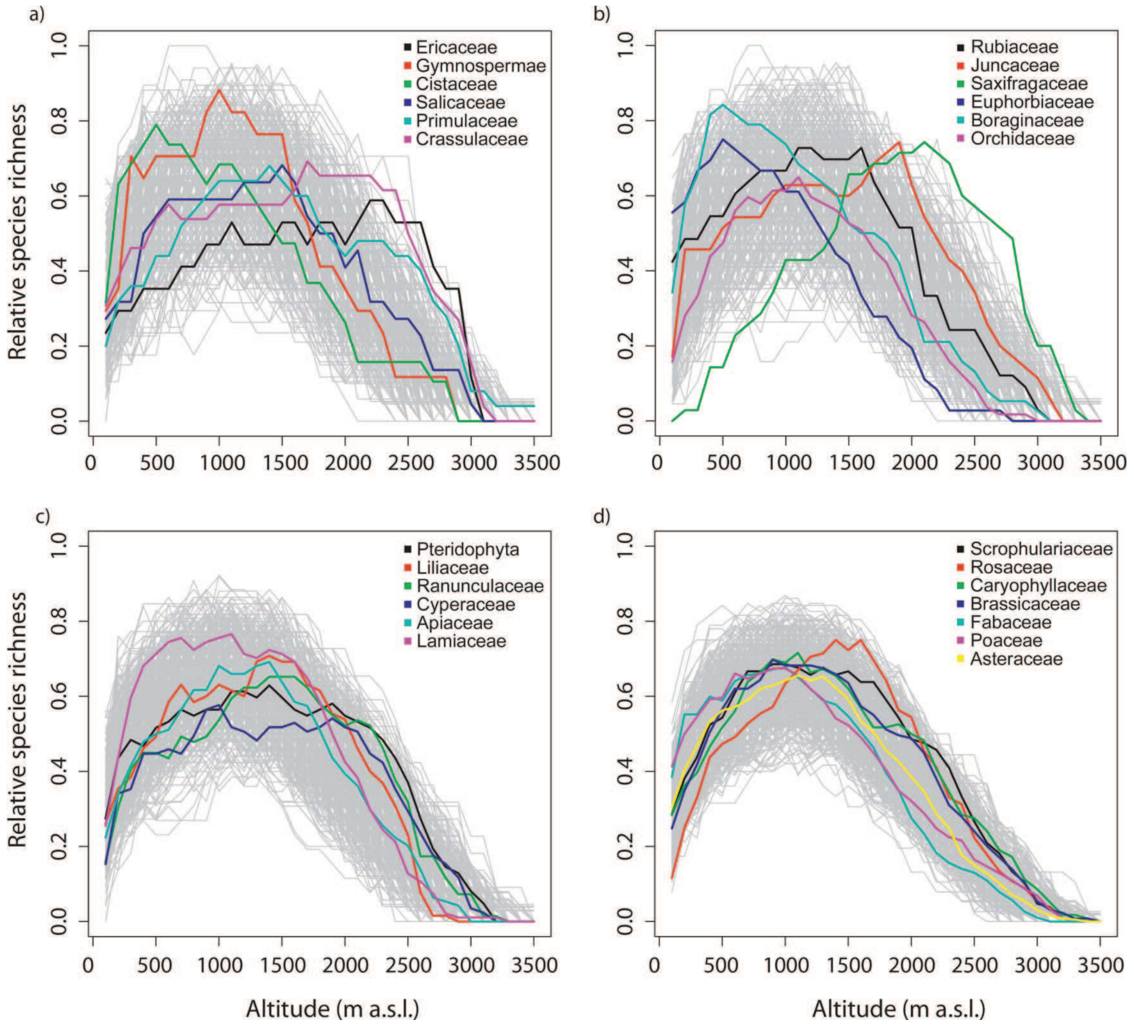

Figure 5. (a–d). Interpolated species richness for the most common families in the Catalan Pyrenees. The families are grouped by size: (a) 17, 17, 19, 22, 25, 26 species, from Ericaceae to Crassulaceae; (b) 33, 35, 35, 36, 38, 57 species, from Rubiaceae to Orchidaceae; (c) 62, 65, 69, 85, 94, 94 species, from Pteridophyta to Lamiaceae; (d) 105, 113, 116, 129, 192, 218, 366 species, from Scrophulariaceae to Asteraceae. The grey lines in the background are based on 1000 random draws of species from the total pool including all families. See Table S1 for statistical significances (supplementary material, available online).

with altitude in the lower part of the vertical gradient, and richness generally varied noticeably from one altitude interval to the next. At higher altitudes all regions showed marked decreasing richness with increasing altitude, but the altitude at which species richness started to decrease varied among mountains. We could distinguish three different patterns: i) mountains lower than 1500 m and showing a plateau in species richness up to around 1000 m (Muntanyes de Prades and Ports de Tortosa-Beseit); ii) mountains over 2500 m and maintaining a more or less constant species richness up to almost 2100 m (Cerdanya, Ripollès, Aigüestortes i Estany de Sant Maurici and Val d'Aran); and iii) mountains with a pattern that varied greatly with altitude, with a decreasing trend from the beginning (Montseny and Montserrat-Sant Llorenç del Munt i l'Obac).

We estimated interpolated species richness for the 25 largest families (or groups of closely related families) in the Pyrenees; the results showed relatively large differences in species richness patterns (Figure 5a–d). Several families showed little or no deviation from the overall pattern (Table S1, available online), i.e. the pattern observed did not deviate from randomly generated patterns. This was particularly the case for large families (e.g. Asteraceae, Poaceae, Brassicaceae and Apiaceae). The most deviating patterns were found for relatively small families, such as Saxifragaceae, Euphorbiacae, Crassulaceae and Boraginaceae, but some families with many species also deviated (i.e. Rosaceae). Ericaceae ($P = 0.001$), Saxifragaceae ($P = 0.001$), Juncaceae ($P = 0.002$), Crassulaceae ($P = 0.018$) and Rosaceae ($P = 0.014$) had their optimum at higher altitudes than the overall pattern when testing the deviation in optimum altitude for species richness. Ranunculaceae also showed a similar pattern, but with a non-significant $P$-value ($P = 0.027$). Euphorbiaceae and Boraginaceae had their optimum at lower altitudes than the total species richness ($P$-values are 0.034 and 0.031, respectively).

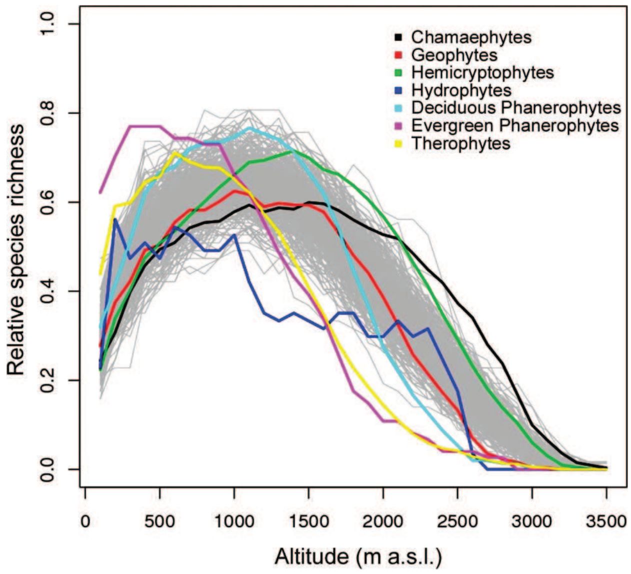

Figure 6. Interpolated species richness patterns of various life-forms along the altitudinal gradient in the Catalan Pyrenees. Chamaephytes (331 species), Geophytes (256 species), Hemicryptophytes (1095 species), Hydrophytes (57 species), deciduous Phanerophytes (163 species), evergreen Phanerophytes (96 species) and Therophytes (650 species). See Table S1 (supplementary material available online) for statistical significance.

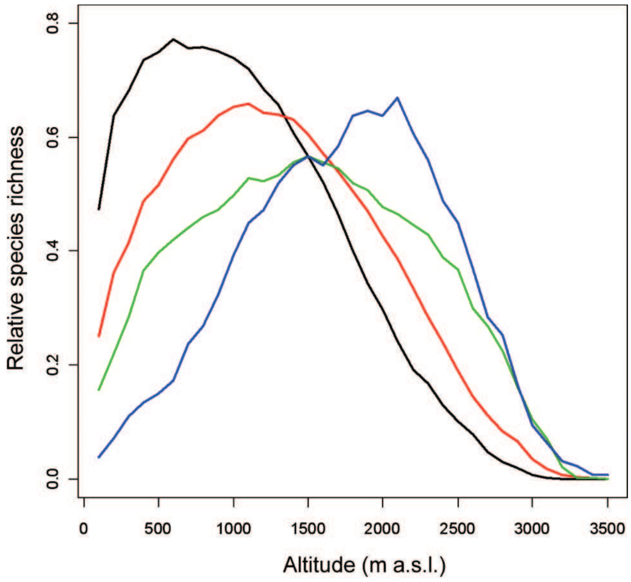

Figure 7. Interpolated richness pattern of groups of distinct range sizes in the Catalan Pyrenees: narrow-ranged endemics (blue, 127 species), wide-ranged endemics (green, 383 species), wide distribution area (red, 1257 species) and very wide distribution area (black, 881 species).

Life-forms differed more among each other in the interpolated species richness pattern (Figure 6) than plant families did. Five of the seven life-form groups had a statistically significant deviation from optimum species richness (Table S1, available online). The optima of chamaephytes and hemicryptophytes were at significantly higher altitudes than the total pool ($P < 0.001$), whereas geophytes and deciduous phanerophytes did not differ from the general pattern. Therophytes, evergreen phanerophytes and hydrophytes showed optima at lower altitudes than expected ($P = 0.001$, 0.003 and 0.001, respectively).

When species were classified into chorological groups with distinct range sizes (Figure 7), we observed that the interpolated species richness of groups with smaller ranges had a peak at higher elevations in the Pyrenees. The number of endemic species with a narrow range peaked at 2100 m; the endemic species with a wide range at 1500 m; the group of species with a wide range at 1100 m; and the group of cosmopolitan species between 1000 and 1100 m.

## Discussion

The altitudinal pattern of species richness observed in Catalonia varied with the method used to quantify the pattern and with the subset of species used to quantify the pattern. The interpolated richness pattern for the Pyrenean dataset showed a clearly humped pattern with a peak around 1100 m (Figure 4). A mid-elevational peak has commonly been observed in other areas (McCain and Grytnes 2010), especially when using interpolation, a method that may create an artificial humped pattern (Grytnes and Vetaas 2002). However, a humped shape is also observed without using this method (Acharya et al. 2011; Karger et al. 2011). The pattern observed in the present study was very similar to that described for the Aragon Pyrenees, directly west from our study area (Villar et al. 2001). However, when including the whole of Catalonia, the altitudinal richness pattern had a low-altitudinal plateau in species richness before it decreased at around 1100 m (Figure 4). A somewhat similar pattern was detected for the Pyrenees when rarefaction was used (Figure 3a). This might indicate that the decrease in species richness with lower altitudes found when using interpolation may be an artefact of the method used and incomplete sampling (Grytnes and Vetaas 2002). When comparing the different geographical subsets, the pattern is surprisingly similar in the lower part of the altitudinal gradient (Figure 3b).

The low-altitude plateau in Pyrenean species richness indicated by the rarefaction analyses (Figure 3a) may be partly explained by a more benign climate in the lower part (warmer temperatures and sufficient precipitation). In addition, the large lowlands adjacent to the Pyrenees may contribute to a noticeable increase in the species pool for the lower part of the Pyrenees. The low and medium altitudes also host a greater diversity of soils and bedrocks (ICC 1989), which contribute to marked physiographic diversity which, in turn, may also contribute to the high diversity at these altitudes. At small and medium scales, such diversity leads to a wide range of habitats, resulting in a wide diversity of the local floristic pool (Pausas et al. 2003). In addition, climatic variability is stronger at low altitudes compared with higher altitudes, since there is greater variability (expressed as standard deviation) of mean annual rainfall, mean spring rainfall and mean summer temperature (data from Ninyerola et al. 2009, not shown). Traditional anthropogenic activities such as farming and forest exploitation may have contributed to the spatial heterogeneity (Lasanta 1990) and to an increase in lowland species richness in the Pyrenees. The mid-domain effect (MDE) predicts a symmetrical humped pattern with altitude (Colwell et al. 2004); however, this was not observed in the Pyrenees. Therefore, the MDE alone cannot explain the pattern observed, but it may modify a linear decrease with altitude caused by other factors, such as climate or habitat heterogeneity (Grytnes and Vetaas 2002).

### *Species richness patterns in different mountains in Catalonia*

A comparison of the pattern for Catalonia as a whole with that for the Pyrenees (Figures 3a and 4) indicates that some of these humped patterns may be a result of the definition of the study area. When examining altitudinal gradients, it is common to define the study area centred on a mountain or a massif. The area of interest in this study was selected to avoid the inclusion of most disturbed areas, which are commonly found in the lower part of the altitudinal gradient (Nogués-Bravo et al. 2008). As a result, the area defined as the Pyrenees in this study included only very small areas at low elevation (Figure 2). The larger area in the lowlands when including all of Catalonia compared with the Pyrenean part is probably responsible for the difference in richness at the lower part (Figure 3a; see also Figure S3, available online)

At a smaller scale, the division into separate mountains (Figure 3b) showed that species richness often had no trend at lower altitudes and that it decreased with altitude. The altitudes at which this decrease started depended on the maximum altitude of the mountain. This could be attributed to the generally harsher life conditions on the mountain peaks than those on slopes at similar altitudes on higher mountains (e.g. more wind exposure). Alternatively, it also fits the predictions made by the MDE, which predicts that the decrease in richness will start at different altitudes, depending on the height of the mountain. The different patterns between the different mountains cannot be explained by differences in climate. If mountains are classified into those with a dry base (Beseit, Prades, Montserrat, Montseny) and those with a humid base (Aran, Aigüestortes, Ripollès, Cerdanya) on the basis of their climate and potential vegetation (based on information from de Bolòs et al. 2004), we observe no clear differentiation in patterns between the two groups. This can be interpreted as contrary to the theory of water–energy dynamics (O'Brien 1993), or it may also be due to too small differences in the intensity of the climatic gradient among the mountains in this region, or that all mountains have a humid base if compared within a larger context.

### *Species richness patterns of plant families*

Considerable variation was observed in species richness patterns among families. In many cases this variation was greater than that expected by randomness. This observation indicates that species which belong to a given family follow a similar altitudinal pattern and tend to be found at the same altitude. This finding is not consistent with hypotheses that uphold similar patterns for distinct taxonomic groups, such as climatic hypotheses based on number of individuals or speciation rates (Currie et al. 2004). However, the niche conservatism hypothesis predicts that each phylogenetic group has its optimum in the area where the group originated (Wiens et al. 2010). For instance, this is the case of Saxifragaceae, where most species are found at relatively high altitudes, where growth conditions are similar to those of boreal or temperate mountain regions, corresponding to their origin and optima (Stevens 2001). The same applies to Euphorbiaceae and Boraginaceae, which show their maximum richness at low altitudes. This observation can be explained by their strong adaptation to their optimal and originally warmer inter-tropical zones (Stevens 2001). Therefore, niche conservatism could help to explain the species richness patterns of plant families along altitudinal gradients, such as the pattern observed in the Pyrenees.

The pattern detected in larger families (e.g. Asteraceae, Poaceae, Fabaceae, Brassicaceae) coincided with that of the total species pool; therefore, it is difficult to separate any ecological signal in this pattern from the effect that the large families have on the total species richness pattern, i.e. the total species richness pattern is a result of the pattern for the largest families.

Additional factors may also explain the pattern observed in other families. For instance, a high number of Rosaceae and Ranunculaceae species were found at high altitude because of the strong diversification of some particular genera within these families (*Alchemilla*, *Potentilla* and *Ranunculus*). In addition, some families that show strong specialization and hence a narrow ecological niche were highly diversified in areas where their specific habitat was more abundant. This was the case for Crassulaceae, which were commonly found in rock crevices (more abundant in high mountains). Another case is Juncaceae, which showed high richness in mid-altitudinal areas; it is precisely in these areas in which the Pyrenees show their greatest diversification of wetlands and other aquatic habitats (Carreras and Diego 2010).

### *Adaptive value of life-forms*

The deviation of most life-forms from the general interpolated pattern was more notable than among families (Figure 6; Table S1, in supplementary material available online) and expressed the functional meaning of these plant groups. As stated by Raunkiær (1934), life-form spectra correspond to marked adaptations to distinct bioclimatic areas and ecological niches. The differences in life-forms are not independent of phylogeny, and some of the differences described for the families above may reflect diversity of life-forms. Hemicryptophytes actively regenerate most of their above-ground structures during the favourable vegetative period in a wide range of bioclimates (e.g. from atlantic to alpine) and were the richest group and extended abundantly up to very high elevations. The pattern observed in chamaephytes corresponded to that of typically slow-growing, stress-tolerant plants (Grime 2001), which can thrive in a wide range of unfavourable habitats, such as rocky slopes, the understory of dry forests and shrubs, and open and infertile habitats, which are often dominant in the high alpine zone.

The asymmetric altitudinal distribution of therophytes reflected their capacity to grow under irregular climatic seasonality or in areas affected by marked disturbance (Grime 2001). This group is favoured by the irregular precipitation patterns of Mediterranean and sub-Mediterranean areas, and by the varied anthropogenic activities common to low and medium altitudes. The small group of evergreen phanerophytes consisted mostly of trees and shrubs adapted to the Mediterranean climate, denoted by their sclerophyllous, leptophyllous, malacophyllous or laurophyllous adaptations; they were also found mostly at low altitudes and decreased in abundance with increasing altitude. In the subalpine belt they formed extensive and dominant perennial forests, but the number of evergreen phanerophytes was very low. Hydrophytes formed a plateau of species richness up to 1000 m and then decreased markedly up to 1300 m, where species richness formed a second plateau up to 2400 m. This observation could be interpreted as a balance between the availability of potential areas for hydrophytes and aquatic habitat diversity. In contrast, the decrease in hydrophyte richness coincided with the very low availability of aquatic areas and habitat diversity at increasing altitudes (Carreras and Diego 2010).

Geophytes and deciduous phanerophytes followed the general pattern, meaning that their life strategy was neutral for the altitudinal gradient. Geophytes are weaker competitors than other groups, as they are forced to use their reserves to grow earlier in the season to avoid competition (Orshan 1989). By initiating early growth, they share the habitat with other groups that are stronger competitors. This strategy is appropriate for thriving in a wide range of habitats, from low-altitude Mediterranean grasslands or scrubs, to mid-altitude meadows and deciduous forests, and to alpine pastures. Deciduous phanerophytes require a relatively long vegetative period, which is inherent to the bioclimate at intermediate and low–medium altitudes. This group belongs mostly to temperate flora, but some species may penetrate the high edge of the upper montane belt on warm slopes while others may descend to very low Mediterranean landscapes along rivers.

### *Influence of altitude on the distribution of species with different range sizes*

The distinct richness patterns of plant groups of distinct geographic range sizes (Figure 7) may support several theories. A larger degree of isolation at higher altitudes is often considered to be a crucial factor contributing to speciation (Vetaas and Grytnes 2002). Broad-scale climatic dynamics strongly affect vascular floras, facilitating hybridization between previously isolated populations followed by polyploidization, which may result in new species adapted to new conditions following climatic change (Petit and Thompson 1999). A higher endemic proportion with increasing altitude has also been found in several mountainous regions such as the Himalayas (Grau et al. 2007), Iran (Noorozi et al. 2011), the Andes (Kessler 2000), the Alps (Casazza et al. 2005; Dirnböck et al. 2011) or the Sierra Nevada (Pauli et al. 2003; Giménez et al. 2004). The increasing fraction of endemics at higher altitudes may be considered as an indication of greater speciation rates at these altitudes; the humped species richness pattern of endemic species may be the result of increased extinction rates towards the highest altitudes.

Most of the wide-range species found in the Pyrenees appear to be associated with Mediterranean or temperate bioclimatic conditions, with fewer species corresponding to boreal-alpine conditions (authors' own data, not shown). This observation would explain why most species were concentrated at low–medium altitudes, where there are favourable habitats for these two major chorological groups (Ninot et al. 2007). Regarding the cosmopolitan and other multi-regional species, most found their ideal conditions in areas with greater anthropogenic influence, which dominate landscapes at low altitude, whereas others were related to maritime or temperate bioclimates. The group also includes alien species (about 238 species; Vigo et al. 2007), which were clearly concentrated in maritime and low-altitude areas.

## Conclusions

The Catalan Pyrenees showed a low-altitude plateau in species richness before it decreased with altitude from around 800 m. This pattern was scale invariant and the regional differences in species richness patterns among the different mountain systems in Catalonia are probably due to small differences in the intensity of climatic gradients across mountains. The clear differences in the richness patterns observed among distinct families, life-forms and species with different distribution ranges indicate a strong phylogenetic and adaptive signal on the altitudinal diversity pattern in the Catalan Pyrenees. This complies with hypotheses related to species tolerances and niche conservatism and the adaptive signal of the different plant groups.

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## References

Acharya BK, Chettri B, Vijayan L. 2011. Distribution pattern of trees along an elevation gradient of Eastern Himalaya, India. Acta Oecologica-International Journal of Ecology 37:329–336.

Améztegui A, Brotons L, Coll L. 2010. Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. Global Ecology and Biogeography 19:632–641.

Batllori E, Gutiérrez E. 2008. Regional tree line dynamics in response to global change in the Pyrenees. Journal of Ecology 96: 1275–1288.

Brown JH. 1995. Macroecology. Chicago (IL): University of Chicago Press.

Carreras J, Diego F. 2010. Cartografia dels hàbitats a Catalunya 1:50.000 [Habitat cartography in Catalonia 1:50.000]. Generalitat de Catalunya. Available from: http://mediambient.gencat.net/cat/el_medi/habitats/inici.htm Catalan.

Casazza G, Barberis G, Minuto L. 2005. Ecological characteristics and rarity of endemic plants of the Italian Maritime Alps. Biological Conservation 123:361–371.

Colwell RK, Rahbek C, Gotelli NJ. 2004. The mid-domain effect and species richness patterns: what have we learned so far? American Naturalist 163:E1–E23.

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guegan JF, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E, et al, 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134.

de Bolòs O, Vigo J, Carreras J. 2004. Mapa de la vegetació potencial de Catalunya 1:250.000 [Map of potential vegetation in Catalonia 1:250,000]. Institut d'Estudis Catalans and Universitat de Barcelona (Spain). Catalan.

de Bolòs O, Vigo J, Masalles RM, Ninot JM. 2005. Flora manual dels Països Catalans [Manual of flora of the Catalan countries]. 3rd ed. Barcelona (Spain): Pòrtic.

Dirnböck T, Essl F, Rabitsch W. 2011. Disproportional extinction risk of high-altitude endemic species under climate change. Global Change Biology 17:990–996.

Font X. 2009. Mòdul de Flora, Banc de Dades de Biodiversitat de Catalunya (BDBC) [Flora section, Biodiversity Data Bank of Catalonia (BDBC)]. Generalitat de Catalunya and Universitat de Barcelona. Available from: http://biodiver.bio.ub.es/biocat/homepage.html Catalan.

Giménez E, Melendo M, Valle F, Gómez-Mercado F, Cano E. 2004. Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes. Biodiversity and Conservation 13:2641–2660.

Gómez D, Sesé JA, Ferrández JV, Aldezábal A. 1997. Altitudinal variation of floristic features and species richness in the Spanish Pyrenees alpine belt. 36th Symposium of IAVS. Universidad de la Laguna, Tenerife. Serie Informes 40:113–123.

Gómez D, Sesé JA, Villar L. 2003. The vegetation of the alpine zone in the Pyrenees. In: Nagy L, Grabherr G, Körner C, Thompson DBA, editors. Alpine biodiversity in Europe. Berlin (Germany): Springer. p. 85–92.

Gotelli NJ, Colwell RK. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391.

Grau O, Grytnes JA, Birks HJB. 2007. A comparison of altitudinal species richness patterns of bryophytes with other groups in Nepal, Central Himalaya. Journal of Biogeography 34:1907–1915.

Grime JP. 2001. Plant strategies, vegetation processes and ecosystem properties. Chichester (UK): John Wiley and Sons.

Grytnes JA, Heegaard E, Ihlen PG. 2006. Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. Acta Oecologica–International Journal of Ecology 29:241–246.

Grytnes JA, Romdal TS. 2008. Using museum collections to estimate diversity pattern along geographical gradients. Folia Geobotanica 43:357–369.

Grytnes JA, Vetaas OR. 2002. Species richness and altitude, a comparison between simulation models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. The American Naturalist 159: 294–304.

ICC. 1989. Institut Cartogràfic de Catalunya. Mapa Geològic de Catalunya, 1:200.000 [Geological Map of Catalonia]. Barcelona (Spain). Catalan.

Karger DN, Kluge J, Kromer T, Hemp A, Lehnert M, Kessler M. 2011. The effect of area on local and regional elevational patterns of species richness. Journal of Biogeography 38:1177–1185.

Kessler M. 2000. Elevational gradients in species richness and endemism of selected plant groups in the Central Bolivian Andes. Plant Ecology 149:181–193.

Körner C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. Trends in Ecology and Evolution 15: 513–514.

Lasanta T. 1990. Diversidad de usos e integración especial en la gestión tradicional del territorio en las montañas de Europa Occidental [Use diversity and special integration in traditional land management in Western Europe mountains]. In: García Ruiz JM, editor. Geoecología de las áreas de montaña. Logroño (Spain): Geoforma Ediciones. Spanish. pp. 235–266

Lomolino MV. 2001. Elevation gradients of species-richness, historical and prospective views. Global Ecology and Biogeography 10:3–13.

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. 3rd ed. Sunderland (MA): Sinauer Associates.

McCain CM. 2007. Area and mammalian elevational diversity. Ecology 88:76–86.

McCain CM. 2010. Global analysis of reptile elevational diversity. Global Ecology and Biogeography 19:541–553.

McCain CM, Grytnes JA. 2010. Elevational gradients in species richness. In: Encyclopaedia of life sciences (ELS). Chichester (UK): John Wiley and Sons, Ltd

Ninot JM, Carrillo E, Font X, Carreras J, Ferré A, Masalles RM, Soriano I, Vigo J. 2007. Altitude zonation in the Pyrenees. A geobotanic interpretation. Phytocoenologia 37:371–398.

Ninot JM, Ferré A. 2008. Plant diversity across five vegetation belts in the Pyrenees (Catalonia, Spain). Collectanea Botanica 27:67–76.

Ninyerola M, Pons X, Roure JM. 2009. Digital climatic atlas of Catalonia. Universitat Autònoma de Barcelona. Available from: http://www.opengis.uab.cat/acdc/en_index.htm

Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C. 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453:216–220.

Noorozi J, Pauli H, Grabherr G, Breckle SW. 2011. The subnival-nival vascular plant species of Iran: a unique high-mountain flora and its threat from climate warming. Biodiversity and Conservation 20:1319–1338.

O'Brien EM. 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa woody flora. Journal of Biogeography 20:181–198.

Oksanen J, Kindt R, Legendre P, O'Hara P, Simpson GL, Solymos P, Steven MHH, Wagner H. 2009. Vegan: Community Ecology Package. R package, version 1:15–3.

Orshan G. 1989. Plant pheno-morphological studies in Mediterranean type ecosystems. Dordrecht (Netherlands): Kluwer.

Pauli H, Gottfried M, Dirnböck T, Dullinger S, Grabherr G. 2003. Assessing the long-term dynamics of endemic plants at summit habitats. In: Nagy L, Grabherr G, Körner C, Thompson DBA, editors. Alpine biodiversity in Europe. Berlin (Germany): Springer (Ecological Studies; vol 167). p. 195–207.

Pausas JG, Carreras J, Ferré A, Font X. 2003. Coarse-scale plant species richness in relation to environmental heterogeneity. Journal of Vegetation Science 14:661–668.

Petit C, Thompson JD. 1999. Species diversity and ecological range in relation to ploidy level in the flora of the Pyrenees. Evolutionary Ecology 13:45–66.

R Development Core Team. 2010. R: a language and environment for statistical computing version 2.10.1. Vienna (Austria): R Foundation for Statistical Computing.

Raunkiær C. 1934. The life forms of plants and statistical plant geography. Oxford (UK): Clarendon Press.

Rosenzweig ML. 1995. Species diversity in space and time. Cambridge (UK): Cambridge University Press.

Stevens PF. 2001. Angiosperm Phylogeny Website, version 9. Available from: http://www.mobot.org/MOBOT/research/APweb/.

Vetaas OR, Grytnes JA. 2002. Distribution of vascular plants species richness and endemic richness along the Himalayan elevation gradient in Nepal. Global Ecology and Biogeography 11:291–301.

Vigo J, Masalles RM, Ninot JM. 2007. A propòsit de les plantes naturalitzades [On naturalised plants]. L'Atzavara 15:73–82. Catalan.

Villar L, Sesé JA, Ferrández JV. 2001. Atlas de la Flora del Pirineo Aragonés [Atlas of the Pyrenean Flora in Aragon]. Vol 2. Instituto de Estudios Altoaragoneses and Consejo de Protección de la Naturaleza de Aragón, Jaca (Spain). Spanish.

Villar L, Sesé JA, Goñi D, Fernández JV, Guzmán D, Catalán P. 1997. Sur la flore endémique et menacée des Pyrénées (Aragon et Navarre). Lagascalia 19:673–684. French.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes JA, Harrison SP, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13:1310–1324.

Willig MR, Kaufman DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution and Systematics 34:273–309.