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Plant diversity across five vegetation belts in the Pyrenees (Catalonia, Spain)

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Abstract

In this paper we analyze the size and habitat partitioning of the vascular floras of five areas of the NE Iberian Peninsula, representing five distinct vegetation belts and three floristic regions: Mediterranean (basal belt), medio-European (submontane and montane belts) and Boreo-Alpine (subalpine and alpine belts). Each area covered over 1000 ha, and was fairly uniform in terms of potential vegetation, bedrock and bioclimate. They excluded large villages and field areas, the landscape being mainly natural or moderately anthropized.

The size of the local floras showed a unimodal function with respect to altitude, with the highest number of species (568) in the submontane belt. The decrease in species richness was moderate toward the neighbouring belts (basal and montane) but more marked from the montane to the subalpine belt and then to the alpine belt (the poorest area, with 217 species). However, considering the size of the areas studied, the montane belt showed higher species richness than the submontane belt. The species impoverishment toward higher altitudes followed general tendencies found in other altitude and latitude gradients, and reflects the increasing environmental constraints and the decreasing habitat diversity of colder landscapes. On the contrary, the richer floras of the submontane and montane areas reflect less stressful general conditions, but also the occurrence within them of a number of taxa from the neighbouring regions (Mediterranean and Boreo-Alpine).

The forest flora in the basal to subalpine landscapes accounted for a small percentage of the local floras (6.5-13.2%). Among the other species, roughly one half (42-46%) made up diverse serial communities (forest clearings, scrubs, pastures) while the other half (44-51%) occurred in particular habitats (water sides, rocky areas) or in anthropogenic habitats. In the alpine area almost half of the taxa were found in the pasture mosaic, and a similar amount thrived in rocky and water-related habitats. Across the studied areas, the size of the flora particular to each main habitat showed no relationship with the surface area occupied by these habitats.

Ongoing changes in land use –mainly rural abandonment– would have little effect on the ruderal floras, which can persist even in very small disturbed patches, and may have no effect on the plants of rocky and water-related habitats. But these changes clearly reduce the extent of secondary habitats (scrubs, pastures), and thus lead to population reduction and fragmentation, and eventually local extinction of the most rare species in these habitats.

Key words: vascular flora, habitat, biodiversity, Iberic Pyrenees, Mediterranean, alpine, altitude zonation, landscape ecology.

INTRODUCTION

Plant species richness in a given landscape depends upon a variety of crude environmental factors, such as bedrock diversity, physiography, vegetation history and bioclimate. The spatial combination of these factors creates particular habitats, which act as environmental filters on the regional floristic pool and give way to particular plant communities. Therefore, diversity at the species level in a given landscape is caused by the combination of habitat diversity (β-diversity) and the diversity of species found in each particular habitat (α-diversity; VAN DER MAAREL, 1997).

Several attempts have been made to determine the relationships between plant diversity and environmental factors, although the dependence of floristic pool size upon a particular factor is difficult to demonstrate. A number of promising approaches have explored the relationship between plant diversity and a few general factors varying in space, such as mean annual temperature or mean rainfall (MALYSHEV *et al*., 1994; ROSENZWEIG, 1995 and references therein). Comparison of areas along such gradients is particularly useful when set along the altitude gradient of mountain systems, since there the environmental gradient proceeds through relatively short distances, and thus the areas compared share the same regional floristic pool (GRYTNES & BEAMAN, 2006).

In this paper, we analyze species richness related to habitat partitioning in five small contrasting areas, with the aim of revealing general patterns of distribution for the five local floras, exploring possible relationships between the size of ecological groups of taxa and their available habitat surface, and evaluating the biogeographic interest of floristic groups. Each case study is representative of one distinct vegetation belt, all typically found in the northeastern part of the Iberian peninsula, from the Catalanidic lowlands and hills to the high mountains of the Pyrenees (NINOT *et al*., 2007). Discussion of the results and the trends drawn might be generalised to other regions stretching from mild Mediterranean to Alpine landscapes.

THE AREAS CONSIDERED

We selected five areas in Catalonia, representing five vegetation belts: basal, submontane, montane, subalpine and alpine. These may be placed in three contrasting phytogeographic regions: Mediterranean (basal belt), medio-European (submontane and montane belts), and Boreo-Alpine (subalpine and alpine belts). All areas were natural and seminatural landscapes, i.e. they did not include any big villages or large agricultural areas, and most of their surface is covered by potential communities, or similar. Each study area covered over 1,000 ha and an altitude range of 400-700 m (Table 1). On a crude scale, each lies on a single type of substratum, and may be taken as a single landscape type.

We calculated a few climate parameters for each area from the climatic atlas of Catalonia (NINYEROLA *et al*., 2000). These parameters are mean values of interpolated data, which are available for each terrain cell of 180 x 180 m; this gives a few hundred (249-385) values for each of the five areas.

The basal area, el Bruc, is located in the central Catalanidic mountains (Fig. 1), lies on Paleozoic slate, and has a hilly relief. The climate is subhumid Mediterranean, with moderate summer water stress, and the potential vegetation is the Catalan mild Mediterranean holm oak forest (*Quercetum ilicis*). Most of its surface is covered by secondary forests related to *Quercetum ilicis*. These are immature forests and maquis of *Quercus ilex* subsp. *ilex* and pinewoods of *Pinus pinea* or *Pinus halepensis* with undergrowth similar to that of the potential holm oak forest. Light scrub, dry pastures, and fields (active or abandoned) make up the rest of the landscape.

The other four areas lie in the central Pyrenees, from the southern to the northern part of the Iberic face of the range. In this sense winter resting period increases, from 3-4 months in the submontane belt to 8-10 months in the alpine belt. Contrarily, the potential evapotranspiration decreases; summer water shortage occurs only in Llesp, the submontane area, though more irregularly than in Mediterranean lowlands. Llesp is mainly made of Devonian lime rocks, and lies in the southernmost part of the Noguera de Tor valley. The potential forest is the meso-xerophilous oak forest of *Quercus pubescens* (*Buxo-Quercetum pubescentis*), which covers a noticeable part of the area in the form of young forests. Pinewoods of *Pinus sylvestris* (partly secondary), extensive pastures, box scrub and hay fields complete the landscape.

Caldes de Boí lies on the medium slopes of Noguera de Tor and Noguera de Sant Nicolau, a rugged area mostly made up of siliceous rocks (granite and slate) but including lime outcrops. The main potential vegetation is a mesic beech forest (*Buxo-Fagetum*) but Scotch pinewoods (*Deschampsio-Pinion, Quercion pubescenti-petraeae*) are also widespread, with pastures, scrubs, and rocky outcrops occupying small patches.

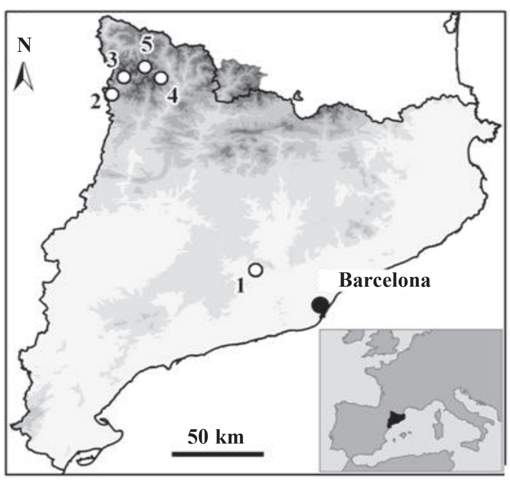
Peguera is the subalpine part of a secondary valley of the Espot valley. It is chiefly made of siliceous rocks (granodiorite and slate), with small lime outcrops. The potential forest, a mountain

Table 1. Main physiographic and climatic features of the areas studied.

	Bruc	Llesp	Caldes	Peguera	Ratera
Altitude range (m)	380	470	525	680	710
Lowest and highest altitudes (m a.s.l.)	360-740	850-1320	1295-1820	1630-2310	2190-2900
Total surface (ha)	978	1,249	783	992	783
Mean annual temperature (ºC)	13.1	9.1	7.3	4.9	2.0
Mean annual rainfall (mm)	683	989	1,157	1,071	1,419
Mean summer rainfall (mm)	143	278	345	289	370

pinewood with alpenrose (*Rhododendro-Pinetum uncinatae*) is dominant. Dryer pinewoods, subalpine pastures, scree and rocky slopes are also found.

The fifth area, Ratera, lies in the supra-forest part of another secondary valley above Espot. Made exclusively by granodiorite, the relief is very rugged and steep; rock and scree cover substantial areas, including impressive cliffs, summits and block fields. The potential vegetation corresponds to acidophilous pastures (*Nardion, Festucion eskiae, Festucion supinae*), which cover



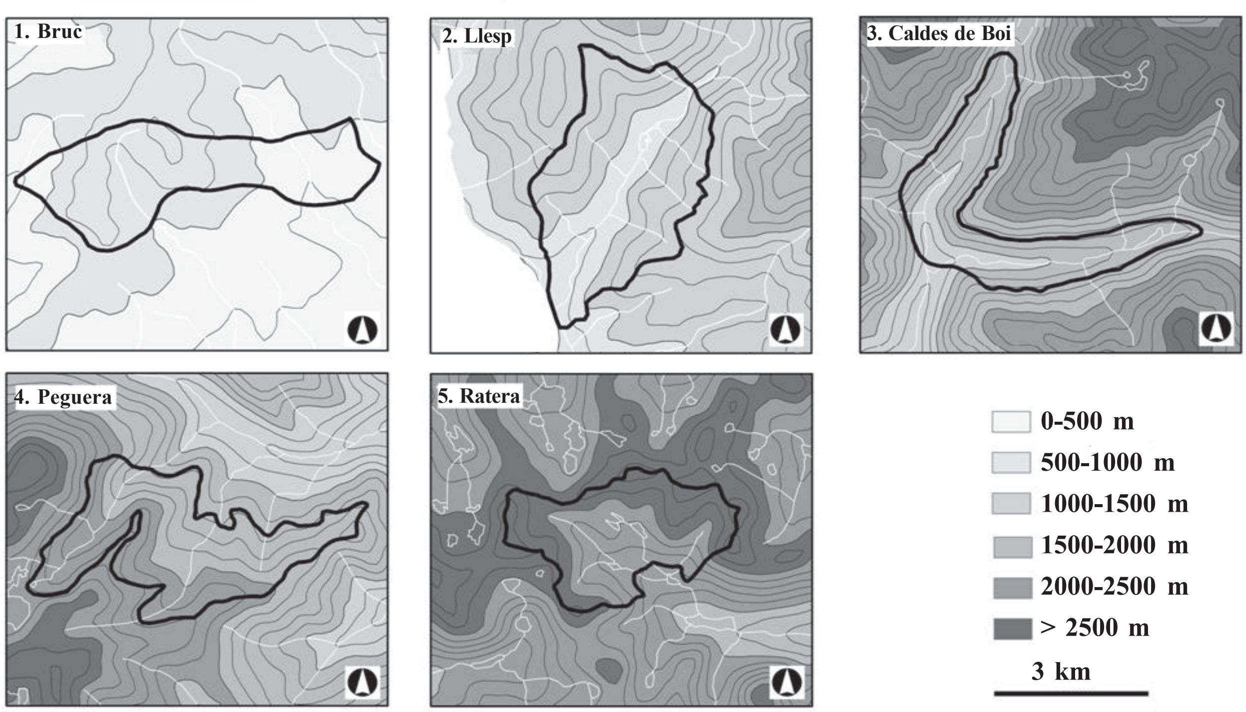


Figure 1. Location and maps of the areas studied.

the gentle slopes where there is some soil, and also many small patches interspersed over the rocky surfaces. Some alpine scrubs (*Rhododendro-Vaccinion, Juniperion nanae*) occur sporadically at the lower altitudes, whilst snow-beds, small lakes and rivulets are common.

METHODS

We used the map of CORINE habitats of Catalonia (CARRERAS & DIEGO, 2007) to asses the ecological partitioning of the areas studied. In this map, the legend units correspond to biotopes, each including various biotic communities but defined by means of plant communities. We classified the legend units into seven main habitats for each area, characterized by ecological, physiognomic and floristic criteria. Thus we obtained simplified maps according to the following main habitats: (1) potential forests; (2) secondary forests; (3) scrubs; (4) pastures and similar herbaceous units; (5) fields and ruderalized sites; (6) habitats related to water (fens, riverine formations, etc.); (7) rocky habitats (rock, scree, fellfields, etc.). Since the scale of the map is 1:50,000 with a minimum area for each polygon of 2.25 ha, the surface area calculated for some habitats (chiefly those related to water and to rocks) was underestimated.

For species richness, we obtained the local floras of the five areas from catalogues (NINOT *et al*., 1999; CARRILLO & NINOT, 1992a); these detail the ecological preferences of each taxon. Several taxa were added to include more recent data (FONT, 2007). Analyses were done at the species level, or at the subspecies level where these were differentiated. We generally followed the taxonomic and nomenclatural units proposed by BOLÒS *et al*. (2005), with a few exceptions. According to this regional flora, Catalonia harbours about 3,200 species, from which about 2,600 inhabit the Catalan Pyrenees; considering also subspecies, the flora of these areas account for about 3,900 and 3,170 taxa, respectively.

The taxa (species or subspecies) listed for each study area were then classified into six groups depending on their ecological preferences, according to the information given in the catalogues, for each of the five areas:

- **Potential forests**: taxa clearly preferring the potential forests (not present in Ratera, the alpine area), though sometimes occurring also in serial communities; a number are almost exclusive to these potential units.

- **Scrubs and clearings**: plants with ecological optimum in shrubby communities or in the vegetation of forest clearings, though sometimes occurring also in forests or in pastures.

- **Pastures**: plants showing a clear preference for these herbaceous units, excluding those with some ruderal tendency. In the first four areas, they form secondary vegetation related to deforestation, or permanent units on rocky slopes, whereas in the alpine Ratera area they mainly inhabit the most balanced habitats (flat areas and gentle slopes).

- **Ruderal habitats**: taxa mainly occurring in fields, fallows, roadsides and other places subject to disturbance.

- **Humid habitats**: plants restricted to streamsides, springs or other habitats that are more humid than the potential areas (such as certain north-facing toeslopes or cliffs). We included here hygrophilous forests, related bramble units, rush formations and fens.

- **Rocky habitats**: taxa occurring on rocks (crevices, rocky shelves), scree and other rocky places.

The two classifications (main habitat type and ecological preferences of the species) were intended to be parallel. However, while secondary forests were important landscape units, we did not use this category as an ecological preference. These forests differ from the potential forests at least in the dominant tree, which normally was more heliophilous (e.g., *Pinus halepensis* instead of *Quercus ilex* in the basal belt, or *Betula pendula* instead of *Fagus sylvatica* in the montane belt). Their undergrowth was made by varying combinations of heliophilous plants and taxa of the potential forests (frequently it includes also juveniles of the potential tree). Thus, the plants living in such heterogeneous forests are more closely associated with potential forests, clearings, scrubs or even pastures.

Since the areas studied differed in size, we calculated the ratio 'log species / log surface size' to allow standardized comparison (ROSENZWEIG, 1995: 9-10).

Table 2. Surface area percentages of main habitats in each area.

	Bruc	Llesp	Caldes	Peguera	Ratera
Potential forests	15	32	53	71	0
Secondary forests	49	15	11	2	0
Scrubs	18	8	6	3	4
Pastures	3	25	15	16	27
Fields and ruderal sites	12	13	1	0	0
Humid habitats	3	5	6	1	5
Rock and scree sites	1	4	9	8	64

RESULTS

As shown in Table 2, all the areas were covered to a large extent by forests, apart from the alpine area. The extent of potential forests increased from the basal belt to the subalpine belt, whilst that of secondary forests decreased correspondingly. Pastures and scrubs covered together 20-30% of the surface in all cases, with scrubs prevailing only in the Mediterranean area. Fields and other anthropized habitats (farms and small villages) covered substantial areas only in the basal and submontane belts. In other areas, they were almost or totally absent, at least at the scale mapped. Humid sites (springs, river and rivulet banks, etc.) covered very small areas in all cases. The alpine area showed the most particular landscape, due in part to the lack of forests, and in part to the large surface area covered by rock, scree, block fields and other rocky relieves.

Table 3 shows the distribution of taxa (species and subspecies) into the broad habitats considered in each area. The richness of the local floras showed a unimodal relation with altitude, the maximum being reached in the submontane belt. Differences between neighbouring belts were the smallest between submontane and montane belts, and the greatest between subalpine and alpine belts. Most of the partial floras of each habitat showed a similarly humped distribution according to altitude, with maxima situated from submontane to subalpine belts, depending on habitat. Only the ruderal flora decreased from the basal belt upwards.

DISCUSSION

Species richness across the five belts

The humped relationship between local floras and altitude is similar to that found in other studies on mountain plant diversity (VILLAR *et al*., 2001; GÓMEZ *et al*., 2003; GRYTNES, 2003; GRYTNES & BEAMAN, 2006), and reflects the so-called 'mid-domain effect'. Most of these studies split the areas treated into small altitude intervals (e.g. 100 m), which gives finer analyses of plant richness by altitude. With regards the areas compared, these altitude partitions result in a noticeable decrease in surface area studied as altitude increases, whereas in our case the extent of the areas compared was similar. If we consider the logarithmic ratio between species richness and area size, the montane belt had the highest species richness; the other areas remain in the order given by the raw number of species, although the submontane and basal belts become more similar (Table 3). Therefore, in spite of methodological and data differences among studies, the mid-domain effect with maximum richness in mid altitudes was reinforced in our study.

Besides the general altitude trends, the richness of local floras is influenced by physiographic diversity (PAUSAS *et al*., 2003), the size of the regional pool (ROSENZWEIG, 1995: 13-14), and the nature of the dominant outcrop. It is well-known that in temperate latitudes lime-rich substrata bear richer floras than lime-poor substrata (CHYTRÝ *et al*., 2003; EWALD, 2003). In our study, the flora of the basal belt may be poorer than expected due to

Table 3. Distribution of taxa (total number of species and subspecies) into the main habitats in each area (percentages over each local flora in brackets). [1] normalized by the lowest value (Ratera)

	Bruc	Llesp	Caldes	Peguera	Ratera
Potential forests	32 (7.4)	37 (6.5)	70 (13.2)	42 (10.8)	0
Scrubs, clearings	61 (14.1)	68 (12.0)	92 (17.4)	37 (9.5)	20 (9.2)
Pastures, grasslands	121 (27.9)	185 (32.6)	127 (24.0)	140 (36.0)	101 (46.5)
Fields and other disturbed habitats	137 (31.6)	134 (23.6)	62 (11.7)	23 (5.9)	8 (3.7)
Humid habitats	58 (13.4)	93 (16.4)	121 (22.8)	88 (22.6)	49 (22.6)
Rocky habitats	25 (5.8)	51 (9.0)	58 (10.9)	59 (15.2)	39 (18.0)
TOTAL	434	568	530	389	217
Ratio log species/ log surface[1]	1.09	1.10	1.17	1.07	1

its relatively gentle relief and the uniformity of its bedrock (slate). On the other hand, the flora of this mild Mediterranean area includes many medio-European and sub-Mediterranean plants (16-19%; NINOT *et al*., 1999) restricted to its mild or humid habitats, and also a number of latetropical plants (including aliens) in warmer and disturbed sites.

The highest floristic richness of the submontane area may be related to its physiographic heterogeneity, to the dominant lime-rich outcrops combined with a few patches of acidic soil, and also to the intrusion of plants from the neighbouring belts: Mediterranean plants mainly restricted to the basal belt grow in a few warm or dry parts of this submontane area, such as south-facing cliffs and rocky slopes. They may account for 20-25% of the local flora of this area (115-140 taxa; CARRILLO & NINOT, 1992a). Also, some medio-European taxa enrich this flora, inhabiting the moister or colder habitats.

The montane area is similarly enriched by taxa from the neighbouring belts. Besides some sub-Mediterranean (and a few Mediterranean) plants that are restricted to warmer spots, boreo-alpine and alpine taxa that are most commonly found in the high mountain occurs also here, mainly on rocky cold slopes and in streamsides. Moreover, the topographic and substrata diversity (steep relief; lime, slate and granodiorite) and the variety of water-related habitats result in a very rich flora. On the contrary, the scarcity of non-forest habitats, and particularly of anthropized units, is a noticeable filter for most of the flora of open sites. Compared with the lower belts, this is particularly apparent in the large decrease in opportunist and ruderal plants.

In Peguera, only the pastures and the rocky habitats have partial floras similar in size to that of the other areas. Forests, scrubs, and humid and ruderal habitats clearly offer less ecological diversity for the corresponding floras, as reflected by their decreasing richness. However, the plant diversity of this area remains relatively high due to the inclusion of a number of calcicolous taxa that are restricted to a few lime outcrops, and to a number of medio-European plants in mild pinewoods and fens.

The relative poorness of the alpine flora reflects a very uniform substrata and the normal altitude decrease observed in other high mountain areas (VILLAR *et al*., 2001; KÖRNER, 2003). This impoverishment is caused by the increasing limitations to plant growth and the decrease in habitat diversity along the altitude gradient. In addition to the lack of forests and true ruderal habitats in this belt, humid sites decrease in physical and chemical diversity, and the simplicity of alpine plant formations include poorer vegetation series. Moreover, the representation of phytogeographical groups other than Boreo-Alpine (Mediterranean orophytes, medio-European) is rather low (GÓMEZ *et al*., 1997). Thus, most of its flora is formed by the more ubiquitous plants of the high mountain pool (i.e. also occurring in the subalpine belt), with smaller proportions of specific taxa of the alpine belt (GÓMEZ *et al*., 2003).

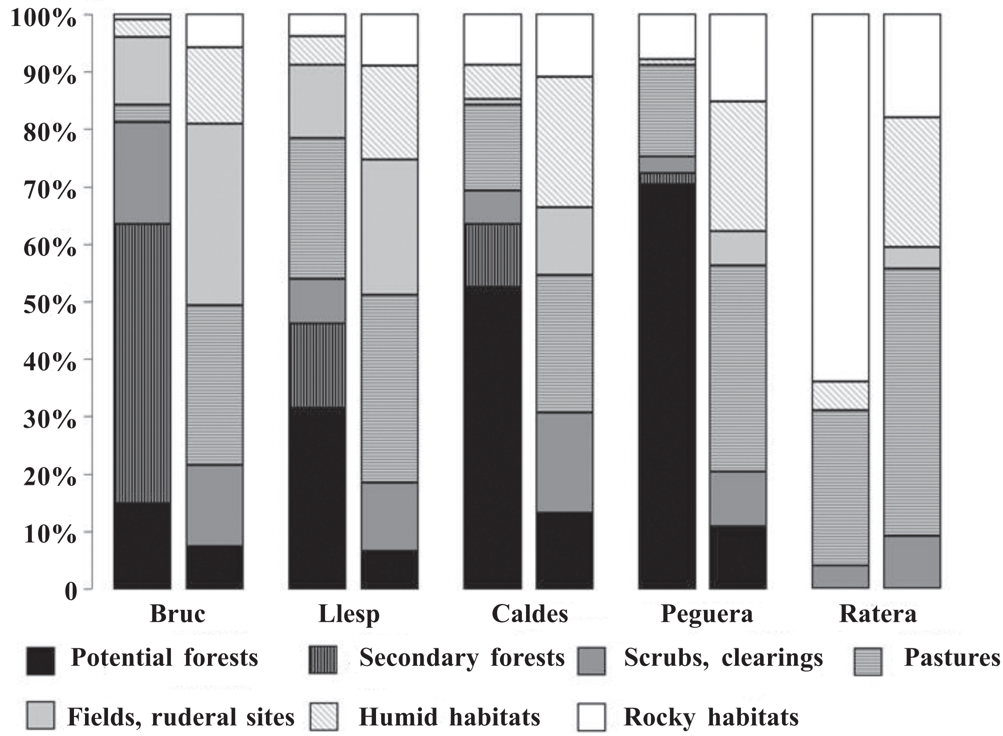


Figure 2. Comparison of percentages of the surface area of the main habitats (left columns in each pair) and of the number of taxa occurring in them (right columns), for the five areas studied.

Therefore, as in other similar studies the general pattern of humped species richness with maximum in the submontane and montane belts may be interpreted as a result of better macroclimate conditions for plant life (BROWN & LOMOLINO, 1998: 463-464). In these mid altitudes, a combination of fair rainfall and moderate temperatures, together with particular microclimates, enhance the co-occurrence of the flora corresponding to the main temperate conditions and other taxa from the neighbouring belts. Summer dryness in the basal belt and cold climate in the high mountain act as filters for most of the regional floristic pool.

Habitat partitioning of the local floras

In all the landscapes under forest domains, the plants restricted to the potential forests represent a small part of the local floras (Fig. 2). It accounts for less than 11% in three cases, and slightly more in Caldes de Boí, where the atlantic forest is rather species rich; moreover, in this area there are other particular potential forests covering small domains. In fact, the number of taxa restricted to potential forests in each belt amounts to only twofold to threefold the number of species which occur in one small (100-200 m^2) representative plot of these forests (CARRILLO & NINOT, 1992b; NINOT *et al.*, in press). In general terms, slightly more than half of these forest-specific taxa are widespread in each study area, while the other half are rare, occurring in only a few woodland locations. Also, the richness of forest species cannot be related to the area covered by potential forests in each example. These percentages of forest flora are similar to those given by ELLENBERG *et al.* (1991) for the whole central-European area (10%), which is much more extensive and includes many potential forest domains.

Scrubs and clearings contained richer partial floras than forests; compared to the forest flora, in el Bruc and Llesp the number of taxa inhabiting these units was twofold higher. Their relative abundance decreased in Caldes and was similar in the subalpine Peguera, where scrubs are not very differentiated among them, and nor from the pinewoods. No relationship between surface area occupied by scrubs (and secondary forests) and species richness was found, since they were widespread in el Bruc, and much scarcer in the other areas. The maximum richness was found in Caldes, probably due to the longer, more complex vegetation series involved in forest succession.

Pastures harboured high diversity in all cases, including between 24-47% of the local floras across the five belts. This high species richness showed no relationship with the area occupied by pastures; in el Bruc, 3% of surface area contained 28% of species, whereas in Caldes 15% of surface area contained 24% of species. From the Mediterranean to the alpine landscapes, pastures showed high within-community species diversity (α-diversity). The mean species richness of pasture relevés was 20-27 species in most cases, with maxima in Mediterranean *Hyparrhenietum hirto-pubescentis* (36 sps./rel.; NINOT *et al.*, in press) and subalpine *Trifolio-Festucetum* (29 sps./rel.; CARRILLO & NINOT, 1992b). Moreover, in pasture landscapes small environmental differences frequently condition rather contrasting communities (β-diversity). In Mediterranean and submediterranean landscapes, soil heterogeneity is reflected by species composition much more in secondary pastures than in forests and scrubs (CASAS & NINOT, 2003). Therefore, the species richness of the pasture habitats is clearly more related to environmental variation on a small scale than to the surface area occupied.

As for the plants of rocky slopes and other particular sites, their percentage increased with rising altitude from the basal belt to the subalpine belt. This indicates a rough relationship with the increasing area of these habitats, but this does not extend to the alpine belt. In fact, the number of species found in these habitats was similarly high in all the Pyrenean areas, and clearly lower in the basal belt. Thus, it seems that the species richness of this group depends more on aspects other than habitat surface area. Other Alpine massifs include rich and particular rupicolous flora spread throughout the altitudinal range (PAWLOWSKY, 1970).

The flora related to water and hygric soils followed a similar trend to that of rocky habitats, though more attenuated. Their total species number reached the maximum in Caldes, decreasing towards upper and lower belts. But the percentage over the local floras increased regularly from the Mediterranean to the montane belt, and then remained the same until the alpine belt. Species richness showed no relationship with the available habitat, which was small and dispersed in all areas, especially in the subalpine belt.

The habitats created by farming and other disturbances harboured a substantial part of the floras in el Bruc and in Llesp, in spite of the moderate percentage of these areas occupied by the corresponding habitats. The ruderal floras clearly decreased along the altitude gradient, related both to the strong size decrease in fields and related habitats and to the general decrease of the ruderal flora in the altitudinal sense. However, this flora was still noticeable in Caldes, and survived in the subalpine and even in the alpine belts, where ruderal habitats were reduced to small patches and a few roadsides. Therefore, a number of ruderal species can maintain sparse populations in a given landscape even if only very small surface areas are occasionally disturbed. Occasional forest clearings, cattle resting places or even avalanches give this dynamic flora a chance in natural areas, such as the high mountain (GÓMEZ *et al.*, 1997).

Biogeographic and dynamic aspects

At our scale of analysis, over one half of the flora was related to extensive habitats (forests, scrubs, clearings and pastures); this amount grew slightly from the basal belt (49.4%) to the high mountain (56.3% and 55.7% in the subalpine and alpine belts respectively). In each area, most of these plants were widespread – although a number were rare or even very rare (BOLÒS *et al.*, 2005). Since they mainly depend on general environmental conditions and vegetation dynamics, their persistence in the local floras seems more certain than that of plants restricted to particular habitats. However, the abandonment of traditional forest and farm exploitation during the last few decades has greatly reduced the extent of fields, pastures and scrubs, at least in the lower belts (from basal to montane; LASANTA, 1990; MONJE, 2003). Thus, the populations of the less common plants of these open habitats have decreased, becoming small and scarce over landscapes dominated by secondary or near-potential forests. Their local survivorship will depend on their particular ability to persist in scattered, fluctuating populations. Whereas most weeds and plants from scrubs and clearings are well adapted to such dynamics, this may be a handicap for some pasture species that are not able to disseminate efficiently or persist in soil seed banks (FENNER & THOMPSON, 2005).

On a global scale, most of the plants from these habitats (from forests to pastures) show medium-sized ranges, which mostly coincide with biogeographic provinces or regions. But in all the areas studied, a small proportion reflects regional variation; for example, a number of endemics inhabit calcicolous pastures (VILLAR & GARCÍA, 1989). So, the flora of these habitats would be only slightly richer if the areas considered were larger, but their proportion would decrease in front of that of plants of particular habitats (MONTSERRAT-MARTÍ & MONTSERRAT-MARTÍ, 1990).

The plants of water-related habitats are rarely endemics, although a good number have their southernmost populations in the Pyrenees. Moreover, most hygrophytes are related to rather specific environmental conditions, and have little chance of survival if these change (VILLAR *et al.*, 1997). They may be doomed to face severe persistence triggers, given their fragmented, scarce habitat and disjunct areas.

In contrast to the other species groups, the ruderal flora mainly consists of ubiquitous plants occurring in whole regions or continents, a few even being cosmopolitan. Many occur in two or even three of the areas studied. Since they are widespread over neighbouring zones, their percentage would decrease if larger areas were considered. Therefore, although they account for a substantial part of the local diversity in the lower belts, their contribution is less singular than that of the other groups.

The most specific flora from the biogeographic point of view was concentrated in the rocky habitats, as stated by other authors (PAWLOWSKI, 1970; BAUDIÈRE & CAUWET-MARC, 1986; VILLAR & GARCÍA, 1989; GÓMEZ *et al.*, 1997; VILLAR *et al.*, 2001). Crevices, shelves, scree and other stressful habitats harboured endemics of any type, mainly in the Pyrenean areas (from the submontane to the alpine areas). The occurrence of a number of very ancient paleoendemisms (e.g. *Ramonda myconi*) proves that these are very conservative habitats, even the dynamic scree and eroded slopes (MONTSERRAT-MARTÍ & MONTSERRAT-MARTÍ, 1990). This flora seems to thrive better than plants of more general habitats during climatic change and land use shifts (MAJOR, 1988; GÓMEZ *et al.*, 2003).

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