Phytocoenologia	37 (3-4)	371-398	Berlin–Stuttgart, December 21, 2007
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Altitude zonation in the Pyrenees. A geobotanic interpretation

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with 4 figures, 1 table and 2 appendices

Dediquem aquest treball al professor Salvador Rivas-Martínez, pal de paller i animador incansable de la fitocenologia ibèrica

Abstract. We present a review of the main trends of vegetation zonation in the entire Pyrenean mountain system, including previous overviews and a great many papers on flora and vegetation. The main floristic territories are roughly set as parallel zones along the main axis. The high mountain zone forms a central core, characterized by the dominant Boreo-Alpine element. The Atlantic mid altitudes and lowlands (mainly on the north face of the chain) and the mid altitudes of the Iberian side bear Medioeuropean flora as their dominant element, but include a good representation of the transitional Submediterranean element. Lower down, the Iberian lowlands harbour dominant Mediterranean flora. This landscape zonation may be understood in terms of the Alpine model, by which high mountains include three belts (subnival, alpine, subalpine), the mid altitudes show one belt on the Atlantic face (montane) and two on the Iberian face (montane, submontane), and the low altitudes form a basal belt with two contrasting faces (Atlantic and Mediterranean).

The vegetation belts are briefly defined in terms of the main potential communities, since these are the most closely related to bioclimate. Thus, the boundaries between belts mostly coincide with boundaries of potential domains, but a few vegetation domains occur in two neighbouring belts. Then, substrata properties and regional climatic variation within the same belt produce noticeable shifts in the potential domains. This makes the basal and montane belts more diverse throughout the Pyrenean range than the high mountain belts. The boundaries between belts run a bit higher on south-facing slopes than on north-facing slopes, reflecting the effect played by topographic thermal and hydric drivers on vegetation. Also, the somewhat higher location of the boundaries in the central sector than towards the edges of the chain is connected with the continental character of the inner Pyrenean area.

Keywords: floristic regions, landscape, vegetation, Alpine mountain, phytocoenology, bioclimate.

1 Introduction

Plant zonation is a very particular phenomenon in the field of environmental sciences that has exerted a powerful attraction on a wide range of scientists. In the great mountain systems contrasting landscapes are set according to their altitude gradient, but also reflect other causal factors at meso- and microscales. The interaction of all these factors, together with human influence, lead to complex arrangements, in which altitude-related factors remain prevalent.

Here we try to synthesize the main trends of vegetation zonation over the whole Pyrenean mountain system. After a number of previous papers, now we attempt a comprehensive review of this topic, trying to bring together broad-range Pyrenean works, local monographs on Flora and vegetation, vegetation maps, results from floristic data banks, and evidence obtained from functional studies on mountain communities.

1.1 Generalities on landscape zonation: latitude and altitude

At the entire biosphere scale and at the scale of mountain systems, various climate gradients define latitude and altitude zonations, made up of contrasting zonobiomes (WALTER 1979). The dominant plant formations have been traditionally used to design some latitude zones (taiga, steppe) and altitude zones (maquis, xeroacanthic, beechwood). However, other zones include complex vegetation patterns, making a simple vegetation descriptor less suitable. Given the main role played by the macroclimate at this ecological level, these zones are designed by adding climate descriptors, mainly in the case of latitude zones (cold deserts, rain forest, etc.). The altitude zones, named belts, are usually defined through specific descriptors (montane, alpine ...), which referred in the first instance to the Alps and later to similar mountains.

In the mid latitudes of Eurasia, Quaternary climatic changes forced floristic pools from various sources to meet during latitude and altitude migrations. This led to the formation of two similar floristic gradients, latitudinal over lowlands, and altitudinal in the mountains. A rule of thumb states that the variation of the main bioclimatic factors 100 km northwards is roughly the same as the change at 100 m greater altitude (WALTER 1979). Shifts in flora and vegetation would follow the same rule. Therefore, latitude and altitude zonations show noticeable parallelisms, from their main ecological factors to vegetation structure and function and to plant composition. Although some of these parallelisms are only superficial – just physiognomic, or referring to a few dominant species – some authors (EMBERGER 1955, OZENDA 1975, RIVAS-MARTÍNEZ 1981) use the same term, belt, to design both latitude and altitude zones. RIVAS-MARTÍNEZ even defines these latitude zones, together with the altitude belts, through climatic descriptors.

1.2 Altitude zonation

Mountain systems may be considered either a particular extension of the latitudinal zone where they are found, or taken as independent entities. The first approach leads to the inclusion of a given landscape (e.g., mountain beechwood) occurring in various mountain systems (Pyrenees, Iberidic range) in different biogeographic regions. The second approach gathers similar mountain systems into the same orobiome. As orobiomes are then treated as biogeographic units differentiated from the lowland zonobiomes, a given biogeographic territory may include detached surface areas. The upper belts of the mountains located in the northern part of the Mediterranean region (Montseny, Moncayo, etc.) are good examples of small Medioeuropean islands surrounded by extensive Mediterranean vegetation lower down (Bolòs 1989).

Following the first approach, RIVAS-MARTÍNEZ (1987a) includes each mountain range, or most of it, in one biogeographic region. Others consider some ranges as a complex transition between adjacent regions or latitude zones. Mountain systems in South Europe would then coincide with the transition between the Medioeuropean (Eurosiberian) and the Mediterranean regions (Quézel 1971, Dupias 1985, etc.), expressed through southern lower belts of Mediterranean character and upper belts coinciding with Medioeuropean mountain belts (Ozenda 1994). In fact, RIVAS-MARTÍNEZ (1987a) expresses almost the same, when including the lower Iberian belts of the Prepyrenees in the Mediterranean region.

A common trend in all these interpretations is that the Pyrenees, like the southwestern Alps, the Apennines and Caucasus, straddle the Medioeuropean and the Mediterranean regions. Therefore, these mountain systems are good examples of interzonal orobiomes, which show two different altitude zonation patterns on the lower part of their two sides.

1.3 The Alpine model

At the beginning of the twentieth century, SCHRÖTER (cited in OZENDA 1985) established a comprehensive system of belts in the Alps, taking into account a good deal of previous proposals from diverse fields. Mainly on the basis of vegetation complexes, he distinguished five belts (colline, montane, subalpine, alpine and nival), sometimes divided into upper and lower parts.

This Alpine model was generally adopted and re-elaborated in geobotanic papers during the past century, mainly for the Alps but also for other 'Alpine' systems (Pyrenees, Apennines, Carpathians, etc.). The schema was broadened sufficiently to encompass the double zonation patterns of such interzonal systems. Thus, the lower vegetation belts include differentiated landscapes and wider transitions between northern and southern faces (OZENDA 1985 and references therein; BOLÒS 1979; RIVAS-MARTÍNEZ 1987b, 1988).

The same zonation model has sometimes been applied to mountain systems that are quite distant from the Alps, but the resulting schemes

become less informative, the further away their regional floristic pool is from the Medioeuropean flora. Partly to avoid this, RIVAS-MARTÍNEZ (2005) proposes a new system of vegetation belts, based on the macrobioclimate where each mountain occurs and on the thermal altitude gradient. What he calls thermotypes correspond to given ranges of thermal indexes (thermicity, annual positive temperature) and are associated with particular landscapes, or belts. In this classification, the French side of the Pyrenees, like most of the Alps, shows the following 'temperate' belts: thermotemperate (formerly, lower colline), mesotemperate (= upper colline or submontane), supratemperate (= montane), orotemperate (= subalpine) and criorotemperate (= alpine and nival). On the Iberian side, the Pyrenees start with Mediterranean belts (mesomediterranean and supramediterranean) and then give way to 'temperate' belts, as on the French side.

1.4 New insights

Growing knowledge of recent environmental changes has allowed a better understanding of the link between bioclimate and vegetation. Relatively small thermal changes occurred from the Holocene onwards have produced noticeable landscape changes, including altitude displacement of belts by a few hundred meters (Montserrat 1992, Carcaillet & Brun 2000, Tinner & Theurillat 2003). It is now clear that some of these changes took place under strong human influence (deforestation, rising cattle, etc.). The altitude and structure of the present treeline, the extensive subalpine and montane areas turned into pastures, and the enhancement of a few tree species (*Pinus sylvestris, P. uncinata*, etc.) are clearly the result of strong landscape modifications.

The most influential aspect of the ongoing global change, i.e. rising temperatures, is expected to produce a noticeable altitude rise of vegetation belts. A rate of upwards displacement between 200–400 m during the next 100 years has been hypothesised for the Alps (Guisan et al. 1995). In the Montseny massif (E Catalonia), diachronic landscape analysis and dynamics of forest structure have been used to show the upwards advance of holm oak Mediterranean forest over the Medioeuropean beechwood (Peñuelas & Boada 2003). The other main change driver, i.e. the strong decrease of traditional land use during the last decades, enhances the spontaneous

return to natural landscapes.

Ancient anthropogenic effects on the vegetation, together with those resulting from the ongoing global change, pose particular difficulties in the interpretation of the Pyrenean landscape. For instance, the knowledge of vegetation domains is biased because most forests in the present landscape lie on rocky landforms, and thus may be more closely related to particular substrata conditions than to general bioclimate. Some serial communities, including anthropized woods, show a noticeable inertia, mostly relating to population dynamics and to the slowness of mountain soil responses to changing climate or land use. This is the case of some eutrophic *Carpinion* forests surrounded by poorer woodlands, reflecting residual fertility due to

ancient farming use. Even the return of the treeline to former positions is a very complex and diversified ecological response to global change. Its rise is particularly slow or unappreciable where it has been lowered least, and where soil has been eroded or transformed more (KÖRNER 2003, HOLTMEIER & BROLL 2005, NINOT et al. 2005).

2 Floristic territories in the Pyrenees

The Pyrenean landscape is built upon a rich flora, estimated to contain some 3,500 species (Duplas 1985). This species richness is partly due to the interzonal character of the Pyrenees, to the varied altitude zonation and to the noticeable endemic element. The first two aspects result in the occurrence in the range of three contrasting floristic elements: Mediterranean in the lower belts of the central part of the Iberian face, Medioeuropean (mainly Atlantic) in the other parts of the same belts, and Boreo-Alpine in the high mountain. Moreover, the Mediterranean and Medioeuropean elements include various subelements, related to regional variations in bioclimate and substrata. Therefore, the floristic territories reaching the Pyrenees partly coincide with the altitude zones.

2.1 Traditional attempts

From the end of the nineteenth century (e.g. Lázaro-Ibiza 1897), considerations on the Pyrenean landscape have been strongly influenced by geomorphic criteria. In this respect, most authors point out the strong contrast between the Northern face-steep, narrow and rainy – and the Southern face – more extended, intricate and dryer. The other aspect in which most coincide is the definition of three sectors along the range (Western, Central and Eastern), showing minor differences in the precise location of the boundaries. The criteria used by most of them (Dantin 1942, Hernández 1932, Gaussen 1965, Lautensach 1967, Ruiz & Ruiz 1976, etc.) may be considered geobotanic in a broad sense, since their grounds were biotic and abiotic factors in various degrees.

The Pyrenean system is treated in a similar way by RIVAS-MARTÍNEZ (1973) in his chorological synthesis of the Iberian peninsula, where the resulting territories (provinces, sectors, etc.) are mainly based on the distribution of taxa and syntaxa, and secondly on other criteria (lithologic, climatic, etc.). Among the floristic data, he places particular weight on endemic flora (patroendemic and paleoendemic) and to the distribution patterns of polyploid complexes. In so doing, the core of the Pyrenees becomes a particular province (Pyrenean) in the Medioeuropean region, formed by three sectors (Western, Central and Eastern), and borders the Atlantic province (north- and westwards) and two Mediterranean provinces (south- and eastwards). This paper was a milestone in chorological syntheses of the Pyrenees, strongly influencing most of the geobotanic work since then. The same author on his own (RIVAS-MARTÍNEZ 1979, 1982, 1988) and in collaboration (RIVAS-MARTÍNEZ et al. 1977, 1983, 1990, 1999, 2002) has

developed his proposals, placing more weight on distribution ranges of syntaxa and vegetation series. In his more recent work, the Spanish Pyrenees are plit into four main sectors, two of which are more or less peripheral and parallel (Prepyrenean and Mediterranean) and two are axial (Central and Eastern).

2.2 Giving protagonism to chorological criteria

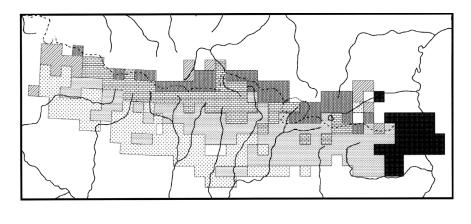
Other phytogeographic Pyrenean syntheses have been constructed solely on the patterns of plant distributions, following the principles given by TAKHTAJAN (1986). In this sense, the proposals of Meusel et al. (1965) and SAINZ & HERNÁNDEZ (1981) result once more in the distinction of three sectors set along the main axis. The second work, referred to endemic monocots, was later developed (SAINZ 1983) through a hierarchical classification analysis of the data, into the first use of this method on Spanish chorological data. There have been a number of other attempts since then, using multivariate analyses on particular taxonomic groups: endemic monocotyledons (Sainz & Hernández 1985; Moreno & Sainz 1997; Moreno et al. 1998), pteridophytes (Márquez et al. 1997, 2001), Ericoideae (OJEDA et al. 1998), Cytiseae (Gómez-González et al. 2004) or endemic plants and animals (GARCÍA-BARROS et al. 2002). In this last article, the authors use a parsimony analysis and distinguish two sectors (Eastern and Western) in the Pyrenees. The strong taxonomic bias given in these papers by the primary data makes the results very dependent on the evolutive history of each group, and thus difficult to compare with more classic geobotanical schemes. However, the proposals of both groups of studies show noticeable affinities, especially when the taxonomic groups taken are broader.

A more specific approach is that of Hernández & Sainz (1984), in which the similarity between Pyrenean sectors is calculated from the quantitative analysis of the Iberian endemic taxa, which leads to the identification of migratory paths and different types of boundaries. They conclude that the Pyrenean boundaries between Eastern and Western sectors are semipermeable, thus giving no support to their distinction at the sector level. In the phylogeographic aspect, the eastern Pyrenees shows noticeable values of exportation westwards (and southwards), which suggests the relevance of

this sector in the preservation and origin of Pyrenean endemicity.

2.3 Analysing the entire Flora

In a contrasting attempt, LÓPEZ & FONT (2006) use the entire vascular flora to draw a phytogeographic scheme of the Spanish Pyrenees and neighbouring areas. The study is based on the distribution of the Pyrenean Flora according to the 10×10 km UTM squares, which implies 4,700 taxa and some 1,200,000 citations, mainly compiled in the data bank BDBC (FONT et al. 2004). The squares are then analysed and clustered according to their particular floristic pool, through the K-means algorithm (BOUXIN 2005).



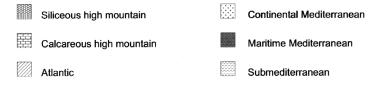


Fig. 1. Division of the Pyrenees into distinct floristic territories, according to the K-means fuzzy analysis of the flora of each 10×10 km UTM square. Open squares mean deficient data.

The first Pyrenean territories distinguished are one central core of squares including high mountain areas versus one surrounding area. Successive partitions give, from the surrounding area, one Atlantic territory, and then one Mediterranean and one Submediterranean area. At more detail, both the Mediterranean outskirts and the high mountain zone become split into two territories each. We consider that this partition of the Pyrenees into six floristic territories (Fig. 1) is the most suitable in phytogeographic terms and at the scale of the whole Pyrenean area.

In this scheme, all the territories except the maritime Mediterranean one draw longitudinal stripes, in part coinciding with that proposed by RIVAS-MARTÍNEZ et al. (2002) and by BOLÒS (1985). The order of appearance of the territories, moreover, gives preeminence to the altitude gradient as most affecting the formation of floristic territories, through particular bioclimates, and highlights the contrasting effects of the main chain on the floristic pool of both Pyrenean sides (N and S). In spite of the low resolution of the 10×10 km squares (each includes contrasting altitudes, slopes and substrata) and the simplicity of the data (presence/absence of the taxa in each square), this approach constructed from vascular flora as a whole responds to the occurrence of three main floristic territories: Medioeuropean (including Atlantic and Submediterranean), Mediterranean and Boreo-Alpine.

The floristic territories drawn correspond well with the altitude belts of vegetation discussed above (cf. 1.2 & 1.3). The belt cliserie shows a gradual shift between two main geoelements (Atlantic and Boreo-Alpine) on most of the French side, as well as on the Iberian side in eastern Navarra and in mild northeastern Catalonia. In contrast, on the rest of the Iberian side and in the Prepyrenees, the Mediterranean lowlands make a complex transition through Submediterranean and Atlantic landscapes to Boreo-Alpine high mountain.

3 Pyrenean belts and vegetation patterns

According to the landscape and floristic criteria discussed above, a rough approach to the Pyrenees distinguishes three main altitude units: high mountain, mid altitudes and low altitudes. The high mountain is clearly characterized by dominant Boreo-Alpine flora and vegetation, together with particular geoforms (glacial relief, steep peaks and crests, etc.), which harbour singular vegetation units. In the mid altitudes, the landscape is mainly Medioeuropean, in spite of the noticeable differentiation between the Atlantic and the Mediterranean sides – the second including transitional Submediterranean landscapes. At low altitudes, this distinction leads to a greater contrast between typical Atlantic territory on one side and Mediterranean territory on most of the other, connected by transitional landscapes in eastern Navarra and northeastern Catalonia.

These three levels may be more precisely treated as six vegetation belts. The surrounding lowlands, including noticeable penetrations along the valleys into the axial range, are here considered a basal belt (= colline belt). The range of mid altitudes may be split into submontane and montane belts in the Mediterranean face, or just taken as a montane belt in the Atlantic face. Finally, the high mountain is divided into subalpine, alpine and subnival belts. This last distinction is primarily based on the decreasing complexity of the potential vegetation (coniferous forests, pastures and open vegetation, respectively), but also on the different role played by particular habitats and on floristic shifts – such as the decreasing number of species.

Altitude belts have been defined geobotanically on the basis of the most mature plant communities, since these are the ones most closely related to bioclimate. Thus, the altitude gradient is better represented by the sequence of potential domains, in which varying mature communities make up altitudinal cliseries. Within the same belt, potential domains also show noticeable shifts, mainly over contrasting substrata (acidic vs. lime-rich) and exposures (north- vs. south-facing). Weaker bioclimatic variation over the Pyrenean surface (continentality, special topoclimates) and the composition of local floristic pools also produce special vegetation patterns.

In the following sections we give a short characterization of the different belts recognized, in terms of potential domains, bearing in mind the abovestated regional variation. This variation occurs from valley to valley, and may be considered along the Pyrenean system (i. e. from the Atlantic to the Mediterranean edges) or, contrarily, across the mountain system (from

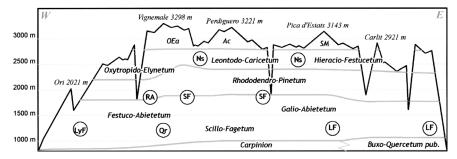


Fig. 2. Schematic distribution of the main potential domains on the French side of the axial Pyrenees, mainly on north-facing exposures. Circles represent domains limited to small territories or to particular conditions. OEa, Oxytropo-Elynetum var. of Artemisia umbelliformis; Ac, Androsacion ciliatae; SM, Saxifrago-Minuartietum sedoidis; Ns, Nardion strictae; RA, Rhododendro-Abietetum; SF, Sorbo-Fagetum; LyF, Lysimachio-Fagetum; Qr, Quercion roboris; LF, Luzulo-Fagetum.

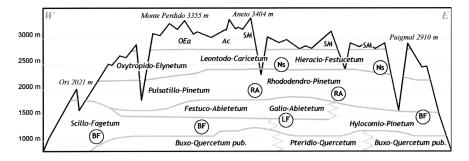
North to South). We synthesize this regional variation of altitude zonation in three comprehensive figures, corresponding to the French face of the axial range (Fig. 2), the Iberian face of the axial range (Fig. 3) and the Iberian Prepyrenees (Fig. 4). Figures 3 and 4 include north-facing and south-facing slopes as independent schemes, whereas other variations are indicated through codes and in the captions.

This synthesis is based on a great many geobotanic papers, from regional studies to local monographs, and includes chorological, phytocoenological and cartographic approaches (see Appendix 1). Most of them have been written during the last two decades, and refer to the Iberian part of the Pyrenees. As a consequence, the Iberian side of the Pyrenees is now more precisely known than the French side, in contrast with earlier.

3.1 Basal belt

This belt spreads up to 600-900 m a.s.l., and includes such contrasting aspects as Atlantic mixed woodlands and Mediterranean sclerophyllous forests.

In the Mediterranean area, i.e. the Prepyrenees and most of the Iberian side of the axial Pyrenees, the basal belt is defined by the overwhelming dominion of Quercus ballota (= Q. rotundifolia) forests. They are very general on south-facing and intermediate exposures, whereas on north-facing aspects they alternate with mesoxerophyllous forests (Quercion pubescenti-petraeae), which come down from the submontane belt. These sclerophyllous forests are rather irregular and species-poor, related to continental conditions. Most of their understorey taxa are a bit heliophilous and generalistic, thus giving poor regional distinction to these communities. Buxo-Quercetum rotundifoliae is the most general association, occurring on lime-rich substrata from the lower Roncal valley to the Llobre-



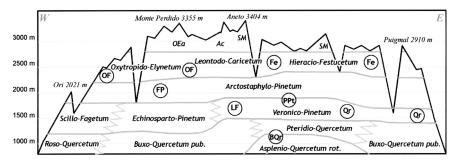


Fig. 3. Schematic distribution of the main potential domains on the Iberian side of the axial Pyrenees, on north-facing slopes (up) and on south-facing slopes (down). OEa, Oxytropo-Elynetum var. of *Artemisia umbelliformis*; Ac, Androsacion ciliatae; SM, Saxifrago-Minuartietum sedoidis; Ns, Nardion strictae; RA, Rhododendro-Abietetum; BF, Buxo-Fagetum; LF, Luzulo-Fagetum; OF, Oxytropido-Festucetum; Fe, Festucion eskiae; FP, *Festuca scoparia-Pinus uncinata* community; PPt, Primulo-Pinetum teucrietosum; Qr, Quercion roboris; BQr, Buxo-Quercetum rotundifoliae.

gat basin. It shifts to Spiraeo-Quercetum rotundifoliae towards the western edge of this range, and to Asplenio-Quercetum rotundifoliae on acidic outcrops of central-eastern valleys. On the Mediterranean maritime northeastern part of the chain, *Quercus ilex* makes richer communities (Asplenio-Quercetum ilicis). The serial vegetation of these sclerophyllous forests includes xerophilous garigues (Rhamno-Quercion cocciferae), light scrub (Rosmarinion, Cistion) and therophytic pastures (Thero-Brachypodion, Helianthemion).

The Atlantic part of this belt is well characterized by mesophilous forests of Carpinion betuli, typically with a mixed deciduous tree layer, but dominated by Quercus robur or Fraxinus excelsior in fresher aspects and by Quercus petraea or Q. pyrenaica in drier biotopes. These forests have in most cases a complex structure (four vegetation strata) and high species richness, mainly due to geophytes and hemicryptophytes. In the most oceanic, western area two main associations are found, related to varying sub-

strata: Blechno-Quercetum roboris on acidic substrata and Isopyro-Quercetum roboris on neutral or basic soils. Eastwards, Isopyro-Quercetum reaches Ariège and even the most humid area of the southeastern Pyrenees (Garrotxa, Ripollès); this is a rather diversified association, relating to substrata, topoclimate and local flora.

The transition from Mediterranean to Atlantic areas within this belt gives way to the dominance of mesoxerophilous oakwoods (Quercion pubescenti-petraeae) in local landscapes, where Quercion ilicis occupies the driest surfaces and Carpinion is secluded to milder toeslopes and river terraces. These Submediterranean landscapes are quite extensive in humid northeastern Catalonia.

3.2 Submontane belt

The submontane belt is well defined on the Iberian face and in the Prepyrenees, where it coincides mostly with the dominance of Submediterranean formations, such as forests of marcescent oaks (Quercus pubescens, Q. faginea and hybrids), related pinewoods (of Pinus nigra subsp. salzmannii or P. sylvestris) and serial mesoxerophilous scrub and pasture (Amelanchiero-Buxenion, Aphyllanthion, Brachypodion phoenicoidis). Its upper limit runs at 1100–1300(1500) m a.s.l., depending on areas and exposures. On the Atlantic side the vegetation of this level is roughly the same as that which occurs upwards till the subalpine belt, and in the transition areas Submediterranean landscapes remain on dry, south-facing slopes. Therefore, the submontane belt becomes progressively thinner and more fragmented in the transition from the Mediterranean to the Atlantic Pyrenees.

Dry oakwoods of *Quercus faginea* (and related hybrids) characterize the Prepyrenees from the Segre valley to western Navarra, and reach the axial range in a few places. The most common association is Violo-Quercetum fagineae, whereas Spiraeo-Quercetum fagineae is found in the western transition area. They are related to lime-rich bedrocks, mostly marls and clays producing gentle relieves and dense soils, and to rather continental climates. Summer dryness is noticeable and is reflected in these deciduous forests by some Mediterranean taxa. Locally, Violo-Quercetum alternates with a related pinewood, Lonicero-Pinetum salzmannii, on steep slopes made of hard limestone or conglomerate, chiefly in the most continental areas.

Quercus pubescens forms mesoxerophilous forests in the axial range and in the upper part of this belt in the Prepyrenees. The most extended association over these areas is the calcicolous Buxo-Quercetum pubescentis, which moreover comes down to the basal belt in the transition zones and even on the Atlantic face, where it remains secluded on dry slopes. On acidic bedrocks, this association is replaced by the poorer Pteridio-Quercetum pubescentis, frequent in central and eastern areas. At the western edge of the Iberian Pyrenees, the Atlantic influence is expressed through two different associations: Roso-Quercetum humilis on limes and Pulmonario-Quercetum pyrenaicae on acid substrata.

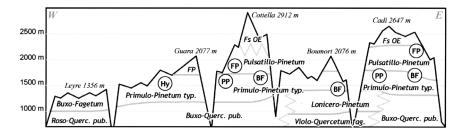
3.3 Montane belt

The domain of this belt corresponds to mesic deciduous woodlands or, in more continental areas, to analogous coniferous forests. Its upper limit is mainly at 1,600–1,700 m a.s.l. on north-facing exposures and at 1,700–1,900 m a.s.l. on south-facing aspects. Due to the varying development of the submontane belt over the Pyrenees, the montane belt has a broader altitude range on the Atlantic side. It includes the greatest diversity of land-scapes at the regional scale, according to variation of bioclimate and substrata. The same trend is also reflected in greater species richness at this altitude level, where various floristic elements coincide (VILLAR et al. 2001).

Beechwoods are the most characteristic montane forests on the Atlantic face and in areas with some Atlantic influence. In the latter, mixed forests of Fagus sylvatica and Abies alba are more extended than pure stands of Fagus sylvatica. These forests dominate the landscape of most of the belt on the north side of the main range, become less extensive in the transition areas, and reach the driest ranges, such as the Prepyrenees, secluded on particular north-facing slopes. On the other hand, Fagus sylvatica is almost absent in the continental area stretching from Cerdanya to Pallars, where it nevertheless makes a few, small stands. Under the broad ecological range of this dominant tree, beechwoods show a noticeable differentiation across the Pyrenean range, reflected in a number of associations and subassociations, related to local conditions and species pools.

Eutrophic, species-rich beechwoods may be mainly included in the broad Scillo-Fagetum, which includes various subassociations. They are widespread on the Atlantic face, where they are found on diverse exposures and bedrocks, excluding the driest or more acidic slopes. On the Iberian face, they become less frequent in the transition zones (eastern Navarra, northeastern Catalonia) and remain secluded in the most humid places of a few wet valleys of the central sector. Acidophilous beechwoods are generally less diverse, though various associations have been distinguished along the main range. Luzulo-Fagetum covers the acidic north-facing slopes of the eastern areas on both sides of the chain, and reaches the central and western parts on south-facing exposures, where it gives way to the mesohygrophilous Lysimachio-Fagetum on north-facing slopes; and Galio rotundifoliae-Fagetum occurs on acidic substrata of the western Prepyrenees. The calcicolous beechwoods include various mesoxerophilous taxa in the understorey, thus making the transition from the typical Medioeuropean Fagion to the Submediterranean Quercion pubescentipetraeae. They occur on the Mediterranean side of the main range, from Vallespir to the Irati valley (Navarra), and in the Prepyrenees, where it is almost the only beechwood type. In spite of their regional diversification, they may be included in the same association, Buxo-Fagetum.

The montane belt also includes acidophilous oakwoods, which are common on the Atlantic side, are restricted to acidic bedrocks of the central and eastern Iberian face, and do not reach the Prepyrenees. The main association is Lathyro-Quercetum petraeae, related to poor substrata, but



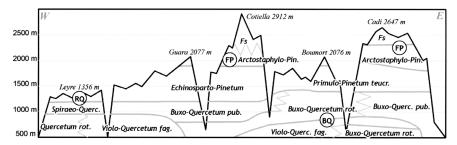


Fig. 4. Schematic distribution of the main potential domains in the Iberian Prepyrenees, on north-facing slopes (up) and on south-facing slopes (down). Fs, Festucion scopariae; OE, Oxytropido-Elynetum; FP, Festuca scoparia-Pinus uncinata community; Hy, Hylocomio-Pinetum; PP, Polygalo-Pinetum; BF, Buxo-Fagetum & Buxo-Abietetum; RQ, Roso-Quercetum humilis; BQ, Buxo-Quercetum pubescentis.

in the wetter places of the Iberian part occurs the richer mesohygrophilous Veronico-Betuletum.

Natural forests of *Pinus sylvestris* cover wide surfaces and are greatly diversified on the Iberian side of this belt. They dominate the forested landscapes in the areas where the climate is too continental or too dry for Fagus or Abies, i.e. the central part of the Iberian side and Prepyrenees. In other Pyrenean areas, these pinewoods are more restricted to unfavourable sites (poor soils, dry shelves, rocky slopes, etc.). Hylocomio-Pinetum catalaunicae is a well-characterized calcifuge mesic type, including a noticeable moss layer and a number of boreal taxa. It covers noticeable northfacing slopes of the Catalan Pyrenees. On dry, acidic substrata the Scots pine forms the xerophilous Veronico-Pinetum sylvestris, less related to the Boreo-Alpine coniferous forests. In the lime-rich areas of the Iberian main range and in the Prepyrenees, the same Pinus species forms pinewoods of the Submediterranean alliance Quercion pubescenti-petraeae. The most general association, Primulo-Pinetum sylvestris, develops in the central and eastern parts, differentiated into one xeric and one mesoxerophilous subassociation (teucrietosum and typicum). The xerophilous Echinosparto-Pinetum pyrenaicae is an open pinewood found in the central and

western sectors, defined by the endemic *Echinospartum horridum*; and other pine associations (Polygalo-Pinetum, Goodyero-Pinetum), which depend on particular ecological factors, are also found.

Finally, Abies alba forms pure firwoods, in some places very extensive, in the areas with mild, subcontinental bioclimate, where Fagus is rare or absent. Galio-Abietetum plays a great role from the Hecho to the Aran valleys on the Atlantic side, and in the Pallaresa valley on the Iberian side. This dense, species-poor forest covers mainly north-facing slopes on acidic bedrocks, in the upper part of the belt and in the lower subalpine belt. Richer associations occur in more eutrophic soils of the same range (Festuco-Abietetum) and in the lime-rich southwestern Pyrenean edge, in the Roncal valley (Coronillo-Abietetum).

Deforestation in the montane belt produces a wide variety of scrubs, pastures and grasslands. Acidophilous heaths of Sarothamnion scopariae and Calluno-Genistion characterize the Atlantic areas, whereas calcifugue Cytision oromediterranei and calcicolous *Buxus sempervirens* formations are general in the Iberian areas. Grasslands and pastures show a parallel shift between both Pyrenean faces. Thus, on the Atlantic side the mesic Arrhenatheretalia meadows are widespread and the mesoxerophilous Bromion pastures are restricted to drier sites. And in the Mediterranean parts Arrhenatheretalia are limited to milder substrata, whereas Bromion and xerophilous Xerobromion cover extensive slopes.

3.4 Subalpine belt

This is mainly the domain of *Pinus uncinata*, which is ubiquitous, since it forms forests of diverse type, mainly combining north- and south-facing, and acidic and lime-rich soils. Whereas there is noticeable variation in the species composition of pinewoods according to these main ecological factors, regional variation in the Pyrenees remains small. However, these pinewoods may be dense and well-structured in the lower part of the belt (mainly to 2,000 a.s.l.), and become lighter and more irregular further up, or on less favourable substrata. The highest pinewoods occur at 2,500 m a.s.l. in Neouvielle, and at slightly lower altitudes in the continental area from Pallars to Cerdanya.

The landscape of this belt has been strongly deforested for centuries to extend the pasture surface: what is known as the 'alpinisation' of the subalpine belt. This is clearest on the Atlantic face (Ariége, Hautes Pyrénées), and in the Iberian valleys with gentle relief (Cabdella, Castanesa), where subalpine forest is very scarce or absolutely absent. Present abandonment of traditional land use combined with rising temperatures enhances forest recovery, expanding from the remaining forests and mainly in the lower part of the belt. Indeed, in greatly deforested areas and where the treeline had been lowered less, no upward forest progression has been observed (Camarero & Gutiérrez 1999).

However, low scrubs (Juniperion nanae, Rhododendro-Vaccinion) and pastures (Nardion strictae, Festucion eskiae) occur in the

subalpine belt not only as serial vegetation, but as permanent communities related to thin, irregular soil or to other particular conditions. As a general rule, this non-forest vegetation, together with open rock and scree communic.

nities, become more extended in the upper part of the belt.

The most general pinewood domain is that of Rhododendro-Pinetum uncinatae, which is related to acidic, humic, mild soils and to near-continuous snow cover in winter. These conditions occur on north-facing slopes and on gentle or flat relieves, where this pinewood covers great surfaces. However, the present landscape includes large surfaces of these pinewoods only in the eastern half of the main range, whereas from the Maladata massif westwards they occur only as small, dispersed stands.

Irregular or variable snow cover, which occurs in south-facing, steep or windy areas, give way to other forest communities more tolerant to low winter temperatures and to drought events through the year. Arctostaphylo-Pinetum uncinatae, which corresponds to open, irregular pinewoods with xerophilous subshrub layer, occurs over the entire area, both on siliceous bedrocks (typicum) and on lime materials (rhamnetosum alpi-

nae).

Other forest types are more closely related to ecological conditions, such as Veronico-Pinetum pinetosum uncinatae, which covers siliceous, dry slopes of the lower subalpine belt, and Pulsatillo-Pinetum uncinatae, settling on carbonated mild soils found on steep, north-facing slopes. In lime-rich areas, calcicolous pinewoods poorly characterized (*Pinus uncinata* and *Festuca gautieri* community) develop where dry conditions prevent soil leaching, e.g. on the south-facing, lower surfaces of the axial range

and in most of the Prepyrenean ranges.

In the lower subalpine belt, Pinus uncinata, Abies alba and a few deciduous trees vary along the axial range, mainly on north-facing exposures. Abies forests with Rhododendron and Pinus (Rhododendro-Abietetum) are scarce in the eastern and central parts of the axial Pyrenees (on the mildest, gentle slopes), whereas in suboceanic areas of the central Pyrenees (e.g. Aran, high Pallars) the extensive firwood Galio-Abietetum protrudes from the montane belt up to 1,800-1,900 m a.s.l. In the Atlantic western valleys, the reconstruction of forest domains become more hypothetical, due to stronger deforestation. The domain of Pinus uncinata seems noticeably narrowed, as pinewoods remain only on steep, rocky slopes. Firwoods (Rhododendro-Abietetum) occupy more favourable surfaces of the lower subalpine belt, whereas deciduous, species-rich forests occur sparsely on other relieves, frequently in the form of small spots above the fir forests. Subalpine beechwoods (Sorbo-Fagetum) have been found up to 1,850 m a.s.l., and birch thickets (Thelipterido-Betuletum) reach 1,950 m a.s.l.

The upper boundary of the subalpine belt, or treeline, provides the clearest discontinuity in Pyrenean zonation. It consists of a dense ecotone (100–200 m wide) in which the open, irregular pinewood gives way to a patchy area formed by small spots of dwarf-scrub, low forest and pasture, and to a typical alpine mosaic still with scarce small-grown pines or krummholz.

Table 1. Distribution of main vegetation domains through belts and sectors of the Pyrenees. N, on the Atlantic side; S, on the Mediterranean side; A, on both sides; P, in the Iberian Prepyrenees; Ca, calcicolous; Si, calcifugue.

	Western area	Central area	Eastern area	altitude
	Axial: Irati - Roncal - Anie Prepyrenees: Leyre	Axial: Anie - Perdido - Maladeta Prepyrenees: Oroel - Guara - Turbón	Axial: Aran - Ribagorça - Canigó Prepyrenees: Cis - Moixeró	
Subnival		Salicetea herbaceae (A) (Ga-Si) Minuartio sedoidis-Androsacetum ciliatae (A) (Si) Minuartio cerastiffoliae-Androsacetum ciliatae(A) (Ca) Oxytropido-Elynetum myosuroidis var. of Artemisia (A) (Ca) Saxifrago bryodis-Mi	ierbaceae (A) (Ca-Si) stae (A) (Sl) ciliatae(A) (Ca) Saxffrago bryodis-Minuartietum sedoidis (A) (Sl)	to 3404 from (2600) 2800
Alpine		Leontodonto-Caricetum curvulae (A) (Si)	Hieracio-Festucetum supinae (A) (Si)	to 2800 2600
		Oxytropido-Elynetum myosuroidis (A) (Ca) Oxytropido-Festurestim sconariae (A) (Ca) Festurestim sconariae (A) (Ca)	Festicetim scopariae (A) (Ca)	
		Saponario-Festucetum gautieri (P) (Ca)	Oxyropido-Caricetum humilis (P) (Ca)	
		Dryado-Salicetum pyrenaicae (A) (Ca)		
		Cetrario-Loiseleurietum (A) (Si) Empetro-Vaccinietum (A) (Si)	urietum (A) (Si) nietum (A) (Si)	
		Saxifrago-Rhododendretum (A) (Si) Cytiso-Arctostaphyletum (A) (Si)	endretum (A) (Si) hyletum (A) (Si)	2400 from 2200
Subalpine		Rhododendro-Pinetum uncinatae (A) (Si)		to 2400 (2500)
		Arctostaphylo-Pinetum uncinatae typicum (A) (Si)	(Si)	(2100)
			Veronico-Pinetum pinetosum uncinatae (S) (Si)	
		Pulsatillo-Pinetum uncinatae (A)(Ca)		
	Arctosta F	Arctostaphylo-Pinetum uncinatae rhamnetosum alpinae (A) (Ca) Festuca gautieri-Pinus uncinata community (S) (Ca)	ae (A) (Ca)) (Ca)	from (1700) 2000
		Sorbo-Fagetum (A) (Ca-Si) Thelypteridi-Betuletum (A) (Ca-Si)	m (A) (Ca-Si) etum (A) (Ca-Si)	to 1900 from 1700

Table 1 (cont.)

Montane		Galio-Abietetum (A) (Si)		to 1700 (1900)
	Lysimachio-	Lysimachio-Fagetum (N) (Si)	Luzulo-Fagetum (A) (Si)	
		Scillo-Fagetum (A) (Ca-Si)		
		Buxo-Fagetum (A) (Ca)		
	Coronillo-Abietetum (S) (Ca) Galio rotundifoliae-Fagetum (P) (Si)		Buxo-Abietetum (P) (Ca)	from (600) 1000
		Polygalo-Pinetum	Veronico-Pinetum sylvestris (S) (Si) Polygalo-Pinetum sylvestris (S) (Ca)	to 2000
		Primuio-Pinetum sylvinum Primu	Primuio-Prinetum sylvestris typicum (5) (Ca) Primulo-Pinetum sylvestris teucrietosum (S) (Ca)	
		Hylocomio-Pinetum catalaunicae (S) (Si)		
	Echinosparto-Pine	Echinosparto-Pinetum sylvestris (S) (Ca)		1300
		Lathyro-Quercetui	Lathyro-Quercetum petraeae (A) (Si)	to 1700
			Veronico-Betuletum (S) (Si)	to 1800
				TOTH 1200
Submontane	Roso-Quercetum humilis (S) (Ca)	Buxo-Quercetum pu	Buxo-Quercetum pubescentis (A) (Ca)	to 1200
	Festuco-Quercetum pyrenaicae (P) (Si)		Pteridio-Quercetum pubescentis (S) (Si) Aceri-Quercetum petraeae (N) (Si)	
	Spiraeo-Quercetum fagineae (P) (Ca)	Violo-Quercetum	Violo-Quercetum fagineae (S)(Ca)	
		Lonicero-Pinetum salzmannii (P) (Ca-Si)		from 800
Basal Atlantic	Hyperico-Quercetum roboris (A) (Si)	lsopyro-Quercetum	Isopyro-Quercetum roboris (A) (Ca-Si)	to 800
			Brachypodio-Fraxinetum (S) (Ca-Si) Buxo-Quercetum pubescentis (A) (Ca)	
Basal	Spiraeo-Quercetum rotundifoliae	Buxo-Quercetum rc	Buxo-Quercetum rotundifoliae (S) (Ca)	to 900 (1200)
Mediterranean	(S) (Ca)		Asplenio-Quercetum rotundifoliae (S) (Si) Asplenio-Quercetum ilicis (A) (Si)	

The treeline occurs at varying altitudes, mostly between 2,200–2,450 m, depending on continentality, exposure and landform (CARRERAS et al. 1996). The most basic ecological factor defining the treeline's location must be the mean temperature of the rhizosphere during the growing season (around 7°C, as in the southern Alps and Apennines; KÖRNER & PAULSEN 2004).

3.5 Alpine belt

This belt stretches from the Anie to the Canigó peaks, up to 2,800 m a.s.l. Alpine landscapes are typically small-scale mosaics, in which contrasting plant communities express topographic and microclimatic heterogeneity. The related ecological factors involve stronger variation in vegetation than regional floristic shifts do. At the local scale, particular plant communities inhabit the most extreme habitats (rocks, scree, snow-beds), whereas various types of short grasslands cover more balanced soils (ILLA et al. 2006).

The calcifuge grasslands more closely related to standard alpine conditions are Hieracio-Festucetum supinae and Leontodonto-Caricetum curvulae. The former is a tussock-like, mesoxerophilous grassland widespread in the eastern part of the axial range, where winter may involve periods without snow cover. It occurs also on the mildest Prepyrenean summits and on dry shelves and slopes of the central axial range. The Leontodonto-Caricetum shows an opposite pattern along the main range, since it is a mesophilous community related to more snowy climates. Thus, it is more common in the central and western parts, where thicker snow cover leads to later phenology and milder soil conditions, and is limited to concavities and other favourable sites in the eastern Pyrenees. This complementary role between both associations is similar to that shown in the Alps by Festucetum halleri and Caricetum curvulae (Ozenda 1985). Also on siliceous substrata, Festuca eskia forms open grasslands on steep slopes affected by solifluxion (Festucion eskiae) and dense grasslands on gentle surfaces with acidic soils (Nardion strictae).

On calcareous rocks, where the poor edaphic evolution produces carbonated soils, pasture communities are richer and more differentiated. Oxytropido-Elynetum occurs along the main chain and even in some Pyrepyrenean ranges, though showing some regional variation. This short pasture is typical of flat or north-facing surfaces with rocky substrata, under cold, windy microclimates. Mesoxerophilous, irregular, tussock-like Festuca gautieri grasslands are more extended, since they settle on various landforms (summits, south-facing areas, gliding slopes). These species-rich communities are included into various associations, according to varying floristic composition. Thus, two mesoxerophilous associations share the main range and the milder surfaces of the Prepyrenees (Oxytropido-Festucetum scopariae in the western half, and Festucetum scopariae in the eastern half), and two xerophilous associations occur at the dryer Prepyrenean summits and on the higher slopes (Saponario-Festucetum gautieri and Oxytropido-Caricetum humilis, respectively).

Low scrub characterizes the lower part of the alpine belt, where they settle on particular landforms. Rhododendron scrub (Saxifrago-Rhododendretum ferruginei) on north-facing slopes and Arctostaphylos carpets (Cytiso-Arctostaphyletum uvaeursi) on south-facing exposures are very common in rocky areas, frequently in connection with subalpine forests. Other types are more restricted to particular landforms, such as the calcicole Dryado-Salicetum pyrenaicae or the calcifuge Empetro-Vaccinietum uliginosi and Cetrario-Loiseleurietum.

Other plant communities related to special habitats occur over the entire alpine belt, but are more frequent and extended in its higher part. This is the case of a few associations related to snow-beds (Arabidion caeruleae, Salicion herbaceae, chionophilous Nardion) and of a number of associations settling on rocky surfaces (Saxifragion mediae, Androsacion vandellii) and scree (Iberidion spathulatae, Senecion leucophylli), mainly species-poor but harbouring noticeable endemics and other particular taxa.

3.6 Subnival belt

This belt only occurs on some small surfaces corresponding to abrupt peaks, crests and cliffs, in the central part of the main range. Its particularity is the strong dominance of rocks and scree, and the scarcity of surfaces bearing soil. These conditions are general from 2,800 m a.s.l. upward, but are also found at lower altitude summits (up to c. 2,600 m). There, alpine pastures become scarce and very irregular, settling on small shelves or concavities and in rock discontinuities. Two associations are found in these areas: Saxifrago-Minuartietum sedoidis on siliceous rocks, and an extreme form of Oxytropido-Elynetum (var. of Artemisia umbelliformis) on limestone.

In the subnival landscape, sparse rupicolous vegetation settling on rock crevices, chionophilous carpets covering a few concavities and a few communities related to scree and other rocky surfaces are more frequent. Among these, the alliance Androsacion ciliatae is specific to the subnival belt.

The last, vanishing Pyrenean glaciers may be taken as a tiny expression of the nival belt. They are located in the Maladeta and Perdido massifs, where the vegetation is reduced to a few vascular plants and bryophytes dispersed among the rocks and ice, together with rupicolous lichens. Following a noticeable altitude rule general in the alpine belt (KÖRNER 2003), vascular Pyrenean flora is reduced to 153 taxa above 3,000 m, and to 24 above 3,300 m (Sesé et al. 1999).

4 Concluding remarks

The analysis of particular landscape transections and general schemes provides evidence for several facts and driving ecological factors. The most important are:

- The floristic analysis of the Pyrenees supports the partition based on vegetation domains and belts. Thus, the shift from montane to subalpine may be considered to coincide with the limit between Medioeuropean and Boreo-Alpine regions. As for the border between Medioeuropean and Mediterranean regions found on the southern face of the Pyrenees, it mostly coincides with that between basal and submontane belts, but runs at higher altitudes on dominant rocky surfaces in the central valleys, and at lower altitudes – off the Pyrenean chain – in mild Navarra and northeastern Catalonia.

- The vegetation belts recognized in the Pyrenees are chiefly defined through potential domains, though a few of these defining communities show noticeable irregularities in their range. Some examples are the sclerophyllous forests occupying most of the submontane belt on south-facing rocky slopes, the range of Galio-Abietetum including high montane and low subalpine belts in the central sector, and the expansion to the basal belt of mesoxerophilous oakwoods (Quercion pubescenti-petraeae) in the transition areas between Atlantic and Mediterranean territories. However, serial vegetation is in some of these cases more in accordance with the definition of the corresponding belts. These apparent irregularities illustrate the role played by particular ecological factors on the distribution range of dominant species.
- Within the same mountain area, the boundaries of homologous vegetation units and belts occur at higher altitudes on south-facing slopes than on north-facing ones. This is connected with the wetter and colder local climates on north-facing aspects. However, this altitude difference decreases towards the summits, suggesting that vegetation of low and mid altitudes is more influenced by the local water balance than high-mountain vegetation is.
- Along the whole area considered, the boundaries between vegetation belts run higher in the central parts than at the western and eastern ends. Such altitude differences are at their maximum in the case of the Iberian face of the axial range (more than 200 m on south-facing aspects), and are the lowest on the French face of the axial range. A similar rising effect of vegetation belts has been described in other mountain systems. It relates to continentality and is in accord with the 'inner area' bioclimatic character found in some valleys (from Pallars to Cerdanya; IZARD in DUPIAS 1985).
- As a general feature, landscape zonation is more complex in the axial Pyrenees than in the Prepyrenean ranges, mainly due to greater altitude differences, but also to more local biodiversity (more diverse flora) and to wider range of local substrata and climates.
- Within the axial range, the area between the central and eastern parts of the Iberian face (from Ribagorça to Alt Urgell) shows the most complex zonation patterns, which is connected with the most complex gradient of altitude climates and floristic territories. In this sector, the lower belts clearly have a more xeric character than any other, while the higher belts are on the contrary, rainier.

- Oceanity is clearly seen in the Pyrenean vegetation of lower and mid altitudes of most of the French face and of the western edge. This character also has a noticeable influence at the same altitudes of the eastern edges, particularly in the Prepyrenees. At higher altitudes (subalpine and alpine belts) of the axial range, the vegetation shows some oceanic influence on the French face and in the central sector of the Iberian face (eastwards to Pallars).
- As for the highest belts (alpine and subnival), the vegetation shows a more xerophilous and continental character in the eastern sector than in the central and western parts, mainly connected with less snow cover in winter.

Acknowledgements. This study was partially supported by the Spanish ministries of Research and of Environment (projects REN2002-04268-C02-01 and 69/2005).

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Appendix 1. Main references used to build the vegetation synthesis given in section 3.

Regional geobotanic works: Braun-Blanquet 1948, 1952; Bolòs 1960, 1979; Gruber 1978, 1992; Dupias 1985; Rivas-Martínez 1988; Rivas-Martínez et al. 1991, 2002; Vigo & Ninot 1987; Villar et al. 1997, 2002.

Local geobotanic monographs, Axial range: Benito 2006; Bolòs 1957; Carreras et al. 1993a; Carrillo & Ninot 1992; Nègre 1969, 1972; Rivas-Martínez & Costa 1998; Vigo 1996; Villar 1982.

Local geobotanic monographs, Prepyrenees: Carreras 1993; Gómez 1989; G. Montserrat-Martí 1986; J. M. Montserrat-Martí 1987; Ninot et al. 1993; Romo 1989; Soriano 2001; Vives 1964.

Regional vegetation maps (and joined reports): Bolòs et al. 2004; Dupias et al. 1982; Gaussen 1964, 1972; Loidi & Báscones 1995; Noirfalise 1987; Rivas-Martínez 1987b.

Local vegetation maps (and joined reports): Carreras et al. 1993b, 1994, 1997a, 1997b, 1997c, 1999, 2000, 2001, 2002, 2005; Carrillo et al. 2003; Soriano & Devis 2004; Vigo & Masalles 1996.

Appendix 2. Complete names and main synonyms of the syntaxa cited.

Aceri opali-Quercetum petraeae Br.-Bl. 1952

Amelanchiero ovalis-Buxenion sempervirentis (O. Bolòs & Romo) I. Soriano & Sebastià 1990

Androsacion ciliatae Rivas-Martínez 1988

Androsacion vandellii Br.-Bl. 1926

Aphyllanthion monspeliensis Br.-Bl. 1952

Arabidion caeruleae Br.-Bl. 1926

Arctostaphylo uvaeursi-Pinetum uncinatae Rivas-Martínez 1968 typicum et rhamnetosum alpinae Rivas-Martínez et al. 1991

Arrhenatheretalia elatioris Pawlowski 1928

Asplenio onopteridis-Quercetum ilicis (Br.-Bl.) Rivas-Martínez 1975

Asplenio adiantinigri-Quercetum rotundifoliae (Carreras et al.) Rivas-Martínez 2002

Blechno spicantis-Quercetum roboris Tüxen et Oberd. 1958

Brachypodio sylvatici-Fraxinetum excelsioris Vigo 1968

Brachypodion phoenicoidis Br.-Bl. ex Molinier 1934

Bromion erecti Koch 1926 (Mesobromion erecti Zoller 1954)

Buxo sempervirentis-Abietetum albae Vigo 1974

Buxo sempervirentis -Fagetum sylvaticae Br.-Bl. & Susplugas 1937 (Helleboro occidentalis-Fagetum O. Bolòs 1957)

Buxo sempervirentis-Quercetum pubescentis Br.-Bl. 1932

Buxo sempervirentis-Quercetum rotundifoliae Gruber 1974

Calluno vulgaris-Genistion pilosae Duvigneaeud 1944

Caricetum curvulae Rübel 1911

Carpinion betuli Issler 1931

Cetrario-Loiseleurietum procumbentis Br.-Bl. 1926

Cistion ladaniferi Br.-Bl. ex A. & O. Bolòs 1950

Coronillo emerici-Abietetum albae Rivas-Martínez, Báscones, T. E. Díaz, Fernández-González & Loidi 1991 Cytision oromediterranei Tüxen 1958 (Genistion purgantis Tüxen 1958)

Cytiso oromediterranei-Arctostaphyletum uvaeursi Br.-Bl. 1948 (Genisto-Arctostaphyletum Br.-Bl. 1948)

Dryado octopetalae-Salicetum pyrenaicae Chouard ex Vanden Berghen 1970

Echinosparto horridi-Pinetum pyrenaicae Rivas-Martínez 1987

Empetro hermaphroditi-Vaccinietum uliginosi Br.-Bl. 1926

Fagion sylvaticae Luquet 1926

Festucetum halleri Br.-Bl. 1926

Festucetum scopariae Br.-Bl. 1948

Festucion eskiae Br.-Bl. 1948

Festuco altissimae-Abietetum albae Rivas-Martínez 1968

Festuco braunblanquetii-Quercetum pyrenaicae Br.-Bl. 1967

Galio rotundifolii-Abietetum albae O. Bolòs 1957 (Goodyero repentis-Abietetum Rivas-Martínez 1968)

Galio rotundifolii-Fagetum sylvaticae Rivas Martínez 1962

Goodyero repentis-Pinetum sylvestris Bannes Puyg. 1933

Helianthemion guttati Br.-Bl. 1940

Hieracio pumili-Festucetum supinae Br.-Bl. 1948

Hylocomio splendentis-Pinetum catalaunicae Vigo 1968

Hyperico pulchri-Quercetum roboris Rivas-Martínez, Báscones, T. E. Díaz, Fernández-González & Loidi 1991

Iberidion spathulatae Br.-Bl. 1948

Isopyro thalictroidis-Quercetum roboris Tüxen & Diemond 1936

Lathyro montani-Quercetum petraeae Rivas-Martínez 1983 (Prunello hastifoliae-Quercetum Rivas-Martínez & Costa 1998)

Leontodonto pyrenaici-Caricetum curvulae Br.-Bl. 1948 (incl. Gentiano alpinae-Caricetum curvulae Nègre 1969, Oreochloo blankae-Caricetum curvulae Rivas-Martínez 1974)

Lonicero xylostei-Pinetum salzmannii Gamisans & Gruber 1988

Luzulo niveae-Fagetum sylvaticae (Susplugas) Br.-Bl., Roussine & Nègre 1952

Lysimachio nemorum-Fagetum sylvaticae Gruber 1973

Minuartio cerastiifoliae-Androsacetum ciliatae Chouard 1943

Minuartio sedoidis-Androsacetum ciliatae Rivas-Martínez 1988

Nardion strictae Br.-Bl. 1926

Oxytropido amethysteae-Caricetum humilis Carrillo & I. Soriano 1997

Oxytropo foucaudii-Elynetum myosuroidis Chouard 1943 (Carici roseae-Elynetum Rivas-Martínez 1987, Elyno-Oxytropidetum halleri (Br.-Bl.) Küpfer 1974)

Oxytropido pyrenaicae-Festucetum scopariae Rivas-Martínez, Báscones, T. E. Díaz, Fernández-González & Loidi 1991

Polygalo calcareae-Pinetum sylvestris (Vigo) Rivas-Martínez 1983

Primulo columnae-Pinetum sylvestris Molero & Vigo ex Vigo, Carreras & Carrillo 1995 typicum et teucrietosum Carreras & Carrillo 1995

Pteridio aquilini-Quercetum pubescentis (Susplugas) O. Bolòs 1983

Pulmonario longifoliae-Quercetum pyrenaicae Oberdorfer & Tüxen 1958 (Festuco heterophyllae-Quercetum pyrenaicae Br.-Bl. 1967)

Pulsatillo fontquerii-Pinetum uncinatae Vigo 1974

Quercion ilicis Br.-Bl. ex Molinier 1934

Quercion pubescenti-petraeae Br.-Bl. 1932

Quercion roboris Malcuit 1929

Rhododendro ferruginei-Abietetum albae Br.-Bl. 1948 (Homogyno-Abietetum Gruber 1978)

Rhododendro ferruginei-Pinetum uncinatae (Br.-Bl.) Rivas-Martínez 1968 Rosmarinion officinalis Br.-Bl. ex Molinier 1934 (Rosmarino-Ericion auct.)

Roso arvensis-Quercetum humilis Rivas-Martínez, Báscones, T. E. Díaz, Fernández-González & Loidi 1991

Salicion herbaceae Br.-Bl. 1926

Saponario caespitosae-Festucetum gautieri Gruber ex Ninot 1988

Sarothamnion scoparii Tüxen 1949

Saxifragion mediae Br.-Bl. 1934

Saxifrago bryoidis-Minuartietum sedoidis Carrillo & Ninot 1989

Saxifrago geranioidis-Rhododendretum ferruginei Br.-Bl. 1948

Scillo liliohyacinthi-Fagetum sylvaticae Br.-Bl. ex O. Bolòs 1957

Senecion leucophylli Br.-Bl. 1948

Sorbo aucupariae-Fagetum sylvaticae Carrillo & Ninot 2002 (Roso pendulinae-Fagetum sylvaticae Rivas-Martínez, Costa & P. Soriano 2002)

Spiraeo obovatae-Quercetum fagineae O. Bolòs & P. Montserrat 1984

Spiraeo obovatae-Quercetum rotundifoliae Rivas-Goday ex. Loidi & F. Prieto 1986

Thelypterido limbospermae-Betuletum pubescentis Rivas-Martínez 1987 Thero-Brachypodion Br.-Bl. 1925

Veronico urticifoliae-Betuletum pendulae Vigo 1984

Veronico officinalis-Pinetum sylvestris Rivas-Martínez 1968 typicum et pinetosum uncinatae Rivas-Martínez 1968

Violo willkommii-Quercetum fagineae Br.-Bl. & O. Bolòs 1950

Xerobromion erecti Br.-Bl. & Moor 1938