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Estudio integral de los bosques de *Quercus pyrenaica* willd. en la Península Ibérica: características bioclimáticas, sintaxonómicas y especies indicadoras

Comprehensive study of *Quercus pyrenaica willd*. forests at Iberian Peninsula: indicator species, bioclimatic, and syntaxonomical characteristics

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

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Beatriz Vilches De la Serna

Memoria de tesis doctoral

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Foto de portada: Brotes de melojo tomada en Somosierra.
P.B. Vilches

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Memoria Doctoral presentada por Paloma Beatriz Vilches de la Serna para optar al grado de Doctora.

Con la autorización de sus Directores

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Lo perfecto es enemigo de lo bueno.

Indice

Abreviaturas

Para facilitar la lectura, la denominación de las diferentes asociaciones fitosociológicas del roble melojo serán abreviadas en el texto de la siguiente manera:

Adenocarpo decorticantis-Quercetum pyrenaicae (*Adenocarpo-Quercetum*),
Arbuto unedonis-Quercetum pyrenaicae (*Arbuto-Quercetum*),
Berberido hispanicae-Quercetum pyrenaicae (*Berberido-Quercetum*),
Cephalanthero rubrae-Quercetum pyrenaicae (*Cephalanthero-Quercetum*),
Festuco merinoi-Quercetum pyrenaicae (*Festuco merinoi-Quercetum*),
Genisto falcatae-Quercetum pyrenaicae (*Genisto-Quercetum*),
Holco mollis-Quercetum pyrenaicae (*Holco-Quercetum*),
Linario triornithophorae-Quercetum pyrenaicae (*Linario-Quercetum*),
Lonicero periclymeni-Quercetum pyrenaicae (*Lonicero-Quercetum*),
Luzulo baeticae-Quercetum pyrenaicae (*Luzulo baeticae-Quercetum*),
Luzulo forsteri-Quercetum pyrenaicae (*Luzulo-Quercetum*),
Melampyro pratensis-Quercetum pyrenaicae (*Melampyro-Quercetum*),
Pulmonario longifoliae-Quercetum pyrenaicae (*Pulmonario-Quercetum*),
Pyro bourgaeanae-Quercetum pyrenaicae (*Pyro-Quercetum*),
y *Sorbo torminalis-Quercetum pyrenaicae* (*Sorbo-Quercetum*).

Resumen / Abstract

Introduction

Temperate deciduous forests appear distributed over central-western Europe, reaching the north of Iberian Peninsula. In this area of Mediterranean climate domain, the marcescent endemism *Quercus pyrenaica* Willd develops as indicator of the southern limit of European broad-leaved forests. Its distribution area from South-western France to North-eastern Morocco show the wide variety of emplacements and ecological nuances it could cover, which we will try to describe in the present text.

Their formations tend to be closed, although depending on the level of management their overall appearance can range from extremely closed forest to different degrees of openness (and trunk diameter), including the "dehesa" in some parts of the peninsula. A particularly eye-catching feature of this species is the purple color of outbreaks during the early stages of birth of the leaf. The preference for siliceous soils makes it predominates mainly in the northwest quadrant of the Iberian Peninsula, reducing its presence to the south but mostly to the east where calcareous substrates are dominant due to Mesozoic sedimentary processes. The acidic lithology on which it develops is variable: granite, slate, schist, gneiss and locally over decarbonated basic substrates or neutral substrate islands interspersed within limestone soils (Buntsandstein sandstone). These forests form a differential area of favorable "mediterraneity", where the vegetal species most vulnerable to summer drought may be refugees and wildlife also benefits. Moreover, their distribution area indicates per se, that summer drought is one of its limiting factors, avoiding most xeric emplacements. The second – perhaps not so obvious – are winter frosts. Both are factors to which this oak appears to be morphologically and physiologically adapted to survive. *Quercus pyrenaica* forests appear in both Temperate (Euro-Siberian region) and Mediterranean territories. They are differentiated by a period of summer aridity nonexistent in the first and extending up to three months in the second. So the adaptations that allow them to live in Mediterranean areas, usually as mountain forest force them to search for dry or increased drainage locations at Temperate Iberia (sunniest orientations, sandy substrates or steep slopes). Thereby, the Pyrenaean oak is distributed through a wide range of altitudes, from 290 m (Basque Country) to 1800 m (Sierra Nevada), thus thermotypes, always with a minimum summer precipitation of 100 mm (Costa, 1997) and annual rainfall around 600 mm. As a result we could only find them in those territories with ombrothypes ranging from humid to even hyperhumid and thermothypes from meso- to supramediterranean (and meso- supratemperate (Rivas-Martínez et al. 2011a). The latest syntaxonomical classification (Rivas -Martínez, 2011b) has divided the Iberian oaks in 15 climatophilous associations (two more than in the previous (starred in Figure 5), included in class *Querco-Fagetea* Br.-Bl. & Vlieger in Vlieger 1937 alongside other Eurosiberian optimal deciduous forests (Order *Quercetalia roboris* Tx. in Barner 1931, which includes acidophilus oak and beech forests). These associations define a particular alliance *Quercion pyrenaicae* Rivas Goday ex Rivas-Martínez 1965, subdivided into two subaliances: one purely Mediterranean *Quercenion pyrenaicae* Rivas-Martínez 1974 (12 associations), and those corresponding to the temperate areas of the northern peninsula in *Quercenion robori-pyrenaicae* (Br-Rl., P. Silva & Rozeira 1956) Rivas-Martínez 1975 (3 associations).

Due to its high level of biodiversity, *Quercus pyrenaica* forests are protected at European level by Directive 92/43/EEC and included in the NATURA 2000 initiative, participating in different habitat classification schemes.

Aims & Structure

The aforementioned background on these forests, their uniqueness as marcescent endemism in southern Europe, the current situation of global change and existing real threat for its conservation and particularly of the flora that harbor in the Mediterranean boundary has maid of their study an urgent need. We have reviewed in detail the differences in the full extent of its distribution in the Iberian Peninsula, trying to quantify different levels of conservation, and floristic singularity. To do this, we have studied local and regional nuances, but also the connections that have allowed the continuity in the floristic composition of *Quercus pyrenaica* forests which usually difficult its classification. In parallel we have tried to develop a methodology that allows us to define its different shades but without leaving the floristic basis common to the entire Iberian Peninsula.

The specific objectives of this study were:

(i) Define the main climatic characteristics that explain the phytogeographic distribution pattern of *Quercus pyrenaica* forests in Spain and get the bioclimatic limits that best define these vegetation types.

(ii) Determine the set of species that best indicate different forest environmental influences Levantine, both common and differential.

(iii) Find floristic patterns at different levels of work presenting the main ecological factors of the Pyrenaean oak forests of the northern peninsula, and to determine whether these patterns can be considered drivers of community assembly.

(iv) Find the main groups of floristic similarity of *Quercus pyrenaica* forests of the Iberian Peninsula, indicator species that drive this differentiation and its correlation with actual hierarchical structure.

(v) Describe in a bioclimatic and floristic way those differentiated group of Eastern peninsula relevés and its replacement communities.

Results & Conclusions

- Iberian *Quercus pyrenaica* forests can be discriminated briefly:
    - In the East, based on the cadences of rainfall, which will be maxim in summer while increasing the influence of the Mediterranean humid air currents (Jaén, Castellón), or maxim in winter while increasing the influence of Atlantic Ocean airflow (Sierra Nevada).
    - In the West, annual temperature increases (particularly in summer) in a north-south gradient. Being the minimum winter temperature, discriminant mainly for Temperate (orocantábricos minimum) but also for Mediterranean climates (Central system minimum), being associated with continentality gradients. Level and cadence of rainfall appeared associated with Atlantic influence: decreasing towards the center. Interestingly the effect of the Azores anticyclone increase in the same sense over the west (Central System precipitation will be higher in summer than western ones).
- In general, in those forests with high levels of oceanity, topography and microclimatology were important as vegetation modelers in both Temperate and Mediterranean area.
- Analysis of the East Peninsular forests made possible to distinguish the confluence of two types of vegetation: the mountainous one, with temperate biome character

and the Mediterranean. Higher affinity forests were those from Cuenca, Teruel and Tarragona, leaving a side those belonging to the Sierra de Espadán in Castellón, warmest and with a great Mediterranean influence. This differentiation led to the generation of a new type of community: *Minuartio valentinae-Quercetum pyrenaicae* ass nova over Buntsandstein rodena.

- Throughout this thesis we have suggested different methods in order to find floristic patterns working at different scales. In turn, we suggest obtaining hierarchical levels of assembly. First by obtaining, with unsupervised classification methods, those most consistent clusters of the set and the subsequent search of floristic identifiers and similarity patterns that define and relate them.
- The application of indicator species analysis with combinations of groups on the Iberian Northwest forests allowed us to observe the differential shades at different scales of work as well as those areas represented of higher affinity through co-occurring species. Throughout the 42nd parallel, we found a high floristic affinity between forests, which relate to the existence of a transitional area between temperate Mediterranean climate and able to accommodate a large and varied number of indicator species.
- In Chapter IV we find that the west / east division axis, which separates the peninsula based on the predominance of the influence of the Atlantic / Mediterranean influence, and the acid / base substrates is slightly off to the east. Two-thirds of the Peninsula are therefore grouped based on the cadences of rainfall and Atlantic influence. The East, on the other hand, is characterized by greater isolation of their forests, and lower floristic similarity.
- Western Iberian Peninsula showed a more complex differentiation, unlike other authors we do not suggest the fusion of those close associations as *Genisto-Quercetum* and *Holco-Quercetum* but a change of definition, what seems to have included Rivas-Martínez in his last review (2011b). *Sorbo-Quercetum* and *Arbuto-Quercetum* showed in turn two internal nuances related to the distance to the Atlantic coast of their different localities.

INTRODUCCIÓN GENERAL

Introducción

El paisaje vegetal de la Península Ibérica ha sufrido los efectos de la actividad humana desde el Neolítico, período en el que se reconocen las primeras influencias humanas. Estrabón y Plinio coincidían hace más de veinte siglos en describir a la Península Ibérica como un país tan densamente cubierto de tupidos bosques que habitarlo no debía ser tarea fácil para sus primeros pobladores. Sin embargo, algunos botánicos del siglo XIX llegaron a atribuir una vocación esteparia a los territorios ibéricos interiores en los que apenas se encuentran ya vestigios de las formaciones forestales que debieron existir en tiempos pretéritos y que sucumbieron a diversos eventos producto de la intervención del hombre entre los que destacan la agricultura, la ganadería y el desarrollo urbanístico, principalmente, además de otros derivados como los incendios, la contaminación ambiental e incluso la propia silvicultura. En cualquier caso, la vocación forestal de la Península Ibérica incluiría todo el territorio, excepto las cumbres de las altas montañas, los territorios de ombrotipos semiárido y árido (Rivas-Martínez et al. 2011a) y determinados lugares de topografía más o menos abrupta sometidos a fenómenos intensos de erosión que impiden el desarrollo de suelo necesario para la implantación con éxito del bosque (Sánchez-Mata & Fernández-González, 1989).

Los bosques de rebollo o melojo (*Quercus pyrenaica* Willd.) ocupan importantes extensiones en las montañas silíceas ibéricas, estando bien adaptado a climas lluviosos con moderada sequía estival. El ambiente favorable y, en algunos casos la dificultad de acceso, ha permitido que en las zonas templadas los melojares conserven cierta superficie y densidad perdida sin embargo en otras áreas mediterráneas donde la intensa explotación, junto con una difícil regeneración del bosque (Pulido, 2002), ha conseguido relegarlos a pequeñas manchas acantonadas en umbrías y zonas de montaña e incluso a algunos pies diseminados como es el caso de Pina de Montalgrao (Roselló, 1994). Esta fragmentación acusada es consecuencia de su transformación en zonas cultivadas o para el ganado, favorecida en parte por ser eficaces formadores de suelos fértiles (el bombeo de bases a través de su raíz pivotante favorecen un pH cercano a la neutralidad y la generación de la denominada "tierra de melojar"). Pero también por su sustitución por cultivos de especies de crecimiento rápido como el pino (*Pinus pinaster*, *P. radiata*, *P. sylvestris*) y el eucalipto (*Eucalyptus globulus*), pero también para el cultivo de castaño (*Castanea sativa*) (entrando en conflicto con la protección dada a ciertos castañares (código 9260 Red Natura 2000)). Así se ha ido disminuyendo progresivamente la extensión de melojar ibérico, de manera que incluso en la ficha del hábitat 9230 de la red natura 2000, García & Jiménez (2009) reconocen la dificultad para determinar con exactitud la superficie ocupada dentro de su área de distribución, al igual que ha pasado con otros tipos de bosques. Además debido al ambiente que generan, en zonas mediterráneas el melojar constituye un oasis para muchas especies nemorales, de ambientes templados que lo acompañan por toda la península; es buen regenerador de suelo pero además lo retiene gracias a sus raíces laterales (de crecimiento superficial), efecto muy importante en áreas ganaderas y degradadas (Blanco et al. 2005) donde es útil para evitar su pérdida.

A pesar de que su madera no es muy apreciada, ha sido históricamente explotado para carboneo, pero también como madera para la construcción, estacas, leña o incluso vías de ferrocarril. Corteza y agallas fueron usadas para el curtido de pieles. En la actualidad este bosque continúa siendo aprovechado en régimen de monte bajo-medio e incluso es adehesado (Allué 1995), sin embargo el abandono de las prácticas históricas señaladas hace que se esté observando cierta regeneración y recuperación de areas potenciales antes deforestadas (Herreros 2010).

Quercus pyrenaica Willd., especie dominante de estos bosques (generalmente monoespecíficos) es un árbol endémico del occidente europeo, que a lo largo de la historia ha recibido diversas denominaciones: *Quercus tauzin* Pers., *Quercus toza* Gillet ex Bosc in Lam. (quizás el más usado), *Quercus stolonifera* Lapeyr. o *Quercus palensis* Palassou. Debido a su variabilidad foliar y las frecuentes hibridaciones dentro del género, incluso actualmente existen discrepancias en cuanto a su denominación en ciertos puntos de España (p.ej. *Quercus pauciradiata* Penas et al. (López 2001)). Sus nombres vernáculos más utilizados "melojo" y "rebollo" (aunque son diversos: marojo, roble negro, tozo, roure reboll en levante, caxigu o toziu en asturias; carvallo negro, cerqueiro o cerquiño en galicia, ametza en país vasco, carvalho negral en Portugal) parecen derivar de los numerosos rebrotes de raíz que genera, pero la adjudicación del nombre científico definitivo: *Quercus pyrenaica* por parte de Carl Ludwig von Willdenow en 1805 se debió a un desafortunado error en la etiqueta de herbario que describía el espécimen original en los Pirineos, lugar donde su presencia es prácticamente nula. Sorprendentemente en 1813 Christian von Steven volvió a darle el mismo nombre (The International Plant Names Index 2012).

El aspecto más frecuente de esta fagácea es el de un árbol de altura moderada (10-15 m), tronco derecho, copa irregular, lobulada, y corteza pardo-grisácea de poco espesor, agrietada longitudinalmente. Sólo en algunos casos en los que se ha respetado su crecimiento, el melojo puede alcanzar alturas de hasta 25 metros con diámetros de un metro de grosor (López 2001) estando en estos casos frecuentemente incluido en catálogos de árboles singulares como el de la Comunidad de Madrid o Castilla la Mancha.

Fig. 1. Estructura general del bosque de *Quercus pyrenaica* Willd., y detalles de sus hojas jóvenes e inflorescencias. Elaboración propia.

Sus formaciones tienden a ser cerradas, aunque en función del nivel de manejo su aspecto general puede ir desde un bosque extremadamente cerrado a diferentes grados de apertura (y de diámetro de tronco) que pueden llegar hasta el adehesado en algunos puntos de la península. Una característica muy llamativa y particular de esta especie, es el color purpúreo de los brotes durante las primeras fases de nacimiento de la hoja (fig.1).

La preferencia por los terrenos silíceos hace que el melojar predomine principalmente en el cuadrante noroeste de la Península Ibérica, reduciéndose su presencia hacia el sur pero sobre todo hacia el este donde son dominantes los substratos calizos debido a procesos sedimentarios mesozoicos lacustres y marinos (López-Gómez & Arche 1992; Alonso et al. 1991). La litología de carácter ácido sobre la que se asienta es variable: granitos, pizarras, esquistos, gneises y sólo puntualmente aparece sobre terrenos básicos descarbonatados (Aralar-Bidasoa en el País Vasco) o en islas de sustrato ácido intercaladas dentro de terrenos calizos como ocurre en los melojares leoneses de Barrios de Luna o en el levante español, donde suele crecer sobre gres y argilitas rojas del Buntsandstein (Herreros, 2010). Pero no es solo el substrato el que define la distribución geográfica de estos bosques en la Península Ibérica; son numerosos los autores que resaltan el carácter transicional del melojar entre el clima templado y el mediterráneo, ocupando emplazamientos que algunos autores han denominado como submediterráneos. El conjunto forma un área diferencial, de mediterraneidad favorable, donde las especies más vulnerables a la sequía estival pueden quedar refugiadas y de la que la fauna también se ve beneficiada (Martínez-Lirola 2011). Esta distribución ha sido utilizada por diversos autores para delimitar zonas biogeográficas ibéricas, como Polunin (1977, 1989) que a través del área del melojo prolongó la Región Eurosiberiana hasta el Sistema Central e incluso Bolòs (1985) se basó en ella para delimitar lo que llamó el territorio Carpetano-Atlántico (Costa 1997). Dejando a un lado sus aplicaciones biogeográficas, el hecho de que este roble se ubique en estas localizaciones es indicativo *per se*, de que la sequía estival es uno de sus factores limitantes; el segundo, quizás no tan evidente, son las heladas invernales. Ambos, factores a los que el roble parece haberse adaptado morfológica y fisiológicamente para poder sobrevivir.

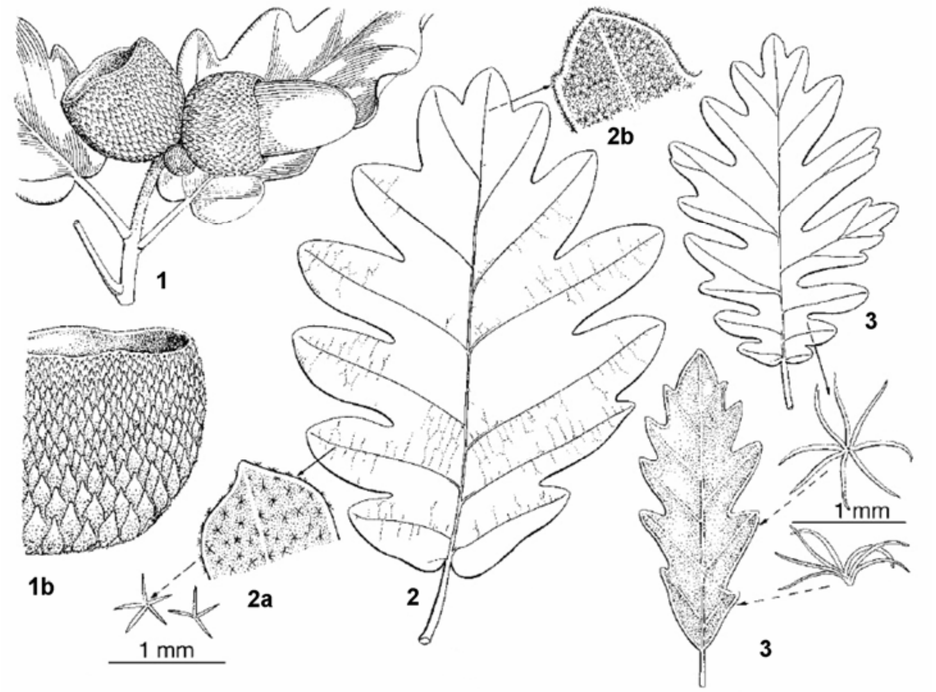


Fig. 2. Imagen modificada de Flora iberica. 1. Rama fructífera (cúpula, aquenio), 1b. Detalle de las escamas imbricadas de la cúpula, también vellosa; 2. Hoja: detalle de la haz (2a) y el envés (2b), 3. Haz y envés, detalle de los pelos estrellados del envés (8-10 radios).

En primer lugar, sus hojas: de lobadas o pinnatífidas a pinnatipartidas, variabilidad probablemente asociada al nivel de estrés hídrico que soporten (Sisó 2001); con pelos foliares estrellados (fig. 2) en la haz y el envés (principalmente en el envés de las hojas maduras, 2b) que minimizan la pérdida de agua por evapotranspiración (Charco et al. 2002, Sisó et al. 2001). En segundo lugar, su raíz pivotante que le permite extraer agua del subsuelo (útil también en el bombeo de nutrientes); y, finalmente, un xilema de tipo ciclospóreo*,* (se renueva y modifica en cada estación: en verano se desarrollan vasos más estrechos para evitar la cavitación) (fig. 3) que les protege frente a cierta carestía hídrica estival (Gil-Pelegrín et al. 2005).

Por otro lado son el carácter marcescente de sus hojas, que las hace permanecer sobre las yemas foliares hasta bien entrada la primavera, y su foliación retardada los caracteres funcionales que les sirven de protección frente a las heladas tardías que son frecuentes en la Iberia más continental.

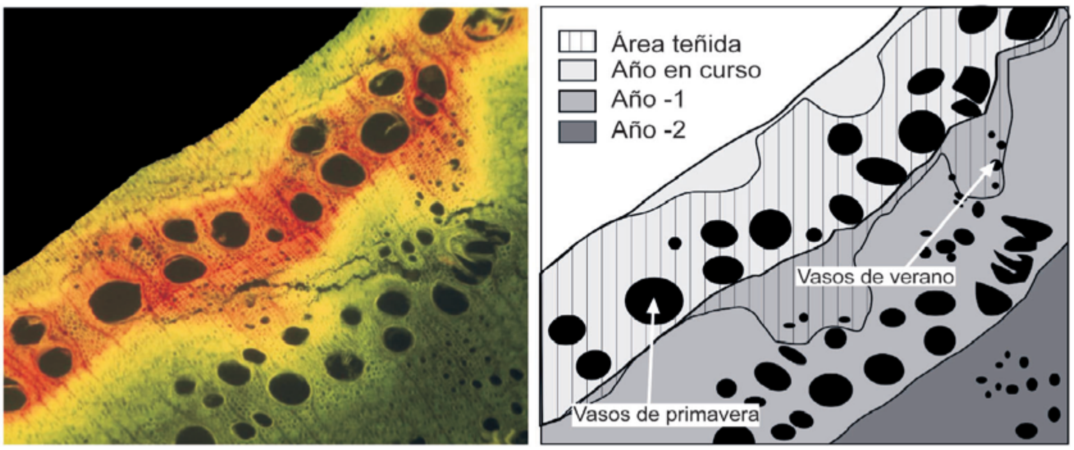


Fig. 3. Fotografía (parte izquierda) y esquema (parte derecha) de un corte transversal de xilema de *Quercus pyrenaica* (Fuente: Gil-Pelegrín et al. 2005).

La división principal de los melojares ibéricos es precisamente en base a estos dos factores: continentalidad y aridez estival. Se produce entre los territorios de macroclima Templado (región Eurosiberiana) y Mediterráneo (ver fig. 4), diferenciables por un período de aridez estival prácticamente inexistente en el primero y que se prolonga hasta tres meses en el segundo. Así las adaptaciones que les permiten vivir en la Iberia mediterránea, generalmente como bosque de montaña, les obligan en la Iberia templada a buscar ubicaciones más secas o con drenaje incrementado, como solanas, zonas de baja altitud, sobre sustratos arenosos o pendientes pronunciadas. Todo ello hace que, a lo largo de la Península Ibérica, el melojar se distribuya por un amplio rango de altitudes, desde los 290 msnm (País Vasco) hasta los 1800 msnm (Sierra Nevada), siempre manteniendo precipitaciones de verano no inferiores a 100 mm (Costa, 1997) y, generalmente, una mínima precipitación anual entorno a 600 mm. Es decir, sólo los encontraremos en aquellos territorios con ombroclimas que van del subhúmedo hasta incluso el hiperhúmedo (Tabla 1). De la misma manera, existe una correlación entre las temperaturas y la presencia de estos bosques. Dado que existen secuencias altitudinales y latitudinales operando sobre esta variable, en bioclimatología se han establecido los denominados termotipos (o termopisos) dentro de cada región. En general, los melojares ocupan únicamente dos pisos bioclimáticos (o termotipos) en las dos regiones climáticas Ibéricas, Meso- y Supramediterráneo en la Mediterránea y sus equivalentes: Colino y Montano en la región Templada o Eurosiberiana (Tabla 2).

Ombrotipo	Mediterráneo	Templado	Io
Árido	<200mm	-	0.4-0.1
Semiárido	200-350 mm	-	1.0-2.0
Seco	350-600 mm	-	2.0-3.6
Subhúmedo	600-1.000 mm	500-900 mm	3.6-6
Húmedo	1.000-1.600 mm	900-1.400 mm	6.0-12.0
Hiperhúmedo	>1600mm	>1400mm	12.0-24.0

Tabla 1. Ombrotipos Ibéricos y valores de precipitación media anual aproximada (tabla creada a partir de Rivas-Martínez, 1987 y Rivas-Martínez, 2011a). (Io=(Pp/Tp)10; siendo Tt: Temperatura positiva anual, Tª media de los meses de T>0ºC y Pt, precipitación positiva anual, sumatorio de la P media de los meses de T>0ºC). En azul ombrotipos que ocupa *Quercus pyrenaica.*

	Región Mediterránea	Tp (Itc)	Región Eurosiberiana / Templada	Tp (Itc)
Pisos bioclimáticos	Inframediterráneo	> 2400 (450 – 580)	Infracolino	> 2350 (>410)
	Termomediterráneo	2100 – 2400 (350 – 450)	Termocolino	2000 – 2350 (290 – 410)
	Mesomediterráneo	1500 – 2100 (220 – 350)	Colino o Mesotemplado	1400 – 2000 (190 – 290)
	Supramediterráneo	900 – 1500 ((120) – 220)	Montano o supratemplado	800 – 1400 ((120) – 190)
	Oromediterráneo	450 – 900 (–)	Subalpino o Orotemplado	380 – 800 (–)
	Crioromediterráneo	1 – 450 (–)	Alpino o criorotemplado	1 – 380 (–)

Tabla 2. Termotipos Ibéricos tabla creada a partir Rivas-Martínez, 1987 y Rivas-Martínez, 2011a, Siendo: Tp: temperatura positiva anual (sumatorio de las T medias mensuales de los meses de Tmedia >0ºC (Tp=(Ti>1ºC)), Indice de termicidad (It)=(T+M+m)10. En azul pisos bioclimáticos que ocupa *Quercus pyrenaica.*

La biogeografía combina climatología y distribución de las especies para establecer territorios de diferente extensión con cierto grado de homogeneidad ecológica. En la figura 4 detallamos la división biogeográfica de la Península ibérica y junto a ella incluimos la distribución de *Quercus pyrenaica*. Esta, abarca un gran número de provincias (Rivas-Martínez et al. 2011b); desde la Europea-Atlántica (nº 1 en fig. 4: Orocantábrica (1b) y Cántabro-Atlántica (1a)) en la región Eurosiberiana (o templada) pasando por la Catalana-Provenzal-Balear (5b: Catalana-Valenciana), Mediterránea-Ibérica-Central (4b: Oroibérica), Bética (8), Lusitano-Andaluza Litoral (6), o Mediterránea-Ibérica-Occidental (3) en la región Mediterránea, siendo en esta última donde predomina.

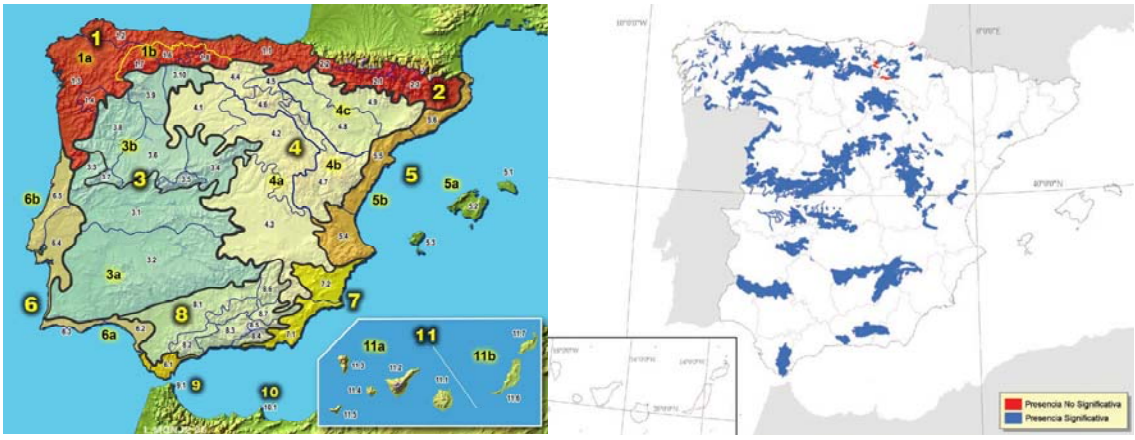


Fig.4. Izq. Regiones biogeográfica (Rivas-Marttínez, 2011): *Región Eurosiberiana* (en rojo): 1. Prov. Atlántico-Centroeuropea (SubProv.: a.Cántabro-Atlántica, b.Orocantábrica) 2. Prov. Alpino-Caucásica; *Región Mediterránea:* 3. Prov. Mediterránea Ibérica Occidental (SubProv.: a.Luso-extremadurense, b.Carpetano-Leonesa), 4.Prov. Mediterránea Ibérica Central (SubProv.: a.Castellana, b.OroIbérica, c.BajoAragonesa), 5.Prov. Catalana-Provenzal-Balear (Subprov. a Baleárica b. Catalano-Valenciana), 6.Prov. Lusitano-Andaluza Litoral (SubProv.: a.Gaditano-Algarviense, b.Sadense-Divisorio portuguesa), 7.Prov.Murciano Almeriense, 8.Prov. Bética. Drcha. Lugares de Interés Comunitario con presencia del hábitat 9230 en la Red Natura 2000. Fuentes Fig. 4 Izq., Peinado et al. (2008); Fig. 4 Drcha. García & Jiménez (2009)

En base a las mismas podemos realizar una breve descripción general de los melojares peninsulares, marcada en primer lugar por las diferentes comunidades forestales con las que entran en contacto en cada región biogeográfica. En la Iberia templada el melojo se encuentra inmerso en un ambiente dominado por frondosas, creando en muchas ocasiones bosques mixtos con *Quercus robur* y entrando en contacto con *Fagus sylvatica* o *Quercus petraea*. Sin embargo en la Iberia mediterránea suele crear islas de vegetación marcescente en un entorno predominantemente perennifolio, pudiendo incluir en función de la altitud y situación geográfica algún pie de *Quercus suber*, *Quercus broteroi* o *Quercus* *rotundifolia* Lam., entrando en contacto con sus comunidades así como con las de coníferas como *Pinus sylvestris* o *Pinus pinaster* (Blanco et al. 2005).

De la misma manera sus cortejos florísticos van variando en función de su ubicación. La clasificación sintaxonómica más reciente (Rivas-Martínez et al. 2011b) ha dividido los melojares ibéricos en 15 asociaciones climatófilas (dos más que en la anterior (con asterisco en la fig. 5), incluidas en la clase *Querco-Fagetea* Br.-Bl. & Vlieger in Vlieger 1937 junto a otros bosques caducifolios de óptimo eurosiberiano (Orden *Quercetalia roboris* Tx. in Barner 1931, que incluye robledales y hayedos acidófilos). Estas asociaciones climatófilas definen una alianza particular *Quercion pyrenaicae* Rivas Goday ex Rivas-Martínez 1965, y quedan subdivididas en dos subalianzas: por un lado las puramente mediterráneas en *Quercenion pyrenaicae* Rivas-Martínez 1974 (tabla 3, en azul), y aquellas correspondiente a las áreas de clima templado del norte peninsular en *Quercenion robori-pyrenaicae* (Br-Rl., P. Silva & Rozeira 1956) Rivas-Martínez 1975 (tabla 3, en verde).

Subalianza Quercenion pyrenaicae	Prov	Código Red natura	Termotipo	Ombrotipo		
				sH	H	HH
MELOJARES del INTERIOR IBÉRICO:						
Luzulo forsteri-Quercetum pyrenaicae	3b-4	9230/823028	SM	x	x	
* *Festuco merinoi-Quercetum pyrenaicae*	3b		SM		x	x
Holco mollis-Quercetum pyrenaicae	3b-1a	9230/823027	M-ST / MM		x	x
Pulmonario longifoliae-Quercetum pyrenaicae	4b-3b	9230/823025	ST / SM	x	x	
Genisto falcatae-Quercetum pyrenaicae	3b	9230/823026	ST / M-SM	x	x	x
* *Pyro bourgaeanae-Quercetum pyrenaicae*	3b		SM	x	x	
Arbuto unedonis-Quercetum pyrenaicae	3a-8	9230/823022	MM	x	x	
Sorbo torminalis-Quercetum pyrenaicae	3a	9230/823029	SM	x	x	
MELOJARES LEVANTINOS:						
Cephalanthero rubrae-Quercetum pyrenaicae	4b-5b	9230/823024	SM	x	x	
MELOJARES BÉTICOS:						
Berberido hispanicae-Quercetum pyrenaicae	8	9230/823023	SM	x	x	
Adenocarpo decorticantis-Quercetum pyrenaicae	8	9230/823021	SM	x		
Luzulo baeticae-Quercetum pyrenaicae	6a	9230/?	MM			x
Subalianza Quercenion robori - pyrenaicae						
MELOJARES CANTÁBRICOS:						
Linario triornithophorae-Quercetum pyrenaicae	1b	9230/823014	M-ST		x	
Melampyro pratensis-Quercetum pyrenaicae	1a	9230/823013	M-ST	x	x	
MELOJARES del NOROESTE IBÉRICO:						
Lonicero periclymenii-Quercetum pyrenaicae	1a	9230/?	M-ST/M-SM		x	x

Tabla 3. Relación de asociaciones fitosociológicas, provincia biogeográfica, piso bioclimático y ombroclima (en base a Rivas-Martínez, 2011b), y sus correspondencias con los códigos de la red natura 2000 y tipos de hábitat (Atlas y Manual de los Hábitats Naturales y Seminaturales de España). Abreviaturas: MM/SM, meso- y supramediterráneo; MT/ST, meso-supratemplado; SH, subhúmedo, H, Húmedo, HH, Hiperhúmedo. Con asterisco aquellas asociaciones no incluidas como tal en la red, sino formando parte de las inmediatamente superiores.

Subalianza Quercenion pyrenaicae (Mediterránea)

Ocupan posiciones muy variables en función del ombrotipo y situación geográfica, como característica diferencial podemos incluir la entrada como comunidades de sustitución (aparte del matorral retamoide y piornal) de gramíneas y cistáceas. A continuación hacemos una breve descripción de las asociaciones incluidas dentro de la alianza *Quercenion pyrenaicae.*

Festuco merinoi-Quercetum, Luzulo forsteri-Quercetum, Genisto falcatae-Quercetum, y *Pyro bourgaeanae-Quercetum.*

Son formaciones presentes a lo largo del oeste peninsular en territorios con diferentes grados de continentalidad y volumen de precipitaciones. El melojar es sustituido por piornales que dan paso a jarales y berciales.

Holco mollis-Quercetum, y *Pulmonario longifoliae-Quercetum.* Contactan con la región biogeográfica Eurosiberiana (macroclima Templado) por lo que aun reciben precipitación abundante; el matorral de sustitución sigue incluyendo brezales y no jarales.

Arbuto unedonis-Quercetum, y *Sorbo torminalis-Quercetum.* Son formaciones presentes en la submeseta sur (prov. Luso-Extremadurense) y Sierra morena. La orientación de sus sierras (E-O) permite la entrada de vientos atlánticos que incrementan la humedad ambiental y reducen los contrastes térmicos. El madroño, el lentisco, el rusco y el quejigo lusitano *Quercus broteroi* incrementan su presencia y el matorral de sustitución vuelve a incluir brezales. Estos melojares (*Arbuto unedonis-Quercetum)* aparecen a altitudes bajas, (≤ 1000 msnm) enriqueciéndose con especies termófilas típicas de encinares y alcornocales húmedos con los que conectan por debajo. A veces, ascienden como ocurre en Toledo por encima de los 1000 msnm (*Sorbo torminalis-Quercetum)* incluyendo serbales (*Sorbus torminalis*, *Sorbus aria*) y perdiendo ese fuerte carácter termófilo.

Cephalanthero rubrae-Quercetum pyrenaicae. Presente en la provincia Catalano-Valenciano-Provenzal, forma masas relictas sobre islas de sustrato ácido en un entorno predominantemente calizo, entran en contacto con encinares al bajar en altitud, y pinares silvestres al ascender.

Berberido hispanicae-Quercetum, Luzulo baeticae-Quercetum, y *Adenocarpo decorticantis-Quercetum.* Formaciones presentes en la prov. Bética y Gaditano-Onubo-Algarviense. Son las masas de melojo más al sur de la península por lo que suelen localizarse en umbrías y cabeceras de valle incrementando la altitud para conseguir mejores condiciones ambientales. El bosque se enriquece con mostajo (*Sorbus aria*), encina (*Quercus rotundifolia* Lam.) o arce (*Acer granatense* Boiss.). Piornales, codeseras (*Adenocarpus decorticans*) y agracejos

(*Berberis hispanica* Boiss. & Reut.) aparecen como matorrales de sustitución, siendo sustituidos por gramíneas con la degradación.

Subalianza Quercenion robori-pyrenaicae (Templada)

En general, en esta zona los melojares ocupan posiciones de media montaña, con elevada precipitación, estando el extremo geográfico cántabro-euskaldún (*Melampyro pratensis-Quercetum)* enriquecido con especies pirenaicas y el astur-galaico (*Linario triornithophorae-Quercetum,* y *Lonicero periclymeni-Quercetum)* con aquellas más atlánticas. El matorral de sustitución suele ser el piornal-brezal o brezal-tojal (*Daboecia*, *Calluna*, *Ulex*, *Erica*) (Rivas-Martínez 2010; Costa 1997; Díaz-González 2010).

Conservación

Por su elevado nivel de biodiversidad, los bosques de *Quercus pyrenaica* están protegidos a nivel europeo por la Directiva 92/43/CEE e incluidos en la red NATURA 2000, participando en diferentes esquemas de clasificación de hábitats: EUNIS Habitat Classification 200410 (G 1.7 Thermophilous deciduous woodland) (Davies, 2004), Paleartic Habitat Classification 1996 (41.6 *Quercus pyrenaica* forests), CORINE biotopes (Moss, 1994) (p. ej. 41.563, 41.564 Luso-Galician acidophilous oak forests). Están además incluidos como espacios de interés en algunas comunidades autónomas como Cataluña, e integrados en listas rojas con cierto nivel de protección como es el caso de Andalucía (incluido como "vulnerable" en el Decreto 104/1994, B.O.J.A.) (López 2001).

La red NATURA 2000, en particular, los incluye dentro del grupo de "bosques mediterráneos caducifolios" (92) con el código *9230: Robledales de Quercus pyrenaica y robledales de Quercus robur y Quercus pyrenaica del noroeste ibérico.* Bajo este título sin embargo y como ya se advierte en la revisión de 2009 (García & Jiménez), se definen la mayor parte de melojares ibéricos, pero además aquellos robledales de *Quercus robur* donde entra *Quercus pyrenaica.* Debido a que la última revisión sintaxonómica se produjo en 2011 (Rivas-Martínez et al. 2011b), en la Fig. 4 hemos intentado incluir la actual clasificación correlacionándola con la utilizada en la red natura 2000. Así las asociaciones incluidas en la Tabla 3 con un asterisco se encontrarían incluidas en la red dentro de las inmediatamente superiores, y la asociación incluida en la tabla 3 como *Pulmonario longifoliae-Quercetum* se trataría de la actual denominación de la asociación *Festuco braun-blanquetti-Quercetum* dentro del esquema de comunidades de la red.

Objetivos generales

La fuerte presencia de los bosques de *Quercus pyrenaica* en la Península Ibérica, con una superficie estimada en España que supera las 650.000 Ha. hace que sea el segundo fanerófito más abundante detrás de la encina (*Quercus rotundifoliae* Lam.) (III Inv. Forestal Nacional). Por ello y por su singularidad como endemismo marcescente de la Europa meridional estos bosques han sido objeto de muchos estudios, entre los que destacan los de vegetación, desde los puramente descriptivos realizados a lo largo del siglo XX y culminando recientemente con las últimas clasificaciones sintaxonómicas (Braun-Blanquet (1956, 1964, 1967), Tüxen & Oberdorfer (1958), Amaral (1958), Rivas-Martínez et al. (1962, 1984, 1987, 1991, 2002, 2007), Rivas Goday (1964), Mayor (1965), Bolòs (1967), Vigo (1968), Ladero (1970), Navarro (1974), López (1976), Báscones (1978), Velasco (1978), Martínez-Parras et al. (1982), Loidi (1983), Mateo (1983), Romero (1983), Navarro & Valle (1983), Mendiola (1983), Amigo (1984), Llamas García (1984), Mesón (1985), Barrera (1985), Fuente (1985), Penas & Díaz-González (1985), Navarro (1986, 1989), Losa (1986), Onaindía (1986), Tárrega (1986), Arambúru (1987), Catalán (1987), Fernández Prieto (1987), Nieto & Cabezudo (1988), Cano (1988), Valle (1988), López Pacheco (1988), Pérez Morales (1988), Puente García (1988), Sánchez-Mata (1989), Herrero (1989), Cano (1990), García González (1990), Silva Pando (1990), Ferrer Plou (1990), Peralta (1990), Amor (1991), Fernández-González (1991), Peralta (1992), Amor (1993), Ferrer (1993), Galán de Mera (1993), Medrano (1994), Gavilán (1994), Sardinero (1994), De la Cruz (1994), Roselló (1994), Allue (1995), Herrera (1995), Pérez Latorre et al. (1996), López Vélez (1996), Ortiz et al. (1997), Loidi (1997), García-Mijangos (1997), Melendo (1998), El Aallali (1998), Aguiar Goçalves (2001), Soutinho et al. (2001), Alonso (2002), Ladero (2003, 2008), García Baquero (2003), Pérez Latorre (2004), Sardinero (2004), Entrocassi et al. (2004), Cantó (2004), Belmonte (2008), Herreros (2010), Honrado (com. pers.), Merle & Ferriol (2008), Vicente (2008), Pereira (2009), Rodríguez Guitián (2010)). También han sido estudiado otros aspectos del melojar, como son la relación con sus líquenes epífitos, dendrocronología, hibridación, ciclo de nutrientes, restauración, impacto de vertebrados o aplicaciones como el envejecimiento de vinos (Avalos (1986), Calvo (1993), Pérez Antelo (1995), Gómez (2003), Blanco et al. (2005), Valbuena (2005), Castro (2006), Cadahía (2008), Tárrega (2006), Martínez-Lirola (2011), Urbieta (2011), Belinchón et al. 2012).

Los antecedentes antes mencionados sobre estos bosques, la actual situación de cambio global y la amenaza real existente para su conservación y la de la flora que albergan en la Cuenca Mediterránea nos ha llevado al estudio de los mismos. Hemos revisado de forma detallada las diferencias en toda la extensión de su distribución en la Península Ibérica, tratando de cuantificar sus diferentes niveles de conservación, y también de singularidad florística. Para ello, se han estudiado sus matices locales y regionales, pero también las conexiones que han permitido esa continuidad en la composición florística del melojar y que muchas veces dificulta su clasificación. Paralelamente hemos intentando desarrollar una metodología que nos permita definir sus matices diferenciales pero sin abandonar la base florística común a toda la Península Ibérica.

Los objetivos específicos de este trabajo han sido:

(i) Definir las principales características climáticas que explican el patrón de distribución fitogeográfica de los bosques de *Quercus pyrenaica* en España y obtener los limites bioclimáticos que mejor definen estos tipos de vegetación.

(ii) Determinar el conjunto de especies que mejor indican las diferentes influencias ambientales o características de los bosques relictos levantinos, y en base a ellas las características comunes y diferenciales de los mismos.

(iii) Encontrar patrones florísticos a diferentes niveles de trabajo que representen los principales factores ecológicos de los melojares del norte peninsular y a que escala lo son, así como averiguar si estos patrones pueden ser considerados conductores del ensamblaje de la comunidad.

(iv) Encontrar los principales núcleos de similitud florística de los bosques de *Quercus pyrenaica* de la Península Ibérica, aquellas especies indicadoras que impulsan esta diferenciación y su correlación con la estructura jerárquica actual.

(v) Describir bioclimática y florísticamente el grupo diferenciado de inventarios del levante y sus comunidades de substitución.

Materiales y Métodos

Se ha realizado una revisión bibliográfica exhaustiva de todos aquellos trabajos en los que se ha estudiado estos bosques. Se incluyen datos válidamente publicados y también inéditos. En total se recopilaron hasta un total de 712 inventarios fitosociológicos recogidos siguiendo la metodología de Braun-Blanquet (1932), que incluyen más de 800 especies y que cubren ampliamente la distribución geográfica de estos bosques.

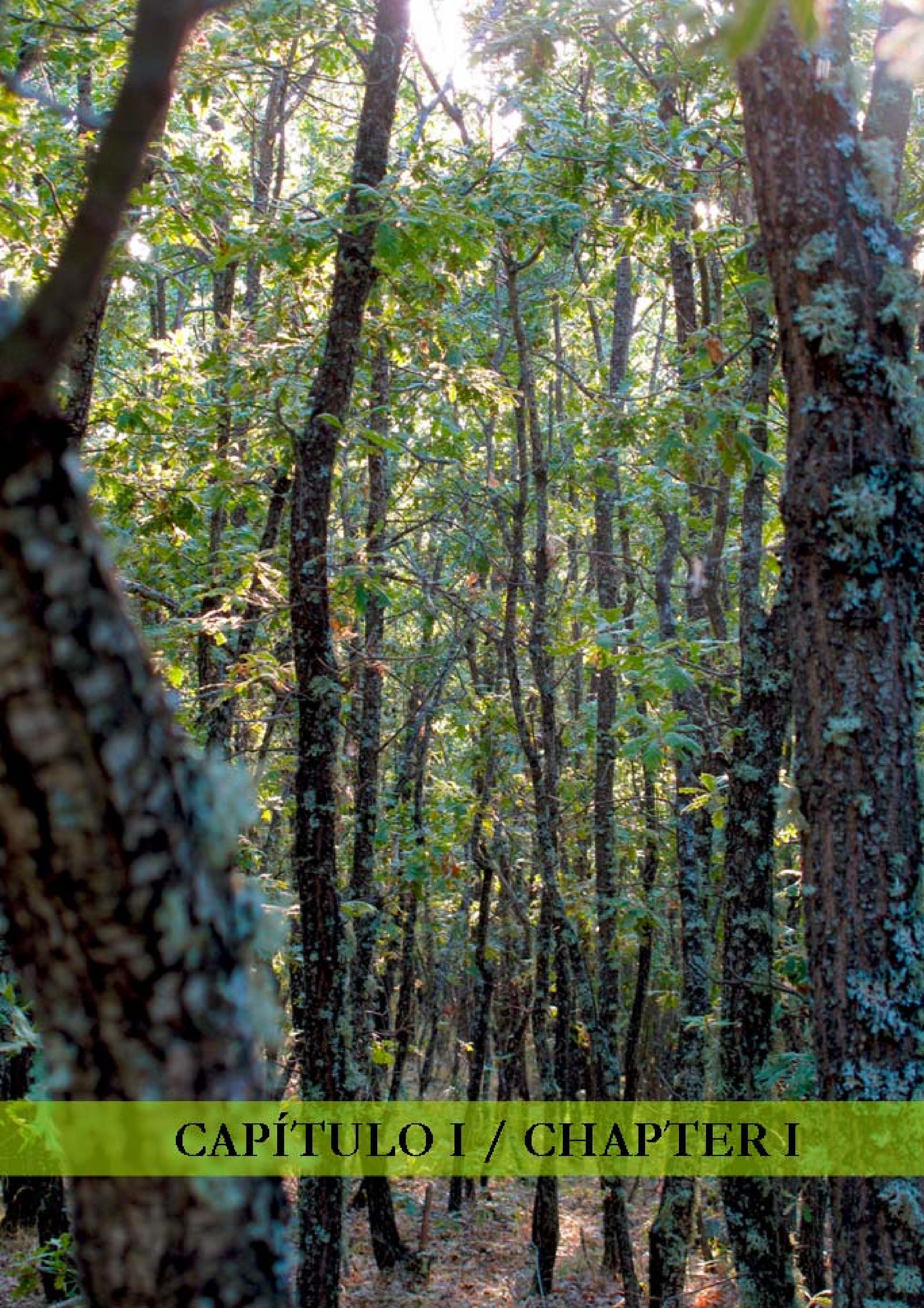
Como paso previo al análisis de los datos se realizó una homogeneización: corrección nomenclatural y de sinonimias, de las especies incluidas en los inventarios a escala peninsular, basándonos principalmente en los números publicados de Flora iberica (Castroviejo et al. 1986-2010) si la autoría no está indicada, y la recopilación de Euro+Med PlantBase (2006-2013) para el resto. Sólo en ciertas regiones ha sido necesario recurrir a la flora local, como es la de los Paisos Catalans (Bolòs & Vigo (1984-1995)), así como diferentes monografías (*Festuca* (Fuente & Ortuñez, 1998) o *Hieracium* (Mateo Sanz, 2001)). En aquellas ocasiones en las que la distribución geográfica de la especie en cuestión no aparecía claramente delimitada a nivel peninsular, se decidió mantener la denominación del autor. De igual manera ciertas subespecies aunque no reconocidas en la flora de referencia, sí (según esa misma flora) mantenían caracteres diferenciales, en estos casos se ha preferido mantener su denominación de cara a no perder información que a nivel de campo pudiese ser relevante. A su vez, hemos seguido las propuestas de Rivas-Martínez et al. (2007, 2011b), para la caracterización biogeográfica y bioclimática de los bosques estudiados.

Se realizó también la localización y registro de las coordenadas UTM de cada inventario – cuando el autor no aportaba la información – utilizando mapas militares 1:50.000 (Servicio Geográfico del Ejército, 1985).

El almacenamiento de toda esta información se hizo a través de la creación de una base de datos con el programa TURBOVEG (Hennekens, 1998-2013), mientras que para la edición y análisis de los datos fitosociológicos se utilizó JUICE (Tichý, 1999-2013) junto con los paquetes estadísticos vegana, indicspecies y vegclust (entre otros), incluidos en el software R (Gentleman et al. 1997).

Cuando fue necesario todos aquellos inventarios con coberturas de *Quercus pyrenaica* inferiores al 20% fueron eliminados de la matriz (en ocasiones interesaba conservar las comunidades de sustitución), así como aquellas duplicidades encontradas incluso entre diferentes autores. Las coberturas florísticas fueron transformadas para su análisis posterior bien en presencia-ausencia (Chytrý et al. 2002), bien en abundancias (siguiendo la escala dada por van der Maarel, 1979). La primera preferiblemente para localidades aisladas y muy fragmentadas, la segunda para áreas de elevada continuidad florística como es el norte peninsular donde la precipitación ejerce un efecto homogeneizador y la dominancia nos pareció más adecuada a la hora de identificar las especies indicadoras.

Los análisis realizados sobre la matriz y sus particiones son explicados en cada uno de los capítulos por separado. En todos ellos se ha realizado un análisis multivariable previo para conseguir una visión general de la distribución de los datos. Y en la mayoría de los capítulos hemos utilizado para la identificación de especies indicadoras la función “multipatt” del paquete del proyecto-R: “indicspecies”. Esta herramienta nos ha permitido, no solo identificar aquellas especies representativas de áreas concretas con el índice IndVal (Dufréne & Legendre, 1997) sino aquellas que son representativas de superficies mayores que las agrupan, consiguiendo así conocer conexiones florísticas y áreas de dominancia.



CAPÍTULO I / CHAPTER I

Chapter I: Modeling current distribution of Spanish *Quercus pyrenaica* forests using climatic parameters

Abstract

The geographical distribution of *Quercus pyrenaica* forests in the Iberian Peninsula is analysed from a climatic point of view. 438 phytosociological relevés were collected and 28 climatic parameters were derived from their geographical features using the ESTCLIM model. The objectives of our work were to define the main climatic characteristics that explain the particular distribution pattern of *Quercus pyrenaica* forests in Spain and to obtain the climatic envelopes that best define these vegetation types. For this purpose, four floristic and their corresponding climatic matrices were analyzed by means of Canonical Correspondence Analysis (CCA). Results show the importance of some climatic features that define the Mediterranean climate: summer dryness and winter precipitation, both of which serve to separate some types of forest. It is the case of Adenocarpo-Quercetum and *Berberido hispanicae-Quercetum* in southern Spain or *Pulmonario longifoliae-Quercetum* and *Luzulo forsteri-Quercetum*, in the center of the Iberian Peninsula, which are separated in terms of summer dryness. *Luzulo baeticae-Quercetum* is well separated from the other two associations it was compared with (*Arbuto unedonis-Quercetum* and *Sorbo torminalis-Quercetum*) by winter precipitation. Exposure also plays an important role in some ranges such as the Sierra Madrona where a different type of forest appears in warmer or cooler exposures. Finally, other phytosociological adscriptions of relevés to a type of association presented problems due to a very similar floristic composition, as is the case of *Genisto falcatae-Quercetum* and *Holco-Quercetum*. Regarding the differences between Eurosiberian forests and northern Mediterranean ones, separation resulted difficult since some of them (*Linario triornithophorae-Quercetum*) showed a certain overlap with those Mediterranean forests they were compared (*Genisto falcatae-Quercetum*, *Holco mollis-Quercetum*) in terms of the climatic variables analysed, although they showed a very different floristic composition.

Keywords: modeling vegetation distribution, *Quercus pyrenaica*, Canonical correspondence analysis, phytosociology, bioclimatology.

Introduction

The vegetation of any region is the reflection of environmental factors present in it, and climate is one of the most crucial. The relationships between climate and vegetation distribution has long been established (Von Humboldt 1807, Grisebach 1838) and it has been widely studied from different points of view: the study of ecophysiological responses of plants (Woodward 1987); life-form types as a response to the diversity in climate (Box 1981, 1987); plant functional types (Woodward & Cramer 1996); zonation or distribution of vegetation types (Rivas-Martínez et al. 2002, Del Río et al. 2007); the creation of a world wide bioclimatic typology (Rivas-Martínez & Rivas Sáenz 2007); and most recently, the prediction of species distribution for global change (Guisan et al. 1998, Guisan & Thuiller 2005).

The climate of an area is a complex entity comprising numerous elements: temperature, moisture, precipitation, wind, etc., usually quantified in terms of means, extremes or maximum or minimum values, durations, etc. Any climatic element or combination of elements could potentially be assumed to influence plant life (Tuhkanen 1987), since climate provides all the physical or environmental constraints within which physiological features and other aspects of plant/vegetation ecology must operate. Simple climatic parameters have been used to quantify and determine this influence of climate, either in the form of bioclimatic indices or by themselves (Gavilán 2005; Beaumont et al. 2005; Körner & Paulsen 2004). Other bioclimatic approaches include climatic envelopes of vegetation and plant distributions as a reasonable means for treating the climatic limits and ranges of a large numbers of entities (Box et al. 1993, Box 1981, Holdridge 1947, 1967). A climatic envelope is the climatic space corresponding to the geographic range within which a vegetation formation or a plant or taxon is considered to grow and reproduce under natural conditions. Such a climatic space can be defined in terms of available climatic data (temperature and precipitation variables) for which relatively long-term records are available at a number of sites in a study region (Box et al. 1993; Crumpaker et al. 2001, 2002).

Quercus pyrenaica is a species whose natural distribution covers the Iberian Peninsula, where it forms mainly mountain forest, to western France and north-western Morocco. These Iberian forests live under meso-supramediterranean and mesotemperate areas and subhumid, humid and hyperhumid ombroclimate (Rivas-Martínez et al. 2002) living on siliceous soils, or soils impoverished in basic ions. From a biogeographical point of view they occupy extended areas of the Mediterranean region, mainly in the Carpetan-Leonese, the Lusitan-Extremadurean and the OroIberian subprovinces and are extended in smaller areas of the Betic, Gaditan-Algarvian, Castilian and Catalonian-Valencian subprovinces, while in the Eurosiberian region they can be found throughout the OroCantabrian and Cantabrian-Atlantic subprovinces (Rivas-Martínez et al. 2002). *Quercus pyrenaica* forests, as other vegetation types, are subject to intense pressure from human use, and have been traditionally used for extracting wood, grazing, etc., which has reduced their distribution area; in some cases their use has led to changes in their floristic pattern (Gavilán et al. 2000). A variety of conservation tools are needed to recover and conserve them.

They have been the subject of numerous phytosociological studies (Braun-Blanquet et al. (1956), Amaral Franco (1958), Rivas-Martínez (1962), Braun-Blanquet (1964), Rivas Goday (1964), Ladero (1970), López (1976), Velasco (1978), Martínez-Parras & Molero (1983), Mateo (1983), Navarro & Valle (1983), Rivas-Martínez et al. (1984), Fuente (1986), Penas & Díaz-González (1985), Losa et al. (1986), Fernández Prieto & Vázquez (1987), Cano (1988), López Pacheco (1988), Nieto & Cabezudo (1988), Pérez Morales (1988), Valle et al. (1988), Navarro (1989), Sánchez-Mata (1989), Amor (1991), Fernández-González (1991), Galán Mera (1993), García-Mijangos (1994), Gavilán (1994), Sardinero (1994), Herrera (1995), Pérez Latorre et al. (1996), Loidi et al. (1997), Ortiz et al. (1997), Aguiar Goçalves (2001), Ladero et al. (2003) and Honrado (com. pers.), but so far all the information has not been analyzed and checked, except in a few works (Rivas-Martínez 1987, 2007, Entrocassi et al. 2004).

The objectives of this paper are to define the main climatic characteristics that explain the phytogeographic distribution pattern of *Quercus pyrenaica* forests in Spain and to obtain the climatic envelopes that best define these vegetation types. For this purpose we analyzed an environmental-climatic dataset derived from ESTCLIM a climatic model which summarizes climatic parameters over a geographical distribution range of a plant community; in our case, for every site where a phytosociological relevé exists. Thus, a floristic dataset containing phytosociological relevés for the large distribution of *Quercus pyrenaica* in the Iberian Peninsula was studied using the climatic dataset as an environmental constraint for a particular floristic composition in a determined location.

Materials and methods

Quercus pyrenaica forests in Spain are comprised by 10 associations following the Braun-Blanquet phytosociological approach. Over 800 relevés can be found in the bibliography on *Quercus pyrenaica* studies from the Iberian Peninsula (see Introduction), of which 438 are from Spain (see Map 1.1). They include more than 800 plant species. The whole dataset of relevés has been analyzed and discussed in a previous paper (Entrocassi et al. 2004). The relevés were entered into TURBOVEG (Hennekens 1996) to be able to manage this great quantity of information.

Map 1.1. Studied localities and authors' adscription: 1&2.Ibías and Narcea river watersheds (Fernández Prieto & Vázquez 1987, sub *Linario-Quercetum pyrenaicae*). 3. Peña Trevinca and Sierra do Eixo (Ortiz et al. 1997, sub *Genisto falcatae-Quercetum* and *Holco-Quercetum pyrenaicae*). 4. Bernesga and Curueño river watersheds (Penas & Díaz González 1985, sub *Genisto falcatae-Quercetum pyrenaicae*; Pérez Morales 1988, López Pacheco 1988, sub *Linario-Quercetum pyrenaicae*). 5. Picos de Europa (La Liébana) Rivas-Martínez et al. 1984). 6. Asón river watershed (Herrera 1995, Loidi et al. 1997, sub *Melampyro-Quercetum pyrenaicae*). 7. Montes Obarenes (García Mijangos 1997, sub *Melampyro-Quercetum pyrenaicae*). 8. Sierra de La Demanda (Loidi et al. 1997, sub *Pulmonario-Quercetum pyrenaicae*). 9. Zámora (Tábara, Alba and Aliste territories, Navarro & Valle 1983, sub *Holco-Quercetum pyrenaicae*). 10. Sierra de Gata (Gavilán 1994, sub *Genisto falcatae-Quercetum* and *Holco-Quercetum pyrenaicae*). 11. La Vera and Sierra de Tormantos (Amor 1991, Sardinero 1994, sub *Luzulo-Quercetum pyrenaicae* s.l.). 12. Sierra de Gredos (Sánchez Mata 1989, sub *Luzulo-Quercetum pyrenaicae* s.l.). 13. Sierra de Guadarrama (Fernández-González 1991, sub *Luzulo-Quercetum pyrenaicae* s.l.). 14. Sierrra de Ayllón (Fuente 1985, sub *Luzulo-Quercetum pyrenaicae* and *Pulmonario-Quercetum pyrenaicae*). 15. Sierra del Moncayo (Braun-Blanquet 1964, Navarro 1989, sub *Pulmonario-Quercetum pyrenaicae* and *Luzulo-Quercetum pyrenaicae* s.l.). 16. Sierras de Mira y Talayuela (Mateo 1983, sub *Luzulo-Quercetum* s.l.) 17. Serranía de Cuenca (López 1976, sub *Luzulo-Quercetum pyrenaicae* s.l.). 18. La Jara and Serranía de Ibor, Guadalupe and Villuercas (Ladero 1970, sub '*Leuzeo-Quercetum pyrenaicae*'). 19. Montes de Toledo (Velasco 1978, sub '*Leuzeo-Quercetum pyrenaicae*'). 20. Sierra de Madrona, Quintana and San Andrés (Rivas Goday 1964, sub '*Genisto tournefortii-Quercetum pyrenaicae*', Cano 1988, sub *Arbuto-Quercetum pyrenaicae*). 21. Sierra de Segura 21. Sierra de Segura (Valle et al. 1988, sub *Berberido-Quercetum pyrenaicae*). 22, 23. Sierra del Aljibe and Tarifa (Galán de Mera 1993, Pérez Latorre et al. 1996, sub. *Arbuto-Quercetum pyrenaicae* and sub '*Cytiso triflori-Quercetum pyrenaicae*', respectively). 24. Sierra de Tejeda and Almijara (Nieto & Cabezudo 1988). 25 and 26. Sierras de Cázulas, Alfácar, Sierra Nevada and Las Alpujarras (Martínez Parras & Molero Mesa 1983, Losa Quintana et al. 1986, sub *Adenocarpo decorticantis-Quercetum pyrenaicae*).

Climatic data

For the climatic characterization of *Quercus pyrenaica* forest we used ESTCLIM (Sánchez Palomares et al. 1999), a climatic model which summarizes up to 28 climatic parameters over the biological range of any known plant community. It is a correlative modeling tool that interpolates up to 28 climatic parameters for any location for which the latitude, longitude and elevation are known. In our case, elevation data are usually included in all phytosociological relevés, and sometimes the geographical location (UTM coordinates); however they often need to be located on topographical maps with a suitably accurate scale (1:50000). The parameters calculated for every site by means of ESTCLIM are: annual mean temperature (TY), monthly mean temperature (T1-T12), maximum mean temperature of the warmest month (TMXC), minimum mean temperature of the coldest month (TMF), annual precipitation (PY) and monthly precipitation (P1-P12).

Vegetation data?

The large number of species and localities compiled (438 relevés), made it very difficult to manage the whole dataset with statistical programs, so we subdivided the former matrix into other smaller ones, according to syntaxonomical, biogeographical and bioclimatic criteria, including some altitudinal features (Table 1.1), following the more recent typologies (Rivas-martínez et al. 2002 and 2011). For this work, we have considered *Luzulo-Quercetum* as a big complex covering extended areas from eastern parts of Iberian Sistema Central to western ones. Even more it has been recently segregated and other associations has been proposed, like *Festuco merinoi-Quercetum* (Sánchez-Mata, 1999).

Finally, the analyses have been applied to eight matrices: four climatic and four floristic matrices.

Ordination

When the whole dataset of 438 sites was compiled, we used canonical analyses (CCA, canonical correspondence analyses) to compare it with the floristic datasets. This is a useful multivariate method for determining variables that best define differences among vegetation groups which has been used frequently in ecology (Moreno et al. 1990, Gavilán & Fernández-González, 1997). It uses biotic (in our case the phytosociological matrix) and abiotic data (the matrix derived from ESTCLIM) simultaneously as in other canonical multivariate analyses such as discriminant analysis. It is also suitable for detecting both primary and secondary gradients while reducing the dimensionality of the data space (Williams 1983, Sun & Feoli 1991). The analyses were performed using CANOCO ver. 4.1 (ter Braak & Smilauer 1998). From the analyses, homogeneous groups of relevés were obtained; from them two tables were derived Table 2 for monthly data and Table 3 for seasonal data.

Associations	**N. relevés**
Matrix I:	28
Adenocarpo decorticantis-Quercetum pyrenaicae Martínez-Parras & Molero 1983	20
Berberido australis-Quercetum pyrenaicae F. Valle, Gómez-Mercado & Mota 1988	8
Matrix II:	76
Arbuto unedonis-Quercetum pyrenaicae (Rivas Goday in Rivas Goday et al. 1960) Rivas-Martínez 1987	63
Luzulo baeticae-Quercetum pyrenaicae Rivas-Martínez in Rivas-Martínez et al. 2002 (=*Cytiso triflori-Quercetum pyrenaicae* Pérez, Galán, Deil & Cabezudo 1996	8
Sorbo torminalis-Quercetum pyrenaicae Rivas Goday ex Rivas Martínez 1987 (= *Genisto tournefortii-Quercetum pyrenaicae* Rivas Goday 1964)	5
Matrix III:	243
Luzulo forsteri-Quercetum pyrenaicae s.l. Rivas-Martínez 1963	155
Pulmonario longifoliae-Quercetum pyrenaicae Oberdorfer in Tüxen & Oberdorfer 1958	42
Sorbo torminalis-Quercetum pyrenaicae Rivas Goday ex Rivas Martínez 1987	46
Matrix IV:	91
Holco mollis-Quercetum pyrenaicae Br.-Bl., P. Silva & Rozeira 1956	11
Genisto falcatae-Quercetum pyrenaicae Penas & T.E. Díaz ex Rivas-Martínez et al. 2002 (incl. *Pyro-Quercetum pyrenaicae* Ladero, Amor, Santos, Sánchez & Ferro 2004)	23
Linario triornithophorae-Quercetum pyrenaicae Rivas-Martínez et al. 1984	28
Melampyro pratensis-Quercetum pyrenaicae Rivas-Martínez ex Rivas-Martínez et al. 1984	29

Table 1.1 Matrices of phytosociological associations of *Quercus pyrenaica* forest studied. Numbers correspond to relevés studied in every association.

Table 1.2. Monthly mean precipitation and temperatures of Spanish *Quercus pyrenaica* groups, extracted from the CCA, between parenthesis the minimum and maximum value obtained (range). Numbers in the first column refers to the matrix and the relevés group of figures 1-4.

Group	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
1,1	112,8 (80,153)	116,8 (78,165)	112 (77,153)	80,2 (64,103)	60,7 (41,86)	18,6 (12,23)	4,3 (3,7)	6,55 (5,8)	26,35 (19,37)	80,5 (71,97)	92,8 (71,124)	125,7 (93,166)
1,2	79 (78,81)	75,8 (75,78)	72,63 (71,75)	82,6 (80,84)	64,9 (63,)68	37,75 (37,39)	16,5 (15,18)	20,5 (20,21)	42,38 (41,44)	65,25 (64,67)	62 (61,63)	93,3 (92,96)
2,1	86 (84,87)	84,4 (83,85)	73,4 (73,74)	53,4 (53,54)	61 (60,62)	41,4 (40,42)	9 (9,1)	7 (7,8)	36,4 (35,37)	71,6 (70,73)	81 (79,82)	79,6 (79,80)
2,2	255,8 (200,271)	255,2 (197,272)	232,7 (191,246)	186,9 (133-207)	146,1 (106,161)	42,9 (29,48)	5,5 (4,6)	11,09 (9,12)	73,79 (56,81)	160,4 (131,169)	181,2 (136,192)	266,4 (209,282)
2,3	83 (62,181)	86,8 (63,168)	83 (63,165)	68 (53,103)	56,7 (48,84)	32,33 (32,41)	5,67 (7,8)	8,16 (7,10)	32,66 (26,71)	68,66 (55,143)	80,5 (57,196)	95,5 (74,122)
2,4	154,09 (95,184)	148,4 (91,176)	155,2 (100,192)	94,5 (69,113)	84 (70,97)	41,45 (36,48)	8,36 (6,11)	11,09 (9,16)	65,63 (44,80)	120,54 (78,143)	163,7 (106,204)	126,9 (96,164)
2,5	179,25 (166,208)	172,3 (158,192)	175,3 (161,184)	114,8 (100,141)	95,8 (81,127)	47 (41,59)	9,75 (7,13)	13,5 (9,21)	78,75 (73,95)	151,75 (136,181)	207 (198,222)	151,5 (127,191)
2,6	155,58 (82,182)	167,6 (73,174)	136,5 (79,200)	80,5 (61,124)	78,2 (61,94)	41,17 (36,47)	5,94 (2,13)	10,29 (9,15)	63,41 (41,85)	120,88 (68,175)	169,4 (88,248)	124,9 (77,161)
3,1	74,46 (69,85)	67,4 (62,78)	78,46 (73,90)	90,8 (86,102)	85,3 (82,94)	60,3 (59,63)	33,46 (32,36)	40,23 (38,44)	50,38 (47,58)	73,92 (68,87)	92,6 (85,107)	94,6 (80,104)
3,2	119,5 (111,129)	131 (121,142)	95,8 (91,101)	90,8 (86,96)	78,3 (77,80)	85,25 (81,90)	31,5 (30,33)	35 (33,37)	51 (51,52)	123,75 (113,136)	134,8 (124,147)	125 (117,134)
3,3	48,06 (35,113)	44,7 (32,96)	52,83 (43,104)	55,1 (46,81)	65,2 (60,86)	64 (58,86)	31,61 (58,67)	27,11 (26,34)	50,06 (24,30)	47,67 (43,58)	60,9 (38,90)	59,9 (47,128)
3,4	89,68 (65,130)	88,6 (52,127)	80,75 (61,119)	78,7 (55,127)	74,6 (41,103)	56,21 (12,77)	20,75 (3,35)	19,71 (6.0,35)	54,86 (19,75)	84,25 (56,121)	106,8 (65,173)	96,1 (66,143)
3,5	73 (54,111)	76 (64,100)	75,66 (57,113)	61,3 (53,77)	70,3 (64,83)	73 (47,52)	19,5 (19,20)	22,5 (25,20)	58 (47,69)	82 (60,104)	97 (56,138)	90 (63,117)
3,6	91 (60,230)	91,2 (862,198)	93,07 (67,188)	67,1 (51,147)	68,1 (53,132)	42,07 (37,61)	13,93 (9,22)	12,93 (5,21)	54,25 (36,92)	85,93 (63,188)	108,4 (75,230)	96,4 (60,199)
3,7	132 (31,281)	135 (61,264)	167,86 (33,459)	96,1 (41,162)	77,6 (35,121)	41,71 (25,64)	12,43 (9,16)	10,86 (4,14)	75,71 (20,207)	155 (35,469)	212,4 (30,681)	119 (71,172)
3,8	98 (66,136)	104,9 (66,143)	100,53 (63,133)	65,9 (52,86)	67 (53,77)	38,19 (30,45)	7,44 (2,10)	6,66 (5,11)	38,88 (28,48)	78,69 (58,106)	99,2 (60,126)	104,4 (70,147)
4,1	123 (73,234)	100,6 (64,174)	96,1 (74,160)	114,8 (84,198)	98 (80,170)	66,38 (54,113)	43,31 (31,81)	49,45 (39,70)	63,38 (48,94)	105,34 (69,191)	122,4 (86,178)	129,9 (82,192)
4,2	124 (108,133)	110,3 (97,119)	116,33 (102,125)	96 (82,105)	97,7 (84,106)	72,67 (66,77)	31,33 (29,33)	35 (32,37)	66,33 (60,71)	104 (91,113)	150 (133,162)	130,3 (113,141)
4,3	121 (90,180)	102,4 (80,148)	106,56 (85,143)	83,3 (68,120)	85,7 (71,111)	64,89 (56,82)	28,39 (21,41)	32,06 (25,50)	62,61 (52,89)	95,17 (76,135)	133,7 (110,171)	123,6 (93,174)
4,4	330 (98,894)	235,9 (85,585)	262,33 (84,685)	178,5 (64,450)	147,3 (69,315)	90,47 (53,182)	53,53 (20,137)	83,4 (23,249)	141 (48,368)	226 (73,587)	309 (107,802)	300,7 (101,780)
4,5	384 (154,840)	269,7 (127,551)	292 (116,641)	201,33 (92,418)	158,3 (89,294)	99,67 (65,167)	63,33 (31,127)	106 (42,233)	166,67 (77,345)	254,33 (106,547)	343 (138,750)	344,3 (149,732)
4,6	117 (47,227)	110,4 (52,220)	109,74 (50,216)	72,79 (38,134)	73,2 (40,120)	39,53 (27,57)	11,11 (8,18)	13,47 (8,20)	56,21 (36,92)	93,11 (47,171)	124,8 (62,263)	104,9 (45,211)

Group	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**T7**	**T8**	**T9**	**T10**	**T11**	**T12**
1,1	4,87 (3.1, 7.0)	5,76 (4.4, 7.4)	7,44 (6.1, 9.0)	9,88 (8.3, 11.0)	10,05 (5.6, 14.9)	17,55 (14.8, 18.6)	22,04 (19.5, 23.2)	18,95 (15.3, 22.7)	17,99 (15.5, 19.5)	12,76 (11.6, 14.2)	8,3 (6.9, 10)	5,09 (3.2, 7.2)
1,2	4,01 (3.6, 4.3)	4,52 (4.3, 4.7)	6,75 (6.5, 6.9)	9,4 (9.2, 9.6)	13,41 (12.8, 13.8)	17,36 (17.2, 17.5)	21,6 (21.4, 21.7)	21,12 (20.9, 21.3)	17,25 (16.6, 17.6)	11,67 (11.3, 11.9)	7,64 (7.2, 7.9)	4,41 (4.0, 4.7)
2,1	4,22 (4.1, 4.4)	5,22 (5.1, 5.4)	7,12 (7.0, 7.3)	9,92 (9.8, 10.1)	14,3 (14.2, 14.5)	17,18 (16.9, 17.6)	23,56 (23.4, 23.8)	23,8 (23.7, 24.0)	20,26 (20.2, 20.4)	13,66 (13.6, 13.8)	8,06 (8.0, 8.2)	3,98 (3.8, 4.3)
2,2	7,6 (7.3, 8.0)	8,52 (8.3, 8.9)	9,89 (9.6, 10.4)	12,38 (12.1, 13.1)	14,22 (13.5, 16.4)	18,31 (17.9,19.9)	21,8 (21.4, 23.6)	21,57 (20.9, 23.8)	19,2 (18.8, 20.5)	15,31 (15, 15.9)	11,12 (10.9, 11.9)	7,92 (7.7, 8.1)
2,3	5,56 (4.8, 6.9)	6,86 (6.2, 8.1)	9 (8.4, 10.3)	12,1 (11.7, 13.1)	14,8 (13.7, 17.4)	20,31 (19.6,21.9)	24,8 (23.9, 25.5)	23,46 (21.5, 25.3)	20,63 (19.6, 21.6)	14,85 (14, 16.1)	9,3 (8.7, 9.9)	5,7 (4.9, 6.7)
2,4	6,37 (4.8, 7.3)	7,23 (5.8, 8.4)	9,86 (8.5, 10.7)	12,66 (11.3, 13.5)	16,4 (14.6, 17.8)	20,56 (19.0,22.2)	24,65 (24.0, 25.8)	24,15 (22.9, 25.2)	20,55 (18.7, 21.9)	15,37 (13.4, 16.6)	9,64 (8.4, 10.5)	6,39 (5.2, 6.9)
2,5	5,52 (4.0, 6.4)	6,35 (4.5, 7.6)	8,9 (7.1, 9.9)	11,65 (9.7, 12.7)	15,27 (12.9, 16.8)	19,47 (16.8,21.4)	23,73 (21.6, 25.2)	23,22 (21.1, 24.7)	19,43 (17.2, 20.9)	14,25 (12.2, 14.7)	8,77 (7.3, 9.5)	4,73 (4.4, 6.4)
2,6	6,17 (5.1, 7.5)	7,15 (6.2, 8.1)	9,66 (8.7, 11.0)	12,47 (11.5, 13.7)	16,34 (15.1, 17.5)	20,67 (19.2,21.7)	24,63 (23.5, 25.4)	24,15 (23.0, 24.9)	20,45 (19.2, 21.3)	15,16 (13.9, 16.7)	9,37 (8.5, 10.7)	6,24 (5.5, 7.1)
3,1	3,28 (2.8, 3.5)	3,8 (3.2, 4.1)	6,2 (5.6, 6.5)	8,04 (7.4, 8.4)	11,28 (10.6, 11.7)	14,85 (14.2,15.3)	17,7 (17.0, 18.1)	18,05 (17.4,18.4)	15,86 (15.2, 16.2)	11 (10.4, 11.3)	6,51 (6.1, 6.8)	4,19 (3.8, 4.4)
3,2	1,73 (1.6, 1.8)	0,78 (0.3, 1.2)	3,48 (3.0, 3.9)	3,93 (3.1, 4.7)	8,08 (7.3, 8.8)	10,9 (9.8, 11.9)	15,33 (14.3, 16.3)	15,6 (14.7, 16.4)	12,85 (12.2, 13.5)	8,3 (7.8, 8.8)	3,3 (2.9, 3.7)	0,2 (-0.2, 0.6)
3,3	2,24 (0.9, 3.4)	2,85 (1.7, 4.2)	5,75 (4.5, 7.2)	8,03 (7.3, 9.7)	11,81 (9.8, 13.4)	16,09 (13.7, 17.8)	19,46 (16.7, 21.1)	19,14 (16.4, 20.8)	16,02 (13.6, 17.6)	10,52 (9.3, 12.0)	5,75 (4.5, 7.0)	2,99 (1.4, 4.2)
3,4	2,26 (-0.2, 6.7)	2,94 (0.0, 7.2)	4,82 (0.0, 8.7)	7,24 (2.0, 10.7)	11,36 (6.1, 14.6)	15,47 (11.3, 18.6)	19,34 (14.2, 23.2)	18,93 (13.7, 22.7)	15,56 (11.9, 19.2)	10,31 (6.9, 14.0)	5,12 (1.2, 9.7)	2,43 (-1.4, 7.0)
3,5	2,87 (1.1, 3.8)	3,63 (1.3, 4.8)	5,65 (3.8, 7.5)	7,85 (5.8, 9.9)	11,65 (9.6, 13.7)	15,8 (13.6, 18.0)	19,65 (17.5, 22.1)	19,45 (17.2, 21.7)	15,85 (13.7, 18.0)	10,8 (8.9, 12.7)	6,43 (4.4, 7.5)	3,3 (1.5, 4.5)
3,6	2,79 (1.3, 4.9)	3,45 (1.7, 5.4)	6,28 (4.2, 8.6)	8,67 (6.3, 11.2)	12,05 (10.1, 14.6)	16,2 (14.2, 18.0)	20,87 (18.0, 23.3)	20,36 (17.6, 22.8)	16,12 (14.2, 18.5)	11,06 (9.2, 13.7)	6,34 (4.5, 8.6)	3,1 (1.6, 5.0)
3,7	3,73 (2.3, 5.3)	4,47 (2.9, 6.7)	7,19 (4.8, 9.6)	9,86 (7.3, 12.5)	12,96 (10.8, 15.6)	17,1 (14.7, 20.5)	22,57 (19.4, 26.2)	21,99 (18.9, 25.5)	17,14 (15.2, 20.6)	11,94 (10.2, 14.6)	7,33 (5.4, 9.3)	4,1 (2.6, 5.6)
3,8	4,67 (2.9, 5.9)	5,57 (3.3, 7.0)	8,24 (6.4, 9.8)	11,03 (9.0, 12.7)	14,24 (11.4, 16.2)	18,23 (15.2, 20.4)	24,28 (22.1, 26.0)	23,85 (21.4, 25.4)	19,25 (15.7, 21.4)	13,53 (10.7, 15.3)	8,59 (6.8, 9.5)	4,87 (3.1, 6.1)
4,1	3,89 (3.2, 6.2)	4,67 (3.9, 6.9)	6,81 (6.0, 8.6)	8,58 (7.2, 10.1)	11,84 (10.5, 13.6)	15,5 (13.9, 16.4)	18,28 (16.8, 19.3)	18,23 (16.7, 19.2)	16,24 (15.2, 17.1)	11,81 (11.1, 13.5)	7,21 (6.5, 9.0)	4,74 (4.0, 6.7)
4,2	0,2 (-0.2, 0.8)	0,97 (0.5, 1.7)	3,83 (3.3, 4.7)	5,97 (5.4, 6.9)	8,93 (8.4, 9.8)	12,73 (12.1, 13.7)	15,67 (15.1, 16.5)	15,4 (14.9, 16.2)	12,73 (12.2, 13.6)	8,63 (8.2, 9.4)	4,07 (3.7, 4.7)	1,1 (0.8, 1.6)
4,3	1,33 (0.5, 5.2)	2,17 (1.0, 6.1)	4,96 (3.9, 7.9)	7,01 (6.0, 9.4)	10,09 (9.0, 12.5)	13,88 (12.7, 15.7)	16,86 (15.8, 18.2)	16,58 (15.6, 18.2)	14,02 (12.9, 16.2)	9,74 (8.7, 12.5)	5,21 (4.0, 8.3)	2,04 (1.1, 5.9)
4,4	2,17 (1.1, 3.5)	2,84 (1.6, 4.4)	5,29 (4.1, 6.4)	6,45 (3.4, 8.4)	9,17 (4.5, 11.4)	13,05 (8.1, 15.5)	16,13 (12.6, 18.3)	15,78 (11.4, 17.9)	14,3 (13.3, 15.0)	9,87 (8.9, 10.9)	5,57 (4.1, 7.3)	3,66 (1.1, 8.9)
4,5	4,47 (4.3, 4.7)	5,37 (5.2, 5.6)	7,2 (7.0, 7.4)	7,7 (6.0, 8.7)	10,1 (6.8, 11.9)	13,47 (10.6, 15.0)	16,17 (13.4, 17.6)	16,07 (13.1, 17.6)	15,43 (14.9, 15.8)	11,63 (11.2, 12.0)	7,8 (7.7, 8.0)	6,7 (5.2, 9.3)
4,6	4,1 (3.2, 4.9)	4,85 (4.2, 5.6)	7,6 (7.0, 8.5)	9,99 (9.4, 11.1)	13,36 (13.2, 14.8)	17,28 (17.3, 19.1)	20,92 (21.0, 23.1)	20,39 (20.5, 22.5)	17,12 (17.1, 18.6)	12,44 (12.0, 13.7)	7,37 (6.7, 8.4)	4,13 (3.4, 5.2)

group	pwin	pspr	psum	paut	py	twin	tspr	tsum	taut	ty
1,1	355,25	252,80	29,45	199,65	837,15	5,24	9,12	19,51	13,02	11,72
1,2	248,00	220,13	74,75	169,63	712,51	4,31	9,85	20,03	12,19	11,60
2,1	250,00	187,80	57,40	189,00	684,20	4,47	10,45	21,51	13,99	12,61
2,2	777,40	565,68	59,49	415,39	1817,96	8,01	12,16	20,56	15,21	13,99
2,3	265,33	207,66	46,16	181,82	700,97	6,04	11,97	22,86	14,93	13,95
2,4	429,35	333,63	60,90	349,89	1173,77	6,66	12,97	23,12	15,19	14,49
2,5	503,00	385,75	70,25	437,50	1396,50	5,53	11,94	22,14	14,15	13,44
2,6	448,10	295,29	57,40	353,64	1154,43	6,52	12,82	23,15	14,99	14,37
3,1	236,46	254,52	133,99	216,91	841,88	3,76	8,51	16,87	11,12	10,06
3,2	375,50	264,75	151,75	309,50	1101,50	0,90	5,16	13,94	8,15	7,04
3,3	152,72	173,06	122,72	158,61	607,11	2,69	8,53	18,23	10,76	10,05
3,4	274,43	234,07	96,68	245,93	851,11	2,54	7,81	17,91	10,33	9,65
3,5	239,00	207,26	115,00	237,00	798,26	3,27	8,38	18,30	11,03	10,24
3,6	278,50	228,25	68,93	248,57	824,25	3,11	9,00	19,14	11,17	10,61
3,7	386,00	341,57	65,00	443,14	1235,71	4,10	10,00	20,55	12,14	11,70
3,8	306,88	233,47	52,28	216,72	809,34	5,03	11,17	22,12	13,79	13,03
4,1	353,76	308,90	159,14	291,10	1112,90	4,43	9,08	17,34	11,75	10,65
4,2	364,33	310,00	139,00	320,33	1133,67	0,76	6,24	14,60	8,48	7,52
4,3	347,06	275,56	125,33	291,50	1039,44	1,84	7,35	15,77	9,66	8,66
4,4	866,33	588,20	227,40	676,00	2357,93	2,89	6,97	14,98	9,92	8,69
4,5	998,00	651,67	269,00	764,00	2682,67	5,51	8,33	15,23	11,62	10,18
4,6	332,11	255,68	64,11	274,16	926,05	4,36	10,32	19,53	12,31	11,63

Table 1.3. Annual and seasonal precipitation and mean temperatures of Spanish *Quercus pyrenaica* groups, extracted from the CCA. Numbers in the first column refers to the matrix and the relevés group of figures 1-4. Abbreviations are the combination of p, precipitation or t, temperature to: win: winter, spr: spring, sum: summer, aut: autumn, py: yearly precipitation and ty: mean annual temperature.

Results

As mentioned above, for the general biogeographic and bioclimatic description of forest we have used the Rivas-Martínez bioclimatic belts and biogeography sectorization typologies for the Iberian Peninsula (Rivas-Martínez et al. 2002).

MATRIX I: *Adenocarpo decorticantis-Quercetum pyrenaicae* and *Berberido australis-Quercetum pyrenaicae* (Fig. 1.1, Tables 1.2, 1.3)

Supramediterranean deciduous oak forest of Nevadense and Subbetic sectors (Betic subprovince), respectively.

These communities form mountain forests in Sierra Nevada and Sierra de Cazorla in elevations above 1200 m. The sample plots had a maximum altitude of 1800 m. in Sierra Nevada and 1350 m in Sierra de Cazorla. They are the southernmost mountain forests in Spain, since Sierra Nevada and the nearby mountains are the only areas in southern Spain with sufficient altitude for this kind of forest. Cazorla is a calcareous range so this forest appears in limited areas where soils have leached the highest proportion of calcium.

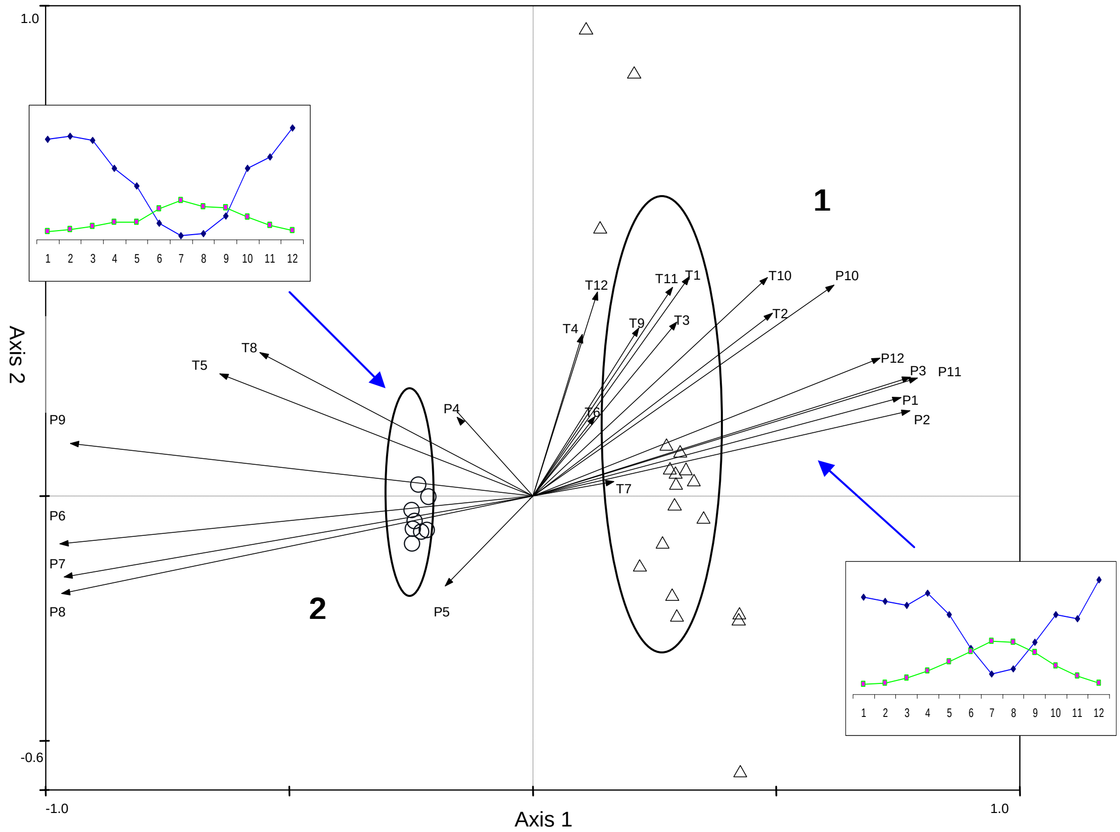


Figure 1.1. CCA of Matrix I of *Quercus pyrenaica* relevés and its corresponding climatic matrix. Diagram shows the two first axis (eigenvalues for axis 1 and 2: 0.7019, 0.4734). Open circles correspond to *Berberido-Quercetum*; open triangles to *Adenocarpo.-Quercetum*, see text for explanations.

The CCA (Fig. 1.1) shows separation of relevés along the first axis based on rainfall: summer (P6, P7, P8) or late summer rainfall (P9), together with mean monthly temperature in May and August (T5, T8) separates the *Berberido-Quercetum* forest in the negative part of the diagram. The positive part shows *Adenocarpo-Quercetum* relevés separated by winter precipitation (P12, P1, P2) and early spring or late autumn precipitation (P3, P10, P11). Autumn, winter and some spring temperatures (T1-T4, T9-T12) also serve to separate these forests. Following these results *Adenocarpo-Quercetum* receives more precipitation in winter than *Berberido-Quercetum*, but less precipitation in summer, even in September (P9) when soil water content begins to refill. Late spring (May, T5) and late summer (August, T8) temperatures also show differences *Adenocarpo-Quercetum* sites are almost three degrees Celsius cooler than *Berberido-Quercetum* sites.

MATRIX II: *Arbuto unedonis-Quercetum pyrenaicae* and *Luzulo baeticae-Quercetum pyrenaicae* (Fig. 1.2, Tables 1.2, 1.3). Mesomediterranean deciduous oak forest of Toledan-Taganean, Marianic-Monchiquensean sectors (Lusitan-Extremadurean subprovince, Mediterranean western Iberian province) and Gaditan-coastal Onubensean sector (Gaditan-Algarvian subprovince, coastal-Lusitan-Andalusian province).

Matrix characterized by the presence in the herb layer of not only *Querco-Fagetea* species with high cover values, but also by species from evergreen oak forests (*Quercetea ilicis*). They appear in altitudes between 500-900 m.a.s.l. in the central-western and southern Iberian Peninsula. We have differentiated six groups in the CCA which show good separation along the two first axes; Group 1 in the most positive part of axis 1 includes relevés from Sierra Madrona (Toledo) showing lower temperatures and precipitation than the rest. This group is formed by five relevés, three of them were adscribed to *Genisto tournefortii-Quercetum* by Rivas Goday (1964), now synonymized to *Sorbo torminalis-Quercetum* (Rivas-Martínez et al. 2002), however we wanted to include them in this matrix since they have a similar altitude than others relevés, from the same locality and in the same paper, adscribed by the author to *Arbuto-Quercetum* (the other two relevés that appear in group 1).

Group 2, with *Luzulo baeticae-Quercetum* relevés is very well segregated along the most positive part of the second axis, due to the higher winter rainfall and also to the warmer temperatures in the same season. The remaining groups belong to *Arbuto-Quercetum* and are split in the diagram, showing a gradation from the drier sites of Sierra Madrona to the more humid sites of the Tiétar valley. We have separated them into 4 groups: group 5 includes four sites from the Tiétar valley and Sierra de Gata that show higher precipitation records throughout the whole year, although with the most pronounced difference in summer (mostly in July, usually the driest month in most Mediterranean territories). This group is also the coolest of the *Arbuto-Quercetum* groups. Groups 4 and 6, which include most of *Arbuto-Quercetum* sites, have very similar temperatures and precipitations; the only difference appears in winter precipitation, which is higher in group 6. Finally, group 3 is separated from the others in terms of dryness with a difference in annual precipitation of 900-1300 mm. Temperature is, however, similar although the mean thermal amplitude is 1°C higher than the more typical groups 4 and 6.

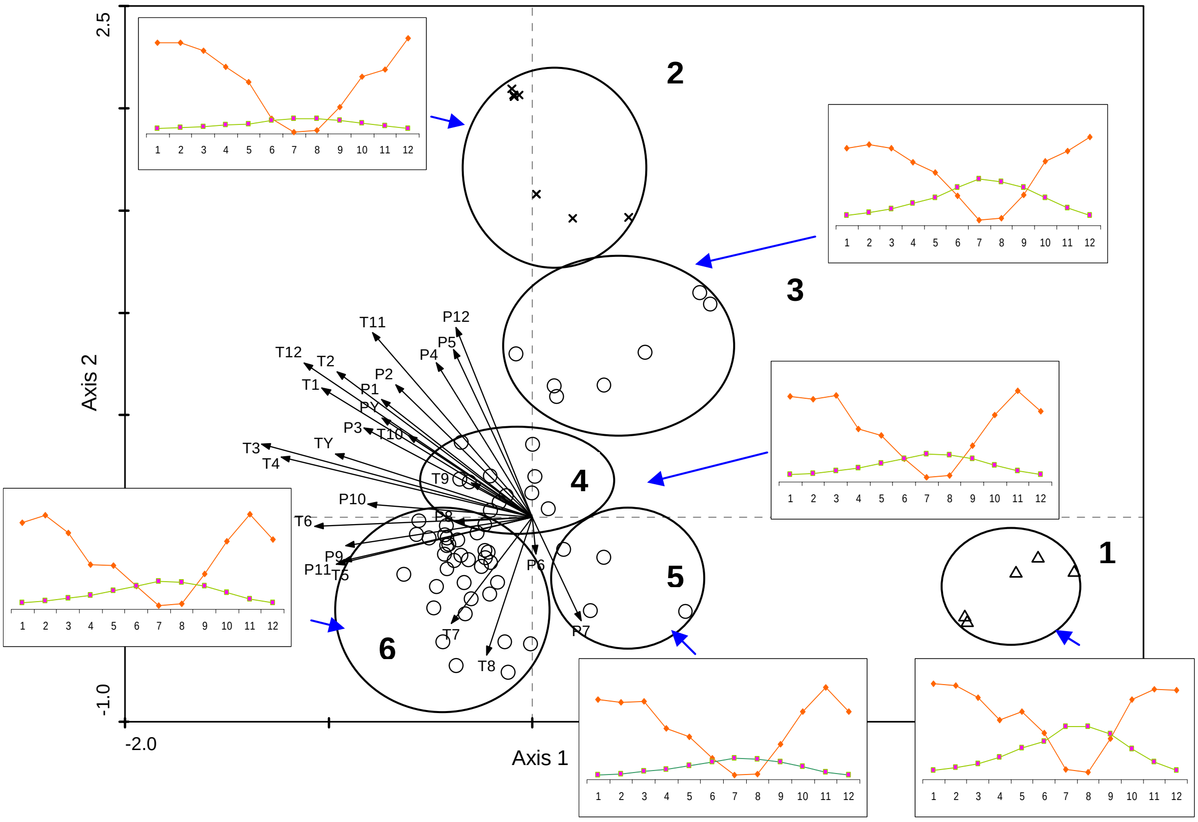


Figure 1.2 CCA of Matrix II of *Quercus pyrenaica* relevés and its corresponding climatic matrix. Diagram shows the two first axis (eigenvalues for axis 1 and 2: 0.3828, 0.3397). Open circles correspond to *Arbuto-Quercetum*, open triangles to *Sorbo torminalis-Quercetum* and x-marks to *Luzulo baeticae-Quercetum*, see text for explanations.

Matrix III: *Luzulo forsteri-Quercetum pyrenaicae* s.l., *Pulmonario longifoliae-Quercetum pyrenaicae* and *Sorbo torminalis-Quercetum pyrenaicae* (Fig. 1.3, Tables 1.2, 1.3). Supramediterranean deciduous oak forest of Guadarramean, Bejarano-Tormantino and Ayllonense subsectors (Carpetan-Leonese subprovince, Mediterranean west Iberian province), that reach the OroIberian subprovince (Mediterranean west Iberian province). The third association extends to the Toledan-Taganean and Marianic-Monchiquensean sectors (Lusitan-Extremadurean subprovince). They are found between 1000-1500 m.a.s.l.

The first axis of the CCA (Fig. 1.3) shows separation by summer precipitation, with groups that receive more amount of rainfall appearing on the right of this axis. The second axis shows separation by temperature records, mainly in winter, so those relevés withstanding lower temperatures in winter appear in the upper part of the figure. The CCA shows separation of the two *Pulmonario-Quercetum* groups (1 and 2) from the rest; however they also are clearly separated one from the other, and group 1 appears in the lower right corner of the graph. It has more annual rainfall than 2 (about 400 mm more) and includes a set of relevés from Burgos province.

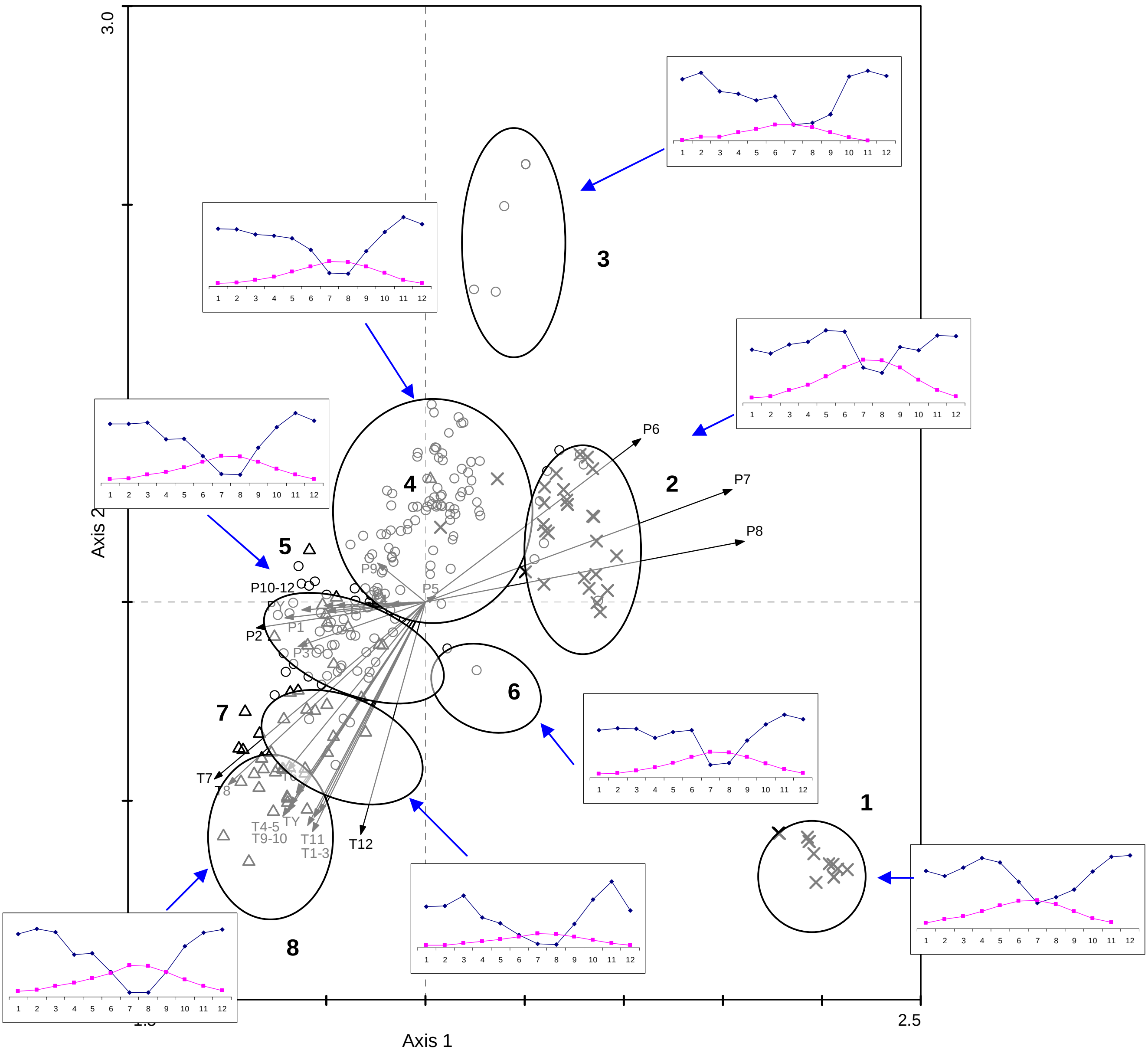


Figure 1.3. CCA of Matrix III of *Quercus pyrenaica* relevés and its corresponding climatic matrix. Diagram shows the two first axis (eigenvalues for axis 1 and 2: 0.4657, 0.3730). Open circles correspond to *Luzulo-Quercetum*, open triangles to *Sorbo torminalis-Quercetum* and x-marks to *Pulmonario-Quercetum*, see text for explanations.

The *Sorbo-Quercetum* forest (group 8) results separated in the lower left corner of the graph are mainly based on higher temperatures throughout the whole year, with differences in winter temperatures of between 1ºC and 4ºC from the other groups. In the case of *Luzulo-Quercetum*, relevés are separated into five groups, following a climatic gradient from the very cold areas of the northern Castilian plateau to the most humid, mainly in winter, areas of Sierra de Guadarrama and Gredos. Thus group 3 shows the lowest temperatures in the whole data set, while groups 6 and 7 show warmer temperatures in the *Luzulo-Quercetum* groups since the relevés are from altitudes lower than 1000 m.a.s.l. in the Sistema Central or on southern exposures when at slightly higher altitudes. Finally, group 4 includes relevés from Sistema Central over 1000 m.a.s.l.

MATRIX IV: *Holco mollis-Quercetum pyrenaicae*, *Genisto falcatae-Quercetum pyrenaicae* (incl. *Pyro cordatae-Quercetum pyrenaicae*), *Linario triornithophorae-Quercetum pyrenaicae* and *Melampyro pratensis-Quercetum pyrenaicae*. (Fig. 1.4, Tables 1.2, 1.3). Supramediterranean deciduous oak forests of Lusitan-Duriense, Bercian-Sanabriense and Leonese sectors (west Iberian Mediterranean province, Carpetan-Leonese subprovince), reaching the Eurosiberian region (Cantabrian-Euskaldún sector, Cantabrian-Atlantic subprovince, European Atlantic province) and OroCantabrian subprovince.

The first axis of the CCA (Fig. 1.4) shows low correlations of climatic variables. Among precipitation variables, only July and June precipitation show the highest correlations (around 0.3, see the magnitude of arrows in figure 1.4). Temperatures show higher correlation than precipitation, being summer variables (T7, T8) the only that account for higher correlation values (around 0.5). Looking at this, it is difficult to interpret the separation of groups along this axis. The second axis shows separation in terms of temperature, mainly in winter, but also throughout the rest of the year, and the magnitude of the arrows is sufficient to explain the separation of groups.

Melampyro-Quercetum forest (group 1) is split from the nearest groups (3-5) in the most positive part of the first axis of the CCA, however this separation is difficult to interpret, as it has been explained above: summer precipitation in Group 1 is higher than in group 3, but lower than in 4 or 5, being these two groups the most humid of the dataset (see tables). Mainly summer but also spring temperatures are higher in group 1 than in groups 3, 4 or 5. *Linario-Quercetum* is separated into two groups (2 and 3) in the upper part of the diagram, showing a high variability, from drier localities (group 3) to those with colder winters (group 2). Group 2 is colder in winter, but wetter in summer and autumn than group 3. However there are a few relevés of *Linario-Quercetum* that are split into groups 4 and 5, together to other relevés adscribed to *Genisto-Quercetum* and *Holco-Quercetum*. They are found in León and southern Galicia and they have the highest records in precipitation, as mentioned above. Group 6 represent *Genisto falcatae-Quercetum* and *Holco-Quercetum* relevés from Sierra de Gata and Peña de Francia localities (Sistema Central). They are the warmest and the driest of the whole dataset.

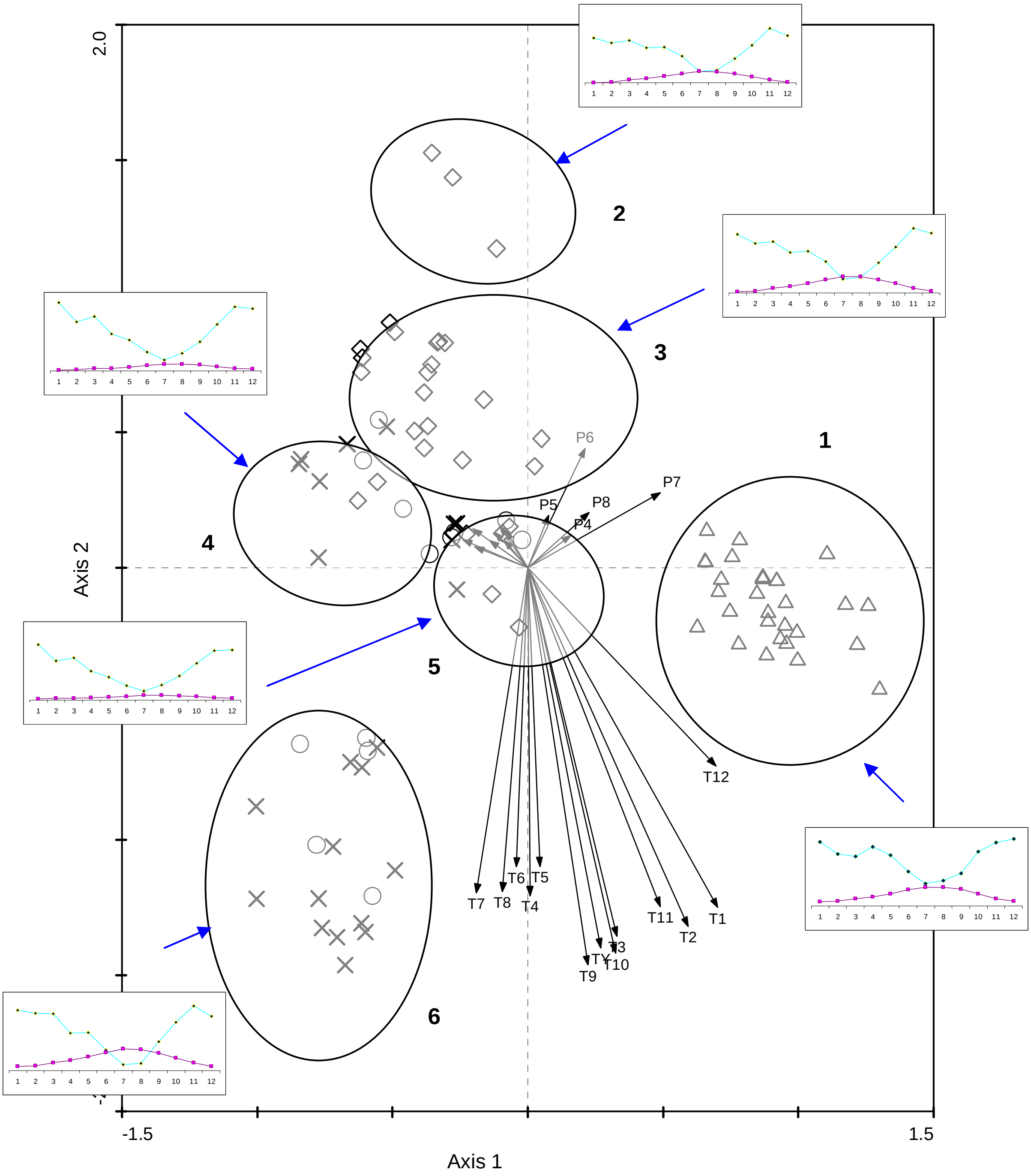


Figure 1.4 CCA of Matrix IV of *Quercus pyrenaica* relevés and its corresponding climatic matrix. Diagram shows the two first axis (eigenvalues for axis 1 and 2: 0.4486, 0.4228). Open circles correspond to *Holco-Quercetum*, open triangles to *Melampyro-Quercetum*, x-marks to *Genisto falcatae-Quercetum* and open squares to *Linario-Quercetum*, see text for explanations. Arrows in the upper left part of the diagram correspond to PY, P10-P3.

Discussion

Quercus pyrenaica forests are a type of potential vegetation which is very widespread in Spain, although intense management in the form of cutting, fires or grazing have caused them to disappear in many places. In spite of this, we have collected enough relevés to be able to infer climatic data from their basic geographical information. According to the current typologies on bioclimatology, most of them are situated in the supramediterranean belt, as mountain forests (over 1000 m.a.s.l), since dryness in the Mediterranean region makes them unsuited to growing at lower altitudes. They also appear in western Mediterranean areas in altitudes of around 500 m.a.s.l., owing to the westerly winds exposure, which usually bring the greatest amount of water to the Iberian Peninsula, mostly in winter. They may also appear in the Eurosiberian region, but less frequently, since other oaks or even *Fagus sylvatica* occupy the same areas. It is also important to remember that the actual climatic pattern of *Quercus pyrenaica* forest is not the unique source to interpret the floristic pattern, but also historic events, like climatic changes during the Holocene, fluctuations of the vegetation belts or refugia of these forests, should be also taken into account.

The two main climatic features of Mediterranean territories are summer dryness and rainfall concentration in winter (Emberger, 1954, Nahal, 1981, Box, 1987) and our analyses show separation of vegetation following these climatic patterns, as in the case of the Andalusian forest. Although Andalusia is generally thought to be a very dry region, it includes territories like the Sierra de Cazorla which is one of the rainiest areas in Andalusia, together with the mountains of the Sierra de Segura (near the Sierra de Cazorla), Cádiz and Málaga, most of which are on basic substrata. *Quercus pyrenaica* forests only occur in particular areas of the Sierra de Cazorla (surroundings of Madera river) due to leaching of the carbonate existing in the soils (Rubio & Escudero, 2005), otherwise these forests would not appear.

Sierra de Cazorla sample sites (*Berberido-Quercetum*) are separated from those of Sierra Nevada (*Adenocarpo-Quercetum*) in terms of higher quantities of rain in summer (June to August), and even in September when the first rains come and the soils begin to refill after the summer, usually very dry. So the annual rainfall is more likely to also be higher. Together with some specific soil characteristics of the substrata, this fact should be one of the main causes for the appearance of *Quercus pyrenaica* in areas where it would never normally appear. *Adenocarpo-Quercetum* forests are separated in terms of winter precipitation;

winter is in many parts of the Iberian Peninsula (mostly in western areas but also the east) the rainiest season when soils are refilled.

Summer precipitation also appears in other analyses as separating vegetation types: in matrix III, it separates *Holco-Quercetum* forests from the rest. Summer in the central Iberian Peninsula is marked by a contrast between western and eastern territories: the western territories come under the influence of the Azores anticyclone which brings warm temperatures but also dryness; while in the east the Mediterranean Sea warms up during summer, which causes large quantities of seawater to evaporate, creating clouds which usually run inland where they discharge water. The vegetation responds accordingly, thus the floristic composition of *Pulmonario-Quercetum* is different from that of a closed forest such as *Luzulo-Quercetum.*

Another interesting feature is the particular exposure of some territories that define different types of vegetation. This is the case of Sierra Madrona, an east-west running range with two very different exposures giving rise to two types of forest: thermal forests (*Arbuto-Quercetum*) in southern exposures, and forests withstanding lower temperatures (*Sorbo torminalis-Quercetum*) in northern exposures but both with similar altitudes; both these types occur on drier sites than the other relevés in the analyses, but both groups are well separated from each other and from the rest of the relevés.

The separation of northern Iberian Peninsula forest is difficult and although groups of different forest types are separated by some monthly or annual temperature or rainfall parameters, the diagram (fig. 1.4) shows that the dimension and position of arrows does not clearly indicate a real climatic difference among groups. This is the case of the datasets of *Holco-Quercetum*, *Genisto falcatae-Quercetum*, *Linario-Quercetum* and *Melampyro-Quercetum*. *Holco-Quercetum* and *Genisto falcatae-Quercetum*, two northern Mediterranean associations, show no separation between them probably due to a similar floristic composition of their floristic dataset; this has been detected previously (Ladero et al. 2003). The Eurosiberian *Melampyro-Quercetum* forest is very well separated from the remaining groups, but shows a similar summer rainfall than the Mediterranean groups.

Some very widespread forests such as *Luzulo-Quercetum* or *Arbuto-Quercetum* have a very marked climatic gradation from one territory to another, highlighting the particularities of every territory. However as some overlap has been detected, further studies may be required.

The number of sites analyzed is sufficient to carry out a study of the characteristics we include. These models usually work with regression algorithms that tend to be sensitive to the accuracy of the basic data they use, in the form of data recorded in meteorological stations. Therefore the accuracy of the data provided by these models is the main drawback. In our case, this potential problem is eliminated due to the number of sites we have for every *Quercus pyrenaica* forest associations. There are other problem areas where the analysis does not work properly (such as the northern part of the Iberian Peninsula, see matrix IV), usually in areas which have very strong humang impact or where there is contact with a different forest type. In many cases it is difficult to obtain a complete floristic relevé and these forests are usually assigned to a particular phytosociological association according to altitudinal or biogeographical criteria. The ordination of those relevés show proximities in their floristic composition, and more phytosociological data are therefore necessary to obtain the required accuracy for determining their climatic features from these models.

Acknowledgements

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CAPÍTULO II / CHAPTER II

Chapter II: Indicator species of broad-leaved oak forests in the eastern Iberian Peninsula.

Abstract

The degraded state, scattered distribution and substrate type of *Quercus pyrenaica* forests in eastern Spain make them a subject of particular interest, as well as a priority for conservation efforts. An extension of Dufrêne & Legendre's indicator value (IndVal) analysis was applied to one hundred relevés. This extension of the IndVal method allowed us, by considering the preference of species for combinations of relevé groups, to obtain those species that represent local, but also regional, characteristics (as a new practical use). Our objective was to identify the species that best indicate the main ecological features of these broad-leaved oak forests. The usefulness of our analysis was evidenced at two levels: local indicator species, showing the characteristic species of individual sites and including the presence of endemics in the area; and indicator species of combinations of two or more sites, reflecting the affinities or relationships between these scattered forests.

Most singular forests showed a higher number of local indicator species. The indicator species of each site combination represent the main ecological traits shared by these groups –such as proximity to the coast, land uses or postglacial migration pathways– thereby defining their relationships. Indicator value analysis with site group combinations (*Multipatt* function) proved to be a useful tool for the identification of different species that could serve both to determine the local forest conservation status and aid in its preservation, as well as contributing to an understanding of the life history of larger territories.

Keywords: *Multipatt* function, indicator species analysis, conservation, *Quercus pyrenaica eastern* forest.

Introduction

The *Quercus pyrenaica* forests in eastern Spain are remnants of the broad masses that occupied the peninsula in cooler eras and are now found predominantly in the northwest. These forests are therefore unique examples of sub-Mediterranean broad-leaved forests in this area, with an additional special feature: their substrate, which comprises Buntsandstein sandstones and rodenas surrounded by limestone. This uniqueness makes them prime targets for conservation. In many cases, habitat fragmentation has gradually reduced the quality and extent of these scattered forests, mainly due to grazing and felling for charcoal manufacture or to favour other forest species such as pine (Calvo et al. 1999). The impact of these disturbances in eastern Spain has been particularly severe, as forest regeneration is not straightforward in this area (Pulido et al. 2002). Thus there is an urgent need for prompt action to understand their main ecological traits, together with the species range that best defines their particularities. Indicator forest species take on key interest when discussing the conservation status of forests, since they reflect their life history (MacNally & Fleishman 2004). The close relation they show with the different aspects of the habitat makes them useful tools for a range of purposes, since they can be used as indicators of diversity, richness, and disturbance (McGeoch 1998).

Today, there is an even greater need in both conservation and management for detailed knowledge of key species and their autecology (Rubio et al. 2011). According to Grumbine (1994), three of the main goals in ecosystem conservation and management are the maintenance of native species, the protection of representative examples of native ecosystems, and the adaptation of human activities to these principles. The identification of native species and ecosystems, community types and traditional land uses therefore becomes an issue of vital importance for the preservation of an ecosystem, especially when communities are isolated from each other and surrounded by a more or less hostile environment. In this regard, Dufrêne & Legendre (1997) developed a methodology to identify indicator species, assuming that for a species to be an appropriate indicator of a given target type (e.g., a habitat type, environmental state or a community type), most of its occurrences should be concentrated in the target type, as well as being present with a certain frequency. The aim of the present study was to determine a set of species that best indicated the different environmental influences or features of the ecological mosaic of territories, such as land use, scattered distribution, altitude or substrate type. Since we needed a method that made it possible to obtain this wide range of information, we chose a recent modification of Dufrêne & Legendre indicator species analysis (De Cáceres et al. 2010). This modification allows the determination – by analysing each site separately as well as in combination – of a set of both local and shared floristic indicators. The specific questions we addressed were: What are the indicator species of these *Quercus pyrenaica* forests? What do they indicate? Which of them are common species to these scattered forests? As original *Quercus pyrenaica* forests are described growing on purely siliceous soils, could this tool find species that indicate changes in substrate type?

Materials and Methods

Study area and data gathering

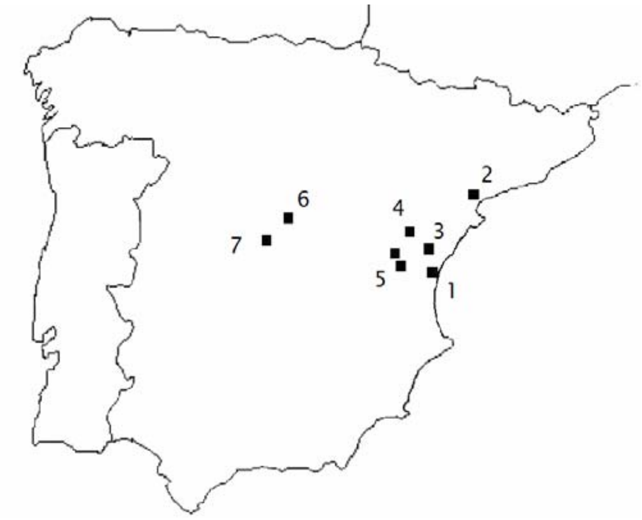

Figure 2.1. Location of Quercus pyrenaica forest studied: 1. Sierra de Espadán (pre-coastal Castellón Massif), 2. Sierra de Prades; 3-5. Sistema Ibérico: 3. Penyagolosa Massif (Inner Castellón province), 4. Albarracín Massif (Tremedal), 5.Serranía de Cuenca (two localities: Boniches and Ranera); Sistema Central: 6. Ayllón Massif, 7. Guadarrama Massif.

We focused our study on the *Quercus pyrenaica* forests in the eastern Iberian Peninsula (Fig.2.1), and collected 100 floristic relevés (i.e. the list of species, along with an estimate of their cover values, found within an explicit plot, which in these forests is usually above 100 m^2) (Braun-Blanquet, 1932). Relevé data are normally presented in a relevé-by-species matrix, which we summarize in Table 1. Located at altitudes of between 950 and 1700 m, these oak forests persist in three different mountain ranges (fig. 2.1): the pre-coastal ranges of Sierra de Espadán (1) and Sierra de Prades (2), and the inner Sistema Ibérico range (including 4 localities: Penyagolosa (3), Albarracín (4) and Cuenca (5)

(Boniches and Ranera) massifs. Each locality (site) is therefore represented by a group of relevés (Table 1).

Although soils in the eastern part of the Iberian Peninsula are predominantly calcareous, our forests are mainly located on sites with a special kind of siliceous soil known as Triassic rodenas (Buntsandstein sandstones and argillites). As some influence of surrounding calcareous soils can be expected on the flora, data from forests growing on purely siliceous substrata (granite and gneiss) in the Sistema Central range (central Iberian Peninsula) were included, in order to control for floristic differences due to substrate type. We therefore considered two additional massifs (sites) –Ayllón (6), and Guadarrama (7) (Fig.2.1)–, and their corresponding relevés, for this purpose.

Num.	Abbr.	Locality	Province	D. coast	Altitude	N. relevés	% excl. spp.
1	E	Espadán	Castellón	35 km	900-1106	15	43.94
2	Pr	Prades	Tarragona	27 km	950-1050	6	40.31
3	P	Penyagolosa	Castellón	58 km	1250-1500	10	26.26
4	Al	Albarracín	Teruel	235 km	1500-1700	9	28.77
5	B	Boniches	Cuenca	170 km	1000-1200	4	15.38
	R	Ranera		120 km	1280-1380	4	20.45
6	Ay	Ayllón	Guadalajara	430 km	960-1350	8	17.07
7	G	Guadarrama	Madrid	480 km	1170-1500	43	47.65

Table 2.1. Summary of locations studied. For every location the information presented is: the number assigned to every locality in Figure 1 (Num.), Abbreviation (Abbr.), Spanish political division (Province), distance to the coast (D. coast), altitudinal range (Altitude), data gathering (N. relevés), and percentage of exclusive species per forest (% excl. spp.).

Statistical analysis

We first used Principal Components Analysis (PCA) on the relevé-by-species matrix containing presence-absence values, in order to display the compositional variation among the *Quercus pyrenaica* woodlands in the study area. Given a relevé-by-species matrix and a classification of the relevés into groups, the Indicator Value (IndVal) index was defined by Dufrêne & Legendre (1997) as the product of two components: A_{ij} and B_{ij}; where A_{ij} is a measure of species i specificity or positive predicting value as an indicator of the relevé group j; and B_{ij} is the probability of finding the species when the relevé belongs to the relevé group j (De Cáceres & Legendre 2009). As ecological niches cannot normally be reduced to closed compartments, De Cáceres et al. (2010) extended the Indicator Value method to cope with the variation of species niche breadth. Specifically, they extended indicator value analysis by considering all possible combinations of relevé groups (i.e., combinations of sites in our case) and selecting the combination for which the species can best be used as an indicator. The analysis produces the set of indicator species significantly associated to each relevé group or relevé group combination. Among these, we selected those species with IndVal value greater than 0.5 (i.e. the most constant and specific species). Thus, only species which were frequent and also statistically significant were shown as representative of site or site combinations ("shared differential species", Willner et al. 2009).

Indicator value analyses were performed using the *'multipatt'* function of the R package 'indicspecies', using IndVal as the statistical index. To control for the effects of using relevé groups of unequal size, the sum of the mean overall groups in its *A* component was included, following the recommendations of De Caceres & Legendre (2009). Only presence-absence values were used in these analyses. The use of presence / absence data implies that the indicator species obtained are specific and frequent, but not dominant, and are diagnostic on their own “not only when exceeding a certain cover value” (Willner et al. 2009). The low weighting of rare species that characterizes IndVal is also reduced with presence-absence data (De Cáceres & Legendre 2009). In our indicator value analyses we assumed that initial groups (sites) were floristically homogeneous. In order to check that the compositional variation within each site was not excessively high, we calculated the beta diversity of its corresponding group of relevés, using the beta-diversity index suggested by Legendre & Peres-Neto (2005). Specifically, we transformed our values using the chord transformation (Legendre & Gallagher 2001), and then calculated the overall variation for each group of relevés. Multivariate centroids were also calculated in order to confirm the floristic proximity between sites.

In this paper we suggest using the number and identity of the indicators to determine how different geographical locations could be related, and the autoecology of the representative species of site combinations to identify shared environmental characteristics.

Results

Together, the first two PCA axes explained 22.1% of the total variance (Fig. 2.2). This low percentage can be understood in terms of a wide ecological gradient, thus indicating the floristic heterogeneity of the relevé data. The first axis separated the pre-coastal relevés with the lowest altitudes in the whole set – Sierra de Espadán (downward triangles) – in the most positive part of the diagram, from the rest. Sistema Central relevés – Guadarrama (solid circles) and Ayllón (upward triangles) massifs – are in the negative part, whereas the remaining relevés are in the middle. The second axis separated the Guadarrama massif (solid circles) and Sierra de Espadán (downward triangles) in its negative part, whereas the rest of the eastern relevés appeared in the positive part. Thus, the first PCA axis could be interpreted as a continentality gradient, with relevés from the central Iberian Peninsula as the most continental; while the second axis could be related to a summer humidity gradient, with the relevés with shorter or compensated summer drought located in the positive part.

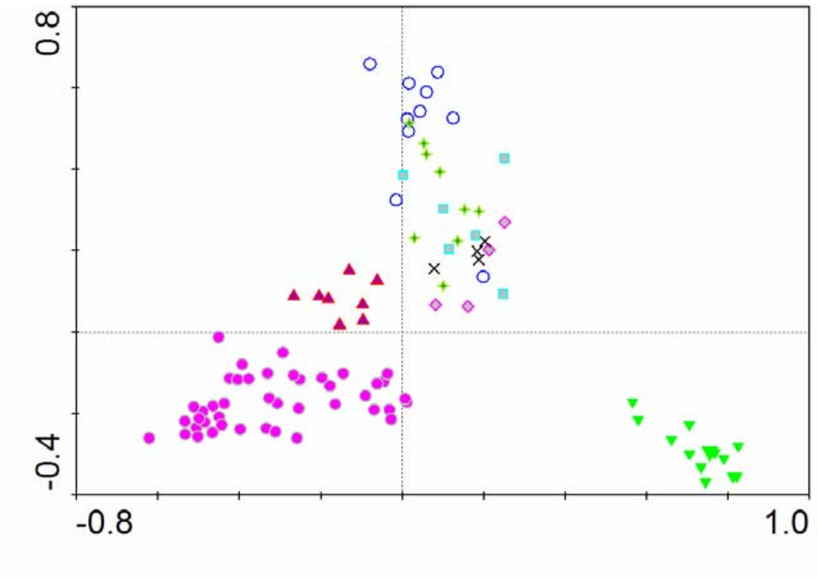

Figure 2.2 Principal Component Analysis of eastern Quercus pyrenaica forests: Sierra de Espadán (Downward triangles), Sierra de Prades (Solid boxes); Sistema Ibérico: Penyagolosa (Open circles), Albarracín Massif (Stars) & Serranía de Cuenca: Boniches (X-marks), Ranera (Diamonds); Sistema Central: Ayllón (Upward triangles), Guadarrama (Solid circles).

Site indicator species

The *multipatt* function produced, on a first level, the species which are representative of individual sites (see Appendix 2.1):

Sierra de Espadán: this site obtained the highest number of indicator species in the whole set. Its northwest-southeast orientation favours the retention of rainfall associated with easterly (Levante) winds, producing summers with reduced drought. Its proximity to the coast also causes warm winters, and allows the inclusion of frost-sensitive species. These factors have permitted the development of a *Quercus pyrenaica* forest in altitudes that are generally not suited to this species in the Iberian Peninsula. The indicator species that best characterize this forest are endemics such as *Minuartia valentina*, some of which – like *Biscutella calduchii* – are silicicolous, and others – such as *Helianthemum marifolium* subsp. *molle* – are calcareous. Serial thermophilous shrubs such as *Ulex parviflorus* subsp. *parviflorus* are also significant indicators of this locality, while *Quercus suber*, a tree that forms part of the canopy layer, was also appointed as indicator species.

Sierra de Prades: this was the northernmost locality studied, and had the highest percentage of species with a temperate distribution. Twelve species were selected as indicators, with *Euphorbia amygdaloides* and *Campanula persicifolia* as the most important, both of which are common species in beech forests. In contrast, heliophilous herbs (*Anthriscus sylvestris, Festuca marginata*), and serial shrubs such as *Cistus salviifolius* which were extracted as significant, highlight the open character of these forests.

Sistema Ibérico: on one hand, the Boniches massif in the Serranía de Cuenca showed a mixture of silicicolous and calcicolous indicators (i.e. *Quercus faginea*, see Appendix A), due to the favourable conditions of the Buntsandstein substrate (López 1976), in addition to endemics (*Thymelaea subrepens*). In contrast, the Ranera massif, also in the Serranía de Cuenca, is the only locality where annual and highly competitive species such as *Urtica dioica* appear as the main indicators, giving an idea of the degraded state of the forest.

In contrast, the Albarracín massif was represented by typical mountainous species, and also by plants with preferences for stony land such as *Leontodon hispidus* (see Appendix 2.1). The Penyagolosa massif – the coldest location in its area – was represented mostly by temperate species such as *Geranium sanguineum*, and also by species typical of temporarily flooded substrates such as *Rubus caesius*.

Sistema Central: the main indicator species of these forests were typical plants of the herb layer such as *Holcus mollis* or *Melica uniflora*, in addition to some shrubs such as *Cytisus scoparius*; all of them show a distribution in the north-western area of the Iberian Peninsula, where granite and schist are the most common substrata in this type of forest. The second massif, Ayllón, showed a lower number of indicator species, including humid grassland species, indicating its typical management as open forest (Fuente, 1985), but also suggesting the particular moisture supply of this area.

Indicator species of site-group combinations

The second kind of information obtained from the *multipatt* function concerned the species that are not specific to a single site but are associated to combinations of two or more sites that share ecological characteristics (see also Appendices 2.2 and 2.3).

We present these results in combinations of two sites, three sites, and so on, in consecutively combined sites (Table 2.2). The highest number of shared species appears at the level of two combined sites, with Prades and Boniches as the two sites which appear most frequently in combinations.

Prades was also the site with the highest degree of indicator species in its combinations with other sites. It shared a large number of indicator species mainly with Espadán, Penyagolosa and Albarracín (see Appendix 2.2), thus showing a high degree of relationship with these sites. These indicators express three main patterns in Prades: 1) the influence of the Mediterranean Sea (at approx. 27 km from the coast) represented by thermo-Mediterranean species in the combination Prades-Espadán, which are the most coastal massifs; 2) the moderately continental character of species corresponding to the combination Prades-Penyagolosa; and 3) the mountainous character of species selected in the combination Prades-Albarracín, also characterized by mesophytic grassland and typical species from the northern Sistema Ibérico.

The second site most frequently appearing in two-site combinations was Boniches (Table 3). Its floristic composition related this site to its geographically closest site, Ranera, through perennial and calcareous species belonging to pioneer communities *(Conopodium arvense*); but also to calciphilous species that have a central-European optimum, and link it with the Penyagolosa massif *(Cephalanthera rubra*, *Inula salicina)*. Forest fringe shrubs, such as *Genista florida* in what is probably its easternmost location – related Boniches with the Guadarrama massif.

Combinatory level	E	Pr	P	Al	B	R	Ay	G	Total indicator species
2 sites	3	6	3	4	6	3	5	4	32
3 sites	4	8	6	4	4	8	4	4	16
4 sites	3	4	7	6	4	4	5	3	9
5 sites	0	3	3	3	1	2	2	1	3
6 sites	0	2	2	1	2	2	2	1	3
7 sites	0	1	1	1	1	1	1	1	1
Total nº combinations	10	24	22	19	18	20	19	14	

Table 2.2 Number of combinations of each site inside each combinatory level and total number of combinations of each site group. Abbreviations in Table 2.1.

	E	Pr	P	Al	B	R	Ay	G
E		0.90	0.94	0.96	0.97	0.98	1.06	0.95
Pr	4		0.70	0.73	0.87	0.78	0.84	0.72
P	4	13		0.70	0.79	0.84	0.83	0.71
Al	2	10	13		0.81	0.86	0.78	0.73
B	4	7	9	7		0.88	0.89	0.84
R	3	12	9	8	10		0.89	0.83
Ay	2	8	8	9	5	9		0.65
G	1	7	7	4	4	4	9	

Table 2.3 Results extracted from Multipatt analysis. Lower left part: number of combinations between pairs of sites. Upper right part: distances between site-centroids. Abbreviations in Table 2.1.

Combinations of more than two groups were represented by no more than 32 species that generate a real division of the data. Based on our objective, we established three types of site combinations (Appendix C) according to the best differentiated groups in the PCA: combinations of any sites that occur with the Sistema Central, those that occur with Espadán, and those that do not relate to either:

- Species associated to combinations of the Sistema Central and other site groups were typical of dense cool oak forests such as *Poa nemoralis* or *Cruciata glabra*; open forest but with iberoatlantic preferences such as *Arenaria montana, Dactylis glomerata*; or those with their optimum in the temperate biome such as *Viola riviniana.*

- Species associated to combinations of Espadán and other site groups were thermophilous, in addition to those with humid atmosphere requirements such as *Hedera helix,* or calcareous requirements such as the Mediterranean shrub *Teucrium chamaedrys*, *Viola alba* or *Prunus spinosa.*

- Species associated to site combinations that did not include any of the former two sites tended to be representative of serial or degraded stages. Examples are species belonging to anthropogenic grasslands and meadows on deeper Eurasian soils such as *Arrhenatherum elatius* and *Trifolium pratense*. Prades, Penyagolosa and Albarracín include areas still in use for livestock feed. They are the most frequently combined sites in the whole set (see Table 2.3), indicating the high floristic affinity between these sites. Moreover, eastern relevés were more frequently combined with each other than with the Central or Espadán massifs. As seen in Table 2.3, the greater the number of combinations, the higher the floristic relationships among sites. The distance between multivariate centroids was generally in accordance with the results of *multipatt* function, but not always. Less frequently combined groups were not always the most distant in the species compositional space. An example of this is Ranera or Ayllón, which were the most distant from Espadán but obtained more significant combinations with it than with Guadarrama, which was much closer.

Above the level of four combined sites (Table 2.2) the number of statistically significant indicator species was considerably reduced, and due to their singularity some cases, such as Espadán, did not generate any combinations. Indicator species of more than four site combinations were species often related to land use or forest species present in the herb layer (nemoral species). This was the case of typical oak-forest or forest-edge species such as *Poa nemoralis* or *Clinopodium vulgare*.

Discussion

This study presents a new and interesting pratical use of indicator value analysis with combinations of relevé groups to study the floristic affinities between sites. Indeed, the use of the *multipatt* function in our dataset showed the wide variety of ecological traits that define or characterize each site through its indicator species (including local endemics or anthropogenic influences) but also gave an idea of its floristic affinities with other sites. These affinities can be interpreted environmentally and geographically as the result of common present (or past) shared ecological features between sites. Each site has shown its particular indicator species, including the presence of local endemics, or anthropogenic influences.

In the comparison between eastern and central forests, all the indicator species of the Sistema Central were mostly silicicolous plants. Species with more stringent requirements for moisture, and thus with north-western preferences, were also relegated here, and comprised mesophyllous vegetation occurring in the east (Cuenca, Espadán).

Different types of results gave different types of information:

a) Number of indicator species – A high number of indicator species for a given site gave an idea of its degree of uniqueness. A high number of indicator species relating a combination of sites may indicate that the ecological traits these species share is especially important as a descriptor of these sites, and also helps to distinguish these sites from others.

b) Number of combinations – The more floristically distinct a site is, the fewer indicator species were obtained for combinations of this site with others. The least frequently combined site was Espadán, precisely the only one that has a meso-Mediterranean character and a greater maritime influence, with species forced to adapt to post-glacial changes. At the other extreme was Prades (Catalan pre-coastal range), with twenty-four indicator species related to combinations of this site with others, showing the multiple influences that are grouped in this area, including land use and frequent fires. Most of its combinations occur with Penyagolosa and Albarracín (Sistema Ibérico); these are the three sites with the highest degree of floristic affinity. Several authors point to the role of these three mountain ranges as migratory vegetation routes in the postglacial period, highlighting Albarracín as a connection between the Iberian and Catalan pre-coastal ranges (Bolós, 1989). These affinities were also observed in the PCA (Fig. 2), with a differentiated set of relevés in the upper part (Penyagolosa, Albarracín and Prades), and also with the Espadán set standing in isolation at the right, in accordance with its specific character.

Implications for conservation

Espadán and Boniches were the locations with the highest number of endemics as indicator species, half of which are included on European red lists. The protection of species with restricted distribution is crucial, and these sites should therefore be preferential areas for conservation. Five of the seven sites also obtained indicator species included on lists of ancient forest species (Hermy et al. 1999). The presence *per se* of these species is not directly correlated with the degree of conservation of the forest, but indicates the vulnerability of the set due to the species' limited dispersal rate and their low competitive ability. Hermy et al. (1999) noted the difficulty of these species to regenerate, since many of them do not form a persistent seed bank. Furthermore, the isolation of these eastern forests – mainly of their temperate species – may hinder the complete recovery of the community, even in the case where the arboreal mass can be recovered. Pollen flow is quite low between isolated populations of small sizes, thus isolation decreases the genetic diversity of forest species, and consequently reduces their capacity to adapt to change (Honnay et al. 2005). The effect of anthropogenic disturbances on these forests is therefore more damaging, and makes their recovery harder.

We have shown different degrees of conservation, with grazing as the main land use observed. At least half the study sites have typical pastureland species in common (various authors confirm this use; Barrera (1983) also confirms the existence of peat lands in Albarracín), even though some are included in protected areas. Gómez-Aparicio et al. (2004) indicated herbivory as a major limiting factor of deciduous forest regeneration, given the preferential predation of these phanerophytes over evergreens. Hence control of herbivory in these locations would be of particular relevance to improving their forest quality and regeneration. Ranera is the most degraded site, with annual and highly competitive species as its main indicators. As *Quercus pyrenaica* forests are typically closed formations, a high number of nemoral indicator species could represent areas which continue to be more densely forested: Guadarrama, Prades and Boniches.

Conclusions

Determining species habitat preferences may be an objective in itself, but it is also a tool for achieving a better understanding of habitat ecological information (Dufrêne & Legendre, 1997). We emphasize the usefulness of indicator species analysis with site group combinations, not only for a better and more thorough understanding of our study areas, but also to make decisions about which sites should be preferential for conservation efforts. Furthermore, we have shown the wide variety of traits in the set of sites, which enables identification and preservation of the maximum amount of variability within this type of forest, as suggested by Mandelik (2010). This is an important point in relict forests such as these, which are unique and especially vulnerable to any change in climate and in management.

Through the chorology of their main indicator species, we have found the various traits that define each area (calcareous (Boniches, Ranera), thermophilous (Espadán) and sub-Mediterranean species (Penyagolosa, Albarracín, but also Prades)). In addition, floristic affinities (shown by the number of indicators related to site combinations) confirmed the differentiation of east-west Pyrenean oak forests defined by the siliceous character and high-Atlantic influence of the central group, and the entry of limestone species with a greater or lesser mesophilic character in the eastern forests.

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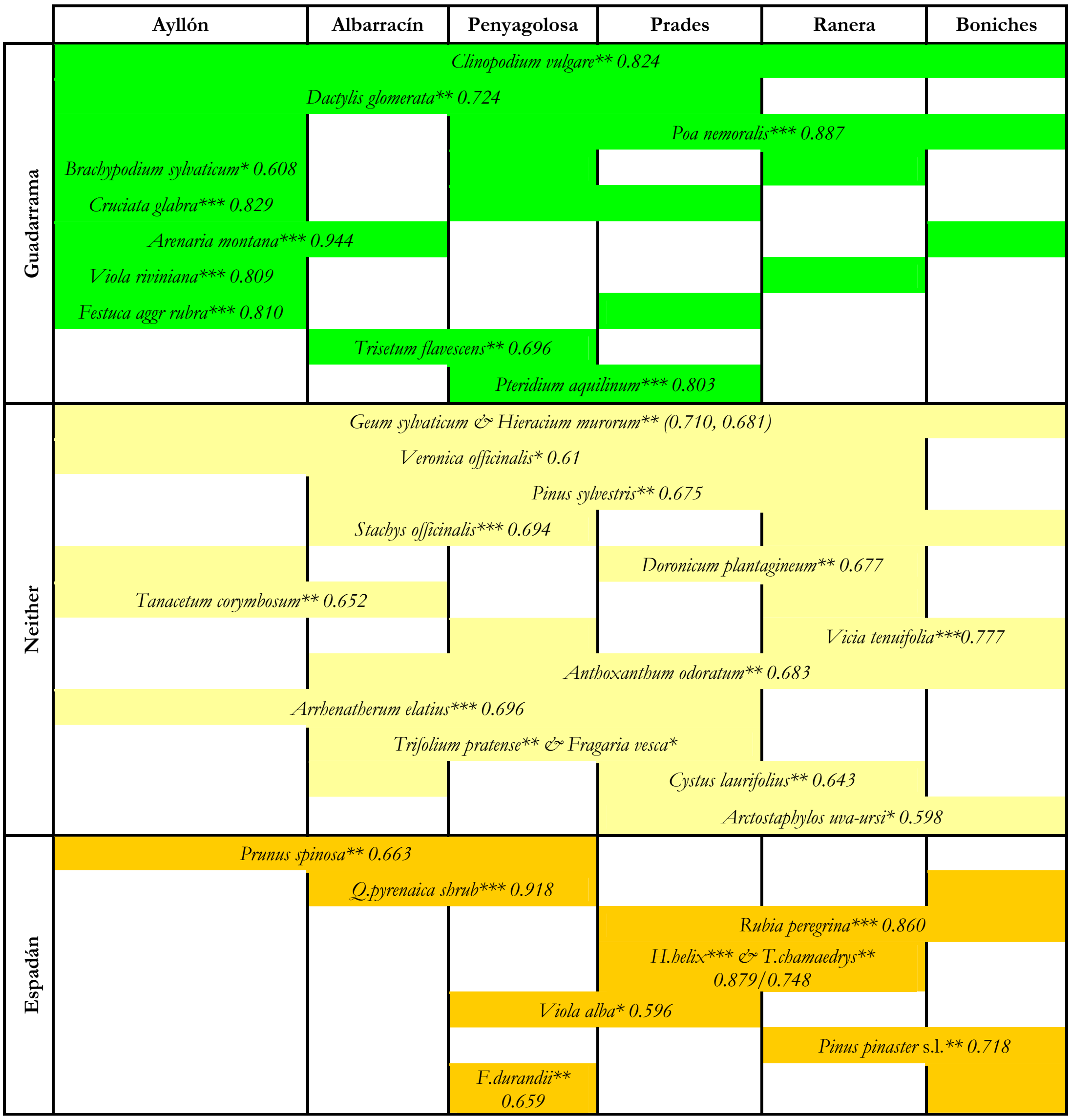
Appendix 2.1. Indicator species of the eastern Iberian Peninsula *Quercus pyrenaica* forest (endemics in bold; *= $p < 0.05$; ** = $p < 0.01$; ***= $p < 0.001$).

Espadán	No. Indicator species: 15 ***Biscutella calduchii* (0.966,***),** *Brachypodium retusum* (0.966,***), ***Minuartia valentina* (0.966, ***)**, *Galium maritimum* (0.953,***), *Rubus ulmifolius* (0.932,***), *Quercus suber* (0.894,***), ***Helianthemum marifolium* subsp *origanifolium* (0.856,***),** *Euphorbia flavicoma* (0.816,***), *Ulex parviflorus* (0.816,***), *Polypodium cambricum* (0.683,**), *Daphne gnidium* (0.632,**), *Geranium robertianum* (0.578,*), *Hieracium amplexicaule* (0.577,*), *Lonicera implexa* (0.577,*), *Silene inaperta* (0.516,*).
Prades	No. Indicator species: 12 *Euphorbia amygdaloides* (0.913,***), *Campanula persicifolia* (0.816,***), *Silene nutans* (0.744,***), *Corylus avellana* (0.707,***), *Polypodium vulgare* (0.707,**), *Sedum sediforme* (0.667,**), *Anthriscus sylvestris* (0.577,**), *Festuca* aggr *marginata* (0.577,**), *Ilex aquifolium* (0.577,**), *Rumex acetosella* (0.577,**), *Thymus vulgaris* (0.577,**), *Cistus salviifolius* (0.527,*).
Penyagolosa	No. Indicator species: 11 *Filipendula vulgaris* (0.837,***), *Asphodelus cerasiferus* (0.775,**), *Geranium sanguineum* (0.760,**), *Peucedanum oreoselinum* (0.707,**), *Rubus caesius* (0.707,***), *Hieracium sabaudum* (0.690,**), *Rosa pimpinellifolia* (0.662,**), *Achillea millefolium* (0.653,**), *Malus sylvestris* (0.632,*), *Brachypodium phoenicoides* (0.548,*), *Ranunculus bulbosus* (0.548,*)
Albarracín	No. Indicator species: 4 *Galium idubedae* (0.704,**), *Lathyrus linifolius* (0.681,**), *Potentilla rupestris* (0.667,**), *Leontodon hispidus* (0.577,*)
Serranía de Cuenca Boniches	No. Indicator species: 5 *Viola reichenbachiana* (1.000,***), *Milium effussum* (0.707,**), ***Thymelaea subrepens* (0.707,**)**, *Quercus faginea* (0.691,**), *Acinos alpinus* (0.614,**).
Serranía de Cuenca Ranera	No. Indicator species: 6 *Geranium lucidum* (1.000,***), *Amelanchier ovalis* (0.989,***), *Moehringia pentandra* (0.866,***), *Origanum virens* (0.707,**), *Dryopteris filix-mas* (0.691,**), *Urtica dioica* (0.662,**).
Ayllón	No. Indicator species: 6 *Ranunculus paludosus* (0.866,***), *Vicia orobus* (0.707,***), *Allium scorzonerifolium* (0.612,**), *Anthoxanthum aristatum* (0.612,*), *Bryonia dioica* (0.612,*), *Lathyrus niger* (0.595,*)
Guadarrama	No. Indicator species: 11 *Holcus mollis* (0.928,***), *Melica uniflora* (0.747,***), *Viola odorata* (0.682,**), *Rumex acetosa* (0.647,**), *Cytisus scoparius* (0.629,**), *Lapsana communis* (0.610,*), *Potentilla sterilis* (0.591,*), *Deschampsia iberica* (0.571,*), *Hyacinthoides non-scripta* (0.571,*), *Lactuca viminea* (0.528,*), *Potentilla micrantha* (0.528,*)

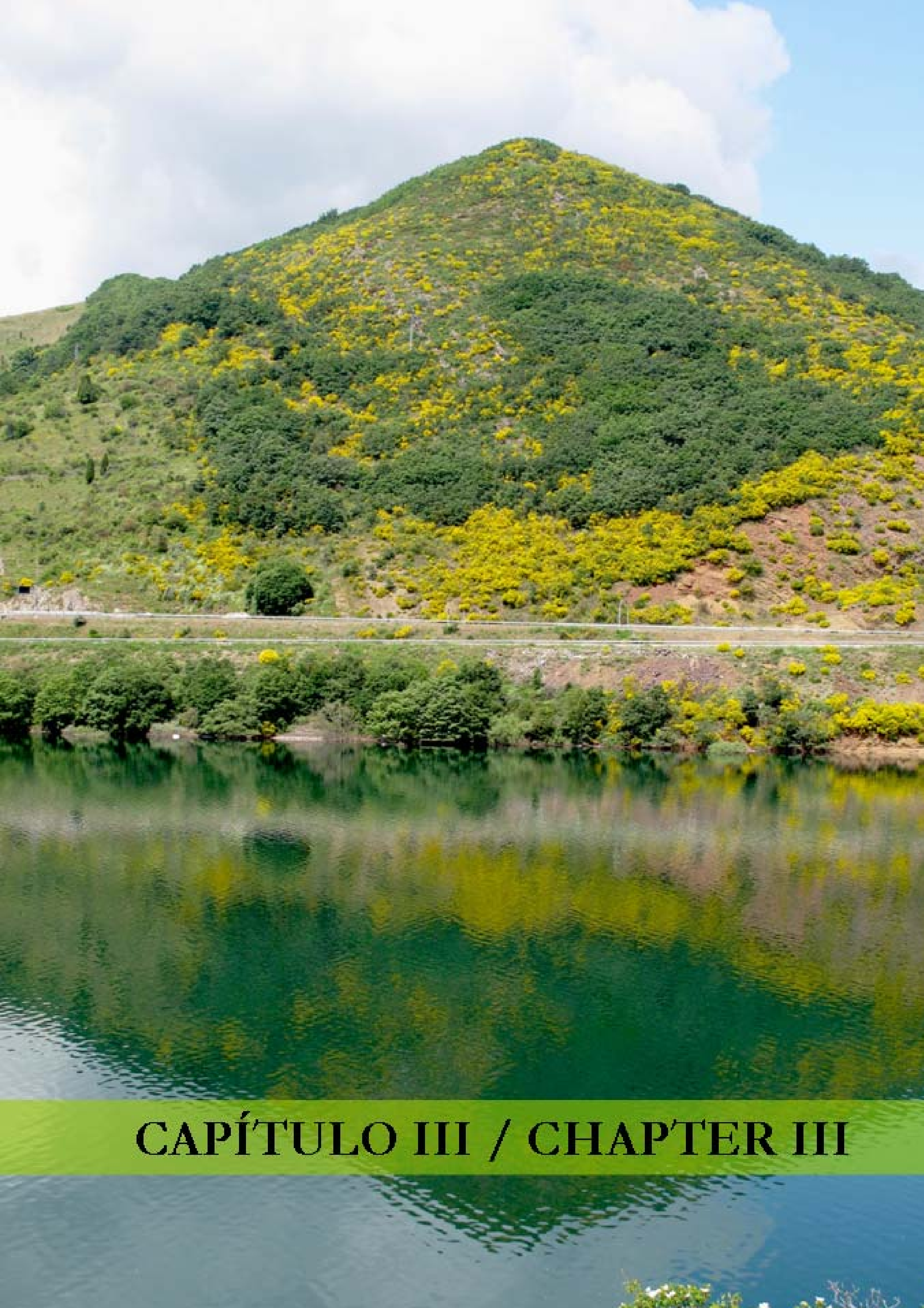
Appendix 2.2. Significant indicator species representing pairs of sites (only sites that share species are included; *= $p< 0.05$; ** = $p < 0.01$; ***= $p < 0.001$).

	Espadán	**Prades**	**Penyagolosa**	**Serranía de Cuenca Boniches**	**Ayllón**	**Guadarrama**
Prades	*Asplenium onopteris* *** *Rosa pouzinii* *** *Quercus ilex* subsp *ilex* *** *Cistus albidus* ** *Hieracium glaucinum* *		*Vicia sepium* *** *Lathyrus pratensis* ** *Juniperus communis* ** *Carex caryophyllea* ** *Helleborus foetidus* * *Galium verum* *	*Astragalus glycyphyllos* *		*Sedum forsterianum****
Penyagolosa				*Cephalanthera rubra* *** *Inula salicina* * *Campanula rapunculus* *		
Albarracín		*Lotus corniculatus* *** *Vicia cracca* *** *Centaurea triumfetti* subsp *lingulata* ** *Helianthemum numularium* *			*Conopodium pyrenaeum* *** *Melampyrum pratense* ***	
Serranía de Cuenca Ranera		*Rubus canescens* *** *Carlina vulgaris***		*Conopodium arvense* **	*Hypericum montanum* **	
Ayllón	*Erica arborea* ***			*Arrhenatherum bulbosum* ** *Aristolochia paucinervis* **		*Lonicera hispanica* *
Guadarrama	*Carex muricata* subsp *pairae* **			*Genista florida* **		

Appendix 2.3 Combinations between more than two groups. Coloured rows represent combined sites: representative species of combinations with Guadarrama in green, among themselves in yellow; with Espadán at the bottom of the table in orange (*= p< 0.05; ** = *p* < 0.01; ***= *p* < 0.001).



		Ayllón	Albarracín	Penyagolosa	Prades	Ranera	Boniches
Guadarrama	*Clinopodium vulgare*** 0.824	🟩	🟩	🟩	🟩	🟩	🟩
	*Dactylis glomerata*** 0.724	🟩	🟩	🟩	🟩		
	*Poa nemoralis**** 0.887	🟩		🟩	🟩	🟩	🟩
	*Brachypodium sylvaticum** 0.608	🟩		🟩		🟩	
	*Cruciata glabra**** 0.829	🟩		🟩	🟩		
	*Arenaria montana**** 0.944	🟩	🟩				🟩
	*Viola riviniana**** 0.809	🟩				🟩	
	*Festuca aggr rubra**** 0.810	🟩			🟩		
	*Trisetum flavescens*** 0.696		🟩	🟩			
	*Pteridium aquilinum**** 0.803			🟩	🟩		
Neither	*Geum sylvaticum & Hieracium murorum*** (0.710, 0.681)	🟨	🟨	🟨	🟨	🟨	🟨
	*Veronica officinalis** 0.61	🟨	🟨	🟨	🟨	🟨	
	*Pinus sylvestris*** 0.675		🟨	🟨	🟨	🟨	
	*Stachys officinalis**** 0.694		🟨	🟨		🟨	🟨
	*Doronicum plantagineum*** 0.677	🟨			🟨	🟨	
	*Tanacetum corymbosum*** 0.652	🟨	🟨			🟨	
	*Vicia tenuifolia****0.777			🟨		🟨	🟨
	*Anthoxanthum odoratum*** 0.683		🟨	🟨	🟨	🟨	🟨
	*Arrhenatherum elatius**** 0.696	🟨	🟨	🟨	🟨		
	*Trifolium pratense*** & *Fragaria vesca**		🟨	🟨	🟨		
	*Cystus laurifolius*** 0.643		🟨		🟨	🟨	
	*Arctostaphylos uva-ursi** 0.598				🟨	🟨	🟨
Espadán	*Prunus spinosa*** 0.663	🟧	🟧	🟧			
	*Q.pyrenaica shrub**** 0.918		🟧	🟧			🟧
	*Rubia peregrina**** 0.860				🟧	🟧	🟧
	*H.helix**** & *T.chamaedrys*** 0.879/0.748				🟧	🟧	
	*Viola alba** 0.596			🟧	🟧		
	Pinus pinaster s.l.** 0.718					🟧	🟧
	*F.durandii*** 0.659			🟧			🟧



CAPÍTULO III / CHAPTER III

Chapter III: Floristic patterns at different scales in broad-leaved oak forests from northern Iberia.

Abstract

After the compilation of a set of 273 relevés representing Northern Iberia forests dominated by *Quercus pyrenaica*, divided in twelve groups. By using a variant of indicator species analysis that generates indicators for each group of sites but also for different combinations of them, we searched for those floristic affinities that best define the inner structure of *Quercus pyrenaica* forests. We took the order of a site group combination indicated by a species, as an indication of the geographical scale of that floristic pattern, and we used the traits of the indicator species to understand the nature of potential drivers.

The compositional patterns of *Quercus pyrenaica* forests in North Iberian Peninsula are varied and have complex relationships. Through indicator species we could identify different ecological traits driving compositional variation among scales of analysis: Local to regional species assemblages and substrate type or disturbance indicators were shown at low and intermediate levels (i.e. involving a one or a small number of groups), whereas those indicators representing the temperate climate that prevails in most of this territory emerged at higher levels (i.e. involving a large number of groups). Based on the chorology of co-occurring species, we can observe two major gradients that determine the floristic composition of our groups, Mediterranean / temperate and oceanity / continentality and more locally silicicolous / calcicolous (due to a peninsular east-west differentiation by substrate).The set of species selected by indicator species analyses at a given order of site-group combinations reflects the ecological drivers that filter different species traits at that scale of analysis. Niche assembly exerts a recognizable effect at small scale (i.e., for combinations involving few groups), but the prevalent floristic patterns observed at larger scales of work seem to be driven by historical assemblages closely related to broader climatic variables.

Keywords: Community patterns, Indicator species, *Quercus pyrenaica*, Community assemblage, Ecological traits.

Introduction

The importance of scale in community ecology became a fact decades ago, but today has become a major factor and many studies have demonstrated its influence over different study subjects: fragmentation (Rescia et al. 1997), spatial structure heterogeneity (Wagner & Fortin 2005), relations heterogeneity-diversity and niche limitation at spatial scales (Tamme et al.. 2010), etc. Generally, enhancing its effect on vegetation-environment relationships: how do they change through scale? (Reed et al. 1993), how scale influences different environmental factors? (Siefert et al. 2012).

The analysis of floristic patterns at community level is central in community ecology because of the role played by some species to the community structure and processes (Meffe et al. 1997). The impact of particular species could be large for the communities or even for the ecosystems where they live, acting as real drivers (Walker, 1992, Holling, 1992). As indicators or even key stone species (Power et al. 1996), they could be used to monitor environmental changes and assess the impacts of disturbances over an ecosystem (Carignan & Villard, 2002), but also evaluating their fidelity, could be referred as diagnostic species in vegetation studies (Chytry et al. 2002). McGeoch (1998) suggested the use of indicator species in three ways: to reflect the biotic or abiotic state of the environment; to reveal evidence for the impact of environmental changes; and to indicate the diversity of communities within an area. Either diagnostic or indicator species refer to the same concept, the use of a species for predictive purposes. This concept is frequently applied in conservation, land management, and reserve design (De Cáceres & Legendre, 2009).

The vegetation-environment relationship makes species frequency and specificity within an area strongly related to its bioclimatic characteristics (Dufrene & Legendre, 1997, Gavilán et al. 2007), but also makes them dependent on the context and scale of the analysis (Chytry et al. 2002). Dufrene & Legendre in 1997 created the Indicator value method which allows to identifying those species that characterize a set of samples, assuming that for a species to be indicator most of its occurrences should be concentrated in its target type, having a frequency, being a "within-species abundance and occurrence comparisons" method. De Cáceres (2010) added to the Dufrene & Legendre method the possibility of combining those groups of samples, analyzing the species representativeness for each group separately as well as in combination. The application of their method to a geographic division of the data should generate species groups representing dominant patterns at different scales. In the present work, we want to determine whether indicator species summarizing floristic patterns at different scales are useful to gain information about the ecological processes operating at those scales. In order to do this, we take the result of indicator species analysis and use the ecological traits of the selected species to obtain information about the potential drivers of community assembly.

As study case, we take the floristic patterns of broad-leaved forest of *Quercus pyrenaica* in the Northern Iberian Peninsula. Northern Iberian Peninsula includes territories with different climatic conditions, from temperate to Mediterranean, but also with a different degree of conservation and different history of management practices. All of these features conform a mosaic of situations that we expect will influence the result of indicator species analysis. Through the inspection of the traits of the selected species, we expect to identify the factors that drive the compositional differentiation of *Quercus pyrenaica* forests. In particular, we are interested in the following questions: Could be the compositional variability related to assembly processes? Can we relate the indicator species obtained at different combinatory levels with different sets of ecological traits?

Methods

Study area and data gathering

The present study was conducted on *Quercus pyrenaica* forest of Central-Northern Iberian Peninsula. This broad-leaved oak forest reaches northern to cover some extended areas in Southwestern France (coming to the Loire mouth), but also in North-Western Morocco, being the Iberian Peninsula the larger territory of its distribution, where occupies more than 650,000 ha. With a preference for silicicolous substrata and a broad climatic range (between 7 ºC and 14.50 ºC for the mean annual temperature and between 607 mm and 2682 mm of annual rainfall), *Quercus pyrenaica* live mainly in Mediterranean conditions (where summer drought remains one of its limiting factors) but also in temperate emplacements (where due to substrata characteristics or slope terrain, soils do not retain much water). In southern areas it is considered a mountain forest species, whereas it covers some extensions of valleys in the temperate north. Therefore, topography exerts a significant effect as buffering of climatic conditions. We have considered Sierra de Guadarrama in Central Spain as the most south-eastern territory that can help to elucidate the relationship with the floristic patterns of close areas like those of north-eastern ranges (Moncayo, North-Iberian System) but also most western ones (Portugal, Salamanca, Table

3.1). Only those relevés with a *Quercus pyrenaica* cover over 25% were included and we revised taxonomic nomenclature to avoid synonymies.

Climate	**Geographic id.**	**Nº samples**	**βdiversity**	**Ios**	**It**	**altitude**
TEMPERATE						
1 41N, 1W	Moncayo	26	0.573	3.2	126	1108 ± 31.3
2 42N, 2W	Northern Sistema Ibérico	33	0.689	2.7	118	1191 ± 31.7
3 43N, 1-2W	Basque Country	46	0.612	2.9	208	693 ± 19.5
5 43N, 5-6W	Cantabrian coastal valleys	11	0.586	2.7	231	669 ± 43.9
6 43N, 6W	Cantabrian range	27	0.687	2.0	147	1171 ± 22.6
INTERMEDIATE						
4 43N, 3W	Burgos	8	0.520	1.8	204	814 ± 7.8
8 42N, 7W	Orense	10	0.468	1.7	189	1013 ± 48.4
9 43N, 4W	Palencia	18	0.593	1.9	102	1170 ± 22.5
11 41-42N, 7W	Portugal	6	0.624	1.9	198	884 ± 84.6
MEDITERRANEAN						
7 42N, 6W	Inner North plateau	26	0.617	1.3	173	1176 ± 21.1
10 41N, 6W	Salamanca	18	0.564	1.0	242	856 ± 28.8
12 40N, 4W	Sierra Guadarrama	13	0.461	1.6	125	1326 ± 28.5

Table 3.1 General data, sites grouped through bioclimatic characteristics (based on Ios value). First column: Climate/ latitude,longitude. Values: *Ombrothermic index of summer* (Ios= 10 (Ppd/Tpd): Ppd = positive precipitation of the driest three months, Tpd = positive temperature of the driest three months); *Thermicity index* (It= (T+M+m) 10: T = annual mean temperature, M = mean daily maximum temperature of the coldest month, m = mean daily minimum temperature of the coldest month) (based on Rivas-Martínez, 2011);. *Beta-diversity* (average of squared pairwise dissimilarities between relevés).

We compiled 273 floristic relevés (514 species) covering the whole distribution of these forests in valleys and mountains. Some of these relevés were obtained from the Iberian and Macaronesian Vegetation Information System (SIVIM) (Font et al. 2010), while others had to be digitized from bibliographic sources. The resulting compositional data matrix was divided into twelve groups following geographical criteria (Table 3.1), although the compactness and isolation of these geographical grouping was confirmed after obtaining similar divisions in numerical classification analyses (*K*-means partitioning with different numbers of groups, results not shown). Cover values in Braun-blanquet scale were transformed into abundance data (van der Maarel, 1979).

Indicator species analyses

The statistical index used to identify indicator species was IndVal defined by Dufrêne and Legendre (1997) as the product of two components: Aij a measure of species i specificity and Bij, the probability of finding the species when the relevé belongs to the relevé group j (A_{ij} x B_{ij} x 100). This method is based on the abundance and occurrence of each species without comparisons between them.

As ecological niches cannot normally be reduced to closed compartments, De Cáceres et al. (2010) extended the Indicator Value method to cope with the variation of species niche breadth. In order to identify floristic patterns and among-group affinities, we used this extension, which determines indicators for individual groups of sites as well as for combinations of them (De Cáceres et al. 2010). Specifically, if k is the number of groups of the initial classification or partition this extended method can potentially produce indicator species for 2^k-1 combinations. In our case, by considering site-group combinations we could identify indicator species for individual groups but also those species that represent the floristic composition of two or more groups. To control for the effects of using relevé groups of unequal size, the sum of the mean overall groups in its A component was included, following the recommendations of De Cáceres and Legendre (2009). As criteria to select indicators we kept only those species with a statistic (IndVal) over 0.5 and *p-value* below 0.05.

Order of site group combination and geographical scale of the floristic pattern

Since the initial classification of sites had been defined using geographical criteria, the different combinations of site-groups could be interpreted as associated to different geographic scales, ranging from a single study site - group indicators (upper cone) - through various combinations thereof (i.e. progressively wider areas) to almost the whole study area - multiple combinations - (see schematic diagram in Figure 3.1). Accordingly, our indicator species analysis produced indicators that represented different geographic levels. To observe the floristic patterns in the whole area it is important to establish the main floristic affinities between pairs of sites. To address this, we counted the number of indicators relating each pair of sites, assuming that the higher the number of indicators the greater the affinity between two groups.

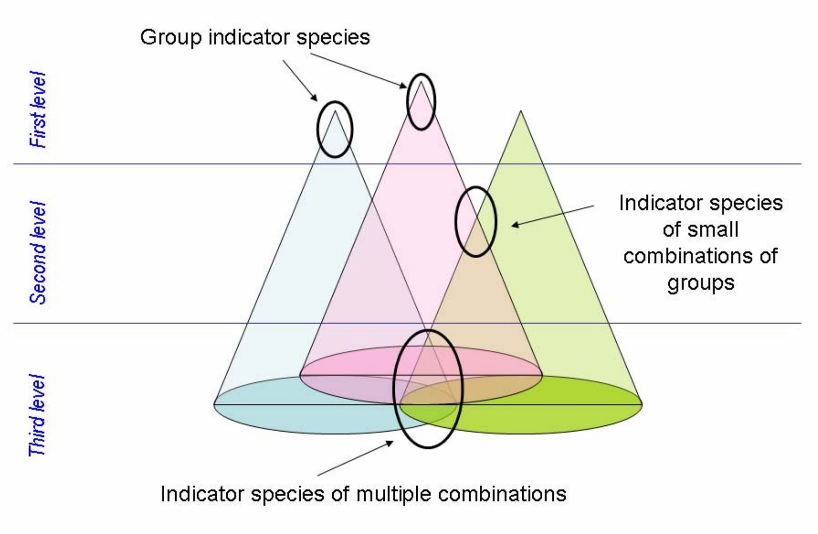


Figure 3.1 Scheme of *multipatt* function results generated through combinations of groups of sites. Three levels have been differentiated corresponding to the geographical structure of data: first one, indicator species for each group, generally exclusives; second one, indicator species of small combination of groups (local to regional floristic affinities) and third level, indicator species of multiple combinations or wide areas.

Examination of the ecological traits of indicator species

To identify ecological traits related to patterns of variation in species composition, we collected information about the autecology of each indicator species. Thus, we compiled the main characteristics of each species, in terms of distribution and niche preferences guided mainly by the work of Grime et al. (2007), Castroviejo (1986/2013), Tutin et al. (1964/1980) and Rubio et al. (2011). Afterwards we identify most frequent indications at each combinatory level.

Results

Group indicator species (first level)

At this level indicator species are those mostly exclusive to each area, usually with a higher frequency. Thus their number correspond to the floristic singularity (understood as differentiation from the rest) of the group respect to the whole set. From the twelve groups analyzed, the number of indicator species obtained reached up to 24 in Portugal (through annuals and disturbance indicators), followed by Sierra de Guadarrama in central areas (9) (through granitic shrubland), and Burgos (8) (through phanerophytes and calcicolous flora) (Table 3.2, Appendix S1).

	Endemism		Substrate	Disturbed habitats	Ancient forest	Syntaxonomical indicators	%Nemoral species	Main variables
	Iberian	Iber-Fr-Moroccan						
x1	9	3	8	10	9	4	25	Singularity
x2	3	3	1	7	2	3	34	
x3	1	2		4	3	3	36	
x4	1	1			2	4	54	
x5	1	1			1	2	83	
x6				1	3	1	71	
x7				1		1	80	
x8					1	1	75	
x9					3		85	
x10					1	1	100	Prevalence

Table 3.2 Summary of indicators traits at different combinatory levels.

Only one group did not generate indicator species: the group from the Northern Sistema Ibérico that included two mountain ranges, Sierra de Urbión and Sierra de la Demanda. This is justified by their location close to temperate areas which exert influence on the composition of these forests, but also a strong contrast between slopes that is reflected in a larger degree of internal heterogeneity respect to the remaining groups (see beta-diversity values in Table 3.1), although closely followed by the group of the Cantabrian range, also in the Temperate-Mediterranean boundary, that got only one indicator from the herb layer, the temperate *Mercurialis perennis*.

We have also observed at this level representatives of the main climatic features of the Iberian Peninsula: temperate forests species representing the hiperhumid northern groups from the Basque country and Cantabrian coastal valleys (*Ulex spp.*, *Hedera hibernica*), and typical Mediterranean species from Central Spain, represented by forest herbs (*Aquilegia vulgaris* subsp. *hispanica*, *Viola odorata*) or serial scrub communities of such territories (*Genista florida*, *Cytisus scoparius*) but also grasses (*Avenula marginata*) in managed forest of western Iberian Peninsula (northern plateau, Salamanca). Other temperate territories, like Portugal are rich in anthropogenic disturbance indicators, including annuals such as *Viola kitaibeliana*, *Stellaria media* or *Carduus carpetanus*. This group showed the highest number of indicator species (due to its singularity) that could be splitted into two groups, one representing the North-Atlantic floristic dataset (related to an oceanic climate) and a second one related to the influence of inland territories with dryer ones. Finally we have also detected a mixture of silicicolous and calcicolous indicators in Moncayo, where the Buntsandstein substrate exerted its influence on *Quercus pyrenaica* forest.

The highest number of endemism appeared also at this level (Table 3.2), some temperate as *Anemone trifolia* subsp. *albida* in Portugal, some Mediterranean as *Adenocarpus hispanicus* in Central range.

Indicator species of small combination of groups (second level).

In a second level we inspected the number of species associated to site-group combinations involving two to six groups. The number of species found as indicators decreased with the increasing number of combined groups (i.e. with the increase in the geographical area considered), which makes sense if we accept that local affinities are much stronger than broad ones: the number of species associated to combinations of two groups was 26, while 14 species were associated to combinations of three groups, 11 to combinations of four groups and so on (Appendix S1). Combinations between less than four groups were those that best represented the level of affinity. Floristically closest groups will create a larger number of combinations. Moreover, at this level their combinations could have more than one species as indicator, what we have interpreted as species co-ocurrence.

Co-occurrences: Set of indicator species

They appear only in combination of two and three site groups, as groups of species that are frequent but also they are frequent together, they are co-occurring in those geographic areas that we can consider of higher floristic affinity (Fig. 3.2). Many of these co-occurrences included species with restricted distributions in the study area, such as *Cruciata laevipes*, *Viola reichenbachiana*, *Potentilla montana* (northeastern), and endemism: *Festuca elegans* subsp. *merinoi, Aquilegia vulgaris* subsp. *dichroa* (Northwestern), *Cytisus multiflorus* (western-central areas), *Genista hispanica* subsp *occidentalis* (south-eastern)*,* in what seems to be an east-west polarity. Other co-ocurrences indicates broad ecological features as temperate climate or Atlantic influence. Is the case of *Quercus robur* and *Pseudarrhenatherum longifolium* (also a Iberic-France-Moroccan endemism) selected as the indicator species of those locations (Portugal, Cantabrian coastal valleys) with a maritime influence (highlighting the change in species composition of those *Quercus pyrenaica* forests protected by the Cantabrian range, where the presence of these two species is minimal). And also that co-occurrences indicating a temperate influence (see Fig. 3.2) in Eastern Mediterranean territories (Burgos, Sistema Ibérico Norte and Moncayo), with somewhat basophilous character, highlighting the complexity of an area, enriched with a common life-history of migratory movements.

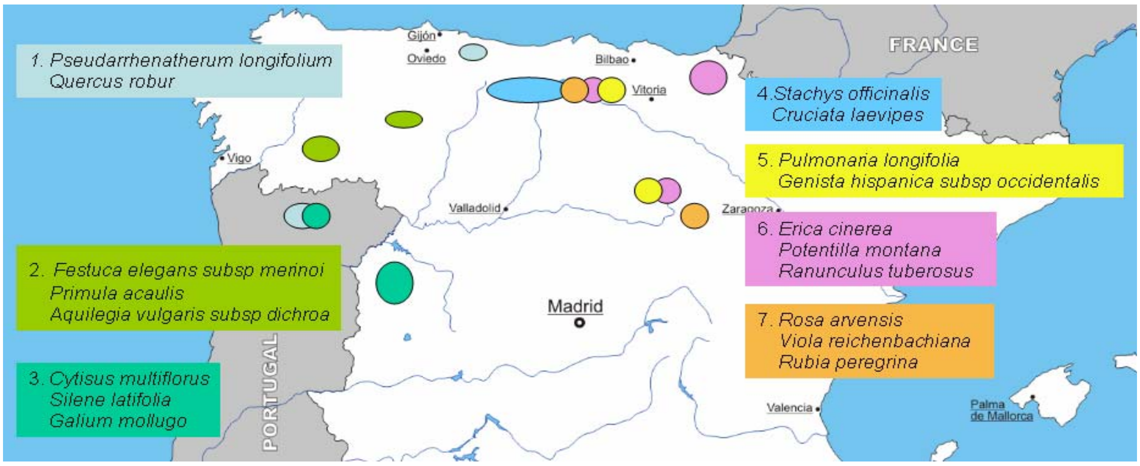


Figure 3.2 Local co-ocurrences. Species indicating together the same area were called, co-ocurrences. They represent high floristic affinity areas (author: B.Vilches from a map obtained at: http://d-maps.com).

Maximum abundances of *Stachys officinalis* in Nothern Iberia coincides with maximum values of the restricted distribution herb *Cruciata laevipes* but also (with a low IndVal value) *Succisa pratensis*, a stress tolerator specie (as *Stachys*) that use to occupy unshaded grassland and heath habitats over slightly calcareous soils (also co-ocurring in Grime et al. 2007) in species-rich habitats.

Single indicator species

Single species detected at this second level are mainly representatives of the forest herb layer (60%, including those nemoral herbs), sciophilous species as *Crepis lampsanoides* and *Ilex aquifolium*, but also those coming from seral communities (15%) like heath-gorse communities in the east. Surprisingly 25% of indicator species at this level are related to managed or disturbed areas (but restricted to two and three combined groups).

Forest species and phanerophytes represent again an east-west division e.g. *Castanea sativa* (west) and *Ilex aquifolium* (east). Some of them indicate traits as continentality (*Lathyrus niger* in north plateau surrounding areas), or basic substrate influence like *Melica uniflora,* a typical species of beech forest herb layer, also found in well conserved *Quercus pyrenaica* forest of Eastern territories from north locations to central ones. At this level there is a bigger set of sciophilous, forest herbs, usually dispersal-limited and sensitive to disturbance and forest age (Hermy et al. 1999).

Finally, this level included some endemism with restricted distribution areas as *Linaria triornithophora* (identified in those groups ranging from Palencia to northern Portugal) or *Festuca braun-blanquetii* (intermediate positions between temperate and mediterranean climate as Cantabrian range or Moncayo) frequently used as community indicators by the authors.

In shrub communities, the locally dominant group - especially in Eastern areas- are those of heathlands (*Calluna vulgaris*, *Ulex spp.*). They are, in general, silicicolous species or species with a certain preference for oligotrophic soils, except *Erica vagans* which tends to appear over limy or washed limestone terrains. This is correlated with its strong presence in Sistema Ibérico, where siliceous substrata dominate but surrounded by limestone. Slightly wider is the representativeness of *Daboecia cantabrica*, ranging from the Basque territories to the cantabrian coastal valleys, confirming its preference for high humidity sites, especially with summer rains (Bay of Biscay influence).

Finally, the most common indicator species coming from managed or disturbed communities are those derived from anthropogenic influence, either nitrophilous annuals such as *Galium aparine* or perennials, such as *Lapsana communis*, but others more typical of humid meadows and pastures such as *Holcus lanatus*, *Rumex acetosa* or *Dactylis glomerata*. These species appear to be particularly common at medium altitudes, Salamanca, Burgos and Central. Furthermore, *Brachypodium pinnatum* subsp. *rupestre*, is one of the most strongly associated with the Basque group, Burgos and Orense. It is a common species in mesophytic grasses with some limestone component.

Indicator species of wide combinations (third level)

This section included as indicators of large areas (regional) those species presented in combinations of more than six groups, thus generalists of those forests.

Forest species are the most common at this level (79%): in addition to the typical shade perennials such as *Poa nemoralis*, *Viola riviniana* or *Luzula forsteri*, we also find those more common in open forest or forest edges such as *Anthoxanthum odoratum* or *Fragaria vesca*. We have found small trees such as *Crataegus monogyna*, common in their canopy layer, but also in the spiny forest-fringe. But perhaps the most interesting are those that represent different nuances or forest types: species as *Anemone nemorosa, Stellaria holostea,* or *Hypericum* *pulchrum* typical of temperate deciduous oak (*Quercus robur*, *Q. petraea*) and beech communities; similarly, *Physospermum cornubiense* shared by those western groups. Moreover, the species that represents the combination of more groups, *Melampyrum pratense*, is common in beech forest confirming the predominant temperate influence in our work area. It represents ten of the twelve groups, only avoiding dry areas of central Spain: Sierra de Guadarrama and Salamanca.

Respect to shrub species they form the second more representative group (17%). The analysis showed three main types of communities at this level: Mediterranean: silicicolous, edapho-xeric broom communities dominated by *Cytisus* (*C. scoparius*); open forest but also deep soils *Pteridium aquilinum*; and Mediterranean heathlands in open forests but also as fresh, shady thickets (*Erica arborea*).

Indicator species from managed or disturbed communities represent only the 4% of the total; but are species frequent in open woodlands as *Potentilla erecta*, another acidophilous herb.

Floristic patterns at different level of combinations

Main floristic affinities between pairs of sites - number of species representing each - are summarized in Table 3.3. In general, the number of combinations showed a higher relation within Eastern and Western groups separately, despite the whole dataset included widespread species (Appendix S1). Moreover the maximum number of paired combinations occurs between western sites (red boxes in Table 3.3).

At least one third of the total combinations involved Cordillera Cantábrica, Ourense and Portugal combining with each other and western ones. Burgos, an eastern location showed also a high number of paired combinations but with eastern and center localities.

This could be interpreted as a strong effect of the Atlantic winds generating an important humidity gradient from the coast to inland (Gavilán & Fernández-González, 1997), reaching even Central localities but not the Northeastern Iberian peninsula where the influence of winds coming from the Bay of Biscay would be more important (summer rains).

	M	NIb	Bq	B	P	Ccv	Cr	NP	Ou	Port	Sal	SG
Moncayo		4	2	7	1	4	6	3	3	2	2	5
Northern Sistema Ibérico	15		3	5	1	0	4	3	2	0	1	2
Basque country	7	8		5	2	4	1	1	1	1	1	0
Burgos	16	15	14		2	2	2	1	2	0	3	5
Palencia	7	9	7	10		3	4	1	3	2	1	2
Cantabrian coastal valleys	12	9	12	12	10		4	2	2	5	2	1
Cantabrian range	15	15	8	13	16	14		7	6	4	2	3
North plateau	8	10	7	9	8	10	16		3	3	1	2
Orense	13	14	7	12	12	14	19	11		6	5	3
Portugal	13	12	8	12	11	17	17	12	20		5	3
Salamanca	10	10	7	13	10	11	14	7	18	19		5
SªGuadarrama	12	10	5	14	10	8	14	7	13	13	18	
Nªtotal comb.	24	25	21	32	21	26	29	21	31	32	28	27

Table 3.3 Number of combinations between pairs of sites. Right quadrant shows combinations of less than 6 groups, left quadrant shows total combinations of paired groups. The last row represents the total number of combinations. The color of the boxes is more intense as the number of combinations increased (from white to green in combinations of less than 6 groups, from yellow to red in wide combinations).

We also calculated the total combinations of each site (see last row of Table 3.3) that inform us on how a site is combined and how particular it is respect to the whole. Considering this, Basque country, Leon plateau and Palencia are the less combined groups (21). Conversely, the maximum number of combinations appeared in Orense, Portugal and Burgos, transitional areas between the Mediterranean and Temperate territories considered as species richness hotspots due to their wide bioclimatic range (Rey Benayas & Scheiner, 2002), but as a consequence also historically managed territories and therefore use to include a wide range of species such as a high level of phanerophytes in Burgos.

In general, combinations between not close groups (e.g.Burgos and Cantabrian range) can be interpreted in terms of the existing migratory routes, confirmed by the type of species that represent them (temperate-west / Mediterranean-central) and pointed out by several authors (Olalde, 2002, Petit, 2002) but also to forward and reverse phases of plant communities throughout history (North-western Iberia was an oak and beech shelter during glaciations (Comes & Cadereit, 2004, Hewitt, 2001)).

Discussion

Floristic patterns

Vegetation can be regarded as a fractal entity, and its patterns can be observed at different spatial scales (Palmer 1988, 1990, 2007). We hypothesized that these patterns (which are highly related with the "geometry of the environment") should be observable through different groups of species representatives of the key ecological processes. IndVal analysis with combination of groups allowed us to recognize the most representative species of our territory at different levels of combination (146 species have been selected from a total of 514, indicating that 28% of all species defines the main structure of the set). Identifying the species and the level (scale of combination) they act as indicators, allowed us to approximate their geographical area of prevalence, which could be related with the prevalence of their preferential niche. As expected, nemoral species, typical of the forest herb layer, increased their percentage when increasing the number of group combinations (Table 3.2) indicating their prevalence over the set, while those species from seral communities (shrublands or scrub communities), and those belonging to open forest communities such as meadows, grasslands or even ruderals, reduced it. In fact, substitution species can be also used at an intermediate combinatory level, for distinguishing the main biogeographical features. It is the case of eastern territories throughout basophilic heathland and moorland with dwarf shrubs; temperate-oceanic areas in northern Spain, throughout heather-gorse substitution shrubs. And finally western territories, mainly formed by the northern plateau and surrounding areas are recognized throughout graminoid substitution communities. As expected, those species mentioned in bibliography as syntaxonomically diagnostic also have appeared at first combinatory levels (between 1 and 5), where community differentiation still possible. As seen in Table 3.2, "differentiation" (in a floristic way, but also different traits and niche indicators) dominated first combinatory levels whereas general traits of the data matrix dominated last ones. This agree with results obtained by Sieferd et al. 2012, which found greater representativeness of soil variables and land uses on a small scale, factors of primarily local influence.

Floristic patterns, defined as species common to several groups, exhibit variations along the different levels of work. The maximum number of shared species occurs locally (in less than 5 combined groups appeared 84% of indicator species, moreover below 4 combined groups appeared co-ocurrence species), which is consistent with the idea that local affinity is stronger than regional (Wiens, 1989). This is also a symptom of the increase in heterogeneity that occurs when increasing the study area (Palmer, 2007), causing few species to appear as significant indicators at wide combinatory levels in our study. Similarly the number of indicator species obtained per each combination fell after three combined groups, and only one species will result as indicator thereafter.

Assembly rules

Twenty-five (17%) of the 146 indicator species are included in the ancient forest plant list of Hermy et al. (1999) with short dispersal modes, mainly endozoochores to myrmecochores. The prevalence of these dispersal-limited species at higher levels of combination -thus in most of North Iberian forest - indicates these forests long life history and vulnerability, but also a better conservation stage as marcescent forest than for example eastern ones (Vilches et al. 2013). In addition Indicator species type of dispersion, is highly related with community assembly rules, in this case at a particularly local and regional level.

Similarly endemic species, are related with community assembly rules in the sense of dispersion and differentiation. We have found two types of endemics as indicators: those exclusives of the Iberian Peninsula and those that are shared with the southern France and Northern Africa (i.e. the geographic distribution of *Quercus pyrenaica*) (Table 3.2). Wide-distribution endemism could be used as indicators of the phylogeographic assembly pointed by Götzenberger et al. (2011), where speciation, extinction and migration define regional species pool. While Iberian ones that used to appear as co-ocurrence species with a narrow distribution - even within the peninsula - could represent dispersal assembly, defining local species pool.

As we have observed, floristic composition patterns vary with scale, are related to species traits, hence they are a function of the assembly rules and ecological traits prevailing at each scale level. Assembly processes such as competition do influence single and local patterns primary (observable only using groups of quite small areas), whereas historical processes including broader or stronger environmental influences or changes are detected at a regional scale (Weiher et al. 2011). The species traits as nemoral character results in a niche assembly, but the composition of each community itself is in addition due to historical assemblies (Weiher et al. 2011, Drake, 1991).

Compositional variation

In this work we have also seen groups that are highly combined and with geographically different groups. They can be interpreted as areas of high environmental heterogeneity (Tamme et al. 2010) or mosaic diversity (Rey Benayas & Scheiner , 2002), reflected in a greater number of indicator species both locally and in combination with other groups. Is the case of Burgos, Portugal, Orense, but also Cantabrian range. They occupy transitional areas between Mediterranean or Temperate territories, allowing greater variety of species (Rey Benayas & Scheiner, 2002). As a consequence they were also historically managed, which could be observed in the wide variety of phanerophytes included as indicators of Burgos area. In contrast, other groups have a low number of combinations and also indicator species. Is the case of the Basque group, one of the most humid areas, which differential ecological characteristics made it combine only with nearby groups. Based on the chorology of co-occurring species, we can observe two major gradients that determine the floristic composition of our groups, Mediterranean / temperate, oceanity / continentality and more locally silicicolous/calcicolous (due to a peninsular east-west differentiation by substrate, with a calcareous domain in eastern areas (Vilches et al. 2013)).

Conclusions

We have found floristic patterns at different scales that appeared related with historical and abiotic traits. Our results support the idea of Siefert et al. (2012) about the variation with the scale of the environmental factors influence on community composition, but also Götzenberger et al. (2011), showing indicators of phylogeographic assembly, dispersal assembly and finally at a local level ecological assembly. Main conclusions are:

- Group Indicator species could be interpreted as main descriptors of each area.
- Highly related sites, generated high number of combinations, mainly at a small scale and their combinations are often represented by co-occurring species.
- Most of the species used by the phytosociologists as diagnostics of the different *Quercus pyrenaica* communities, appeared at a second level of combination, thus substitution shrubs but also species representing land uses and nemoral ones. Wide areas (third level) were represented by typical species of *Quercus pyrenaica* forests.The analysis resulted useful for an

in-deep description of the area. Furthermore, the identification of representativeness scales of the species, allow to better define communities but also their geographic variations.

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Appendix 3.a Indicator species at each combinatory level.

	locality		Orense	Inner north plateau	Portugal	Salamanca	Cantabrian range	Cantabrian (Coast)	Sierra Guadarrama	Palencia	Burgos	Northern Sistema Ibérico	Basque Country	Moncayo	
	lat		7	6	7	6	6	6	4	4	3	2	2	1	
	long		42	42	41-42	41	43	43	40	43	43	42	43	41	
	IndVal / p value		NW	NW	W	W	N	N	C	N	NE	NE	NE	NE	
Galium estebanii	0.673	***												x	x1
Arctostaphylos uva-ursi	0.572	**												x	
Viola hirta	0.502	**												x	
Ulex gallii susp gallii	0.621	**											x		
Euphorbia amygdaloides	0.531	**											x		
Serratula tinctoria	0.875	***									x				
Juniperus communis	0.644	***									x				
Corylus avellana	0.636	***									x				
Ligustrum vulgare	0.592	***									x				
Cornus sanguinea	0.587	**									x				
Rosa pimpinellifolia	0.563	**									x				
Quercus faginea	0.534	**									x				
Sorbus torminalis	0.516	**									x				
Hedera hibernica	0.739	***						x							
Glandora prostrata	0.603	***						x							
Pyrus cordata	0.542	***						x							
Saxifraga spathularis	0.522	**						x							
Ulex gallii subsp *breoganii*	0.522	**						x							
Mercurialis perennis	0.564	***					x								
Allium victorialis	0.588	***		x											
Galium papillosum	0.764	***	x												
Melittis melissophyllum	0.634	***	x												
Epilobium montanum	0.632	***	x												
Myosotis arvensis	0.548	***	x												
Periballia involucrata	0.548	***	x												
Helleborus viridis	0.607	***								x					
Trifolium medium	0.594	***								x					
Conopodium subcarneum	0.853	***				x									
Carex muricata subsp *lamprocarpa*	0.690	***				x									
Bryonia dioica	0.686	***				x									
Daphne gnidium	0.667	***				x									
Acinos alpinus subsp *meridionalis*	0.577	**				x									
Avenula marginata subsp *marginata*	0.534	**				x									
Cardamine hirsuta	0.816	***			x										
Hyacinthoides hispanica	0.816	***			x										
Lamium maculatum	0.800	***			x										
Ranunculus ficaria	0.798	***			x										
Digitalis purpurea	0.728	***			x										
Pyrus communis	0.719	***			x										
Anemone trifolia subsp *albida*	0.707	***			x										
Carex spicata	0.707	***			x										
Hypericum linariifolium	0.707	***			x										
Viola kitaibeliana	0.707	***			x										
Carduus carpetanus	0.707	***			x										

		locality	Orense	I. N. plateau	Portugal	Salamanca	Cantabrian R	Cantabrian C.	Sª Guadarram	Palencia	Burgos	N. Sist.Ibérico	B.C.	Moncayo	
Ceratocapnos claviculata	0.661	***			**x**										x1
Brachypodium pinnatum	0.638	***			**x**										
Saxifraga granulata	0.618	***			**x**										
Cerastium fontanum subsp *vulgare*	0.577	***			**x**										
Draba muralis	0.577	***			**x**										
Ranunculus gregarius	0.577	***			**x**										
Stellaria media	0.577	***			**x**										
Asplenium adiantum-nigrum	0.552	**			**x**										
Veronica arvensis	0.548	***			**x**										
Luzula multiflora	0.543	**			**x**										
Rumex papillaris	0.522	***			**x**										
Cytisus scoparius subsp *reverchonii*	0.520	***			**x**										
Legousia scabra	0.520	**			**x**										
Carex muricata subsp *pairae*	0.734	***							**x**						
Adenocarpus hispanicus	0.679	***							**x**						
Viola odorata	0.663	***							**x**						
Potentilla micrantha	0.642	***							**x**						
Geum urbanum	0.635	***							**x**						
Vicia tenuifolia	0.622	***							**x**						
Aquilegia vulgaris subsp *hispanica*	0.620	**							**x**						
Moehringia trinervia	0.614	***							**x**						
Silene vulgaris	0.577	**							**x**						
Rosa arvensis	0.744	***									**x**			**x**	x2
Viola reichenbachiana	0.655	***									**x**			**x**	
Pulmonaria longifolia	0.749	***									**x**	**x**			
Genista hispanica subsp. *occidentalis*	0.522	**									**x**	**x**			
Agrostis capillaris	0.646	***									**x**		**x**		
Viola canina	0.577	***						x					**x**		
Blechnum spicant	0.527	***		x									**x**		
Euphorbia dulcis	0.521	**			x								**x**		
Stachys officinalis	0.649	***								**x**	**x**				
Cruciata laevipes	0.566	***								**x**	**x**				
Holcus lanatus	0.647	***				**x**					**x**				
Festuca rubra	0.670	***							**x**		**x**				
Pseudarrhenatherum longifolium	0.673	***			**x**			**x**							
Quercus robur	0.524	**			**x**			**x**							
Festuca elegans subsp. *merinoi*	0.793	***	**x**	**x**											
Primula acaulis	0.681	***	**x**	**x**											
Aquilegia vulgaris subsp. *dichroa*	0.543	***	**x**	**x**											
Galium aparine	0.582	***		**x**	**x**										
Agrostis castellana	0.587	**	**x**			**x**									
Jasione montana	0.531	**	**x**		**x**										
Lapsana communis	0.666	***	**x**						x						
Galium mollugo	0.548	***			**x**	**x**									
Aristolochia paucinervis	0.736	***				x			x						
Melica uniflora	0.706	***							x		x			x	x3
Polypodium vulgare	0.523	***			x			x						x	
Festuca braun-blanquetii	0.709	***		x			x							x	
Potentilla montana	0.621	***									**x**	**x**	**x**		
Erica cinerea	0.567	***									**x**	**x**	**x**		
Ranunculus tuberosus	0.561	***									**x**	**x**	**x**		

		locality	Orense	I. N. plateau	Portugal	Salamanca	Cantabrian R.	Cantabrian C.	Sª Guadarrama	Palencia	Burgos	N. Sist. Ibérico	B.C.	Moncayo	
Calluna vulgaris	0.553	***				x						x	x		
Euphorbia angulata	0.605	***	x	x								x			
Brachypodium pinnatum subsp. *rupestre*	0.730	***	**x**								**x**		**x**		
Ilex aquifolium	0.615	***						x		x			x		
Rumex acetosa	0.571	***				x			x		x				
Crepis lampsanoides	0.724	***	x		x		x								
Primula veris	0.566	***			x				x	x					
Dactylis glomerata	0.751	***			**x**	**x**			**x**						
Erica vagans	0.752	***									**x**	**x**	**x**	**x**	x4
Lathyrus linifolius	0.662	***							**x**		**x**	**x**		**x**	
Deschampsia flexuosa	0.575	***					**x**	**x**					**x**	**x**	
Genista polygaliphylla	0.508	**		x			**x**	**x**						**x**	
Potentilla sterilis	0.570	***		x			**x**		**x**			**x**			
Daboecia cantabrica	0.674	***						**x**		**x**	**x**		**x**		
Lonicera peryclimenum	0.539	**		**x**	**x**		**x**	**x**							
Castanea sativa	0.629	***	**x**		**x**	**x**		**x**							
Lathyrus niger	0.576	***		**x**			**x**		**x**	**x**					
Campanula rapunculus	0.578	***	**x**			**x**	**x**			**x**					
Genista falcata	0.671	***	**x**	**x**	**x**	**x**									
Veronica chamaedrys	0.529	**		x			x				x	x		x	x5
Hieracium murorum	0.570	***	x				x			x		x		x	
Lonicera peryclimenum subsp. *hispanica*	0.712	***				x		x	x		x			x	
Vicia sepium	0.529	***	x				x		x		x			x	
Sedum forsterianum	0.620	***	x		x	x			x					x	
Linaria triornithophora	0.617	***	**x**		**x**		**x**	**x**		**x**					
Hypericum pulchrum	0.646	***	**x**					**x**			**x**	**x**	**x**	**x**	x6
Brachypodium sylvaticum	0.625	***					**x**		**x**	**x**	**x**	**x**		**x**	
Fragaria vesca	0.577	***					x		x	x	x	x		x	
Potentilla erecta	0.589	***		x	x			x			x	x	x		
Anemone nemorosa	0.514	**		x			x	x		x	x		x		
Cytisus scoparius	0.681	***	**x**			**x**	**x**	**x**	**x**	**x**					
Viola riviniana	0.722	***	x		x	x		x	x	x					
Anthoxanthum odoratum	0.624	***	x		x	x		x			x	x		x	x7
Luzula forsteri	0.753	***	x		x	x			x		x	x		x	
Erica arborea	0.726	***	x	x	x		x	x				x		x	
Silene nutans	0.627	***	x		x	x	x		x			x		x	
Physospermum cornubiense	0.744	***	**x**	**x**	**x**	**x**	**x**			**x**	**x**				
Hedera helix	0.600	***		x	x	x		x	x		x		x	x	x8
Crataegus monogyna	0.748	***			x	x	x		x	x	x		x	x	
Prunella grandiflora	0.501	**		x	x	x	x		x	x	x	x			
Holcus mollis	0.835	***	**x**		**x**	**x**	**x**	**x**	**x**		**x**		**x**		
Teucrium scorodonia	0.804	***	**x**		**x**	**x**	**x**	**x**		**x**		**x**	**x**	**x**	x9
Stellaria holostea	0.778	***	**x**	**x**	**x**		**x**	**x**		**x**	**x**	**x**		**x**	
Arenaria montana	0.762	***	x		x	x	x	x	x		x	x		x	
Poa nemoralis	0.789	***	x	x	x	x	x		x	x		x		x	
Cruciata glabra	0.755	***	x	x		x	x		x	x	x	x	x		
Clinopodium vulgare	0.791	***	x	x	x	x	x	x	x	x		x			
Pteridium aquilinum	0.787	***	x	x	x	x	x	x	x		x		x		
Melampyrum pratense	0.841	***	**x**	**x**	**x**		**x**	**x**		**x**	**x**	**x**	**x**	**x**	x10

Appendix 3.b Type of indicator species at each level of combination, A: Forests species (in a broad sense) the canopy, ombrophilous herb layer and other companions like *Rosaceae*. B: Pasture species, open forest indicators

A	*Agrostis castellana, Festuca elegans, Pseudarrhenatherum longifolium, Silene latifolia,Galium mollugo, Rosa arvensis,Stachys officinalis, Aquilegia vulgaris, Pulmonaria longifolia, Blechnum spicant, Euphorbia dulcis, Primula acaulis, Quercus robur, Viola reichenbachiana, Aristolochia paucinervis, Cruciata laevipes, Rubia peregrina, Viola canina.*
B	*Galium aparine, Lapsana communis, Festuca* aggr. *Rubra, Agrostis capillaris , Holcus lanatus, Jasione montana,Genista hispanica* subsp *occidentalis, Cytisus multiflorus,*
A	*Brachypodium pinnatum* subsp *rupestre, Dactylis glomerata, Potentilla montana, Ranunculus tuberosus, Crepis lampsanoides, Primula veris, Euphorbia angulata, Polypodium* sp. pl.,, *Festuca braun-blanquetii, Melica uniflora, Ilex aquifolium.*
B	*Rumex acetosa, Erica cinerea, Calluna vulgaris*
A	*Campanula rapunculus, Lathyrus niger, Deschampsia flexuosa,Potentilla sterilis, Lathyrus linifolius, Castanea sativa, Lonicera peryclimenum*
B	*Erica vagans, Daboecia cantabrica,Genista florida* subsp *polygaliphylla, Genista falcata*
A	*Lonicera peryclimenum hispanica, Sedum forsterianum, Hieracium murorum, Veronica chamaedrys, Vicia sepium*
B	*Linaria triornithophora*
A	*Brachypodium sylvaticum, Viola riviniana, Anemone nemorosa,Hypericum pulchrum*
B	*Cytisus scoparius, Fragaria vesca, Potentilla erecta*
A	*Silene nutans, Physospermum cornubiense, Luzula forsteri*
B	*Anthoxanthum odoratum, Erica arborea*
A	*Crataegus monogyna, Hedera helix, Holcus mollis*
B	*Prunella grandiflora*
A	*Pteridium aquilinum, Clinopodium vulgare, Cruciata glabra, Stellaria holostea, Poa nemoralis, Teucrium scorodonia, Arenaria montana*
B	
A	*Melampyrum pratense*
B	

CAPÍTULO IV / CHAPTER IV

Fotografía: Melojar de Riaza

Beatriz Vilches

Chapter IV: Updating vegetation types, a two-way method and its application to Iberian Peninsula broad-leaved oak forest

Abstract

Noise Cluster analysis was performed over Pyrenaean oak forests data matrix from the whole Iberian Peninsula. After the creation of an updated set of "assigned clusters" we propose to use indicator species analysis with combinations of groups (*multipatt* function) to obtain a triple result: first, an appropriated description of these clusters through their main representative species, second *validating* their robustness from a compositional perspective but third create connections – not necessarily hierarchical – that helps to elucidate or approximate the real structure of our data set. After obtaining twelve clusters with Noise Clustering method (NC), the application of indicator species analysis confirmed the congruence - from a floristic point of view- of eleven, as independent units. The cluster with no indicator species correspond to the zone of maximum presence of *Quercus pyrenaica* in the whole Iberian Peninsula: North plateau and neighboring areas. In turn, this cluster established the maximum number of floristic connections at higher levels of combination. In the opposite side was a group at eastern Iberia, with the maximum number of indicator species but one of the less combined of the whole. Its the group with the higher percentage in xeric species of the set, thus, the most differentiated. The results are -in general- consistent with the current biogeographic division of the Iberian Peninsula. Seven of the twelve clusters are also concordant with the taxonomical adscription of their relevés. The other five clusters gather highly complex areas, such as transitional zones between macroclimates (Mediterranean and Temperate).

The combined use of unsupervised classification methods and indicator species analysis, allowed to obtaining more consistent groups or communities, while enabling the observation of floristic connections between them, which could be used as indicators of higher units. Furthermore, it facilitates the observation of large affinity areas as well as those that require more thorough analysis to be fully understood. In turn, we suggest the observation of the level (number of divisions) of occurrence of each cluster to assess their preliminary degree of differentiation.

Keywords: Unsupervised classification methods, Noise Clustering, Indicator species analysis, *Quercus pyrenaica*.

Introduction

Classification of plant communities or other biotic entities has been, traditionally, an important research subject to understand the complexity of biodiversity. Moreover, the study of the life of those organisms living together in a limited space and their interrelations becomes 'easier' if the plant community is deeper known (Rabeler 1960; Braun-Blanquet 1979). Vegetation classification can focus on different attributes of vegetation, including its physiognomy, structure and species composition but also climate data, soil conditions or plant functional traits (e.g. Walter 1973; Pfister & Arno 1980; Adams 1999; Adams 1999; Dengler et al. 2008; Jennings et al. 2009). Vegetation classification is fundamental to understand and predict biodiversity because it is a tool underlying vegetation mapping, monitoring components, management of conserved areas, etc.

The approaches to define vegetation types are many, although some authors have pointed out the need for a formal and standard methodology when working with vast territories (Wiser & De Cáceres 2013; Dengler et al. 2011; etc.). Standardizing vegetation classification would make easier the comparison of vegetation patterns at large scales (Bruelheide & Chytry 2000). While there is not a universal valid approach for defining vegetation types, new numerical methods continue to being proposed (De Cáceres et al. 2010; Schmidtlein et al. 2010; Dengler & al. 2011; Tichy et al. 2011; Wiser & De Cáceres 2013), although certain conceptual nuances still unresolved (Willner 2006; Pignatti et al. 1995; Dale 1994; De Cáceres & Wiser 2011).

Vegetation analyses of large datasets integrating information from vegetation surveys are nowadays common (Eliáš et al. 2013; Jiménez-Alfaro 2008; Pausas 2003, Garzón 2006; Wiser & De Cáceres 2013). Many European countries have compiled thousands plot records into vegetation databases (Kleyer 2008; Schaminée et al. 2009; Font 2010), which are helping to develop large-scale classification systems. In this sense, numerical syntaxonomy is trying to solve some of those problems of classic Phytosociology, calculating absolute or relative similitude between samples (relevés), or the homogeneity of any hierarchic level to obtain most objective one, but also combining numerical and classic classifications to obtain a more repeatable and formal classification system (Feoli & Lausi 1981; Escudero et al. 1994).

Unfortunately, despite the efforts of numerical classification some problems related to hierarchical levels still arise because of nested relationships between syntaxonomic categories (Dengler et al. 2005). Recently, the use of indices to detect species indicators of syntaxonomic units can be useful to solve the troubles with hierarchies that only consider the combinations of nested levels instead of all possible combinations at the same time. To consider all combinations of groups of sites could bring us some advantages, since we can get a characterization of the species that have preference for a concrete habitat from qualitative data, providing the species that characterize individual groups but those that relate two or more (Dufrêne & Legendre 1997; De Cáceres & Legendre 2009; De Cáceres et al. 2010b). When working with Noise Clustering method simultaneously, indicator species analysis creates floristic connections between those clusters merged from the cloud of noise. Number of indicator species individually and in combination gives an idea about the level of singularity of each cluster, which are more connected and through which species (Vilches et al. 2013). Therefore, could establish hierarchies, while giving their floristic characterization. Community assembly and species coexistence become a determinant factor in this hierarchical structure. Indicator forest species take on key interest when discussing the conservation status of forests, since they reflect their life history (MacNally & Fleishman 2004). The close relation they show with the different aspects of the habitat makes them useful tools for a range of purposes, since they can be used as indicators of diversity, richness, and disturbance (McGeoch 1998). They have been the subject of numerous phytosociological studies from the middle XX century (Braun-Blanquet et al. 1956; Amaral Franco 1958; Rivas-Martínez 1962; Braun-Blanquet 1964; Rivas Goday 1964), to recent works (Aguiar Goçalves 2001; Ladero et al. 2004), including preliminary approaches to a global numerical classification (Entrocassi et al. 2004), or recent studies focused in higher rank syntaxa (Rivas-Martínez et al. 2011; Mucina et al. in press.). Used in phytosociology, diagnostic species could give different meanings in different contexts such as *character*, *differential* and *absolute* character species (Willner 2006). In this sense Noise cluster give community cores but Indicator species analysis with combining groups of sites will give us the context of indication of their different diagnostic species.

Quercus pyrenaica is a species whose natural distribution covers the Iberian Peninsula mainly as mountain forest, to western France and north-western Morocco. As other vegetation types, have been subjected to intense human pressure, what gradually reduced their quality changing their floristic patterns and distribution area (Gavilán et al. 2000; Rubio et al. 2009) and transforming certain areas in particularly vulnerable ones (Pulido 2002; Vilches 2013). Therefore, there is an urgent need for prompt action to understand their main ecological traits, together with the species range that best define their particularities. Its large distribution along Iberian Peninsula makes this forest suitable to develop a new classification, adding new plot data recently published, but also through the use of recently developed numerical techniques. Hence, our central aims was to update the current classification of *Quercus pyrenaica* forests using a non-hierarchical unsupervised method and identify the species representing individual and common diversity patterns. Complementarily, we also determined the set of species that best indicate their different environmental features, through the study of co-ocurring species ecological traits.

Materials and methods

Study area and Data gathering

Our study focused on the *Quercus pyrenaica* forests of the whole Iberian Peninsula. These broad-leaved forests are found under meso-supramediterranean and mesotemperate areas with subhumid, humid and hyperhumid ombroclimate (Rivas-Martínez 2002) on siliceous soils, or soils impoverished in basic ions (Buntsandstein rodenas (Vilches et al. 2013)). Searching for a minimum summer precipitation of 100 mm in Mediterranean areas and avoiding most humid situations in Temperate ones, these forests are located along a range of altitudes between 200 and 1800 masl; appearing in different mountain ranges (and slopes) but also in valleys.

We collected 671 floristic relevés obtained following the method of the Sigmatist School (Braun-Blanquet 1932) from several bibliographical resources including (Font et al. 2010) database (Table 4.1). Relevé locations were distributed throughout the Peninsula, both in the Temperate (North Iberia) and in the Mediterranean regions. After revising the taxonomic nomenclature to avoid synonymies, the community data matrix contained 882 species, whose cover values were transformed from Braun-Blanquet to Van der Maarel abundance scale (Van der Maarel 1979).

Ordination analysis

Given the large area considered and its orographic variability, a DCA ordination analysis was first conducted to display the main compositional gradients of the data (Figure 4.1).

Noise clustering

Observation of vegetation, thus field surveys and personal experience is the main basis of the current classification of our forests, as Iberian Peninsula is a deeply studied region. We explored alternative classifications of *Quercus pyrenaica* forests using a non-hierarchical unsupervised clustering method, Noise Clustering (NC, Dave 1991). This method represents an improvement over Fuzzy C-means (FCM) (Bezdek 1981) for vegetation classification, because clusters are less influenced by transitional relevés (De Cáceres et al. 2010a). Specifically, the NC method defines ball-shaped clusters around each prototype vector (centroid), and leaves aside outliers and transitional relevés in a different cluster called *Noise*. This noise class obtained is composed of data that lie further than a user-specified distance (δ) from the rest of cluster centroids. Such distance should be decided depending on the desired size of clusters, which in turn depends on the distance coefficient used to measure the resemblance between plot records. Both this parameter and the fuzziness exponent (m) will depend on the data set at study (Wiser & De Cáceres 2013, De Cáceres et al. 2010a). Thus, using NC requires choosing a dissimilarity coefficient as well as choosing values for the distance to noise class, the fuzziness coefficient, and the optimum number of clusters (De Cáceres et al. 2010a; Wiser & De Cáceres 2013).

The difference between plot records clearly assigned and those deemed transitional is a matter of distances. Assigned clusters were those that collected all relevés close to or consistent with the prototype vector defining them. In turn, transitional relevés were those located at the same distance to all prototypes. As working with distance among each object (relevé) and the comparison between cluster centres, not with dense regions (as PCM does) NC does not need a previous re-sampling of the data set. In fact, the NC ability to avoid transitional relevés could be also interpreted as a way of re-sampling to increase the distinctiveness of vegetation types. In general, resampling methods are useful to reduce the influence of oversampled areas over the analysis, but do not reinforce the representative degree of undersampled ones.

As already indicated in previous works with hierarchical and non-hierarchical methods (Wiser & De Cáceres 2013; Dufrene & Legendre 1997), the number of clusters is a major decision when searching for the most representative and congruent scheme of the vegetation type. Partition coefficient criterion (De Cáceres et al. 2010a), limitation of the variability of vegetation types (Hellinger distance), maximization of number or value of indicator species (Dufrene & Legendre 1997), minimizing plot records for each cluster and limiting cluster variance ((HCR) Wiser & De Cáceres 2013) and also the selection of those clusters represented through the highest number of diagnostic species (Optimclass, Tichý et al. 2010) are alternative methods that may help us to decide where to stop dividing. In our case number of indicator values, together with volume of noise cluster will be our "where to stop diving" criterion.

Indicator species analyses

We propose to use indicator species analysis with combinations of groups (De Cáceres et al. 2010b) to obtain a triple result: first, an appropriated description of these clusters through their main representative species, second *validating* their robustness from a compositional perspective but third create connections – not necessarily hierarchical – that helps to elucidate or approximate the real structure of our data set.

De Cáceres et al. (2010b) extended it to cope with the variation of species niche breadth by considering all possible combinations of relevé groups and selecting that for which the species can best be used as an indicator. The analysis produces the set of indicator species significantly associated to each relevé group or relevé groups combination through their specificity and constancy. Indicator value analyses were performed using the 'multipatt' function of the R package 'indicspecies', using as statistical value IndVal (Dufrêne & Legendre 1997). To control for the effects of using groups of unequal size, the sum of the mean overall groups in its A component was included (De Cáceres & Legendre 2009).

In order to select the best number of clusters we conducted several NC analyses, each searching for a different number of clusters. We calculated different statistics for each resulting classification have: volume of Noise cluster (transitional and non-assigned relevés), number of unassigned relevés and sum of Indicator species (with Indicator Value > 0.4 and significance level (alpha) < 0.05) obtained for each group (criterion used by Dufrene & Legendre 1997).

In this paper we also suggest using the number and identity of the indicators to determine how NC clusters –i.e. data matrix hard groups - could be related, and the autoecology of the representative species of site combinations to identify shared, and differential, environmental characteristics. This step can also be useful to define vegetation types at higher level of abstraction, which focus on common ecological traits of species (e.g. alliances).

Results

Ordination analysis

Previous DCA of broad-leaved oak forest showed a clear separation of the sites in terms of summer drought, a typical Mediterranean feature. Thus typical Mediterranean territories (i.e. Sierra Nevada, Sierra de Espadán) are well separated in the most positive part of both axis (Fig. 4.1), together to forest growing on decarbonated substrata. The rest of the Iberian forest including temperate, transitions and those from northern Mediterranean territories appear more concentrated at the negative part of the diagram.

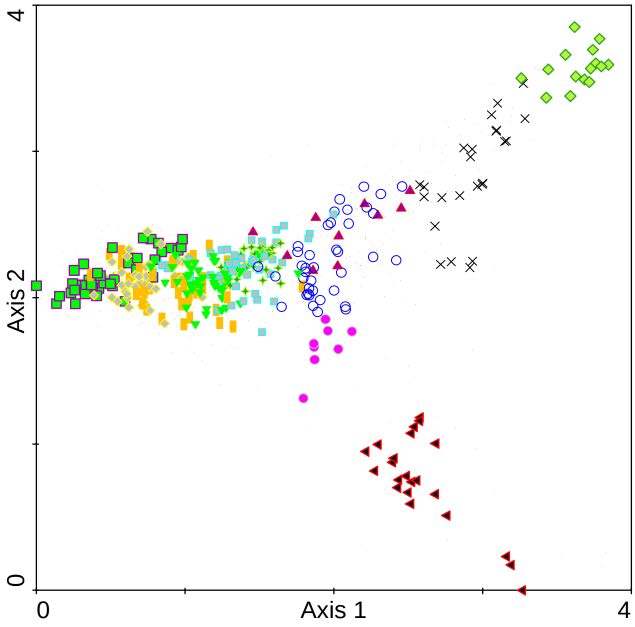

Figure 4.1 Abundance DCA: General appearance of data matrix. Symbols represent Noise Clustering results: Green stars correspond to cluster 1 in fig.4.4, open circle is cluster 2, green down triangles cluster 3, grey squares cluster 4, green square cluster 5, orange rectangle cluster 6, grey diamond cluster 7, cross cluster 8, left black triangle cluster 9, pink circle cluster 10, green diamond cluster 11, up triangles cluster 12, and tiny red points represent noise cluster relevés.

Noise clustering

In order to select the best number of clusters we have performed consecutive divisions, which have generated different reference values (fig. 4.2): Volume of Noise cluster (transitional and non-transitional relevés), number of unassigned relevés and sum of Indicator species obtained at each level for each group. As seen noise cluster volume decreased when number of divisions increased. At certain point Noise cluster and unassigned relevés reached a plateau and simultaneously number of indicator species reaches its maximum value followed by a steep descent. Both signals were chosen to select the cut point in 12 clusters. Nevertheless increased number of clusters seems to increase the division of these twelve groups, but did not create new differential ones. The second reason to stop dividing in twelve clusters is to aim a congruent representation of the main division of Pyrenaean oak communities, i.e. those with a floristic and chorological meaning although not necessarily hierarchical. It is important to note the punctual appearance - along the sequence of divisions - of a cluster represented by *Pteridium aquilinum*. This cluster is not desirable as group different types of forests with an openness character (but high compositional heterogeneity) and whose main species in common is this heliophilous fern, already indicated by many authors as representative of these forests and their potential locations (Rivas-Martínez 2002).

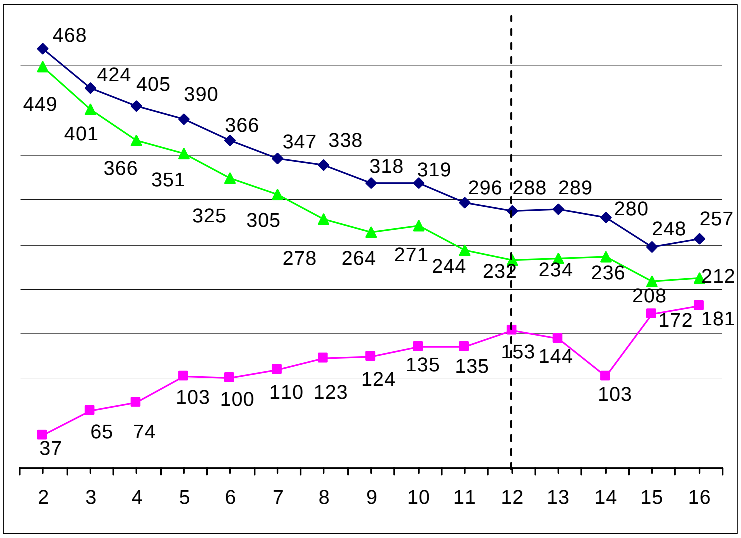

Figure 4.2 Graph of consecutive divisions of data matrix. Total number of indicator species (pink), noise cluster volume (blue) and number of unassigned relevés (memb. value ≥ 0.5) (green) obtained at each division level.

The observation of the consecutive clustering, allows identify different types of clusters; some divisions or groups of relevés appeared almost from the beginning while others emerged from the cloud of noise much later. This different sequence of emergence appears to be associated with the consistency of each group, and ultimately their level of differentiation from the rest. Thus, each cluster ("*community*") seems to have its own level of appearance, thus its own ecological breadth in the same manner as species. Compact and isolated clusters are the first to be identified with low number of divisions (thus clusters) (*a* in fig.4.3). Those that are sparser and less distinct are only identified with larger numbers of divisions and may be less robust (*b* in fig.4.3). It can happen that one of these clusters is divided into two sub-clusters when increasing the number of clusters. Some small groups merged at high division levels (or clustering levels), in what seems to correspond to those forests with a local differentiation (usually small surface area forests).

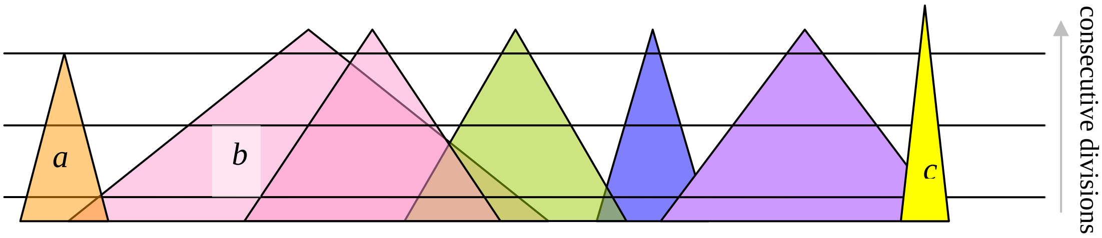

Figure 4.3 Diagram of the different sequences of appearance. Each community merging at different levels, with different width of representation. Each line indicates a clustering level.

After selecting the number of clusters, calculation of distances between centroids allow us to show its representation as dendrogram (twelve site groups and one more as the noise cluster) (fig 4.4). Compositional relationships between clusters were shown in ordination of fig. 4.1, but main hierarchical relations appear represented in this dendrogram (*ward* method). It divides clusters in two big groups: Western Iberia (green) receiving Atlantic rainfall to a greater or lesser extent, and Eastern Iberia - thus most mediterranean sites (group D, orange) - with a pronounced summer drought. In previous work we had already detected this western Iberia similarity, relating it to the strong influence of the Atlantic Ocean over this area.

Main cluster or western division (green in fig.4.4) separated - at the highest similarity level - ten groups, including the most typical forest growing on siliceous soils in its first branch (groups A and B) and those southernmost locations in its second one (C). This last cluster subdivided those forests groups developed at low altitudes (Cáceres, Córdoba, Jaén y Cádiz (8 in fig.4.4)) (200-1000 m.a.s.l.) and those south-eastern but supramediterranean forests (Granada, S^a Nevada (9 in fig.4.4)) (1150-1800 m.a.s.l.).

First branch: Group A, cover the whole altitudinal spectrum of central-western forests (Atlantic influences) (S^a de Gredos (1 in fig.4), Sistema Central (3 in fig.4.4), Northern plateau and Portugal (4 in fig.4.4), Montes de Toledo, Cáceres (2 in fig.4.4)), from low altitudes in western areas of southern plateau to higher altitudes in Sistema Central. But also the noise group that included relevés spread –mainly over central-western territory, clustered at a very low level of similarity (0.35) to one of the groups with highest internal heterogeneity (2 in fig.4.4).

In the other hand, second branch or group B (fig.4.4) included those areas of humid summers -Temperate trend-, northernmost forests from Galicia to Basque country.

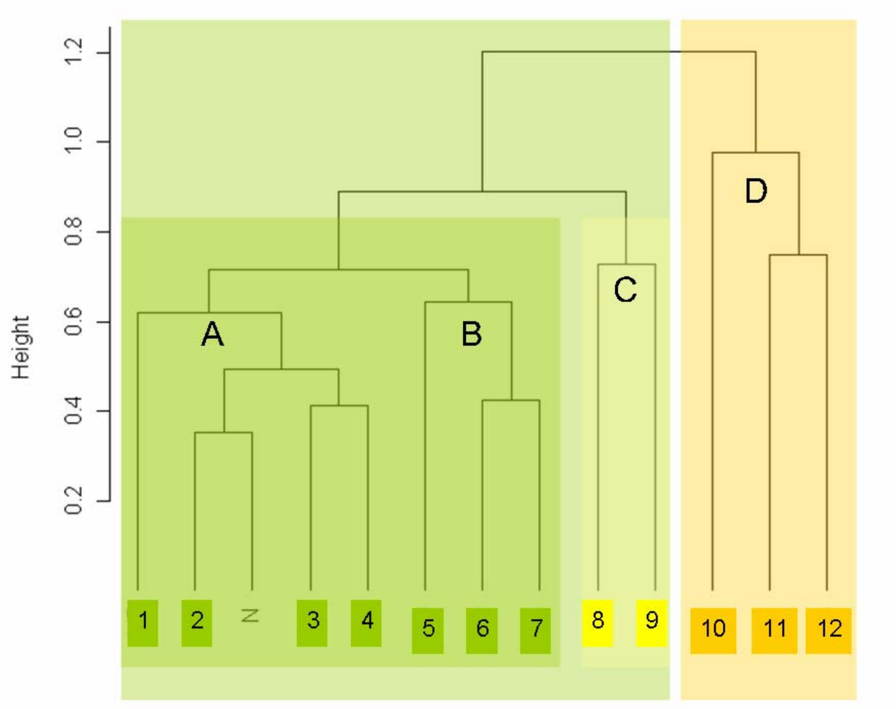

Figure 4.4 NC analysis dendrogram from cluster centroids distances (ward method). A, Group of western relevés; B, group of Northern localities (temperate and transitional climate ones); C, Southern localities; and D, Eastern Iberia clusters.

Group D or most Mediterranean cluster (orange in fig.4.4) included likewise two groups, from those easternmost forests of the Iberian Peninsula (Espadán (11 in fig.4.4), Serranía de Cuenca y Teruel (12 in fig.4.4)) to a third coming from the south-eastern (Río madera Jaén (10 in fig.4.4)) (Sierra del Segura). They have in common basophilous species in the canopy layer due to the prevalence of basic substrata in such areas.

Through between-centroids-distances (fig.4.4) we could observe a higher cohesion within clusters A-B than C-D; being the most distanced group of the whole data set cluster 11, Sierra de Espadán (Castellón), a Mediterranean pre-coastal range. Seven of the twelve clusters are formed by relevés originally assigned to a unique association (Table 4.1). The other five clusters gather highly complex areas, with high level of internal affinity such as transitional zones between macroclimates (Mediterranean and Temperate). They seem to correspond to communities, with greater ecological breadth, that can be divided into lower units through their internal nuances.

	Sorbo	*Arbuto*	*Luzulo*	*Festuco*	*Lonicero*	*Genisto*	*Holco*	*Pulm.*	*Linario*	*Melam.*	*Berb.*	*Adeno.*	no adscrip
1				100									
2	64	28	8										
3	2		98										
4		6	52			19	21		2				
5					9			7	4.5	79.5			
6			22			30	24	9	15				
7			15					66	19				
8		100											
9												100	
10											100		
11													100
12			100										

Table 4.1 Compositional scheme of each cluster, refering to percentage of assigned relevés to current clasification. Sorbo, *Sorbo torminalis-Quercetum,* Arbuto, *Arbuto unedonis-Quercetum,* Luzulo, *Luzulo forsteri-Quercetum,* Festuco, *Festuco merinoi-Quercetum,* Lonicero, *Lonicero peryclimeni-Quercetum,* Genisto, *Genisto falcateae-Quercetum,* Holco, *Holco molli-Quercetum,* Pulm., *Pulmonario longifoliae-Quercetum,* Linario, *Linario triornithophorae-Quercetum,* Melam., *Melampyro pratensis-Quercetum,* Berb., *Berberido hispanicae-Quercetum,* Adeno., *Adenocarpo decorticantis-Quercetum,* no adscription correspond to recently proposed *Minuartio valentinae-Quercetum* (Vilches et al. 2013).

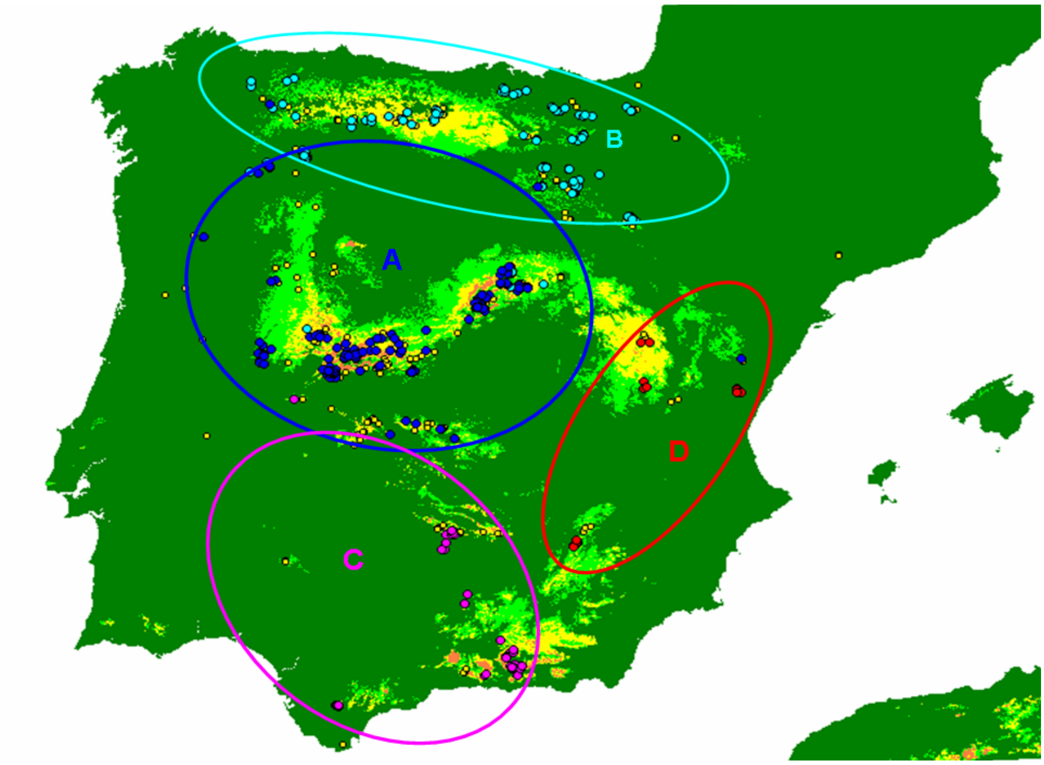

Figure 4.5 Geographical distribution of the different clusters along Iberian Peninsula. Noise cluster plots as Yellow points. A, B,C & D correspond to each main clusters of figure 4.4.

Indicator species analysis

Justify in a compositional way our clustering results but also create connections not observable at a first glance. The analysis selected 209 species from the twelve groups analyzed (629 total species). Indicator species analysis results are presented in Appendix II. Species appearing at this level use to represent association character species from current hierarchical classification (Rivas-Martínez 2011). From those seven clusters (above mentioned) (composed by a unique association relevés), five generated as indicators, species currently described as association characteristics (Appendix 4.1). The other two clusters are Central System (3 in fig. 4.4), and relevés from Cuenca-Teruel (12 in fig. 4.4). The first one, do not showed as indicators those species described in the literature as characteristics, whether they are observable in the lists of specificity (Appendix 4.2). The latter, belongs to one of the major associations of *Quercus pyrenaica*: *Luzulo-Quercetum*, however their indicator species were those originally assigned to the Levantine association *Cephalanthero-Quercetum.*

First step: Indicator species of each cluster

In this section we showed those indicator species with higher frequency that could be exclusive to each cluster (Appendix 4.1). Richer groups in individual indicator species were usually those that showed higher floristic singularity (Vilches et al. 2013), but are also those which included species with a most particular autecology.

It is worthy to note that at least a quarter of the species that appear in this first step are trees or shrubs. These species belong to the canopy layer, forest fringe or those seral communities that firstly appear when the forest is destroyed or cleared. Looking at Appendix II we observed that these fanerophytic or chamaephytic species are common in those groups separated in the dendrogram in the 0.7 of similarity, coinciding with those represented by the highest number of indicator species in the total pool (10, 11, 12 in fig. 4.4), thus most Mediterranean ones (certain openness character). In these clusters the presence of basic particles in soils facilitates the appearance of a particular flora (Vilches et al. 2013), but they are also the most isolated emplacements with a higher level of endemics.

The Northernmost cluster (5 in fig. 4.4), is also another highly represented one, including typical temperate trees and shrubs (*Quercus robur*, *Daboecia cantabrica*, *Ulex gallii*). As said, all of them could be said as the most singular groups of the whole set, together with group C - the southernmost - well characterized, also through endemics. The rest of clusters, showed less than 10 indicator species; being those with less indicator species those that appeared inside group A but also second branch of group B, due to the high internal floristic similarity.

Second step: Indicator species as linkers between clusters.

From this point Indicator species represented floristic similarities among or within clusters, keys to understand the organization of the dendrogram explained above.

From a phytosociological point of view most of these connections could represent higher nested levels. However we had observed that this type of analysis generates floristic similarities more linked with the real continuity of the vegetation than those taxonomical hierarchies.

In general, these "second step species" are mostly shade species from the herb layer. Given that, *multipatt* function, shows as indicators species ever more generalists; reducing the level of uniqueness as it increases the number of groups combined (Vilches et al. 2013).

We have detected interesting groups of species representing higher affinity connections as *Stellaria holostea* and *Festuca braun-blanquetii* co-ocurring as indicators of Cantabrian range (cluster B), *Aquilegia vulgaris* subsp *hispanica* and *Hyacinthoides non-scripta* for groups of central Iberian forest, or *Festuca durandoi*, *Rubia peregrina* or *Geum sylvaticum* in Eastern groups (notice that at this step calcareous east is represented by silicicolous species in contrast to individual indicator species above commented). But also indicate those clusters in which the altitude plays an important role by increasing moisture, as in the case of *Hepatica nobilis* or *Sanicula europaea* connecting central relevés with eastern Sistema Ibérico, or *Melittis melissophyllum* and *Genista falcata* appearing at higher altitudes of central-western groups. All of them – specially co-ocurrences – are useful to find highly connected clusters but also to resolve complex groups, i.e. those represented by a low number of species at first step, i.e. temperate influenced (6 and 7 in fig. 4.4) or central-western ones (3 and 4 in fig. 4.4).

As seen in Appendix 4.1, those low represented clusters – low number of own indicator species – could be differentiated by groups of co-ocurring species with a definite distribution and autecology. Is the case of cluster group B, connected through *Lonicera* *periclymenum* subsp *periclymenum* and *Vaccinium myrtillus.* It includes the distinct cluster 5, the most temperate (linkable, with the subaliance *Quercenion robori-pyrenaicae*), but two more clusters with transitional character between Mediterranean and Temperate macroclimate: 6 and 7 in fig. 4.4. Indicator species analyses showed – through number of co-ocurring species – a higher connection between clusters 5 and 7 - the temperate region and the northern Sistema Ibérico - already found in previous analyzes and different authors (Vilches in press).

Stellaria holostea and *Festuca braun-blanquetii* represent those transitional climate clusters (7 & 6 in fig. 4.4). Western cluster 6 showed a higher mediterraneity level with an increased Atlantic influence (see its connections with central-western sites through species like *Genista falcata* and *Melittis melissophyllum*), while eastern cluster 7 is more influenced by the Bay of Biscay, pirenaean species and calcareous substrata.

The westernmost cluster (2) and the central-western ones (3 & 4 in fig. 4.4) have a most difficult analysis. First one is the cluster that brings together all the communities of the west Mediterranean, collecting high compositional heterogeneity but two main nuances: Atlantic influence and floristic connection with southern areas with drought-tolerant species as *Daphne gnidium* or *Paeonia broteroi.* Clusters 3 & 4 are highly floristically connected clusters, joining sites of the Northern plateau and the Sistema Central. It is probably their central location, which makes these two clusters share species with most of A but also B groups (even D (cluster 12)). They come together most typical silicicolous communities of *Quercus pyrenaica.* In fact, this Northwestern quadrant is the best represented at wide combinatory levels, mainly through nemoral herbs with certain humidity requirements as *Holcus mollis* or *Poa nemoralis*, but also those with certain heliophilous and acidophilous character as *Pteridium aquilinum* or *Sedum forsterianum.*

Other species indicated connections between zones, f.e. *Dactylis glomerata* and *Genista florida* between Sistema Central and southern Sistema Ibérico, *Arenaria montana* with the northern, or *Melampyrum pratense* between temperate areas and southern Sistema Ibérico. But most of these wide combinations indicate those species natural to this oak-wood that could be understood as generalists, thus west Iberia species as *Cruciata glabra*, *Teucrium scorodonia* or *Cytisus scoparius. Crataegus monogyna*, a small tree from spiny seral communities and *Luzula forsteri*, a very common herb in those forests are the indicator species in combinations of eight groups. From 9 groups up we have not detected any indicator species.

Discussion

In general, Noise Clustering of our data matrix seems to be concordant with the biogeographical division of the Peninsula, although more distanced groups do not correspond - as could be expected- to the different macroclimatic areas in the Iberian Peninsula, i.e. Mediterranean and Temperate (North Iberia). Rather, the preliminary classification set aside Southeast relevés, bringing together in a single cluster the rest: Temperate and what is often called sub-mediterranean areas (mountain areas of inner Iberia). Thus floristic composition seems to be enriched in Eurosiberian species going northwest but in Mediterranean going southeast, showing the strong East-West division of this type of marcescent forest.

It is worth notice that *Quercus pyrenaica* forests appear most often in western Iberia, particularly at Inner Northwest areas. Thus western area has generated much more within affinities (less distanced clusters but also, represented through a highest number of indicator species) than eastern ones. This could be justify from a biogeographical perspective, first through plateau and Hesperian massif characteristics (including their siliceous soil prevalence), and second due to the strong effect of Atlantic Ocean influence reaching Sistema Ibérico (winds, rainfall cadences, azorean anticyclone). These affinities make classification a more complex task in certain western areas compared to southeast ones, where this forests become an unusual community due to the calcareous soils dominance, and where isolation become a definite factor within differentiation, fact reflected in the number of endemism that represent them as indicator species.

The main Pyrenaean oak area in western Peninsula could be divided in three groups in base of their indicator species: Central (A), North (B) and South (C), being the temperate region forests (5 in fig. 4.4) inside the second one, the best represented. In general, western clusters - as already said – had Atlantic species in their composition, with a Mediterranean species increment from north to south and thermophilous from inner to coastal.

Group B covers (in addition to temperate cluster) a large area represented by intermediate macroclimate clusters (6 and 7) that almost follow latitude 43 with a clear floristic similarity (but also with the most heterogeneous cluster of the whole set: num. 6). This connection could be understood as historical exchange of species within these areas and a changing topography that makes that only endemism with restricted distribution and those species related with *Quercus robur* forests could differentiate them locally (is the case of *Linaria triornithophora*, *Luzula sylvatica* (maximum presence in cluster 6), as is the case of

Orocantabric forests. In turn, these two groups could be, differentiated through atlantic (6 in fig. 4.4) and eastern (Pyrenees but also calcareous) (7 in fig. 4.4) species.

On the other hand Central group (A) showed a remarkable low number of species indicating 3 and 4 clusters, due to the high number of species in common between them and the whole west in what could be an effect of "Central Association" (Willner 2006). Finally southwest forests (A&C) showed two different shades: one moister and oceanic, and other inner, thus drier and warmer.

To include Indicator species analysis to any classification or clustering method, help to reinforce best defined clusters (which show their singularity with a high number of indicator species) but also help to understand not as stronger ones. Furthermore, added evidence of the connections between different communities, a way to acknowledge the *continuum* within our classification. Once again site history seems to have something to say on the current composition of our communities (MacNally & Fleishman 2004; Weiher 2011; Mucina 1997).

Noise clustering used together with Indicator species analysis with combined groups of sites, helps to study in depth large data matrix from two ways: numerical (grouping by inventories) and compositional (grouping by species). Some floristic connections could be explained through climatic influences but their establishment has no sense without historical processes of migration, and maintenance. Phylogeographic assembly rules (Götzenberger et al. 2012) could be factors to take into account when describing a community. Obviously defining concrete units, distinguishable from each other, entails some loss of information related to the *continuum*. The use of IndVal analysis with site group combinations - over any type of classification - would not only establish the level of floristic affinity between units, but also - closely related to this - the level of historical-geographical isolation of each. This facilitate the inclusion in this type of analysis of the *continuum* concept, moreover through the identification of the appearance areas we could easily define which species are good diagnostic for each unit. Although a controversial issue - as Mucina (1997) pointed out - vegetation classification should not ignore its continuous character, but this continuity do be included as a factor to take into account in order to identify the proper “definite floristic composition” (Willner 2006) of an association. No study was performed in this sense over *Quercus pyrenaica* communities along Iberian Peninsula.

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Appendix 4.1 Indicator species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**8**	**10**	**11**	**12**
Festuca elegans subsp *merinoi*	0.823	-		-		-						
Carex lamprocarpa	0.643	-	-	-					-			
Andryala integrifolia	0.503	-		-		-						
Acinos alpinus subsp *meridionalis*	0.495	-	-	-								
Festuca rothmaleri	0.448	-	-	-								
Allium massaessylum		0.703	-	-				-				
Hyacinthoides hispanica		0.470						-				
Festuca aggr rubra			0.711	-	-	-	-					
Viola odorata			0.519	-								
Geum urbanum			0.461	-		-	-					
Potentilla micrantha			0.437				-					
Brachypodium pinnatum subsp *rupestre*				-	0.768	-						
Daboecia cantabrica					0.752	-	-					
Potentilla erecta					0.739	-	-					
Euphorbia dulcis					0.645	-						
Agrostis capillaris			-	-	0.613	-	-					
Potentilla montana					0.609		-					
Ulex gallii subsp *gallii*					0.584							
Erica cinerea					0.575	-	-					
Euphorbia amygdaloides					0.491		-					
Ulex europaeus					0.477							
Danthonia decumbens		-			0.468							
Serratula tinctoria					0.461		-					
Agrostis curtisii					0.452			-				
Carex pilulifera					0.426							
Frangula alnus	-			-	0.426	-	-					
Simethis mattiazzii		-		-	0.416		-					
Quercus robur				-	0.408							
Pseudarrhenatherum longifolium				-	0.402							
Crepis lampsanoides				-		0.461	-	-				
Allium victorialis						0.417						
Astrantia major						0.417						
Vicia orobus			-			0.417						
Galium estebanii				-			0.468					
Genista florida subsp *polygaliiphylla*					-	-	0.463					
Arbutus unedo		-		-	-			0.965				
Viburnum tinus								0.791				
Cistus ladanifer		-						0.750				
Phillyrea angustifolia		-						0.747				
Cistus salviifolius		-			-		-	0.541	-	-	-	
Luzula forsteri subsp *baetica*								0.456				
Avenula marginata subsp *albinervis*								0.408				
Lavandula stoechas								0.408				
Pistacia terebinthus								0.408				
Ulex borgiae								0.408				
Festuca elegans									1.000			

Adenocarpus decorticans									0.853			
Myrrhoides nodosa		-							0.524			
Dactylorhiza insularis									0.522			
Arrhenatherum album		-		-					0.505			
Digitalis purpurea subsp *purpurea*				-	-				0.482			
Lonicera arborea									0.477			
Cerastium gibraltaricum									0.426			
Nepetea granatensis									0.426			
Paeonia coriacea									0.426			
Smyrnium perfoliatum									0.426			
Rubus canescens										0.935		
Filipendula vulgaris		-				-				0.913		
Agrimonia eupatoria		-						-		0.912		-
Quercus faginea					-			-		0.873		-
Cytisus scoparius subsp *reverchonii*										0.866		
Viburnum lantana				-	-		-			0.818		
Berberis hispanica									-	0.804		
Quercus xneomairei		-						-		0.764		
Sorbus torminalis			-		-		-		-	0.729		
Origanum vulgare							-			0.697		
Prunus insititia										0.612		
Amelanchier ovalis							-			0.598		
Trifolium ochroleucon	-	-	-	-		-	-		-	0.585		-
Elymus caninus			-							0.578		
Daphne laureola									-	0.513		
Monotropa hypopitys										0.500		
Primula acaulis				-	-	-	-			0.480		
Epipactis helleborine			-	-						0.444		
Galium maritimum											1.000	
Biscutella calduchii											0.966	
Brachypodium retusum											0.966	
Minuartia valentina											0.966	
Asplenium onopteris		-		-		-		-			0.881	
Helianthemum marifolium subsp *origanifolium*											0.856	
Teucrium chamaedrys						-	-				0.838	
Euphorbia flavicoma											0.816	
Ulex parviflorus									-		0.785	
Pinus pinaster s.l.		-		-				-			0.693	-
Cistus albidus											0.683	
Carex muricata subsp *pairae*			-	-							0.670	
Polypodium cambricum						-	-				0.653	
Rubus ulmifolius		-	-	-	-	-	-	-	-	-	0.634	
Hieracium glaucinum											0.632	
Viola alba											0.632	
Hieracium amplexicaule											0.577	
Sedum sediforme											0.577	
Silene inaperta											0.516	

Lonicera implexa								-			0.504	
Phleum phleoides	-		-	-							0.485	
Orobanche alba											0.447	
Arrhenatherum elatius subsp *bulbosum*	-	-	-	-	-	-	-					0.643
Phleum pratense												0.632
Potentilla rupestris												0.548
Helianthemum nummularium							-					0.529
Leontodon hispidus							-					0.523
Galium idubedae											-	0.507
Cephalanthera rubra		-	-				-				-	0.499
Lotus corniculatus				-		-	-					0.458
Ranunculus auricomus gr.												0.447
Thymelaea subrepens												0.447
Trifolium medium			-	-		-	-					0.442
Milium effusum							-					0.415
Acinos alpinus			-									0.409
Polygala vulgaris		-	-	-	-	-	-					0.401
Hypochaeris radicata	0.450	0.254		-								
Aquilegia vulgaris subsp *hispanica*			0.360	0.255								
Hyacinthoides non-scripta	-	-	0.326	0.285		-		-				
Agrostis castellana	0.597	-	-	0.311		-	-	-				
Ornithogalum pyrenaicum	0.273			0.357								
Galium mollugo	0.312	-		0.292		-						
Euphorbia oxyphylla	0.322	-		0.280								
Conopodium subcarneum	0.458	-	0.208	0.459		-						
Melittis melissophyllum		0.281	-	0.253		0.369	-					
Genista falcata	-	0.285		0.210		0.372						
Rumex acetosa	0.164	-	0.381	0.329	-		-					
Poa pratensis	0.125		0.359	0.234		-	-					
Paeonia broteri	-	0.472	-	0.211				0.208				
Physospermum cornubiense	-	-	-	0.488	-	0.364	0.242					
Melica uniflora		-	0.506	-		-	0.581					
Mercurialis perennis						0.128	0.233					
Stellaria holostea			-	-	-	0.401	0.679					
Festuca braun-blanquetii		-			-	0.528	0.494					
Lonicera periclymenum				-	0.291	0.268	0.324					
Vaccinium myrtillus					0.274	0.343	0.183					
Erica vagans					0.577	-	0.408					
Hypericum pulchrum				-	0.424	-	0.422					
Rosa arvensis					0.291		0.522					
Fagus sylvatica			-		0.253		0.452					
Deschampsia flexuosa			-		0.411	-	0.288					
Ranunculus tuberosus			-		0.434		0.227					
Pulmonaria longifolia			-		0.359	-	0.296					
Carex distachya	-	0.580	-	-				0.264				
Tamus communis	-	0.389	-	-	-		-	0.362				
Doronicum plantagineum		0.328	-	-		-	-	-	0.592			-

Daphne gnidium	-	0.379		-				0.539			0.261	
Quercus rotundifolia		-	-	-			-	0.432	0.192		0.361	
Quercus suber								0.508			0.647	
Helleborus foetidus			-	-		-	-		0.466	0.137		
Acer opalus subsp *granatense*									0.422	0.164		
Prunus spinosa			-	-	-	-	-			0.661	0.394	-
Rosa pouzinii		-	-						-	0.324	0.635	
Hedera helix	-	-	-	-	-	-	-		-	0.260	0.512	
Festuca durandoi		-									0.396	0.299
Rubia peregrina	-	-		-	-		-	-	-	0.337	0.539	0.233
Origanum virens	0.311	0.274		0.152		-		0.225	-			
Clinopodium vulgare subsp *arundanum*	0.549	0.398	0.239	0.242				-				
Holcus mollis	0.404	-	0.329	0.496	0.440	-	-		-			-
Dactylis glomerata	0.209	-	0.437	0.461	-	-	-				-	0.133
Genista florida	0.123	-	0.323	0.190		-						0.110
Conopodium pyrenaeum	0.245	-	0.265	0.167	-	-	-		0.123			0.312
Arenaria montana	0.492	-	0.458	0.269	-	-	0.242					0.280
Melampyrum pratense			-	-	0.366	0.453	0.544					0.194
Erica arborea	-	-	-	-	-	0.351	0.249	0.404			0.546	
Geranium robertianum		0.138	0.222	-	-	-	0.249				0.375	
Lathyrus linifolius		0.180	0.241	-	0.253	-	0.374					0.357
Veronica officinalis	0.067		0.172	-	-	0.204	0.276			0.192		0.223
Poa nemoralis	-	-	0.507	0.296		0.267	0.514			0.209		-
Cruciata glabra	0.445	0.249	0.328	0.284	0.193	0.404	0.125					
Teucrium scorodonia	0.173	0.257	-	0.442	0.328	-	0.421	0.122				
Pteridium aquilinum	0.465	0.315	0.247	0.309	0.396	-	-	-	-	0.220	-	
Brachypodium sylvaticum	-	0.200	0.389	0.124		0.117	0.290	0.121	-	0.270		
Lonicera periclymenum subsp *hispanica*	0.212	0.174	0.239	0.362	-	-	-	-	-	0.533		
Cytisus scoparius	0.406	0.164	0.161	0.371	-	0.174	0.173	-	0.141			
Anthoxanthum odoratum	0.344	0.250	-	0.251	-	0.120	0.282		0.118			0.156
Crataegus monogyna	-	-	0.230	0.203	0.362	0.141	0.189	-	0.210	0.496	0.212	0.195
Luzula forsteri	0.299	0.349	0.313	0.223	-	-	0.320	-	0.115	0.216	0.212	0.280

Appendix 4.2 exclusive species of each cluster

Group A List of species with specificity values (Ind Val, A component) over 0.5							
M7		**M1**		**M2**		**M6**	
Adenocarpus aureus	1.000	*Anisantha sterilis*	1.000	*Adenocarpus hispanicus*	1.000	*Anemone trifolia* subsp *albida*	1.000
Halimium umbellatum subsp. *viscosum*	1.000	*Asparagus acutifolius*	1.000	*Ajuga x rotundifolia*	1.000	*Anthericum liliago*	1.000
Helianthemum apenninum	1.000	*Asphodelus cerasiferus*	1.000	*Bellis sylvestris*	1.000	*Asphodelus ramosus*	1.000
Sedum amplexicaule	0.867	*Carlina corymbosa* subsp *hispanica*	1.000	*Biscutella valentina* subsp *pyrenaica*	1.000	*Biscutella laevigata*	1.000
Galium mollugo subsp *erectum*	0.750	*Celtis australis*	1.000	*Carlina vulgaris*	1.000	*Cucubalus baccifer*	1.000
Andryala integrifolia	0.735	*Cistus monspeliensis*	1.000	*Cytisus oromediterraneus*	1.000	*Euphorbia nevadensis*	1.000
Stipa gigantea	0.714	*Coincya monensis* var. *setigera*	1.000	*Festuca iberica*	1.000	*Genista hystrix*	1.000
Vicia angustifolia	0.613	*Conopodium capillifolium*	1.000	*Galeopsis ladanum*	1.000	*Hieracium schmidtii*	1.000
Erica umbellata	0.600	*Dactylis glomerata* subsp. *lusitanica*	1.000	*Geranium pyrenaicum*	1.000	*Muscari comosum*	1.000
Lavandula pedunculata	0.583	*Dianthus armeria*	1.000	*Koeleria crassipes*	1.000	*Nepetea coerulea*	1.000
Thymus pulegioides	0.579	*Dictamnus albus*	1.000	*Lathyrus sphaericus*	1.000	*Omphalodes nitida*	1.000
Festuca elegans subsp. *merinoi*	0.564	*Digitalis pupurea*	1.000	*Legousia scabra*	1.000	*Peucedanum lancifolium*	1.000
Pilosella officinarum	0.560	*Erysimum lagascae*	1.000	*Leontodon bourgaeanus*	1.000	*Pilosella castellana*	1.000
Malva tournefortiana	0.545	*Festuca paniculata* subsp *baetica*	1.000	*Linaria nivea*	1.000	*Rhaponticum exaltatum*	1.000
Carduus nutans subsp. *platypus*	0.500	*Lamium hybridum*	1.000	*Lotus pedunculatus*	1.000	*Thalictrum minus*	1.000
Hypochaeris radicata	0.500	*Legousia scabra*	1.000	*Mycelis muralis*	1.000	*Thalictrum speciosissimum*	1.000
Genista cinerascens	0.500	*Osyris alba*	1.000	*Myosotis ramosissima*	1.000	*Thesium humifusum*	1.000
		Bituminaria bituminosa	1.000	*Phleum serotinum*	1.000	*Torilis arvensis*	1.000
		Ranunculus gregarius	1.000	*Pimpinella major*	1.000	*Trachynia distachya*	1.000
		Rhagadiolus stellatus	1.000	*Polygonum bistorta*	1.000	*Ulex minor*	1.000
		Scrophularia scorodonia	1.000	*Rosa obtusifolia*	1.000	*Cytisus multiflorus*	0.844
		Stachys recta	1.000	*Rosa rubiginosa*	1.000	*Rubus castellarnaui*	0.824
		Vicia hirsuta	1.000	*Rosa tomentosa*	1.000	*Epilobium montanum*	0.800
		Viola lactea	1.000	*Rubus brigantinus*	1.000	*Pentaglottis sempervirens*	0.692
		Allium massaessylum	0.920	*Saxifraga dichotoma*	1.000	*Ornithogalum pyrenaicum*	0.690
		Hyacinthoides hispanica	0.909	*Silene legionensis*	1.000	*Myosotis arvensis*	0.667
		Cynosurus effusus	0.818	*Thlaspi stenopterum*	1.000	*Euphorbia oxyphylla*	0.548
		Ruscus aculeatus	0.811	*Viola suavis*	1.000	*Cytisus striatus*	0.545
		Urginea maritima	0.800	*Potentilla micrantha*	0.897	*Galium mollugo*	0.529
		Geranium purpureum	0.789	*Festuca rivas-martinezii*	0.864	*Sorbus aucuparia*	0.500
		Quercus faginea broteroi	0.714	*Moehringia trinervia*	0.838	*Genista tinctoria*	0.500
		Arabis nova iberica	0.667	*Geum urbanum*	0.789	*Carex leporina*	0.500
		Carex distachya	0.633	*Viola odorata*	0.730	*Rubus caesius*	0.500
		Conopodium arvense	0.600	*Festuca aggr rubra*	0.724	*Vicia sativa*	0.500
		Lathyrus aphaca	0.600	*Arrhenatherum elatius*	0.714	*Taxus baccata*	0.500
		Orchis mascula	0.600	*Urtica dioica*	0.714	*Cardamine hirsuta*	0.500
		Geranium lucidum	0.583	*Silene vulgaris*	0.706	*Cistus psilosepalus*	0.500
		Paeonia officinalis subsp *microcarpa*	0.571	*Ranunculus paludosus*	0.706	*Festuca ampla*	0.500
		Cardamine hirsuta	0.500	*Lactuca viminea*	0.684	*Carduus nutans* subsp *platypus*	0.500
		Cistus psilosepalus	0.500	*Primula veris* s.l.	0.667		
		Orobanche rapum-genistae	0.500	*Sanguisorba minor*	0.667		
		Stellaria media	0.500	*Epilobium lanceolatum*	0.667		
		Torilis japonica	0.500	*Geranium pyrenaicum* subsp *lusitanicum*	0.667		
				Aquilegia vulgaris hispanica	0.611		
				Arum cylindraceum	0.588		
				Sanicula europaea	0.585		
				Trisetum flavescens	0.576		
				Allium scorzonerifolium	0.556		
				Ajuga pyramidalis	0.538		
				Milium vernale	0.538		
				Juniperus communis subsp *hemisphaerica*	0.531		
				Anthriscus caucalis	0.500		
				Dryopteris filix-mas	0.500		
				Phleum phleoides	0.500		
				Acinos alpinus	0.500		
				Asphodelus aestivus	0.500		
				Genista cinerascens	0.500		
				Genista tinctoria	0.500		
				Potentilla argentea	0.500		
				Ranunculus ficaria	0.500		
				Rosa blondaeana	0.500		
				Saponaria ocymoides	0.500		

Group B. List of species with specificity values (A) over 0.5.

M10		M12		M3	
Acer pseudoplatanus	1.000	*Allium victorialis*	1.000	*Biscutella auriculata*	1.000
Agrostis canina	1.000	*Astrantia major*	1.000	*Brachypodium phoenicoides*	1.000
Agrostis xfouilladei	1.000	*Campanula glomerata*	1.000	*Briza media*	1.000
Alnus glutinosa	1.000	*Carex praecox*	1.000	*Centaurea jacea*	1.000
Betula alba	1.000	*Centaurea montana*	1.000	*Ceratocapnos claviculata*	1.000
Carex pilulifera	1.000	*Chamaespartium sagittale*	1.000	*Chaerophyllum aureum*	1.000
Carex sylvatica	1.000	*Dactylorhiza maculata*	1.000	*Cynosurus cristatus*	1.000
Centaurea debeauxii	1.000	*Galium parisiense*	1.000	*Cytinus hypocistis* subsp. *macranthus*	1.000
Cirsium filipendulum	1.000	*Genista micrantha*	1.000	*Daucus carota*	1.000
Colchicum autumnale	1.000	*Halimium lasianthum*	1.000	*Dianthus carthusianorum*	1.000
Hedera hibernica	1.000	*Hieracium umbellatum*	1.000	*Dianthus hyssopifolius*	1.000
Jasione laevis	1.000	*Laserpitium latifolium*	1.000	*Festuca nigrescens*	1.000
Luzula multiflora	1.000	*Laserpitium nestleri*	1.000	*Galium aparine spurium*	1.000
Molinia caerulea	1.000	*Ornithogalum bourgaeanum*	1.000	*Gymnocarpium dryopteris*	1.000
Peucedanum gallicum	1.000	*Piptatherum paradoxum*	1.000	*Jacobaea adonidifolia*	1.000
Pimpinella saxifraga	1.000	*Ranunculus platanifolius*	1.000	*Knautia nevadensis* subsp. *nevadensis*	1.000
Pyrus cordata	1.000	*Sedum rupestre*	1.000	*Limodorum abortivum*	1.000
Quercus ilex	1.000	*Senecio lividus*	1.000	*Melampyrum cristatum*	1.000
Quercus xnumantina	1.000	*Silene italica*	1.000	*Myosotis decumbens*	1.000
Thalictrum tuberosum	1.000	*Thesium pyrenaicum*	1.000	*Plantago lanceolata*	1.000
Thymelaea ruizii	1.000	*Thymus praecox*	1.000	*Platanthera bifolia*	1.000
Ulex europaeus	1.000	*Veronica alpina*	1.000	*Polystichum aculeatum*	1.000
Ulex gallii subsp. *breoganii*	1.000	*Vicia pyrenaica*	1.000	*Ribes alpinum*	1.000
Ulex gallii subsp. *gallii*	1.000	*Luzula sylvatica* subsp. *henriquesii*	0.880	*Rubus gr. hirtus*	1.000
Xolantha sect. tuberaria	1.000	*Halimium umbellatum*	0.789	*Rubus gr. rubus*	1.000
Danthonia decumbens	0.967	*Vicia orobus*	0.781	*Seseli cantabricum*	1.000
Euphorbia dulcis	0.961	*Jasione montana*	0.773	*Succisa pratensis*	1.000
Serratula tinctoria	0.933	*Euphorbia hyberna*	0.750	*Veronica serpyllifolia*	1.000
Carex flacca	0.929	*Teesdalia nudicaulis*	0.750	*Viola hirta*	1.000
Quercus robur	0.905	*Oxalis acetosella*	0.727	*Viscum album*	1.000
Agrostis curtisii	0.892	*Ranunculus nigrescens*	0.714	*Galium estebanii*	0.909
Brachypodium pinnatum subsp. *rupestre*	0.886	*Aquilegia vulgaris* subsp. *dichroa*	0.667	*Genista hispanica* subsp. *occidentalis*	0.750
Euphorbia amygdaloides	0.881	*Luzula campestris*	0.667	*Heracleum sphondylium*	0.714
Pseudarrhenatherum longifolium	0.879	*Narcissus triandrus*	0.667	*Polystichum setiferum*	0.714
Carex caryophyllea	0.867	*Nardus stricta*	0.667	*Ranunculus acris*	0.714
Potentilla montana	0.852	*Periballia involucrata*	0.667	*Polypodium vulgare*	0.680
Daboecia cantabrica	0.852	*Stachys sylvatica*	0.600	*Rosa arvensis*	0.670
Erica cinerea	0.851	*Glandora diffusa*	0.577	*Asplenium adiantum-nigrum*	0.667
Rosa squarrosa	0.824	*Leucanthemum vulgare*	0.571	*Fraxinus excelsior*	0.667
Potentilla erecta	0.823	*Crepis lampsanoides*	0.543	*Lonicera xylosteum*	0.667
Viola canina	0.807	*Primula acaulis*	0.529	*Genista florida* subsp. *polygaliiphylla*	0.660
Agrostis capillaris	0.774	*Erythronium dens-canis*	0.500	*Galium verum*	0.645
Quercus xandegavensis	0.750	*Orobanche rapum-genistae*	0.500	*Quercus petraea*	0.643
Euonymus europaeus	0.714	*Anthriscus caucalis*	0.500	*Mercurialis perennis*	0.625
Rubus lainzii	0.714	*Cardamine flexuosa*	0.500	*Arctostaphylos uva-ursi*	0.619
Frangula alnus	0.621	*Carex leporina*	0.500	*Fragaria vesca*	0.594
Simethis mattiazzii	0.617	*Dryopteris filix-mas*	0.500	*Fagus sylvatica*	0.593
Dryopteris affinis	0.600	*Polygala microphylla*	0.500	*Stellaria holostea*	0.588
Pyrus communis	0.600	*Quercus xtrabutii*	0.500	*Primula veris columnae*	0.578
Symphytum tuberosum	0.600	*Rubus caesius*	0.500	*Helleborus viridis* subsp. *occidentalis*	0.561
Corylus avellana	0.586	*Vicia sativa*	0.500	*Ligustrum vulgare*	0.550
Ranunculus tuberosus	0.577			*Asphodelus aestivus*	0.500
Solidago virgaurea	0.571			*Potentilla argentea*	0.500
Acer campestre	0.563			*Ranunculus ficaria*	0.500
Glandora prostrata	0.556			*Rosa blondaeana*	0.500
Galium saxatile	0.556			*Saponaria ocymoides*	0.500
Ilex aquifolium	0.552			*Veronica chamaedrys*	0.500
Erica vagans	0.532			*Cardamine flexuosa*	0.500
Cornus sanguinea	0.500			*Quercus xtrabutii*	0.500
Rhamnus catharticus	0.500			*Knautia arvensis*	0.500
Taxus baccata	0.500			*Cornus sanguinea*	0.500
				Stellaria media	0.500
				Bellis perennis	0.500
				Geranium rotundifolium	0.500

Group C: List of species with specificity values (Ind Val, A component) over 0.5

M8		**M9**	
Avenula marginata subsp *albinervis*	1.000	*Adenocarpus decorticans*	1.000
Brachypodium gaditanum	1.000	*Anacyclus clavatus*	1.000
Carlina racemosa	1.000	*Anthriscus sylvestris*	1.000
Cistus populifolius subsp *major*	1.000	*Aristolochia baetica*	1.000
Digitalis mariana	1.000	*Armeria alliacea*	1.000
Erica scoparia	1.000	*Artemisia barrelieri*	1.000
Erophaca baetica	1.000	*Artemisia campestris* subsp *glutinosa*	1.000
Genista tridens	1.000	*Biscutella sempervirens*	1.000
Gladiolus illyricus	1.000	*Brachypodium boissieri*	1.000
Helichrysum stoechas	1.000	*Carduus nigrescens* subsp *hispanicus*	1.000
Juniperus oxycedrus subsp *macrocarpa*	1.000	*Carex muricata*	1.000
Lavandula stoechas	1.000	*Cerastium gibraltaricum*	1.000
Lonicera etrusca	1.000	*Cytisus grandiflorus*	1.000
Luzula forsteri subsp *baetica*	1.000	*Dactylorhiza insularis*	1.000
Osmunda regalis	1.000	*Euphorbia characias*	1.000
Pimpinella villosa	1.000	*Festuca elegans*	1.000
Pistacia terebinthus	1.000	*Festuca scariosa*	1.000
Poa trivialis	1.000	*Hedypnois rhagadioloides*	1.000
Pyrus bourgaeana	1.000	*Leontodon boryi*	1.000
Quercus canariensis	1.000	*Lobaria pulmonaria*	1.000
Quercus xfontqueri	1.000	*Lonicera arborea*	1.000
Rosmarinus officinalis	1.000	*Marrubium supinum*	1.000
Senecio lopezii	1.000	*Nepeta tuberosa*	1.000
Silene aellenii	1.000	*Nepetea granatensis*	1.000
Stauracanthus boivinii	1.000	*Ononis natrix*	1.000
Teucrium fruticans	1.000	*Paeonia coriacea*	1.000
Ulex borgiae	1.000	*Primula veris veris*	1.000
Viburnum tinus	1.000	*Ptilostemon hispanicus*	1.000
Vicia disperma	1.000	*Rosa deseglisei*	1.000
Cistus ladanifer	0.943	*Salix atrocinerea*	1.000
Phillyrea angustifolia	0.932	*Salix caprea*	1.000
Arbutus unedo	0.882	*Smyrnium perfoliatum*	1.000
Cistus populifolius	0.846	*Thymus serpylloides*	1.000
Cytisus eriocarpus	0.833	*Thymus zygis*	1.000
Pterospartum tridentatum	0.750	*Vicia onobrychioides*	1.000
Cynosurus echinatus	0.727	*Acer granatense*	0.909
Calamintha nepeta nepeta	0.714	*Myrrhoides nodosa*	0.783
Epipactis tremolsii	0.714	*Cystopteris fragilis*	0.778
Lavandula stoechas luisieri	0.667	*Digitalis purpurea purpurea*	0.733
Cistus salviifolius	0.596	*Arrhenatherum album*	0.682
Quercus suber	0.593	*Alliaria petiolata*	0.600
Vincetoxicum nigrum	0.571	*Daphne laureola*	0.538
Conopodium marianum	0.538	*Eryngium campestre*	0.500
Juniperus oxycedrus	0.533		
Geranium rotundifolium	0.500		
Rosa micrantha	0.500		
Polygala microphylla	0.500		

Group D: List of species with specificity values (Ind Val, A component) over 0.5

M4		**M11**		**M5**	
Catananche caerulea	1.000	*Aira elegantissima*	1.000	*Conopodium majus* subsp. *marizianum*	1.000
Cistus crispus	1.000	*Anagallis arvensis*	1.000	*Dactylorhiza elata*	1.000
Cytisus scoparius subsp. *reverchonii*	1.000	*Antirrhinum litigiosum*	1.000	*Geum hispidum*	1.000
Monotropa hypopitys	1.000	*Arenaria serpyllifolia*	1.000	*Nepeta latifolia*	1.000
Prunus insititia	1.000	*Asplenium trichomanes*	1.000	*Phleum pratense*	1.000
Prunus mahaleb	1.000	*Asterolinon linum-stellatum*	1.000	*Plantago media*	1.000
Rubus canescens	1.000	*Atractylis humilis*	1.000	*Potentilla rupestris*	1.000
Origanum vulgare	0.857	*Biscutella calduchii*	1.000	*Ranunculus auricomus gr.*	1.000
Filipendula vulgaris	0.792	*Brachypodium retusum*	1.000	*Rhinanthus pumilus*	1.000
Quercus xneomairei	0.789	*Carduus defloratus paui*	1.000	*Stellaria graminea*	1.000
Amelanchier ovalis	0.778	*Cistus albidus*	1.000	*Thymelaea subrepens*	1.000
Agrimonia eupatoria	0.750	*Crepis pulchra*	1.000	*Trifolium montanum*	1.000
Berberis hispanica	0.692	*Euphorbia flavicoma*	1.000	*Trifolium repens*	1.000
Geranium sylvaticum	0.625	*Festuca arundinacea*	1.000	*Galium idubedae*	0.800
Viburnum lantana	0.585	*Galium maritimum*	1.000	*Helianthemum nummularium*	0.750
Elymus caninus	0.563	*Genista hispanica*	1.000	*Leontodon hispidus*	0.692
Quercus faginea	0.545	*Helianthemum marifolium* subsp *origanifolium*	1.000	*Inula salicina*	0.600
Sorbus torminalis	0.526	*Hieracium amplexicaule*	1.000	*Milium effusum*	0.571
		Hieracium glaucinum	1.000	*Bellis perennis*	0.500
		Leontodon saxatilis subsp *rothii*	1.000	*Acinos alpinus*	0.500
		Lotus angustissimus	1.000		
		Minuartia valentina	1.000		
		Narduroides salzmannii	1.000		
		Orobanche alba	1.000		
		Scrophularia tanacetifolia	1.000		
		Sedum sediforme	1.000		
		Silene inaperta	1.000		
		Sorbus domestica	1.000		
		Viola alba	1.000		
		Ulex parviflorus	0.893		
		Teucrium chamaedrys	0.880		
		Polypodium cambricum	0.778		
		Helichrysum italicum subsp. *serotinum*	0.667		
		Lonicera implexa	0.667		
		Pinus pinaster s.l.	0.618		
		Quercus pyrenaica arbustivo	0.611		
		Asplenium onopteris	0.610		
		Eryngium campestre	0.500		

CAPÍTULO V / CHAPTER V

Chapter V: *Minuartio valentinae-Quercetum pyrenaicae*: A new Iberian broad-leaved oak forests in the eastern coastal mountains and their seral plant communities.

Abstract

The study of *Quercus pyrenaica* forests in eastern areas of the Iberian Peninsula has differentiated a set of relevés from Castellón. They are located in subhumid sites in the upper mesomediterranean to low supramediterranean thermotype territories of Sierra de Espadán, in the Valenciano-Tarraconense biogeographical sector. A new forest *Minuartio valentinae-Quercetum pyrenaicae* is therefore described here, together with its main seral communities.

Key words: broad-leaved oak forests, Mediterranean vegetation, new association, community ecology, Sierra de Espadán.

Resumen

El estudio de los bosques de *Quercus pyrenaica* del centro y este ibérico ha discriminado un conjunto de inventarios procedentes de Castellón. Están situados en emplazamientos de termotipos mesomediterráneo superior-supramediterráneo inferior y ombrotipo subhúmedo de la Sierra de Espadán, incluidos en el sector biogeográfico Valenciano-Tarraconense. Así, se describe la nueva asociación de melojares *Minuartio valentinae-Quercetum pyrenaicae* y las comunidades seriales que forman una nueva serie de vegetación para la Península Ibérica.

Palabras clave Bosques marcescentes, melojares, vegetación mediterránea, nueva asociación, ecología de las comunidades, Sierra de Espadán.

Introduction

The distribution of the marcescent Pyrenean oak on the Iberian Peninsula is concentrated mainly in sites with a sub-Mediterranean climate (moderate or compensated summer drought) in the northwest. This, together with its preference for siliceous soils (less common in the east), means that only reduced samples remain in eastern mountain zones, and usually in protected areas surrounded by evergreen (generally basophile) vegetation. They appear over 1000 m.a.s.l. and have traditionally been included in the supra-mediterranean association *Cephalanthero rubrae-Quercetum pyrenaicae*. All are at risk of local extinction due to their level of isolation (mainly edaphic) and fragmentation (Pérez Badía, 2003). The Prades mountains in Catalonia, Pina, Penyagolosa, Castielfabib, and Tuéjar in Valencia are sites for which there is bibliographic evidence of the presence of this oak forest (Braun-Blanquet, 1934, Font Quer, 1934, Bolòs, 1967, Vigo, 1968, Costa et al. 1985, Herreros, 2010; Roselló, 1994, Mateo & Aguilella, 1990), and Prades and Penyagolosa are its best representations in the eastern Iberian peninsula. Its composition is high in nemoral herbs, and often includes other phanerophytes in the arboreal stratum with which it is in contact, mainly *Pinus sylvestris* s.l., in addition to *Juniperus communis*. Different *Cytisus* and *Erica* appear frequently in the shrub layer, also accompanied by the typical spiny border shrubs *Crataegus monogyna* or *Prunus spinosa*.

Although the vegetation of the Sierra de Espadán has been studied, as a whole, by various authors (Beltrán, 1911; Rivas Goday & Borja, 1961; Bolòs, 1967, 1975, Bolòs & Vigo, 1979, Mateo & Aguilella, 1990), its oak forests are the least studied of all those on the eastern Iberian Peninsula. This can be explained by its isolated location and relatively difficult access, and partly because historically this has been a managed area, as it is located in cooler locations that are ideal for farming (Merle & Ferriol, 2008), reducing the forest area, currently under regeneration.

The Espadán Triassic mountain range, although not very high in altitude (highest peak: La Rápita at 1106 m.a.s.l.) captures more rain and humidity than nearby territories. Its NW-SE orientation leads to an annual average rainfall of over 600 mm on the lower slopes, in addition to the contribution of the frequent mists in the area. Espadán soils comprise mainly Buntsandstein sandstones and argilites, characterized by neutral pH, and locally by the formation of deep argillic horizons that allow good water reserves. Both these factors are instrumental in making cork oak the main vegetation in the mountain range, with a predominance of maritime pine (*Pinus pinaster* s.l.) in drier areas. Heathlands are found on the forest fringes; they are the main substitution shrubs for cork oak forests (Costa et al. 1985) in sites with a cooler microclimate and for *Quercus pyrenaica* formations. Several authors have highlighted the special floristic character of this site where Temperate, Iberian-Moroccan and endemic species converge (Rivas-Goday & Borja, 1961; Mateo & Aguilella, 1990); some have also delimited an independent chorologic element inside the Valenciano-Tarraconense sector, supported by endemics such as *Minuartia valentina*, *Centaurea paui*, *Dianthus multiaffinis* or *Biscutella calduchii* (O. Bolòs & Masclans) Mateo & M.B. Crespo (Roselló 1994; Costa et al. 1985).

The main aim of our paper is to describe a new association of broad-leaved oak forests in the Sierra de Espadán. This objective was developed as part of a larger study of all the *Quercus pyrenaica* forests on the Iberian Peninsula. The results of this study emphasised the significant floristic difference between the forests described here and the rest, even when they appear at similar altitudes and bioclimatic belts. We have also analysed –from a purely phytosociological point of view– the following main seral plant communities: heathlands appearing as forest fringes or as a substitution plant community when the forest is destroyed; and shrublands representing a more degraded stage.

Materials and methods

We compiled a data set of published relevés on *Quercus pyrenaica* forests in eastern areas of the Iberian Peninsula (Table 1). These relevés were previously analysed to check the relationships between central and eastern *Quercus pyrenaica* forests (Vilches et al. 2013).

No	Original assignment	Locality	Province	Distance to coast	Altitude	References
1	*Luzulo forsteri-Quercetum*	Guadarrama	Madrid	480 km	1170-1500 mosl	Fernández-González, 1991
2	*Luzulo forsteri-Quercetum*	Ayllón	Guadalajara	430 km	960-1350 mosl	Fuente, 1985
3	*Luzulo forsteri-Quercetum*	Albarracín	Teruel	235 km	1500-1700 mosl	Barrera, 1983
4	*Luzulo forsteri-Quercetum*	Boniches	Cuenca	170 km	1000-1200 mosl	López, 1976
	Luzulo forsteri-Quercetum	Ranera		120 km	1280-1380 mosl	Mateo, 1983
5	*Cephalanthero-Quercetum*	Penyagolosa	Castellón	58 km	1250-1500 mosl	Vigo, 1968
6	*Cephalanthero-Quercetum*	Prades	Tarragona	27 km	950-1050 mosl	Braun-Blanquet, 1934; Font Quer, 1934, Bolos, 1967
7	None	Espadán	Castellón	35 km	900-1106 mosl	Merle & Ferriol, 2008

Table 4.1. Summary of data gathering according to the locations studied.

We used Principal Components Analysis (PCA) on the site-by-species matrix containing presence-absence values to display the compositional variation among the *Quercus pyrenaica* woodlands in the study. Using indicator species analyses with site group combinations ('multipatt' function of the R package 'indicspecies') we determined the indicator species of each massif, in addition to the common species in forests belonging to those different massifs. The number and identity of the indicators suggest how the different geographical locations could be related.

For the seral communities we studied the data published in the Catalano-Valenciano biogeographical subprovince (Valenciano-Tarraconense sector), which includes: Braun-Blanquet (1940), Zeller (1959), Bolòs (1967) Mateo (1983), Mateo & Mansanet (1982), Costa & *al.* (1985), García-Fayos (1991), Merle & Ferriol (2008).

We follow the taxonomic nomenclature proposed by the published issues of Flora Ibérica (Castroviejo et al. 1986-2013) if the authority is not indicated; and the compilation of the Euro+Med PlantBase (2006-2013) for the rest, in addition we follow the proposals of Rivas-Martínez et al. both for Biogeography (2007) and Bioclimatology (2011b).

Results & Discussion

Minuartio valentinae-Quercetum pyrenaicae ass. nova hoc loco

[*Holotypus ass.* Table 2, rel. 2; (Merle & Ferriol 2008)]

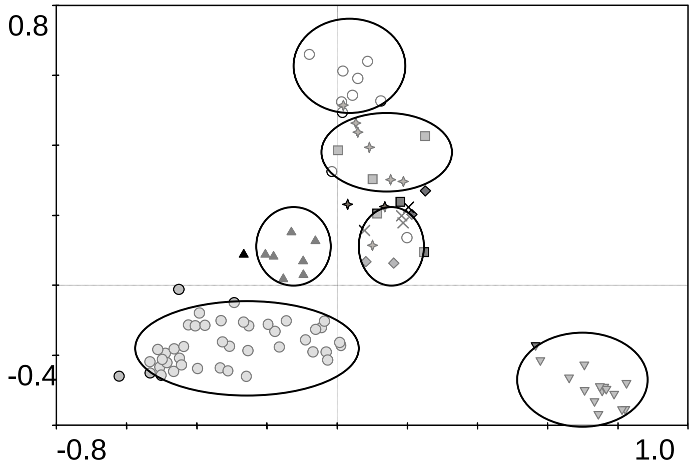

Figure 5.1 First two axes of the Principal Component Analysis carried out with data from Sierra de Espadán (downward triangles), Sierra de Prades (solid boxes), Sistema Ibérico: Penyagolosa (open circles), Albarracín Massif (stars) and Serranía de Cuenca: Boniches (X-marks), Ranera (diamonds), Sistema Central: Ayllón (upward triangles), Guadarrama (solid circles).

The first axis of the PCA (Fig. 5.1) separated the pre-coastal relevés with the lowest altitudes –Sierra de Espadán (downward triangles)– in the most positive part of the diagram, with the most central relevés –Sierra de Guadarrama (solid circles) and Sierra de Ayllón (upward triangles)– in the negative part. The relevés assigned to *Cephalanthero-Quercetum pyrenaicae* O. Bolòs & Vigo in O. Bolòs 1967 and *Luzulo-Quercetum pyrenaicae* Rivas-Martínez 1964 in the eastern localities of Cuenca, Teruel, Valencia and Catalonia appeared only in the middle, leaving Penyagolosa, the highest peak in the upper section. Thus the first PCA axis could be interpreted as a continentality-oceanity gradient, with relevés from the Sierra de Espadán near the coast, and clearly separated from the relevés of the central Iberian Peninsula.

The second axis could be related to a Mediterranean (aridity) gradient, with relevés with shorter or compensated summer drought located in the most positive part, clearly separated from the Sierra de Espadán and Sistema Central, which undergo higher summer dryness. Most of these forests are located at higher altitudes than the coastal Sierra de Espadán (fig. 5.1), where retention of clouds formed by evaporation from the Mediterranean Sea becomes a factor of vital importance to compensate aridity. Precipitation and fog increase the atmospheric humidity of these mountains, where it is common to find ferns and other cryptogrammic species such as *Asplenium onopteris*, *Polypodium cambricum* or *Polypodium vulgare* (Mateo & Aguilella 1991).

The Sierra de Espadán generated the maximum number of exclusive indicator species, including a high number of endemisms that separated it from relevés ascribed to *Cephalanthero-Quercetum pyrenaicae* from Penyagolosa and Prades (Vilches et al. 2013). Both mountains have almost three months of frost risk in winter, and both *Quercus pyrenaica* forests are related to *Pinus sylvestris s.l.* and *Cistion laurifolii* seral communities. Only the pre-coastal location of Prades (Cataluña) shares certain species with Espadán –such as *Rosa pouzinii, Cistus albidus* or *Asplenium onopteris*– in addition to some thermophilous and calcareous species, although the analysis (fig. 5.2) confirmed a differentiated floristic composition of the latter. In fact this difference was also apparent when this community was compared to the whole Iberian Peninsula (Vilches et al. in press).

Minuartio valentinae-Quercetum pyrenaicae corresponds to silicicolous subhumid forests of *Quercus pyrenaica*, appearing over rodenos in the upper mesomediterranean to lower supramediterranean belts of the Sierra de Espadán (Castellón). It is found in sites with reduced continentality and increased humidity due to crypto-precipitations and also to the deep limy soils. Its distribution is thus reduced and localized, specifically on the northern slope of the highest peak: La Rápita (as indicated by Mateo & Aguilella 1990; Roselló 1994). The territory has been cultivated for centuries, and some individuals of *Quercus pyrenaica* can be found growing on abandoned terraces. The forests have a strong level of regeneration and usually include evergreen phanerophytes from the forests with which they are in contact, such as *Quercus suber*, *Quercus rotundifolia* and *Pinus pinaster s.l.*, in addition to shrubs (*Erica arborea*, *Ulex parviflorus*, *Prunus spinosa*). *Quercetea ilicis* species are widely represented in these forests, in contrast with the *Quercus pyrenaica* locations of the supramediterranean *Cephalanthero-Quercetum pyrenaicae* (Penyagolosa or Prades), which have an increased Eurosiberian species composition (Vilches et al. 2013). Thus the absence of some species such as *Astragalus glycyphyllos, Primula veris* subsp. *columnae*, *Veronica officinalis, Poa nemoralis, Campanula trachelium* and *Lapsana communis*, together with its chorology and dynamism, differentiate it from *Cephalanthero-Quercetum pyrenaicae.*

As is known, Pyrenean oak requires a minimum annual rainfall of 600 mm to become established, as well as a site that compensates the Mediterranean summer drought (Costa 1997). The timing of the rainfall in this area (autumn-spring-winter-summer) facilitates a faster recovery of water reserves (Roselló 1994), enough for *Minuartio-Quercetum pyrenaicae* to grow in the most humid sites throughout the entire Sierra de Espadán, specifically sub-humid locations (Vall de Almonacid, 670 mm; Bolòs & Vigo 1979; Ninyerola & al. 2005).

There is an absence of most of the drought tolerant species of the Valenciano-Tarraconense sector such as *Phillyrea angustifolia* (including the subhumid *P. latifolia*), *Rhamnus alaternus* or *Pistacia lentiscus*; but also a lack of thermophilic shrubs frequent in other mesomediterranean *Quercus pyrenaica* forests (*Arbutus unedo*, *Viburnum tinus*). On southern slopes or in more exposed areas, these forests come into contact with the Valencian cork forests of *Asplenio onopteridis-Quercetum suberis*, and also with *Hedero-Quercetum rotundifoliae* in drier areas. Our community shares more species with the former, mainly in the understory, where the rocky silicicolous substrate allows the inclusion of *Minuartia valentina* and other related Espadán endemisms such as *Biscutella calduchii* or *Scrophularia tanacetifolia*; it also shares the heathland fringe community described below.

Hedero helicis -Ericetum arboreae (Costa, Peris, Figuerola & Stübing 1985) Rivas-Mart. et al. 2011 (=*Cytiso villosi-Ericetum arboreae* Costa, Peris, Figuerola & Stübing 1985 non Zéller 1959)

We agree with Costa et al. (1985) regarding the floristic composition of seral scrub plant communities that form part of the vegetation series of *Minuartio-Quercetum pyrenaicae*. *Hedero-Ericetum* is not only the first degraded plant community of *Asplenio-Quercetum suberis* in the Sierra de Espadán; it is also present as a seral state of *Minuartio-Quercetum*, although impoverished in scrubs such as *Cytisus villosus* or *Ruscus aculeatus* (Merle & Ferriol 2008). It is found in shady areas where soils retain enough water, and has a coastal influence in the upper mesomediterranean to lower supramediterranean bioclimatic belt. They are included in *Quercetea ilicis* and not in *Cytisetea* as it could be expected (Rivas-Martínez et al. 2011b; Gavilán et al. 2011).

We followed the criteria of Rivas-Martínez et al. (2011) to distinguish Espadán heathlands (*Cytiso villosi-Ericetum arboreae* Costa, Peris, Figuerola & Stübing 1985), from the species reported by Zeller (1959) to describe a similar plant community in Catalonia dominated by *Erica arborea* and *Cytisus villosus*, together with other brooms such as *Teline monspessulana* and *Cytisus scoparius* subsp. *reverchonii*. Espadán heathlands are lacking most of these species, although may include *Cytisus villosus*. Moreover, as mentioned above, in the territory of *Minuartio-Quercetum pyrenaicae* there is an absence of drought-tolerant and thermophilic species inside the *Hedero-Ericetum,* such as *Ruscus aculeatus*, *Smilax aspera*, *Clematis flammula*, etc. (Table 5.2).

Ulici parviflorae-Cistetum albidi ass. nova hoc loco
[*Holotypus ass.* Table 5.4, rel. 1; (Merle & Ferriol 2008)]

They represent rockrose-gorse shrublands that appear in a more degraded stage than *Hedero-Ericetum arboreae*. Of all the associations described in the area, the relevés included in the new association *Ulici-Cistetum* are close to those of *Pino pinastri-Cistetum salvifolii* Bolòs 1967 given by Costa et al. (1985) and recently synonymized by Rivas-Martínez & al. (2002) to *Calicotomo spinosae-Cistetum crispi* Br.-Bl. 1940. The original relevés given by Braun-Blanquet in 1940 showed the dominance of *Calicotome spinosa*, *Cistus crispus*, and even *Erica cinerea* in Catalonia (on granitic soils). Bolòs (1967) included maritime pine (*Pinus pinaster s.l.*), *Lavandula stoechas* and *Erica arborea* to the set, and indicated in a previous work the enormous local variability of this association, in which he suggested including gorse bushes with various *Cistaceae* that appeared in Espadán and neighbouring mountains

(Bolòs 1957; Rivas-Martínez 1979). In our case, the community lacks these species (*Calicotome spinosa, Cytisus villosus or Lavandula stoechas*) and is particularly enriched with *Rosmarinetea* species such as *Cistus albidus* and *Ulex parviflorus*.

The absence of thermophilous taxa such as *Calicotome spinosa* or *Cistus crispus* in *Ulici-Cistetum* can be also explained in terms of altitude (900-1106 m.a.s.l.), with the latter found at higher altitudes than taxa of *Calicotomo-Cistetum*. Frequent fires also favour the dominance of *Ulex parviflorus* and *Cistus albidus*, which are quite common in some areas of the Sierra de Espadán such as La Rápita (Merle & Ferriol 2008).

Conclusions

Minuartio valentinae-Quercetum pyrenaicae can be framed perfectly in the *Quercion pyrenaicae* alliance, which includes mesophytic *Quercus pyrenaica* forests from the meso- to supramediterranean bioclimatic belts. Previous studies (Herreros 2010; Vilches et al. 2013) already reflected a clear distinction between this and the adjacent communities, specifically *Luzulo forsteri-Quercetum pyrenaicae* and *Cephalanthero rubrae-Quercetum pyrenaicae*.

The series 'Minuartio valentinae-Querco pyrenaicae sigmetum' corresponds to silicicolous subhumid forests of *Quercus pyrenaica*, appearing on rodenos in the upper mesomediterranean to lower supramediterranean bioclimatic belts of the Sierra de Espadán (Valenciano-Tarraconense biogeographical sector). *Hedero helicis-Ericetum arboreae* and *Ulici parviflorae-Cistetum albidii* are their main seral plant communities.

Syntaxonomical scheme

QUERCO-FAGETEA SYLVATICAE Br.-Bl. & Vlieger in Vlieger 1937
  Quercetalia roboris Tx. in Barner 1931
    Quercion pyrenaicae Rivas Goday ex Rivas-Mart. 1964
      Minuartio valentinae-Quercetum pyrenaicae Vilches, Merle, Ferriol, Sánchez-Mata & Gavilán *ass. nova*
QUERCETEA ILICIS Br.-Bl. ex A. & O. Bolòs, 1950
  Pistacio lentisci-Rhamnetalia alaterni Rivas-Mart. 1975
    Ericion arboreae (Rivas-Mart. ex Rivas-Mart. & al. 1986) Rivas-Mart. 1987
      Hedero helicis-Ericetum arboreae Costa & al. 1985 in Rivas-Mart. 2011
CISTO-LAVANDULETEA Br.-Bl. in Br.Bl., Molinier &Wagner 1940
  Lavanduletalia stoechadis Br.-Bl. in Br.Bl., Molinier &Wagner 1940 em. Rivas-Martínez 1968
    Cistion ladaniferi Br.-Bl. ex A. & O. Bolòs 1950
      Ulici parviflorae-Cistetum albidi Vilches, Merle, Ferriol, Sánchez-Mata & Gavilán *ass. nova*

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Appendix Chapter V

Table 2
Minuartio valentinae-Quercetum pyrenaicae ass. nova
(*Quercion pyrenaicae, Quercetalia roboris, Querco-Fagetea*)

Plot size (m^2)	50	50	50	50	50
Exposure	N	N	N	N	N
Slope	30	30	30	30	30
Relevé N.	1	2	3	4	5
Characteristics					
Quercus pyrenaica	5	5	5	4	5
Hedera helix	1	1	+	1	+
Hieracium glaucinum	+	.	.	1	+
Luzula forsteri	1	+	.	1	.
Moehringia trinervia	.	.	.	+	+
Biscutella calduchii	1	+	+	+	+
Minuartia valentina	4	3	2	.	+
Polypodium cambricum subsp. *cambricum*	+	+	+	.	.
Hieracium amplexicaule	.	+	.	.	+
Differentials					
Erica arborea	2	+	2	1	2
Asplenium onopteris	1	1	1	1	1
Rubia peregrina	+	+	+	1	1
Galium maritimum	+	+	+	1	+
Quercus suber	1	.	+	2	1
Quercus rotundifolia	.	.	.	2	1
Daphne gnidium	.	.	1	+	.
Lonicera implexa	+	+	.	.	.
Companions					
Brachypodium retusum	3	.	3	2	2
Pinus pinaster s.l.	1	.	1	1	2
Carex muricata	+	+	.	1	+
Prunus spinosa	1	.	1	+	+
Rubus ulmifolius	1	.	+	+	+
Teucrium chamaedrys	+	.	+	+	+
Geranium robertianum	.	+	.	+	+
Crataegus monogyna	.	+	1	+	.
Euphorbia flavicoma	+	.	+	+	.
Ulex parviflorus	1	+	1	.	.
Helianthemum origanifolium	+	+	+	.	.
Phleum phleoides	.	.	.	+	+
Orobanche alba	.	.	+	.	+
Sedum sediforme	.	+	.	.	+
Silene inaperta	+	.	.	.	+
Festuca paniculata subsp. *durandii*	.	+	.	+	.
Cistus albidus	+	.	+	.	.

Other species*:* *Crepis pulchra*, *Carduus paui* and *Helichrysum italicum* + in 2; In 3*:* *Cephalanthera rubra*, *Thapsia villosa* and *Viola alba subsp. dehndartii* + in 3; *Sorbus domestica* + in 4; *Hieracium sabaudum*, *Pteridium aquilinum*, *Juniperus oxycedrus Atractylis humilis*, *Anagallis arvensis*, *Asterolinon linum-stellatum*, *Aira elegantissima*, *Narduroides salzmannii*, *Lotus angustissimus* and *Leontodon taraxacoides* subsp. *longirrostris* + in 5.
Localities: All relevés from Sierra de Espadán (Pico La Rápita) between 900-1106 m.a.s.l. *Holotypuss ass.* rel. 2

Table 3

Hedero helicis-Ericetum arboreae (Costa, Peris, Figuerola & Stübing 1985) Rivas-Mart. & al. 2011
(*Pistacio lentisci-Rhamnetalia alaterni*, *Ericenion arboreae*, *Quercetea ilicis*)

Plot size (m^2)	50	50	50	50	50	50
Exposure	N	N	N	N	N	N
Slope	30	30	30	30	30	30
Relevé number	1	2	3	4	5	6
Characteristics						
Erica arborea	5	5	4	4	4	2
Asplenium onopteris	+	+	+	+	+	+
Rubia peregrina	+	+	+	1	.	.
Quercus rotundifolia	1	1	1	.	.	1
Galium maritimum	+	.	.	+	1	+
Daphne gnidium	1	.	.	.	1	+
Quercus suber	.	+	1	+	1	.
Lonicera implexa	.	1	.	2	.	.
Companions						
Brachypodium retusum	4	3	1	+	3	4
Cistus albidus	1	1	+	1	1	3
Biscutella calduchii	+	+	+	+	+	+
Euphorbia flavicoma	+	+	+	.	+	+
Minuartia valentina	+	1	+	+	.	+
Rubus ulmifolius	.	1	1	+	2	1
Ulex parviflorus	2	.	.	1	2	4
Prunus spinosa	1	1	.	1	.	+
Helianthemum origanifolium	+	+	.	+	.	+
Crataegus monogyna	.	1	+	1	+	.
Thapsia villosa	+	.	.	.	.	2
Cistus salviifolius	.	1	.	.	.	1
Phleum phleoides	+	.	.	.	+	.
Hedera helix	.	.	1	+	.	.
Polypodium cambricum	.	.	+	+	.	.

Other species*: Sedum sediforme +, Quercus pyrenaica* 1 in 1; *Sorbus domestica, Galium idubedae* and *Viola alba* subsp. *dehndartii* + in 2; *Vicia tenuifolia, Cistus populifolius* and *Quercus faginea* + in 3; *Asplenium trichomanes*, *Hieracium amplexicaule*, *Antirrhinum barrelieri*, *Scrophularia tanacetifolia, Geranium robertianum* and *Luzula forsteri* +in 4; *Helichrysum italicum*, *Mercurialis tomentosa*, *Crepis pulchra*, *Carduus paui*, *Echium vulgare*, *Rhaponticum coniferum* and *Crepis capillaris* +, *Pinus pinaster s.l.* 1 in 5; *Senecio lividus* + in 6.

Localities: All relevés from Sierra de Espadán (Pico La Rápita) between 900-1106 m.a.s.l.

Table 4
Ulici parviflorae-Cistetum albidii ass. nova
(*Cistion ladaniferi, Lavanduletalia stoechadis, Cisto-Lavanduletea*)

Plot size (m^2)	50	50	50	50
Exposure	N	N	N	N
Slope	30	30	30	30
Relevé number	1	2	3	4
Characteristic				
Ulex parviflorus	3	5	4	2
Cistus albidus	4	3	3	4
Cistus salviifolius	.	1	1	.
Companions				
Brachypodium retusum	4	3	3	3
Trifolium campestre	+	+	1	+
Biscutella calduchii	+	+	+	+
Asplenium onopteris	+	+	+	+
Sedum sediforme	+	+	+	+
Galium maritimum	+	+	+	+
Dactylis glomerata	.	+	+	+
Euphorbia flavicoma	+	.	+	1
Prunus spinosa	1	+	.	1
Silene inaperta	+	.	.	+
Hedera helix	.	+	.	2
Rubus ulmifolius	.	.	1	1
Minuartia valentina	.	.	1	1
Trifolium arvense	.	.	+	1
Geranium robertianum	.	.	+	+
Thapsia villosa	1	.	1	.
Daphne gnidium	+	.	+	.
Senecio lividus	+	.	+	.
Polypodium cambricum	.	1	+	.
Helianthemum origanifolium	.	+	+	.
Quercus rotundifolia	.	+	+	.
Phleum phleoides	.	+	+	.

Other species*: Cynosurus elegans* and *Quercus suber* + *Quercus pyrenaica* 1 in 2; *Hieracium amplexicaule* and *Pteridium aquilinum* + in 3; *Bituminaria bituminosa* +, *Carex muricata*, *Galium idubedae*, *Lonicera implexa*, *Poa pratensis*, *Rubia peregrina*, *Scrophularia tanacetifolia* and *Vicia tenuifolia* + in 4.

Localities: All relevés from Sierra de Espadán (Pico La Rápita) between 900-1106 m.a.s.l. *Holotypus ass.* rel. 1

DISCUSIÓN GENERAL

Discusion general

Patrones climáticos de los melojares ibéricos

Los bosques de *Quercus pyrenaica* son por lo general bosques de montaña, especialmente en la Iberia mediterránea. Ocupan, por tanto, cuatro pisos de vegetación (termotipos) exclusivamente, dos en cada región biogeográfica, equivalentes entre sí: supramediterráneo y mesomediterráneo por un lado, y supratemplado (montano) y mesotemplado (colino) por otro. Al ser la sequía estival un factor limitante de su desarrollo estos bosques ocupan a su vez territorios de ombroclima al menos subhúmedo. Los datos derivados a partir del programa ESTCLIM concuerdan con estos límites bioclimáticos, pero a la vez muestran la amplia gama de matices climáticos que permiten discriminar unas comunidades de otras, con medias de precipitación anual que van desde los 600 mm superando los 3000 mm y temperaturas medias anuales entre los 6 y los 15 ºC.

Sin dejar de lado la diferente distribución en pisos de vegetación -que supone un gradiente altitudinal evidente- comprobamos que la sequía estival, continentalidad y distribución de las precipitaciones a lo largo del año, son los principales patrones climáticos que diferencian las comunidades de melojar peninsular. Existe, y es notoria, una gradación principalmente latitudinal, de norte a sur, pero también una variación longitudinal -de este a oeste- en el rango y secuencia de las precipitaciones.

Los patrones generales de sequía estival en los bosques de la Península Ibérica son los marcados por los límites entre las regiones biogeográficas Eurosiberiana y Mediterránea, por lo que los bosques relacionados con una y otra región fueron analizados por separado. En general, de manera longitudinal, las regiones más cercanas al Océano Atlántico serán las que mayor nivel de precipitaciones reciban. En la región Eurosiberiana (sequía estival prácticamente nula) y sus límites biogeográficos, las cantidades de precipitación son en general más abundantes y esta gradación oeste-este queda especialmente marcada. Las asociaciones del oeste (*Linario-Quercetum*), y especialmente aquellos bosques localizados en áreas transicionales entre regiones bioclimáticas, localizados en Galicia e incluso León (*Holco-Quercetum y Genisto-Quercetum*), son los que reciben mayor nivel de precipitación del norte. Estos últimos mostraron -incluso en verano- mayores precipitaciones que la asociación eurosiberiana *Melampyro-Quercetum* sobre la que el Golfo de Vizcaya ejerce su máxima influencia.

En este margen oriental de la región Eurosiberiana, se observa además un gradiente de humedad de la costa hacia el interior que se ve reflejado en la composición florística de estos bosques. Así dejando a un lado el máximo de humedad estival de la zona en la asociación *Melampyro-Quercetum*, podemos encontrar dos asociaciones muy próximas entre sí (ya en el Sistema Ibérico Septentrional) como son *Pulmonario-Quercetum* (veranos más húmedos) y ya en el interior y orientaciones más secas: *Luzulo-Quercetum*. Esta gradación se hizo patente en la separación por su reducida sequía estival de un grupo de inventarios procedentes de Burgos, adscritos a *Pulmonario-Quercetum* y que también se diferenció en los análisis de especies indicadoras posteriores (capítulo III) situándolo más próximo a *Melampyro-Quercetum* ya en la región Eurosiberiana (templada).

En la región Mediterránea, podemos establecer una línea vertical de separación este/oeste, que coincide aproximadamente con los límites orientales de la provincia biogeográfica Mediterránea Ibérica Occidental, pero también con los límites de la influencia atlántica. En verano, el anticiclón de las Azores trae sequedad a los territorios occidentales, pero hemos observado que también aquí existe un gradiente, recibiendo más lluvias en este periodo las comunidades del Sistema Central (*Luzulo-Quercetum*) que aquellas situadas en pisos bioclimáticos similares en el Oeste (*Sorbo-Quercetum*) (*Festuco merinoi-Quercetum* aunque no incluido como tal en el análisis quedaba en este sentido en posiciones intermedias entre los ambos).

Como ya hemos indicado, todo el occidente de nuestra área de estudio sufre una fuerte influencia Atlántica, representada principalmente por una acusada distribución de lluvias entre el invierno y el verano (épocas estacionales de máximos y de mínimos, respectivamente). A medida que bajamos latitudinalmente y vamos entrando en el área mediterránea, se produce un incremento de la temperatura media por lo que la sequía estival se vuelve cada vez más determinante en la composición de las comunidades. *Arbuto-Quercetum* y *Sorbo-Quercetum* son las asociaciones que ocupan el área luso-extremadurense, en los ambientes más cálidos y de veranos más secos de toda la matriz de datos. En esta zona las orientaciones de las sierras resultarán determinantes, pues de ellas dependerá la retención o no de las lluvias; este hecho se hace especialmente patente en Sierra Madrona donde la comunidad más termófila – *Arbuto-Quercetum* – pero de mayor precipitación anual ocupa exposiciones sur, mientras que *Sorbo-Quercetum* ocupa laderas norte. Tanto en el capítulo I como en el IV, estas dos comunidades parecen tener dos matices diferentes, el luso-extremadurense por un lado y el localizado en los límites de este sector biogeográfico:

Toledo-Ciudad Real cuyas características los acercan más a comunidades más meridionales como *Luzulo baeticae-Quercetum*. Esto parece responder a gradientes de temperatura invernal, relacionados a su vez con gradientes de continentalidad.

Estos gradientes también resultaron discriminantes en otros territorios como es el caso de los grupos de inventarios adscritos a asociaciones eurosiberianas: *Melampyro pratensis-Quercetum*, *Linario triornithophorae-Quercetum*, y aquellas asociaciones mediterráneas biogeográficamente más próximas: *Holco mollis-Quercetum* y *Genisto falcatae-Quercetum*. Dado el nivel de precipitaciones de la zona -especialmente homogeneizador- se observó que junto con las precipitaciones de verano son las temperaturas invernales las que separan estos bosques. Así, la asociación orocantábrica – *Linario-Quercetum* – se separó en base a sus bajas temperaturas mientras que las dos asociaciones mediterráneas ligadas a ella (*Holco-Quercetum* y *Genisto-Quercetum*), no mostraron ninguna separación entre sí. Sin embargo, aunque superpuestas, estas dos asociaciones generan una división clara en dos grupos: uno puramente mediterráneo, más seco y continental formado por inventarios de Salamanca (Peña de Francia, Sª de Gata) y otros dos de características bioclimáticas aparentemente transicionales entre lo mediterráneo y lo eurosiberiano (Ourense, León) (de veranos mucho más húmedos) pero también con dos niveles de continentalidad diferentes. Atendiendo al conjunto de la matriz, *Melampyro-Quercetum* y aquellos inventarios astur-cantábricos (4.5) dentro de los que se encuentran localidades incluidas como *Linario-Quercetum* y posteriormente adscritas a *Lonicero-Quercetum* serían los de mayor influencia oceánica, con inviernos más suaves. Mientras que los grupos más frescos son los orocantábricos (4.2) y aquellos correspondientes a inventarios de *Luzulo-Quercetum* y *Pulmonario-Quercetum* del interior peninsular (3.2) (en general los de mayor altitud).

Los patrones de distribución de la precipitación parecen ser la tercera variable discriminante dentro de los bosques de *Quercus pyrenaica* ibéricos. En contraste con el occidente, de lluvias predominantemente invernales, las lluvias de verano y otoño son típicas de aquellas localidades del este peninsular, e influencia variable del mar Mediterráneo. Suponen una recuperación rápida de la capacidad freática del suelo en áreas de especial aridez donde, de otra manera, la supervivencia del melojar estaría comprometida; es el caso por ejemplo de las Sierras andaluzas, como el entorno del río Madera en la Sierra del Segura (*Berberido-Quercetum*) o Sierra Nevada (*Adenocarpo-Quercetum*). Se diferencian entre sí por la cadencia de precipitaciones: principalmente invernales en

Sierra Nevada (de influencia principalmente atlántica) y más abundantes en verano (junio a agosto e incluso en septiembre) en Sierra del Segura.

Luzulo baeticae-Quercetum (2.2) en Cádiz, y áreas transicionales templado-mediterráneas del noroeste (inventarios adscritos a *Linario-Quercetum*, *Holco-Quercetum* y *Genisto-Quercetum*) (4.5 y 4.4) son, según el análisis, los grupos que reciben mayor precipitación anual, y principalmente en el periodo invierno-primavera. Sin embargo, los picos de precipitación en el periodo verano-otoño (además de las áreas transicionales), se producen en los grupos de *Melampyro-Quercetum* (4.1) en verano (Golfo de Vizcaya) y *Luzulo-Quercetum* y *Sorbo-Quercetum* (3.7) en otoño (vientos ábregos).

En el análisis sólo hemos tenido en cuenta las variables climáticas (no se incluyeron otras como evapotranspiración) pero en base a ellas podemos decir que, en general, las zonas de interior con mayor temperatura anual (y principalmente estival), reciben mayores precipitaciones dentro del periodo otoño-invierno que invierno-primavera. Es el caso de la matriz I de inventarios supramediterráneos (*Berberido-Quercetum* vs. *Adenocarpo-Quercetum*), pero también de la II (*Arbuto-Quercetum*) que incluye inventarios principalmente mesomediterráneos. Sin embargo aquellos bosques cercanos a la costa como *Luzulo baeticae-Quercetum* no siguen esta norma; su reducida evapotranspiración debida a elevados niveles de humedad ambiental les permiten soportar mejor el verano por lo que no dependen de la recuperación de la capacidad freática para resistir la sequía. Aunque no incluidos en este apartado los bosques del levante siguen también esta secuencia aunque el efecto del mar Mediterráneo como atenuador térmico e hídrico sea mucho más moderado. Vemos que, en general, lo más templado no es necesariamente lo más húmedo. *Quercus pyrenaica* tiene que encontrar ubicaciones con un equilibrio entre disponibilidad de agua (precipitaciones, capacidad de retención del sustrato, secuencia de lluvias) y evapotranspiración. Las comunidades de melojar ibéricas parecen diferenciarse fácilmente en base a las tres variables mencionadas (sequía estival, continentalidad y distribución de las precipitaciones). Se producen, no obstante, algunas superposiciones o situaciones de ambigüedad que pueden ser debidas a fenómenos microclimáticos pero también -puesto que se ha respetado la adscripción original de los inventarios- podrían deberse a asignaciones erróneas o zonas degradadas de difícil clasificación. Es necesario recordar además, que el patrón climático de los bosques de *Quercus pyrenaica* no es la única fuente para interpretar su patrón florístico, sino que también eventos históricos como los cambios climáticos durante el Holoceno y las fluctuaciones de los pisos de vegetación (termotipos) o refugios de estos bosques, deben ser también tenidos en cuenta y así lo hacemos en capítulos posteriores.

Con la recopilación de nuevos inventarios florísticos, la aparición de propuestas o adscripciones sobre los bosques asentados en substratos neutros en el este peninsular (ródenos del Buntsandstein) y la falta de estudios completos de los melojares levantinos, nos propusimos conocer qué especies los representan y en base a ellas cuáles son los modelos florísticos que definen a estos bosques. En este trabajo no se utilizó la adscripción previa de los inventarios en base a asociaciones fitosociológicas, sino que se prefirió trabajar en un ámbito más geográfico, separando los distintos bosques por macizos montañosos en los que se desarrollan. Esto nos permitió por un lado evitar posibles errores en dicha adscripción (sobre todo teniendo en cuenta que en muchas localidades no estaba clara) y por otro un conocimiento más exhaustivo de unos territorios muy particulares desde el punto de vista geológico y edáfico. La aplicación del método IndVal y en concreto de la función *multipatt* a los inventarios de levante nos dio la posibilidad de obtener especies indicadoras no sólo de cada macizo montañoso, sino de las conexiones existentes entre ellos en forma de afinidades florísticas. En el presente trabajo sugerimos, además, que estas afinidades, podrían ser interpretadas como el resultado de características ecológicas compartidas (presentes y/o pasadas) en base a la autoecología de las especies indicadoras. Utilizamos por tanto las preferencias ambientales de las especies como herramienta para lograr una mejor comprensión de la información ecológica del hábitat donde aparecen.

La localidad más singular en base al número de especies indicadoras fue la Sierra de Espadán (Castellón), que fue a su vez la de menor número de combinaciones representativas, posiblemente por ser la única de carácter mesomediterráneo y con mayor influencia marítima, lo que deriva en un enriquecimiento en especies mediterráneas termófilas.

En el extremo opuesto apareció la comarca de Prades (cordillera pre-litoral catalana), con un elevado número de especies indicadoras representando sus distintas combinaciones. El análisis mostró un grupo (Prades y Espadán) caracterizado por especies termófilas que prefieren un ambiente de alta humedad (costero) y un segundo grupo (Penyagolosa, Albarracín) caracterizado por especies típicas de las zonas montañosas y de bioclima templado. Los inventarios de Prades compartieron especies con ambos grupos, mostrando que este área agrupa múltiples influencias, y mayor heterogeneidad que el resto, derivada también de los usos del suelo y frecuencia de incendios (Boldú, 1975). La mayoría de sus combinaciones se producen con Penyagolosa y Albarracín (Sistema Ibérico), siendo las tres localidades con el mayor grado de afinidad florística de la matriz. Varios autores señalan el papel de estas tres cadenas montañosas como rutas migratorias de vegetación en el período postglacial, destacando Albarracín como conexión entre el Sistema Ibérico y la cordillera pre-litoral catalana (Bolòs, 1989).

En resumen, encontramos entre los bosques del levante tres tipos de combinaciones: aquellas que se realizaron con el Sistema Central, centradas en especies nemorales e ibero-atlánticas; combinaciones con la Sierra de Espadán representadas por especies mediterráneas y termófilas y, por último, las combinaciones mayoritarias, entre el resto de grupos orientales que suelen estar relacionadas con especies calcícolas y representantes de usos del suelo. No debemos olvidar que tanto el Maestrazgo como en general el Sistema Ibérico han sido rutas de trashumancia durante siglos, y estos bosques manejados principalmente en régimen de monte bajo (Allué, 1995) se encuentran muy conectados por estas prácticas.

Ranera, en Cuenca, es la localidad más degradada, con especies anuales y altamente competitivas como principales indicadoras. La aparición de un número elevado de especies indicadoras nemorales en Guadarrama, Prades y Boniches la interpretamos como indicación de un bosque en mejor estado de conservación.

Debido a su aislamiento, el nivel de endemicidad se ha incrementado en la mayoría de los macizos orientales; sin embargo, las condiciones particularmente finícolas de los bosques de Espadán han impulsado con mayor fuerza la diferenciación de su vegetación, siendo junto a Boniches los emplazamientos con mayor número de endemismos actuando como especies indicadoras.

En general, los diferentes estados de conservación que hemos encontrado dentro de los melojares levantinos, junto a su nivel de aislamiento son los factores más preocupantes para la supervivencia futura de estos bosques. El bajo flujo de polen entre poblaciones aisladas de extensión reducida contribuye a disminuir la diversidad genética de las especies forestales, y por lo tanto reduce su capacidad de adaptación al cambio (Honnay et al. 2005). El efecto de la perturbación en estos bosques es más perjudicial, y de difícil recuperación, especialmente teniendo en cuenta el elevado porcentaje de especies indicadoras de bosque primario que las describen (Hermy, 1.999), más vulnerables y de menor tasa de dispersión y capacidad competitiva. Si sumamos a este aislamiento la frecuente entrada del ganado y el mayor riesgo de incendio en estas zonas, observaremos que ante una subida de las temperaturas estos bosques acantonados en rincones más o menos frescos tienen pocas oportunidades de mantenerse, al menos como comunidad forestal. La protección de las especies con distribución restringida es crucial, por lo que en estos emplazamientos debería ejercerse un mayor control de la herbivoría así como deberían ser considerados áreas preferenciales para la conservación (algunas de ellas ya incluidas en la red de parques naturales).

Norte Peninsular

Tras el estudio de los melojares finícolas de levante, nos propusimos analizar los patrones florísticos comunes y diferenciales que dominan en la zona de prevalencia de nuestro bosque, el noroeste peninsular, dado que además en el capítulo I no pudimos obtener un patrón climático tan claro como en otros territorios. Se trató de buscar esa diferenciación de nuevo a través de la aplicación *multipatt*, comprobando además su aplicación sobre áreas más amplias tras los buenos resultados obtenidos en el estudio del levante. El análisis IndVal con combinaciones de grupos permitió reconocer las especies más representativas de este área en distintos niveles de trabajo (el 28% de las especies definió la estructura principal del conjunto). La identificación de estas especies y el nivel (escala de combinación) en el que actúan como indicadores, nos permitió aproximar su zona geográfica de prevalencia, relacionándolo con su nicho preferencial.

Dado el carácter mayoritariamente templado de la zona, las especies nemorales y acidófilas, típicas del estrato herbáceo del bosque, aparecieron como indicadoras al aumentar el número de grupos combinados, es decir, como indicadoras del noroeste peninsular en general. Mientras tanto, aquellas especies pertenecientes a comunidades seriales (matorrales o comunidades arbustivas), características locales del sustrato o que se adentran en bosques con cierto grado de apertura como las propias de prados, pastizales y ruderales, aparecieron principalmente a niveles individuales e intermedios de combinación. De hecho, las especies de sustitución pueden ser utilizadas en estos niveles como descriptores biogeográficos: los territorios del nordeste serían identificables a través de arbustos y brezales basófilos, las zonas de clima templado oceánico en el norte de España a través de tojales-brezales de sustitución y, por último, los territorios más occidentales de nuestro área de estudio (meseta norte y territorios aledaños) reconocidos a través de comunidades de sustitución graminoides y retamoides.

Los patrones florísticos generales -definidos a través de las especies comunes a varios grupos- presentan variaciones a lo largo de las diferentes escalas de trabajo. El número máximo de especies compartidas se produce a nivel local (así como las especies co-ocurrentes o co-indicadoras) y al aumentar el número de combinaciones, el área y por tanto, la heterogeneidad aumentan (Palmer, 2007), reduciendo el número de especies significativas. Además, como ya hemos indicado previamente, la gama más amplia de hábitats representados aparece también entre los primeros niveles de combinación reduciéndose progresivamente de ahí en adelante. Existe por tanto una mayor representatividad a pequeña escala de las variables de influencia local como son las características edáficas o los usos del territorio (Sieferd et al. 2012).

Los matices a resaltar en este área templada son: diferenciación en base a la oceanidad (incrementado nivel de precipitaciones), introduciendo vegetación especialmente acidófila como *Pseudarrhenatherum longifolium* y *Quercus robur* (Fig. 2 capítulo III), cuyos valores máximos de indicación se dan en los melojares de valles del noroeste abiertos al cantábrico y el norte de Portugal. Por otro lado, las localidades con influencia del Cantábrico (particular cadencia de lluvias)(*Melampyro-Quercetum, Lonicero-Quercetum*) mostraban como especie conectora *Daboecia cantabrica*, que aparece con menor frecuencia en las localidades protegidas orocantábricas (*Linario-Quercetum*) donde predomina sin embargo la especie *Genista florida* subsp *polygaliiphylla*, dato ya observado por otros autores (Jiménez-Alfaro, 2008).

En general (a pesar de ser favorecido por los incendios) la presencia de especies del género *Ulex* (*Leguminosae*) indica influencia marítima siendo más específica la presencia de *Ulex gallii* s.l. en este sector (*Ulex gallii* subsp. *breoganii* en valles cantabro-astures (*Lonicero-Quercetum*) y *Ulex gallii* subsp. *gallii* en cántabro-euskaldunes), así como *Ulex europaeus* en todo el noroeste.

La región noreste (cántabro-euskaldún pero también Sistema Ibérico Septentrional) muestra, principalmente reconocible a través de las comunidades arbustivas, un gradiente ya mencionado previamente en el capítulo I. Así desde las localidades más cercanas a la costa donde predomina *Ulex gallii* subsp. *gallii* vamos pasando a zonas donde sigue llegando humedad del golfo de Vizcaya y en especial nubes cargadas de lluvia que chocan contra su primera barrera orográfica importante, el Sistema Ibérico. Este área de gradación está representada por la co-ocurrencia de *Erica cinerea*, *Potentilla montana* y *Ranunculus tuberosus* (ver Fig. 2 del capítulo III). Ya en el Sistema Ibérico, hemos observado la entrada de arbustos de preferencia calcícola en las comunidades de melojar, debido al sustrato que los rodea, pero a la vez el contraste entre vertientes favorece el predominio de especies con requerimientos de humedad por un lado (*Viola reichenbachiana*, *Rosa arvensis*) y más mediterráneos por otro (*Rubia peregrina*).

Por otro lado, si atendemos a las co-ocurrencias del occidente de nuestra área de trabajo (ver Fig. 2 del capítulo III) podemos hablar de dos tendencias principales, la de aquellos bosques de Orense y León donde domina *Festuca elegans* subsp. *merinoi*, *Primula acaulis* y *Aquilegia vulgaris* subsp. *dichroa* y aquellos más al sur y con un carácter más mediterráneo entre Portugal y Salamanca representados por *Cytisus multiflorus*, *Silene latifolia* y *Galium mollugo*. De nuevo, como ocurría en el capítulo I el noroeste ibérico aparece dividido en dos grupos principales: uno de elevada precipitación y otro más seco, menos oceánico. En general, encontramos una fuerte polaridad este/oeste, generada principalmente por la influencia atlántica y las especies ligadas a ella como *Cytisus scoparius*, etc., un incremento de las especies acidófilas en dirección noroeste y de las calcícolas en dirección este.

Dentro de los patrones florísticos se observaron áreas de elevada similitud (alto número de combinaciones), áreas alejadas florísticamente (poco combinadas) y áreas de combinación relacionadas a través de muchas especies y con nichos preferenciales variados. Estas últimas suelen coincidir con localidades transicionales entre el macroclima Mediterráneo y el Templado, y que por lo tanto pueden recoger muchas más especies y de diferente indicación, son áreas de elevada heterogeneidad ambiental (Tamme, 2010) o de diversidad en mosaico (Rey Benayas, 2002), lo cual se refleja en un mayor número de especies indicadoras tanto a nivel local como en combinación con otros grupos. Es el caso de aquellos inventarios localizados en Burgos, Portugal y Orense, pero también en la Cordillera Cantábrica.

Un aspecto al que se le ha prestado una especial atención es el de la endemicidad. Muchas de las especies indicadoras de este trabajo son endemismos del occidente europeo, con la misma distribución de *Quercus pyrenaica* (franco-íbero-marroquí) o aún más restringida (norte, oeste ibérico) lo que nos ha llevado a pensar en la existencia de ensamblajes filogeográficos dentro de estas comunidades como migración y especiación (Götzenberger, 2011). Movimientos de regresión y avance de estos bosques a lo largo de la historia podrían ser visibles a través de estas especies.

Reglas de ensamblaje como la competencia influyen principalmente en los patrones individuales y locales de distribución (observables sólo en grupos de área reducida), mientras que los procesos históricos como las influencias climáticas más fuertes se detectan a escala regional. Los atributos de las especies como es el carácter nemoral dan lugar a un *ensamblaje de nicho*, pero la composición de cada comunidad en sí misma es además producida por *ensamblajes históricos* (Weiher, 2011; Drake, 1991).

Dado el enorme volumen de datos obtenido para la realización del estudio en el conjunto de la Península Ibérica, por limitaciones técnicas no se han podido analizar todos los grupos de melojar a la vez. La utilización del *Noise Clustering* nos ofrecía dos ventajas importantes, por un lado la reducción de la matriz de trabajo a través de la formación de un grupo llamado *Noise* dentro del cual quedarían agrupados los inventarios transicionales y *outliers*; y en segundo lugar, la posibilidad de analizar los datos sin manipularlos, es decir, sin necesidad de incluir una clasificación previa de los mismos. Esto nos permitió obtener los grupos más robustos de nuestra matriz de datos, sus especies indicadoras y, al ser un método de clasificación no supervisado, evitar los posibles errores en la adscripción fitosociológica de nuestros inventarios.

Para la identificación de los patrones florísticos toda la matriz de datos tuvo que ser revisada. Diferentes emplazamientos, diferentes autores y diferentes épocas de recogida de datos dan a una matriz de casi 750 inventarios una heterogeneidad que debe ser reducida. Muchas denominaciones sintaxonómicas cambian a lo largo de los años por las sucesivas revisiones, e incluso la propia toma de datos es más o menos detallada en función de la época. Ciertos autores prefieren recurrir a floras regionales, mientras que otros prefieren guiarse por floras que abarquen más superficie. Si nos alejamos más aún en el tiempo incluso la procedencia del fitosociólogo parece influir en las especies que incluye en sus tablas, frecuentemente aquellos autores de origen centro europeo tendían a utilizar táxones más propios de aquellas áreas en sus inventarios (dado lo poco estudiada que estaba la Península). Por todo ello la dificultad principal del estudio global de la península Ibérica radicó en la corrección de sinonimias nomenclaturales de los táxones. Cada especie en cada inventario se analizó para esa región, los táxones infraespecíficos (subespecies) fueron en general obviados y sólo aquellos que han sido utilizados tradicionalmente en la descripción de las comunidades y en particular los que mostraban caracteres fácilmente diferenciables en el trabajo de campo (en su mayoría reconocidos por Flora iberica (Castroviejo,)) han sido mantenidos.

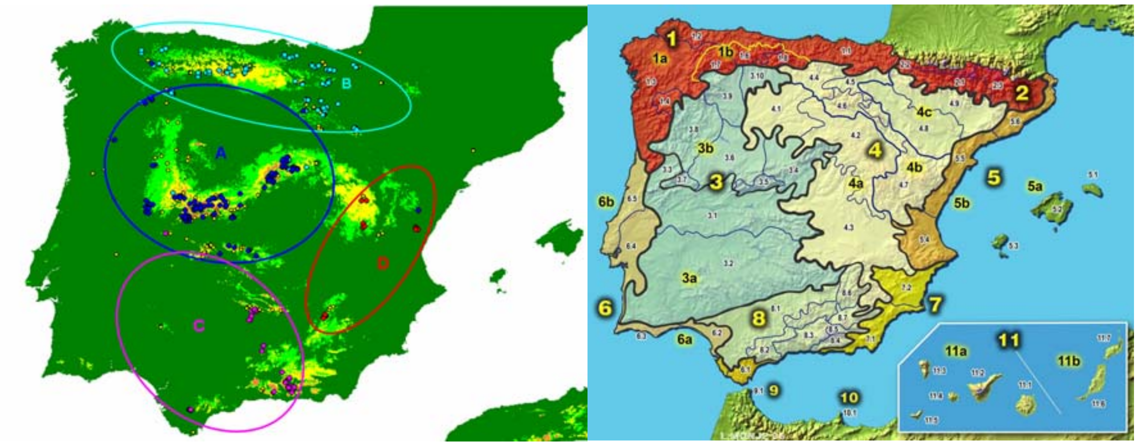


Figure D.1 Geographical distribution of the different clusters along Iberian Peninsula. Noise cluster plots as Yellow points. Biogeographical division of Iberian Peninsula chapter 4 (Peinado et al.2008).

Los resultados generales que agrupan en cuatro zonas de afinidad florística nuestros melojares, parecen concordar con la división biogeográfica de la Península (fig. D.1), mostrando sus principales características ecológicas diferenciales y sus especies indicadoras. Sin embargo, los patrones de afinidad que muestran entre ellos no se corresponden con las dos grandes regiones que dividen el territorio. Esta división principal (fig. 4.3) no está relacionada con los diferentes macrobioclimas existentes (Templado y Mediterráneo), sino que deja a un lado las localidades del este y agrupa lo templado y las denominadas zonas sub-mediterráneas como un área de alta afinidad. Esto puede entenderse además como un signo del carácter transicional de *Quercus pyrenaica,* ya que sus bosques más templados siguen compartiendo especies con el resto de la Península indicando que evita emplazamientos de excesiva humedad.

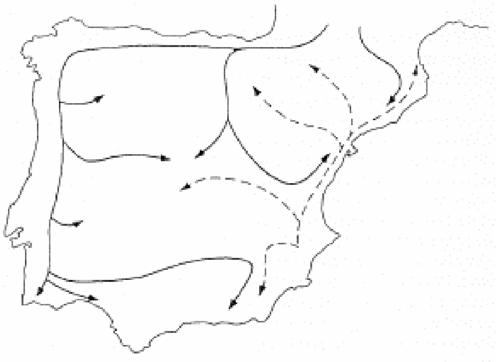


Figure D.2 Mapa de rutas migratorias de especies europeas y norteafricanas tomada de Izco (1984).

A su vez esta primera división puede corresponderse con el alcance de la influencia Atlántica pero también, atendiendo a las vías migratorias que se presuponen en la península (Blanco et al. 1998; Izco 1984; Rivas-Martínez 1973) con la vía de ascenso de especies africanas hacia el norte por el levante y su posterior migración hacia el noroeste desde esos enclaves, desdibujada por los sucesivos avances y retrocesos de la vegetación a lo largo de los periodos interglaciares. Así la composición florística se enriquece en especies eurosiberianas según vamos hacia el noroeste, y en mediterráneas y Norteafricanas hacia el sureste generando una clara polarización ya observada a lo largo de la presente tesis.

Ese gran grupo del oeste, (primera rama del cluster en la figura 4.4) vuelve a separarse en dos, dejando los melojares del sur (SªNevada, Cádiz) a un lado aunque conservando su vinculación con el resto. En un gran grupo aparte queda por tanto, todo el área centro-oeste peninsular, ahora sí separando la zona templada y áreas de transición por un lado (grupo B), y la zona mediterránea por otro (grupo A de la figura 3.4).

Los bosques de carácter más templado, correspondientes al sector cántabro-euskaldún y valles abiertos al mar Cantábrico del sector biogeográfico Galaico-asturiano quedan bien agrupados, mientras que todo el área de transición climática -siguiendo el paralelo 42- aparece dividida en dos: este (con especies pirenaicas y calcícolas) y oeste (con especies acidófilas y atlánticas). Los matices microclimáticos nuevamente quedan enmascarados por las influencias bioclimáticas dominantes, aunque posiblemente surgirían si continuásemos aumentando el número de particiones de la matriz.

El grupo restante, de inventarios del centro-sur-oeste peninsular (grupo A) es el que ha sido más difícil de clasificar en base a sus especies indicadoras. Los más reconocibles son, quizás, los procedentes de la Sierra de Gredos -en el centro-oeste- representado por *Festuca elegans* subsp *merinoi* (cluster 1 Figura 4.4 y 4.5), y la agrupación del suroeste diferenciable en base a especies termófilas. Los otros dos grupos se localizan en el Sistema Central (principalmente Madrid) y Meseta Norte con elevada cercanía florística.

El análisis también confirmó resultados previos como la afinidad entre Teruel y Cuenca con las localidades del noreste (B cluster), y el alcance de la influencia atlántica hasta el interior peninsular, generando mayor afinidad entre estos inventarios del oeste - homogeneizados por la influencia atlántica - que los del este caracterizados por su aislamiento y representados por numerosos endemismos.

En el capítulo I tras la búsqueda exhaustiva de las coordenadas geográficas de todos los inventarios, se procedió a la obtención de las variables bioclimáticas de cada punto a través del programa ESTCLIM. Siempre en base a las adscripciones originales dadas por los autores, se realizaron análisis multivariable (Ter Braak, 1998) por matrices. Estas matrices eran agrupaciones de asociaciones con cercanía geográfica, sólo *Lonicero peryclimeni-Quercetum* y *Cephalanthero rubrae-Quercetum* no estaban incluidas, o aparecían integrando otras comunidades según la clasificación del momento (*Festuco merinoi-Quercetum* en *Luzulo-Quercetum, Lonicero-Quercetum* en *Linario-Quercetum*).

En general la diferenciación climática del conjunto quedaba bien establecida, pero ciertas áreas resultaron complicadas por la superposición de sus bosques. Es el caso de inventarios adscritos a *Sorbo-Quercetum* y *Luzulo-Quercetum,* pero también *Holco-, Genisto-* y *Linario-Quercetum.* Tanto *Linario-Quercetum* como *Sorbo-Quercetum* y *Luzulo-Quercetum* dejaban núcleos bien aislados a pesar de la superposición de ciertas áreas, no siendo así en el caso de *Genisto* y *Holco-Quercetum.* Estas dos asociaciones, sugeridas ya como sinónimos por otros autores (Ladero et al. 2003), formaron dos grupos diferentes, uno más oceánico al norte y otro más al sur hacia el interior; esto nos llevó a pensar que quizás una modificación en su definición como comunidad sería mucho más apropiada que una sinonimización. A esto parece querer dar respuesta Rivas-Martínez en su revisión de 2011 en la que deja *Genisto-Quercetum* como serie berciano-sanabriense (supratemplada y meso-supramediterránea) y *Holco-Quercetum* (meso-supratemplada y mesomediterránea) como carpetano occidental y lusitano-duriense. Incluye por tanto, el área planileonesa en el *Pulmonario-Quercetum* (*Festuco heterophyllae-Quercetum* en la revisión de 2002), eliminando la referencia a Salamanca en *Genisto-Quercetum* y a León en *Holco-Quercetum.* En general, es el fuerte carácter oceánico del área noroeste el que genera esa homogeneidad, aunque con matices microclimatológicos. La clasificación de los sectores transicionales ha sido discutida en numerosos trabajos en los que se pretendía delimitar con mayor precisión la frontera entre las dos regiones macroclimáticas ibéricas. A este respecto cabe destacar el trabajo de Rodríguez-Guitián y Ramil-Rego (2008) donde realizan un resumen de las revisiones existentes, y una nueva propuesta corológica del noroeste, sacando a debate la propia definición de clima Templado en este área, relacionándola con el establecimiento del melojar. Como ya hemos comentado anteriormente este tipo de bosque ha sido utilizado para la demarcación biogeográfica de la Península en diversas ocasiones. Esta zona de carácter extremadamente húmedo para el melojo, incluye comunidades transicionales -como evidencian los resultados de nuestro análisis- pero no podemos olvidar la tendencia hacia la continentalidad (en el sentido hídrico de la palabra) que estos bosques adquieren aquí, comportándose de manera "opuesta" al resto de la Península al intentar reducir su exposición a la humedad. Ese componente hídrico de la continentalidad (Tuhkanen 1980) fue ya indicado por Gavilán & Fernández-González (1997) como uno de las variables discriminantes de los bosques de melojo del área oeste ibérica, concretamente la Lusitano-Duriense. Existe por tanto en todo el área de distribución de las asociaciones: *Genisto-Quercetum*, *Holco-Quercetum*, *Pyro bourgeana-Quercetum* e incluso *Sorbo-Quercetum* y *Arbuto-Quercetum* un gradiente de humedad desde el Oeste peninsular hacia el interior, así como patrones de distribución de la precipitación especialmente relevantes en los meses previos al verano para discriminar las comunidades del cuadrante suroeste y durante el propio verano para las del cuadrante noroeste (Moreno et al. 1990; del Río et al. 2007; Gavilán & Fernández-González 1997; Entrocassi et al 2004). Es este gradiente, que combina temperatura y humedad, el que permite observar diferenciaciones importantes dentro de asociaciones como *Arbuto-Quercetum* y *Sorbo-Quercetum* en el análisis numérico del capítulo IV. Estas asociaciones del suroeste, aparecieron incluidas en dos grupos (M1 y M8 (sur)): *Arbuto-Quercetum* mostrando una división interna entre los inventarios ubicados en Sierra Madrona y Plasencia (con un alto componente de especies de la clase fitosociológica *Quercetea ilicis*) relacionados con *Luzulo baeticae-Quercetum* (M8) y los ubicados en Salamanca, Ávila y Cáceres con un alto componente de especies atlánticas como *Holcus mollis* o incluso *Genista falcata* hecho ya apuntado por Entrocassi et al. (2004). *Sorbo-Quercetum* de la misma manera se reparte entre un grupo rico en especies atlánticas y del orden *Agrostietalia castellanae*, y otro que incluye especies del *Festucion merinoi* en el estrato herbáceo (*Festuca paniculata* subsp. *baetica, Festuca elegans* subsp. *elegans*). A este respecto hemos encontrado que el grupo atlántico de estas dos asociaciones está representado por *Allium massaessylum.*

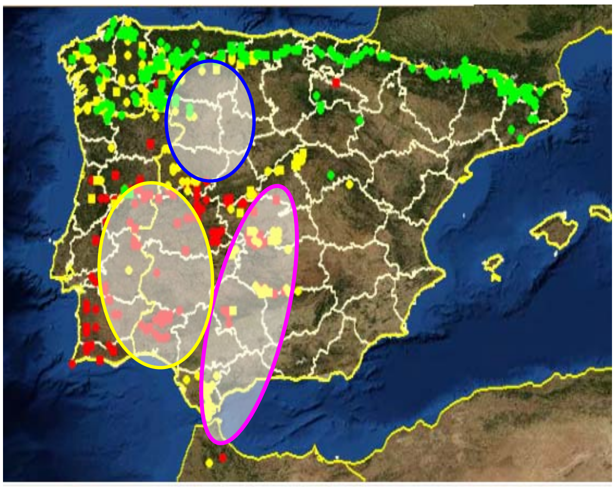


Figura D.3 Datos de presencia incluidos en la base de datos anthos. En rojo *Allium massaessylum*, *Allium scorzonerifolium* en amarillo y *Allium victorialis* en verde.

De hecho, los bosques de *Quercus pyrenaica* del oeste mediterráneo podrían ser diferenciados a grosso modo en base a tres especies de este genero que parecen representar tres áreas diferenciales: Meseta Norte (*Allium victorialis*), centro-sur (*Allium scorzonerifolium*) y oeste-sur (*Allium massaessylum*) (fig D.3). Los inventarios adscritos a *Pyro bourgeana-Quercetum* (Ladero et al. 2003) aparecen como transicionales en este análisis. Según la definición dada por Rivas-Martínez (2011) esta asociación parece querer agrupar aquellos inventarios de Salamanca y Maragatería, de interior y plenamente mediterráneos, que en nuestros análisis estaban representados por especies como *Allium victorialis* o *Conopodium subcarneum*.

Por otro lado, en las zonas occidentales son *Festuco merinoi-Quercetum*, y las asociaciones más templadas *Melampyro-Quercetum* y *Lonicero-Quercetum* (5 en la fig.4.4), las más claramente identificadas. La comunidad templada de *Quercus pyrenaica* restante, *Linario triornithophorae-Quercetum,* quedó integrada en el grupo que denominamos de transición climática del Oeste (6 en la fig.4.4) junto con las asociaciones relacionadas con la influencia atlántica: *Linario-Quercetum*, *Holco-Quercetum* y *Genisto-Quercetum*. Éstas conectan con el Sistema central a través de la Meseta, Sierra de Gredos o Peña de Francia (4 en la fig.4.4).

Mientras, el grupo de transición del este (7 en la fig.4.4) agrupa asociaciones relacionadas con el Pirineo y Golfo de Vizcaya conectando con el Sistema Central a través del sistema Ibérico norte (*Pulmonario-Quercetum*, *Luzulo-Quercetum*).

Las comunidades del sur y el este quedan bien representadas, sin superposición de ningún tipo. Dentro del grupo del Sur (C): *Luzulo baeticae-Quercetum* (8 en la fig.4.4) y *Adenocarpo-Quercetum* (9 en la fig.4.4), y en levante (D): *Berberido-Quercetum* (10 en la fig.4.4) pero también la Sierra de Espadán (11 en la fig.4.4), nuevamente diferenciada del resto. El grupo 12 (fig. 4.4) representa inventarios de Cuenca y Teruel, siendo su principal especie indicadora *Cephalanthera rubra*.

Nueva asociación en la sierra de Espadán

A lo largo de los diversos análisis realizados en la presente tesis, un grupo de inventarios quedó claramente diferenciado del resto. Correspondía a datos recientes tomados en la Sierra de Espadán (Castellón) (Merle & Ferriol, 2008). Tanto en los análisis de afinidades florísticas realizados en los macizos de levante (capítulo II), como en el "*Noise Clustering*" utilizado en el capítulo IV este bosque muestra una composición diferenciada, con cierta influencia marítima y repre4sentado por un elevado numero de endemismos. Esta nueva comunidad mesomediterránea, de claro carácter finícola se ve enriquecida en especies de *Quercetea ilicis* ya que a pesar de ocupar los emplazamientos más húmedos y frescos de esta Sierra su ombroclima no deja de ser subhúmedo.

La ausencia de especies como *Astragalus glycyphyllos, Primula veris* subsp. *columnae*, *Veronica officinalis, Poa nemoralis, Campanula trachelium* y *Lapsana communis*, junto con su corología y dinamismo, lo diferencian de la asociación *Cephalanthero rubrae-Quercetum pyrenaicae*. Esta asociación supramediterránea, descrita para los melojares de Prades y Penyagolosa de alto componente templado conecta con formaciones de *Pinus sylvestris* y *Quercus ilex* en contraste con los alcornocales y pinares marítimos dominantes en el llamado "sector espadánico".

Todos estos datos resultaron en la definición de una nueva comunidad de melojar: *Minuartio valentinae-Quercetum pyrenaicae ass. nova* cabeza de la serie climatófila espadánica sobre ródenos triásicos, correspondiente a bosques oceánicos subhúmedos, localizados en los pisos bioclimáticos mesomediterráneo superior al supramediterráneo inferior, de *Quercus pyrenaica* con *Minuartia valentina*, *Asplenium onopteris* y *Biscutella calduchii* (Merle & Ferriol 2008, Table 1, *holotypus*: relevé 4).

Esta comunidad comparte con el alcornocal espadánico (*Asplenio-Quercetum suberis*) diversas especies de sotobosque, exclusivas de su substrato neutro de areniscas de Buntsandstein; pero además la degradación de ambas formaciones forestales deriva en una similar comunidad de sustitución *Hedero helicis-Ericetum arboreae* Costa et al. 1985 in Rivas-Mart. 2011. Con la diferencia de que en el caso del melojar esta comunidad arbustiva carece de sus típicas especies termófilas y tolerantes a la sequía, como *Ruscus aculeatus*, *Smilax aspera*, *Clematis flammula*, etc

Aportamos a su vez una tercera comunidad de sustitución, en el estado de máxima degradación formada principalmente por *Ulex parviflorus* y *Cistus albidus* (*Ulici parviflorae-Cistetum albidii ass nova.*) y particularmente enriquecida en especies de *Rosmarinetea.*

Por todo ello proponemos la nueva serie 'Minuartio valentinae-Querco pyrenaicae sigmetum' correspondiente a los bosques subhúmedos silicícolas de *Quercus pyrenaica* sobre ródenos en los pisos bioclimáticos mesomediterráneo superior y supramediterráneo inferior de la Sierra de Espadán (sector biogeográfico Valenciano-Tarraconense).

Esquema sintaxonómico

QUERCO-FAGETEA SYLVATICAE Br.-Bl. & Vlieger in Vlieger 1937
  Quercetalia roboris Tx. in Barner 1931
    Quercion pyrenaicae Rivas Goday ex Rivas-Mart. 1964
      Minuartio valentinae-Quercetum pyrenaicae Vilches, Merle, Ferriol, Sánchez-Mata & Gavilán *ass. nova*
QUERCETEA ILICIS Br.-Bl. ex A. & O. Bolòs, 1950
  Pistacio lentisci-Rhamnetalia alaterni Rivas-Mart. 1975
    Ericion arboreae (Rivas-Mart. ex Rivas-Mart. et al. 1986) Rivas-Mart. 1987
      Hedero helicis-Ericetum arboreae Costa et al. 1985 in Rivas-Mart. 2011
CISTO-LAVANDULETEA Br.-Bl. in Br.Bl., Molinier & Wagner 1940
  Lavanduletalia stoechadis Br.-Bl. in Br.Bl., Molinier & Wagner 1940 em. Rivas-Martínez 1968
    Cistion ladaniferi Br.-Bl. ex A. & O. Bolòs 1950
      Ulici parviflorae-Cistetum albidi ass. nova

CONCLUSIONES GENERALES

Conclusiones Generales

- Bioclimáticamente los bosques de *Quercus pyrenaica* Ibéricos pueden discriminarse: -en el este en base a las cadencias de precipitaciones, que serán máximas en verano al incrementar la influencia de las corrientes húmedas mediterráneas (Jaén) o máximas en invierno al aumentar la influencia de corrientes de aire Atlánticas (Sierra Nevada). En el oeste, se incrementa la temperatura anual (particularmente la de verano) en un gradiente Norte-Sur. Siendo la Temperatura de invierno discriminante tanto en el área templada (mínimos orocantábricos) como en la mediterránea (mínimos en el sistema Central), estando además asociada a gradientes de continentalidad. En esta zona el nivel y la cadencia de lluvias está asociado a la influencia Atlántica (reduciéndose hacia el centro), pero por otro lado el efecto del anticiclón de las azores será más fuerte cuanto más al oeste (Precipitación del Sistema Central en verano será superior).
- En general en los bosques con elevados niveles de oceanidad la topografía y la microclimatología serán muy importantes como modeladores de la vegetación, tanto en el área Templada como Mediterránea.
- El análisis de los bosques de levante permitió distinguir la confluencia de dos tipos de vegetación: la montana, de bioma templado y aquella de carácter más mediterráneo. Los bosques de mayor afinidad fueron los de Cuenca-Teruel-Tarragona quedando a un margen los pertenecientes a la Sierra de Espadán en Castellón por ser más térmicos y de mayor influencia mediterránea. Esta diferenciación dio lugar a la generación de un nuevo tipo de comunidad: *Minuartio valentinae-Quercetum pyrenaicae ass nova* sobre ródenos.

- La aplicación del análisis de especies indicadoras con combinaciones de grupos sobre los melojares del Noroeste Ibérico nos permitió observar los matices diferenciales a diferentes escalas de trabajo, así como aquellas zonas de máxima afinidad representadas por especies co-ocurrentes.

- Las especies de sustitución pueden ser utilizadas en estos niveles como descriptores biogeográficos: los territorios del Nor-este serían identificables a través de arbustos y brezales basófilos, las zonas de clima templado oceánico en el norte de España a través de tojales-brezales de sustitución; y por último los territorios más occidentales de nuestro área de estudio (meseta norte y sus alrededores) reconocidos a través de comunidades de sustitución graminoides y retamoides.

- A lo largo del paralelo 42 encontramos una elevada afinidad florística entre bosques, que relacionamos con la existencia de un área transicional entre el clima mediterráneo y templado capaz de albergar un amplio y variado numero de especies indicadoras.

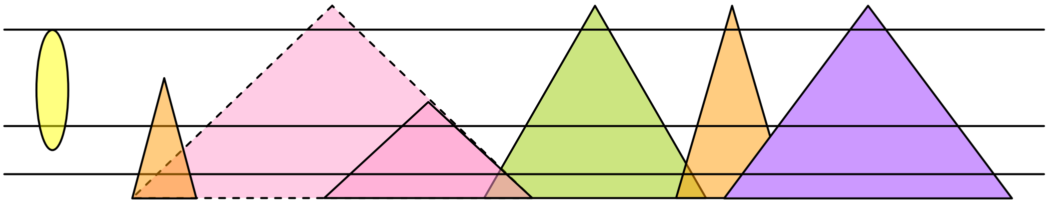
- Las zonas de mayor influencia oceánica pueden ser diferenciadas en base a especies del género *Ulex* s.l.. Así el territorio cántabro-euskaldún será representado por *Ulex gallii* (subsp *gallii* al este, subsp *breoganii* al oeste en valles perpendiculares a la costa), *Ulex europaeus* representando todo el área templada, *Ulex minor* particularmente importante en Sur de Galicia y Portugal, *Ulex parviflorus* en levante y la especie *Ulex borgiae* en Cádiz.

- En el capitulo IV encontramos que el eje de división este/oeste que separa la península en base al predominio de la influencia atlántica y mediterránea y los substratos acido/base se encuentra ligeramente desviado hacia el este. Dos terceras partes de la península quedan por tanto agrupadas en base a las cadencias de lluvias y la influencia atlántica. El este sin embargo se caracteriza por un mayor aislamiento de sus bosques, y una menor similitud florística.

- El área más occidental de la Península Ibérica es la que muestra una diferenciación más complicada, a diferencia de otros autores no sugerimos la sinonimización de asociaciones próximas como *Genisto* y *Holco* sino un cambio de definición que ya parece haber incluido Rivas-Martínez en su última revisión. *Arbuto-Quercetum* y *Sorbo-Quercetum* muestran además dos matices internos relacionados con la distancia a la costa Atlántica.

- Finalmente la presente tesis muestra una diferente representatividad de las especies a diferentes escalas de trabajo, aun cuando trabajamos con métodos numéricos de clasificación no supervisados. Es especialmente en estos casos en los que sugerimos exista un criterio para el establecimiento de jerarquías en base al nivel de aparición de las diferentes comunidades. Hemos observado también el reconocimiento a través de estos análisis de los sectores biogeográficos clásicos.

- Las comunidades al igual que las especies muestran diferentes formas y amplitudes ecológicas. El uso del análisis de especies indicadoras con combinaciones de grupos nos permite observar esas áreas, pero también conexiones pasadas y presentes entre los melojares de toda la Península ibérica.



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Apéndice florístico

Acer campestre L.
Acer granatense Boiss.
Agrostis × *fouilladei* P.Fourn.
Agrostis capillaris L.
Agrostis curtisii Kerguélen
Aira elegantissima Schur
Anacyclus clavatus (Desf.) Pers.
Anisantha sterilis (L.) Nevski
Arrhenatherum album (Vahl) Clayton
Artemisia barrelieri Besser
Artemisia campestris subsp. *glutinosa* (Besser) Batt.
Avenula marginata subsp. *albinervis* (Boiss.) Romero Zarco
Bellis perennis L.
Berberis hispanica Boiss. & Reut.
Biscutella calduchii (O. Bolòs & Masclans) Mateo & Crespo
Brachypodium boissieri Nyman
Brachypodium gaditanum Talavera
Brachypodium phoenicoides (L.) Roem. & Schult.
Brachypodium pinnatum (L.) P.Beauv. subsp. *rupestre* (Host) Schübl. & G.Martens
Brachypodium retusum (Pers.) P. Beauv.
Briza media L.
Carduus nigrescens subsp. *hispanicus* (Franco) Bolòs & Vigo
Carduus nutans subsp. *platypus* (Lange) Greuter
Catananche caerulea L.
Centaurea debeauxii Godr. & Gren.
Centaurea jacea L.
Centaurea montana L.
Cirsium filipendulum Lange
Coincya monensis var. setigera (Lange) Leadlay
Conopodium capillifolium (Guss.) Boiss.
Crepis lampsanoides (Gouan) Tausch
Crepis pulchra L.
Cynosurus cristatus L.
Cynosurus echinatus L.
Danthonia decumbens (L.) DC.
Elymus caninus (L.) L.
Festuca ampla Hack.
Festuca arundinacea Schreb.
Festuca braun-blanquetii (Fuente & al.) Rivas-Mart. & al.
Festuca elegans Boiss.
Festuca elegans subsp. *merinoi* (Pau) Fuente & Ortúñez
Festuca iberica (Hack.) K. Richt.
Festuca nigrescens Lam.
Festuca paniculata subsp. *baetica* (Hack.) Markgr.-Dann.
Festuca scariosa (Lag.) Asch. & Graebn.
Genista florida subsp. *polygaliphylla* (Brot.) Cout.
Gladiolus illyricus W. D. J. Koch
Hedypnois rhagadioloides (L.) F. W. Schmidt
Helichrysum italicum subsp. *serotinum* (DC.) P. Fourn.
Helichrysum stoechas (L.) Moench
Hypochaeris radicata L.
Inula salicina L.
Jacobaea adonidifolia (Loisel.) Pelser & Veldkamp
Koeleria crassipes Lange
Leontodon boryi DC.
Leontodon bourgaeanus Willk.
Leontodon hispidus L.
Leontodon saxatilis subsp. *rothii* Maire
Leucanthemum vulgare (Vaill.) Lam.
Luzula forsteri subsp *baetica* P. Monts.
Luzula sylvatica subsp. *henriquesii* (Degen) Pirajá
Milium effusum L.
Molinia caerulea (L.) Moench
Mycelis muralis (L.) Dumort.
Narduroides salzmannii (Boiss.) Rouy
Nardus stricta L.
Periballia involucrata (Cav.) Janka
Phleum pratense L.
Phleum serotinum Jord.
Piptatherum paradoxum (L.) P. Beauv.
Poa trivialis L.
Pseudarrhenatherum longifolium (Thore) Rouy

Quercus rotundifolia Lam.
Rhagadiolus stellatus (L.) Gaertn.
Rhamnus catharticus L.
Senecio lividus L.
Senecio lopezii Boiss.
Serratula tinctoria L.
Solidago virgaurea L.
*Trachynia distachya (*L.) Link