Marcescent Forests of the Iberian Peninsula: Floristic and Climatic Characterization

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Abstract

Forests dominated by marcescent oak species represent the transition between deciduous forests adapted to rainy summers and cold winters, on the one hand, and evergreen sclerophyllous Mediterranean forests. In the Iberian Peninsula marcescence is shown by some oak species, including *Quercus pubescens, Q. pyrenaica, Q. faginea* and *Q. canariensis*; it suggests an old evergreen habit forced to become deciduous by the cold winters. In this paper we analyse the floristic diversity of marcescent forests in the Iberian Peninsula and their proportion of evergreen broad-leaved and sub-Mediterranean species, and relate them to climatic conditions. This analysis uses 494 phytosociological relevés from the Information System of Iberian and Macaronesian Vegetation (SIVIM) and the BIOVEG data-bases. The data-set was submitted to an agglomerative clustering, which produced four clusters. An NMDS gradient analysis was also applied, in order to assess the relationship between the clusters and bioclimatic variables. The hierarchical and syntaxonomical classifications show a high correspondence, as reflected in the dominance of different *Quercus* species in each cluster. *Quercus broteroi* and *Q. canariensis* forests show a higher proportion of evergreen broad-leaved species, while *Q. pubescens* and *Q. faginea* forests are characterized by sub-Mediterranean species. As for climatic relationships, *Q. broteroi* and *Q. canariensis* forests present the highest values of thermicity (It) and the lowest values of the ombrothermic (Io_2) index. These values indicate their Mediterranean, thermophilous character, which in turn is related to their high proportions of evergreen broad-leaved species. As a conclusion, it can be stated that marcescence is not related to evergreeness, the latter being linked to mediterraneity. Therefore, the idea of considering marcescence as a residual feature of ancient evergreen laurophyll forests is not supported by our results. Those marcescent forests, particularly the basophilous ones, are related to the sub-Mediterranean floristic element.

Keywords

Numerical classification • *Quercus* • Sub-Mediterranean forest • Evergreen broad-leaved • NMDS • Thermicity • Ombrothermic index

1 Introduction

The late Tertiary and Pleistocene were times of dramatic climatic changes, which led to massive extinctions and migrations in the European flora. The changes started with progressive aridification and the emergence of the Mediterranean climate in the late Miocene, with episodes such as the

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Messinian salinity crisis (Hsu et al. 1977). This resulted in a reversal of the rainfall seasonality from a summer to a winter maximum, with the appearance of summer drought along the southern fringe of the European continent. Subsequently, successive ice ages occurred during the Quaternary. All these events caused deep changes and extinctions in this part of the world. Those episodes, combined with the uplift of several mountain ranges throughout the Cenozoic, fostered the differentiation of mountain floras and set up barriers hampering southward migrations in each of the extension phases of the glacial period. The thermophilous laurophyll flora and vegetation of the mid-Tertiary practically disappeared in Europe, while remaining much better preserved on the Atlantic islands (Macaronesia), i.e., the Azores, Madeira and the Canaries (Rodríguez-Sánchez and Arroyo 2011).

Nevertheless, continental Europe has preserved some remains of the laurophyll vegetation (mesophytic palaeoclimatic relicts, in the sense of Honrado et al. 2001), which is generally recognized based on living populations of *Rhododendron ponticum* ssp. *baeticum* or *Prunus lusitanica* (Calleja et al. 2009). Even the more widespread bay laurel (*Laurus nobilis)* can be related to this group (Rodríguez-Sánchez and Arroyo 2008, 2011; Rodríguez-Sánchez et al. 2010). Some ferns, including *Culcita macrocarpa, Davallia canariensis, Stegnogramma pozoi, Woodwardia radicans, Hymenophyllum tunbrigense* and *Vandenboschia speciosa*, are also related to this relict element from the mid-Tertiary. The three southern European peninsulas, i.e., the Iberian, Italian and Balkan, are known to have been refuges for the thermophilous flora, including *Quercus* species, during the cold periods of the Pleistocene (Dumolin-Lapègue et al. 1997; Brewer et al. 2002; Ferris et al. 1998; Olalde et al. 2002). Nowadays these peninsulas, particularly Iberia, are mainly covered by sclerophyllous, often scrubby vegetation well adapted to the Mediterranean climate. Temperate Europe, on the other hand, is dominated by deciduous summergreen broad-leaved forests that reached their maximum extension by approximately 6,000 BP (Brewer et al. 2002). These forests now extend over most of Europe and are adapted to a seasonal climate with rainy summers and more or less cold winters. The transition between these forests and the evergreen Mediterranean vegetation is formed by forests in which the dominant species are marcescent oaks, whose leaves wither in autumn but remain dry on the branches until spring, when they are shed. This practice is shown by many European oak species: *Quercus pubescens, Q. pyrenaica, Q. faginea, Q. canariensis, Q. cerris, Q. frainetto, Q. ithaburensis, Q. trojana*, etc., and resembles the old evergreen practice, which has been forced into deciduousness by the cold winters. In fact, one of these species, *Q. canariensis*, is even “almost evergreen”: it keeps some of its large leaves functioning during winter until spring, when they are shed immediately before the sprouting of the new leaves.

This woody vegetation dominated by oaks could be interpreted historically as a remnant of the mid-Tertiary vegetation, and these marcescent species as direct descendants of some of the evergreen oaks that covered the mid-latitudes of Europe, as they still do on other continents, particularly in East Asia (Japan, China, and southernmost Korea).

We have carried out a survey of these forests in the Iberian Peninsula, analyzing their flora and the climatic conditions they are linked to. We highlighted the evergreen broad-leaved species living in the canopy or understory of these forests, as they can be used as indicators of evergreens in the communities of Tertiary origin. Many of these species are now considered to be Mediterranean species, as they show a certain sclerophylly (hardness in the leaves); in the context of Mediterranean vegetation, though, they always occur in wet or rainy areas. Another relevant group of plants is the sub-Mediterranean forest species, considered to be the genuine or characteristic species of these forests.

The aims of our study are: (1) to analyse the floristic diversity of the marcescent forests of the Iberian Peninsula; (2) to analyse the proportion of evergreen broad-leaved and sub-Mediterranean species across the different marcescent forest types; and (3) to determine the climatic features linked to different marcescent forests.

We consider the Iberian Peninsula as particularly well suited for performing this survey because of the climatic evolution of the post-glacial Holocene period (Benito Garzón et al. 2007; Rodríguez-Sánchez et al. 2010) and the current climatic variability, from the wettest extreme near the Atlantic to the most extreme Mediterranean climate (summer drought) in some areas of southeastern Spain.

2 Materials and Methods

2.1 Study Area

The study area (Fig. 1) covers the Iberian Peninsula (ca 582,000 km^2), located in the transition zone between the Euro-Siberian and Mediterranean biogeographic regions. The climate changes eastward, from temperate hyperoceanic to semi-continental mediterranean (Rivas-Martínez 2007). In the transition between the mediterranean and temperate climates, we consider the submediterranean variant. This can be defined as the type of climate in which there is only one summer month with $p < 2t$, i.e., only one dry month in the warm season. Formally, Rivas-Martínez (2007) included this variant in the temperate macroclimate, since at least two dry months are needed to be included in the mediterranean macroclimate. This submediterranean variant

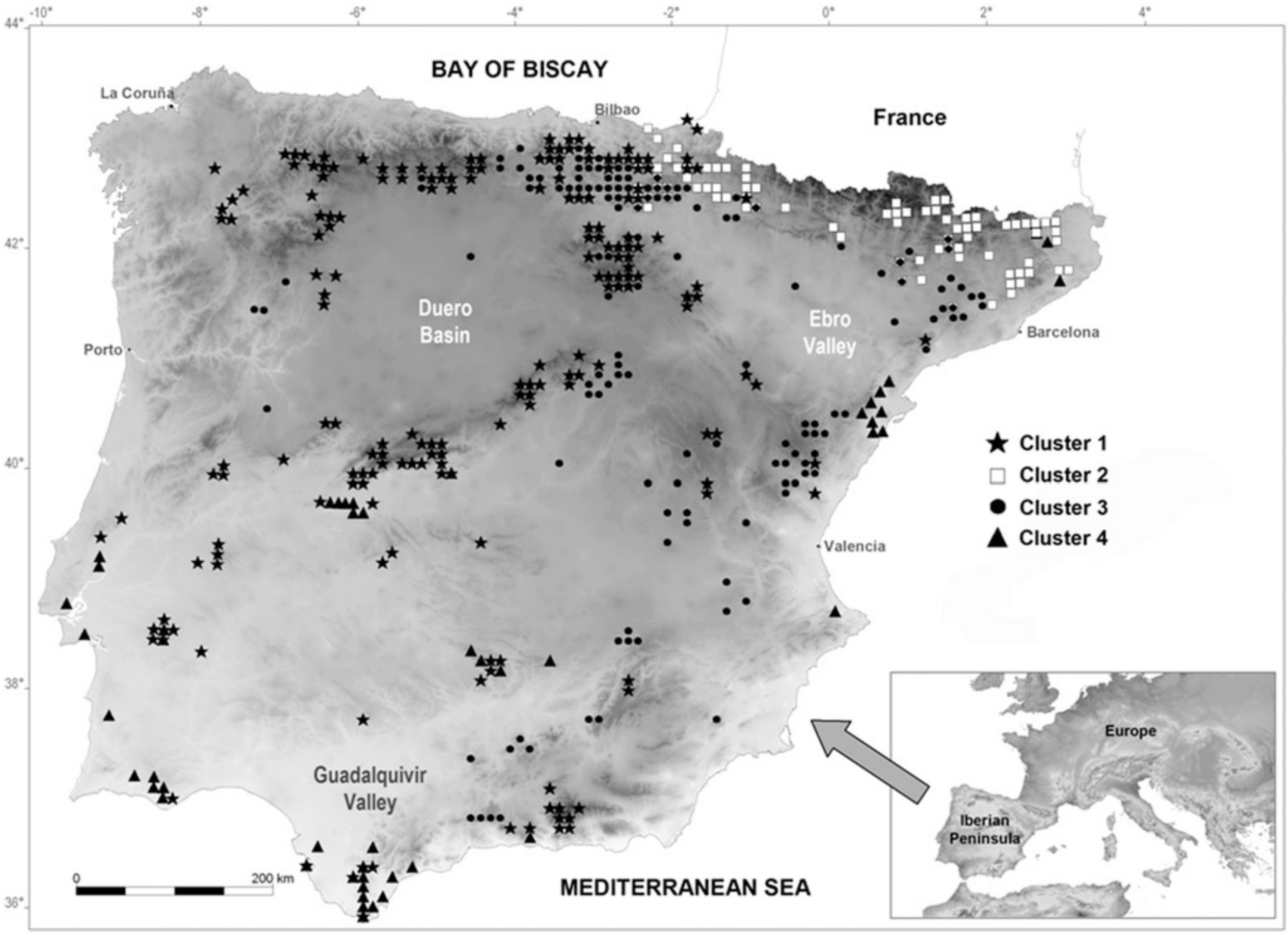

Fig. 1 Location of the study area (*Iberian Peninsula*) in southwestern Europe and distribution of forest cluster types resulting from floristic classification. *Dark areas* correspond to uplands and *light areas* to lowlands

is widespread in the Iberian Peninsula, as well as in other parts of southern Europe, providing a favourable climatic context for this survey. It also seems similar to the concept of warm-temperate deciduous areas in parts of East Asia and southeastern North America.

2.2 Data Collection and Preparation

To construct the primary data-set, phytosociological relevés were obtained from the Information System of the Iberian and Macaronesian Vegetation (SIVIM, Font et al. 2010) and the BIOVEG data-base of the University of the Basque Country. Relevés dominated (tree cover >3) by the marcescent tree species *Quercus pyrenaica, Q. faginea* ssp. *faginea* (from now on *Q. faginea*), *Q. faginea* ssp. *broteroi* (from now on *Q. broteroi*), *Q. pubescens* and *Q. canariensis* were selected. All relevés were compiled using the module QUERCUS of the VEGANA Package (De Cáceres et al. 2003). The primary data-set grouped 1,284 relevés representing 39 associations and five communities (see syntaxonomic scheme in Appendix 1). Floristic nomenclature follows *Flora Iberica* (Castroviejo et al. 1986–2011), and *Flora Europaea* (Tutin et al. 1976, 1980) for taxa not included in the former. The references for these sources are listed in Appendix 2.

The effects of possible oversampling of some areas or particular vegetation types were reduced by a stratified re-sampling (Knollová et al. 2005). The data-set was stratified geographically in such a way that only one relevé for each type of dominant tree was selected for each 10 × 10 km UTM grid.

After stratified re-sampling, a floristic homogeneization was performed by removing bryophytes (many relevés have no records of this group) and by assuming that *Hedera helix* s.l. includes *Hedera helix* L., *Hedera maderensis* K. Koch ex A. Rutherf. ssp. *iberica* McAllister and *Hedera hibernica* (G. Kirchn.) Bean; that *Rubus sp*. includes *Rubus* sect. *Corylifolii* Lindl. and *Rubus* sect. *Rubus*; that *Lonicera periclymenum* s.l., *Juniperus oxycedrus* s.l. and *Sanguisorba* *minor* s.l., include all subspecies within each genus in the territory; and that *Viola* gr. *sylvestris* includes *Viola riviniana* Rchb. and *V. reichenbachiana* Jord. ex Boreau. *Quercus faginea* Lam. includes *Q. alpestris* Boiss, and *Q. pubescens* Willd. includes *Q. subpyrenaica* Villar. Finally, all *Quercus* hybrids were included in the parent species dominant in the relevé or in the surroundings. So the dataset was reduced to 494 relevés and 1,003 species.

Climatic variables were calculated from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005), using a grid of 200 m pixel size generated from the existing network of meteorological stations and the official digital elevation model (DEM) of 100 m pixel size. The mean values of annual temperature (°C), annual rainfall (mm) and summer rainfall (sum of rainfall in June, July and August) per 10 × 10 km UTM cell were calculated, as well as five bioclimatic indices proposed by Rivas-Martínez (2007): continentality index (Ic), thermicity index (It) and the ombrothermic index of the warmest 1, 2 and 3-month periods (Ios_1, Ios_2, Ios_3, respectively). In order to reduce colinearity in potential explanatory climatic variables, a Pearson correlation matrix was calculated and variables with pairwise $|r| > 0.75$ were eliminated. In this way, mean annual temperature, summer rainfall, and Ios_1 and Ios_3 were seen as superfluous and excluded.

Ordinal species abundance estimates were replaced by metric average values prior to data analysis (r and +: 0.5%. 1: 5%. 2: 17.5%. 3: 37.5%. 4: 62.5%. 5: 87.5%). Percentages of evergreen broad-leaved species and sub-Mediterranean species were calculated in each relevé and normalized by an arcsine-square-root transformation, as recommended by Sokal and Rohlf (1987) for proportional data. Species present only in three relevés or fewer were deleted (0.6% of the total number). In this way, a definitive matrix with 494 relevés and 521 species was obtained.

2.3 Statistical Analysis

The GINKGO program of the VEGANA package (De Cáceres et al. 2003) was used to perform the floristic-numerical analysis. After transformation of cover values, the relevé data were √-transformed to reduce the impact of large cover values in the subsequent floristic analysis (McCune and Grace 2002). A dissimilarity matrix was constructed using Bray-Curtis distance. The definitive dataset was submitted to agglomerative clustering, according to species composition, using the hierarchical β-flexible cluster algorithm (Lance and Williams 1967; Wesche and von Wehrden 2011), with $\beta = -0.25$.

The Ochiai fidelity index (De Cáceres et al. 2008) of each species, for the four clusters from the numerical classification, was calculated in order to decide which species are the most diagnostic for each cluster.

Gradient analysis by NMDS (Kruskal 1964a, b; Mather 1976) was applied to assess the relationship between clusters and bioclimatic variables. NMDS has the advantage of not relying on a species response-curve model and can be used with various dissimilarity measures (McCune and Grace 2002; Podani 2006). Correlations between ordination axis and variables were evaluated by Pearson's correlation coefficient (r).

Relationships between the clusters and the proportion of both evergreen broad-leaved species (EB) and sub-Mediterranean species (SM) were assessed by the non-parametric Kruskal-Wallis test. The same test was used to evaluate the affinities between clusters and bioclimatic indices. When differences among the clusters were significant ($p < 0.05$), Mann-Whitney's U-test was applied to determine the categories among which those differences were given. All univariate statistical analyses were performed using SPSS 19.0 statistics package.

3 Results

3.1 Forest Classification

Numerical analysis leads to a classification into four main clusters at dissimilarity level 3.3 (Fig. 2), which reflects the syntaxonomical classification. Cluster 1 includes all relevés dominated by *Quercus pyrenaica* belonging to the *Quercion pyrenaicae* alliance (98.5%), except those of the *Arbuto unedonis-Quercetum pyrenaicae* dominated by *Quercus broteroi*. Cluster 2 comprises relevés corresponding to the *Quercion pubescenti-petraeae* (75.6%) and *Quercion roboris* (17.1%) alliances and some relevés of the *Aceri-Quercion fagineae* dominated by *Quercus pubescens*. Relevés of the *Aceri-Quercion fagineae* dominated by *Quercus faginea* are mainly grouped in cluster 3, and those corresponding to the *Quercion broteroi* and *Querco-Oleion sylvestris* alliances inside the *Quercetea ilicis* class are grouped in cluster 4. In this latter the dominant trees are *Quercus broteroi* and *Q. canariensis*, but some relevés from the eastern coastal mountains, dominated by *Quercus faginea* or *Quercus pubescens* and assigned to *Violo willkommii-Quercetum fagineae*, are also included. Table 1 shows the correspondence between clusters, dominant *Quercus* species and alliance.

The geographical distribution of relevés is represented in Fig. 1, with different symbols for each cluster. *Quercus pyrenaica*, *Q. pubescens* and *Q. faginea* forests assigned to the *Querco-Fagetea* class have a sub-Mediterranean distribution, whereas *Q. broteroi* and *Q. canariensis* forests have a Mediterranean distribution and are included in the

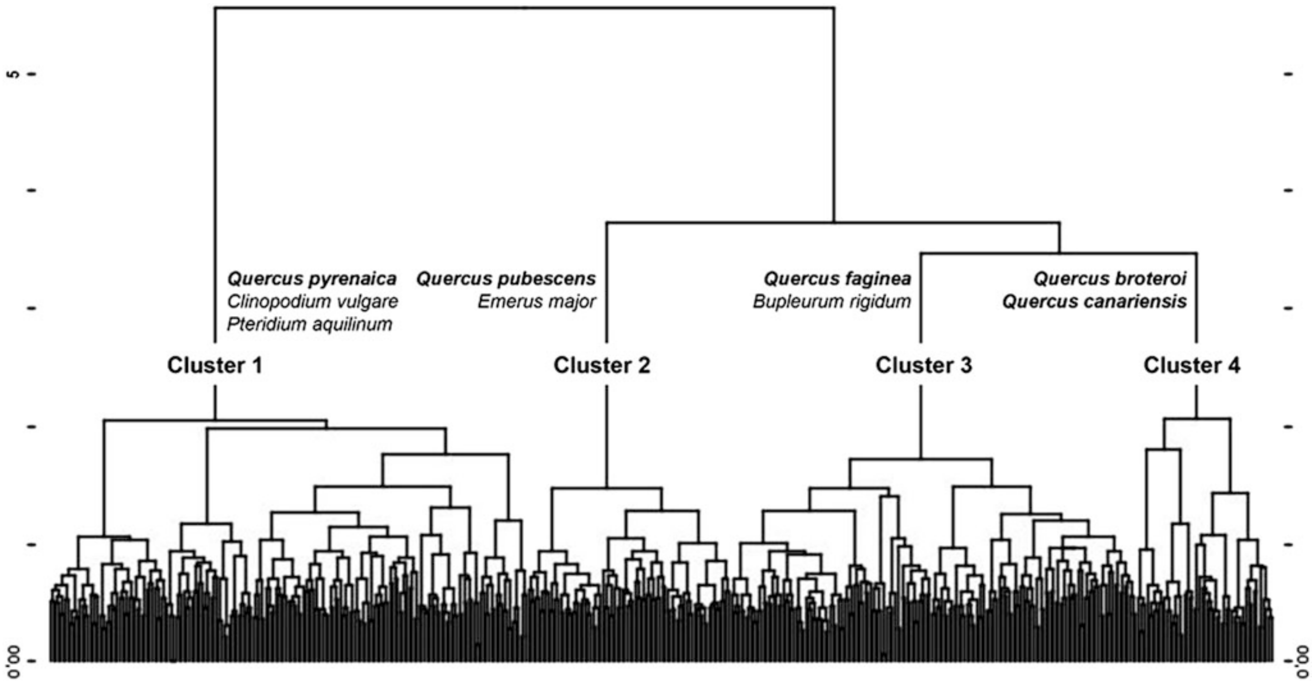

Fig. 2 Dendrogram resulting from the agglomerative clustering analysis explained in the main text. Principal discriminant species, based on their values of the Ochiai fidelity index, are shown. Pearson's *r* cophenetic correlation: 0.758; Spearman's *r* cophenetic correlation: 0.706; Gower Distance (Stress 1): 1472825.37261

Table 1 Correspondence between clusters obtained from hierarchical numerical analysis, tree dominance and alliances for marcescent and related forests in the Iberian Peninsula. The correspondence (%) between clusters, dominant *Quercus* species and alliances is shown in parentheses. N = number of relevés; % EB = percentage of evergreen broad-leaved woody species (median values and interquartile range; $X^2 = 198.89$; df = 3; $p < 0.001$). % SM = percentage of sub-Mediterranean species (median values and interquartile range; $X^2 = 127.1$; df = 3; $p < 0.001$). The values followed by the same letter (a) within a column do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test and a *post hoc* Mann-Whitney U-test

Cluster	N	Tree	Alliance	% EB	% SM
1	193	Q. pyrenaica (98.5%)	*Quercion pyrenaicae* (98.5%)	3 (0–7.1)	7.7 (4.8–10.7)
2	82	Q. pubescens (98.8%)	*Quercion pubescenti-petraeae* (75.6%)	10.4 (4.7–16.2)[a]	12 (7.8–17.6)[a]
			Quercion roboris (17.1%)		
3	164	Q. faginea (98.8%)	*Aceri-Quercion fagineae* (97%)	12.8 (7.1–20)[a]	11 (7.1–15)[a]
4	55	Q. broteroi (47.3%)	*Quercion broteroi* (40%)	40 (27.3–47.4)	2.7 (0–5.3)
		Q. canariensis (21.8%)	*Querco-Oleion sylvestris* (25.5%)		
		Q. faginea (21.8%)[1]	*Aceri-Quercion fagineae* (20%)[2]		

Quercetea ilicis class. *Quercus pyrenaica* forests (Cluster 1) occur mainly throughout the western half of the Iberian Peninsula, associated with acidic soils. Cluster 2 includes *Quercus pubescens* forests from the Pyrenees. Basophilous forests of *Quercus faginea* (Cluster 3) are found in the mountains of the eastern half of the Peninsula. Ecotones are frequent mainly in the north, where the presence and even dominance of hybrids is common.

The classification of the four clusters, with statistically determined diagnostic species for each cluster, is presented in Table 2. Cluster 1 is well defined by *Quercus pyrenaica* (0.97), *Clinopodium vulgare* (0.65), *Pteridium aquilinum* (0.64), *Holcus mollis* (0.63), *Teucrium scorodonia* (0.63), *Arenaria montana* (0.59), *Luzula forsteri* (0.59), *Melampyrum pratense* (0.57), *Lonicera periclymenum s.l.* (0.55), *Physospermum cornubiense* (0.52) and *Poa nemoralis* (0.50). This cluster is characterized by acidophilous species, which supports their inclusion in the *Quercetalia roboris* order.

Clusters 2 and 3 share some diagnostic species with sub-Mediterranean distributions, such as *Viburnum lantana, Primula veris, Acer monspessulanum*, *Buxus sempervirens* (classified as EB)*, Helleborus foetidus* and *Cytisophyllum sessilifolium,* together with other species with a wider distribution, such as *Acer campestre*, *Cornus sanguinea, Juniperus communis, Lonicera xylosteum, Corylus avellana*

Table 2 Floristic interpretation of the clusters obtained (**see main text**). The value of the Ochiai fidelity index is shown for each cluster of the most frequent species

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Diagnostic species of cluster 1					
Quercus pyrenaica	*200*	**0.97**	–	0.03	0.05
Clinopodium vulgare	*145*	**0.65**	0.08	0.14	0.06
Pteridium aquilinum	*154*	**0.64**	0.10	0.11	0.15
Teucrium scorodonia	*113*	**0.63**	0.06	0.01	0.15
Holcus mollis	*81*	**0.63**	0.01	0.01	–
Luzula forsteri	*98*	**0.59**	0.08	0.03	0.08
Arenaria montana	*83*	**0.59**	0.01	0.03	0.04
Melampyrum pratense	*84*	**0.57**	0.02	0.09	–
Lonicera periclymenum s.l.	*134*	**0.55**	0.07	0.18	0.13
Poa nemoralis	*91*	**0.50**	0.17	0.07	0.01
Diagnostic species of cluster 2 and 3					
Juniperus communis	*107*	0.06	**0.40**	**0.46**	0.01
Cornus sanguinea	*85*	0.02	**0.41**	**0.40**	0.01
Acer campestre	*66*	0.04	**0.43**	**0.28**	0.02
Lonicera xylosteum	*65*	0.02	**0.40**	**0.33**	–
Corylus avellana	*70*	0.11	**0.38**	**0.24**	0.03
Amelanchier ovalis	*79*	0.01	**0.34**	**0.45**	–
Diagnostic species of cluster 2					
Quercus pubescens	*97*	–	**0.92**	0.08	0.07
Galium pumilum	*25*	–	**0.38**	0.08	0.08
Campanula trachelium	*19*	–	**0.35**	0.07	0.03
Diagnostic species of cluster 3					
Quercus faginea	*196*	0.06	0.05	**0.91**	0.13
Teucrium chamaedrys	*75*	0.01	0.20	**0.50**	0.03
Genista scorpius	*62*	0.01	0.20	**0.47**	–
Bupleurum rigidum	*60*	0.01	0.11	**0.44**	0.12
Diagnostic species of cluster 4					
Quercus broteroi	*43*	0.11	–	0.01	**0.66**
Quercus canariensis	*16*	–	–	–	**0.54**
Asparagus acutifolius	*32*	0.05	0.04	0.11	**0.43**
Arisarum simorrhinum	*10*	0.02	–	–	**0.38**
Sub-Mediterranean species (SM)					
Physospermum cornubiense	*55*	**0.52**	–	0.01	–
Lathyrus niger	*38*	**0.30**	0.13	0.04	0.04
Genista falcata	*17*	0.24	–	0.06	–
Viburnum lantana	*115*	0.05	**0.34**	**0.55**	–
Primula veris	*78*	0.18	**0.30**	0.28	–
Acer monspessulanum	*74*	0.08	0.28	**0.33**	0.11
Helleborus foetidus	*58*	0.10	0.25	**0.31**	–
Cytisophyllum sessilifolium	*17*	–	0.21	0.17	–
Emerus major	*36*	–	**0.50**	0.10	0.02
Acer opalus	*11*	–	**0.30**	0.05	–
Campanula persicifolia	*11*	–	0.27	0.05	0.04
Hypericum montanum	*13*	0.08	0.21	0.04	–
Saponaria ocymoides	*21*	–	0.07	**0.31**	–
Cephalanthera rubra	*30*	0.07	0.12	0.27	–
Acer granatense	*10*	0.02	–	0.20	0.04
Sorbus aria	*40*	0.17	0.19	0.17	–
Paeonia microcarpa	*14*	0.12	–	0.17	–
Sorbus torminalis	*28*	0.10	0.19	0.16	0.03
Viola hirta	*11*	0.09	0.10	0.09	–

(*continued*)

Table 2 (continued)

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Evergreen broadleaf woody species (EB)					
Rubia peregrina	*220*	0.14	**0.31**	**0.58**	0.36
Hedera helix s.l.	*179*	0.24	**0.35**	**0.43**	0.19
Quercus rotundifolia	*96*	0.06	0.17	**0.51**	0.12
Ligustrum vulgare	*89*	0.05	0.23	**0.51**	–
Buxus sempervirens	*86*	–	**0.57**	**0.32**	–
Ruscus aculeatus	*86*	0.18	0.19	0.13	**0.47**
Daphne gnidium	*66*	0.24	–	0.16	**0.37**
Smilax aspera	*58*	0.09	0.06	0.10	**0.60**
Arbutus unedo	*57*	0.17	0.03	0.06	**0.55**
Rhamnus alaternus	*53*	0.04	0.11	0.28	0.30
Ilex aquifolium	*49*	0.24	0.16	0.15	0.06
Quercus coccifera	*47*	0.03	0.08	0.26	0.31
Viburnum tinus	*45*	0.10	–	0.06	**0.62**
Quercus suber	*39*	0.21	0.04	0.01	**0.39**
Phillyrea latifolia	*36*	–	0.06	0.08	**0.61**
Lonicera implexa	*32*	0.03	0.02	0.11	**0.50**
Pistacia lentiscus	*31*	–	0.02	0.06	**0.63**
Phillyrea angustifolia	*28*	0.05	0.02	0.01	**0.56**
Rosa sempervirens	*25*	–	0.04	0.11	**0.43**
Quercus ilex	*25*	0.04	0.29	0.08	0.11
Daphne laureola	*23*	0.03	0.25	0.13	0.06
Olea europaea	*20*	0.11	–	0.03	**0.33**
Arctostaphylos uva-ursi	*19*	0.05	0.05	0.25	–
Chamaerops humilis	*16*	–	–	–	**0.54**
Cistus populifolius	*15*	0.13	–	–	0.28
Cistus laurifolius	*14*	0.15	–	0.13	–
Myrtus communis	*13*	0.06	–	–	**0.37**
Ruscus hypophyllum	*8*	–	–	–	**0.38**
Vinca difformis	*6*	–	–	0.03	0.28
Rhamnus oleoides	*5*	–	–	–	0.30
Ceratonia siliqua	*4*	–	–	–	0.27
Other species					
Crataegus monogyna	*283*	**0.42**	**0.37**	**0.50**	0.17
Rubus sp.	*191*	0.43	0.27	0.28	0.23
Prunus spinosa	*171*	0.22	**0.34**	**0.53**	0.02
Tamus communis	*140*	0.22	0.26	0.32	0.31
Brachypodium sylvaticum	*134*	0.37	0.30	0.24	0.09
Cruciata glabra	*118*	**0.48**	0.21	0.14	0.05
Stachys officinalis	*108*	0.26	0.27	0.29	0.08
Viola gr. sylvestris	*97*	0.31	0.33	0.19	0.03
Geum sylvaticum	*82*	0.30	0.07	0.28	0.09
Hepatica nobilis	*79*	0.09	0.36	0.33	0.02
Tanacetum corymbosum	*76*	0.21	0.11	0.35	0.05
Carex flacca	*68*	0.03	**0.37**	**0.33**	0.03
Silene nutans	*68*	0.31	0.13	0.21	0.02
Stellaria holostea	*67*	0.37	0.20	0.09	0.02
Lathyrus linifolius	*66*	**0.41**	0.11	0.09	0.05
Viola gr. alba	*65*	0.02	0.36	0.30	0.10
Cytisus scoparius	*64*	**0.43**	0.04	0.04	0.15
Fragaria vesca	*53*	0.19	**0.36**	0.09	0.04
Dactylis glomerata	*53*	0.24	0.26	0.12	0.02
Brachypodium phoenicoides	*52*	0.08	0.17	**0.35**	0.02

(*continued*)

Table 2 (continued)

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Euphorbia amygdaloides	*51*	0.14	0.26	0.20	0.04
Anthoxanthum odoratum	*50*	0.41	0.11	0.02	0.02
Brachypodium retusum	*40*	0.01	0.07	0.32	0.19
Thalictrum tuberosum	*38*	0.01	0.20	0.30	0.04
Juniperus oxycedrus s.l.	*34*	0.02	0.08	**0.35**	0.05
Agrostis capillaris	*29*	0.28	0.08	0.01	0.08
Calluna vulgaris	*29*	0.28	0.08	0.01	0.08
Osyris alba	*28*	0.04	0.04	0.12	**0.38**
Pinus sylvestris	*26*	0.04	**0.37**	0.08	0.03
Pistacia terebinthus	*25*	0.01	0.07	0.17	0.27
Frangula alnus	*25*	0.29	0.02	0.03	0.05
Calamintha nepeta	*22*	0.14	0.05	0.02	0.29
Holcus lanatus	*21*	0.27	0.02	0.02	0.06
Galium maritimum	*19*	0.02	0.28	0.11	0.03
Erica vagans	*92*	0.29	0.21	0.29	–
Brachypodium rupestre	*91*	0.19	0.29	0.34	–
Pulmonaria longifolia	*57*	0.29	0.15	0.18	–
Rosa arvensis	*56*	0.12	0.31	0.24	–
Potentilla montana	*54*	0.27	0.12	0.19	–
Genista occidentalis	*48*	0.07	0.22	0.30	–
Vicia sepium	*48*	0.19	0.37	0.08	–
Festuca rubra	*39*	0.28	0.12	0.10	–
Trifolium ochroleucon	*36*	0.26	0.18	0.05	–
Bromus erectus	*35*	0.02	0.15	0.33	–
Helleborus occidentalis	*31*	0.25	0.04	0.14	–
Hypericum pulchrum	*31*	**0.35**	0.02	0.04	–
Potentilla sterilis	*29*	0.25	0.14	0.04	–
Helictotrichon cantabricum	*27*	0.01	0.19	0.26	–
Daboecia cantabrica	*27*	**0.35**	0.02	0.02	–
Rosa micrantha	*26*	0.07	0.06	0.28	–
Origanum vulgare	*23*	0.05	0.25	0.15	–
Anemone nemorosa	*23*	**0.32**	0.02	0.02	–
Trisetum flavescens	*23*	**0.32**	0.02	0.02	–
Briza media	*22*	0.03	0.09	0.27	–
Ranunculus tuberosus	*21*	0.27	0.05	0.03	–
Coronilla minima	*20*	0.02	0.07	0.28	–
Fraxinus excelsior	*18*	0.03	**0.34**	0.06	–
Trifolium pratense	*17*	0.26	0.03	0.02	–
Helianthemum nummularium	*16*	0.04	0.06	0.23	–
Lonicera etrusca	*59*	–	0.24	0.38	0.09
Carex halleriana	*41*	–	0.07	**0.35**	0.17
Viola willkommii	*37*	–	0.15	**0.36**	0.02
Juniperus phoenicea	*16*	–	0.03	0.25	0.07
Paeonia broteri	*37*	0.25	–	0.05	0.27
Origanum virens	*45*	0.30	–	0.06	0.24
Aristolochia paucinervis	*50*	0.34	–	0.10	0.15
Campanula rapunculus	*49*	0.37	–	0.08	0.12
Sanguisorba minor s.l.	*25*	0.04	–	0.28	0.11
Asphodelus albus	*40*	0.08	–	0.15	0.23
Thapsia villosa	*21*	0.25	–	0.05	0.06
Potentilla erecta	*23*	0.32	–	0.02	0.03
Asphodelus albus	*33*	**0.39**	–	0.01	0.02
Erica arborea	*75*	**0.46**	0.05	–	0.25

(*continued*)

Table 2 (continued)

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Festuca heterophylla	*37*	**0.37**	0.07	–	0.04
Knautia nevadensis	*15*	0.09	0.26	–	0.03
Castanea sativa	*18*	0.27	0.03	–	0.03
Hyacinthoides hispanica	*15*	0.11	–	–	0.31
Conopodium marianum	*14*	0.13	–	–	0.25
Cytisus striatus	*20*	0.26	–	–	0.12
Doronicum plantagineum	*24*	0.29	–	–	0.11
Polygonatum odoratum	*23*	0.29	–	0.07	–
Lapsana communis	*20*	0.26	–	0.07	–
Carex lamprocarpa	*18*	0.25	–	0.06	–
Sedum forsterianum	*20*	0.27	–	0.05	–
Genista polygaliphylla	*16*	0.25	–	0.04	–
Avenula sulcata	*24*	**0.32**	–	0.03	–
Rumex acetosa	*23*	**0.33**	–	0.02	–
Ulex gallii	*22*	**0.32**	–	0.02	–
Conopodium pyrenaeum	*20*	**0.31**	–	0.02	–
Erica cinerea	*14*	0.25	–	0.02	–
Quercus robur	*14*	0.25	–	0.02	–
Festuca elegans	*22*	**0.34**	–	–	–
Linaria triornithophora	*21*	**0.33**	–	–	–
Pseudarrhenatherum longifolium	*20*	**0.32**	–	–	–
Crepis lampsanoides	*18*	**0.31**	–	–	–
Vaccinium myrtillus	*17*	0.30	–	–	–
Simethis mattiazzi	*15*	0.28	–	–	–
Hyacinthoides non-scripta	*13*	0.26	–	–	–
Blechnum spicant	*12*	0.25	–	–	–
Deschampsia flexuosa	*35*	0.34	0.13	–	–
Veronica officinalis	*22*	0.29	0.07	–	–
Conopodium majus	*20*	0.27	0.07	–	–
Clematis vitalba	*32*	–	0.31	0.22	–
Aphyllanthes monspeliensis	*30*	–	0.18	0.30	–
Genista hispanica	*26*	–	0.15	0.29	–
Carex humilis	*25*	–	0.20	0.25	–
Pinus salzmannii	*23*	–	0.07	**0.33**	–
Rhamnus saxatilis	*21*	–	0.10	0.29	–
Catananche caerulea	*18*	–	0.05	0.29	–
Spiraea obovata	*16*	–	0.06	0.27	–
Euphorbia nicaeensis	*13*	–	–	0.28	–
Leuzea conifera	*12*	–	–	0.27	–

and *Amelanchier ovalis*. The characteristic species that separate the two groups of relevés are:

– For cluster 2, *Quercus pubescens* (0.92), *Emerus major* (0.50) and *Acer opalus* (0.30) among sub-Mediterranean species and *Galium pumilum* (0.38) and *Campanula trachelium* (0.35) among widespread species; and
– For cluster 3, *Quercus faginea* (0.91), *Teucrium chamaedrys* (0.50), *Genista scorpius* (0.47), *Bupleurum rigidum* (0.44) and the evergreen broad-leaved species *Rubia peregrina* (0.58) and *Quercus rotundifolia* (0.51) (see Table 2).

Finally, cluster 4 is characterized by *Quercus broteroi* (0.66), *Quercus canariensis* (0.54), *Asparagus acutifolius* (0.43), *Arisarum simorrhinum* (0.38) and a large group of evergreen broad-leaved species such as *Pistacia lentiscus* (0.63), *Viburnum tinus* (0.62), *Phillyrea latifolia* (0.61), *Smilax aspera* (0.60), *Phillyrea angustifolia* (0.56), *Arbutus unedo* (0.55), *Chamaerops humilis* (0.54), *Lonicera implexa* (0.50), *Ruscus aculeatus* (0.47), *Rosa sempervirens* (0.43) and *Quercus suber* (0.39). This cluster is quite well defined by thermophilous evergreen broad-leaved species, many of which are sclerophyllous, together with the absence of

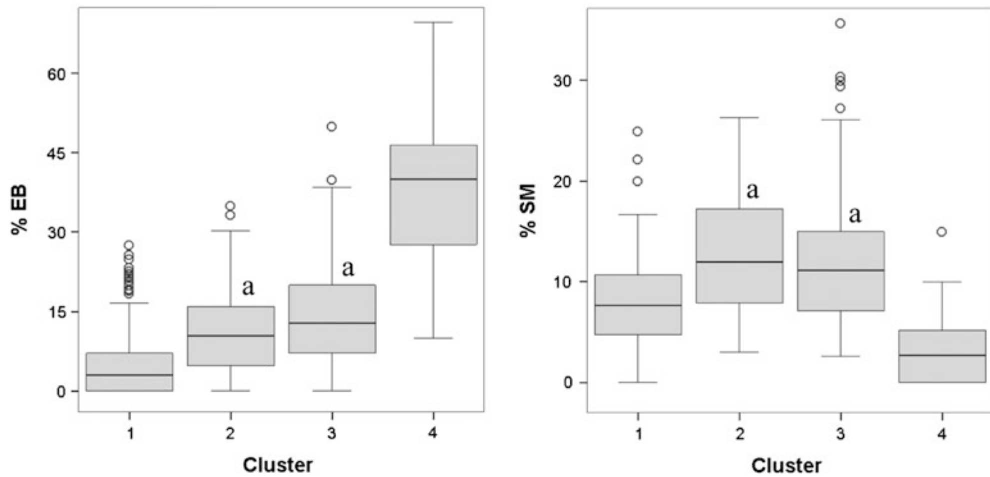

Fig. 3 Comparison of clusters obtained from the clustering analysis (see main text), using the proportions of evergreen broad-leaved species (EB) and sub-Mediterranean species (SM). *Boxes* and *whiskers* include 25–75% and 5–95% of the observed values, respectively, and *lines* inside the *boxes* are medians. Clusters marked with the same letter (a) do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test and a *post hoc* Mann-Whitney U-test

Table 3 Median and interquartile ranges (50% of cases, in parentheses) of climatic parameters for the clusters from hierarchical numerical classification (see main text). Values followed by the same letter (a,b) within a row do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test (X^2) and a *post hoc* Mann-Whitney U-test. N = 494. df = 3. *** = $p < 0.001$. ** = $p < 0.01$

Cluster	1	2	3	4	X^2
P	838 (673–1,141)[a]	858 (752–1,069)[a]	652 (567–829)[b]	699 (626–871)[b]	80.99***
Ic	16.1 (14.8–18.2)[ab]	16.7 (15.6–17.9)[a]	17 (15.3–18.6)[a]	15.1 (13.7–17.5) [b]	16.86**
It	183 (131–247)[a]	179 (125–207)[a]	195 (172–216)[a]	353 (322–382)	123.8***
Io	6.5 (4.9–8.7)[a]	7.1 (5.5–9.5)[a]	4.9 (3.8–6.4)	3.6 (3.2–4.4)	122.3***
Ios_2	1.4 (0.7–2.3)[a]	3 (2.1–4.2)	1.6 (1.1–2.1)[a]	0.3 (0.2–0.8)	162.3***

nemoral plants of the *Querco-Fagetea* class. In fact, these forests belonging to the *Quercion broteroi* and *Querco-Oleion sylvestris* alliances have traditionally been assigned to the *Quercetea ilicis* class.

3.2 Floristic Analysis

Table 1 summarizes, for each cluster, the proportion of evergreen broad-leaved species (EB) and sub-Mediterranean species (SM) present in the relevés. The highest average percentage of EB species (40%) is in cluster 4, which comprises *Quercetea ilicis* forests (65.5%) and those of the *Aceri-Quercion fagineae* alliance (20%) located in the warmest areas. The average percentages of *Q. pubescens* (cluster 2: 10.4%) and *Q. faginea* (cluster 3: 12.8%) forests are quite similar. Cluster 1 shows the lowest mean value (3%). For SM species, clusters 2 and 3 have the highest values (mean of 12% and 11% respectively), followed by *Q pyrenaica* forests (7.7%), and cluster 4 (2.7%). The Kruskal-Wallis test was significant for the percentage of EB and SM species ($p < 0.001$). Comparison of clusters (Fig. 3) shows that there is no difference between clusters 2 and 3 for both types of species (EB and SM), but clusters 1 and 3 differ significantly from them and also between them for both variables (Table 1).

3.3 Climatic Analysis

Climatic characterization of the four clusters is summarized in Table 3, and clusters for climatic parameters and indices are compared in the box diagram of Fig. 4. The Mediterranean character of a climate is expressed by low values of Ios_2 (the 2-month summer ombrothermic index: Rivas-Martínez 2007). *Quercus pubescens* forests (cluster 2) show the highest median values (3.0), corresponding to a temperate climate, with significant differences ($p < 0.001$) with respect to the other three clusters, which are linked to a more mediterranean climate. Cluster 4 shows the lowest value, which indicates its mediterranean character; clusters 1 and 3 have intermediate values, in agreement with a submediterranean climate. The annual ombrothermic index (Io) also shows significant differences among clusters, but in this case *Quercus*

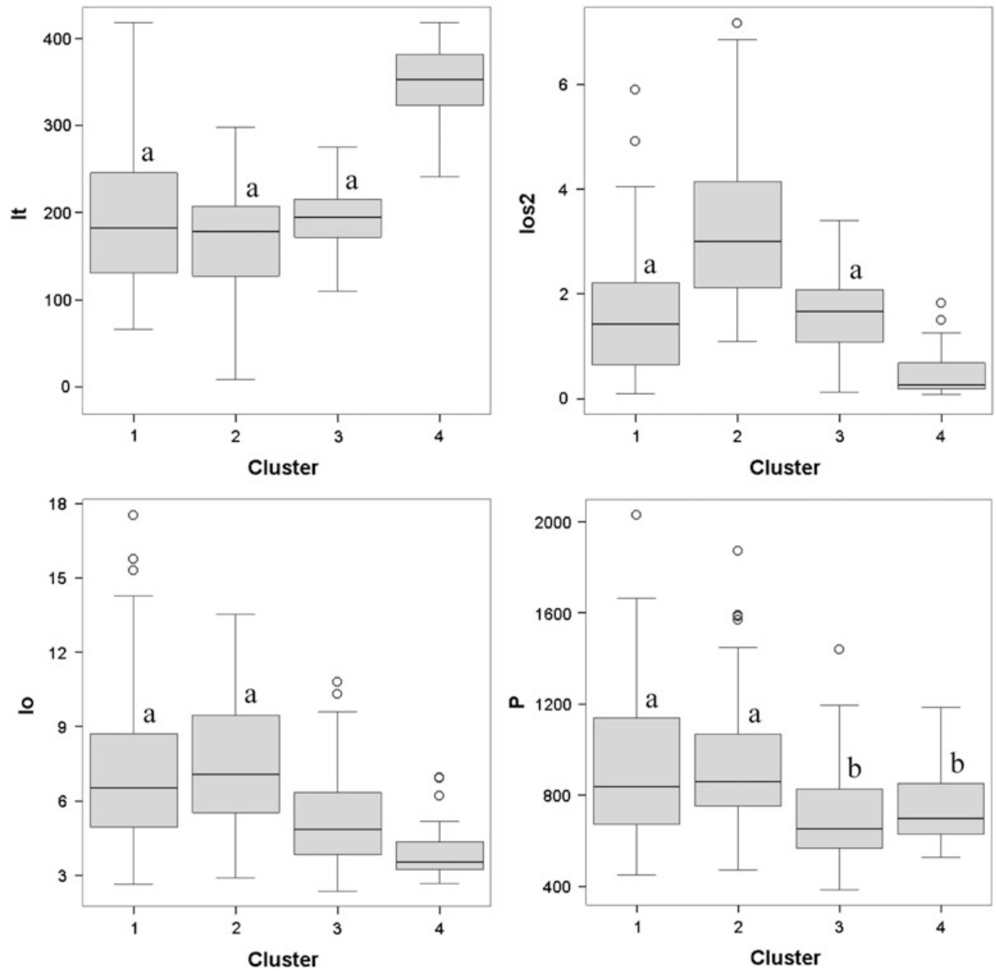

Fig. 4 Comparison of the clusters obtained (see main text) using climatic parameters. *Boxes* and *whiskers* include 25–75% and 5–95% of the observed values, respectively, and *lines* inside the *boxes* are medians. Clusters marked with the same letter (a,b) do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test and a *post hoc* Mann-Whitney U-test

pyrenaica forests (cluster 1) show values similar to those of *Q. pubescens* forests (cluster 2), indicating their affinity for the humid ombrotype; clusters 3 and 4 are related to the subhumid ombrotype (upper and lower, respectively). There is no difference, however, between clusters 3 and 4 in terms of annual precipitation (P), which suggests that temperature controls the dominance by *Q. faginea*, *Q. broteroi* or *Q. canariensis*.

Regarding temperature, cluster 4 bears the highest thermicity index (353) and is significantly different from the other three clusters, which have similar values. This reflects the location of relevés belonging to cluster 4 in the thermo-Mediterranean belt. Continentality does not show any clear differences between clusters ($X^2 = 16.86$).

The diagrams made by NMDS analysis show a clear segregation of the clusters obtained in the hierarchical classification, along axes 1, 2 and 3 (Figs. 5 and 6). These three axes are correlated with climatic indices (Table 4), explaining 33.49% of the accumulated variance. Axis 1 explains the highest accumulated variance (18.25%) and is negatively correlated with annual precipitation (P; $r = -0.319$; $p < 0.001$) and ombrothermic index (Io; $r = -0.313$; $p < 0.001$). Axis 2 shows a large negative correlation with Ios_2 ($r = -0.619$; $p < 0.001$). The diagram representing axes 1 and 2 separates clusters 1, 2 and 3 (Fig. 5). The relevés of cluster 1 (*Q. pyrenaica* forests) are grouped in the first quadrant of the diagram, linked to higher precipitation. The position of relevés of cluster 2 (*Q. pubescens* forests) indicates their temperate character, due to the positive relation with Ios2. Axis 3, which is negatively correlated with the thermicity index (It; $r = -0.702$; $p < 0.001$), involves relevés of cluster 4 (Fig. 6).

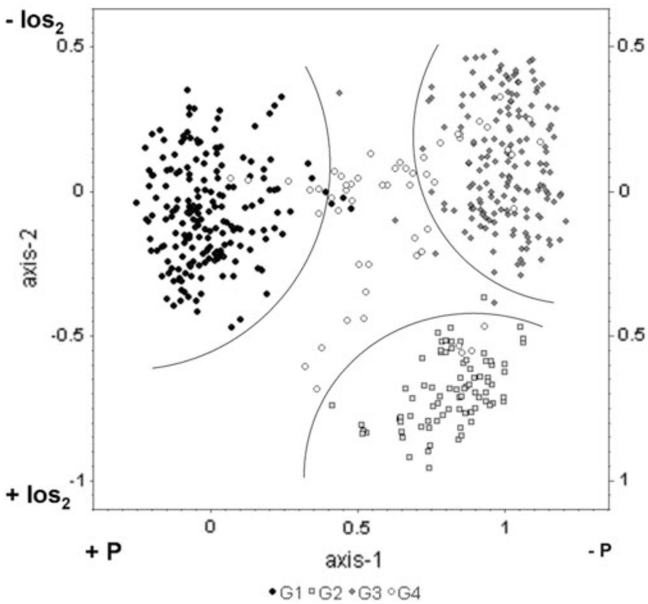

Fig. 5 NMDS ordination of the data-set (see main text), showing axes 1 and 2. G1 – Cluster 1, G2 – Cluster 2, G3 – Cluster 3, G4 – Cluster 4

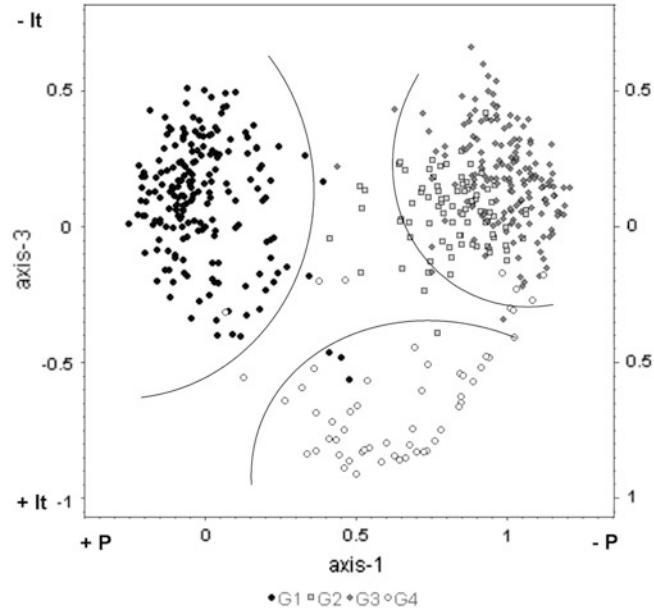

Fig. 6 NMDS ordination of the data-set (see main text), showing axes 1 and 3. G1 – Cluster 1, G2 – Cluster 2, G3 – Cluster 3, G4 – Cluster 4

Table 4 Pearson's correlation coefficients for climatic variables with axes from NMDS ordination analysis (see main text). Accumulated variance explained (Var) by the first three axis = 33.49%. *= $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant

Axe	Var	P	Ic	It	Io	Ios_2
Axis 1	18.25%	−**0.319*****	0.098*	0.078 ns	−0.313***	0.083 ns
Axis 2	8.82%	−0.309***	0.112 ns	0.295***	−0.392***	−**0.619*****
Axis 3	6.42%	0.090*	0.053 ns	−**0.702*****	0.356***	0.419***

4 Discussion

The results of the numerical classification mostly match current syntaxonomy (Rivas-Martínez 2011). Four groups are clearly differentiated, each related to the dominance of one or more *Quercus* species: *Quercus pyrenaica* (cluster 1), *Q. pubescens* (cluster 2), *Q. faginea* (cluster 3) and *Q. broteroi* plus *Q. canariensis* (cluster 4). Nevertheless, some differences can be seen: the associations *Pteridio aquilini-Quercetum pubescentis* and *Carici depauperatae-Q pubescentis*, currently in *Quercion roboris (Quercetalia roboris),* are included in cluster 2, and we propose to change them from *Quercion roboris* to *Quercion pubescenti-petraeae (Quercetalia pubescenti-petraeae).*

Relevés of the *Quercion broteroi* and *Querco-Oleion sylvestris* alliances are grouped together into cluster 4, due to the high number of *Quercetea ilicis* species that they share. Thus we accept their current assignment to this class, which groups both sclerophyllous and marcescent forests from Mediterranean Ibero-Atlantic territories with dry to hyperhumid ombrotypes (Rivas-Martínez 2011). Some relevés dominated by *Q. faginea* and *Q. pubescens* from the eastern coast of the Iberian Peninsula are also included in this cluster 4. These relevés belong to the *Fraxino orni-Quercetum fagineae* and *Violo willkommi-Quercetum fagineae* associations in the *Aceri-Quercion fagineae* alliance.

Fraxino orni-Quercetum fagineae was described by Rivas Goday et al. (1960), who included it in the class *Quercetea ilicis* due to the presence of the Mediterranean species *Lonicera etrusca*, *Arbutus unedo*, *Viburnum tinus*, and *Juniperus oxycedrus*. They admitted, however, that it was quite deviant, as shown by the presence of mesophytic species such as *Acer granatense*, *A. monspessulanum, Quercus faginea*, *Rhamnus infectoria*, and *Colutea arborescens*. Later on, Rivas-Martínez (1972) proposed that the new syntaxon *Aceri-Quercion fagineae* within *Quercetalia pubescenti-petraeae* should go together with *Q. faginea* forests and other mixed sub-Mediterranean Iberian forests developed on base-rich soils. This new syntaxon would occupy, according to Rivas-Martínez (1972), the southern and westernmost areas within the range of *Quercetalia pubescentis*. He also proposed the *Fraxino orni-Quercetum fagineae* association as the type of the new syntaxon. On the other hand, the subassociation *Violo willkommii-Quercetum* *fagineae asparagetosum acutifolii* includes marcescent forests from Catalonian coastal ranges (Royo 2006). It is characterized by the presence of many evergreen character species of *Quercetea ilicis (Viburnum tinus, Smilax aspera, Phillyrea angustifolia, Arbutus unedo, Lonicera implexa*, and *Asparagus acutifolius).*

The syntaxonomic location of *Fraxino orni-Quercetum fagineae* and *Violo willkommii-Quercetum fagineae asparagetosum acutifolii* might not be very appropriate, and their future reassignment to the class *Quercetea ilicis* should be considered.

The almost complete correspondence of the numerical classification with dominance by a particular tree species indicates the existence of a companion flora for these forests. This fits with the syntaxonomic classification, in which the alliances are characterized by tree species together with other diagnostic species (Rivas-Martínez et al 2002).

Quercus pubescens and *Q. faginea* forests have many diagnostic species in common, many of them occurring in sub-Mediterranean areas. Most of the diagnostic species common to clusters 2 and 3 are deciduous, whereas the proportion of evergreen broad-leaved species is only 10% and 12% respectively, not enough to support the idea that these forests originated from the evergreen Tertiary forests.

The evergreen broad-leaved species are linked to cluster 4, which includes the most thermophilous, mediterranean forests, mainly *Q. canariensis* and *Q. broteroi* forests belonging to *Quercetea ilicis*, as stated in the syntaxonomic discussion. In fact, these forests hold many of the lauro-philous Tertiary species that became adapted to submediterranean conditions (*Viburnum tinus, Arbutus unedo, Myrtus communis* and others) (Costa et al. 2015). *Quercus broteroi* and *Q. canariensis* have been defined as semi-deciduous species with Mediterranean distributions (Sánchez de Dios et al. 2009), in contrast to *Q. faginea* and *Q. pyrenaica,* which are marcescent and have sub-Mediterranean distributions. Abadia et al. (1996) also considered that it is the ability to cope with cold winters that differentiates submediterranean marcescent forests from thermophilous Mediterranean forests. In fact, in thermo-mediterranean areas, *Q. broteroi* and *Q. canariensis* can only live in especially humid places, such as ravines or north-exposed cloud forests (Cantó 2004; Rivas-Martínez et al. 1990; Pinto and Paiva 2005), where they replace evergreen sclerophyllous forests.

The small number of sub-Mediterranean and especially of evergreen broad-leaved species in the *Quercus pyrenaica* forests, grouped in cluster 1, may be caused by the acidic soils combined with cooler conditions and high annual rainfall. The *Q. pyrenaica* forests in the south, where it is warmer, have more evergreen broad-leaved species (Cano and Valle 1990; Pereira 2009). This confirms the relation of such plants with warm climates. A comparative study of these forests together with temperate and true Mediterranean acidophilous forests would be of interest, in order to find out how the submediterranean character is reflected in their floristic composition.

The optimum for marcescent forests seems to be linked to sub-Mediterranean areas characterized by an attenuated summer drought with only one arid month in the warm season (Rivas-Martínez 2007). Studies on forests in Castile and Leon indicated that the ombrothermic indices (Io and Ios) are the best bioclimatic indicators for discriminating between marcescent forests (Del Río and Penas 2006). They concluded that the annual ombrothermic index (Io) discriminates between *Q. pyrenaica* and *Q. faginea* forests, the former requiring more humidity than the latter. This agrees with our results, which show significant differences between these forests and also between *Q. faginea* and *Q. pubescens* forests. On the contrary, regarding Ios_2, there is no difference between *Q. faginea* and *Q. pyrenaica* forests but there are significant differences between these forests and *Q. pubescens* forests, which suffer only one month of summer drought. Values of the continentality and thermicity indices do not show differences among these three forests types. *Q. canariensis* and *Q. broteroi* forests, though, differ clearly from the rest in temperature levels, and this fact could explain the relict character of these latter forests in the Mediterranean area.

Marcescence is thus an adaptation to submediterranean areas with winter frost. Many authors have studied the advantages of marcescent vegetation when competing with deciduous or evergreen forests. Montserrat Martí et al. (2004) attributed it to an early budding in spring and delayed leaf senescence in autumn. Marcescent leaves are capable of some photosynthetic activity in the last 1–2 months of the growing season, unlike senescent ones (Abadía et al. 1996). The companion flora of these marcescent forests is also adapted to a submediterranean and somewhat continental climate, as seen by its distribution; it may have been associated with deciduous forests that could have migrated to the south in the Quaternary, since the Pyrenees may not have formed a strong barrier to colonization after the last ice age (Petit et al. 2003).

Quercus broteroi and *Q. canariensis* forests have high proportions of evergreen species and are related to thermo-philous areas with clear summer drought. *Quercus canariensis* is considered to be a semi-deciduous tree (Bingre et al. 2007), as it keeps some of its large leaves functional during winter and then sheds them in spring immediately before the sprouting of the new leaves. This adaptation to mild winters may suggest an evergreen laurophyllous origin partially adapted to summer drought and thus sheltered in especially humid biotopes in thermo-mediterranean territories.

As a conclusion of this survey, it can be stated that the marcescent condition is not related to evergreeness. The abundance of evergreen plants is linked to mediterraneity, and thus the idea of considering marcescence as a residual feature of ancient evergreen laurophyll forests is not supported by our results. Those marcescent forests, particularly basophilous forests, are related to the sub-Mediterranean floristic element.

We propose to move the associations *Pteridio aquilini-Quercetum pubescentis* and *Carici depauperatae-Quercetum pubescentis* into *Quercion pubescenti-petraeae* from the *Quercion roboris* alliance. We also suggest the inclusion of the syntaxa *Fraxino orni-Quercetum fagineae* and *Violo willkommii-Quercetum fagineae asparagetosum acutifolii* in *Quercetea ilicis*. Nevertheless, further studies considering all the associations of *Quercetalia ilicis* and *Quercetalia pubescentis* are necessary.

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Appendix 1. Syntaxonomical Scheme

SALICI PURPUREAE-POPULETEA NIGRAE (Rivas-Martínez & Cantó ex Rivas-Martínez, Báscones, T.E. Díaz, Fernández-González & Loidi 1991) Rivas-Martínez & Cantó 2002

POPULETALIA ALBAE Br.-Bl. ex Tchou 1948

Populion albae Tchou 1948

Fraxino angustifoliae-Ulmenion minoris Rivas-Martínez 1975

1. *Querco pyrenaicae-Fraxinetum angustifoliae* Rivas Goday 1964 corr. Rivas-Martínez, Fernández-González & A- Molina in Fernández-González & A. Molina 1988

QUERCO-FAGETEA SYLVATICAE Br.-Bl. & Vlieger in Vlieger 1937

QUERCETALIA ROBORIS Tüxen 1931

Quercion roboris Malcuit 1929

Quercenion robori-petraeae Rivas-Martínez 1978

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