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ORIGINAL ARTICLE

New insights into the biogeography of south-western Europe: spatial patterns from vascular plants using cluster analysis and parsimony

Juan Carlos Moreno Saiz[1,2*], Mariano Donato[2], Liliana Katinas[2,3], Jorge V. Crisci[2,3] and Paula Posadas[2]

[1]Departamento de Biología (Botánica), Universidad Autónoma de Madrid, Madrid, Spain, [2]Laboratorio de Sistemática y Biología Evolutiva, Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina, [3]División Plantas Vasculares, Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina

*Correspondence: Juan Carlos Moreno Saiz, Departamento de Biología (Botánica), Facultad de Ciencias, Universidad Autónoma de Madrid, Calle Darwin 2, E-28049 Madrid, Spain.
E-mail: jcarlos.moreno@uam.es

ABSTRACT

Aim We analysed the distributional pattern of the vascular flora of the Iberian Peninsula and Balearic archipelago using cluster and parsimony methods to delineate a biogeographical scheme for south-western Europe and to compare the results with previous regionalizations. Additionally, we aim to identify areas of endemism.

Location South-western Europe (Iberian Peninsula and the Balearic Islands).

Methods Pattern analysis of a chorological dataset, consisting of the occurrences of 3041 vascular plant species in each of the 50 km × 50 km UTM cells of a grid covering Iberia and the Balearic Islands, was based on cluster analysis (unweighted pair-group method using arithmetic averages; UPGMA) and parsimony analysis of endemicity (PAE). The Jaccard similarity index was used in the UPGMA, and the set of most parsimonious trees from the PAE were summarized in a 75% majority consensus tree.

Results The UPGMA dendrogram delineated two main branches in the study region: (1) an eastern area of six sectors including the Balearic Islands plus those regions of Iberia with basic substrates, and (2) a western area with three sectors comprising the regions with acidic soils. The majority rule consensus tree of 53 most parsimonious trees from PAE showed eight main clades similarly separating eastern Iberia plus the Balearic Islands with their basic substrates, from western Iberia with its acidic and basic substrates; in addition the PAE tree showed some previously undetected chorological patterns.

Main conclusions The use of large and inclusive datasets allows for the recognition of different spatial patterns from those obtained using a limited number of endemic or indicator species. The analyses support some floristic regions previously recognized for Iberia, but not the classic Eurosiberian–Mediterranean division, and some transition territories. Our recognition of 19 areas of endemism consisting of two or more cells and 60 consisting of one cell in south-western Europe is new.

Keywords

Areas of endemism, Balearic Islands, classification, conservation biogeography, dendrogram, Iberian Peninsula, multivariate methods, PAE, phytogeography, regionalization.

INTRODUCTION

In recent years, the importance of robust systems classifying biogeographical patterns (i.e. regionalizations) has been emphasized (Olson *et al.*, 2001; Whittaker *et al.*, 2005; Mackey *et al.*, 2008; Procheş, 2008; Kreft & Jetz, 2010). Besides their use in providing a taxonomy of distributional areas based on taxa, they serve as the basis for conservation planning (see Mackey *et al.*, 2008 and literature therein). Mackey (2008) noted that such analyses of species distribu-

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tions provide information concerning prior and predicted future distributional and evolutionary events.

Biogeographical regionalizations provide a basic summary of how life on Earth is patterned as a result of history and current physical and biological determinants (Kreft & Jetz, 2010). Therefore, they provide an indispensable background for answering basic and applied questions in biogeography, evolutionary biology, systematics and conservation (Morrone, 2009; Posadas *et al.*, 2010). Two methods that have been widely applied to define biogeographical regionalizations are cluster analysis (Sneath & Sokal, 1973; Kreft & Jetz, 2010) and parsimony analysis of endemicity (Crisci *et al.*, 2000, 2003; Crisci, 2001; Katinas *et al.*, 2004; Crisci & Katinas, 2009). Both methods provide objective approaches for classifying biotas into a hierarchical system because they use quantitative measures of similarity among areas to reveal natural patterns of distribution (López *et al.*, 2008).

The agglomerative cluster algorithm, unweighted pair-group method using arithmetic averages (UPGMA), is one method that has been used to analyse distributional information of taxa (Márquez *et al.*, 2001; Moreno Saiz & Lobo, 2008). Sneath & Sokal (1973) and, more recently, Kreft & Jetz (2010) have shown that the UPGMA algorithm produces less distortion in relation to the original similarities than complete, single and other average linkages, and performs better for biogeographical regionalization than other algorithms.

Parsimony analysis of endemicity (PAE; Rosen, 1988) is a method that classifies areas (localities or quadrats) according to their shared taxa, resulting in a hierarchical classification of the geographical units. It aids recognition of biotic assemblages and generates biogeographical regionalizations. According to Rosen (1988), PAE cladograms probably reflect geological factors and other prevailing ecological conditions without being able to discriminate among the influences of each factor.

Parsimony analysis of endemicity also allows recognition of areas of endemism, defined as the congruent distributions of two or more species (Platnick, 1991), sometimes resulting from evolution of different taxa that share the same isolated regions (Rosen, 1978) and thus evolve under the same ecological and historical conditions.

Here, we present an example of the application of these techniques for the Iberian Peninsula (Spain, Andorra, Portugal and part of France) and the Balearic Islands. This region is a particularly good model because:

1. The Mediterranean area is exceptionally rich in biological diversity (Blondel & Aronson, 1999) and many studies have been carried out in it (Thompson, 2005; Blondel & Médail, 2009). The main centres of Mediterranean plant diversity are located primarily on its islands and peninsulas, that is: Anatolian, Balcan, Italian, and Iberian (Médail & Quézel, 1997). These islands and peninsulas have had an important role not just as cradles of biodiversity (evolution, radiation) but as refugia, especially during Quaternary glaciations (Taberlet *et al.*, 1998; Hewitt, 1999). For example, 25% of the Mediterranean glacial refugia identified by Médail & Diadema (2009) are located in Iberia and the Balearic Islands.

2. Biogeographical analyses of the Iberian Peninsula together with the Balearic archipelago have been carried out to establish spatial patterns using different taxonomic groups (i.e. Sainz Ollero & Hernández Bermejo, 1985; García Barros *et al.*, 2002; Rivas-Martínez *et al.*, 2002; Carrascal & Lobo, 2003; Moreno Saiz & Lobo, 2008; Romo & García-Barros, 2010; see Table 1). However, other authors have studied Iberia separately to avoid the complications that inclusion of species of the archipelago may create (Márquez *et al.*, 1997, 2001; Vargas *et al.*, 1998).

3. Previous studies of south-western Europe were based on incomplete or insufficiently large datasets, representing fewer taxa and so did not include the full range of plant biodiversity.

We compiled the largest vascular plant database used so far in a biogeographical study of this area, including all fern and gymnosperm species and a large number of angiosperm species. The use of such databases that include information on a large portion of a region's biodiversity is potentially critical to avoid biases introduced by limited geographical data (Soria-Auza & Kessler, 2008 and references therein).

Therefore, our objective is to analyse the distributional pattern of the vascular flora of the Iberian Peninsula and Balearic archipelago. Both cluster and parsimony methods are applied to delineate a biogeographical scheme for south-

Table 1 Primary models of biogeographical regionalizations based on vascular plants for south-western Europe.

Reference	Study group	Area	Geographical grain	Method
Sainz Ollero & Hernández Bermejo (1985)	Endemic dicotyledons (n = 1200)	SW Europe	OGUs of varying size	Ward, Lance-Williams
Moreno Saiz *et al.* (1998)	Endemic monocotyledons (n = 182)	SW Europe	100, 50 and 10 km UTM squares	TWINSPAN, DECORANA
Márquez *et al.* (2001)	Pteridophytes (n = 113)	Iberian Peninsula	OGUs of varying size	UPGMA
García Barros *et al.* (2002)	Endemics (129 plants + 351 animals)	SW Europe	100 km UTM squares	UPGMA, PAE
Rivas-Martínez *et al.* (2002)	A number of taxa and plant communities	SW Europe and Canary Islands	–	Expert knowledge
Moreno Saiz & Lobo (2008)	Pteridophytes (n = 123)	SW Europe	50 km UTM squares	Ward

n, number of taxa considered; OGUs, operational geographic units; PAE, parsimony analysis of endemicity; UPGMA, unweighted pair-group method using arithmetic averages.

western Europe. Additionally, PAE will allow the definition of areas of endemism, defined as groups of cells that share two or more exclusive species or as individual cells with at least two exclusive taxa (autapomorphies; Morrone, 1994). These areas of endemism would be considered as potentially relevant for biodiversity conservation (Posadas, 1996).

MATERIALS AND METHODS

Description of the study area

The study area in south-western Europe comprises the Iberian Peninsula (continental Portugal and Spain, Andorra and a small portion of France, totalling 580,000 km^2) and the Balearic archipelago. The latter consists of four main islands (Majorca, Minorca, Ibiza and Formentera) and several close islets extended over 5000 km^2. The islands are also grouped as the eastern Gymnesic Islands (Majorca and Minorca) and the western Pine or Pityusic Islands (Ibiza and Formentera).

The topography of the area includes inner plateaus surrounded by mountain ranges (the Pyrenees and Cantabrian Range in the north, the Baetic System in the south) mainly oriented in an east–west direction, except for the Iberian System, which is oriented in a predominantly north-west to south-east direction (Fig. 1a).

Acidic substrates and silicate soils tend to predominate in the western half of the peninsula because of the underlying Hercynian massif, which is made up of Palaeozoic schists

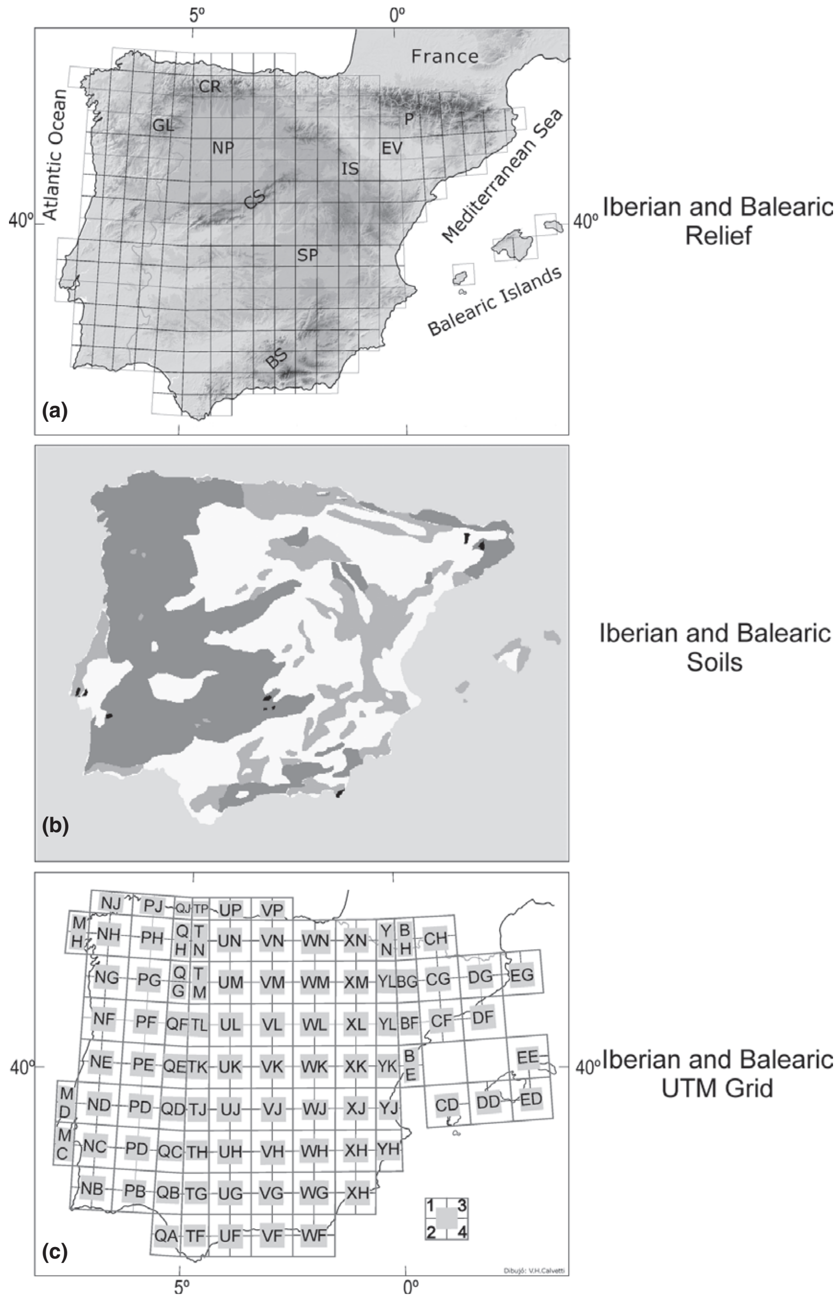

Figure 1 (a) Map showing Iberian and Balearic topography, overlain by a 50 km × 50 km UTM grid and showing geographical areas referred to as follows: BS, Baetic System; CR, Cantabrian Mountain Range; CS, Central System; EV, Ebro Valley; GL, Galician-León Mountains; IS, Iberian System; NP, North Plateau; P, Pyrenees; SP, South Plateau. (b) Area geology: silicate soils (dark grey), calcareous soils (light grey), clayey soils (white) and volcanic soils (black). (c) Cell names: each 100 km × 100 km cell is named by the pair of letters in its centre; each 50 km × 50 km cell within each 100 km × 100 km cell is numbered as indicated in the square in the lower right corner of Fig. 1.

and quartzites. Triassic and Jurassic sandstones, marls and limestones predominate in the eastern half (Fig. 1b). The Baetic Mountains are part of a Cenozoic geosyncline that extends from Gibraltar north-eastwards across south-eastern Spain to the Balearic Islands and consists of an extremely complicated mixture of micaschists, peridotites, limestones and dolomites (Gutiérrez Elorza, 1994; Martínez de Pisón & Molina Holgado, 2002).

Areas in the north and along the Atlantic coast have a temperate climate, while the areas south of the Pyrenean–Cantabrian axis and the Balearic Islands have a Mediterranean climate. The greatest contrast in Iberia is between the high humidity of the north-west and the dryness of the south-east. Montane climates with high insolation and strong thermal contrasts typify various mountain ranges, and continental climates are characteristic of the inner plains and the Ebro Basin.

Species distribution data

A grid of 50 km × 50 km UTM was superimposed on a map of the Iberian Peninsula and the Balearic Islands. Only cells with at least 20% of their surface area not covered by seawater were considered. Cells close to longitudinal lines in southern Iberia are reduced to small trapezoids and so were combined with their respective adjacent squares to minimize strong differences in areas among cells. In the Balearic Islands, Minorca was treated as a single cell, Majorca as two cells, and the smaller Pityusic Islands (Ibiza and Formentera) were joined in a single cell. The resulting grid included a total of 254 cells (Fig. 1a & c).

Distributional data were compiled from various sources: (1) *Atlas Florae Europaeae*, which used the same 50 km × 50 km UTM grid (Jalas & Suominen, 1972–1994; Jalas *et al.*, 1996), with their maps updated using data from subsequent monographs (e.g. Salvo *et al.*, 1984) and sparse records published after each atlas volume until 2011; and (2) maps of Iberian and Balearic vascular plants using 10 km × 10 km UTM cells, comprising about 1750 additional maps published in regional floristic atlases and red data books (e.g. Amaral Franco & Rocha Afonso, 1982; Villar *et al.*, 1997–2001; Bolòs, 1998; Bañares *et al.*, 2004–2011). Most of these maps took their information from sheets deposited in public herbaria and from recent fieldwork associated with several national or regional chorological projects. The resulting database is the largest assembled to date with 79,194 records corresponding to 3041 taxa, with no less than 40% of the whole Iberian and Balearic vascular flora included, estimated at 7500 species and subspecies (cf. Castroviejo, 1997, 2010). Nomenclature follows Castroviejo (1986–2010).

Pattern analyses

Cluster analysis was performed using the Jaccard index and UPGMA (Sneath & Sokal, 1973) implemented in the program PAST 2.08b (Hammer *et al.*, 2001). Although Real & Vargas (1996) proposed a method to quantify the statistical significance of the observed similarity values obtained, the calculus of the probabilities associated with the Jaccard index is computationally very complex and therefore difficult to apply (Real, 1999). This problem is further magnified by the size of the matrix analysed here. For these reasons no estimate of statistical significance was calculated for the cluster analysis performed.

Parsimony analysis was carried out with TNT 1.1 (Goloboff *et al.*, 2000, 2008) under maximum parsimony using equal weights to group areas and define areas of endemism. The tree search was performed using a combined search strategy of ratchet plus tree-fusing (Goloboff, 1999; Nixon, 1999), using the default setting for both algorithms. In order to ensure that the best results were found, an initial analysis was performed until the best score was hit 10 times, and this procedure was repeated, increasing the number of hit findings by 10. In this way, the best score was stabilized in 20 hits; to corroborate this result, the analysis was continued until 30 hits gave the same results. Branch support was estimated using jackknife analysis performing 1000 pseudoreplicates and using the same setting as in the original analysis but stopping after hitting the best score once.

Areas of endemism were recognized after applying PAE and were delimited as groups of cells defined by at least two shared species or as individual cells with two or more exclusive species (Morrone, 1994). All species were used in the analysis although 345 of them were exclusive to a single quadrat and therefore treated as autapomorphies.

RESULTS

Each cell of the dataset contained an average of 313 taxa, ranging from fewer than 100 taxa (83 taxa in WJ3 and 94 in WJ1, both from the Southern Plateau) to around 700 taxa (701 taxa in YN2, 708 in DG1, both from the Pyrenees). Figure 1c shows the nomenclature used for the 50 km × 50 km UTM cells, following the system used by Jalas & Suominen (1972–1994).

UPGMA

The dendrogram from the cluster analysis (Fig. 2; see Appendix S1 in Supporting information for the full size dendrogram) provides evidence for recognizing 10 main sectors, some of which comprise districts, 16 in all (Table 2). We selected only those clusters (groups) of cells with a similarity value of more than 0.2 and which are biogeographically meaningful. The choice of a value of 0.2 seemed reasonable because of the large size of the data matrix. The dendrogram shows two main branches correlated to a noticeable longitudinal territorial component (see the red line in Fig. 2): (1) an eastern area where basic substrates dominate (Sectors 1–6), and (2) a western area where acidic soils tend

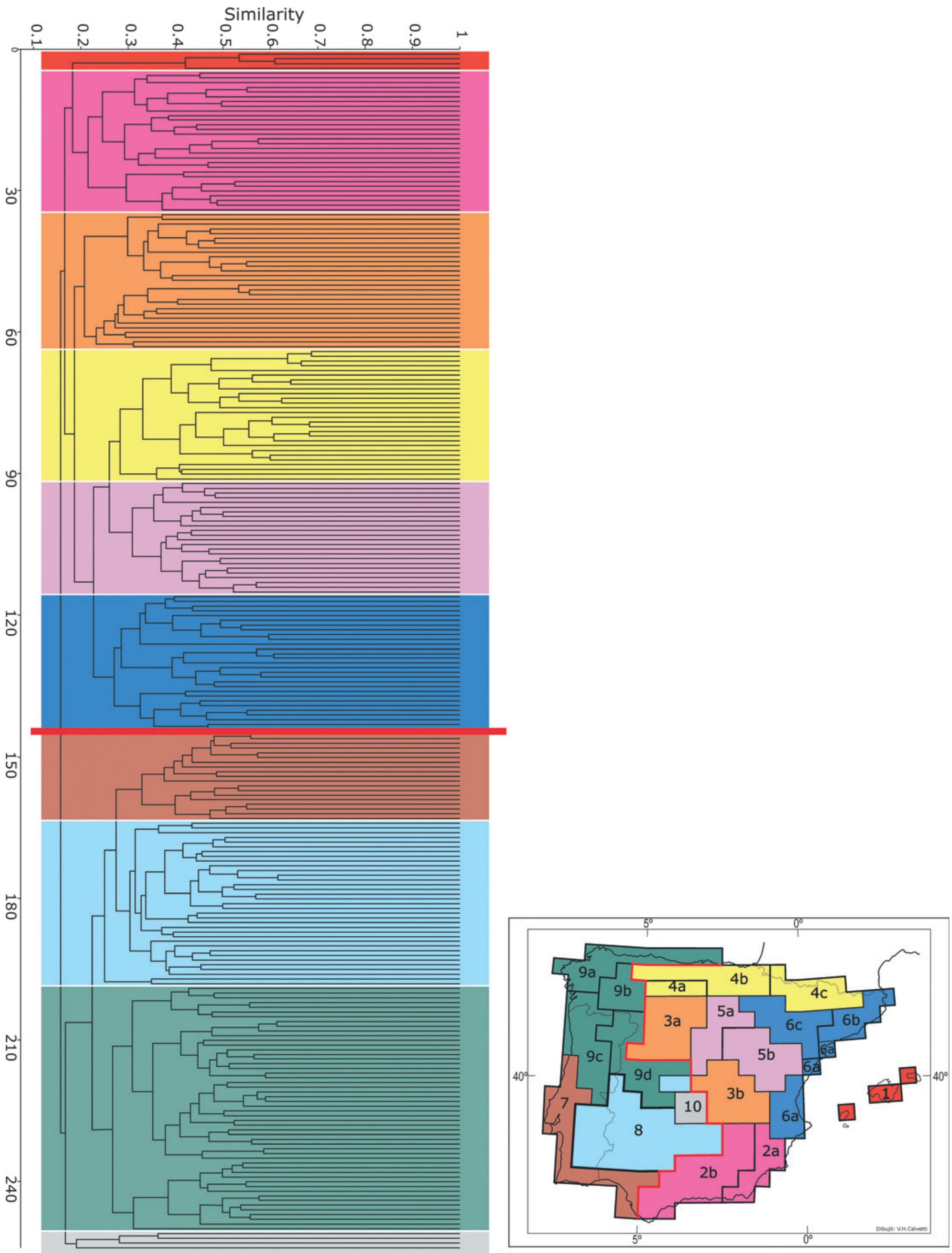

Figure 2 Dendrogram and map resulting from UPGMA analysis of the distribution of vascular plants in the Iberian Peninsula and Balearic archipelago. The red line in the dendrogram indicates the primary division of the 50 km × 50 km cells into the floristic regions shown on the map. The 10 main sectors are numbered in the same order as they appear in the dendrogram, and abbreviations of sectors and districts are given in Table 2.

to dominate and which additionally has climates strongly influenced by the Atlantic Ocean (Sectors 7–9). Sector 10 is characterized by poor data and human disturbance and is associated with this western branch.

The detailed composition of the 10 sectors is as follows (Table 2):

1. Balearic sector: comprising the Balearic archipelago (Table 2; Fig. 2). It is characterized by a high degree of endemicity; the uniqueness of its biota has long been recognized (Sainz Ollero & Hernández Bermejo, 1985; Moreno Saiz *et al.*, 1998; García Barros *et al.*, 2002). The dendrogram first groups the minor western islands (Pytiusic Islands) with the

Table 2 Floristic regions in the Iberian Peninsula and Balearic archipelago based on UPGMA cluster analysis for distributional data from vascular plants.

Sectors	Districts
Eastern	
1. Balearic	
2. South-eastern	2a. Murcian-Almerian
	2b. Baetic
3. Manchego-Castillian	3a. Castillian
	3b. Manchego
4. Cantabrian-Pyrenean	4a. Pre-Cantabrian
	4b. Basque-Cantabrian
	4c. Pyrenean
5. Iberian System	5a. North Iberian System
	5b. Maestracense
6. North-eastern	6a. Valencian
	6b. Catalonian
	6c. Ebro Basin
Western	
7. Coastal south-western	
8. Luso-Extremadurense	
9. Hercynian	9a. Coastal Northatlantic
	9b. Galician-León
	9c. North Portuguese
	9d. Carpetanian
10. Poor data	

eastern ones (Gymnesic Islands), and then groups the two Gymnesic Islands: Menorca and Majorca.

2. South-eastern sector: comprising most of the Baetic Mountains, *sensu lato*, from the Straits of Gibraltar to the south-eastern Iberian coast, the driest area in continental Europe (Kunkel, 1993; Armas *et al.*, 2011). The large number of shared endemics within the sector provides evidence against the usual recognition of two sectors here, the Baetic and Murcian-Almerian (Moreno Saiz *et al.*, 1998; Rivas-Martínez *et al.*, 2002), which we treat as districts (Districts 2a & 2b in Table 2 & Fig. 2).

3. Manchego-Castillian sector: comprising the inner plateaus and depressions characterized by basic substrates and a continental climate, subdivided into a northern part representing the inner part of the Duero Depression, and a southern one corresponding roughly to the La Mancha area (Districts 3a & 3b in Table 2 & Fig. 2). The disjunction could be an artefact of grid size. The long history of human disturbance has undoubtedly resulted in the homogenization of the floras of both tablelands. A similar territory had been recognized by Moreno Saiz *et al.* (1998) and Rivas-Martínez *et al.* (2002).

4. Cantabrian-Pyrenean sector: comprising the northern mountain chains. Sainz Ollero & Hernández Bermejo (1985) and Márquez *et al.* (2001) also treated the area as a single sector because of the mountains' shared endemic dicots and ferns. These mountains are usually considered part of the Eurosiberian region (Rivas-Martínez *et al.*, 2002). The dendrogram provides evidence for considering the sector to consist of three districts: the Pre-Cantabrian, the Basque-Cantabrian, and the Pyrenean districts (Districts 4a, 4b & 4c in Table 2 & Fig. 2).

5. Iberian System sector: comprising the Iberian System plus the eastern limit of the Central System. These two montane areas include both acidic and basic substrates and have never previously been treated as a single phytogeographical area. However, the area has served as the only roughly longitudinal corridor for migration since the Miocene and has also facilitated contact between northern and southern elements (Martín Cano & Gurrea, 2003). Two districts are here recognized, the North Iberian System and a more southern Maestracense district (Districts 5a & 5b in Table 2 & Fig. 2).

6. North-eastern sector: comprising most of the Mediterranean littoral plus the Ebro Valley. The two coastal districts, Valencian (6a) and Catalonian (6b) have a maritime climate, while the inner Ebro Basin (6c) has a continental climate and is underlain by evaporites. It has not been recognized in previous Iberian phytogeographical classifications. A pattern similar to our North-eastern sector based on the distribution of endemic vascular plants has been suggested (Sainz Ollero & Hernández Bermejo, 1985; Moreno Saiz *et al.*, 1998).

7. Coastal south-western sector: comprising the Atlantic coast from the Straits of Gibraltar to central Portugal. Widely recognized because of its endemic plant taxa and physiognomic communities (Sainz Ollero & Hernández Bermejo, 1985; Moreno Saiz & Sainz Ollero, 1997; Rivas-Martínez *et al.*, 2002), this sector with its maritime climate probably served as a major refuge during Quaternary glaciations (Moreno Saiz & Sainz Ollero, 1997; Gómez & Lunt, 2007).

8. Luso-Extremadurense sector: comprising the inland areas of south-western Iberia. This sector is roughly coincident with the region of the same name proposed by Rivas-Martínez *et al.* (1990, 2002) for inland parts of the Guadiana and Guadalquivir River basins.

9. Hercynian sector: comprising an arc of cells extending from the Gulf of León to the Central System, mainly over acidic substrates. This is the largest sector and comprises several districts (Districts 9a–d in Table 2 & Fig. 2): the northern coast (9a), Galician-León mountain ranges (9b), northern Portugal (9c), and the inland acidic mountains from the Central System to the Toledo Mountains (9d). Pteridophytes show a similar distributional pattern (Moreno Saiz & Lobo, 2008), and Bolòs (1985) proposed a similar Carpetanian–Atlantic territory, although previous regionalizations have never related the Cantabrian coast to the rest of this sector.

10. Finally, a small sector at the base of the dendrogram clusters some grid cells from the South Plateau that have a long history of agriculture and cattle rearing. The few remaining natural areas here have probably discouraged floristic studies that would provide a better understanding of the sector's relationships to other Iberian sectors.

Parsimony analysis of endemicity

Parsimony analysis of endemicity (PAE) yielded 53 trees with length (L) 35,854, consistency index (CI) 0.85, and retention

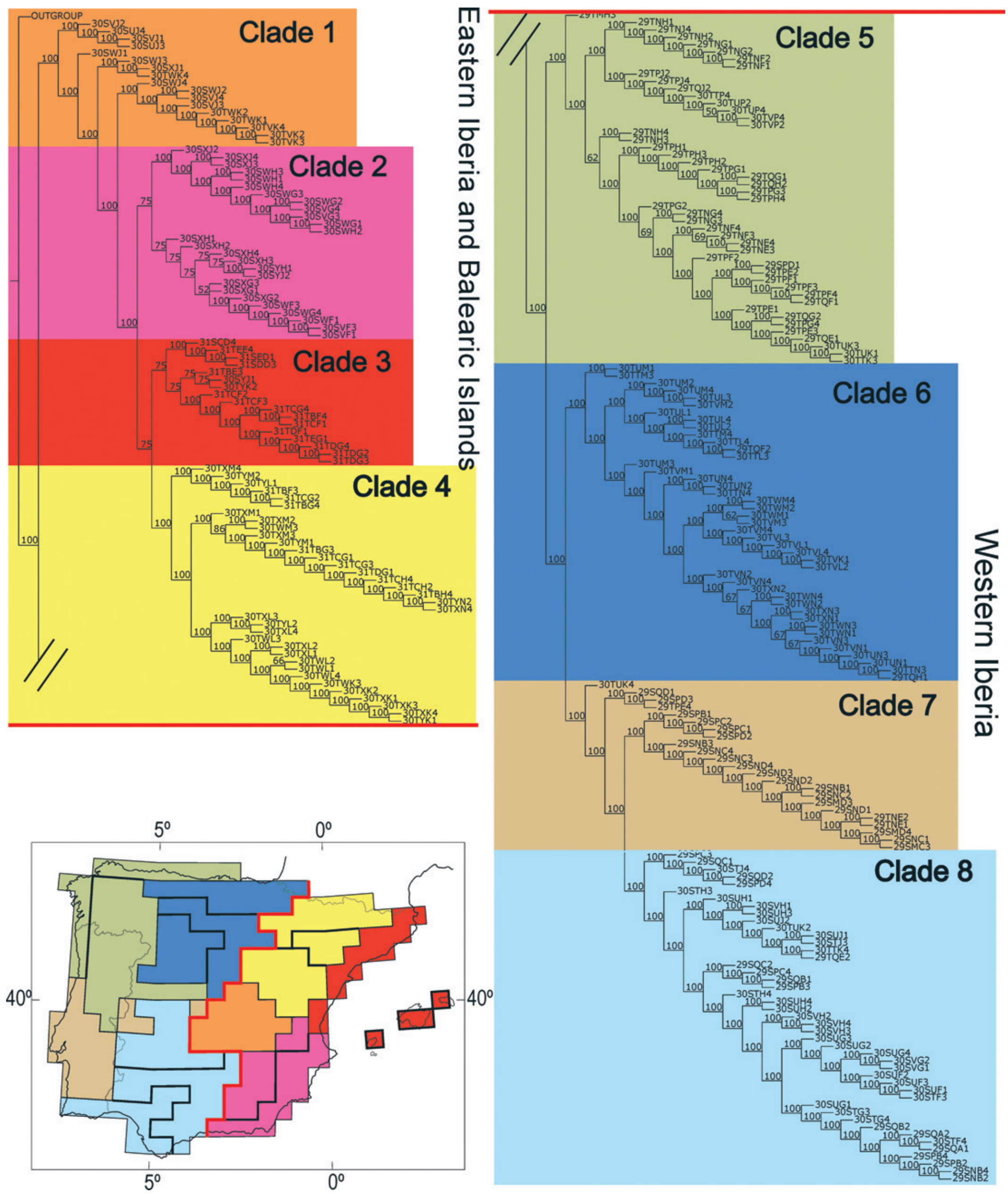

Figure 3 Seventy-five percent majority-rule consensus tree of 53 equally parsimonious trees from parsimony analysis of endemicity (PAE) of the distribution of vascular plants in the Iberian Peninsula and Balearic archipelago (length = 35,854; consistency index = 0.85; retention index = 0.52). For each node its frequency of occurrence in the set of equally most parsimonious trees is given. The primary division of cells into geographical areas is shown by the red line in the cladogram and in the map.

index (RI) 0.52. A consensus tree was constructed applying the 75% majority-rule, that is, by retaining only those clades that were present in 75% or more of the 53 trees. The tree was highly resolved (99%) (Fig. 3). (The complete structure of the tree including the position of each cell is given in Appendix S2).

Jackknife support values were low for most groups, except for a few groups of cells within clade 5. We selected the main monophyletic groups following the hierarchical structure of the final cladogram. Thus, the two main basal clades defined the primary division of the area (see red line in Fig. 3). Clades 1–8 were similarly defined, as were the main subclades within them (Fig. 3).

Like UPGMA, PAE finds that the main division of the total Iberian–Balearic set of cells is primarily longitudinal, splitting eastern Iberia plus the Balearic Islands (Clades 1–4 in Fig. 3) from western Iberia (Clades 5–8). However, PAE differs from UPGMA in restricting cells in the eastern branch to those closer to the Mediterranean Sea (compare red lines in Figs 2 & 3) and including the Baetic and Iberian mountain systems with their acidic and basic substrates in

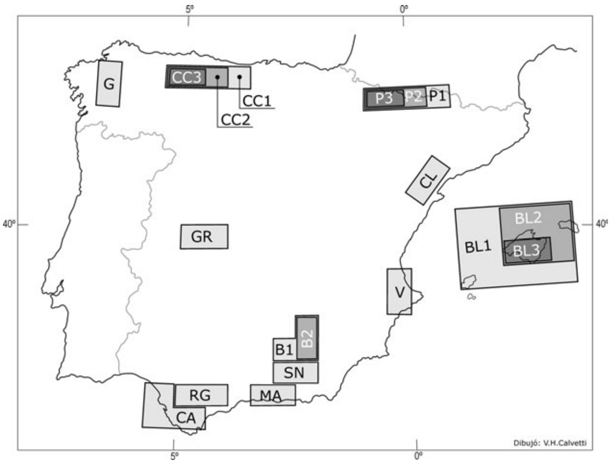

Figure 4 Areas of endemism of vascular plants in the Iberian Peninsula and Balearic archipelago consisting of two or more cells supported by the presence of at least two endemic taxa within the 50 km × 50 km grid. B, Baetic System; BL, Balearic Islands; CA, Cádiz; CC, Cantabrian Mountain Range; CL, Catalonian Cordillera Littoral; G, Galician Mountains; GR, Sierra of Gredos; MA, Málaga-Granada; P, Pyrenees; RG, Sierras of Ronda and Grazalema; SN, Sierra Nevada; V, coastal Valencia.

the western branch. Further branching gives up to eight groups along a mainly latitudinal gradient.

The branches formed by PAE are not exactly those formed by cluster analysis. However, those in the north-western and south-eastern parts of Iberia are very similar to the Hercynian and South-eastern sectors (see Figs 2 & 3). In contrast, PAE apportions some of the cells in the Cantabrian-Pyrenean sector to the eastern and some to the western branches of the first split of the PAE. Also, PAE puts the Balearic archipelago into a larger clade with the Valencian and Catalonian coastal areas.

Areas of endemism

Nineteen areas of endemism were identified, each consisting of two or more cells and containing two or more endemic taxa (Fig. 4). Table 3 lists the taxa supporting each area. These 19 areas can be grouped into 12 main areas as follows: Sub-Baetic System, Balearic Islands, Cádiz, Cantabrian Mountain Range, Catalonian Cordillera Littoral, Galician Mountains, Sierra of Gredos, Málaga and Granada, Pyrenees, Sierras of Grazalema and Ronda, Sierra Nevada, and Coastal Valencia. Four of these main areas contain subsets of cells, which are treated as additional discrete areas of endemism, resulting in the aforementioned 19 units. Nested areas of endemism are present in the Sub-Baetic System (B2 in Fig. 4), the Cantabrian Mountain Range (CC2 and CC3), the Pyrenees (P2 and P3) and the Balearic Islands (BL2 and BL3). The case of the Balearic Islands is especially interesting because its hierarchical structure of nestedness reflects the sequence of isolation between the archipelago and the continent (see below).

Table 3 Areas of endemism of vascular plants in the Iberian Peninsula and Balearic archipelago constituted by two or more cells and their supporting taxa. Square nomenclature as shown in Fig. 1(c).

Area	Taxon
B1: Sub-Baetic System (squares VG3 + WG1 + WH2; n = 2 taxa)	*Crepis granatensis*
	Saxifraga rigoi
B2: Sub-Baetic System (WG1 + WH2; n = 5 taxa)	*Alyssum reverchonii*
	Dianthus subbaeticus
	Erodium cazorlanum
	Hieracium granatense subsp. *granatense*
	Hieracium pallidum subsp. *vulcanicum*
BL1: Balearic Islands (CD4 + EE4 + DD3 + ED1; n = 13 taxa)	*Aetheorhiza bulbosa* subsp. *willkommii*
	Bellium bellidioides
	Carex rorulenta
	Cyclamen balearicum
	Hippocrepis balearica subsp. *balearica*
	Micromeria filiformis
	Micromeria microphylla
	Ophrys balearica
	Romulea assumptionis
	Scabiosa cretica
	Sibthorpia africana
	Silene mollissima
	Verbascum creticum
BL2: Balearic Islands (Gymnesian Islands: EE4 + DD3 + ED1; n = 25 taxa)	*Allium antoni-bolosii* subsp. *antoni-bolosii*
	Aristolochia bianorii
	Arum pictum
	Astragalus balearicus
	Crepis triasii
	Crocus cambessedesii
	Cymbalaria aequitriloba
	Digitalis minor
	Dorycnium pentaphyllum subsp. *fulgurans*
	Dracunculus muscivorus
	Erodium reichardii
	Euphorbia maresii subsp. *maresii*
	Helichrysum ambiguum
	Launaea cervicornis
	Lotus tetraphyllus
	Paeonia cambessedesii
	Pastinaca lucida
	Phlomis italica
	Polycarpon polycarpoides subsp. *colomense*
	Rhamnus ludovici-salvatoris
	Scrophularia ramosissima
	Senecio rodriguezii
	Teucrium asiaticum
	Thapsia gymnesica
	Thymelaea velutina

Table 3 Continued

Area	Taxon
BL3: Balearic Islands (Majorca: DD3 + ED1; n = 24 taxa)	*Brassica balearica*
	Brimeura duvigneaudii
	Calamintha rouyana
	Cephalaria squamiflora subsp. *balearica*
	Delphinium pictum subsp. *pictum*
	Dryopteris pallida subsp. *balearica*
	Fedia caput-bovis
	Galium balearicum
	Genista acanthoclada subsp. *fasciculata*
	Genista majorica
	Globularia cambessedesii
	Helleborus lividus
	Hieracium praecox subsp. *brachypus*
	Limonium marisolii
	Primula acaulis subsp. *balearica*
	Ranunculus weyleri
	Scutellaria balearica
	Sesleria insularis subsp. *insularis*
	Soleirolia soleirolii
	Solenopsis minuta subsp. *balearica*
	Teucrium cossonii subsp. *cossonii*
	Teucrium marum subsp. *occidentale*
	Thymus richardii subsp. *richardii*
	Viola jaubertiana
CA: Cádiz (QA1 + QA2+TF4; n = 2 taxa)	*Narcissus viridiflorus*
	Scrophularia sambucifolia subsp. *mellifera*
CC1: Cantabrian Mountain Range (QH1 + TN3 + UN1 + UN3; n = 3 taxa)	*Hieracium lainzii*
	Ranunculus alpestris subsp. *leroyi*
	Salix breviserrata
CC2: Cantabrian Mountain Range (QH1 + TN3 + UN1; n = 4 taxa)	*Hieracium vegaradanum*
	Nepeta cantabrica
	Ranunculus seguieri
	Salix cantabrica
CC 3: Cantabrian Mountain Range (QH1 + TN3; n = 2 taxa)	*Callianthemum coriandrifolium*
	Centaurea janeri subsp. *babiana*
CL: Catalonian Cordillera Littoral (CF1 + BF4; n = 2 taxa)	*Armeria fontqueri*
	Salix tarraconensis
G: Galician Mountains (NH3 + NH4; n = 3 taxa)	*Armeria merinoi*
	Centaurea janeri subsp. *gallaecica*
	Leucanthemum gallaecicum
GR: Sierra of Gredos (TK3 + UK1; n = 3 taxa)	*Antirrhinum grosii*
	Armeria vestita
	Santolina oblongifolia
MA: Málaga and Granada (VF1 + VF3; n = 3 taxa)	*Arenaria delaguardiae*
	Narcissus rivas-martinezii
	Rosmarinus tomentosus
P1: Pyrenees (XN4 + YN2 + BH4 + CH2; n = 2 taxa)	*Androsace ciliata*
	Saxifraga pubescens subsp. *iratiana*
P2: Pyrenees (XN4 + YN2 + BH4; n = 2 taxa)	*Cystopteris montana*
	Eriophotum scheuchzeri
P3: Pyrenees (XN4 + YN2; n = 3 taxa)	*Festuca altopyrenaica*
	Odontites pyrenaeus subsp. *abilianus*
	Taraxacum ptilotoides
RG: Sierras of Grazalema and Ronda (TF3 + UF1; n = 4 taxa)	*Avenula gervaisii* subsp. *arundana*
	Daucus brachylobus
	Helictotrichum filifolium subsp. *arundanum*
	Koeleria dasyphylla
SN: Sierra Nevada (VG4 + WG2; n = 6 taxa)	*Agrostis canina* subsp. *granatensis*
	Centaurea pulvinata
	Epilobium atlanticum
	Erodium rupicola
	Herniaria boissieri
	Sempervivum minutum
V: Coastal Valencia (YJ2 + YH1; n = 8 taxa)	*Centaurea rouyii*
	Convolvulus valentinus subsp. *valentinus*
	Hippocrepis valentina
	Limonium rigualii
	Pseudoscabiosa saxatilis
	Silene diclinis
	Teucrium flavum
	Thymus webbianus

Finally, we found 60 single cells containing at least two autapomorphies (i.e. exclusive plant taxa), which could be considered as supplementary areas of endemism (see Table 4). Their distribution again highlights the role of the Balearic Islands, the Mediterranean coast and the Baetic, Pyrenean and Cantabrian mountain ranges as centres of plant diversity in south-western Europe (Fig. 5).

DISCUSSION

Phytogeographical classifications for south-western Europe based on plant taxa and plant communities are summarized in Table 1. Many are exclusively defined by endemic plants, based on the idea that they are bioindicators (Braun-Blanquet, 1923; Hernández Bermejo & Sainz Ollero, 1984; but see Hengeveld, 1990). For example, Sainz Ollero & Hernández Bermejo (1985) recognized a Balearic sector and five homogeneous areas within the Iberian Peninsula, with three transition zones in NE, NW and SW Iberia, respectively. Moreno Saiz *et al.* (1998) discussed the effect of grid size in regionalizations and proposed up to 14 regions at the scale of 50 km.

Márquez *et al.* (2001) used the distribution of pteridophyte species within political units and identified three strong boundaries dividing the Iberian Peninsula into four main regions. Later, Moreno Saiz & Lobo (2008) noted that such results are based on inadequate operational geographic units (OGUs) and incomplete data and they proposed a classification of 10 regions for fern species; they also used discriminant analysis to identify the environmental variables that are most highly correlated with such regions.

Table 4 Areas of endemism of vascular plants in the Iberian Peninsula and Balearic archipelago consisting of a single cell. Square nomenclature as shown in Fig. 1(c).

Cell	No. exclusive taxa
DD3	28
CD4	20
EE4	16
TF4	15
VG4	12
WF1	11
CH2	9
VF1	9
WG1	8
YN2	7
DG1	7
DG3	6
EG1	6
BF4	6
WF3	6
NJ4	5
QH1	5
BH4	5
CH4	5
ED1	5
YH1	5
WG2	5
TF3	5
UF2	5
UN3	4
BE3	4
XG3	4
UN1	3
WN3	3
XN3	3
PH4	3
PG4	3
UK1	3
XH1	3
XH4	3
VG3	3
UF1	3
UN4	2
XN4	2
WM1	2
CG3	2
NG4	2
VL1	2
DF1	2
WK4	2
XK2	2
YK2	2
MD3	2
WH1	2
WH3	2
WG3	2
XG1	2
NB2	2
QB2	2
UG4	2
VG2	2
WG4	2
QA1	2
UF3	2
VF3	2

Rivas-Martínez *et al.* (1990, 2002) have been publishing a series of proposals for regionalization of the area based on physiography, distribution of indicator plants, and especially potential natural vegetation. Their phytocoenological systems have been widely used, even though their methodology has never been made explicit. Their last system splits south-western Europe into Eurosiberian and Mediterranean regions, and these in turn into eight provinces (Rivas-Martínez *et al.*, 2002).

García Barros *et al.* (2002) studied both the endemic flora and fauna in south-western Europe, using PAE and a coarse grid (100 km × 100 km) to identify up to 36 endemic areas, many corresponding to mountain chains, with the areas grouped into four main sectors, based on overall similarity.

Some previous studies focused only on Iberian biogeography to avoid ecological or evolutionary concerns related to Balearic insularity. However, our analyses have shown the pertinence of combining the Balearic archipelago together with the Iberian Peninsula in biogeographical analyses of the western Mediterranean, as in some previous studies (e.g. Pichi Sermolli *et al.*, 1988; Carrascal & Lobo, 2003; Moreno Saiz & Lobo, 2008; but see Romo & García-Barros, 2010). Both cluster analysis and PAE retained the Balearic Islands as an *ingroup* of the eastern Iberian–Balearic territory and only separated the two at higher branching levels. The issue of how much of southern French territory should be included as part of south-western Europe study area is yet to be determined.

Neither UPGMA nor PAE analyses supported the classical division between Eurosiberian (or Circumboreal *sensu* Takhtajan, 1986) versus Mediterranean regions in south-western Europe, a latitudinal division roughly paralleling the Pyrenean–Cantabrian montane axis. Although several faunal, floral and phytocoenological studies do suggest such a division (i.e. Rivas-Martínez *et al.*, 1990, 2002; Carrascal & Lobo, 2003; Galicia *et al.*, 2010; Rueda *et al.*, 2010), its primacy has not been supported by other studies, including our own (Moreno Saiz *et al.*, 1998; García Barros *et al.*, 2002). Floristic studies of both endemic and non-endemic plants show that this Eurosiberian–Mediterranean boundary has not been impermeable; many taxa at different times have crossed it in both directions for reasons related to ecology and history (Hewitt, 1999; Vargas, 2003; Gómez & Lunt, 2007). Our large database highlights the importance of connections between Atlantic and Mediterranean climatic regions for a larger number of species than for the small subset of strictly Eurosiberian and Mediterranean floristic elements. Again, the

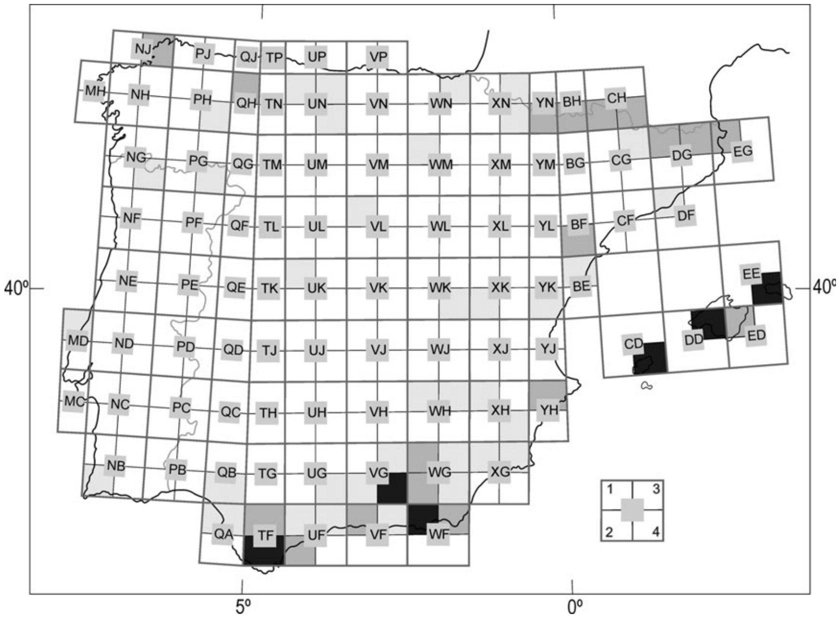

Figure 5 Individual cells that constitute areas of endemism of vascular plants in the Iberian Peninsula and Balearic archipelago supported by the presence of at least two exclusive endemic taxa. Light grey: cells containing from two to four endemic taxa. Dark grey: cells containing from five to nine endemic taxa. Black: cells containing more than 10 endemic taxa.

first dichotomy in both our analyses reflects the strongly longitudinal division between acidic and basic substrates in Iberia (Fig. 1b).

The cluster analysis (UPGMA) enabled us to recognize nine sectors in south-western Europe, representing the Balearic Islands, different mountain ranges, inner plateaus, and the south-western maritime areas. This emphasizes the Iberian physiography and thus the importance of environmental constraints. Human disturbance gives rise to a 10th cluster, made up of a small number of inland cells, transformed by agriculture centuries ago and having a depauperate flora.

PAE similarly showed two main longitudinal clades, but with the longitudinal division located further east. Unlike the cluster analysis, it splits the Cantabrian from the Pyrenean Mountains and the Baetic and Iberian systems. The basal position of La Mancha and surrounding areas (Clade 1 in Fig. 3) could be related with the use of a hypothetical all-zero outgroup for PAE. These plains on the south plateau have been under cultivation for thousands of years, resulting in the extinction of many species. The paucity of species here is exacerbated by the lack of attention by botanists to this degraded landscape.

The linking of the Balearic Islands to Valencian and Catalonian coastal cells (Fig. 3) also was seen for endemic monocots (Moreno Saiz *et al.*, 1998) and is supported by common phytocoenological patterns (Rivas-Martínez *et al.*, 2002). These coastal areas and the Balearic Islands were influenced by the same Alpine uplift, but their similarity could also have been increased by eustatic Mediterranean sea-level changes. At the end of the Miocene and during the Pleistocene, the distance of the western-most islands from the mainland was periodically decreased, enabling, at the height of the glacial periods, more frequent exchanges between their floras (Sáez & Rosselló, 2001; Rosselló & Castro, 2008); during interglacial periods, sea levels rose and the distance again increased. This cyclical process resulted in periodic isolations of plant populations, allowing them to differentiate.

Clade 8 largely consists of the drainages of the Guadiana and Guadalquivir rivers. It also includes the western end of the Baetic Sierras, i.e. the elevations of Ronda and Grazalema, which stood separated from the rest of the Baetic System by a depression (the present valley of the Guadalhorce River), during the lower Messinian (Medina-Cazorla *et al.*, 2010). This sector somewhat resembles the Andalusian pteridological region of Moreno Saiz & Lobo (2008), a territory characterized by some relictual taxa and a large number of fern species. Environmental factors explain less variability here than in the rest of south-western Europe, so historical constraints may have played an important role (Moreno Saiz & Lobo, 2008).

Finally, PAE identified 19 pluricelled areas of endemism, which can be subsumed into 12 Iberian and Balearic areas due to the spatial overlap of some of them (Fig. 4). As congruent distributions of two or more species are the result of evolution under the same ecological and historical conditions (Rosen, 1978), the integration of ecology and history may not only discern processes of spatial arrangement but also highlight some areas of conservation interest (Crisci *et al.*, 2006).

The areas of endemism determined from PAE analysis are mostly concentrated in montane areas, particularly elevations nearer the coast. Such a correlation was already noted by García Barros *et al.* (2002) and by Castro Parga *et al.* (1996) and Lobo *et al.* (2001) in their studies on richness and endemism. Lobo *et al.* (2001) found a strong positive correlation between plant diversity and elevational range throughout south-western Europe in general.

The nested pattern shown by some areas of endemism found in this analysis supports establishment of certain areas for conservation purposes based on their species richness (Posadas, 1996): Pyrenees (cells XN4 + YN2), western Cantabrian Mountain Range (QH1 + TN3), part of the Baetic System (Sierras of Mágina, Cazorla-Segura, and La Sagra, WG1 + WH2) and Majorca. They harbour a significant fraction of the south-western European flora, have probably served as refugia during the Quaternary glaciations, and constitute local hotspots of endemicity (Castro Parga *et al.*, 1996; Araújo *et al.*, 2007; Gómez & Lunt, 2007). Although the Sierra Nevada is considered among the richest floristic areas of the Mediterranean Basin (Gómez-Campo, 1985), it was not supported as a whole in our analysis by a high number of endemic species (Table 3). However, parts of Sierra Nevada are well supported as areas of endemism including single cells areas of endemism (VG2, VG4, WG2; Table 4). These areas of endemism in Sierra Nevada are so rich in endemic taxa that deserve to be considered, as the Sierra already was, an important area for conservation. Other single cells that contain a great number of endemics and therefore could be considered as relevant for conservation purposes are listed in Table 4 and mapped in Fig. 5.

CONCLUSIONS

In summary, our study shows how large datasets allow a more representative assessment of biodiversity and biogeographical pattern. Importantly, it identifies a primary longitudinal division of Iberia between a basic eastern and an acidic western region. The placement of this division in the PAE somewhat eastward of that in the UPGMA reflects a greater emphasis on historical versus ecological factors on plant distributions. The traditional distinction between Eurosiberian and Mediterranean regions is not supported here.

The regionalization we are presenting here is based on the most comprehensive distributional dataset compiled for the area, considerably exceeding the number of taxa used on previous proposals. Also, our regionalization system has the additional advantage of being established through explicit and repeatable methods.

Finally, the identification of areas of endemism recovered by PAE concentrated in the mountain systems of Iberia is consistent with previous studies and strongly supports the arguments for conserving these Quaternary refugia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 More detailed dendrogram from UPGMA cluster analysis of the distribution of vascular plants in the Iberian Peninsula and Balearic archipelago as shown in Fig. 2.

Appendix S2 Seventy-five percent majority-rule consensus of 53 equally parsimonious trees from PAE as shown in Fig. 3.

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BIOSKETCHES

Juan Carlos Moreno Saiz works on different aspects of biogeography and conservation biology of the Mediterranean flora. He co-edited the *Spanish Red Data Book* and coordinated the current Spanish Red List of vascular plants.

The rest of the team belong to Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de La Plata, Argentina. Their research interests are principally focused in the spatial-temporal patterns of southern South America biodiversity, including fossil and extant organisms.

Author contributions: All authors conceived the ideas; J.C.M.S. collected and M.D. analysed the data; all authors analysed and discussed the results and collaborated in the writing, which was led by J.C.M.S. and P.P.

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