Iberian–Balearic fern regions and their explanatory variables

Juan Carlos Moreno Saiz · Jorge M. Lobo

Abstract This article delineates the compositional regions present in the Iberian–Balearic fern flora and compares these regions to previously proposed biogeographic units. It also assesses the extent to which environmental variables could explain the regions and the fern species richness gradients found within them. A combination of 40 previously published and new maps were used to compile the distribution of 123 pteridophytes on a 50×50 km UTM grid. Cluster analysis of the resulting 257 squares was used to classify 10 regions based on fern species assemblages. Discriminant function analysis identified the environmental variables that best explained these fern composition regions. Using generalized linear models; the number of species in each square was regressed against topography, climate, geology, environmental diversity, land use and spatial variables within each region. Two main latitudinal pteridophyte zones can be recognized in the Iberian Peninsula. These two zones are longitudinally subdivided into two sub zones. The 10 regions established significantly differ both in species richness and influential environmental variables. Climatic variables discriminate the most among regions, followed by topography, heterogeneity and geology. Pteridophyte richness varies, with richer areas being located along the coast and the main mountain ranges and the poorest areas being in the central plateaus and some north eastern and south western river basins. Species richness variation in Iberia is positively correlated with altitude range, precipitation, maximum altitude and area with siliceous soils. It is negatively correlated with the total annual days of sun, however. The fact that species richness is explained by different variables within each of the 10 regions indicates that the specific factors determining the spatial distribution of species richness vary from region to region. Some coastal regions are poorly explained by the model, and display a negative correlation with the selected causal factors. This finding suggests that persistent historic effects might play a local role in determining species assemblages in these regions.

Keywords Biogeography · Biotic regions · Cluster analysis · Generalized linear models · Pteridophytes · Variance partitioning

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Introduction

Distribution patterns and the processes underlying their existence have been recurrent topics in descriptive

and experimental biogeography (sensu Birks 1976). Many different and confounding explanatory variables can account for the variation in species richness or floristic composition (Ricklefs and Schluter 1993; Rahbeck and Graves 2001; Whittaker et al. 2001; Hawkins et al. 2003; Lomolino et al. 2005). It is difficult to ascertain the relative contribution of these variables due to the lack of experimental results. Furthermore, when correlations between certain variables and species richness are found, these associations may suggest, but not prove, the existence of causal factors. Any preliminary attempt at explaining distribution patterns must explore the relationships of biological, environmental, spatial and historic variables (Huston 1994; Hengeveld 1996), as this article intends to do.

Pteridophytes are a group with a long evolutionary history. Members of the group are mainly associated with low latitude, tropical and subtropical humid conditions (Smith 1972; Page 1979a; Parris 1985; Kato 1993). Shared biological (spore dispersion over long distances and establishment ability) and ecological characteristics (dependence of sexual reproduction on liquid-phase water, microhabitat preferences) of ferns and allies have resulted in their use as indicators of specific environmental conditions, in spite of their commonly accepted paraphyletic origin (Márquez et al. 2001; Lehmann et al. 2002; Guo et al. 2003). Fern spores, which are good colonizers (Tryon 1970; Kramer 1993), can disperse over large distances (Smith 1972, 1993; Page 1979a, b; Barrington 1993) to connect disjunct areas (Muñoz et al. 2004). This characteristic, along with the lack of co-evolved relationships with pollen or seed vectors (Barrington 1993), plus the asexual reproduction of certain species, enhance the colonizing abilities of ferns (Guo et al. 2003). Thus, the current distribution of the majority of fern species seems to be greatly influenced by environmental conditions (Birks 1976; Richard et al. 2000).

Among the recognized factors relevant to pteridophyte richness, the most noticeable is the importance of moisture or rainfall, a necessary resource for their life history (Page 2002). Since ferns require a continuous supply of water, this variable has been found to be positively correlated with local and regional species richness (Kornas 1993; Clinebell et al. 1995; Lwanga et al. 1998; Kessler 2001; Bhattarai et al. 2004; Bickford and Laffan 2006). Fern richness has also been negatively associated with potential evapo-transpiration. The effect of this variable is attributed to the joint influence of moisture availability and length of growing season (Bhattarai and Vetaas 2003; Bhattarai et al. 2004). In some cases (probably due to a sharp gradient), temperature appears to be an important variable in determining individual fern distributions (Lehmann et al. 2002), probably because pteridophytes are generally associated with warm and tropical conditions (Klekowski 1972; Parris 1985; Kramer 1993). Of the non-climatic factors, soil fertility or C/N ratio can explain the distribution of fern species richness (Tuomisto et al. 1995; Tuomisto and Poulsen 1996; Lwanga et al. 1998). Fertile soils harbour more species-rich assemblages, probably because they offer suitable conditions for gametophyte establishment. Historic or contingent factors, such as the proximity of Pleistocene refugia, have also been suggested to explain the number of fern species in certain areas (Lwanga et al. 1998). Both ecological and geographic isolation also seem to have played a significant role in the conformation of some endemic areas (Tryon 1972).

The Mediterranean basin, a biodiversity hotspot of worldwide importance, is remarkable among other temperate zones in terms of its plant species richness and endemism (Médail and Quézel 1997; Myers et al. 2000). Nevertheless, the Mediterranean does not play a pre-eminent role in terms of pteridophyte diversity, and has been considered a secondary centre of diversity in this group (Pichi Sermolli 1979; Given 1993). Within the Mediterranean region, the Iberian Peninsula is one of the richest areas in floristic diversity due to its palaeogeography and environmental heterogeneity (Sainz Ollero and Moreno Saiz 2002). Patterns of richness related to altitude have been identified (Castro Parga et al. 1996; Lobo et al. 2001; Rey Benayas and Scheiner 2002) and attributed to the fact that mountain chains have probably been the centres of both speciation and refuge, not only during the climate oscillations of the Pleistocene, but also after humans drastically altered lower-elevation plains and valleys. This is particularly true for the Pyrenees (a barrier between the isthmus and the continent) and the Baetic system, which comprises the southernmost elevations with a dominant Mediterranean climate (Gómez Campo et al. 1984; Hernández Bermejo and Sainz Ollero 1984).

General patterns of variation in Iberian and Balearic fern richness and rarity are relatively well

known (Moreno Saiz et al. 1996), but the comparative relevance of different types of environmental variables has been investigated primarily in smaller areas (e.g. Herrero-Borgoñón et al. 1989; Pausas and Sáez 2000; Quintanilla et al. 2003), highlighting the importance of soil types in determining fern species composition. On a larger spatial scale, two major studies carried out at a 50×50 km UTM grid resolution for the entire Iberian Peninsula (Márquez et al. 1997; Ferrer-Castán and Vetaas 2005) suggested the positive influence of rainfall, energy availability and altitudinal range on fern species richness.

The turnover rates in ferns seem to be lower than those in flowering plants (Williams-Linera et al. 2005), and compared to flowering plants, ferns display relatively slow evolutionary rates and high-dispersal capacity (Smith 1972; Kato 1993; Kramer 1993). However, these characteristics do not seem to have enough influence on fern distribution to promote compositional homogeneity across the Iberian Peninsula. There are three hypotheses that have been proposed for defining pteridophyte regionalization in the Iberian Peninsula (Fig. 1). The first hypothesis, according to Birks (1976), divided Iberia into a northern Mediterranean region, extending from northern Portugal to the Italian Peninsula, and a southern Mediterranean region, from southern Portugal to the Balkans, including the Balearic Islands (Fig. 1a). Later, Pichi Sermolli et al. (1988) used the fern composition of Iberia to delimit seven regions (Fig. 1b), which included two large northern and southern areas surrounded by smaller peripheral units. Lastly, Márquez et al. (2001) compared the performance of natural and administrative lattices (11 river basins, 22 physiographic regions and 56 administrative provinces), and concluded that the administrative grid provided the best fern regionalization hypothesis. Accordingly, three strong boundaries divide the Iberian Peninsula into four main regions (Fig. 1c).

Taking advantage of the major increase in pteridophyte distribution information published for the whole area in the last two decades, our first objective in this study is to perform a new analysis to delimit

Fig. 1 Different Iberian plant region proposals based on pteridophytes: (a) from Birks (1976), with indication of previous number of Iberian–Balearic pteridophytes in brackets and currently accepted figure; (b) from Pichi Sermolli et al. (1988); (c) from Márquez et al. (2001)
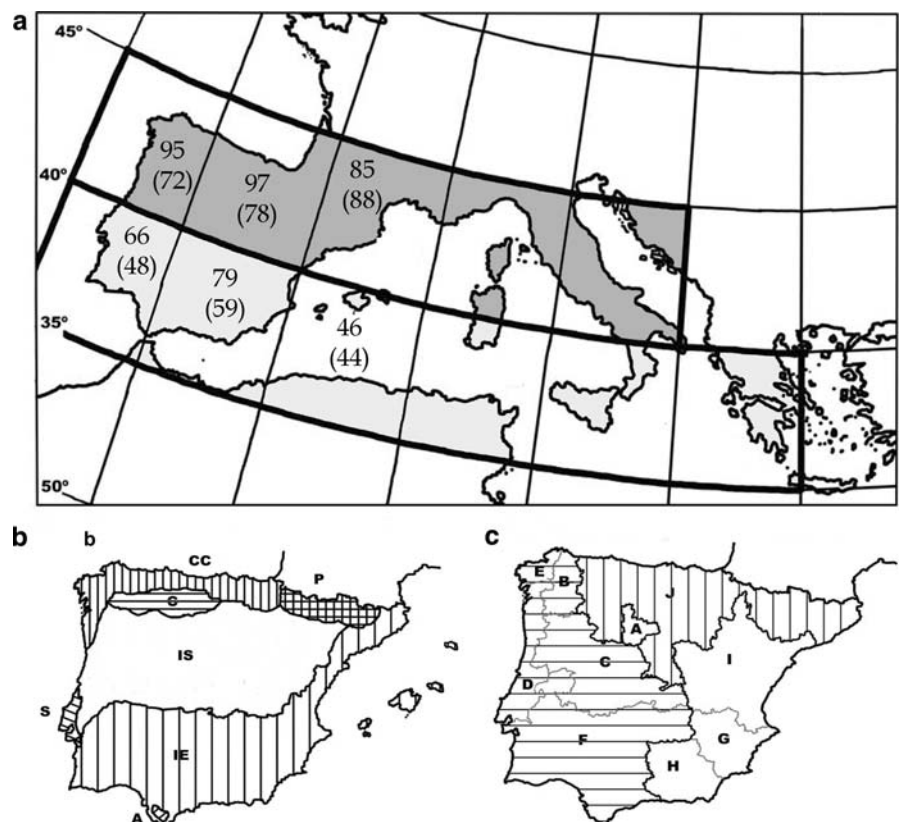
Iberian and Balearic fern regions. We do this by considering both compositional differences and spatial distance between similar species assemblages. In doing so, we review the validity of previously determined regions. Once Iberian pteridophyte regions have been established, we examine the capacity of several types of explanatory variables to discriminate between them. In other words, can the compositional differences between regions be explained by environmental variables? Although previous studies have revised the role of historical and ecological determinants in Iberian and Balearic pteridophyte species richness, we review the relative importance of several variables for explaining fern species richness across the entire Iberian Peninsula. Most importantly, we estimate the comparative influence of these variables for each Pteridological region, and attempt to recognize the relevant predictor variables for fern species richness when compositional differences are minimized. As it has been hypothesized previously (Rosenzweig 1995), variables that produce a coherent signal in species richness vary with scale. These scale changes, and their relationship with the relevance of environmental variables, allow us to determine which factors are of possible influence across the entire territory and how their influence differs across a given region.

Methods

The study area

The Iberian Peninsula covers 581,000 km^2 and harbours a variety of climates, topographic relief, soils and vegetation types. The two climate zones, the Atlantic in the northern fringe and the Mediterranean in the remaining section, overlap to some extent. The climate tends to be continental towards the centre of the Peninsula. Acidic rocks dominate the lithology in the western half of Iberia, and basic rocks dominate in the eastern half. Several mountain chains with predominantly E-W orientation (Pyrenees, Cantabrian Range, Central System and Baetic System) give rise to complex orography that could have acted as barriers to migration during Quaternary climate oscillations.

In the Balearic archipelago (ca. 5,000 km^2), an isolated prolongation of the Baetic System that includes four main islands and several islets, basic soils predominate. Its floristic relationships with the eastern peninsular coast are well documented.

Origin of the data

The list of Iberian and Balearic pteridophytes considered in this study follows the taxonomic proposal of Castroviejo et al. (1986) in *Flora Iberica*, with a few exceptions: the inclusion of *Asplenium obovatum* Viv. subsp. *obovatum* (Pangua et al. 1990), *Hymenophyllum wilsonii* Hook (Soñora et al. 1992) and *Isoetes brochonii* Moteley (Prada and Rolleri 2003), and the removal of the naturalized species (*Azolla carolliniana* Willd., *A. filiculoides* Lam., *Lycopodiella cernua* (L.) Pichi-Serm., *Pteris cretica* L., *Salvinia natans* (L.) All. and *Selaginella kraussiana* (G. Kunze) A. Braun). The final number of native Iberian and Balearic pteridophytes is 123 species and subspecies.

About 80 Iberian and Balearic fern distribution maps have been published within the 10 × 10 km UTM grid format, mainly in chorological sections of the journals *Fontqueria* and *Botanica Complutensis*. Maps for the rest of the Iberian taxa at the same scale were produced for this work (available upon request) and include: the information gathered for the ANTHOS project (http://www.anthos.es); the 'pteridology notes' of the journal *Acta Botanica Malacitana;* and various atlases published in recent years. Since sampling at this resolution is clearly incomplete, data on species presence/absence were later referred to 50 × 50 km UTM grid cells. Distribution data were processed with WORLDMAP software (Williams 2000).

For the 257 Iberian and Balearic 50 × 50 km UTM cells where at least 15% of the surface area was not covered by seawater, 16 simple environmental variables were selected and recorded: topography (maximum, minimum and mean altitude), geology (area with siliceous, calcareous and clay soils), climate (minimum mean temperature, maximum mean temperature, annual mean temperature, total annual precipitation, total summer precipitation and annual days of sun), and four variables that measured environmental diversity (altitude range, annual rainfall variation, annual temperature variation and geologic diversity). Moreover, 16 land-use variables from the 44 land-cover categories provided by the

European Environmental Agency (CORINE Programme 1985–1990) were also used, together with two spatial variables (central latitude and longitude of each grid cell). All explanatory variables are continuous. A detailed description of the sources and GIS procedures used to obtain these variables are provided by Lobo et al. (2001).

Statistical analysis

The Jaccard index estimate of a triangular similarity matrix of the 257 UTM cells, using the presence–absence matrix, was transformed into a distance matrix by calculating the difference between the unity and each value of the Jaccard index. Using the Euclidean UTM coordinates of each square (x and y), another distance matrix was created to represent the spatial distance (on a 0–1 scale) among all cell pairs. The product of both triangular distance matrices was used to identify clusters of adjacent cells with similar flora (Legendre and Legendre 1998). Thus, the number of cell clusters located on the boundary between two or more regions, which have the possibility of being slightly dissimilar, was minimized. This procedure also maximizes the distinction among cell clusters with comparable composition that are separated by geographic or historical factors and, consequently, have a higher probability of containing taxonomic differences.

Ward's Method (recommended in Legendre and Legendre 1998) was used as the linkage rule to obtain hierarchical clusters. An arbitrary number of clusters, not greater than 12, were chosen from the hierarchical tree plot obtained and tested by the k-means clustering algorithm. Using this algorithm, the selected number of clusters was chosen at random and cases were moved between them to minimize variability within clusters and maximize variability between clusters. For each nested dichotomy in the hierarchical tree obtained through this procedure, significant environmental variables whose values differed between the two groups were identified by the non-parametric Mann–Whitney U-test with a Bonferroni-corrected significance level (Siegel and Castellan 1988).

Environmental variables considered were also analysed using the Discriminant Function, to identify those variables that most influenced each pair of groups, according to the number of cells correctly classified (StatSoft Inc. 2001). The percentage of well-classified cells in each region was taken as a measure of an environmental variable's ability to explain the floral composition groups.

Generalized linear models (GLM; McCullagh and Nelder 1989; Dobson 1990) summarized the relationship between the number of species and the explanatory variables considered. A Poisson error distribution for the number of fern species was assumed and linked to the set of predictor variables via a logarithmic link (see Crawley 1993). The model's goodness-of-fit was measured by the deviance statistic and the change in deviance, F-ratio tested (McCullagh and Nelder 1989; Dobson 1990) with a 5% significance level. The percentage of retained deviance was also calculated for each model (see Dobson 1990) in order to estimate the percentage of explained variation.

As a first step, the total number of Iberian–Balearic pteridophytes in 50 km UTM cells were related separately, one-by-one, with each environmental variable. The linear, quadratic or cubic term that was statistically significant and best-explained species richness variation was selected from each environmental variable. Afterwards, environmental variables of the same type (topography, climate, geology and environmental diversity) were backward stepwise processed in order to determine their explanatory capacity. Subsequently, all the significant environmental variables were backward stepwise processed jointly to obtain a final model. Since pteridophyte species richness could also be explained by anthropic factors and different landscape types, land-use variables were included afterwards in the final model in order to determine their added relevance. Similarly, the nine terms of a third-degree polynomial of cell central latitude and central longitude were processed with a backward regression (after environmental and land-use variable processing), since spatial variables can help represent remaining unaccounted-for explanatory variables with a spatial structure (Legendre and Legendre 1998). The order of inclusion of explanatory variables (first environmental, second land-use and lastly spatial) was chosen in an attempt to isolate the supplementary explanatory capacity of anthropic and related unaccounted-for factors.

In order to examine the spatial structure of Iberian pteridophyte species-richness, Moran's I autocorrelation

coefficient with a Bonferroni-corrected significance level (Sawada 1999) was calculated for 50-km distance classes. After dependent-variable regression analysis with the various groups of explanatory variables, residuals were also checked for autocorrelation. Spatial autocorrelation in regression-analysis residuals is an indication that one or several important spatially structured explanatory variables can be omitted from the model (Cliff and Ord 1984; Legendre and Legendre 1998; Keitt et al. 2002).

Results

Iberian fern regions

Two main Iberian–Balearic pteridophyte zones, forming a latitudinal pattern, can be seen (Fig. 2, branches A and B). Their boundary crosses near the centre of the Iberian Peninsula, following the Central System and the southern extreme of the Iberian System. Each zone can be further classified into two clearly distinguishable north-eastern and south-western sub-zones (A1, A2 and B1, B2 in Fig. 2). In some zones smaller units can be distinguished that may, in turn, be classified into regions. The Balearic archipelago does not constitute a unit separate from some eastern Iberian coastal cells. Finally, cluster analysis distinguishes a total of ten territorial divisions or regions (Fig. 2), which are well-supported by k-means partitioning. Out of the 123 species considered, 104 (85.2% of the total) show significant differences between the clusters. F scores for all species vary from 5.15 ($P < 0.0001$) to 0.74 ($P = 0.67$).

The sub-divisions of the 50×50 km Iberian cells are explained well by environmental differences, which generally explain a high proportion of the cells assigned to each subdivision (Fig. 3). Only sub-zone A2 (regions 5 and 6 comprising northeast Iberia and the Balearic Islands) seems to be poorly distinguished by environmental variables. Regions 6 and 9 are the only other zones in which environmental discriminant functions explain less than 70% of the variance. Of the explanatory variables considered in all pair-wise comparisons, climate is statistically significant in 22 cases, while topography, heterogeneity and geology

Fig. 2 Main UTM cell groups derived from cluster analysis of pteridophyte presence–absence data. The triangular distance matrix was the product of a Jaccard distance matrix (one minus the Jaccard similarity score) and a spatial distance matrix in which the Euclidean spatial UTM scores of each cell were considered. The Ward method was used as the linkage rule. The map shows the geographic location of the various clusters, while the combination of letters and number in the tree represent the various hierarchical territorial subdivisions
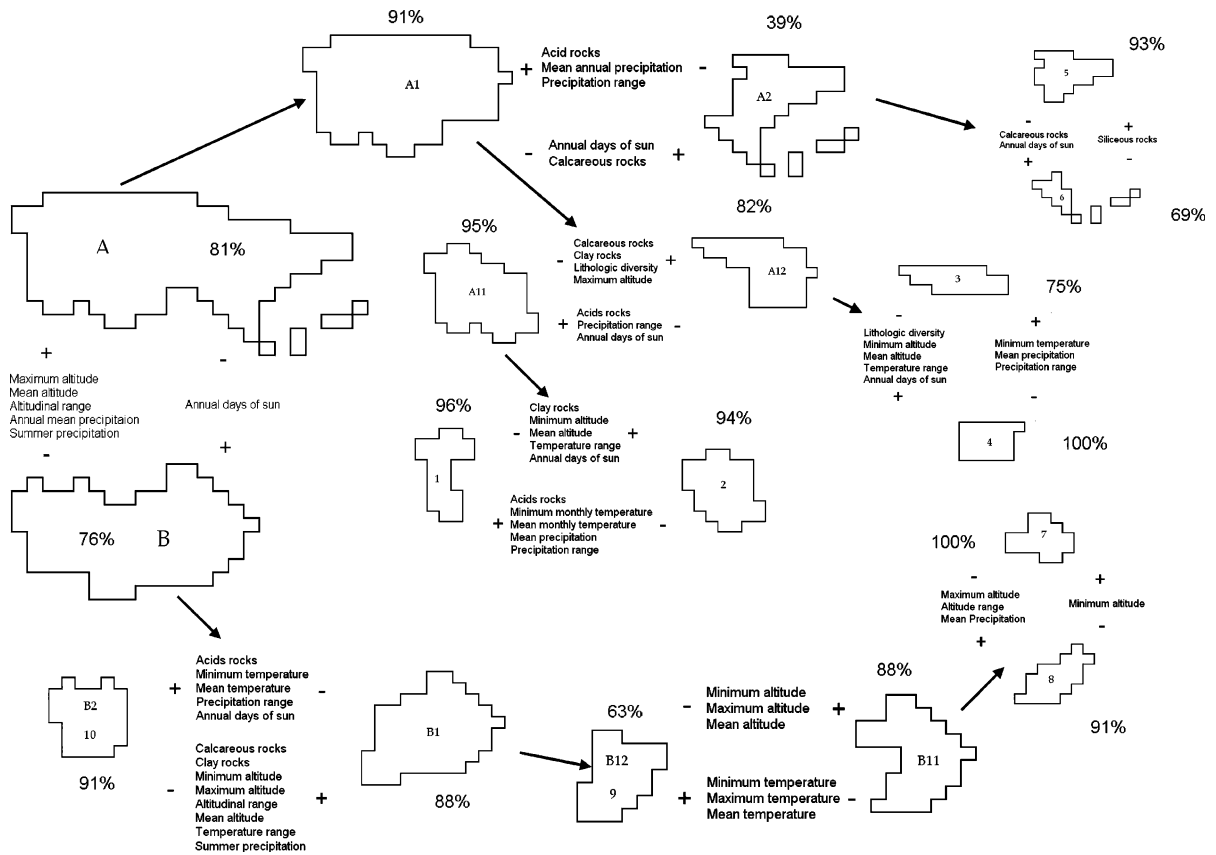
Fig. 3 Environmental differences for each of the hierarchical territorial subdivisions observed in the Cluster Analysis (Fig. 2). Only significant environmental variables whose values differ between any pair of groups are mentioned. Differences were estimated using the non-parametric Mann–Whitney *U*-test with a Bonferroni corrected significance level. Positive and negative symbols near each territorial division illustrate the sign of the influence of each environmental variable. Percentages represent the proportion of squares that were correctly classified by the classification terms of a Discriminant Function Analysis carried out with the same environmental variables

variables are significant in 15, 13 and 12 cases, respectively (Fig. 3).

The first-order Iberian pteridophyte areas, A and B, significantly differ in both total number of taxa and mean cell richness (Table 1). Northern zone A contains 97.5% of total fern taxa, with 28% of them being exclusive to this zone. On the contrary, only 3% of the species present in the southern zone B are exclusive, although a relatively large proportion of the Iberian fern taxa can be found in this zone (69%).

The mean number of species per cell in the ten regions selected differs significantly (Kruskal–Wallis ANOVA by Ranks test = 83.07, *P* < 0.0001). Mean species richness is highest in the Cantabrian region 3 and poorest in the South Plateau region 7 (Fig. 4). The mean number of taxa per UTM cell is positively

and significantly correlated with the total number of taxa (*r* = 0.86; *P* = 0.001) and the number of taxa present in one or two regions (*r* = 0.79; *P* = 0.006) (Table 1).

Iberian species richness

Variation in pteridophyte richness shows the greatest values in the Pyrenees (maximum cell species richness; $S_{max} = 59$), Cantabric mountains ($S_{max} = 54$), Iberian Central System ($S_{max} = 38$), Toledo mountains ($S_{max} = 44$), Sierra Nevada ($S_{max} = 39$ species), the sierra of Algeciras near Gibraltar ($S_{max} = 38$), and the north Atlantic Portuguese coast ($S_{max} = 43$).

Table 1 Number of 50 × 50 UTM cells (N) for each of the 10 Iberian pteridophyte regions (Fig. 2), mean species richness by cell (±standard error), total number of species (S_{TOT}), and number of rare species present only in one or in two regions

|	N	Name	S ± SE	S_{TOT}	One region	Two regions
Zone A	155	Northern	26.8 ± 1.0	119	34	–
Zone B	102	Southern	18.2 ± 0.7	86	3	–
Region 1	26	Galicia	28.5 ± 1.8	85	6	3
Region 2	38	North Plateau	24.8 ± 1.5	72	0	0
Region 3	24	Cantabrian	38.9 ± 1.9	91	2	4
Region 4	21	Aragonian	20.9 ± 2.0	72	0	0
Region 5	30	Catalonia	27.2 ± 1.7	94	6	3
Region 6	16	Valencian-Balearic	17.7 ± 2.3	67	1	3
Region 7	19	South Plateau	12.2 ± 2.1	54	0	0
Region 8	22	Southeastern	21.1 ± 1.9	71	0	1
Region 9	27	Andalusia	19.0 ± 1.8	74	2	0
Region 10	34	Southwestern	19.1 ± 1.6	74	1	0
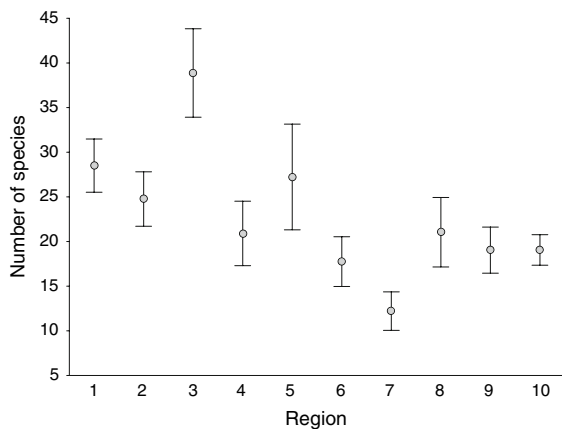
Fig. 4 Mean number of fern taxa per 50 × 50 UTM cell (±95% confidence interval) for each of the ten Iberian Peninsula regions, according to pteridophyte composition (Fig. 2)

The cubic function of maximum altitude is the most important topographical variable, explaining 23% of total deviance in species richness. Both the quadratic function of mean altitude and the linear function of minimum altitude also account for significant percentages of deviation in species richness (Table 2a). The quadratic function of maximum altitude together with the linear function of minimum altitude remain backward after selection carried out with only the topographic variables, accounting for 38% of total species richness variance. The number of taxa decreases with minimum altitude, but increases with mean and maximum altitude, increasing notably above 1,500 m maximum altitude (Fig. 5). The cubic function of clay area, the most

important geologic variable, accounts for 11% of total richness deviance. This means the number of species decreases slightly with the increase in cell clay area (Fig. 5). The quadratic function of siliceous area is the other significant geologic variable (Table 2a). Backward stepwise processing of both geologic variables together leaves only the cubic function of clay area. The most relevant climate variables, the cubic functions of mean monthly precipitation and annual days of sun, as well as the linear function of summer rainfall, account for 32%, 30% and 28% of total deviance, respectively. The quadratic functions of maximum and mean temperatures are additional significant climate variables (Table 2a). Backward stepwise processing of all significant climate variables together selects the cubic function of mean monthly precipitation and the cubic function of annual days of sun, together with the linear function of summer rainfall (44.1% of total species richness variability).

Of the heterogeneity variables, the linear function of altitude range, the most explanatory variable of all variables considered, accounts for 33% of total richness deviance (Table 2a). The results show that the greater the difference in altitude in a territory, the greater the number of taxa (Fig. 5). Other less significant heterogeneity variables are the cubic function of annual rainfall variation and the quadratic function of annual temperature variation (Table 2a). Backward stepwise processing of the linear function of altitude range, together with quadratic function of annual rainfall variation and the linear function of temperature variation, selects these heterogeneity

Table 2 Significant environmental explanatory variables for total Pteridophyte species number (a) in the 50 × 50 km UTM grid cells of the Iberian Peninsula (Fig. 2), and parameters of the final model taking into account environmental, land-use and spatial variables (b)

Variables	Selected term	Deviance	% Explained deviance	Sign	Selected in SMR
a					
Altitude range	Linear	866.1	33.4	+	Y
Mean monthly precipitation	Cubic	881.7	32.2	+ − +	Y
Annual days of sun	Cubic	907.4	30.2	− + +	Y
Summer rainfall	Linear	937.0	27.9	+	
Maximum elevation	Cubic	998.2	23.2	+ + −	Y
Annual rainfall variation	Cubic	1141.6	12.2	+ − +	
Clay area	Cubic	1152.2	11.3	− − +	
Maximum temperature	Quadratic	1147.0	11.7	− +	
Mean elevation	Quadratic	1180.1	9.2	+ +	
Annual temperature variation	Quadratic	1198.5	7.8	− −	
Siliceous area	Quadratic	1215.8	6.4	+ −	Y
Mean temperature	Quadratic	1228.8	5.4	− +	
Minimum elevation	Linear	1254.2	3.5	−	

	Estimate	Standard error	Wald statistics	P
b				
Intercept	3.059	0.020	23181.82	<0.001
Altitude range	0.277	0.035	62.24	<0.001
Mean monthly precipitation	0.118	0.024	24.94	<0.001
Mean monthly precipitation^2	−0.013	0.006	3.79	0.05
Annual days of sun	−0.119	0.016	53.35	<0.001
Maximum elevation	−0.108	0.038	8.13	0.004
Maximum elevation^2	0.045	0.015	8.56	0.003
Maximum elevation^3	−0.012	0.006	3.92	0.05
Siliceous area	0.043	0.016	7.66	0.006
Including land-use variables				
Antropic pasturelands	0.037	0.012	9.29	0.002
Broad-leaf forest	0.068	0.014	22.55	<0.001
Including spatial variables				
Longitude × latitude	0.000	0.000	7.54	0.006

Deviance and percentage of explained deviance from a full model (deviance = 1299.7, df = 256). Linear, quadratic or cubic functions of each variable accounting for statistically significant change in deviance with a probability lower than 0.05 were selected. Only variables accounting for at least 3% of total deviance are represented. Variables are arranged in order of decreasing explanatory power. The sign in the columns corresponds to the sign of each function. The functions selected in a multiple backward stepwise regression (SMR) are indicated (Y)

variables as significant, and accounts for 49.88% of the total species richness variability.

Backward stepwise processing of all the significant environmental variables above produces a complete environmental model (Table 2b) accounting for 56.2% of the variability in the species richness. The residuals of this model are normally distributed. The relationship between the predicted values and the residuals form a cloud around the centre, and no aberrant characteristics can be detected in the residuals of this term. However, these residuals can be partially explained by two current land-use variables (the area of broad-leaf forest and the area of anthropic pasturelands) and by a spatial variable (the
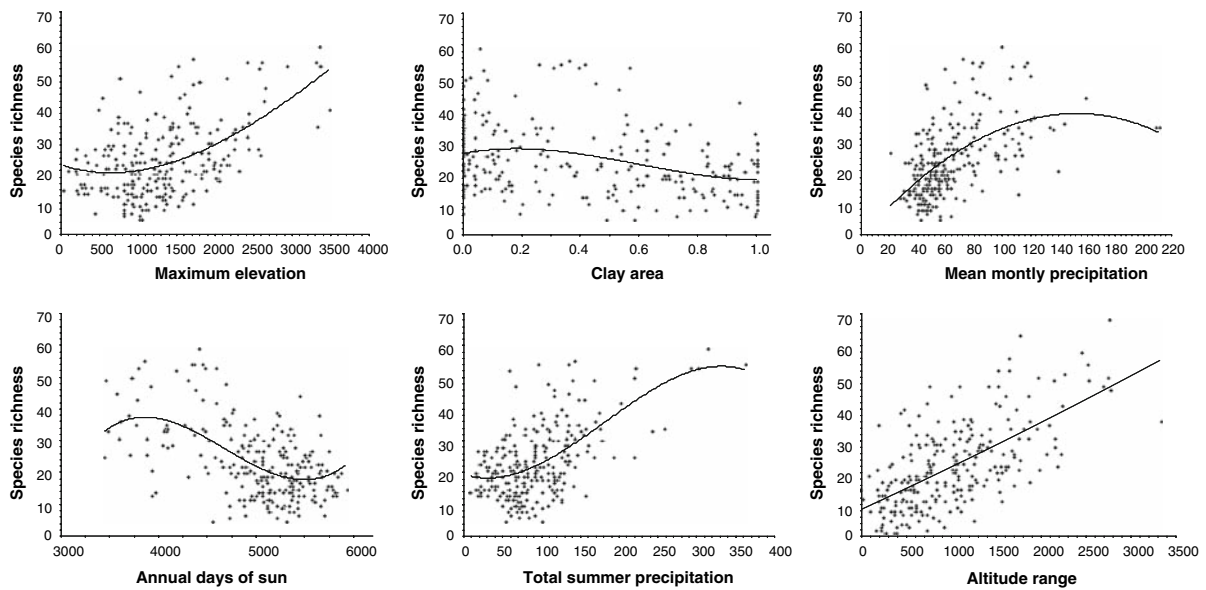
Fig. 5 Relationship between the number of pteridophyte species in the 50 × 50 km Iberian UTM cells and the main GLM-selected explanatory variables (see Table 2). The line represents the linear or curvilinear quadratic or cubic functions
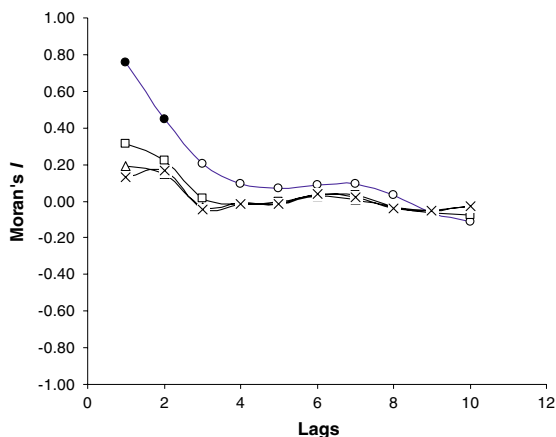

Fig. 6 Moran's *I* autocorrelation scores for the number of fern species (circles), residuals of the model built with environmental variables (squares), the model built with environmental and land-use variables (triangles), and the model built with environmental, land-use and spatial variables (crosses). The lag distance is 50 km. Black circles represent significant autocorrelation scores at $P < 0.05$

interaction between latitude and longitude). Inclusion of the land use variables increases the prediction accuracy of the environmental model to 61.8% of total deviance. A further incorporation of spatial variables increases explained variability in the distribution of spatial richness scores to 62.6% of their total variability (Table 2b).

There is a clear gradient in pteridophyte species richness in Iberia and the Balearic Islands, with positive and significant Moran's *I* scores up to the first 100 km. However, the residuals of the obtained environmental model are not significantly autocorrelated; sequential inclusion of land-use and spatial variables diminishes the degree of positive autocorrelation (Fig. 6). Thus, the gradient detected in species richness seems to be explained by the variables considered.

Inter-region species richness

The explanatory importance of the environmental variables varies between the two main Iberian pteridological zones (A and B in Fig. 2). In the richer northern zone, the main explanatory variables are basically those related to Iberian Peninsula species richness (Table 3). However, in the southern zone, lithology variables, as well as those variables related to total annual days of sun and temperature, lack relevance.

The relevance of fern species richness variables also differs according to region. In the north-western region 1, only annual mean precipitation, annual rainfall variation and summer precipitation (more species in rainy areas) seem to explain (slightly) the

regional variation in number of fern species (17%, 12% and 10% of deviance, respectively). However, in the contiguous richest region 3 (Cantabrian), topography, heterogeneity and lithology variables have a special explanatory power and highlight the great relevance of minimum elevation (more species in cells at low altitudes; i.e., sea coast), and the positive influence of siliceous soils (Table 4). Similar variables play the same role in regions 2 and 4, although heterogeneity variables are noticeably important in those regions. There seem to be more fern species in heterogeneous, low altitude, siliceous and humid cells in the north-western sub-zone (A1 in Fig. 2).

None of the environmental variables considered explain the variation in fern species richness in region 6. In region 5, solar radiation and temperature variables are significantly negatively correlated with the number of species, while lithology variables seem to be less important. In general, there are more fern species in environmentally heterogeneous, high-altitude, shaded and rainy cells in this region (Table 4).

Region 7 is the poorest in terms of species richness (Fig. 4); only lithological diversity and clay area (19% of deviance) appear positively and negatively related with the number of fern species in that region (Table 4). In the neighbouring south-eastern region 8, in contrast, heterogeneity, topography and climate variables account for significant fern richness variability. The relationships of the other significant variables indicate that more species occur in heterogeneous, high-altitude, and rainy cells with a low number of annual sunny days and low temperatures. The pattern in region 9 is not observed in any other region. The greatest species richness is positively correlated with mean annual and summer precipitation, but also with the number of annual sunny days (more species in rainy and sunny cells, Fig. 7). Lastly, in the south-western region 10, no environmental variable seems highly predictive, although the number of ferns species is positively related to mean monthly precipitation (10% of deviance), but negatively correlated with annual days of sun (10% of

Table 3 Significant environmental explanatory variables for the pteridophyte species-number in the main northern and southern Iberian composition zones (zones A and B, Fig. 2), deviance and percentage of explained deviance from a full model

	Selected function	Deviance	% Dev	Sign
Zone A				
Altitude range	Linear	535.25	36.44	+
Annual days of sun	Cubic	628.53	25.36	− + +
Mean monthly precipitation	Cubic	631.58	25.00	+ − +
Summer precipitation	Linear	639.90	24.01	+
Maximum altitude	Linear	679.74	19.28	+
Clay area	Linear	693.23	17.68	−
Siliceous area	Quadratic	711.25	15.54	+ −
Annual temperature variation	Quadratic	717.50	14.80	− −
Maximum temperature	Linear	734.46	12.78	−
Annual rainfall variation	Cubic	744.83	11.55	+ − +
Minimum temperature	Cubic	755.48	10.29	− + −
Zone B				
Mean monthly precipitation	Lineal	179.95	29.69	+
Altitude range	Cubic	187.87	26.63	+ + −
Maximum altitude	Cubic	198.24	22.62	+ + −
Annual rainfall variation	Quadratic	206.66	19.37	+ −
Summer precipitation	Quadratic	210.03	18.07	+ +
Mean altitude	Cubic	215.36	16.01	− + +

Linear, quadratic or cubic functions of each variable accounting for statistically significant change in deviance with a probability lower than 0.05 were selected. Only variables accounting for at least 10% of total deviance are represented. The sign of the columns corresponds to the sign of the functions of each function

Table 4 Significant environmental explanatory variables for peridophyte species number in each of the ten Iberian composition regions (Fig. 2), deviance and percentage of explained deviance from a full model

Region	Variables	Selected function	Deviance	% Dev	Sign
2	Lithology diversity	Linear	55.09	60.1	+
	Minimum elevation	Quadratic	74.71	45.8	− −
	Altitude range	Quadratic	77.60	43.7	+ −
	Siliceous area	Linear	83.51	39.4	+
	Clay area	Linear	87.84	36.3	−
	Annual rainfall variation	Cubic	96.81	29.8	+ − +
	Mean monthly precipitation	Quadratic	103.77	24.7	+ −
	Annual temperature variation	Linear	105.06	23.8	−
3	Minimum elevation	Cubic	30.85	63.6	− − +
	Altitude range	Linear	43.28	48.9	+
	Siliceous area	Cubic	44.30	47.7	+ − +
	Clay area	Quadratic	49.24	26.2	−
	Lithology diversity	Quadratic	60.04	22.0	+ −
4	Altitude range	Quadratic	25.97	62.0	+ −
	Lithology diversity	Quadratic	30.52	55.3	+ −
	Maximum elevation	Linear	39.25	42.6	+
	Mean elevation	Quadratic	45.54	33.4	− +
	Mean temperature	Linear	51.41	26.8	−
	Clay area	Quadratic	50.43	26.2	− +
	Minimum temperature	Linear	53.82	21.2	−
5	Annual days of sun	Linear	63.77	76.2	−
	Altitude range	Linear	85.19	68.2	+
	Maximum elevation	Linear	99.61	62.8	+
	Minimum elevation	Cubic	104.76	60.9	+ + −
	Summer rainfall	Quadratic	109.18	59.2	+ −
	Mean monthly precipitation	Quadratic	129.27	51.7	+ −
	Mean elevation	Linear	149.47	44.2	+
	Clay area	Quadratic	174.43	34.8	+ −
	Maximum temperature	Cubic	176.05	34.2	− + +
	Mean temperature	Quadratic	182.26	31.9	− +
	Annual temperature variation	Quadratic	187.57	29.9	− −
	Minimum temperature	Quadratic	189.57	29.2	− +
	Siliceous area	Quadratic	192.79	28.0	+ −
7	Lithology diversity	Linear	22.60	21.5	+
8	Altitude range	Quadratic	24.41	68.6	+ −
	Maximum elevation	Linear	25.18	67.6	+
	Mean elevation	Linear	44.88	42.3	+
	Annual days of sun	Linear	49.34	36.6	−
	Annual rainfall variation	Linear	50.34	35.3	+
	Mean monthly precipitation	Linear	52.95	32.0	+
	Minimum temperature	Linear	57.48	26.1	−
	Minimum elevation	Quadratic	58.82	24.4	+ +
	Annual temperature variation	Linear	58.91	24.3	+
	Mean temperature	Linear	59.46	23.6	−

Table 4 continued

Region	Variables	Selected function	Deviance	% Dev	Sign
9	Mean monthly precipitation	Linear	33.85	37.4	+
	Annual days of sun	Quadratic	34.94	35.4	+ −
	Minimum elevation	Linear	36.14	33.2	−
	Annual rainfall variation	Linear	39.10	27.7	+
	Annual temperature variation	Quadratic	40.43	25.2	− −

Linear, quadratic or cubic functions of each variable accounting for statistically significant change in the deviance with a probability lower than 0.05 were selected. Only variables accounting for at least 20% of total deviance are represented. Regions 1, 6 and 10 are not represented because none of the explanatory variables account for more than 20% of total deviance. The sign of the columns corresponds to the sign of each function

deviance), as can be said for almost all Iberian regions with a Mediterranean climate.

Discussion

The general species-richness pattern of Iberian ferns

Richness hotspots were found in major mountain chains including the central and western Pyrenees, Cantabrian Range, Central System and to a lesser extent, in Sierra Nevada (near Granada), Serras de Arrábida-Sintra (in the SW Iberian quadrant) and the mountains close to the Straits of Gibraltar. The geographical patterning of the *hottest* hotspots remains roughly unchanged by the addition of these

Fig. 7 Contour plot of the total number of fern species in the Andalusia region (number 9) in the space delimited by the standardized scores of mean monthly precipitation and annual number of days of sun. Regions outside the depicted region represent non-existent combinations of variables

new distributional records (see Moreno Saiz et al. 1996). These findings highlight the critical conservation role of the Iberian mountains and, in particular, the coastal *sierras*.

The new map of Fig. 8 not only reflects a finer chorological work, but also illustrates the most current accepted pteridophyte taxonomy. Paradoxically, numbers in certain cells are lower than those found by Moreno Saiz et al. (1996). This is because some taxa are no longer recognized due to synonymization or misidentification as Iberian species, or because certain Iberian regions have not yet been included in detailed atlases. Regardless, most cell richness is greater than that reported in former studies. Diversity maxima in northern mountain range cells (Pyrenees and Cantabrian System) are a continued reflection of the tendency for pteridophyte richness to increase towards the wetter Atlantic (Eurosiberian) band (Birks 1976; Pausas and Sáez 2000). The effect of the additional information incorporated in this study is evident in the comparison shown in Fig. 1a; values in all but one area are higher than those in Birk (1976: 260), even though French and Italian cells were not included in our analysis.
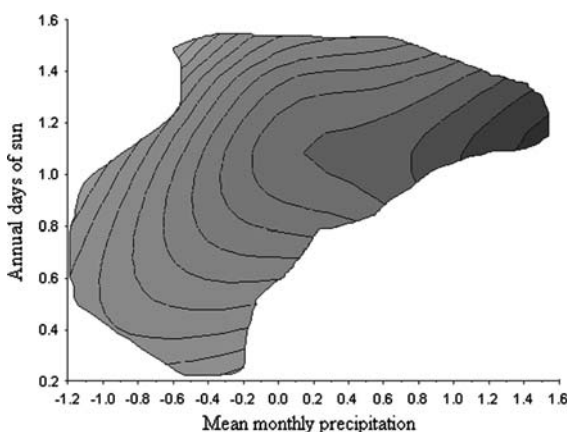
Iberian–Balearic fern regions

Although some authors have suggested that basic patterns have emerged in Iberian biotic regionalization (Real et al. 1996; Gómez-González et al. 2004; Arroyo et al. 2004), divergence among published proposals still emerges (i.e. Vargas et al. 1998; Rivas Martínez and Loidi 2000; García Barros et al. 2002). Divergence in region designation arises not only from

Fig. 8 Number of pteridophyte species in the 257, 50 × 50 km Iberian UTM cells (left). Tones of grey represent the four species richness quartiles

different taxa, variations in the chosen operational geographic units, and differences in analytical methodologies, but also from differences in basic species distribution information. There are striking dissimilarities even within the same group, pteridophytes for example, between the Iberian regions previously published (Fig. 1) and those established herein. The 20-year lapse since the compilation of Salvo et al. (1984) may explain a major part of this disagreement, as prior studies have basically used the same dataset. The 'pteridogeography units' of Pichi Sermolli et al. (1988) coincide poorly with those of later proposals. These authors not only used distributions but also explicit assumptions about the origin of every taxon (Pichi Sermolli 1979), and implicit methods to classify their geographical units.

In our analysis, a major latitude boundary divides Iberia into two zones. This boundary, however, exists further south of the classic delimitation between the Eurosiberian and Mediterranean biogeographic regions. This main boundary runs along the inner Peninsular mountain ranges (Central and Iberian Systems). Pichi Sermolli et al. (1988) also separated their Iberian-submediterranean and Iberian-eumediterranean units along a partially coincident frontier (Fig. 1b).

The significantly different environmental characteristics of the Iberian pteridophyte regions proposed in this study can explain, to a large extent, fern compositional dissimilarities. Only in sub-zone A2, and to a lesser extent in its region 6, does pteridophyte composition differ more than environmental variables. This is probably because many peninsular fern species are not found in Balearic cells due to geographic and historical factors. Interestingly, the environmental variables do not seem to discriminate the Andalusian region 9 well (<70%). Environmental differences explain the main major division, as the northern zone (which includes the Balearic Islands) is distinguished by variables positively related to altitude and availability of water. Such conditions, prevailing in the mountains of the Peninsula centre, probably help to fix the south-western distributional limits of several European species (Pichi Sermolli et al. 1988). The isthmus together with the Pyrenees–Cantabrian axis does not constitute an effective barrier for several mesic ferns, or for other vascular plants (Bolòs 1985). Therefore, the Eurosiberian region, as defined by pteridophyte occurrence, should be enlarged in the Iberian Peninsula (Médail and Quézel 1997; Rivas Martínez and Loidi 2000).

Partitions in the cluster analysis divide Iberia into four quadrants, as a longitudinal boundary further separates western and eastern sub-zones. These longitudinal divisions can be explained by topography, climate and, especially, bedrock variables; acidic rocks predominate in the western half and basic rocks in the eastern portion. Southern Iberia

was also divided by longitude by Márquez et al. (2001), but they did not find any significant division in northern Iberia. In the south-western corner, a temperate south-Atlantic region can be recognized (region 10, Fig. 2), as published in various phytogeographic papers (Sainz Ollero and Hernández Bermejo 1985; Moreno Saiz et al. 1998; Rivas Martínez and Loidi 2000). This sub-zone is strongly supported by a wide range of environmental variables (lower minimal and mean temperatures, lower altitudes, etc.) affecting pteridophytes (Fig. 3). In contrast, group B1 is characterized by higher altitude (Baetic mountains), more area with calcareous soils and increased summer precipitation levels. North-western sub-zones are explained by the presence of acid soils, higher precipitations and lower number of sunny days. In the north east, the Pyrenees do not seem to constitute a separate pteridogeographic region according to our results (but see Pichi Sermolli et al. 1988; Sáez 1997). They are not closely connected to region 3 (Cantabrian) either, as their cells are related with those in Catalonia and the middle and lower Ebro basin. However, a finer cluster analysis of the north-eastern region (not shown) separates five northern Pyrenees UTM cells from the others, suggesting that further sub-regions could be delimited when reliable information at a finer resolution is available.

The fern composition of the Balearic archipelago does not seem to be singular either. It belongs to the east coast of the Peninsula, sharing both endemics such as *Asplenium majoricum* Litard. as well as other common taxa. This connection, which affects several taxonomic groups unequally, has prevented agreement on the biogeographic affinities of the Balearic Islands (e.g. Hernández Bermejo and Sainz Ollero 1984; Rivas Martínez et al. 1990; Rivas Martínez and Loidi 2000; García Barros et al. 2002).

Further division tends to separate these four sub-zones (by latitude) into the 10 regions. Current distributional information available on pteridophytes has helped to improve knowledge of their regionalization. For instance, various smaller, peripheral areas recognized by Pichi Sermolli et al. (1988) are not supported by further multivariate analyses. Also, the small central unit (region A in Fig. 1c: Valladolid administrative province) identified by Márquez et al. (2001), which was a complete novelty to Iberian biogeography, is not be recognized in our data. We suspect that this region is an artefact, since fern diversity in this area appears to be very low and lacks adequate sampling.

Regions were explained well by environmental variables, with the exception of the north-eastern Iberian–Balearic region, which was poorly distinguished, most likely due to the insular effect of the Balearic cells. New patterns will probably emerge with analyses carried out using the 10 km UTM grid for Iberia as a whole, but a lapse of some years is to be expected before these analyses are completed. In the meantime, we consider the 50 km UTM grid a reasonable choice since several international projects have successfully used this scale (Humphries et al. 1999; Williams et al. 2000; Araújo et al. 2005; Bickford and Laffan 2006). We recognize the disadvantages of using 'quadrangular' cells with artificial borders in biogeographic analysis (Márquez et al. 2001), but since nearly all distribution information refers to regular grids, we prefer to avoid a later arbitrary transfer of such information to any other physiographic or administrative grid.

Species richness determinants

The variables selected to explain fern richness variation in pteridophyte regions across the Iberian Peninsula highlights the general relevance of heterogeneity, topography and climate in shaping fern species richness. Hidden bias in distribution maps could be obscuring patterns, but current distributional information at this resolution would seem to be sufficient to enable bias detection. The relevance of these variables to the distribution of fern species, emphasized in other studies, can be easily explained by taking into account both the ecological theory and the biological requirements of ferns.

Altitudinal variables, mainly the altitude differences within each cell, are among the most important explanatory variables. Other important variables are annual temperature variation and annual rainfall variation; altitude range is a surrogate for environmental heterogeneity, and is a practical variable that was closely related to fern species richness in earlier studies (Rey Benayas and Scheiner 2002; Ferrer-Castán and Vetaas 2005). In the case of ferns, altitude range could also reflect the existence of rocky cliffs and inaccessible slopes favouring the establishment of many rupestrian fern species. The importance of

the maximum-altitude topographic variable reflects the relevance of the role played by mid and higher mountains (above 1.500 m), which acted as refugia throughout Pleistocene climate cycles for northern and central European species (Vogel et al. 1999). As with all vascular flora (Lobo et al. 2001), Pausas and Sáez (2000) found that north-eastern Iberian diversity correlated positively with maximum altitude (i.e. mountain summits).

Fern dependence on water for reproduction makes mean monthly precipitation a critical climate variable not only in the Iberian Peninsula (Márquez et al. 1997; Ferrer-Castán and Vetaas 2005) but also in other regions (Bhattarai and Vetaas 2003; Bhattarai et al. 2004). Our results indicate that fern species richness increases linearly with precipitation until 120 mm of mean monthly precipitation. Interestingly, annual days of sun, a variable not previously considered but related with the quantity of energy available, is negatively correlated with Iberian fern species richness. It was found that the number of fern taxa decreases linearly with the increase of annual hours of sun up until approximately 5,000 h (200 days). This negative relationship with temperature or energy-related variables, also found in other fern studies (Lehmann et al. 2002; Bhattarai and Vetass 2003), probably arises because of related water loss. Lastly, two bedrock geological variables explain a small but significant amount of the variation in the number of fern species. The first, the proportion of clay area, has a negative effect on the species richness of ferns, which manifested in both plateaus and inner basins. The second, siliceous rock, correlates positively with the number of fern species. Unlike the relationship with vascular Iberian plants, the surface area of basic (calcareous) bedrock is not the main geological variable that is positively related with number of species (Lobo et al. 2001; Rey Benayas and Schiener 2002). Pausas and Sáez (2000) found this relationship in north-eastern Iberia and suggested that calcareous soils retain less water than do siliceous soils, thus affecting the reproductive processes that require humidity. Areas with mixed geology should be further sampled to verify this relationship, since no edaphic preferences have yet been documented in other studies (Kornas 1993).

Lack of autocorrelation in residuals and lack of relevance of spatial variables indicate that Iberian fern-richness variation is adequately explained by environmental variables. However, in addition to these variables that are unrelated to human activity, inclusion of surface area of antropic pasturelands and the area of broad-leaf forest increases the predictive power of the models. This result suggests that the highest fern richness scores can both occur in current forest zones as well as in human-transformed landscapes. As our data came from a broad temporal range, current association with anthropic land uses could indicate a conservation risk.

Our results indicate that Iberian and Balearic pteridophyte regions are similar in area and species richness and highlight the richness of the Cantabrian region and the poverty of the South Plateau region. However, interestingly, species richness variation within the regions that are more environmentally and pteridologically homogeneous can also be predicted with the use of environmental variables. As has been hypothesized (Rosenzweig 1995), variables that explain the distribution of species richness vary with scale. We show here that the relevance of different environmental variables to fern species richness differs within the two main sub-zones. In the northern sub-zone, relationships with environmental variables are similar to those of the whole Iberian Peninsula, but in the southern sub-zone the number of sunny days and lithological variables lack significance. With regard to the various regions established, there are some in which the variation of the number of fern species is poorly explained by the environmental variables. The positive influence of the heterogeneous, low altitude cells with high precipitations and siliceous soils on north-western fern richness is remarkable; as is the larger number of fern species in the heterogeneous north-eastern quadrant, which contains rainy cells with few sunny days and high altitudes.

Lastly, in one pteridophyte region (Andalusia region 9), relationships with predictor variables are unique. The highest richness occurs in lowland, rainy and sunny cells, a pattern not seen in any other Iberian region. Copious regular rainfall combined with warm temperatures creates a favourable *subtropical* environment for noteworthy diversity in the Sierra of Algeciras, where one finds relict tropical and subtropical species such as *Psilotum nudum* (L.) PB., *Christella dentata* (Forsskål) Brownsey and Jermy, *Culcita macrocarpa* K. Presl and *Diplazium caudatum* (Cav.) Jermy. Nevertheless, the variables

used in this study explain less (only 63%) variation in this Andalusian region, suggesting a relevant role for other explanatory variables. These could be partially historical since this area, including low mountains close to the coast and valleys open to wet maritime winds, may have constituted a refuge from Pliocene climate deterioration (Pichi Sermolli et al. 1988; Arroyo et al. 2004).

Supplementary characteristics related to distribution (extant area, migrations) or biological traits (ploidy level, spore type) have been put forward to explain unusual fern composition and the occurrence of many rare species in some diversity hotspots. These hypotheses have not been analysed explicitly in the Iberian Peninsula and will be the focus of future work.

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ERRATUM

Iberian–Balearic fern regions and their explanatory variables

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Figure 8 along with its legends were incorrectly published with errors in the original publication.

This erratum corrects Figure 8 and its legend accordingly.

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Fig. 8 Number of pteridophyte species in the 257 considered 50 × 50 km Iberian UTM cells. Tones of grey represent the four species richness quartiles