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# Pteridophyte richness, climate and topography in the Iberian Peninsula: comparing spatial and nonspatial models of richness patterns

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## ABSTRACT

**Aim** To describe the spatial variation in pteridophyte species richness; evaluate the importance of macroclimate, topography and within-grid cell range variables; assess the influence of spatial autocorrelation on the significance of the variables; and to test the prediction of the mid-domain effect.

**Location** The Iberian Peninsula.

**Methods** We estimated pteridophyte richness on a grid map with *c.* 2500 km<sup>2</sup> cell size, using published geocoded data of the individual species. Environmental data were obtained by superimposing the grid system over isoline maps of precipitation, temperature, and altitude. Mean and range values were calculated for each cell. Pteridophyte richness was related to the environmental variables by means of nonspatial and spatial generalized least squares models. We also used ordinary least squares regression, where a variance partitioning was performed to partial out the spatial component, i.e. latitude and longitude. Coastal and central cells were compared to test the mid-domain effect.

**Results** Both spatial and nonspatial models showed that pteridophyte richness was best explained by a second-order polynomial of mean annual precipitation and a quadratic elevation-range term, although the relative importance of these two variables varied when spatial autocorrelation was accounted for. Precipitation range was weakly significant in a nonspatial multiple model (i.e. ordinary regression), and did not remain significant in spatial models. Richness is significantly higher along the coast than in the centre of the peninsula.

**Main conclusions** Spatial autocorrelation affects the statistical significance of explanatory variables, but this did not change the biological interpretation of precipitation and elevation range as the main predictors of pteridophyte richness. Spatial and nonspatial models gave very similar results, which reinforce the idea that water availability and topographic relief control species richness in relatively high-energy regions. The prediction of the mid-domain effect is falsified.

## Keywords

Biodiversity, ferns, generalized least squares models, geographical grid system, heterogeneity, macroecology, mid-domain effect, spatial autocorrelation, variance partitioning.

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## INTRODUCTION

Understanding geographical patterns of species richness, and predicting suitable habitats of high biological diversity, i.e. hotspots (Reid, 1998), are central to ecology and biogeography. Macroscale patterns in species richness have long been recognized, and numerous hypotheses have been proposed to account

for them (e.g. Currie, 1991; O'Brien, 1993, 1998; Kerr & Packer, 1997; Colwell & Lees, 2000; Rahbek & Graves, 2001; see also Whittaker *et al.*, 2001). Macroclimate factors such as temperature, rainfall, productivity, and other energy-related factors, often account for most of the variation in species richness along broad-scale geographical gradients (Richerson & Lum, 1980; Currie, 1991; Rohde, 1992; Hawkins *et al.*, 2003a,b). Positive

correlations between species richness and water availability are documented from tropical and subtropical regions (e.g. Gentry, 1982; Vetaas, 1992; Givnish, 1999; Bhattarai & Vetaas, 2003), whereas in temperate and cool regions, the importance of energy, i.e. temperature or potential evapotranspiration (PET), becomes more evident (Currie, 1991; Kerr & Packer, 1997; Grytnes *et al.*, 1999; Lehmann *et al.*, 2002). Based on different meta-analyses, Hawkins *et al.* (2003a,b) suggest a latitudinal shift in the relative importance of energy vs. water from the poles to the equator.

Pausas and Austin (2001) have stressed that species richness studies should consider both the level of environmental factors (normally, mean values), and measures of in-site variability or heterogeneity. Habitat heterogeneity has sometimes been described using range variables (see, e.g. Currie, 1991; Kerr & Packer, 1997; cf. Pausas *et al.*, 2003). Thus elevation range, a surrogate for topographic heterogeneity, has emerged as a primary predictor of species richness (Kerr & Packer, 1997; Rahbek & Graves, 2001). Kerr & Packer (1997) stated that energy factors control richness in cold regions, and that two aspects of habitat heterogeneity, i.e. elevation range and PET variability, are important in relatively high-energy regions. Based on a study at different grain sizes, Rahbek & Graves (2001) proposed the hypothesis that 'terrestrial species richness from the equator to the poles is ultimately governed by a synergism between climate and coarse-scale topographic heterogeneity'.

However, analyses of species richness may be influenced by non-environmental factors such as geometric constraints and spatial autocorrelation, in addition to climate and heterogeneity factors. Colwell & Lees (2000) claimed that 'mid-domain' peaks in species richness may appear as a result of geometric constraints or hard boundaries, which represent absolute barriers to the dispersal and survival of species, but this is currently being subjected to critical examination (Hawkins & Diniz-Filho, 2002; Zapata *et al.*, 2003; Colwell *et al.*, 2004; references therein). In the Iberian Peninsula, it means that the number of species should be lower along the coast, i.e. hard boundary, than in the centre of the peninsula.

Spatial autocorrelation implies a lack of independence between pairs of observations at given distances in space, i.e. that the strict assumption of independence in standard statistical tests is violated (Legendre, 1993; Selmi & Boulinier, 2001; Bhattarai & Vetaas, 2003). It has been claimed that spatial autocorrelation in data can produce erroneous results concerning the relationships between the response variable and the predictors in statistical modelling (Legendre, 1993; Lennon, 2000; Selmi & Boulinier, 2001). According to Legendre *et al.* (2002), broad-scale spatial structures in data have a similar effect on classical tests of significance as spatial autocorrelation. Legendre (1993) suggested variance partitioning by partial regression to elucidate how much of the variance is accounted for by the environment, the spatial component, and their overlap. Recent developments in statistical modelling allow the incorporation of spatial correlation structures in the analyses using generalized least squares models (GLS; Selmi & Boulinier, 2001), i.e. spatial models can be performed. Thus, the relative importance of the explanatory variables may differ among spatial and nonspatial models. Diniz-Filho *et al.*

(2003) argue that methods such as partial regression and spatial GLS change the focus from variables with long-distance clinal structures towards variables acting at finer geographical scales. We used variance partitioning and spatial GLS to evaluate the relative importance of macroclimatic factors and range variables, and address the question of whether these methods influence the results sufficiently to change the biological interpretation of the main predictors.

This was done on pteridophytes (i.e. ferns and fern allies) from the Iberian Peninsula. Pteridophytes are an ancient group of vascular plants with a large number of relicts, which provide valuable information on evolutionary processes (Tryon, 1986; Pausas & Sáez, 2000). Although they are receiving increasing attention in current ecology (see, e.g. Kessler, 2001; Lehmann *et al.*, 2002; Bhattarai & Vetaas, 2003; Bhattarai *et al.*, 2004), little is known about spatial patterns of pteridophyte diversity. They are ideal for checking the relative contribution of environmental factors that may act on different spatial scales because they have a reproductive strategy based on high dispersibility of spores, and have a strong dependence on moist conditions for sexual reproduction (cf. Pausas & Sáez, 2000; Lehmann *et al.*, 2002). Thus, pteridophytes are probably more directly linked to abiotic factors than many other groups of plants resulting from the lack of co-evolved relationships with animal vectors (to our knowledge, no pteridophyte is aided by animals for dispersal) (Barrington, 1993; Lwanga *et al.*, 1998; Pausas & Sáez, 2000).

In this article we describe the spatial variation in pteridophyte species richness in the Iberian Peninsula, and evaluate the importance of macroclimate and topography using both mean- and range-data variables. We also assess the prediction of a shift in the relative importance of mean variables and range variables when spatial autocorrelation is taken into consideration, and test the hypothesis of lower richness along the coast relative to the centre of the Iberian Peninsula.

## MATERIALS AND METHODS

### Data sources

The Iberian Peninsula was divided into 240 grid cells c. 50 km × 50 km. Cells with more than 50% of their area in the sea were excluded. We estimated the total richness of pteridophytes of each cell based on published geocoded data (i.e. projected to the Universal Transverse Mercator coordinate system) of 114 taxa. They were obtained from several sources, i.e. databases compiled in journals, mainly in *Fontqueria* (Fernández Casas, 1987–96), 'pteridophyte notes' and papers (most of them in *Acta Botanica Malacitana* and *Anales del Jardín Botánico de Madrid*), chorological atlas and floras (e.g. Aseginolaza *et al.*, 1984; Salvo *et al.*, 1984; de Bolòs & Romo, 1991, and de Bolòs *et al.*, 1993, obtained from <http://www.bio.ub.es/bioveg/orca/Welcome-Orca.html>; Sáez, 1997; Villar *et al.*, 1997; Segura *et al.*, 2000, obtained from <http://jolube.net>). All the included taxa are native species (de Bolòs & Vigo, 1984; Castroviejo *et al.*, 1986), with reliable distributional data. Thus we considered *Asplenium trichomanes* L. *sensu lato* because the distribution of its different

subspecies found in the Iberian Peninsula is still little known (see, e.g. Villar *et al.*, 1997; Segura *et al.*, 2000).

The environmental data were obtained by superimposing the grid system over isoline maps of mean annual precipitation (MAP), mean annual temperature (MAT), and altitude. The latitude and longitude of the midpoint of the grid squares were also calculated. Climate data were extracted from Bosh (1989) and Font Tullot (2000). For Spain, altitude was obtained from Bosh (1989), whereas latitude and longitude were calculated in maps from Rivas Martínez (1986). In the case of Portugal, all geographical variables were obtained from a map of the IGE (2002). Average values and range data of MAP, MAT and elevation were derived from maximum and minimum values in each cell, where the range-data variables reflect the variation within cells (similar procedures have been used by Currie, 1991; Kerr & Packer, 1997; Grytnes *et al.*, 1999; O'Brien *et al.*, 2000; Diniz-Filho *et al.*, 2003). Maximum and minimum value of MAP and MAT in each grid square, as well as the minimum altitude, were estimated as the midpoint between two consecutive isolines, one inside and the other outside of the square. The climate stations, which provide the data for isoline maps, are for obvious reasons not regularly spaced in the Iberian Peninsula. Thus the mean and range-data variables are based on various degrees of extrapolation. In contrast, the topographic maps are more accurate, hence the altitudinal data (mean and range) are of better quality than the climate data, although the correlations between elevation range and the climatic ranges (both temperature and precipitation) are strong (Table 1).

### Relationships between species richness and environmental variables

We used least squares multiple regression to analyse the variation in pteridophyte richness in the Iberian Peninsula. Generalized linear models (GLMs; McCullagh & Nelder, 1989) are often used to analyse the relationships between species richness and environmental factors (e.g. Margules *et al.*, 1987; Vetaas, 1997; Pausas & Sáez, 2000; Bhattarai & Vetaas, 2003; Pausas *et al.*, 2003). We

found that GLMs with Gaussian distribution of errors and identity link were better than those with Poisson distribution and the log link often assumed for counts when examining diagnostic plots. Gaussian GLM is equivalent to ordinary least squares regression. We used GLS (Selmi & Boulinier, 2001) to perform spatial models (see below), and the nonspatial version of GLS is equivalent to ordinary least squares regression, as Gaussian GLM. We used both ordinary regression and nonspatial GLS to evaluate the explanatory variables in a forward stepwise procedure. Thus we used *F*-tests to assess the change in variance explained for comparing nested models within the framework of ordinary regression, as well as other techniques associated to GLS (see further below). For each environmental variable, the linear, quadratic and cubic terms were tested using a strict criterion for their inclusion in the model ( $P < 0.01$ ). Correlations between all variables were also examined. Here we used Bonferroni corrections for assessing the significance of the relationships to avoid spurious results (Sokal & Rohlf, 1995). Thus the critical *P*-values were divided by the total number of tests.

### Autocorrelation and spatial modelling

We performed a variance partitioning in ordinary regression, where latitude and longitude were partialled out in a forward-selection procedure before including the main environmental variables (cf. Legendre, 1993). This revealed the spatial variation of the response variable, the nonspatial environmental variation accounted for by the environmental variables, and the overlap between spatial and environmental components (i.e. the spatially structured environmental variation explained by these variables). We also used spatial GLS, a recent approach where spatial correlation structure can be assessed and added to the model in order to control for autocorrelation in the data (Selmi & Boulinier, 2001; Hawkins & Diniz-Filho, 2002; Diniz-Filho *et al.*, 2003).

To investigate the issue of spatial autocorrelation, we plotted semi-variograms (hereafter, variograms) of the residuals of species richness and the environmental predictors in a null nonspatial GLS (i.e. against no relationship), and after fitting the

**Table 1** Pearson's product moment correlation coefficients between the variables

	Richness	LAT	LON	MELE	ELER	MAP	RAINR	MAT	TEMR
Richness	1.00								
LAT	0.40	1.00							
LON	NS	NS	1.00						
MELE	0.37	0.29	0.46	1.00					
ELER	0.67	NS	0.37	0.74	1.00				
MAP	0.70	0.49	-0.35	NS	0.36	1.00			
RAINR	0.61	0.34	-0.28	0.24*	0.45	0.84	1.00		
MAT	-0.39	-0.73	NS	-0.73	-0.42	-0.36	-0.38	1.00	
TEMR	0.46	NS	NS	0.54	0.69	0.29	0.43	-0.36	1.00

Significant coefficients are shown, where  $P < 0.0001$  unless otherwise indicated: \* $P < 0.01$ ; NS:  $P > 0.05$  (all values subjected to Bonferroni correction for multiple tests). Abbreviations: Richness = pteridophyte richness; LAT = latitude (degrees); LON = longitude (degrees); MELE = mean elevation (m a.s.l.); ELER = elevation range (m); MAP = mean annual precipitation (mm); RAINR = precipitation range (mm); MAT = mean annual temperature ( $^{\circ}$ C); TEMR = temperature range ( $^{\circ}$ C).

explanatory variables at each step of the selection process in the corresponding nonspatial GLS. The variogram is a useful tool for describing spatial structures, which allows the study of autocorrelation as a function of distance (Burrough, 1987; Journel & Huijbregts, 1989; Legendre & Fortin, 1989). An increase in the semivariance in the variogram as a function of distance indicates spatial autocorrelation, whereas a flat variogram indicates lack of autocorrelation, spatial independence or homogeneity across scales (Journel & Huijbregts, 1989). Distance classes were established from the Euclidean distances between pairs of observations using latitude and longitude as covariates (all-directional variogram), and were also calculated for single directions of space (i.e. from north to south, and from west to east). If variation in space is isotropic, the directional variograms should be similar (Burrough, 1987; Legendre & Legendre, 1998).

To perform spatial GLS, different classes of spatial correlation structures such as spherical, Gaussian and exponential (Venables & Ripley, 2002), were evaluated. When constructing the correlation structures, we specified the spatial covariates (latitude and longitude) and the initial values of parameters such as the *range* and *nugget*, which were obtained from the variograms of the residuals in nonspatial GLS. To select the most appropriate spatial correlation structure, if significant, the different spatial GLS were compared to the nonspatial GLS using the Akaike Information Criterion (AIC), where a smaller value indicates a better fit (Chambers & Hastie, 1993; cf. Littell *et al.*, 1996).

### Mid-domain effect (MDE)

We analysed the MDE on the total pteridophyte richness including the endemics, which are very few (cf. below). Most studies on the MDE have used species endemic to the study region, or domain, taking the assumptions in the model by Colwell & Lees (2000) into account. However, Grytnes (2003) has demonstrated that several ecological variants of the MDE model do not need to assume that species are endemic to the domain, but populations

outside the domain should have no influence on populations inside the domain (see also Grytnes & Vetaas, 2002; Colwell *et al.*, 2004).

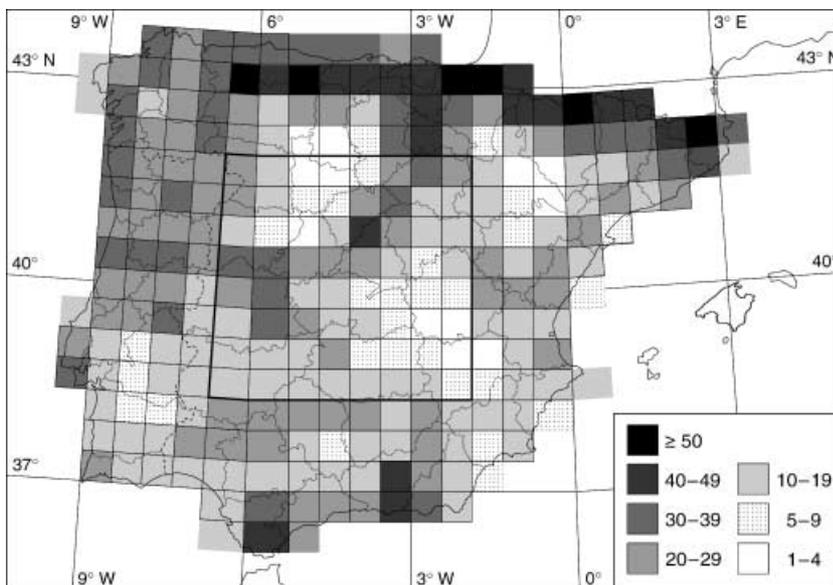
Pteridophytes are able to establish new populations in distant localities, and exhibit lower endemism than other vascular plants probably because of their high dispersibility of spores (Kato, 1993). In the Iberian Peninsula, only *Asplenium adiantum-nigrum* L. ssp. *corunnense* (Christ) Rivas Mart., *Asplenium petrarchae* (Guérin) DC. ssp. *bivalens* (Meyer) Lovis & Reichst., *Dryopteris corleyi* Fraser-Jenkins, *Isoetes velatum* Braun ssp. *asturicense* (Lainz) Rivas Mart. & Prada, and *Marsilea batardae* Launert, have been recognized as endemic ferns (Castroviejo *et al.*, 1986; but see Marchetti, 1997; for a recent review concerning the nomenclature of *Asplenium adiantum-nigrum* ssp. *corunnense* and its general distribution in Europe). This does not allow us to examine whether the variation in richness of endemic pteridophytes in the Iberian Peninsula may relate to geometric constraints or not.

To test whether the MDE applies to total pteridophyte richness, a standard two-sample *t*-test was performed to compare the average number of species in coastal and central cells. If species richness is influenced by geometric constraints, the number of species should be significantly higher in the centre of the Iberian Peninsula than on the coast. Coastal cells are defined here as all those squares with at least a corner in the sea (a total of 64 cells). To obtain a similar number of central cells we selected all squares within a block of 8 × 8 grid cells in the centre of the peninsula (see Fig. 1).

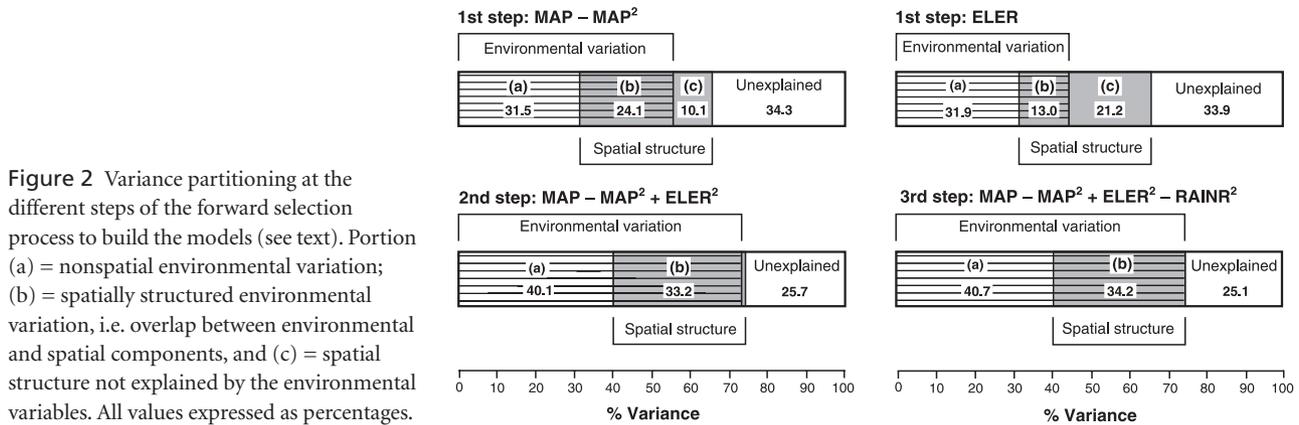
We used S-Plus 6.1 for Windows (Anonymous, 2002) for all analyses and graphical representation (variograms and response surfaces).

### RESULTS

Areas with high pteridophyte richness in the Iberian Peninsula correspond to mountain ranges, in particular to the Cantabrian



**Figure 1** The distribution of numbers of pteridophyte species within 50 × 50 km grid squares in the Iberian Peninsula. The central block of 8 × 8 grid cells used to test the mid-domain effect is indicated. Borders of squares with more than 50% of their area in the sea are not marked.



**Figure 2** Variance partitioning at the different steps of the forward selection process to build the models (see text). Portion (a) = nonspatial environmental variation; (b) = spatially structured environmental variation, i.e. overlap between environmental and spatial components, and (c) = spatial structure not explained by the environmental variables. All values expressed as percentages.

**Table 2** Summary of regression statistics of individual explanatory variables using ordinary least squares regression models (first step of the forward selection procedure), to explain the variation in pteridophyte richness in the Iberian Peninsula. Abbreviations as in Table 1

Predictor	d.f.	F-value	P(F)	% Variance explained
- LAT + LAT <sup>2</sup>	237	51.20	< 0.0001	30.17
- LON + LON <sup>2</sup>	237	6.86	0.0013	5.47
- MELE + MELE <sup>2</sup>	237	29.47	< 0.0001	19.91
+ ELER	238	193.64	< 0.0001	44.86
+ MAP - MAP <sup>2</sup>	237	148.39	< 0.0001	55.60
+ RAINR - RAINR <sup>2</sup>	237	92.31	< 0.0001	43.79
- MAT + MAT <sup>2</sup>	237	26.96	< 0.0001	18.54
+ TEMR	238	65.47	< 0.0001	21.57

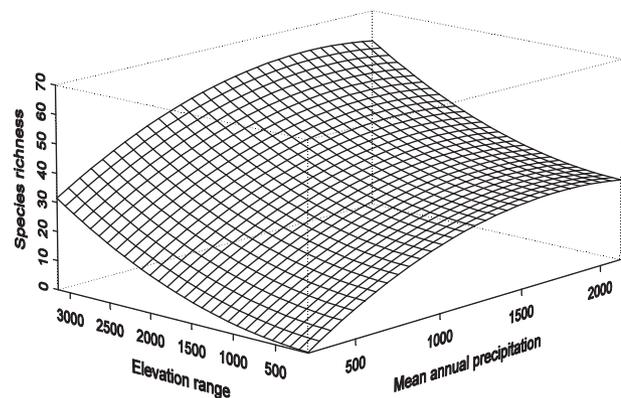
Cordillera, Pyrenees, Central System and Sierra Nevada, whereas both mesetas (i.e. plateaus) and the plains of the Ebro river valley are poor in these species (Fig. 1). Pteridophyte richness is significantly higher along the coast (a hard boundary) than in the 64 grid cells in the centre of the Iberian Peninsula.

Pteridophyte richness is strongly correlated with all environmental (nonspatial) variables (Table 1), and all of them were significant in ordinary regression ( $P < 0.0001$ ) when tested alone (Table 2). Correlations with Bonferroni correction showed that most of the environmental variables are collinear (Table 1). MAP is not significantly correlated with mean elevation, and precipitation range is weakly correlated with this variable. Non-significant correlations were found between elevation range and latitude, and MAT and longitude. The correlation between temperature range and the spatial variables was not found to be significant either.

MAP (second-order polynomial) was the most important variable in ordinary regression, and explained c. 56% of the total variance (Table 2), 24% of which is corresponding to a spatially structured variation, and c. 32% to nonspatial variation (Table 3; Fig. 2). In the second step of the selection process, a quadratic term for elevation range was added ( $P < 0.0001$ ) (at this step, it yielded a better fit than the linear one initially selected). These two variables together account for 73% of the variation, and explain most of

**Table 3** Summary of regression statistics of individual explanatory variables of pteridophyte richness after fitting latitude and longitude using ordinary least squares regression models. The percentage variance explained by the other variables refers in this case to the additional variation explained from the residuals and not from the total variation. Abbreviations as in Table 1

Predictor	d.f.	F-value	P(F)	% Variance explained
- LAT + LAT <sup>2</sup> - LON + LON <sup>2</sup>	235	30.46	< 0.0001	34.15
+ MELE	234	82.03	< 0.0001	17.09
+ ELER	234	219.77	< 0.0001	31.89
+ MAP - MAP <sup>2</sup>	233	107.02	< 0.0001	31.53
+ RAINR - RAINR <sup>2</sup>	233	56.50	< 0.0001	21.51
- MAT	234	30.84	< 0.0001	7.67
+ TEMR	234	83.51	< 0.0001	17.32



**Figure 3** Response of pteridophyte species richness to mean annual precipitation (second order polynomial) and elevation range (quadratic term) in a nonspatial generalized least squares model (i.e. ordinary regression).

the spatial structure in the data (33%) (Fig. 2). According to this model (Fig. 3), maximum pteridophyte richness along the precipitation gradient is found at 1700 mm ( $\geq 30$  species). Pteridophyte richness greatly increases with increasing elevation

range (up to 60 species at 1700 mm of MAP), whereas no species would be found on most arid plains. Although the other environmental variables also remained significant in nonspatial models ( $P < 0.0001$ ), they explained a lower proportion of the variation than elevation range (MAT explained *c.* 4% of the residual variance, and was not significant when the spatial component was accounted for). In a third step of the forward selection process, a quadratic term for precipitation range could also be added ( $P < 0.01$ ), but it explains less than 2% of the residual variance and was not found to be significant once the effect of space (i.e. latitude and longitude) was partialled out (Fig. 2).

After fitting MAP (second-order polynomial) in nonspatial GLS, both the all-directional variogram and the longitudinal variogram of the residuals showed a spatial pattern (variogram without sill) which is similar to the spatial structure exhibited by elevation range (Figs 4 & 5). The latitudinal variogram of the residuals after fitting MAP is almost flat, which implies lack of autocorrelation. After fitting elevation range, all variograms (directional and all-directional) showed similar structures to those of MAP (Figs 4 & 5). When both MAP (second order polynomial) and elevation range (quadratic term) were fitted in a model, a structureless variation was found in all variograms (i.e. they are almost flat in all cases), indicating that most of the spatial autocorrelation was removed from the residuals (Figs 2 & 5). No additional change was found in the variograms after

fitting the quadratic term for precipitation range at the third step of the forward selection procedure.

The best-fitting spatial GLS model incorporated a spherical correlation structure (AIC = 1588, instead of 1655 in nonspatial GLS,  $P < 0.0001$ ). All environmental variables remained significant ( $P < 0.0001$ ) in this model, with the exception of precipitation range (quadratic term) (Table 4). After excluding this term, in general, a similar response of pteridophyte richness to MAP (second-order polynomial) and elevation range (quadratic term) to that in ordinary regression (or nonspatial GLS) was obtained (Figs 3 & 6). In spatial GLS, the maximum number of pteridophyte species (61) is predicted to be found at 1800 mm of MAP, and the minimum fitted value is equal to two species.

## DISCUSSION

### Climate factors and pteridophyte richness

Both spatial and nonspatial models show that variation in pteridophyte richness in the Iberian Peninsula can be related to both the means and ranges of macroclimate factors and topography. All variables are significant in regression models when they are analysed separately including the pure spatial variables latitude and longitude, although pteridophyte richness and longitude were not significantly correlated. This is because correlation

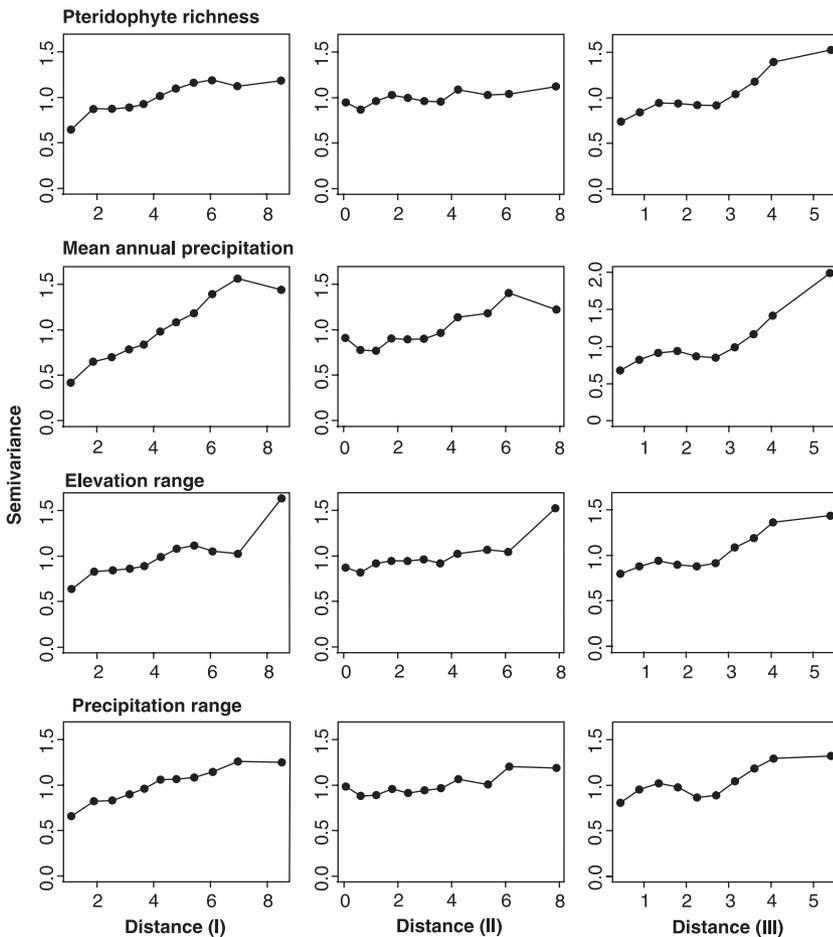
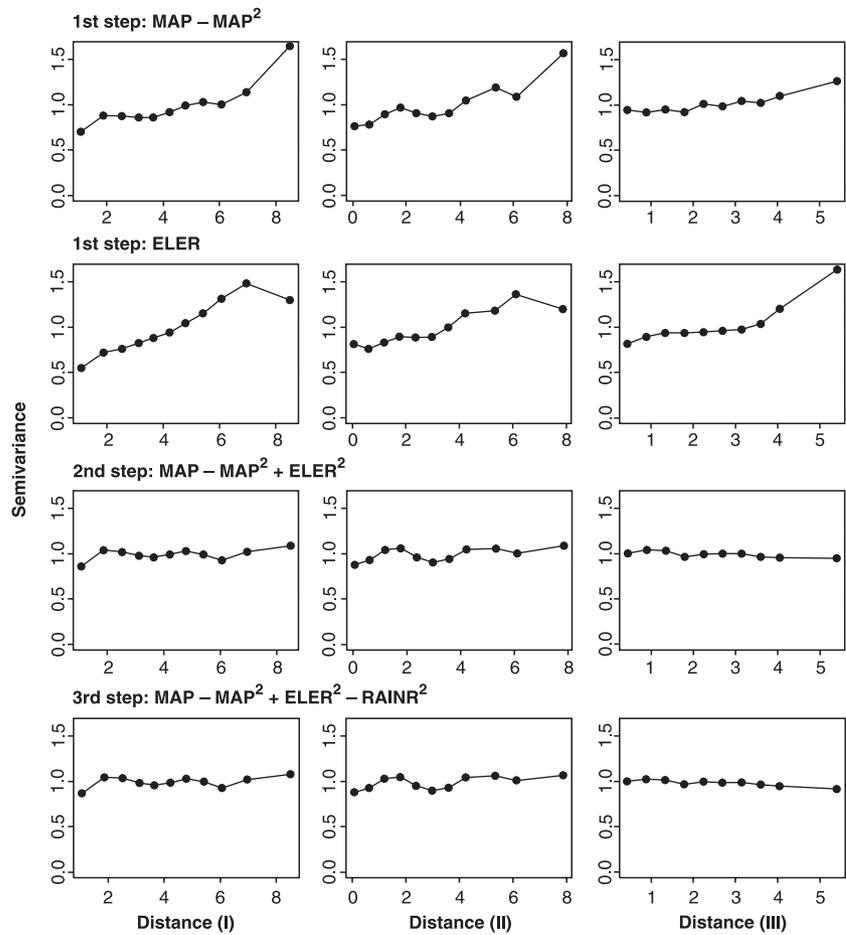


Figure 4 Variograms of the residuals of pteridophyte richness and the main predictors in a null nonspatial generalized least squares model (see text). Distance classes as a function of: (I) latitude and longitude (all-directional variogram), (II) longitude, and (III) latitude, with equal number of observations per group. Maximum latitudinal distance = 800 km; maximum longitudinal distance = 950 km.



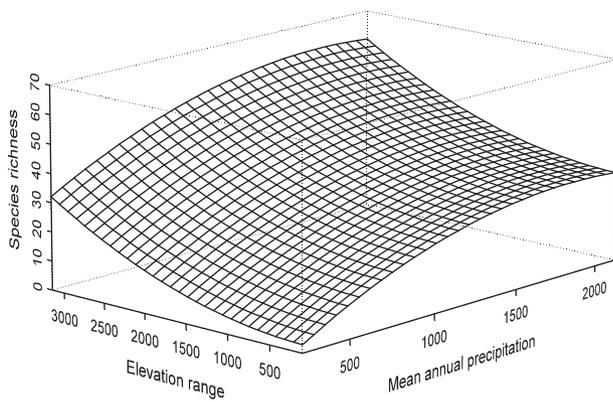
**Figure 5** Variograms of the residuals in nonspatial generalized least squares models after fitting the main variables at each step of the selection procedure (for explanations, see text). Distance classes as in Figure 4.

**Table 4** Coefficients, standard errors and associated *t*-tests for the different terms in the nonspatial generalized least squares model (GLS) of pteridophyte richness in the Iberian Peninsula, and the corresponding spatial GLS with a spherical correlation structure. Abbreviations as in Table 1

Coefficient	Non-spatial GLS				Spatial GLS			
	Value	Std. Error	<i>t</i> -value	<i>P</i> ( <i>t</i> )	Value	Std. Error	<i>t</i> -value	<i>P</i> ( <i>t</i> )
Intercept	$-1.02 \times 10^1$	2.22	-4.62	< 0.0001	$-0.63 \times 10^1$	2.80	-2.25	0.0252
MAP	$4.71 \times 10^{-2}$	$4.81 \times 10^{-3}$	9.80	< 0.0001	$4.10 \times 10^{-2}$	$5.47 \times 10^{-3}$	7.49	< 0.0001
MAP <sup>2</sup>	$-1.22 \times 10^{-5}$	$2.16 \times 10^{-6}$	-5.63	< 0.0001	$-1.07 \times 10^{-5}$	$2.23 \times 10^{-6}$	-4.79	< 0.0001
ELER <sup>2</sup>	$3.21 \times 10^{-6}$	$2.48 \times 10^{-7}$	12.95	< 0.0001	$2.97 \times 10^{-6}$	$3.13 \times 10^{-7}$	9.48	< 0.0001
RAINR <sup>2</sup>	$-3.11 \times 10^{-6}$	$1.09 \times 10^{-6}$	-2.86	0.0046	$-8.72 \times 10^{-7}$	$9.55 \times 10^{-7}$	-0.91	0.3623

deals with linear relationships, whereas regression models make it possible to describe more complex relations. A potential problem in regression analyses relates to multicollinearity among explanatory variables, which seems to be the rule in ecological studies (see, e.g. Vetaas, 1997; O'Brien *et al.*, 2000; Rey Benayas & Scheiner, 2002; Hawkins & Porter, 2003). To minimize this problem, several criteria can be used, e.g. those of simplicity and explanatory power, or the inclusion in the model of variables previously associated with theoretical models, but this does not ensure that the real causal factors will be selected, just a potential set of explanatory factors (see Diniz-Filho *et al.*, 2003; for further discussion on this subject).

In nonspatial modelling, MAP explained the largest proportion of the variation in pteridophyte richness. Analogous results have been obtained by Rey Benayas & Scheiner (2002) for total richness of vascular plants in the Iberian Peninsula, and for moss species richness in Pyrenean forests, north-east Spain (Pausas, 1994). Pteridophyte richness has mainly been found to be related to annual precipitation in tropical regions, e.g. the Andean forests in Bolivia (Kessler, 2001). A relationship between pteridophyte richness and moisture has also been reported in the Himalayas (Bhattarai *et al.*, 2004). This affinity with tropical and subtropical regions is related to the vegetation history of the Iberian Peninsula. The peninsula was covered by tropical and



**Figure 6** Response of pteridophyte species richness to mean annual precipitation (second order polynomial) and elevation range (quadratic term) in a spatial generalized least squares model (Fig. 3).

subtropical vegetation before the development of current Mediterranean climatic conditions (Suc, 1984; Biondi *et al.*, 1985). Thus, numerous relicts in the Iberian Peninsula presumably evolved in tropical-like environments (Herrera, 1992; see also Ferrer-Castán & Vetaas, 2003). Some of them are well-known tropical ferns (Castroviejo *et al.*, 1986), e.g. *Christella dentata* (Forsskål) Brownsey & Jermy, *Pellaea calomelanos* (Swartz) Link, and *Psilotum nudum* (L.) PB.

The explanatory power of MAP for pteridophyte richness in the Iberian Peninsula, and the marginal significance of the energy variable MAT, are consistent with the meta-analyses by Hawkins *et al.* (2003a,b), which show that the relative importance of water increases towards the equator, whereas energy becomes more important towards higher latitudes. The importance of moisture for pteridophytes is probably related to the dependence on external water for reproduction (Pausas & Sáez, 2000; Lehmann *et al.*, 2002). Nevertheless, in tropical regions such as Uganda and western Amazonia (Tuomisto & Poulsen, 1996; Lwanga *et al.*, 1998), soil properties have been found to be important. This may be the result of the relatively uniform macroclimate occurring in these regions (Lehmann *et al.*, 2002). Energy variables, such as PET, have been shown to explain fern richness along the Himalayan elevation gradient (Bhattarai & Vetaas, 2003; Bhattarai *et al.*, 2004), but the operational factor is probably related to the interaction between temperature and water availability. High energy causes excessive loss of water at low elevation, whereas low energy causes inaccessible water through frost at higher elevation (cf. Kessler, 2001; Bhattarai *et al.*, 2004).

### Hard boundaries and mass effect

MDE models predict lower richness in coastal areas, as they exhibit a clear barrier for dispersal (i.e. hard boundary) compared with the inland areas (cf. Colwell & Lees, 2000; Grytnes & Vetaas, 2002). Our analyses show the opposite, where the coastal cells have on average a greater pteridophyte richness than the central grid squares ( $P < 0.0001$ ). This indicates that there is no

MDE, and suggests that the observed pattern of pteridophyte richness in the Iberian Peninsula is primarily caused by environmental factors (cf. Hawkins & Diniz-Filho, 2002; Bhattarai *et al.*, 2004). High richness in the coastal cells may relate to higher habitat diversity, as the grid cells are large enough to include both humid coastal mountains and more arid coastal habitats. Moisture can be locally high as a result of sea mist even in relatively dry coastal environments (see, e.g. Azevedo & Morgan, 1974; Vetaas, 1992; Ferrer-Castán & Vetaas, 2003). Enhanced richness of vascular plants in coastal areas has also been found in Fennoscandia (Grytnes *et al.*, 1999). Another explanation might be that our results do not support the prediction of MDE models because there are very few pteridophytes endemic to the Iberian Peninsula, given the high dispersal capabilities of fern spores, but both Grytnes (2003) and Colwell *et al.* (2004) state that the MDE is not necessarily restricted to endemic species.

Nevertheless, the Pyrenees have even higher richness than the coastal environments (Fig. 1), which may relate to mass effect *sensu* Smida & Wilson (1985) in the transition between the Mediterranean region and the Eurosiberian region (cf. Rey Benayas & Scheiner, 2002). This is also congruent with the fact that the diverse habitats in mountains have high pteridophyte richness, i.e. species richness increases with increasing elevation range (Fig. 6) (cf. Bhattarai *et al.*, 2004). However, high topographic heterogeneity may not only relate to a higher diversity of local climatic conditions but also to greater surface area in mountainous cells compared to cells from plains (O'Brien *et al.*, 2000; see also Rosenzweig, 1997; Vetaas & Grytnes, 2002). This may also explain the fit of a quadratic elevation-range term in the final models instead of the linear one initially selected (cf. O'Brien *et al.*, 2000).

### Range variables and spatial structure

All range variables accounted for a smaller percentage of the variation in pteridophyte richness than the macroclimate variable MAP in the nonspatial models (Table 2), which agrees with several other studies (e.g. Pausas, 1994; Kessler, 2001; Rey Benayas & Scheiner, 2002; see also Pausas & Austin, 2001). In the study by Lwanga *et al.* (1998), elevation range was not found to be significant at all. In our study, elevation range and MAP account for a similar amount of total variance when spatial structure is partialled out (Fig. 2, Table 3), thus elevation range is a primary factor in explaining the variation in pteridophyte richness in the Iberian Peninsula. Several studies have found elevation range to be associated with enhanced richness of a variety of organisms such as mammals (Currie, 1991; Kerr & Packer, 1997), birds (Currie, 1991; Rahbek & Graves, 2001), vascular plants (Grytnes *et al.*, 1999; Rey Benayas & Scheiner, 2002), woody plants (O'Brien *et al.*, 2000), and butterflies (Hawkins & Porter, 2003), in addition to pteridophytes (Pérez Hornero *et al.*, 1996). In two of the above studies (Rahbek & Graves, 2001; Hawkins & Porter, 2003) it was observed that elevation range is important independently of the number of habitats found in the grid cells. For this reason Hawkins & Porter (2003) put into question the link between elevation range and species richness through habitat

diversity. We agree that increased elevation range is a proxy that may relate to more than just habitat diversity, and we have proposed (cf. above) a link to enhanced surface available for the different taxa, which will increase much more than just the two dimensional area of a grid cell.

Grytnes *et al.* (1999) found that the relationship between elevation range and plant richness in Fennoscandia was less significant once the effect of space was partialled out. In contrast, Diniz-Filho *et al.* (2003) found that bird species richness in Europe, North Africa and the Middle East was best predicted by range in elevation when they used spatial GLS, whereas this variable was less significant in ordinary regression. Based on this finding, Diniz-Filho *et al.* (2003) argue that methods such as partial regression (i.e. variance partitioning) and spatial GLS de-emphasize predictors with strong autocorrelation and long-distance clinal structures such as macroclimate variables, giving more importance to variables acting at finer geographical scales, in their case elevation range. Other researchers have claimed that the significance of environmental variables may change depending on whether spatial structure is considered or not, thus if spatial autocorrelation is ignored, the analyses can produce misleading results, i.e. inflated Type I errors (Lennon, 2000; Selmi & Boulinier, 2001; Legendre *et al.*, 2002).

Our results indicate that the statistical significance of the variables in spatial models depends on the correspondence between the spatial structures of both the response variable and the predictors (Fig. 2), and support the statements by Diniz-Filho *et al.* (2003). Thus, if a predictor explains a significant proportion of the spatial structure in the data, it will be de-emphasized when the spatial component is statistically accounted for (partial regression, spatial GLS). In our study, it is particularly the case of MAP (Fig. 2), as it was the case of mean annual temperature and annual evapotranspiration in the study by Diniz-Filho *et al.* (2003). Nevertheless, the differences between the spatial and nonspatial multiple models in our case are very small (Table 4). They only affect the last variable to enter the model, which accounts for very little variance and may do nothing more than correct for lack of fit of the major predictors (i.e. MAP and elevation range). It is likely that our nonspatial models have inflated Type I errors because of a low turnover of species (i.e. most pteridophytes have large geographical range sizes relative to the size of cells), hence adjacent cells are not independent (Diniz-Filho *et al.*, 2003). This may explain that the *t*-values decreased in absolute terms in all cases after including spatial correlation structure in GLS (Table 4), but in spite of that, the overall biological interpretation of the main variables remained the same. Moreover, spatial models have revealed that these two variables explain more than just the spatial structure of the pteridophyte data. This suggests that our findings are quite robust, and reinforces the idea that water availability and topographic relief control species richness in relatively high-energy regions.

As pointed out by Diniz-Filho *et al.* (2003), the results in partial regression, i.e. variance partitioning, are congruent with spatial GLS. The advantage with variance partitioning is that this technique explicitly shows the fraction of variance explained by the spatial and environmental variables together, as well as their

unique contribution. This may be particularly useful in combination with spatial GLS. Spatial GLS can assess the significance of spatial correlation structure, and allow it to influence the significance of the environmental variables in order to reduce Type I errors. However, this will enhance the importance of variables sharing a smaller fraction of spatial structure with the response variable, which can be checked by means of variance partitioning. If a response variable and a predictor covary in space and the predictor becomes nonsignificant after including a spatial correlation structure in the model, one should not reject this predictor based on the spatial-GLS analyses only. The explanatory variable may have biological influence on the target response, and actually be a potential factor explaining the spatial structure of the response variable. To avoid such Type II errors, Diniz-Filho *et al.* (2003) argue for an evaluation of the model by checking the residuals for autocorrelation. If the residuals show a strong spatial trend, it weakens the model and one should expect an important variable to be missing (Diniz-Filho *et al.*, 2003; Bhattarai *et al.*, 2004). The comparison between nonspatial and spatial models, together with variance partitioning, can be useful to clarify mechanisms that may operate on richness at different scales (see Willis & Whittaker, 2002), and this is important for the conservation of biological diversity.

## ACKNOWLEDGEMENTS

We thank the QEP-Research Group at the Department of Biology (UiB), especially J.A. Grytnes, E. Heegaard, and K.R. Bhattarai for valuable suggestions. We are grateful to E. Rico and J.M. Ninot for comments and suggestions about fern data sources. We thank D.J. Currie, B.A. Hawkins and one anonymous referee for their valuable comments on the manuscript, and Barbara Knowles for improving the English text. DFC received financial support to visit the University of Bergen from the Researchers Mobility Program at the University of Salamanca.

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