



Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands

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Using an exhaustive data compilation, Iberian vascular plant species richness in 50×50 UTM grid cells was regressed against 24 explanatory variables (spatial, geographical, topographical, geological, climatic, land use and environmental diversity variables) using Generalized Linear Models and partial regression analysis in order to ascertain the relative contribution of primary, heterogeneous and spatially structured variables. The species richness variation accounted for by these variables is reasonably high (65% of total deviance). Little less than half of this variation is accounted for spatially structured variables. A purely spatial component of variation is hardly significant. The most significant variables are those related to altitude, and particularly maximum altitude, whose cubic response reflects the occurrence of the maximum number of species at the highest altitudes. This result highlighted the importance of Iberian mountains as hotspots of diversity and the relevance of large and small scale historical factors in contemporary plant distribution patterns. Climatic or energy-related variables contributed little, whereas geological (calcareous and acid rocks) and, to a lesser extent, environmental heterogeneity variables (land use diversity and altitude range) seem to be more important. © 2001 The Linnean Society of London

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INTRODUCTION

Species richness, frequently correlated with other measures of ecological, morphological, phylogenetic or functional diversity (Gaston, 1996) provides a reasonably useful measure of biodiversity. As the species richness of a region is frequently not spatially homogeneous, understanding the geographic distribution of diversity and delimiting the main predictor variables that explain the species richness are important goals

for today's biologists. Unfortunately, describing geographical trends in species number and ascertaining the relative importance of different factors are tasks complicated by two principal methodological difficulties (Gaston & Williams, 1996): (i) to consider all the available historical and present biological and geographical species data, while taking into account the unevenness of sampling effort in different areas; and (ii) to differentiate patterns from processes, detecting causal relationships underlying multivariate environmental and spatial correlations.

Richness estimates of different areas are generally unreliable because there is no means of determining

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inventory completeness (Gaston, 1996; Williams, 1993). However, in spite of the lack of sampling effort measurements, one can attempt to describe the main geographical patterns in species richness variation using information based on regional and national atlases, (e.g. Pomeroy, 1993; Williams, Humphries & Gaston, 1994; Väisänen & Heliövaara, 1994; Castro Parga *et al.*, 1996; Blackburn & Gaston, 1996; Qian, 1998 and Davidowitz & Rosenweig, 1998). We will assume in this case that sampling effort unevenness does not completely obscure the geographical species richness pattern.

The first step in analysing the geographical species richness-environment patterns is to identify what factors are correlated with species richness; subsequently, to determine whether these correlations are causal by performing controlled or randomized experiments or assessing the correspondence between the correlations and a causal statistical model (Legendre & Legendre, 1998; Shipley, 1999). As manipulative experiments and causal modelling require stating a priori hypotheses with a small number of variables, factors correlated with the number of species are the raw material for the identification of factors that might lead to species richness patterns (see Hengeveld, 1990; Huston, 1994).

The co-variation and interactions between multiple explanatory variables as well as their spatial autocorrelation and non-linear relationship with the dependent variable must be taken into account to explain species richness patterns (Margules, Nicholls & Austin, 1987; Austin, Pausas & Nicholls, 1996; Gaston, 1996; Gaston & Williams, 1996). To discriminate between different correlated explanatory variables is not a simple task, but model reliability may be heightened by considering interactions between explanatory variables as well as their curvilinear quadratic and cubic functions (Margules *et al.*, 1987; Austin *et al.*, 1996; Heikkinen & Neuvonen, 1997). On a geographical scale most environmental variables are spatially structured and, hence, autocorrelated (i.e. the observed values of the considered variables at any given locality are influenced by values at neighbouring localities). Moreover, these spatial structures in data are a major source of false correlations (Legendre & Legendre, 1998). Partial regression analysis using spatial variables limits the interference of such autocorrelations by removing large-scale trends from environmental variables. It also facilitates both the examination of species richness pattern dependence on different variable groups and the formulation of hypotheses about the processes that may have generated the observed patterns (Borcard, Legendre & Drapeau, 1992; Legendre, 1993; Pinel-Alloul, Niyonsenga & Legendre, 1995; Heikkinen & Birks, 1996; Anderson & Gribble, 1998; Legendre & Legendre, 1998).

The Iberian Peninsula is one of the Mediterranean

areas richest in vascular plant species (Groombridge, 1992). A recent analysis of species richness distribution in this region (Castro Parga *et al.*, 1996) shows that mountain areas score highest in species richness. However, the dependence of species number of Iberian vascular plants on a range of explanatory variables has not been yet analysed. In general, there are not many studies that analyse this question with regard to vascular plants (see Wohlgemuth, 1998 for a brief review). European studies either were carried out in northern or Central European countries (Birks, 1996; Heikkinen, 1996; Heikkinen & Neuvonen, 1997; Wohlgemuth, 1998) or analyse a reduced group of species (Väisänen *et al.*, 1992; Myklestad & Birks, 1993; Pausas, 1994; Márquez *et al.*, 1997).

When research into the environmental factors that determine plant species richness are reviewed (Wohlgemuth, 1998), the most explicative variables are found to relate to either environmental heterogeneity (area, altitude range, etc.) or to productivity (temperature, precipitation, etc.). Environmental heterogeneity, a major determinant of diversity, has received strong empirical support as a species richness determinant (Begon, Harper & Townsend, 1990). However, environmental heterogeneity variables probably summarize other more causal and primary explicative environmental variables, that are more directly related to plant physiological mechanisms, and should be used when detailed environmental information is not available (Austin, 1980).

Using an exhaustive data compilation of Iberian vascular plants found in 50 × 50 km UTM grid cells and 24 explanatory variables of different types for each cell, partial regression analysis was used to estimate the relative importance of spatial and environmental variables in the species richness variation across the Iberian Peninsula. The most important environmental determinants were estimated by modelling Iberian plant species richness, including and excluding environmental heterogeneity variables, removing or including the spatial structure of the explanatory variables and considering curvilinear responses and interactions between variables. Our aim is to ascertain relationships and, if possible, provide a preliminary understanding of the possible underlying causal factors that have led to the current plant richness distribution in the Iberian Peninsula.

METHODS

ORIGIN OF THE DATA

Distributional data for 2687 taxa from 254 50 × 50 km UTM cells with at least 15% surface area not covered by seawater from the Iberian Peninsula and the Balearic Islands was studied (Fig. 1). In total, around 37% of the whole Iberian and Balearic vascular flora was

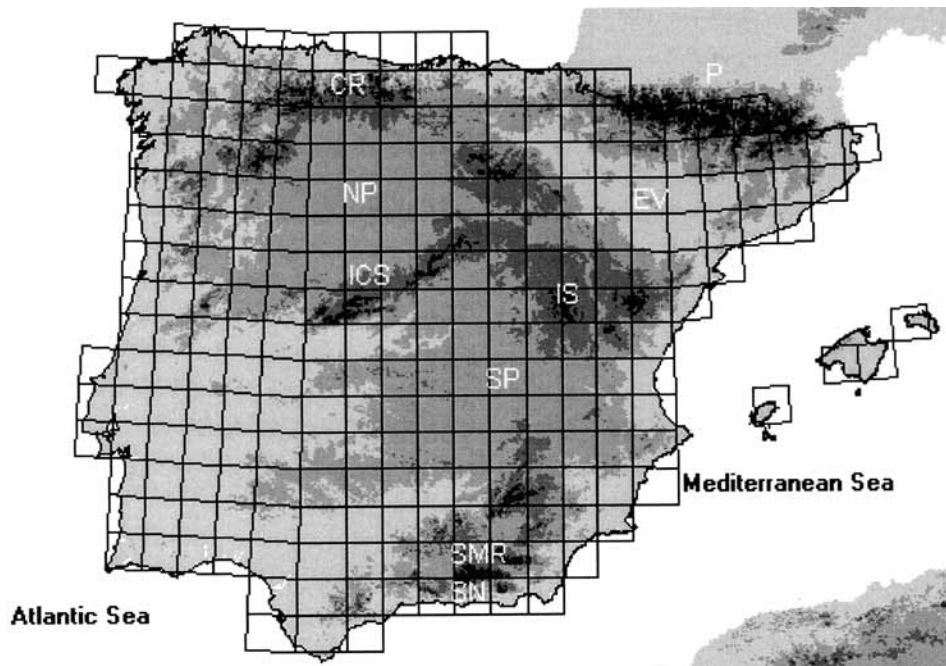


Figure 1. Two hundred and fifty-four Iberian 50×50 UTM grid cells with at least 15% surface area not covered by sea water. The map includes four categories of altitude in metres (0–500, 501–1000, 1001–1500 and 1501+) from light grey to black. CR, Cantabrian Range; EV, Ebro Valley; ICS, Iberian Central System; IS, Iberian System; NP, North Plateau; P, Pyrenees; SMR, Subbaetic Mountain Ranges; SN, Sierra Nevada; SP, South Plateau.

considered (Castroviejo, 1997; Nieto-Feliner, 1999), an increase of 554 species and subspecies from those used by Castro Parga *et al.* (1996). Information concerning plant richness was compiled from: (i) *Atlas Florae Europaeae* (Jalas & Suominen, 1972–1994; Jalas, Suominen & Lampinen, 1996), adding to their maps distributional data from subsequent studies (i.e. Salvo *et al.*, 1984; Gómez-Campo, 1987) or compiling the occasional record published after each atlas volume; and (ii) dispersal maps of Iberian and Balearic vascular plants using UTM 10×10 km grid cells, comprising about one thousand maps published in a series of recent papers, taking advantage of regional atlases (i.e. Amaral-Franco & Rocha-Afonso, 1982; Moreno-Saiz & Sainz-Ollero, 1992). Distributional information was processed with WORLDMAP (Williams, 1994), using the species richness option.

For the 254 UTM cells 24 explanatory variables were recorded (Table 1): two spatial variables (central latitude and longitude of each grid cell); two geographic variables; three topographic variables; two geologic variables; six climatic variables; four land use variables; and five variables that measured the environmental diversity. All explanatory variables are continuous.

The climatic data for each 50×50 km UTM cell were provided by courtesy of W. Cramer (CLIMATE database

version 2; <http://www.pik-potsdam.de/~cramer/climate.htm>). Annual temperature and annual precipitation variations are the differences between monthly extremes. The topographic and spatial data were obtained by overlapping a Digital Elevation Model of the Iberian Peninsula (cell size or spatial resolution of 1 km) and the polygons of UTM cells using a Geographic Information System (GIS). Land use data from the 44 land cover categories in Spain and Portugal were provided by the European Environment Agency raster information (282 m resolution) for Spain and Portugal (CORINE Programme 1985–1990). We also overlaid this information with the 50 km UTM polygons by means of a GIS. The land cover categories have been grouped to obtain the forest surface (all types of forests), scrub surface, grassland surface (natural or artificial), and the surface of areas with strong anthropic influence (urban, industrial and cultivation zones). Land use diversity in each grid cell has been estimated using the Shannon diversity index (see Magurran, 1988):

$$H' = -\sum p_i \log_2 p_i$$

where p_i is the proportion of each one of the 44 land cover categories. Bedrock geology data were obtained by digitizing an Iberian map with three categories:

Table 1. Explanatory variables considered in the 50 × 50 km UTM cells of the Iberian peninsula with their respective code. Deviance and change in the deviance from a full model for total vascular plant species number. The linear, quadratic or cubic functions of each variable have been selected if they account for a statistically significant change in the deviance with a probability of less than 0.01. The sign column corresponds to the sign for each term of each function. Spatial variables were chosen by removing the non-significant terms of a third degree polynomial equation of latitude and longitude by a backward stepwise selection. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

Model	Code	Selected items	Deviance	df	Change in deviance	<i>F</i>	Sign
Full			11299.49	253			
Spatial							
Longitude	LON	LON	9618.92	252	1680.57	44.03***	+
Latitude	LAT	LAT	10993.06	252	306.43	7.02**	+
		LAT + LAT ²	10418.98	251	880.51	21.21***	++
		LAT + LAT ² + LAT ³	9208.49	250	2091.00	56.77***	++-
		LON + LAT + LAT ² + LAT ³	7768.67	249	3530.82	113.17***	+++
		LON + LAT + LAT ² + LAT ³ + LAT ² *LON	7354.22	248	3945.27	133.04***	+++ - +
Geography							
Sea area in grid square	A	A	11299.41	252	0.08	0.002	+
		A + A ²	10874.22	251	425.27	9.82**	+-
Distance from Pyrenees	Dp	Dp	9855.74	252	1443.75	36.92***	-
		Dp + Dp ²	8697.32	251	2602.17	75.10***	- +
Topography							
Minimum elevation	e	e	11292.49	252	7.00	0.16	+
Maximum elevation	E	E	6612.91	252	4686.58	178.59***	+
		E + E ²	6459.64	251	4839.85	188.06***	++
		E + E ² + E ³	6090.64	250	5208.85	213.81***	+++ -
Mean elevation	em	em	9391.21	252	1908.29	51.21***	+
		em + em ²	8975.69	251	2323.80	64.98***	++
Bedrock geology							
Calcareous rock surface	Cr	Cr	9995.90	252	1303.59	32.86***	+
Acid rock surface	Ar	Ar	10801.04	252	498.45	11.63***	-
Climate							
Minimum mean temperature	t	t	10335.57	252	964.92	23.53***	-
		t + t ²	9713.55	251	1585.94	40.98***	- +
Maximum mean temperature	T	T	10395.86	252	903.63	21.90***	-
		T + T ²	9829.30	251	1470.19	37.54***	- +
Annual mean temperature	tm	tm	9979.66	252	1319.83	33.33***	-
		tm + tm ²	9500.45	251	1799.04	47.53***	- +
Total annual precipitation	P	P	10930.63	252	368.86	8.50**	+
		P + P ²	10432.87	251	866.62	20.85***	+-
Total summer precipitation	Ps	Ps	8777.26	252	2522.22	72.41***	+
Annual days of sun	Ds	Ds	10681.75	252	617.74	14.57***	-
		Ds + Ds ²	9915.57	251	1383.92	35.03***	--
Land use							
Cultivated and urban area	U	U	10054.88	252	1244.61	31.19***	-
Forest area	F	F	10125.8	252	1173.69	29.21***	+
Scrub area	S	S	11286.93	252	12.56	0.28	+
Grassland area	G	G	10815.85	252	483.64	11.27***	+
Environmental diversity							
Altitude range	AR	AR	5832.21	252	5467.28	236.23***	+
Annual temperature	TV	TV	11232.14	252	67.35	1.51	+
Variation							
Annual precipitation	PV	PV	11263.65	252	35.84	0.80	-
Variation							
Land use diversity	LUD	LUD	10491.64	252	807.85	19.40***	+
Geologic diversity	GD	GD	9426.28	251	1873.21	49.88***	+

soils on calcareous rocks, soils on acid rocks (siliceous) and soils on clay (spatial resolution of 1 km). Overlaying this map with the 50 km UTM polygons by means of a GIS allowed us to estimate the calcareous and acid rock surface area in each grid cell. Geologic diversity has been estimated also by using the Shannon diversity index with the proportion of the three bedrock categories.

DATA ANALYSIS

Modelling the geographical variation of species richness must take spatial variables into account because spatial structures are a major source of false correlations between autocorrelated variables, and because spatial variables can incorporate the effects caused by ignored historical, biotic or environmental variables (Legendre & Legendre, 1998). Thus, partial regression analysis can be used to separate the response variable variation into a purely environmental fraction (R_{PE}), a spatially structured environmental fraction (R_{SE}), and a purely spatial fraction (R_{PS}) (Borcard *et al.*, 1992; Legendre, 1990, 1993; Legendre & Legendre, 1998). Calculation of the three fractions has been estimated by:

- (i) Computing the multiple regression of plant species number against environmental and spatial variables where the percentage of explained variation is the sum of the three fractions of variation ($R_T = R_{PE} + R_{SE} + R_{PS}$).
- (ii) Computing the multiple regression of plant species number against environmental variables, where the percentage of explained variation is the sum of the purely environmental fraction and the spatially structured environmental fraction ($R_E = R_{PE} + R_{SE}$).
- (iii) Computing the multiple regression of plant species number against spatial variables, where the percentage of explained variation is the sum of the purely spatial fraction and the spatially structured environmental fraction ($R_S = R_{PS} + R_{SE}$).

Taking into account the results of the previous regression analysis, this partial regression analysis approach allows the estimation of the separation of the dependent variable variation into: pure spatial, pure environmental, spatial component of environmental influence, and undetermined (see Legendre & Troussellier, 1988; Legendre & Fortin, 1989; Borcard *et al.*, 1992; Legendre, 1993; Legendre & Legendre, 1998). These four fractions of variation in the dependent variable are obtained by subtraction, where: $R_{PE} = R_T - R_S$; $R_{PS} = R_T - R_E$; and $R_{SE} = R_E + R_S - R_T$. Finally, the unexplained fraction of variation (R_{UN}) can be calculated as $1 - R_T$.

The spatial fraction of variation is calculated by

regressing the number of plant species number in a backward stepwise regression with the third-degree polynomial of the central latitude (LAT) and longitude (LON) of each grid cell (Trend Surface Analysis; see Legendre, 1993): $b_1\text{LAT} + b_2\text{LON} + b_3\text{LAT}^2 + b_4\text{LAT} \times \text{LON} + b_5\text{LON}^2 + b_6\text{LAT}^3 + b_7\text{LAT}^2 \times \text{LON} + b_8\text{LAT} \times \text{LON}^2 + b_9\text{LON}^3$. As recommended by Legendre & Legendre (1998) latitude and longitude have been centred on their respective means prior to submitting the nine terms of the equation to a backward selection procedure to remove the non-significant spatial terms.

Generalized linear models (GLM; McCullagh & Nelder, 1989) of plant species richness were used to estimate the relative importance of environmental and spatial variables in modelling plant species distribution (see Austin, Nicholls & Margules, 1990; Austin *et al.*, 1996; Nicholls, 1989 and Heikkinen & Neuvonen, 1997 for a description of the method and some examples). A Poisson error distribution for the number of plant species was assumed which was linked to the set of predictor variables via a logarithmic link function (see Crawley, 1993). The model goodness-of-fit was measured by the deviance statistic and the change in deviance F -ratio tested (McCullagh & Nelder, 1989; Dobson, 1999) with a 1% significance level. The percentage of explained deviance was also calculated for each model (see Dobson, 1999) in order to estimate the percentage of explained variation in species richness.

As a first step, the total number of Iberian vascular plants in 50 km UTM cells was related separately one-by-one with each environmental and spatial variable. Since the richness and environmental variable relationship may be curvilinear (Austin, 1980), the linear, quadratic or cubic function of each environmental variable was selected by comparing their reduction in deviance with a full model (number of parameters = total number of observations, $n = 254$; see Dobson, 1999).

As a second step, this operation was repeated for the number of vascular plants after eliminating the spatial component of environmental variables. The large-scale environmental variable spatial structure was subtracted using a separate backward stepwise regression for each variable with the third-degree polynomial of the latitude and longitude of each grid cell (Trend Surface Analysis; see Legendre, 1993; Legendre & Legendre, 1998). The retained residuals, a good measure of the predictive power of variables minus their spatial structure, were then analysed as described in the previous step to estimate the most important environmental variables of the purely environmental fraction (R_{PE}).

To obtain the final models of species richness a forward stepwise procedure was used (see Austin *et al.*, 1996 and Heikkinen & Neuvonen, 1997). The linear,

quadratic or cubic function of the variable that accounts for the most important change in deviance was selected. All remaining variables were then tested for significance and the process repeated until no more statistically significant variables remained ($P \leq 0.01$). The importance of all the interactions terms between explanatory variables (see Margules *et al.*, 1987) was subsequently tested by including them sequentially one by one in the previous model. After each step of forward inclusion, the significance of the terms previously selected was also tested by submitting the new model to a backward selection procedure in order to exclude those terms that had become non-significant.

The adequacy of the final models was determined by plotting residuals against the fitted values, and by plotting residuals in a normal probability plot (Dobson, 1999). Independent variables were standardized to eliminate the effect of measurement scale differences. All statistical computations were made using STATISTICA (1999).

As we are also interested in examining the contribution of environmental heterogeneity variables to the species richness variation, models were developed including and excluding the five explanatory variables related to environmental diversity (altitude range, annual temperature variation, annual precipitation variation, land use diversity and geological diversity).

RESULTS

DESCRIPTION OF THE IBERIAN PLANT RICHNESS DISTRIBUTION

The number of species in all areas ranges from 652 to 74, with a mean of 291.8 (standard error = 7.3) (Fig. 2). By some distance, the Iberian northeastern border (including the Pyrenees) not only scores highest within the Peninsula but also has the densest ensemble of cells belonging to the richest categories. Other outstanding areas are the Cantabrian Range, Iberian System, Iberian Central System and the Subbaetic Mountain Ranges, with Sierra Nevada having the only cells with more than 600 taxa outside of the Pyrenees.

The North Plateau, South Plateau, Ebro Valley and the Atlantic belt show the poorest figures in terms of taxon richness. The Mediterranean coast is characterized by moderate levels of diversity, increasing only where mountain areas reach the sea or in other coastal ranges such as Arrábida and the Catalanian massif.

SPATIALLY SIGNIFICANT VARIABLES

A backward stepwise multiple regression of the third-degree polynomial terms of latitude and longitude was used to select a linear function of longitude, a cubic function of latitude and the interaction term between

the quadratic term of latitude and longitude (Table 1). These spatial variables accounted for an important change in deviance (3945.3), and statistically capture 34.9% of the deviance. The cubic function of latitude is the spatial variable that accounted for the most significant change in deviance (18.5% of total deviance). The number of plant species is related to latitude in such a way that the maximum number of Iberian vascular plant species is found at low (about 37° N latitude) and high latitudes (about 42.5° N latitude).

MODELLING WITH SPATIALLY-STRUCTURED ENVIRONMENTAL VARIABLES

Except for minimum elevation, scrub area, annual temperature variation and annual precipitation variation, all the remaining environmental variables were significant when tested separately as either a linear, quadratic or cubic function (Table 1). The variables that explain more than 15% of the deviance in the plant species richness are in decreasing order: altitude range (48.4%), the cubic function of maximum elevation (46.1%), the quadratic function of the distance from Pyrenees (23.0%), total summer precipitation (22.3%), the quadratic function of mean elevation (20.6%), geological diversity (16.6%), and the quadratic function of annual mean temperature (15.9%) (Table 1). As the linear function of altitude range accounted for the most important change in deviance, this variable is the first included in the model (Table 2A). In the second step, the quadratic function of the distance from Pyrenees was selected. Next, calcareous rock surface, the cubic function of maximum elevation, the quadratic function of sea area and land use diversity were sequentially added to the model (Table 2A). After fitting the environmental variables, the only significant interaction term between environmental variables is maximum elevation \times acid rock surface, reflecting the fact that species number is smaller in those places without mountains (lower maximum altitude) where acid rock predominates (Fig. 3). The final model, explaining 64.6% of the deviance was:

$$S = \exp(c + AR + Dp + Dp^2 + Cr + E + E^2 + E^3 + A + A^2 + LUD + E \times Ar)$$

MODELLING WITH SPATIAL AND ENVIRONMENTAL VARIABLES

The final model using all the environmental and spatial variables included in Table 1 contained, in order of entry (Table 2B): altitude range, the cubic function of latitude, acid rock surface, the cubic function of maximum elevation, land use diversity, the quadratic function of minimum mean temperature and the total

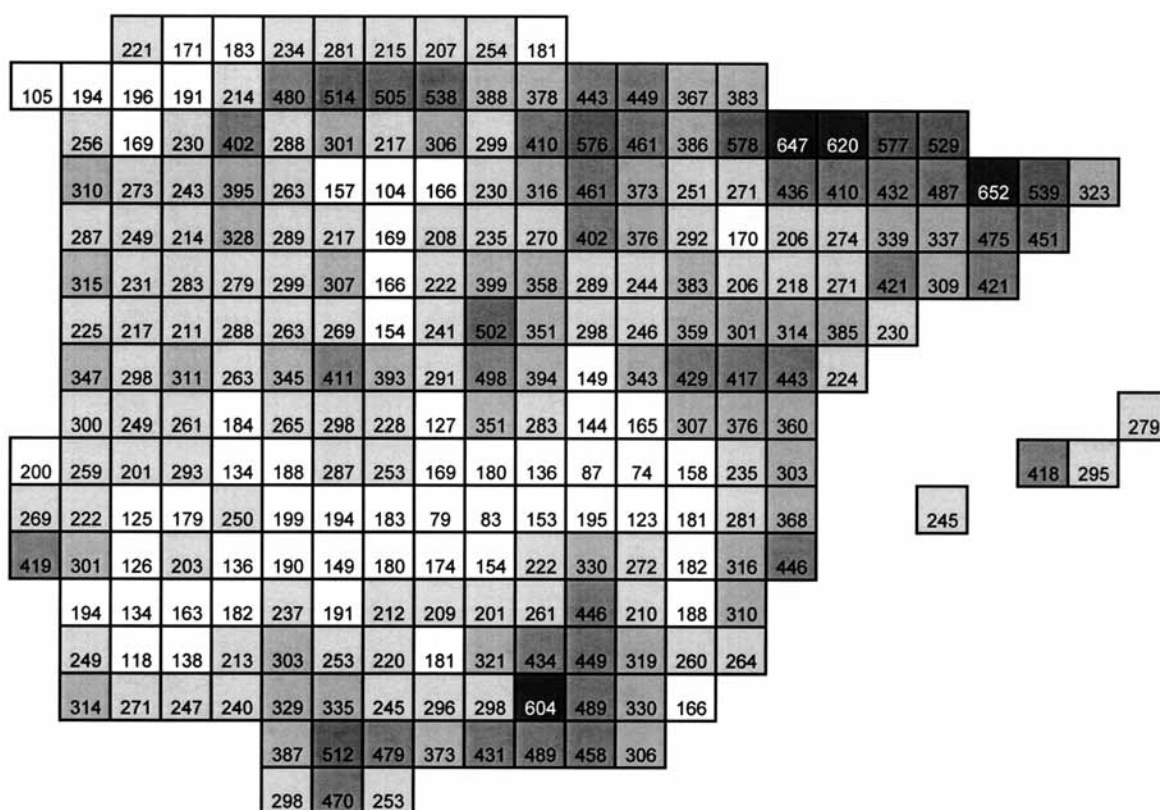


Figure 2. Number of vascular plants species recorded in each of the 254 UTM grid cells of the Iberian Peninsula. The grey scale changes at 200-species intervals.

summer precipitation, although the lineal term of maximum elevation was deleted from the model (change in deviance = 7486.9; $F=475.22$; $P<0.0001$; 66.3% of the deviance). Three interaction terms reflect an additional significant change in the deviance, deleting the linear term of minimum mean temperature: annual days of sun \times distance from Pyrenees, longitude \times maximum mean temperature and forest area \times land use diversity. The species richness is maximum when there is an intermediate number of sunny days, mainly if the distance from the Pyrenees is small (Fig. 4). When the maximum mean temperature is high the species richness is greater in the east than in the west, with the maximum located in eastern and central sites with reduced maximum temperatures. Finally, the response to land use diversity depends on forest surface (Fig. 4) with the maximum species number occurring when there is a high diversity of land use and a high forest surface. The final model explains 71.4% of the deviance and was:

$$S = \exp (c + AR + LAT + LAT^2 + LAT^3 + Ar + E^2 + E^3 + LUD + t^2 + Ps + Ds \times Dp + LON \times T + F \times LUD)$$

whose coefficients and standard errors are given in Table 3A.

MODELLING WITH PURELY ENVIRONMENTAL VARIABLES

Except for the distance from Pyrenees, the sea area in each grid cell, annual temperature variation and annual precipitation variation, all the remaining environmental variables were significant ($P \leq 0.01$) when tested separately after subtracting their spatial component (Table 4). The variables that have the greatest effect on deviance are: the quadratic function of maximum elevation (29.4% of the deviance), altitude range (26.0% of the deviance), the quadratic function of mean elevation (18.8% of the deviance), the quadratic function of total summer precipitation (16.0% of the deviance), the quadratic function of annual mean temperature (15.2% of the deviance), the quadratic function of minimum mean temperature (14.6% of the deviance), and the land use diversity (14.6% of the deviance) (Table 4). The quadratic function of maximum elevation accounted for the most important

Table 2. Summary of the stepwise forward selection of variables to build the models for the species number of vascular plants in the Iberian 50 km UTM cells. Variable codes as per Table 1. (A) With all variables listed in Table 1 except spatial variables. (B) With all variables listed in Table 1. (C) With all variables listed in Table 1 except environmental diversity variables. The change in deviance after including a term in the model has been tested by an *F*-ratio test with a probability of less than 0.01

Model	Deviance	df	Change in deviance	<i>F</i>	%
(A)					
Full	11299.49	253			
Step 1					
AR	5832.21	252	5467.28	236.23***	48.4
Step 2					
Dp	5486.50	251	345.71	15.82***	51.4
+Dp ²	5101.28	250	385.22	18.88***	54.8
Step 3					
Cr	4805.33	249	295.96	15.34***	57.5
Step 4					
E	4803.12	248	2.21	0.11	57.5
+E ²	4792.16	247	10.96	0.56	57.6
+E ³	4532.75	246	259.41	14.08***	59.9
Step 5					
A	4532.17	245	0.58	0.03	59.9
+A ²	4342.21	244	189.96	10.67**	61.6
Step 6					
LUD	4182.71	243	159.50	9.27**	63.0
Step 7					
E × Ar	3971.45	242	211.26	12.87***	64.9
(B)					
Full	11299.49	253			
Step 1					
AR	5832.21	252	5467.28	236.23***	48.4
Step 2					
LAT	5798.94	251	33.27	1.44	48.7
+LAT ²	5796.79	250	2.16	0.09	48.7
+LAT ³	5231.95	249	564.83	26.88***	53.7
Step 3					
Ar	4762.44	248	469.52	24.45***	57.9
Step 4					
E	4717.50	247	44.94	2.35	58.3
+E ²	4611.94	246	105.56	5.63*	59.2
+E ³	4397.52	245	214.42	11.95**	61.1
Step 5					
LUD	4215.56	244	181.96	10.53**	62.7
Step 6					
t	4186.96	243	28.60	1.66	62.9
+t ²	3907.23	242	279.73	17.33***	65.4
Step 7					
Ps	3810.84	241	96.39	6.10**	66.3
-E	3812.59	242	1.75	0.11	66.3
Step 8					
Ds × Dp	3604.32	241	208.27	13.93***	68.1
Step 9					
LON × T	3400.86	240	203.46	14.36***	69.9
Step 10					
F × LUD	3229.85	239	171.02	12.65***	71.4
-t	3232.07	240	2.23	0.17	71.4

continued

Table 2—continued

Model	Deviance	df	Change in deviance	<i>F</i>	%
(C)					
Full	11299.49	253			
Step 1					
E	6612.91	252	4686.58	178.59***	41.5
+E ²	6459.64	251	153.27	5.96*	42.8
+E ³	6090.64	250	369.00	15.15***	46.1
Step 2					
em	5580.26	249	510.38	22.77***	50.6
+em ²	5358.99	248	221.27	10.24**	52.6
Step 3					
LAT	5301.80	247	57.19	2.67	53.1
+LAT ²	5210.56	246	91.24	4.29*	53.9
+LAT ³	4814.87	245	395.69	20.14***	57.4
Step 4					
Cr	4302.42	244	512.45	29.06***	61.9
Step 5					
A	4271.42	243	31.01	1.76	62.2
+A ²	4132.15	242	139.26	8.16**	63.4
Step 6					
LON	3999.22	241	132.94	8.01**	64.6
Step 7					
t × S	3837.04	240	162.18	10.14***	66.0
Step 8					
Ds × Dp	3634.34	239	202.70	13.33***	67.8

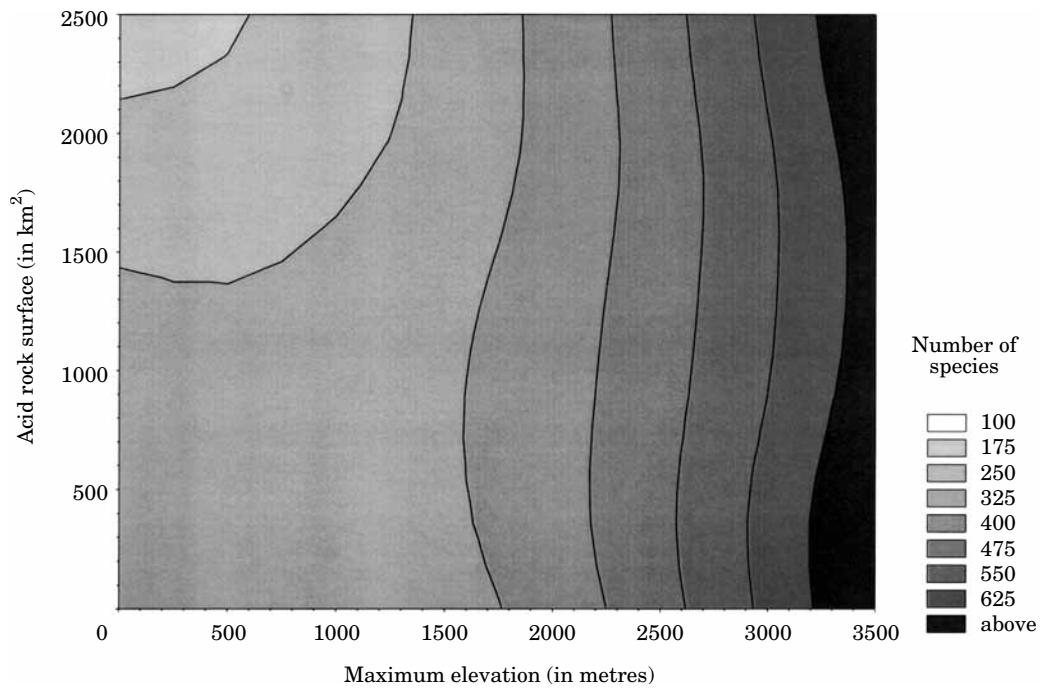


Figure 3. Contour plot of the total number of vascular plant species per 50 km UTM cell in the space delimited by the scores of maximum elevation and acid rock surface.

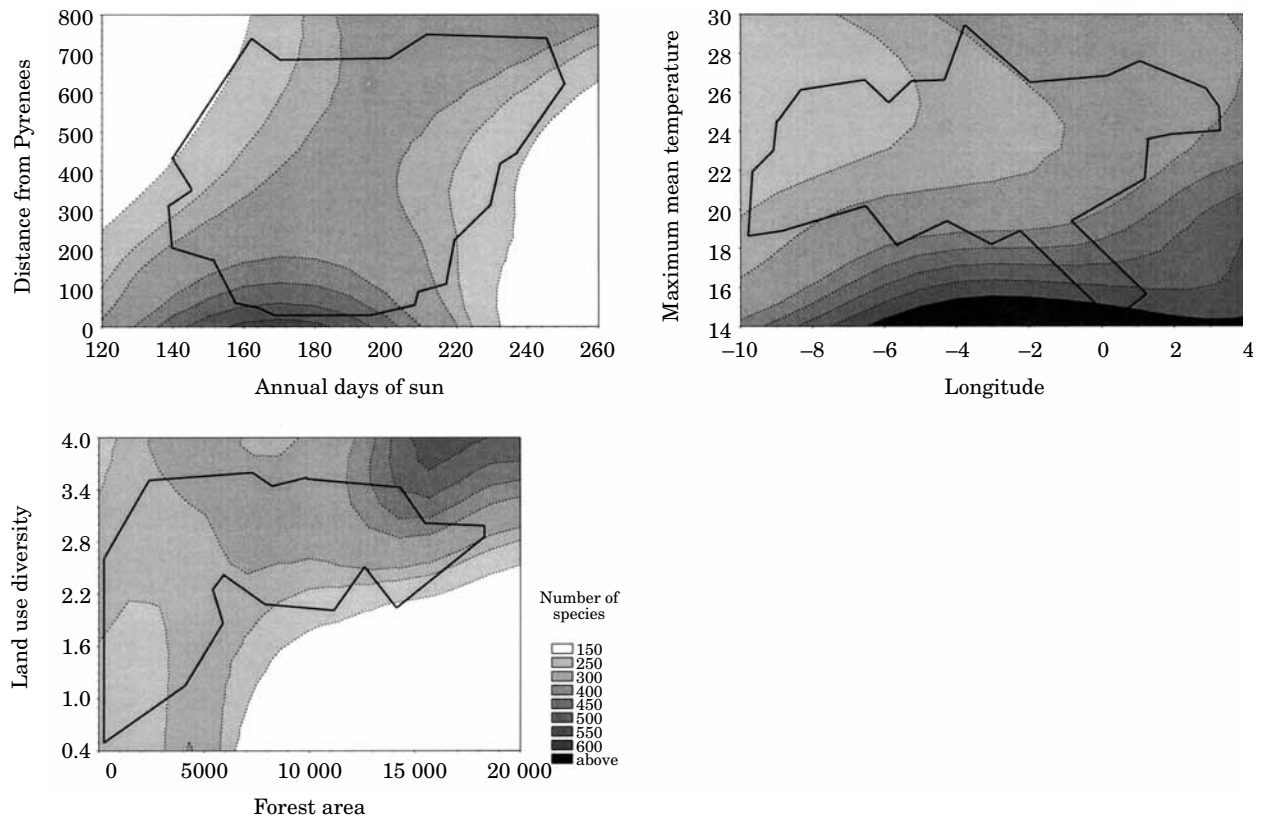


Figure 4. Contour plots of the total number of Iberian vascular plants per 50 km UTM cell in the space delimited by the scores of three pairs of variables. These pairs of variables form the significant interaction terms in the model with the environmental and spatial variables (Table 2B). Regions outside the solid line represent unsampled combinations of variables.

Table 3. Coefficients and standard errors for the parameters of the final model for the Iberian species richness of vascular plants. (A) Considering all the predictor variables listed in Table 1. (B) Considering the predictor variables after their spatial component is subtracted. *c* is the intercept

A			B		
Predictor variables	Coefficient	Standard error	Predictor variables	Coefficient	Standard error
<i>c</i>	5.5340	0.0082	<i>c</i>	5.5769	0.0065
AR	0.2271	0.0061	E	0.2087	0.0099
LAT	0.0998	0.0048	E ²	0.0524	0.0049
LAT ²	-0.0056	0.0014	Ar	-0.1037	0.0062
LAT ³	-0.0118	0.0006	Ar ²	-0.1133	0.0071
Ar	-0.0734	0.0042	LUD	0.1414	0.0057
E ²	0.0458	0.0044	em	-0.0871	0.0099
E ³	-0.0223	0.0017	em ²	0.0760	0.0046
LUD	0.0587	0.0056	A	0.1369	0.0193
t ²	0.0645	0.0040	A ²	0.4473	0.0282
Ps	0.0524	0.0052	A ³	-0.3581	0.0273
Ds × Dp	0.0846	0.0044	Ds	-0.2206	0.0136
LON × T	0.0226	0.0012	Ps	-0.0370	0.0063
F × LUD	0.0654	0.0050	Ps ²	0.0397	0.0034

Table 4. Explanatory variables considered in the 50 km UTM cells of the Iberian peninsula, deviance and change in deviance from a full model for the total number of vascular plant species. In these models the predictor variables are used after their spatial component is subtracted. Each explanatory variable has been regressed with the nine terms of the third degree polynomial equation of latitude and longitude, eliminating non-significant terms by means of a backward stepwise procedure. The linear, quadratic or cubic functions of each variable have been selected if they account for a statistically significant change in the deviance with a probability of less than 0.01. The sign column corresponds to the sign for each term of each function. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

Model	Selected terms	Deviance	df	Change in deviance	F	Sign
Full		11299.49	253			
Sea area in grid square	A	11096.42	252	203.07	4.61*	–
	A + A ²	10708.03	251	591.46	13.86***	– +
	A + A ² + A ³	10403.54	250	895.95	21.53***	– + –
Distance from Pyrenees	Dp	11297.92	252	1.57	0.04	–
Minimum elevation	e	11251.57	252	47.91	1.07	+
	e + e ²	10374.17	251	925.32	22.39***	+ +
Maximum elevation	E	8547.71	252	2751.78	81.13***	+
	E + E ²	7980.49	251	3319.00	104.39***	+ +
Mean elevation	em	9909.62	252	1389.87	35.34***	+
	em + em ²	9173.34	251	2126.15	58.18***	+ +
Calcareous rock surface	Cr	10732.09	252	567.40	13.32***	+
Acid rock surface	Ar	11258.62	252	40.87	0.91	+
	Ar + Ar ²	10795.70	251	503.79	11.71***	+ –
Minimum mean temperature	t	10301.91	252	997.58	24.40***	–
	t + t ²	9650.81	251	1648.68	42.88***	– +
Maximum mean temperature	T	10731.20	252	568.29	13.35***	–
	T + T ²	9897.76	251	1401.73	35.55***	– +
Annual mean temperature	tm	10329.57	252	969.92	23.66***	–
	tm + tm ²	9585.31	251	1714.18	44.89***	– +
Total annual precipitation	P	10813.55	252	485.94	11.32***	+
Total summer precipitation	Ps	10218.03	252	1081.46	26.67***	+
	Ps + Ps ²	9495.51	251	1803.98	47.69***	+ +
Annual days of sun	Ds	11047.41	252	252.08	5.75*	–
Cultivated and urban area	U	10573.52	252	725.97	17.30***	–
Forest area	F	10279.06	252	1020.43	25.02***	+
Scrub area	S	10978.65	252	320.84	7.36**	+
	S + S ²	10613.32	251	686.17	16.23***	+ –
Grassland area	G	10557.21	252	742.28	17.72***	+
Altitude range	AR	8362.97	252	2936.52	88.49***	+
Annual temperature variation	TV	11221.79	252	77.70	1.74	+
Annual precipitation variation	PV	11240.60	252	58.88	1.32	+
Land use diversity	LUD	9653.73	252	1645.76	42.96***	+
Geologic diversity	GD	10777.45	252	522.04	12.21***	+

change in deviance and was first included in the model (Table 5A). The variables that subsequently entered in the model were acid rock surface, land use diversity, mean elevation, sea area, annual days of sun, and total summer precipitation. The explained deviance of this model (51.4%) should not be considered the variation accounted for non-spatially structured environmental variables (R_{PE}), because this stepwise procedure has not been accomplished using only the significant

environmental variables of the stepwise model accomplished with all the environmental and spatial variables. So, both procedures yield different subsets of significant variables. Thus, the final model was:

$$S = \exp(c + E + E^2 + Ar + Ar^2 + LUD + em + em^2 + A + A^2 + A^3 + Ds + Ps + Ps^2)$$

whose coefficients and standard errors are given in Table 3B.

Table 5. Summary of the stepwise forward selection of variables to build the models for the species number of vascular plants in the Iberian 50 km UTM cells. Variable codes as per Table 1. In these models the predictor variables are used after their spatial component is subtracted (see Table 3). (A) With all environmental variables listed in Table 1. (B) With all environmental variables listed in Table 1 except environmental diversity variables. The change in deviance after including a term in the model has been tested by an *F*-ratio test with a probability of less than 0.01

Model	Deviance	df	Change in deviance	<i>F</i>	%
(A)					
Full	11299.49	253			
Step 1					
E	8547.71	252	2751.78	81.13***	24.3
+E ²	7980.49	251	567.22	16.72***	29.4
Step 2					
Ar	7866.56	250	113.94	3.58*	30.4
+Ar ²	7380.98	249	485.58	15.43***	34.7
Step 3					
LUD	6734.72	248	646.26	21.80***	40.4
Step 4					
em	6720.37	247	14.34	0.53	40.5
+em ²	6169.83	246	550.55	20.23***	45.4
Step 5					
A	6154.56	245	15.27	0.61	45.5
+A ²	6082.60	244	71.95	2.86	46.2
+A ³	5841.70	243	240.90	9.66**	48.3
Step 6					
Ds	5627.37	242	214.33	8.92**	50.2
Step 7					
Ps	5625.68	241	1.69	0.07	50.2
+Ps ²	5475.48	240	150.21	6.43*	51.4
(B)					
Full	11299.49	253			
Step 1					
E	8547.71	252	2751.78	81.13***	24.3
+E ²	7980.49	251	567.22	16.72***	29.4
Step 2					
Ar	7866.56	250	113.94	3.58*	30.4
+Ar ²	7380.98	249	485.58	15.43***	34.7
Step 3					
em	7301.89	248	79.08	2.67	35.4
+em ²	6865.56	247	436.33	14.82***	39.2
Step 4					
A	6788.24	246	77.33	2.78	39.9
+A ²	6680.10	245	108.14	3.92*	40.9
+A ³	6472.52	244	207.58	7.61**	42.7
Step 5					
Cr	6223.49	243	249.03	9.39**	44.9
Step 6					
S	6156.42	242	67.07	2.62	45.5
+S ²	6044.85	241	111.57	4.39*	46.5
-A	3048.39	242	3.54	0.14	46.5

THE ROLE OF ENVIRONMENTAL DIVERSITY VARIABLES

The model with all the spatial and environmental variables explains 71.4% of the deviance in species richness (Table 2B). However, if the five environmental diversity variables are ignored, the model explains slightly less (67.8% of the deviance). The final model without the environmental diversity variables includes two interaction terms and was (Table 2C):

$$S = \exp(c + E + E^2 + E^3 + em + em^2 + LAT + LAT^2 + LAT^3 + Cr + A + A^2 + LON + t \times S + Ds \times Dp)$$

The final model using environmental variables after their spatial component was subtracted (Table 5A) explains 51.4% of the deviance. Again, ignoring environmental diversity variables slightly reduces the percentage of explained deviance (46.5%). In this case the final model was (Table 5B):

$$S = \exp(c + E + E^2 + Ar + Ar^2 + em + em^2 + A^2 + A^3 + Cr + S + S^2)$$

No especially aberrant features occur in the residuals plots of anyone of the accomplished models.

VARIATION PARTITIONING

The amount of deviance explained by the statistically significant environmental and spatial variables is high (71.4%; Table 2B). The spatial variation in species richness that is not shared by environmental variables (R_{PS}) is very low (6.5%), while the spatially structured environmental variation in richness (R_{SE}) is 28.4%. The greater fraction of the variability (36.5%) in the number of species is accounted for non-spatially structured environmental variables (R_{PE}).

DISCUSSION

Although an extra number of taxa has been used, the diversity patterns of Iberian and Balearic vascular flora detected mainly coincide with those previously found by Castro Parga *et al.* (1996) and Humphries *et al.* (1999). These patterns may reflect not only ecological, historical and land-use factors but also current knowledge of Iberian plant distribution. Perhaps future data will change the results shown in Figure 2, but these changes should be minor, occurring only after a significant quantum leap in regional distribution knowledge.

The use of 50 × 50 km cells facilitates the analysis of distribution patterns on a regional or large scale (*sensu* Heikkinen & Birks, 1996), helping to discern the evolutionary species' environmental constraints that limit species distribution (Hengeveld, 1990; Wiens

et al., 1986). Studies on such a scale have found environmental and historical background reflected in geographical distributions (e.g. Myklestad & Birks, 1993; Birks, 1996; Márquez *et al.*, 1997; Wohlgemuth, 1998). At present, Iberian Peninsula data availability does not warrant the use of a finer scale for distribution maps (see Castro Parga *et al.*, 1996 for gaps in the 10 km reticule), nor for ecological variables. Even so, Castro Parga *et al.* (1996) found that greatest plant richness correlated with maximum altitudes in 10 km grid cells.

According to the analysis carried out herein, the variation in the Iberian plant species number accounted for by the environmental variables considered on this large scale is reasonably high (around 65%; $R_{PE} + R_{SE}$). This figure fits well with the mean range of variation from previous studies (68%, $n = 13$, maximum = 94%, minimum = 21%, SD = 22%; see Wohlgemuth, 1998), in spite of scale and methodological differences. Considering that the higher percentages of explained variation correspond to studies of larger spatial extent, smaller number of mapping areas or islands (see Wohlgemuth, 1998), we can consider that our Iberian Peninsula model accounts for a considerable proportion of species richness variability. Evidently, some variables not taken into account could be highly explanatory, while other unobserved variables may be correlated with the variables considered, leading to false causal relationships. Furthermore, finding no effect of some variable can mean that on the scale investigated its effect is uniform and cannot be discerned (Hengeveld, 1990).

THE IMPORTANCE OF ALTITUDE VARIABLES

The most significant variables are those related with altitude (altitude range and maximum elevation). Though both variables are correlated ($r = 0.876$; $P < 0.001$), the altitude range is clearly related with the environmental heterogeneity while maximum altitude is a variable related to the existence of high mountain zones. The linear relationship of altitude range with the number of plant species reflects the gradual increase in the species richness with the increase in the altitude range (or environmental heterogeneity) of each cell (Fig. 5A). However, the cubic response of maximum altitude reflects the occurrence of the highest number of species at cells with the highest maximum altitude (higher than 2000 m) (Fig. 5B). Although both altitude variables account for similar scores of change in the deviance (more than two times greater than those of any other environmental variable – 48.4% of the deviance for the altitude range and 46.1% for the cubic function of maximum altitude), the maximum altitude seems of higher causal importance because: (i) variables associated with environmental heterogeneity are

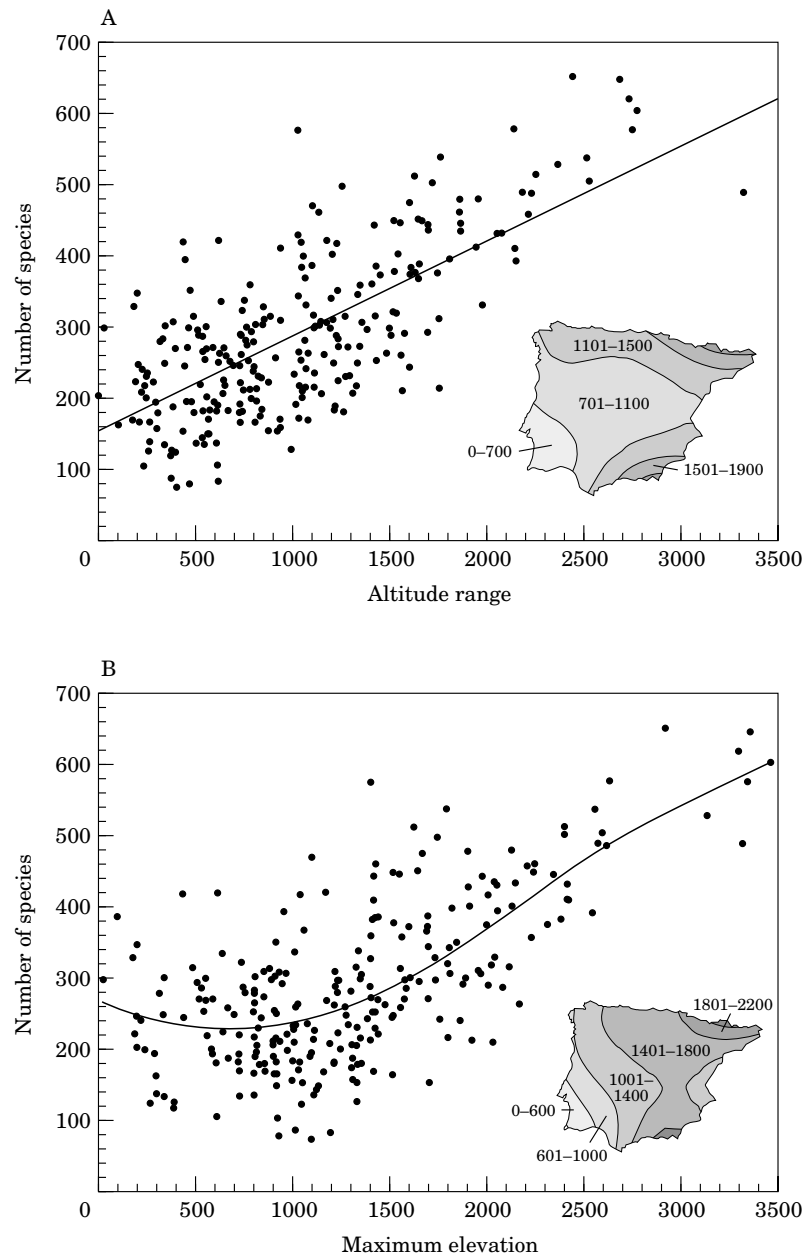


Figure 5. Scatter plots of the total number of Iberian vascular plants recorded against the altitude range (A) and maximum elevation (B) in the 50 km UTM cells. Solid lines are the fitted values derived from the linear and cubic functions of both variables and contour maps represent the Iberian distribution of the altitude range and maximum elevation, respectively.

considered of secondary importance and generally do not exert an influence by themselves (Austin, 1980; Austin *et al.*, 1996); (ii) the incorporation of altitude range produces a final model only slightly more explicative (Table 2); (iii) when altitude range becomes the most explicative variable, maximum elevation continues to be significant, though less important (Table

2B); and (iv) when the spatial structure of variables is removed maximum elevation becomes the most important variable and altitude range does not enter in the model (Table 5), indicating that maximum elevation is also important at a small scale.

When environmental variable spatial structure is eliminated, or when environmental diversity variables

are not included, the quadratic function of mean elevation also appears as a significant variable (see Tables 2C and 5). However, the sign of the first term in the quadratic function is always negative (see Table 3) showing that, when maximum elevation has already been considered, more species also occur at lower mean altitudes. Thus, mean elevation adds a complex ingredient to the generally positive correlation between altitude and species richness: the high altitude cells are characterized by a considerably greater number of species, but lower mean altitude coastal cells also account for an increase in species richness. This pattern could reflect the existence of two different groups of Iberian vascular plants with different environmental tolerances.

THE EFFECT OF MAXIMUM ELEVATION ON SPECIES RICHNESS

That the Mediterranean (unlike the Arctic) mountain *s.l.* does not limit plant richness reinforces the need to examine every pattern in its context. The importance of maximum elevation supports authors who have highlighted Iberian and Balearic mountain ranges as diversity hotspots for different organism groups (Jay-Robert, Lobo & Lumaret, 1997; Médail & Quézel, 1997; Moreno Saiz *et al.*, 1996; Myklestad & Birks, 1993). Species composition and richness of these areas has been related to the traditional Mediterranean land use of ecosystems and their ancient anthropogenic disturbance (Bernáldez, 1981), where lowlands were exploited and the higher slopes were left mainly for cattle raising, thus conserving their more natural state.

Previous studies coincide in that altitude affects diversity, many finding a richness decrease with elevation or an increase in the species richness at intermediate altitudes (i.e. Brown, 1988; McCoy, 1990; Gaston & Williams, 1996; Heikkinen, 1996; Heikkinen & Neuvonen, 1997). Heikkinen and Neuvonen, in their study of a Finnish area, found more plant species at lower altitudes suggesting that altitude can be positively correlated with energy-related variables, essential predictors of the variation in species richness (Currie & Paquin, 1987; Currie, 1991). In fact, mountains of northern latitudes limit productivity (seasonal persistence of permafrost, infrequent sunny days, etc.) to a much greater extent than do temperate zone mountains. The low importance of climatic variables suggests that, at least at present, energy-related variables are not decisive in the plant species richness distribution across the Iberian Peninsula. In the Mediterranean, highest temperatures coincide with lowest rainfall, resulting in decreased or no productivity especially in the lowlands. Rain and humidity persist for longer in higher areas, where the period of drought and hydric stress decreases from months to even days.

Thus, unlike in northern Europe, Iberian Peninsula mountain area relevance perhaps indicates that productivity-related variables can limit species richness at lower altitudes.

The high species diversity of Mediterranean mountain chains may also be due to their role as refuge and 'engine' for speciation and vicariance during Pleistocene contraction/expansion cycles (Bennett, Tzedakis & Willis, 1991; Hewitt, 1996; Taberlet *et al.*, 1998). In southern Europe, more isolated higher altitudes currently support a degree of endemism and coexistence of different evolutionary lineages higher than that of northern Europe (Dennis, Williams & Shreeve, 1998; Myklestad & Birks, 1993). As in other regions (White & Miller, 1988), maximum levels of endemism occur in the upper peaks within Iberia and the Balearics (Moreno Saiz & Sainz Ollero, 1992). Depending on the degree of isolation and orientation of the mountain ranges, high altitude biomes can provide suitable conditions for speciation and refuge for elements originating from lineages distributed at higher latitudes. When this happens at increasing altitudes, mountain elements can clearly be substituted by taxa with different evolutionary histories, and the species richness altitude reduction gradient is attenuated (Lobo & Halffter, 2000; White & Miller, 1988). Nevertheless, as Birks (1996) pointed out, historical and present day ecological variables have to be considered together before assigning historical determinant weight to contemporary distribution patterns.

Finally, it is necessary to compensate for the contribution to the effect of maximum elevation on plant species richness due to the environmental heterogeneity associated with altitude range. As smaller altitude ranges occur in those cells with maximum altitudes of about 1000 m (central plateau of the Iberian Peninsula) and there are no UTM cells with high mountains and small altitude ranges, the effect of maximum elevation on plant species richness may be partially explained by the greater heterogeneity of high altitude environments.

OTHER SIGNIFICANT VARIABLES

The two geographical variables considered (distance from Pyrenees and sea area surface) are also significant Iberian plant species richness explanatory variables. The distance from the Pyrenees has been considered an important variable in explaining the Iberian distribution of some lepidopteran groups (Martín & Gurrea, 1990) that would have entered in recent geological times from northern latitudes. In our case, distance from Pyrenees is only significant when spatial variables are not taken into account or when the spatial structure of the variables has not been subtracted (Table 2A). However, the distance from the Pyrenees

can be expressed very well considering spatial variables. A third degree polynomial of latitude and longitude accounts for 98.41% of the variation in distance from Pyrenees, and the cubic functions of latitude and longitude together explain 88.36% of distance from Pyrenees variation. The response of plant species richness to distance from Pyrenees is quadratic or parabolic, with the maximum number of species at the greatest and smallest distances, a very similar response to that of latitude. Therefore, when the cubic function of latitude is included in the model (see Table 2B,C) the effect of distance from the Pyrenees disappears, showing that it is in reality the consequence of: (i) some ignored spatially structured environmental variables, or (ii) the spatial structure of the variables examined. As the variation explained by the purely spatial variables is very low (6.6%) distance from the Pyrenees hardly explains Iberian plant species richness. The drawback to considering distance from the Pyrenees as an environmental, not spatial, variable is that the real explanatory capacity of the spatially structured environmental variables would then be smaller (Table 2A). However, a fresh analysis using all the environmental variables (Table 1) except distance from the Pyrenees produces a similar predictive model (63.7% of the deviance). Hence, the variation explained by purely spatial variables increase slightly if distance from the Pyrenees is considered a spatial variable (around 8%).

The quadratic or cubic function of UTM cell sea area is one of the significant variables selected in the models (see Tables 2 and 5). The curvilinear response of this variable reflects the fact that, although the minimum number of species can be found both in high and low sea area UTM cells, high sea area cells (i.e. low land surface cells) always contain few species.

Once the variation of altitude and spatial variables has been included, the bedrock geology variables (calcareous rock and acid rock) accounted for the most important change in deviance. When the spatial structure of both variables is not removed a linear response is found (see Table 2): higher plant species numbers occur in cells with larger calcareous or smaller siliceous surfaces (Fig. 6A,B). A general pattern of lower plant richness in the western half of Iberia, where acid rocks predominate, emerges from Figures 2 and 6D. A quite homogeneous and slightly diversified flora inhabits western Iberian older and more uniform relief with permeable or even open flora boundaries (Hernández Bermejo & Sainz Ollero, 1984). Relative poverty in acidic areas has also been found in Switzerland and Finland (Heikkinen & Neuvonen, 1997; Wohlgemuth, 1998), suggesting that alkaline soils with more soluble compounds favour competitively chemically limited weak species and taxa resistant to drought. The significant interaction between acid rocks and maximum

elevation (Table 2A and Fig. 3) would indicate that the poverty of siliceous soils would be still greater in the coastal zones. However, when environmental variable spatial structure is removed, the quadratic function of acid rock surfaces is the most important variable after the maximum altitude (see Table 5). Calcareous as well as siliceous soils are clearly spatially autocorrelated in the Iberian Peninsula (Fig. 6D), therefore it is unexpected that some of these variables will be significant in explaining plant species richness when their spatial structure is eliminated. The curvilinear response of the non-spatially structured acid rocks means that the highest number of species occurs at intermediate siliceous rock contents in UTM cells. As the predicted species richness values by the quadratic function of acid rocks shows (Fig. 6C), the UTM cells with higher species number are those which are located in the eastern calcareous half but with siliceous soil content. In other words, the acidic cells near or in 'basic Iberia' are especially important in terms of diversity. Other authors (Ojeda, Arroyo & Marañón, 1995) have recently pointed out that edaphically isolated acid soils within the basic soil area of southern Spain could have promoted the speciation and endemism of plants.

Plant species richness in the Iberian Peninsula also has a linear and positive relationship with the land use diversity of UTM cells. More species occur in cells with different land cover characteristics. This is a significant predictor variable of plant species richness, regardless of environmental variable spatial structure. The possible interaction between land use diversity and forest surface (Fig. 4) indicates that a higher number of species would appear when UTM cells have both a high land cover heterogeneity and a large forest surface. As forest areas currently harbour more diverse assemblages of species (Margalef, 1974; Scheiner & Rey-Benayas, 1994), a greater contribution of forests to plant species richness should be expected. However: (i) many natural and semi-natural woodlands in Iberia are located in mountain chains, so much of its weight could be absorbed by variables related to altitude; and (ii) areas reforested with species of *Pinus* and *Eucalyptus*, quite common in Iberia, impoverish rather than enrich (Bernáldez, 1991).

The energy-related climatic variables contributed little to the variation of species richness. Minimum and maximum mean temperature, total summer precipitation and annual days of sun are the only significant climatic variables in the models, but their contribution is always marginal. Minimum mean temperature yields a quadratic and positive response (Table 2B), reflecting the occurrence of maximum number of species at the highest minimum temperatures. Maximum temperature only contributes as a part of the interaction with longitude (Table 2B), indicating

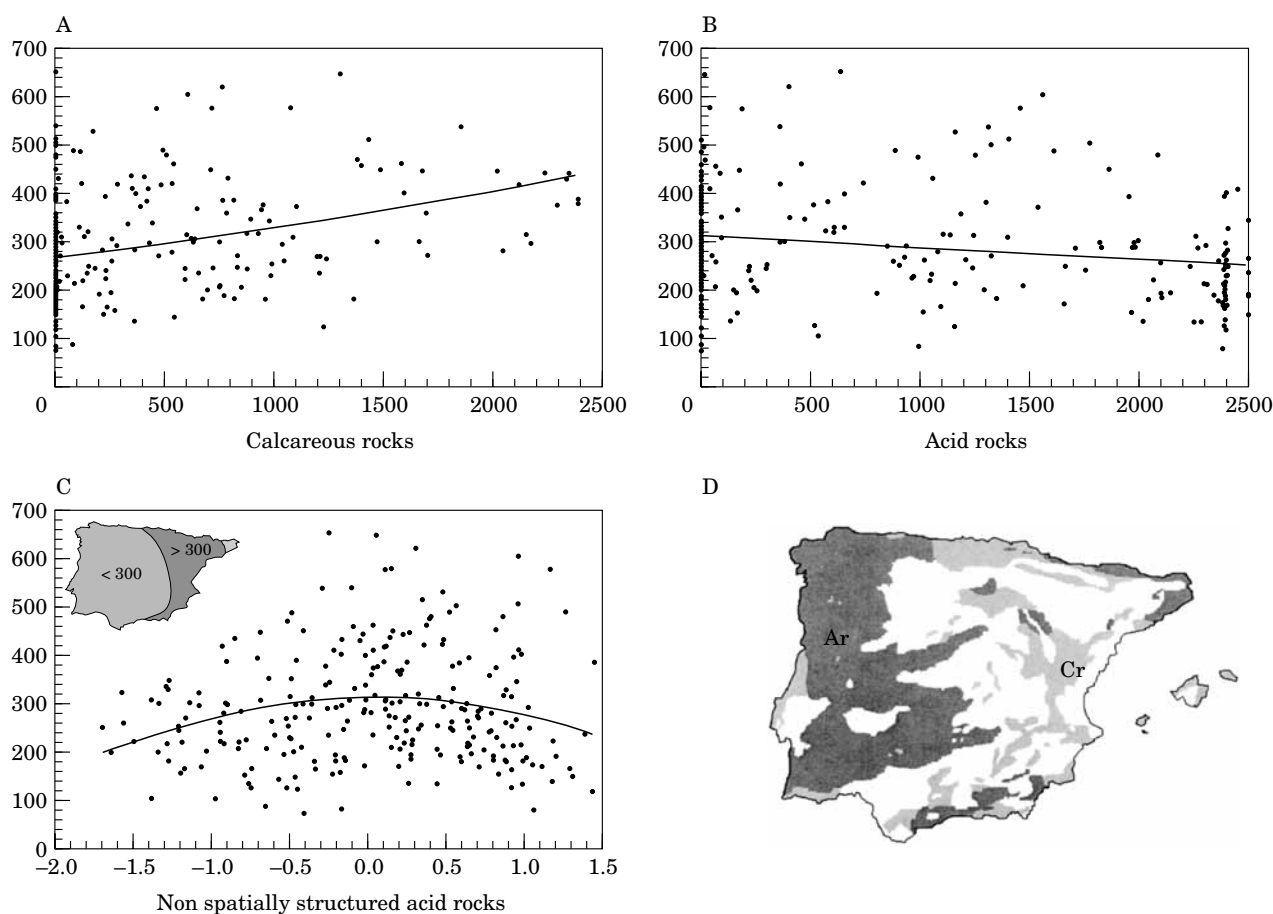


Figure 6. Number of Iberian vascular species in 50 km UTM cells as a function of calcareous rock surface (A), acid rock surface (B), and non-spatially structured acid rock surface (C). Broad scale spatial structure of acid rock surface is eliminated by a Trend Surface Analysis retaining the residuals as a measure of the explanatory power of acid rocks regardless of their spatial structure. The contour map in C represents the geographic variation of the predicted richness (more than 300 species and less than 300 species) according to this function. (D) Iberian distribution of calcareous soils (Cr; light grey) and siliceous soils (Ar; dark grey). Solid lines are the fitted functions.

that eastern UTM cells with lower maximum temperatures contain more species (Fig. 4). Summer precipitation is positively related with the number of plant species, in models with and without spatially structured variables (Tables 2 and 5). Using spatially structured variables, the response to the number of sunny days depends on distance from the Pyrenees, with the maximum number of species at an intermediate number of sunny days ($\cong 180$) and near the Pyrenees (Fig. 4). Finally, with non-spatially structured variables the response to sunny days is linear and negative: few species in UTM cells with many sunny days (the south-eastern coast and the south-western Iberian quadrant). As daylight availability is not productivity limiting in Mediterranean environments, extreme insolation probably reduces productivity due to the negative effect of hydric stress on plant species richness. As commented previously, productivity-related variables could be limiting plant

species richness in low altitude areas. The effect of climatic variables reflects generally moderate conditions in the richest Iberian UTM cells: infrequent summer droughts together with moderate minimum and maximum temperatures as well as intermediate radiance levels.

WHICH FACTORS EXPLAIN IBERIAN PLANT SPECIES RICHNESS?

Causative factors are always difficult to discover unless confirmed by a more direct approach (Legendre & Legendre, 1998). However, topography (primarily), geology and environmental heterogeneity and, less relevantly, climate, are the most important types of variables when looking at Iberian plant richness variation on this scale. Other variables, such as the abundance of watercourses, seem to be important determinants of plant species richness at local or

regional scale (Heikkinen, 1996) but their relevance has not been studied here.

Some studies concerning plants or Iberian Lepidoptera (Martín & Gurrea, 1990; Myklestad & Birks, 1993) reveal an important spatial variable role, while others indicate that there are no Iberian latitudinal trends in the species number of reptiles and amphibians (Busack & Jaksić, 1982; Schall & Pianka, 1977). In our case, the purely spatial component explains a very small fraction of the variation in the number of Iberian plants (between 6 and 8%). This value is at the lower limit of the range of plant species richness explained by purely spatial variation in other studies (between 6 and 19%; see Heikkinen & Birks, 1996), and that is why we believe that the main explanatory variables have been considered in our models. In fact, spatial variables account for a significant percentage of the explained variation when important environmental, historical or biotic variables are ignored in the model (Legendre & Legendre, 1998). To discern the effect of spatial variables with precision, the spatially structured component of the environmental variables must be removed. The inclusion of spatially related variables at the beginning of the regression analysis together with environmental variables can lead to erroneous results, because species richness and environmental variables frequently share a similar spatial structure, which accounts for part of the variation captured by environmental variables.

The positive relationship between species richness and spatial heterogeneity is well documented, so the more heterogeneous a spatial unit the more species could co-exist in it. Plant species richness, according to some (see Wohlgemuth, 1998 and references therein), is highly dependent on heterogeneity variables. However, their importance in explaining species richness patterns is increasingly questioned (Davidowitz & Rosenzweig, 1998; Rosenzweig, 1995) and the interpretation of the correlation could also be in the opposite sense: the more species there are the more finely they subdivide the space into different habitats. In the case of this study, the effect of environmental heterogeneity would be greater depending on the amount of richness variation accounted for by maximum elevation associated with environmental heterogeneity. A partial regression analysis with maximum elevation and altitude range showed that most of the species richness variation accounted for by these variables is due to their combined effect (83%), being very similar. However, we suspect that the importance of heterogeneity-related variables in explaining current Iberian richness patterns is not high. Altitude range and land use diversity, the two main heterogeneity variables positively related with plant species richness, when added to the model (Tables 2 and 5) do not greatly

alter the predictive power of the models (3.6–5%, depending on whether the spatial component of the environmental variables is subtracted). Heikkinen and Neuvonen have found similar results in Finland (1997). This fact demonstrates the need to explain the richness variability employing indirect or complex variables (*sensu* Whittaker, 1967) only after preliminarily testing the role of comparatively more simple environmental variables (Currie & Paquin, 1987; Cowling & Samways, 1995; Austin *et al.*, 1996; Böhning-Gaese, 1997).

Although the search for a unique, simple primary determinant of observed richness gradient can be simplistic, productivity or climate related variables, more directly related to plant physiological mechanisms (see Saetersdal, Birks & Peglar, 1998), have frequently been found to be the main explanatory variables of plant species richness on larger scales (Richerson & Lum, 1980; Currie & Paquin, 1987; Currie, 1991; Linder, 1991; Myklestad & Birks, 1993; Wright, Currie & Maurer, 1993; Dzwonko & Kornas, 1994; Birks, 1996; O'Brien, Whittaker & Field, 1998; Wohlgemuth, 1998). On the contrary, climate and productivity-related variables do not seem very relevant in explaining Iberian plant species richness. In our opinion, this shows that energy availability does not greatly determine current plant species number in the Iberian Peninsula. Climate related variables more probably appear when individual species or homogeneous groups with few species are considered (Myklestad & Birks, 1993; Dzwonko & Kornas, 1994; Austin *et al.*, 1996; Birks, 1996; Wohlgemuth, 1998). Even more important than climate, the type of soil and, therefore, available nutrients could determine the coexistence of a greater number of plant species in the Iberian Peninsula. As has been found in other European studies (Heikkinen & Neuvonen, 1997; Wohlgemuth, 1998), basic soils breed a greater number of plant species than acid soils, above all if siliceous islands exist within the basic territory.

Probably, the most important variables are related with topography, concretely with the maximum elevation. Although the regional coexistence of species is explained by different types of factors, the high predictive power of maximum elevation confers greater weight to historical factors in the determination of Iberian plant species richness (see also White & Miller, 1988). Historical factors would act both on a large scale (refuge and endemism centres) as well as on a shorter-time scale (antropic modifications in the valleys during the last 5000 years). The relevance of land use diversity would also indicate the influence of historical factors. As the Iberian UTM cells with natural vegetation are not actually the richest in species, human disturbance would have promoted a larger number of species in cells with different land cover characteristics. Some

papers suggest that historical events may have disrupted diversity gradients across the Iberian Peninsula (Busack & Jaksic, 1982). Energy or productivity related variables are important in the delimitation of Iberian groups of species with similar distribution patterns (Marquez *et al.*, 1997; Real *et al.*, 1996) and, undoubtedly, productivity-related variables should affect regional distribution of Iberian plants. However, the prolonged and intensive exploitation by man and his livestock in this area has partially wiped out any trace of ancient richness distribution patterns, pointing to the weight of historical processes in the current species richness of Iberian vascular plants.

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