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Coarse-scale plant species richness in relation to environmental heterogeneity

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Abstract. We test to what extent mean environmental conditions and environmental heterogeneity are related to species richness in a regular geographical grid system (UTM) of 10 km × 10 km in the NE Iberian Peninsula (i.e. Catalonia, ca. 31 900 km^2). Species richness of each UTM quadrat was estimated by compiling a large database (more than a million records) from bibliographic references and atlases. Mean environmental conditions of each quadrat were derived from climatic maps. Environmental heterogeneity was estimated from the diversity of geological substrates and climatic classes in each quadrat. The increase in effective (real) area due to topographic complexity was also considered (derived from the digital elevation model). The statistical analysis was performed by a weighted analysis of deviance assuming a negative binomial error distribution. The results suggest that species richness in the study area is a function of both within-quadrat heterogeneity (specifically, effective area, heterogeneity of geological substrates, heterogeneity of January temperature) and mean environmental conditions (mean annual temperature, Thornthwaite moisture index and aspect). All these parameters showed a positive relationship with species richness. Quadrat heterogeneity accounted for ca. 2/3 of the explained deviance, suggesting the importance of environmental heterogeneity when using a geographical grid system. The study fits well with earlier results on the importance of climatic parameters on plant species richness and provides one of the few rigorous, quantitative, coarse-scale studies testing environmental heterogeneity in plant species richness.

Keywords: Diversity; Generalized linear modelling (GLM); Geographical grid system; Species-area relation.

Introduction

Understanding mesoscale (~ 10^{-3}-10^3 km^2) patterns of ecosystem properties is important if we are to effectively monitor, predict and protect our biota. The current threat to biodiversity calls for rapid, cost-efficient approaches (Margules & Redhead 1995; Balmford et al. 2000). Much of the data on species occurrence collected in different surveys and for different purposes can (easily) be compiled into spatially-explicit coarse-scale databases (i.e. geographically gridded systems) and used for needs outside the scope of individual studies. Recent technologies (remote sensing and GIS) provide ways to characterize coarse-scale terrain units. Because of the current threats to biodiversity, there is an increase in the building and analysing of databases on species richness (e.g. Currie & Paquin 1987; Turner et al. 1987; Currie 1991; Harrison et al. 1992; Kerr & Packer 1997; O'Brien et al. 1998; Kerr & Currie 1999). The combination of GIS, databases and advanced statistics is a powerful cost-efficient and comprehensive approach to the identification and prediction of biotically diverse landscapes, and it provides a valuable source of information for generating and testing ecological hypotheses.

Species richness is scale-dependent (Ricklefs 1987; Rosenzweig 1995; Mittelbach et al. 2001). At the local scale, it has been suggested that for an ecological understanding of the patterns of plant species occurrence and richness, close-to-primary parameters (i.e. parameters related to resource availability or parameters having a direct impact on plant growth or resource availability; see review by Pausas & Austin 2001) plus disturbance factors (review by Huston 1994) need to be considered. Gradient studies using these kinds of parameters are making significant contributions to our understanding of species ecology and their interactions (e.g., Austin et al. 1990, 1996; Leathwick 1998; Leathwick & Austin 2001). Indirect factors (parameters that in themselves have no impact on plants or resources availability but may be correlated with one or more primary parameters, e.g., altitude, latitude, distance from the coast) are used when primary parameters are not available (e.g. Glenn-Lewin 1977; Brown & Gipson 1983; Silvertown 1985; Currie 1991; Stevens 1989, 1992; Pausas & Sáez 2000). A few studies have also indicated that spatial heterogeneity may contribute to the control of local plant species richness (Harner & Harper 1976; Vivian-Smith 1997); most of these studies are mainly related to gap dynamics (Ricklefs 1977; Orians 1982; Brandani et al. 1988; Pausas 1994). The increase in heterogeneity implies an increase in niches, allowing more species to coexist. A second possible mechanism, however, is that some species might be favoured by relatively uniform or stable habitats whereas others might be favoured by heterogeneous habitats (Campbell et al. 1991; Grime 1994; Mout et al. 1997; Wilson 2000). As the size of the sites under study increases, within-site topographic complexity becomes an important determinant of plant species richness (Richerson & Lum 1980; Everson & Boucher 1998; O'Brien et al. 2000).

At the coarser scales (e.g. quadrats at a geographical scale), it has been hypothesized that intra-quadrat environmental heterogeneity may be a very important factor in determining species richness (Kerr & Packer 1997; Austin 1999; O'Brien et al. 2000; Pausas & Austin 2001; Rey Benayas & Scheiner 2002). Such quadrats do not represent points along a gradient, but rather a range of conditions; thus, they are likely to contain species not typically associated with the mean conditions of the quadrat (Palmer & Dixon 1990). Quadrats composed of heterogeneous abiotic conditions should provide a greater diversity of potential niches than do homogeneous quadrats. However, many studies analysing species richness in gridded geographical systems have not yet incorporated heterogeneity factors (e.g. Currie & Paquin 1987; Turner et al. 1987; Currie 1991; Harrison et al. 1992; Caley & Schluter 1997; O'Brien et al. 1998, 2000; Kerr & Currie 1999). The importance of these factors may increase with the grain of the sampling unit, and they may be very important in topographically complex or geomorphologically heterogeneous landscapes or when irregular grid systems are used (e.g., those based on latitude and longitude, or on geographical regions).

In the present work, our general hypothesis is that species richness at a coarse scale is a function of the area, the environment and the environmental heterogeneity. Thus, we ask to what extent heterogeneity of the terrain and of the environmental conditions is important in explaining species richness in a 10 km × 10 km grid system of the NE Iberian Peninsula. To test our hypothesis we compile a large amount of records on plant species occurrence in a regular grid system and obtain both the mean environmental values for each quadrat and the heterogeneity of these parameters within the quadrat. Then, we use advanced multiple regression techniques to build a statistical model for generating specific hypotheses on the possible relationships. Because our focus is on environment and environmental heterogeneity, the influences of other parameters (e.g., disturbances, land-use, human population, scale, competition) are not considered.

Methods

The study area

The study area comprises Catalonia (ca. 31 900 km^2), in the northeast of the Iberian Peninsula (Fig. 1); its altitude ranges from sea level to 3143 m (top of the Pica d'Estats). It is situated between ca. 0°15' E - 3°20' E and 40°30' N - 42°40' N. In the northern part of the area (the Pyrenees) the climate is mainly a temperate middle-European type with a cold climate in the higher mountain zones. In the remaining area the climate is typically Mediterranean, with a maritime tendency towards the coast (at the east) and a continental and sub-arid tendency inland (towards the west). This transition between temperate and Mediterranean climates makes the study area very interesting from a biogeographical and biodiversity point of view.

The basic spatial unit for the analysis is the Universal Transverse Mercator (UTM) 10 km × 10 km grid system (100 km^2 projected area). The area studied is composed of 315 such units (quadrats hereafter) included in UTM Zone 31T (DH, CH, BH, EG, DG, CG, BG, DF, CF, CE and BE). Some of the quadrats include the coastline, and so the projected area studied in these quadrats is smaller than 100 km^2. These quadrats were excluded from the analysis. Some quadrats at the border were also excluded if no information was available for

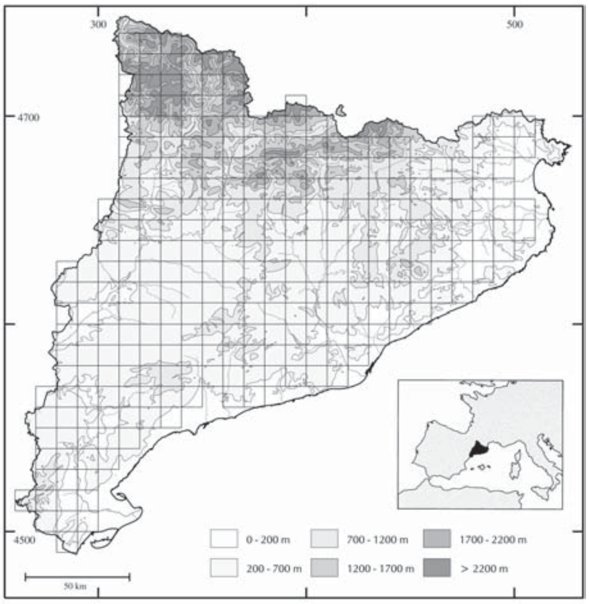

Fig. 1. Location of the study area (Catalonia) with topography (grey scale) and the UTM quadrats used in the first analysis ($n = 285$).

the whole quadrat area (mainly those on the northern border with France; information for many quadrats on the border with other Spanish regions was available). Thus, the total number of quadrats included was 285 (Fig. 1).

The UTM system was used because: (1) it was compatible with several chorologic atlases that include our study area (Jalas & Suominen 1972-1999; Salvo et al. 1984; Anon. 1985-2001; Sáez 1997); (2) it was an appropriate scale for locating most of the records from the literature in which an exact location was not recorded; (3) it is a regular grid system with a constant projected area.

Environmental and terrain parameters

From the topographic map of the study area (with altitude contour lines and rivers) we constructed a triangular irregular network (TIN). This network was then rasterized to 25 m × 25 m pixels (400 × 400 pixels in each quadrat), and from the altitude values of the pixels, we computed the minimum, maximum, mean and standard deviation of altitude for each quadrat (Table 1a, d). The close-to-real (effective) quadrat area (rather than the projected one) and the proportion of the effective area facing the four main directions (N, S, E, W; Table 1a) were also computed from the TIN.

Climatic information was obtained by overlaying climatic contour maps (non-sea-level corrected) of the area (Anon. 1996) on the UTM grid system. Average climatic values for each quadrat were computed as the mean of midpoint contour levels in the quadrat weighted by the area occupied by each level (Table 1b). The number of contour levels in each quadrat was used as an indicator of in-site quadrat heterogeneity (Table 1d). The precision of the climatic contour maps was 1 °C for temperature, 50 mm for total annual precipitation, 20 mm for summer precipitation, and 20 units for the Thornthwaite moisture index (Table 1b).

Bedrock type was obtained from a hydrogeologic map (Anon. 1992) of the study area. The original 39 bedrock types on the map were grouped into seven main

Table 1. List of predictor parameters tested, and the range of environmental conditions in the study area, for the 285 UTM quadrats used in the analysis.

Code	Min	Max	Mean	Units	Description
a) Topographic parameters (derived from TIN)					
Altmin	0.0	1634.2	332.4	m	Minimum altitude
Altmax	5.9	3017.0	1046.6	m	Maximum altitude
Altmean	2.5	2427.0	611.0	m	Average altitude
RArea	100.0	128.5	107.1	km^2	Real (effective) area
N	12.0	68.3	36.9	%	Proportion of the quadrat facing north (315°- 45°)
E	3.6	69.8	20.4	%	Proportion of the quadrat facing east (45°- 135°)
S	3.7	61.1	23.8	%	Proportion of the quadrat facing south (135°- 225°)
W	0.0	45.6	18.0	%	Proportion of the quadrat facing west (225° - 315°)
b) Climatic parameters (derived from climatic atlas)					
Pa	375.0	1203.5	684.3	mm	Total annual precipitation
Ta	4.5	17.5	12.7	°C	Mean annual temperature
Psum	60.8	382.5	160.3	°C	Summer (June, July, August) precipitation
Tjan	–3.3	10.5	4.5	°C	January temperature (daily mean)
Tjul	13.6	25.0	21.5	°C	July temperature (daily mean)
MI	–30.0	109.4	5.2		Thornthwaite moisture index
c) Substrate parameters					
Qua	0.0	100.0	25.0	%	Proportion of the quadrat on quaternary subtrate
Lim	0.0	91.7	15.0	%	Proportion of the quadrat on hard limestone
Mar	0.0	100.0	42.2	%	Proportion of the quadrat on marls
Con	0.0	29.7	1.2	%	Proportion of the quadrat on siliceous conglomerates
Sch	0.0	100.0	8.2	%	Proportion of the quadrat on siliceous schists
Gra	0.0	97.9	7.8	%	Proportion of the quadrat on siliceous granites
Gyp	0.0	18.1	0.5	%	Proportion of the quadrat on gypsum
d) Heterogeneity within the quadrat					
H.Pa	1	10	3.7		Number of Pa levels (50 mm)
H.Ta	1	9	3.4		Number of Ta levels (1°C)
H.Psum	1	8	2.9		Number of Psum levels (20 mm)
H.Tjan	1	8	3.2		Number of Tjan levels (1°C)
H.Tjul	1	10	3.7		Number of Tjul levels (1°C)
H.MI	1	6	2.3		Number of MI levels (20)
H.Geo	0	2.32	1.21		Diversity of geological types (Shannon index)
H.Alt	1.1	444.6	142.4		Standard deviation of the altitude

types. We computed the area occupied by each of these seven main bedrock types in each quadrat (Table 1c) and the Shannon diversity index of the original 39 bedrock types (as an indicator of bedrock heterogeneity, Table 1d).

The flora data

We used a flora database for the study area, which is being built by compiling all the existing references (471 references from journals, books, dissertations, local atlas) together with unpublished information from a botanist network in the study area (Anon. 1985-2001). We considered native (ca. 95%) and naturalized species (ca. 5%), but not exotic unnaturalized species. Presently, there are 1 141 475 records (data entries) in the database. The number of records in each quadrat varies greatly, ranging from 209 to 30693 (mean = 3197, SD = 3666), dependent mainly on two factors: the prospecting intensity (i.e., number of botanical studies done in the quadrat), and the floral richness (the more species in a quadrat, the more entries). With the agreement of the Global Biodiversity Information Facility (GBIF) effort (Edwards et al. 2000), the database has been made available in a searcheable form at http://biodiver.bio.ub.es/BioCat/Homepage.html

Statistical analysis

The relationship between the dependent variable (i.e. species richness) and the independent variables at the quadrat level (i.e. environmental parameters and heterogeneity variables) was tested by a weighted analysis of deviance (Generalized Linear Models). Analysis of deviance is analogous to analysis of variance but assuming non-normal error distribution (McCullagh & Nelder 1989). At first, because the dependent variable included discrete data (counts), the Poisson distribution of errors with a logarithmic link function was assumed (McCullagh & Nelder 1989). However, after building a minimal adequate model, there was strong evidence of overdispersion (dispersion parameter >> 1; variance >> mean), and thus the negative binomial (with the same link function) was assumed to be a more general error distribution. The negative binomial family provides an appropriate parametric alternative of modelling overdispersion (Venables & Ripley 1999). The weight variable used was: $W = \ln(NR / NS)$, where NR is the number of records, NS the number of species in the quadrat, and NR is always greater than NS. This weight was used because it is an indicator of the sampling intensity of the quadrat, and thus, in order to compute the regression coefficients, quadrats with few records (undersampled quadrats) were downweighted. The reasoning behind this weighting is that if the number of records (sampling intensity) is proportional to the species richness, then W is the same for all quadrats, even if some are richer than others. A backward stepwise procedure was employed to obtain the minimal significant model (parsimony), and only variables explaining a significant ($p < 0.01$) amount of deviance were included in the final statistical model. To reduce collinearity problems, we used the following selection criteria for the model building: (1) variables with the most important biological meaning (proximal variables) were preferred (see Pausas & Austin 2001); and (2) variables that explained the most (significant) deviance were preferred. Reduction of collinearity was evaluated by variance inflation factors (Belsley et al. 1980). Significance was evaluated by the χ^2 criterion. Interactions between pairs of significant variables were also tested, and residuals were investigated for alternative response shapes (quadratic and logarithmic). Influence measures of the final model were also computed (Belsley et al. 1980; Cook & Weisberg 1982). Sites with high values with respect to any influential measure (standardized residuals, covariance ratio, Cook's distance) were carefully checked for anomalies. Special attention was given to quadrats with both high residuals and high influence (Sokal & Rohlf 1981). These quadrats were removed and the statistical analysis repeated to check for possible changes in the model coefficients.

Results

The database includes 3087 species (Table 2) belonging to 874 genera and 148 families. The weighted mean number of species per quadrat was 620 (min = 124; max =1222; SD = 230.8).

The most important variables for explaining species richness are those related to area, quadrat heterogeneity, temperature, and water availability (Table 3). All these variables showed a positive relationship with plant species richness in the quadrats (Fig. 2). Water availability is composed of two variables: one of them, MI, is related to climatic factors (precipitation and evapotranspiration),

Table 2. General flora characteristics (number of species, genera, and families) for the whole study area (total number), and mean, weighted mean (wMean), minimum, maximum and standard deviation found within a quadrat of 10 km × 10 km.

	Total number in database	Quadrats				
		Mean	wMean	Min	Max	Sd
Species	3087	548	620	124	1222	231
Genera	874	306	332	97	525	91
Families	148	79	82	39	111	15

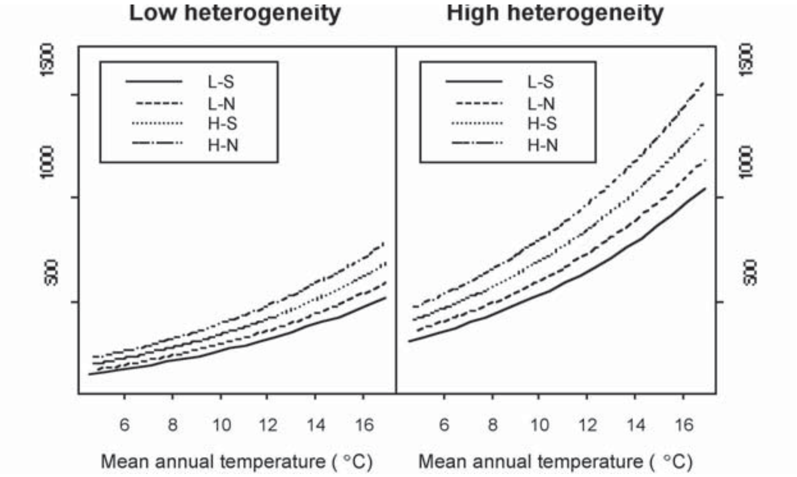

Fig. 2. Predicted relation between plant species richness and mean annual temperature (°C) at low (L) and high (H) moisture index, with low (S) and high (N) proportion of slopes facing north, and with low (left) and high (right) heterogeneity (Table 3). Heterogeneity is measured by (see Table 1) RArea (real area), H.Tjan (heterogeneity of January temperature) and H.Geo (heterogeneity of geological substrates). Fitted lines for high and low heterogeneity are computed from the 80% and 20% (respectively) percentiles of these three heterogeneity variables.

and the other is related to the aspect (N). Environmental heterogeneity is studied with respect to the increase in area related to topography, the temperature variations in January and the variations in the heterogeneity of geological substrates (RArea, H.Tjan and H.Geo, respectively). However, RArea takes into account both the effect of topographic heterogeneity and the strict effect of area. The model explains about 38% of the total deviance, of which more than 2/3 is due to the area and the heterogeneity parameters. No quadratic terms or interactions were significant. Mean variance inflation factor of the final model was ca. 3.3, suggesting that there was not a strong collinearity effect (Belsley et al. 1980).

Table 3. Table of analysis of deviance for the plant species richness in the study area. Explained deviance for each variable is computed as percentage of residual deviance explained from the null model minus the explained deviance from the previous variables. Dispersion parameters (theta) estimates = 7.84 (SE = 0.655). Variables are (see also Table 1): Real effective area (RArea), heterogeneity of January temperature (HTjan), heterogeneity of geological substrates (H.Geo), mean annual temperature (Ta), proportion of the cell facing north (N), moisture index (MI). Significance: ** = $p < 0.01$; *** = $p < 0.001$; **** = $p < 0.0001$.

	Df	Deviance	Resid. Df	Resid. Dev.	Exp. Dev. (%)	P ($>|\chi^2|$)
Null			284	489.23		
RArea	1	63.25	283	425.73	12.98	****
H.Tjan	1	24.98	282	400.65	5.13	****
H.Geo	1	37.60	281	358.27	8.66	****
Ta	1	22.71	280	340.20	3.69	****
N	1	7.60	279	331.35	1.81	**
MI	1	26.12	278	305.03	5.38	****

Checking the residuals, there were neither strong tendencies (e.g. increasing or decreasing residuals in relation to an independent variable) nor outlier sites. Residuals tended to be negative (mean = – 0.23; SD = 1.0), suggesting a slight overall tendency to some overestimation (i.e. predicted > observed richness). Six quadrats were identified as having a relatively high residual and a high value of some of the influential measures used. Removing these quadrats, the model increased slightly in significance and in explained deviance, but the coefficients and the trends remained roughly the same.

Discussion

The study area can be considered of great importance in plant species diversity (3087 species were found in an area of 31 900 km^2). Although it is difficult to compare this with other areas due to the different species criteria, there are biodiversity hotspots about ten times larger than the study area, such as Central Chile, the Californian Floristic Region, or New Zealand, which have a similar number of plant species (2300-4500; Myers et al. 2000).

A positive relationship between richness and temperature has been suggested in several studies at a regional scale (Knight et al. 1982; Pausas & Carreras 1995; Austin et al. 1996), although the opposite has also been found, mainly when water availability is not considered simultaneously (e.g., Richerson & Lum 1980). Many studies have shown a negative relationship between altitude and species richness in different ecosystems (e.g., in coniferous forests by Pausas 1994 and Rey Benayas 1995; in Alaska, Tennessee and Costa Rica reviewed by Stevens 1992) due to a negative correlation between altitude and temperature.

Our study agrees with most of the studies on the positive relationship between plant species richness and water availability to plants (Richerson & Lum 1980; Knight et al. 1982; Currie & Paquin 1987; Gentry 1988; Leathwick et al. 1998), although the wide variety of variables used as a surrogate for water availability (e.g., rainfall, aspect, evapotranspiration, soil depth) makes strict comparisons difficult. We used the Thornthwaite moisture index plus aspect to measure water availability, that is, a macroclimate parameter considering both rainfall and evapotranspiration, plus a microclimate parameter (aspect) in order to take into account both meso- and micro-scale effects. O'Brien (1993) has shown a quadratic (humped) response of woody species richness to minimum monthly potential evapotranspiration in southern Africa (65 grid cells of ca. 20000 km^2); however, in that study, the underlying factor could well change from the effect of temperature (in the first part of the gradient) to the effect of water stress (in the second part of the gradient). A direct indicator of water availability would probably suggest a decrease in species richness with a decrease in water availability. Some studies with large data sets have shown the importance of the interaction between temperature and rainfall for explaining plant species richness (Margules et al. 1987; Austin et al. 1996).

The temperature and water availability combination, which is strongly related to site productivity, can be considered a measure of ambient environmental energy (*sensu* Wright 1983; Currie 1991); thus our study is in accordance with the species-energy hypothesis (Wright 1983). Our analysis suggests that at the scale of this study, within-quadrat heterogeneity is the most important parameter for understanding geographical patterns of species richness. The increase in area due to topography and the variations in temperature and bedrock type showed positive significant relationships with species richness. These results may encourage further research. For example, the quadrat size in the work by Currie and collaborators (Currie & Paquin 1987; Currie 1991; Kerr & Packer 1997; Kerr & Currie 1999) is variable (some quadrats have twice the projected area of others), and some of the unexplained variance from their work could well be related to quadrat environmental heterogeneity.

The model we obtained agrees with the framework by O'Brien et al. (2000) on water-energy dynamics and topographic control of species richness. In fact, our model can be considered an improvement of their model in that it explicitly accounts for effective area, plus two other within-cell heterogeneity parameters (climatic heterogeneity and bedrock type heterogeneity). Our model can be summarized by:

$$S = \mathrm{f}(\ A_1 + E[W, T] + E_\mathrm{h}[A_2, T, G]\ ) + \mathrm{Error} \qquad (1)$$

Where species richness at the coarse scale (S) is a function (f) of the quadrat effective area (A_1), the environment (E, which in our example takes two components: water availability and temperature), and environmental heterogeneity (E_h, with three components in our example: topographic heterogeneity, A_2, heterogeneity of temperature, T, and of geological substrate, G). Although our model considers the increase in area associated with topography, it does not differentiate the strict effect of area (A_1) from the topographic heterogeneity (A_2). A similar model was suggested, although not tested, by Austin (1999). The importance of heterogeneity has also been suggested in other studies for different scales. For instance, Rey Benayas & Scheiner (2002) found a positive relation of regional species richness with altitudinal range (a measure of heterogeneity) in their study at the scale of the whole Iberian Peninsula, and Vivian-Smith (1997) performed an experiment showing the direct (and positive) effect of heterogeneity on species richness at a local scale. The relative contribution of each parameter ($A_{1,}$ E, E_h) will probably depend on the grain and scale of the study, and the complexity of the landscape. A conceptually similar approach was used by Harner & Harper (1976) when studying plant species richness at the local scale (1 - 10 000 m^2) in the western United States. They used an index of environmental heterogeneity (E_h) that integrates the heterogeneity (standard deviations) of eight different parameters and an environment index (E) called favourableness (based on water availability for plants). They also found that the relative importance between E and E_h varies between sites with different environmental conditions, and that the rate of species added with increasing area was more related to E_h than to E.

Our model still has a large amount of unexplained error; to what extent this error is due to other environmental parameters not considered or to other factors (disturbance, agricultural land, sampling problems, etc.) is yet unknown and needs further consideration. For instance, a preliminary test suggested that the proportion of agricultural land (which is highest in flat areas) in each quadrat does not reduce the unexplained deviance when tested after including the environmental parameters in Table 3 (Pausas et al. unpubl.). To what extent this is related to causal factors or to correlations needs further research. Furthermore, errors in the data due to the diverse data sources used, the different sampling intensities, and the interpolation of environmental conditions from maps, may also contribute to unexplained errors.

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