UC Irvine
UC Irvine Previously Published Works

Title

Does plant richness influence animal richness? the mammals of Catalonia (NE Spain)

Permalink

https://escholarship.org/uc/item/8p8041w5

Journal

Diversity and Distributions, 10(4)
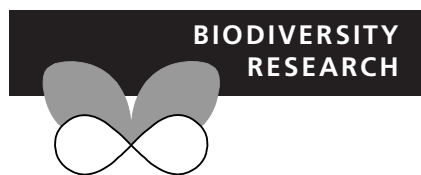
ISSN

1366-9516

Authors

Hawkins, Bradford A.
Pausas, J G

Publication Date

2004-07-01

Peer reviewed

Does plant richness influence animal richness?: the mammals of Catalonia (NE Spain)

Bradford A. Hawkins* and Juli G. Pausas†

Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697 USA. E-mail: bhawkins@uci.edu; and †Fundación Centro de Estudio Ambientales del Mediterráneo (CEAM), C. Charles R. Darwin 14, Parc Tecnològic, E-46980 Paterna, València, Spain. E-mail: juli@ceam.es

ABSTRACT

Although it has long been held that plant diversity must influence animal diversity, the nature of this relationship remains poorly understood at large spatial scales. We compare the species richness patterns of vascular plants and mammals in north-eastern Spain using a 100-km^2 grain size to examine patterns of covariation. We found that the total mammal richness pattern, as well as those of herbivores and carnivores considered separately, only weakly corresponded to the pattern of plants. Rather, mammal richness was best described by climatic variables incorporating water inputs, and after adding these variables to multiple regression models, plant and mammal richness were virtually independent. We conclude that the observed association, although weak, is explained by shared responses of both groups to climate, and thus, plant richness has no influence on the richness pattern of Catalan mammals.

*Correspondence: Bradford A. Hawkins, Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697 USA. E-mail: bhawkins@uci.edu

INTRODUCTION

The number of plant species in an area might be expected to influence the number of animal species, and at small spatial scales such positive associations have been widely found in both experimental and observational studies (Siemann *et al.*, 1998 and references therein; Knops *et al.*, 1999; Haddad *et al.*, 2001). Such associations have also been used to argue that one of the ecosystem functions provided by diverse plant communities is the maintenance of rich animal communities (Knops *et al.*, 1999). However, whether or not this 'function' operates at larger extents or for all animal groups is less certain. At some very gross level plant and animal richness patterns must be congruent, since both increase from the poles to the tropics. But even if true, it begs the more interesting ecological question of the extent that this covariation is causal or coincidental. If plant diversity strongly influences animal diversity at broad scales, then it follows that to understand animal diversity gradients we need only know what drives plant diversity and then explain total biotic diversity as a special case of resource–consumer interactions, whereas if links between plant and animal diversity are non-causal, then we need to understand what aspects of the environment can drive both patterns simultaneously. Given that there is widespread evidence that elements of climate influence both plant and animal diversity gradients at broad spatial scales

(Wright *et al.*, 1993; Hawkins *et al.*, 2003), the key to answering this question is not simply to correlate plant and animal richness gradients, but to include simultaneously both plant richness data and climatic variables in analyses of animal diversity patterns to determine how they covary in concert.

The biggest stumbling block in testing the hypothesis that plant diversity drives animal diversity has been the lack of appropriate plant data. Although range maps of trees and shrubs exist for various parts of the world, the absence of maps for herbaceous plants has severely limited our ability to generate estimates of total plant richness across large regions against which to compare animal diversity data. However, as part of the general interest in understanding diversity gradients, plant diversity patterns are beginning to be documented. In this paper we use a data set generated for Catalonia in north-eastern Spain. Pausas *et al.* (2003) analysed these data with respect to environmental variables and found that measures of area, within-cell environmental heterogeneity, temperature, and water availability best explained the species richness pattern. Their multiple-factor model explained 37.6% of the 'deviance' in plant richness.

To date there have been at least two studies attempting to link mammal and plant richness patterns across broad scales. Boone & Krohn (2000) found that woody plant and mammal richness were strongly positively associated across Maine, USA, but that climate and geomorphology were stronger predictors of mammal

diversity patterns. In contrast, Andrews & O'Brien (2000) found that mammal richness in southern Africa was more strongly correlated with woody plant richness than with a wide range of climatic and topographical variables, at least raising the possibility that the former may indeed drive the latter. On the other hand, they did not conduct any spatial evaluations of the associations, nor did they attempt to determine whether the observed link was direct or was driven by similar responses of both groups to the same environmental driving variables. Thus, it is difficult to evaluate their findings. Further, neither Boone & Krohn (2000) nor Andrews & O'Brien (2000) included herbaceous plant species, so the full relationship between mammal and plant diversity remains unexplored.

METHODS

Study area

The study area is the whole of Catalonia (*c*. 31, 900 km^2). Its altitude ranges from sea level to 3143 m (the peak of Pica d'Estats). It is situated between *c*. 0°15′ E and 3°20′ E longitude and 40°30′ N and 42°40′ N latitude. In the northern part of the area (the Pyrenees) the climate is mainly temperate middle-European with a colder climate in the higher mountain zones. In the remaining area the climate is typically Mediterranean, with a maritime tendency towards the coast (to the east) and a continental and subarid tendency inland (to the west).

The spatial unit for the analysis is the UTM 10 × 10 km grid system (see Pausas *et al.*, 2003). We excluded cells with less than 75% of their projected area within Catalonia (i.e. we excluded small coastal cells and cells largely representing land within adjacent provinces), leaving 318 cells for which we had measurements of all environmental variables.

Plant richness and environmental variables

Plant richness in each grid cell was obtained from Pausas *et al.* (2003). They compiled total plant richness for each cell based on all existing references (articles, books and unpublished dissertations) on plants in the study area and from a botanical network (ORCA, 1985–2001). The data set is founded on 1,141,475 records and includes 3087 species (see Pausas *et al.* (2003) for more details). The number of records in each cell varies greatly (mean = 3197, SD = 3666), but comparing the plant richness model weighted by the number of records (Pausas *et al.*, 2003) with an unweighted model (J. Pausas, unpublished), the main results and tendencies do not change. Thus, although the data are undoubtedly incomplete, we believe they capture the overall richness pattern well.

Climatic data were obtained by overlaying climatic contour maps of the area (ICC, 1996) on the grid system (Pausas *et al.*, 2003). The variables selected for analysis were: mean annual temperature, July temperature, annual rainfall, summer rainfall, and Thornthwaite's moisture index. Average climatic values for each cell were computed as the mean of midpoint contour levels in the cell weighted by the area occupied by each level. 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 Thornthwaite's moisture index. We also included two topographical variables: real area and elevation range. A triangular irregular network (TIN) was constructed from a topographic map of the study area and used to compute the close-to-real cell area (rather than the projected area). The TIN was then rasterized (to 25 × 25 m pixels) to compute the maximum and minimum elevation and the elevation range of each cell (Pausas *et al.*, 2003).

Mammal richness

The number of mammal species in each cell was estimated using two sources (Gosàlbez-Noguera, 1987; Ruiz-Olmo & Agular, 1995). The older reference illustrates ranges as filled-in range maps. We overlaid the grid onto the maps and scored the cells where the reported ranges overlapped. For rodents and insectivores, however, the maps in Ruiz-Olmo & Agular (1995) illustrate ranges as occurrences in the UTM grid, so occupied cells were directly scored. Introduced species were excluded from consideration, leaving 39 species. Finally, mammals were classified as being herbivores, carnivores or omnivores, based on a range of sources, to allow us to generate statistical models of richness for each trophic group. We would expect a priori that plant richness should have stronger effects on herbivore richness than carnivore richness.

Statistical analysis

We conducted simple and step-wise multiple regression using all predictor variables against total mammal richness to generate a statistical explanation of the overall mammal spatial pattern. This tested whether plant richness or elements of climate or topographical relief were stronger predictors of mammal richness, based on the order of entry of each variable into the model. The analysis was then repeated for herbivores and carnivores separately to determine if either group showed strong associations with plants. The four omnivore species were considered too few to merit analysing them separately.

To evaluate the adequacy of the environmental regression models, we generated spatial correlograms at 10 distance classes of the raw richness data and the residual data after fitting the primary climatic predictor variable for each model, using SAAP 4.3 (Wartenberg, 1989) (see Diniz-Filho *et al.*, 2003). Any spatial pattern remaining in residual richness at any distance class indicates that a spatially patterned variable not included in the analysis is probably contributing to the richness gradient.

RESULTS

Mammal richness in each cell ranged from 8 to 33 species. Herbivores and carnivores ranged from 4 to 16 and from 1 to 14 species, respectively. The spatial patterns show a strong northeast to south-west gradient in all three cases, with most species occurring in the Pyrenees and few in the drier south-west
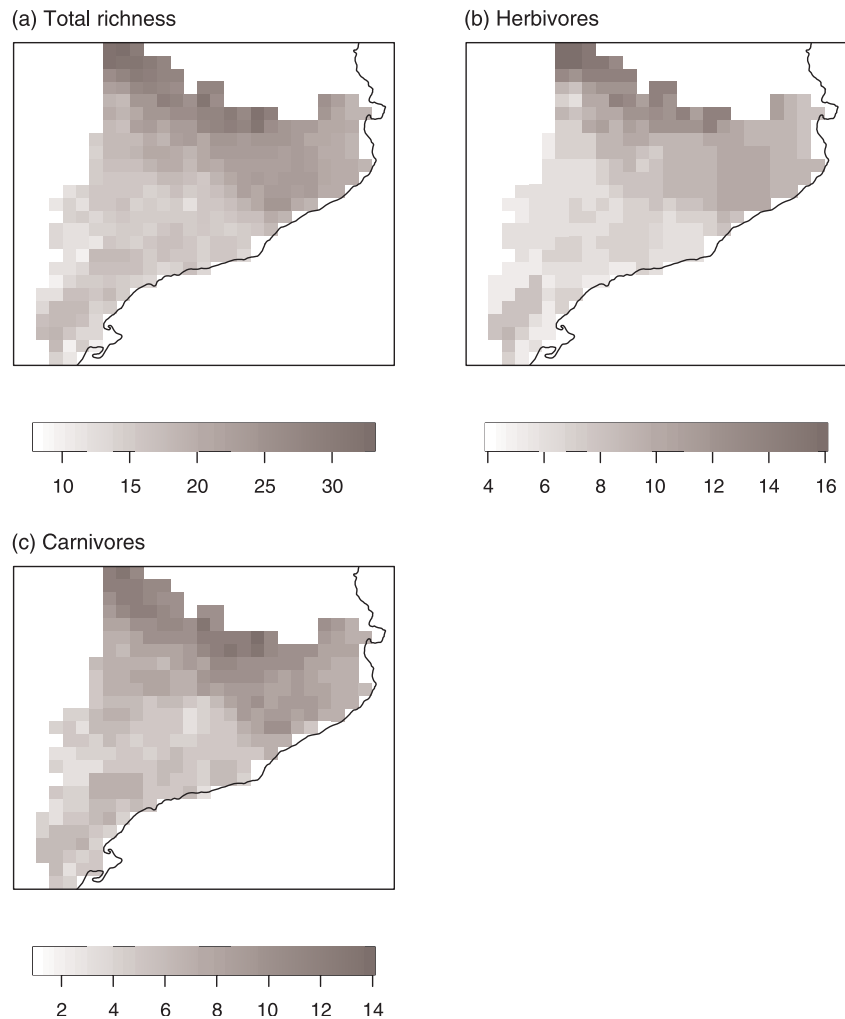
(a) Total richness

(b) Herbivores

(c) Carnivores

Figure 1 Spatial pattern of mammal species richness in Catalonia at 10 × 10 km resolution. (a) All species (b) herbivore species, and (c) carnivore species.

Table 1 Coefficients of determination for linear regressions of environmental variables against the spatial pattern of total mammal species richness, herbivore richness and carnivore richness. Positive and negative regression coefficients are indicated by (+/−), and all regressions are significant at $P < 0.001$

Variable	Total	Herbivores	Carnivores
Moisture index (+)	0.747	0.701	0.692
Summer precipitation (+)	0.724	0.624	0.717
Precipitation (+)	0.716	0.635	0.675
July temperature (−)	0.681	0.674	0.601
Annual temperature (−)	0.596	0.590	0.529
Range in elevation (+)	0.552	0.515	0.498
Area (+)	0.484	0.447	0.442
January temperature (−)	0.483	0.474	0.433
Plant richness (+)	0.109	0.079	0.115

(Fig. 1). When the environmental variables were considered individually, Thornthwaite's moisture index was the best predictor of both total mammal richness and herbivore richness, explaining *c.* 3/4th of the variance in both cases (Table 1, Fig. 2).

For carnivores, summer precipitation ranked slightly higher than moisture content. In all three cases, the moisture index and the measures of seasonal and annual rainfall were essentially interchangeable as predictors, indicating strong collinearity among them. Further, in all cases temperature variables explained less variation than water variables, and all relationships were negative. Notably, plant richness had the weakest relationships with richness of all potential predictor variables for all mammal data sets. Clearly, plant richness is a poor predictor of mammal richness in this region, even without taking into consideration the effects of climate on both gradients.

The multiple regression models further indicate that plant richness has virtually no direct influence on mammal richness (Table 2). Although it entered the models for total and carnivore richness, the improvement in the multiple coefficient of determination was less than 1% in both cases. Plant richness did not enter the herbivore model at all.

The correlogram of the raw data for total species richness (Fig. 3) is typical of a cline, reflecting that richness is highest in the north and decreases steadily to the south and west (Fig. 1). Fitting Thornthwaite's moisture index successfully removed most of the spatial richness pattern, except at the smallest and
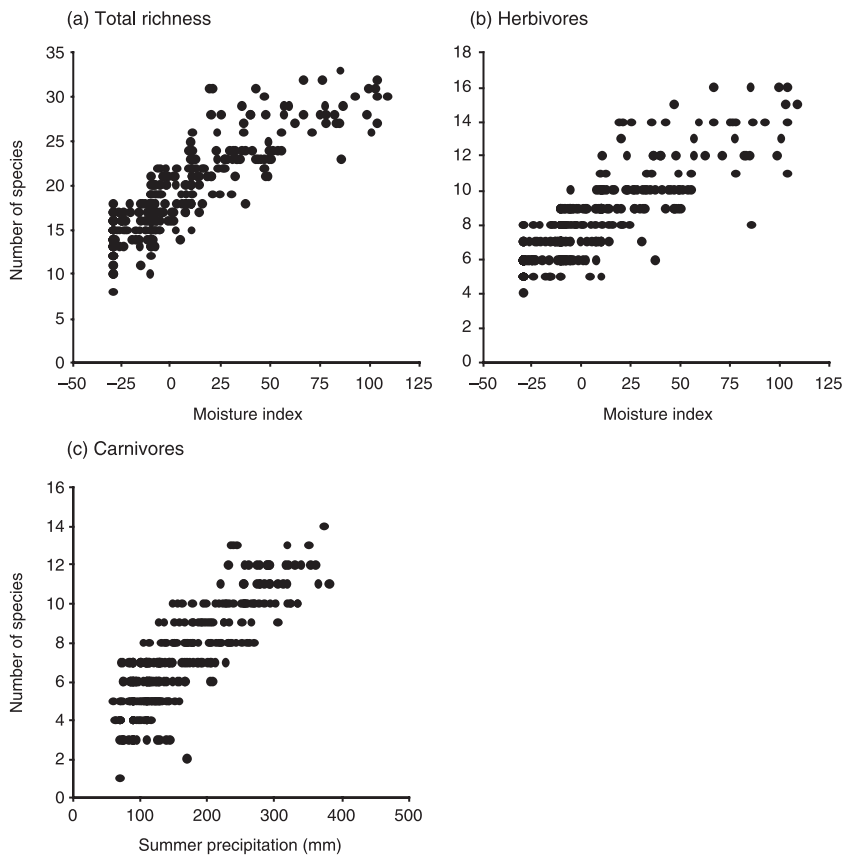
(a) Total richness

(b) Herbivores

(c) Carnivores

Figure 2 Relationships between mammal species richness and the primary explanatory variables in step-wise multiple regression models (see Table 2). (a) All species (b) herbivore species, and (c) carnivore species.

largest distances (Fig. 3). Adding the additional minor variables in the multiple regression did not further reduce the spatial auto-correlation, indicating that although they improved the explana-tory power of the model by a few percent, they contribute little or nothing to explaining the spatial pattern. The correlograms for herbivores and carnivores (not illustrated) were qualitatively identical to those for total richness, which would be expected because both trophic groups have very similar spatial patterns (Fig. 1). Thus, both groups show a clinal pattern of spatial auto-correlation, the primary predictor variables in the respective multiple regressions successfully account for most of the auto-correlation in all but the smallest and largest distance classes, and the minor variables do not further reduce the residual auto-correlation. All three analyses indicate that the primary climatic predictors explain the spatial pattern of mammal richness very well across most distances, although small amounts of residual spatial pattern remain at the extreme spatial scales.

DISCUSSION

We find no evidence that the number of plant species recorded in 100 km^2 cells has any measurable influence on the number of mammal species in each cell. Rather, we find that mammal rich-ness is well described by climatic variables, particularly those related to measures of water and energy inputs. The ability of climate to explain the spatial distribution of species richness at broad spatial scales is now very well established for a wide range

Table 2 Step-wise multiple regression models for total, herbivore, and carnivore mammal species richness. Variables are listed in the order in which they entered the model. Also provided are partial coefficients of determination and significance levels for each variable. (−) after variable name indicates a negative partial regression coefficient

| Variable	R^2	Probability
All species		
Moisture index	0.747	< 0.001
Summer precipitation	0.030	< 0.001
Annual precipitation	0.005	0.006
Annual temperature (−)	0.014	< 0.001
Plant richness	0.005	< 0.007
Model R^2	0.800	
Herbivores		
Moisture index	0.701	< 0.001
July temperature (−)	0.019	< 0.001
Annual precipitation	0.011	< 0.001
Annual temperature (−)	0.008	0.003
Model R^2	0.738	
Carnivores		
Summer precipitation	0.717	< 0.001
Moisture index	0.027	< 0.001
Plant richness	0.008	0.001
Model R^2	0.752	
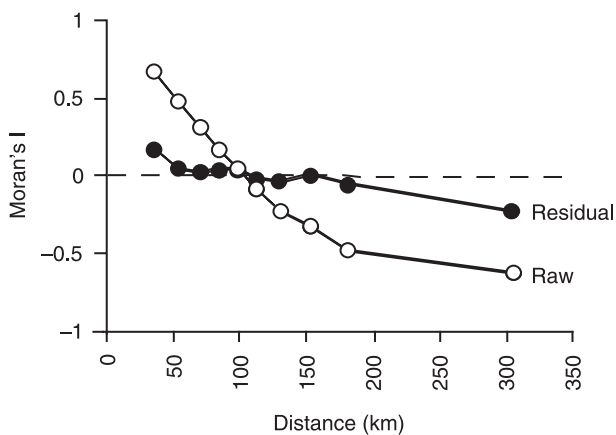
Figure 3 Spatial correlogram across 10 distance classes for raw mammal species richness and for residuals after fitting Thornthwaite's moisture index. Both correlograms are significant ($P < 0.001$, Bonferroni adjusted), indicating that significant residual spatial autocorrelation remains in at least one distance class. Correlograms for herbivore and carnivore richness are very similar.

of terrestrial plant and animal groups (Hawkins *et al.*, 2003). Further, it has been argued that in warm climates water is likely to be the primary limiting factor for both plants and animals, whereas in cold climates temperature is most important. Based on the fact that mammal richness is positively correlated with precipitation measures and negatively correlated with temperature measures, Catalonia can be considered a warm climate with respect to mammals. A strong interaction between water and temperature is further indicated by the very high collinearity among the water and temperature variables, such that most seasonal and annual climate variables have moderate to strong associations with mammal richness when considered individually, whereas in the multiple regression models a single variable accounts for almost all of the explained variance. This collinearity makes it difficult to judge which specific measure of climate is the 'best' predictor of mammal richness, but it does not alter the conclusion that there are more mammal species in the cooler, wetter parts of Catalonia than in the hotter, more arid parts.

In analyses that attempt to link plant and animal richness gradients, we might expect a priori that groups such as mammals will be at best weakly influenced by plant richness gradients, since the herbivorous species tend to have broad food plant ranges. This is in fact probably part of the reason why we found little direct association. However, very limited data suggest that food-plant range does not by itself determine whether or not animal richness gradients are associated with plant richness. For example, Hawkins & Porter (2003) examined this for the butterflies of California and found that plant and butterfly richness were completely independent after fitting an environmental model to both gradients, and it made no difference if the analysis was restricted to strictly monophagous species or included both specialist and generalist species. Also, plants offer more to animals than just food, so if increased plant richness is positively associated with non-trophic factors of importance to animals

(i.e. shelter, nesting sites, refuges from predators, etc.), plant richness could drive animal richness independently of the latter's food-plant ranges, or even that of non-herbivorous species. However, despite these considerations, we cannot conclude that it makes much difference to the outcome of the analysis, at least in the case of Catalan mammals.

A methodological issue related to studies of diversity gradients, whether plant or animal, is the grain size of the analysis. It is universally recognized that the forces driving diversity vary with grain size, such that in very local-scaled plots biotic interactions are more likely to influence richness whereas at larger scales other forces dominate (Willis & Whittaker, 2002). The $10 \text{ km} \times 10 \text{ km}$ cells we used are likely to represent a very local scale from the point of view of many of the larger mammal species that can roam widely, whereas for many plants and small mammals in which entire populations could reside in a few square kilometres, our cells could be considered more regional. This complication could somewhat blur correlations between plants and animals. However, this potential problem is not unique to this study, since body size gradients and differences in mobility among species will almost always influence the effective scale of an analysis. Unfortunately, we do not have enough species of mammals within Catalonia to deal with this issue analytically, but given the weakness of the association between plant and mammal richness, we doubt that this represents a serious problem.

There are currently too few analyses to be able to generalize the results we found. Although there have been a number of studies that have documented positive correlations between animal richness and plant or tree richness across moderate to large distances (e.g. Currie, 1991; Gaston, 1992; Chown *et al.*, 1998; Andrews & O'Brien, 2000; Boone & Krohn, 2000), there have been few attempts to determine if associations are direct or are indirectly driven by shared responses to similar environmental variables. Given that both plant and animal richness gradients are usually strongly correlated with measures of water, heat, or both (Hawkins *et al.*, 2003), it is probable that many observed associations are not directly causal. This does not mean that plants do not influence animals at large scales, since water-energy operates on animal richness at least partially via their effects on plant productivity (Wright, 1983; Wright *et al.*, 1993). Even so, Hutchinson's (1959) simple conjecture, 'The extraordinary diversity of the terrestrial fauna, which is much greater than the marine fauna, is clearly due largely to the diversity provided by terrestrial plants' (pg 148), remains poorly documented.

REFERENCES

Andrews, P. & O'Brien, E.M. (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology*, **251**, 205–231.

Boone, R.B. & Krohn, W.B. (2000) Partitioning sources of variation in vertebrate species richness. *Journal of Biogeography*, **27**, 457–470.

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts, and conservation. *American Naturalist*, **152**, 562–575.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant species richness. *American Naturalist*, **137**, 27–49.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.

Gaston, K.J. (1992) Regional numbers of insect and plant species. *Functional Ecology*, **6**, 243–247.

Gosàlbez-Noguera, J. (1987) *Insectivors I rosegadors de Catalunya*. Ketrea Editora, Barcelona.

Haddad, N.M., Tilman, D., Haarstad, J. & Knops, J.M.H. (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist*, **158**, 17–35.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity?: the case of California butterflies. *American Naturalist*, **161**, 40–49.

Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.

ICC (1996) *Atlas climàtic de Catalunya*. Institut Cartogràfic de Catalunya, Barcelona.

Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Groth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286–293.

ORCA (1985–2001) *Atlas corològic de la flora vascular dels Països Catalans*, pp. 1–11. Institut d'Estudis Catalans, Barcelona.

Pausas, J.G., Carreras, J., Ferré, A. & Font, X. (2003) Coarse-scale plant richness in relation to environmental heterogeneity. *Journal of Vegetation Science*, **14**, 661–668.

Ruiz-Olmo, J. & Agular, A. (1995) *Els grans mamifers de Catalunya i Andorra*. Lynx Ediciones, Barcelona.

Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*, **152**, 738–750.

Wartenberg, D. (1989) *SAAP 4.3: Spatial autocorrelation analysis program*. Exeter Software, New York, NY.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity — scale matters. *Science*, **295**, 1245–1248.

Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496–506.

Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. In: *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 66–74. University of Chicago Press, Chicago, Illinois.