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Plant diversity, biogeography, and environment in Iberia: patterns and hypothesized causal factors

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Abstract. We associated patterns of plant diversity with possible causal factors by considering 93 local regions in the Iberian Peninsula and Balearic Islands with respect to biogeography, environmental favorability, and environmental heterogeneity, and their relationship with measured species diversity at four different scales: mean local species richness standardized at a grain of 100 m^2, total species richness in a community type within a region (regional community richness), mean compositional similarity, and mosaic diversity.

Local regions in biogeographic transition zones to the North African and Atlantic floras had higher regional community richness and greater mosaic diversity than did non-transitional regions, whereas no differences existed in mean local species richness or mean compositional similarity. Mean local species richness was positively related to environmental favorability as measured by actual evapotranspiration, but negatively related to total precipitation and temporal heterogeneity in precipitation. Mean local species richness was greatest in annual grassland and dwarf shrubland communities, and on calcareous bedrock types. Regional community richness was similarly related to actual evapotranspiration and total precipitation, but in addition was positively related to spatial heterogeneity in topography and soil water holding capacity. Mean compositional similarity decreased with increasing spatial heterogeneity and temperature seasonality. Mosaic diversity, a measure of complexity, increased with increasing local and regional richness.

We hypothesize that these relationships can be explained by four ecological and evolutionary classes of causal factors: numbers of individuals, intermediate environments, limits to adaptation, and niche variation. These factors operate at various scales and manifest themselves in various ways. For example, at the site level, apparently processes that increase the number of individuals increase mean local species richness, but at the level of the entire region no such effects were found.

Keywords*:* Available energy; Community type; Environmental heterogeneity; Global change; Mosaic diversity; Resources; Scale; Soil type; Species richness; Transition zone.

Introduction

Understanding the mechanisms and processes that control patterns of species diversity is a synthetic goal of ecology (Rosenzweig 1995). Reaching this understanding is not simple, however, because diversity can be measured in a variety of ways and at different spatial, temporal, and taxonomic scales. Further, the processes that determine patterns of diversity are varied, including phylogenetic, historical, biogeographic, and environmental processes. Moving from pattern to process is one of the grand challenges facing ecology today (Lawton 1999; Brown 1999). In this study we tackle this challenge by moving from patterns of diversity to hypothesizing causes of a few ultimate ecological and evolutionary determinants.

We pose our exercise as one of hypothesis generation. The hypothesized causal factors are not mutually exclusive. The question we address is the relative importance of the processes involved. In ecology, determining the relative importance of processes is arguably at least as important as hypothesis testing (e.g., Quinn & Dunham 1983; Simberloff 1983). We acknowledge the potential importance of other processes operating at other scales (e.g., disturbance operating at local scales, species pool effects operating at continental scales) that may also be determinants of diversity.

Biological diversity is a scale-dependent and hierarchical phenomenon (Ricklefs 1987; Levin 1992; Schluter & Ricklefs 1993; Brown 1995; Rosenzweig 1995; Gaston 1996; Waide et al. 1999). It can be measured and analyzed at scales of meters or hundreds of kilometers, creating a spatial hierarchy due to the size of the analytical units. A second, ecological hierarchy can be defined from among plots within communities, to among communities within a region, to among biomes within and among continents. Another hierarchy exists for measures of diversity. Most diversity studies, especially for large extents, consider only one or two components of diversity, species richness within local communities (α diversity; e.g., Kerr & Packer 1997), species richness within a region (γ diversity; e.g., Currie 1991; Caley & Schluter 1997, Lobo et al. 2001), or similarity between communities (β diversity; e.g., Whittaker 1967, 1972; Shmida & Wilson 1985; Cody 1993; Blackburn & Gaston 1996). Very few studies have looked at local, differential, and regional diversities in large regions (Cowling et al. 1992; Scheiner & Rey Benayas 1994; Cowling et al. 1996). In this study we examined this entire range of diversity measures: mean local species richness, regional community richness, mean compositional similarity, and mosaic diversity (Scheiner 1992).

The diversity hierarchy with its scale dependence can be organized according to three components of scale: grain, focus, and extent (Palmer & White 1994; Scheiner et al. 2000). Grain is the size of the common analytical unit. Focus is the scale at which the grains are aggregated, for example the scale at which a mean is calculated. Extent is the scale at which the entire set of sample-units is analyzed (see Material and Methods). Scale-dependent differences in patterns can help us infer the causal processes responsible and the scale(s) that they are operating. Thus, we need to analyze patterns at multiple scales.

Previous studies have pointed out the joint importance of historical and more recent environmental factors in shaping patterns of plant diversity (Guo et al. 1998; Grace 1999; Ricklefs et al. 1999). In this paper, we look at the interaction of two sets of factors – biogeography and environment – which our analyses identified as potentially important. The effects of biogeography are manifest at transition zones. Environment appears in two ways, as overall favorability, and as environmental heterogeneity, i.e., variation in space and time. We considered these environmental factors because previous studies have shown them to affect species diversity: habitat area (e.g., Arrhenius 1921), spatial heterogeneity (e.g., Williams 1943), temporal heterogeneity (e.g., Sanders 1969), and environmental favorability (e.g., Dobzhansky 1950; Connell & Orias 1964). For favorability we followed the definition of Richerson & Lum (1980): environmental effects that increase productivity. Biogeography and environment are linked to more general determinants of patterns of diversity.

We analyzed plant diversity at different scales in the Iberian peninsula, a part of the world dominated by Mediterranean climate where past and recent environments have led to a complex mosaic of plant communities (Cowling et al. 1996, Blondel & Aronson 1999). Some of the specific questions we aim to answer in this study are the following. What are the patterns of plant diversity in the Iberian Peninsula? What plausible hypotheses can explain them? Can the patterns be attributed to a few basic causal factors? Can we infer basic knowledge useful for conservation and predicting the effects of global change?

Biogeography and environment of Iberia

The Iberian Peninsula and Balearic Islands include a large variety of biomes, relief, climates, and soil types. As such, it is representative of temperate regions and contributes to information about global patterns of diversity. Biomes include deciduous forest, coniferous forest, evergreen woodland and garrigue (Mediterranean “monte”), tall shrubland, dwarf shrubland, perennial grassland, and annual grassland. Variation in bedrock composition gives rise to soils with different water holding capacities and chemical compositions. The areas of our study were representative of Iberia and the Balearic Islands, including salient features of gradients of mean altitude (62 m to 2340 m), total annual precipitation (262.5 mm to 1778.4 mm), and mean annual temperature (5.0^{o}C to 18.6^{o}C). Within local regions, the relative extent of different vegetation types depends not only on the abiotic environmental status, but also on human impacts. Thus, land management may affect diversity patterns (Onipchencko & Semenova 1995; Leiva et al. 1997).

Two major climatic zones, Mediterranean and Atlantic, impinge on Iberia (Font Tullot 1983). The Mediterranean climate is strongly seasonal with warm, dry summers and cool, wet winters. It is characteristic of most of Iberia. In contrast, the Atlantic climate is wetter, cooler and less seasonal. It is found in a band ca. 100 km wide along the western and northern coasts as well as the Pyrenees Mountains. These zones correspond to major floristic regions, the Mediterranean and the Eurosiberian (Peinado & Rivas-Martínez 1987). A northern transition zone is recognized along their border in Iberia. A southern transition zone is recognized within the Mediterranean region. Southern Iberia served as a refugium during Pleistocene glaciations and was the source of much of the current Iberian flora (Hewitt 1996, Taberlet et al. 1998, Vogel et al. 1999). On top of this, in southeastern Iberia, the coastal fringe and adjacent low elevation mountain ranges have a climate similar to that in adjacent northern Africa, and share North African floristic elements (Peinado & Rivas-Martínez 1987). In contrast, the northern transition zone is substantially younger, having emerged only after the glacial retreat.

Material and Methods

Data sets

We analyzed 93 vascular plant data sets (Fig. 1) obtained from the literature (Appendix) or kindly donated by the owners. Each data set consists of information on species presence in a number of sites (i.e., plots) in a local region. A data set had to meet five criteria. First, the data had to include all terrestrial vascular plant species in the individual plots. Second, data sets had to be representative of a region. That is, we had to be able to conclude that plot locations were not obviously geographically biased. A region was defined as the minimum polygon enclosing a set of plots. Generally, we considered regions greater than 100 km^2 and less than 5000 km^2 (mean area = 841.1 km^2, SD = 923.5 km^2). Six regions smaller than 100 km^2 were included because they were deemed representative of larger areas.

Third, each data set was constrained to represent only a single major community type, e.g., only coniferous forests within a forest, shrubland, and grassland mosaic. By restricting a data set to a single community type, data sets were more uniform in sampling methodology (e.g., plot size) and represent a more homogeneous environment. In addition, biases that might have arisen from under- or over-sampling of the different community types within a mosaic were minimized. When a survey included more than one community type, we separated the samples into multiple data sets. The 7 community types considered in this study were: deciduous forest (15 data sets), coniferous forest (9 data sets), evergreen woodland and garrigue (15 data sets), tall shrubland of species such as *Erica* spp., *Cytisus* spp and *Cistus* spp. (22 data sets), dwarf shrubland (8 data sets), perennial grassland (15 data sets), and annual grassland (9 data sets).

Fourth, a data set had to include at least 15 plots (mean number of plots = 27.7, SD = 15.1). Fifth, plots generally had to be at least 20 m^2 and no larger than 200 m^2 (mean plot area = 95.3 m^2, SD = 43.4 m^2). The modal plot size was 100 m^2 (25 data sets; 38 between 90 and 110 m^2). The exceptions were the annual grasslands, which had plot sizes ranging from 0.25 to 6 m^2.

An alternative to the quadrat-based data used here would be data from a species distribution atlas. While such a data set would provide extensive information on species richness within a region (gamma-diversity), it would not address issues of scale and causal factors. Quadrat-based data permits measuring diversity at multiple scales and using multiple measures (see Measures of diversity), leading to more finely dissecting relationships between diversity and its determinants. We recognize that the ideal data set would include dense and uniform quadrat sampling across all of Iberia, but are confident that the current data set includes sufficient sampling to examine patterns and hypothesize causal factors.

Biogeography and environmental characterization

We considered two aspects of biogeography, province within Iberia and location within the transition zones between the Mediterranean Iberia and the Atlantic or North African floras (Fig. 1). The biogeographical provinces were those of Peinado & Rivas-Martinez (1987), and represent the largest biogeographical units within the two major climatic zones. Each data set was classified based on which province contained most of its area. All 11 biogeographical provinces in Iberia were represented in this study. Biogeographical provinces represent relatively homogenous communities as regards to historical processes and current environments.

We classified each data set as transitional or not (Fig. 1). Data sets were defined as transitional if they spanned the border between the Eurosiberian and Mediterranean climate regions. In addition, some data sets defined as transitional were entirely within the Eurosiberian or Mediterranean climate regions, but near the border and described as transitional by the study's author(s). The southern transition zone was defined as the Murciano-Almeriense province. Six data sets were considered transitions to the North African floristic province and twenty-four data sets were considered transitions to the Atlantic floristic province. Preliminary analyses indicated that measures of diversity did not differ between the two transition zones, justifying our treatment of them as a single entity.

We characterized the environment based on relief, climate, and soil using variables grouped into broad categories based on favorability and heterogeneity. Measures of overall favorability included: mean annual temperature, total annual precipitation, actual evapotranspiration (AET), bedrock type, and soil water holding capacity (WHC). Climatic information for each data set were interpolated from the closest weather stations (Instituto Nacional de Meteorología 1995) or obtained from a climate atlas (Instituto Nacional de Meteorología e Geofisica 1982; Font Tullot 1983). AET depends upon the amounts of potential evapotranspiration (PET), on one side, and precipitation and available WHC, on the other side. PET combines information on temperature, radiation, humidity, and wind speed. We used the Monteith´s (1965) method and Rey´s (1999) climate database to measure PET for our data sets. AET value is equal to the minimum value of PET and precipitation plus available WHC. In our study region, AET is more limited by shortage of precipitation than by temperature (see correlations between these variables in Table 3 below). It is a measure of biologically available energy and closely related to net primary productivity (Rosenzweig 1995). To confirm this link we also measured another productivity surrogate, the normalized difference vegetation index (NDVI). NDVI is a measure of vegetation density and the distribution of vegetation patterns and estimates standing crop (Roughgarden et al. 1991; Nohr & Jorgensen 1997). A mean NDVI for the area encompassed by each data set was determined for three time periods, 21-31 March 1995, 22-28 May 1995, and 10-21 August 1995, from

NOAA's AVHRR satellite imagery. The correlation between the mean of these three estimates of NDVI and AET was 0.64 ($N = 93$, $P < 0.0001$).

In our data, we distinguished 5 categories of bedrock and their associated soils: calcareous – basic soils developed from calcareous rocks such as limestone and serpentines (37 data sets); sandstone – neutral to slightly acid soils developed from soft detritic rocks such as sandstone (10 data sets); metamorphic – acid soils developed from metamorphic rocks such as slates, phyllites and schists (17 data sets); granitic – acid soils developed from rocks such as granites and gneisses (28 data sets); volcanic – basic soils developed from calcareous volcanic rocks (1 data set). Each data set was assigned a major bedrock type based upon the descriptions of the author and geological maps. For data sets that included more than one bedrock type ($N = 41$), the classification was based on the most extensive type. Based on bedrock type, WHC was calculated for each data set using a weighted average of the values provided in Gandullo & Muñoz (1986). These authors list for every bedrock type a range of WHC that also depends on how close the vegetation is from the potential vegetation in the area. Soils developed from calcareous bedrocks have the highest WHC and are the most nutrient rich, whereas those from granitic bedrocks have low WHC and are nutrient poor (Porta et al. 1994).

Environmental heterogeneity includes spatial and temporal heterogeneity. Measures of spatial heterogeneity included area extent, altitudinal range, and number of bedrock types. Measures of temporal heterogeneity included the standard deviation (SD) of mean temperatures among months and the coefficient of variation (CV) of total precipitation among months. The SD was used for temperature because of the small correlation with the mean ($r = 0.21$, $N = 93$, $P = 0.04$); the CV was used for precipitation because the SD was highly correlated with the mean ($r = 0.85$, $N = 93$, $P < 0.0001$). We examined a number of additional climatic variables. These variables were each highly correlated with one or more of the other variables, and so were not used in subsequent analyses. The variables used in the analyses were chosen both to represent the range of potentially important environmental factors and to be as statistically independent as possible.

Measures of diversity

Our four measures of diversity can each be defined relative to the three components of scale: grain, focus, and extent. Our study considered two grain sizes: 100 m^2 and the local region. For all measures, the focus was the region because all data points in the analyses represent regional values. That is, they were either mean values taken among plots within a region or values calculated across all plots in a region. The extent for all measures was Iberia.

Our measure of local species richness was the average species richness among plots within a region. Plot species richness was standardized to a grain of 100 m^2. For data sets in which the plot size was 100 m^2, this value was the mean number of species in all plots. If the plot size was other than 100 m^2, mean species richness per 100 m^2 was estimated by linear interpolation or extrapolation of the species-area curves provided by EstimateS (Colwell 1997).

The second diversity measure was total community species richness in a region (regional community richness). For each data set, we used EstimateS to construct a complete species-area curve. Each curve was constructed by determining the number of species in 50 random combinations of plots (pairs, triplets, etc., up to the total number of quadrats). This curve was fit to a logistic model, $S = B/(C + A^{-Z})$, where S is the number of species, A is the sampled area and B, C and Z are constants. The variation explained in all cases was $\geq$99.7%, and was always greater than the fit of either power or exponential functions. In the logistic model, B/C estimates the asymptotic regional community richness. For this measure the grain size was the region.

The third diversity measure, mean compositional similarity, is a measure of β diversity, the degree to which sites share species. Compositional similarity for pairs of plots within a data set was calculated using Jaccard's index (Jaccard 1901). Thus, the grain size was a pair of plots. For each region we then calculated the mean compositional similarity.

The fourth diversity measure, mosaic diversity, is a measure of compositional pattern diversity, the pattern within a site-species data matrix (Istock & Scheiner 1987; Scheiner 1992). This pattern is a function of variation in species richness among communities as well as variation in commonness and rarity among species within a region. A high value for mosaic diversity implies a complex region with many environmental gradients and strong differentiation among communities, from those that are rich in common species to those that are rich in rare species. A previous study of Scheiner & Rey Benayas (1997) showed that mosaic diversity is highly and positively correlated with the variation of site occupancy by species, a component of rarity. Mosaic diversity was calculated using the Affinity Analysis program (Scheiner 1992). Mosaic diversity values are based on patterns across an entire set of plots, so the grain was the region.

Data analyses

Biogeographic and environmental effects on the four diversity measures were assessed in a series of ANOVAs and multiple regressions. For regional community richness, mean compositional similarity, and mosaic diversity, all data sets were used in the analyses. For mean local species richness, however, we excluded the nine annual grassland communities. These communities have a mean local species richness one order of magnitude larger than the other community types (Table 4). These nine data sets are extreme outliers, violating homoscedasticity assumptions of ANOVA and regression, and distorting the analyses. No transformation was possible to allow inclusion of these data.

Because we are generating hypotheses to infer causal factors (i.e., model construction), we explored the effects of biogeography and environment on the various measures of diversity using stepwise multiple regression analyses. Bedrock type was excluded from stepwise regressions because it is a categorical variable. In the final models, standardized partial regression coefficients measured the relative importance of each variable. This statistical procedure is useful for uncovering potential causal relationships, i.e., hypothesis building. We examined the data, both graphically and statistically, for nonlinear relationships, but found none. Therefore, all regressions were based on linear relationships. We used both a forward and backward selection procedure to ensure model robustness. We used a criterion of $P < 0.15$ for inclusion in the model to avoid the problem of missing potentially important factors. However, the final models are those with statistically significant ($P < 0.05$) terms only (Table 2). We did not adjust our criterion for statistical significance to account for multiple analyses and, thus, we were liberal in our search for possible causal factors. Because transitional zones strongly affected diversity (see below), transition zone was included in the multiple regression models as a bivariate dummy variable. All statistical analyses were done using Systat (SYSTAT 6.1 for Windows, SPSS, Inc., Chicago, Illinois).

Results

Biogeographic effects

Biogeography affected regional community richness and mosaic diversity, but did not affect mean local species richness or mean similarity. Biogeographical provinces differed

(Table 1) with the highest values of regional community richness and mosaic diversity corresponding to provinces for which some or all data sets represented transition zones (P, M-A, C-I-L; see Fig. 1). Regional community richness in transition zones averaged 40% higher than those from outside transition zones (transition zone: mean = 230.50, SE = 18.27; non-transition zone mean = 164.52, SE = 10.77; t = 3.29, df = 91, P = 0.014). Similarly, mosaic diversity values were substantially higher in transition zones (mean = 4.43, SE = 0.18) vs non-transition zones (mean = 3.77, SE = 0.10; t = 3.51, df = 91, P < 0.001). Location within a transition zone did not result in differences for mean local species richness (transition zone: mean = 18.80, SE = 1.03; non-transition zone mean = 19.73, SE = 0.91; t = 0.62, df = 82, P = 0.53) or mean compositional similarity (transition zone: mean = 0.218, SE = 0.011; non-transition zone mean = 0.233, SE = 0.010; t = 0.91, df = 91, P = 0.37).

Data sets in biogeographical transition zones were on average more species rich, although the average local site did not contain more species. In turn, increased species richness corresponded with a more complex region. The higher values of mosaic diversity within transition zones indicated that some sites were richer in common species, whereas other sites accumulated rare species. The lack of differences in mean compositional similarity indicates that the two floras were mingling within local sites.

Environmental favorability and heterogeneity

Each of the four measures of diversity were correlated with a different subset of environmental variables (Table 2). The correlations among the environmental variables used in the stepwise regression models are shown in Table 3; only a few of the correlations were statistically significant and all were small enough to minimize problems of collinearity. Variation in mean local species richness was explained by both environmental favorability (AET and total precipitation) and temporal heterogeneity (the CV of precipitation). Mean local species richness increased with increasing AET, but the correlation was low (Fig. 2A). In contrast, areas with higher total precipitation and greater seasonal variation in precipitation had lower mean local species richness. Community types differed significantly, with the highest mean local species richness in dwarf shrublands (Table 4). These communities are generally found in drier areas with more seasonal variability in precipitation. Finally, bedrock types differed significantly in mean local species richness (Table 5), with calcareous and granitic types having the highest species richness.

Variation in regional community richness was related to both environmental favorability and spatial heterogeneity. Regional community richness was correlated positively with AET (Fig. 2B) and correlated negatively with total precipitation. In addition, increasing WHC was related to decreasing regional community richness. An increase in altitudinal range was associated with an increase in regional community richness (Fig. 3A). Community types showed marginal evidence for differences in regional species richness ($P = 0.053$), with coniferous forests and dwarf shrublands having the highest values, and evergreen woodlands and perennial grasslands having the lowest values (Table 4). No correlation between species richness per 100 m^2 and regional community richness was found either among community types ($r_S = 0.60$, $N = 6$, $P > 0.2$) or among data sets ($r = 0.20$, $N = 84$, $P = 0.06$), although the correlations hint at a positive relationship. Bedrock types did not differ significantly in regional community richness (Table 5).

Variation in mean compositional similarity was due to environmental heterogeneity. Increases in both spatial variation [altitudinal range (Fig. 3B) and number of bedrock types] and temporal variation (SD of temperature) were associated with decreases in mean compositional similarity. Neither community types nor bedrock types differed in mean compositional similarity.

Variation in mosaic diversity was related to environmental favorability (i.e., AET and total precipitation), the same factors that explained mean local species richness and regional community richness. Again, increasing regional community richness was associated with sites being richer in common species, and other sites accumulating rare species, resulting in a more complex region. Bedrock types differed in mosaic diversity (Table 5), but community types did not (Table 4).

Discussion

Both biogeographic and environmental factors affected patterns of plant diversity (Table 6). We hypothesize that most of the described patterns are a consequence of ecological and evolutionary processes influencing four classes of causal factors. For convenience we label these classes as: numbers of individuals, intermediate environments, limits of adaptation, and niche variation. Each label refers to a set of processes, detailed below. The processes operate at a range of scales and manifest themselves in a variety of ways. By identifying a limited number of classes of causal factors that may be responsible for patterns of diversity, we take a first step in constructing an overall theory about the factors that control diversity patterns at different scales. We do not mean to imply that we are the first to identify these factors as being potentially important for shaping patterns of species diversity (e.g., Connell 1978, Huston 1979, Shmida & Wilson 1985, Auerbach & Shmida 1987, Palmer 1994). Rather, we make the point that multiple patterns and proximal mechanisms can be associated with a limited number of ultimate causal factors.

Numbers of individuals

As the number of individuals in an area increases, the number of species may increase through increased sampling from the regional species pool and decreased local extinction due to stochastic demographics (Coleman et al. 1982; Rosenzweig 1995). These processes are the basis of the available energy hypothesis of the relationship between productivity and species richness (Wright 1983; Wright et al. 1993). We hypothesize that in Iberia environmental factors may act to increase numbers of individuals in sites and regions in four ways. Data on numbers of individuals were not available for the data sets analyzed here, so our conclusions are based on our general knowledge of density patterns in these regions.

First, mean local species richness and regional community richness were positively correlated with AET. This pattern is similar at both the scale of a site and the scale of a region. Second, regional community richness was negatively correlated with WHC, which we interpret as a consequence of changes in vegetation physiognomy that may be partially related to disturbance intensity. WHC is highest in the deepest soils, which support forests; it is lowest in shallow soils that support grasslands and dwarf shrublands. In this instance a gradient of increasing WHC corresponded to a gradient of decreasing light level and other properties such as litter accumulation and mineralization rates. Third, of all bedrock types, calcareous ones had the highest mean local species richness. These calcareous soils are high in nutrients, and likely result in an increase in productivity. In all three cases, increases in resources (i.e., available energy – which is mostly limited by precipitation – and possibly light and nutrients) very likely increased the number of individuals, ultimately resulting in greater numbers of species. This observation of increasing species richness with increasing productivity is consistent with two literature surveys which found an increasing number of positive relationships between productivity and plant species richness as the geographic scale of the study increased (Rey Benayas 2001, Mittelbach et al. 2001). Conversely, highest diversity at the regional scale has been recorded on the most infertile areas of the South African Cape and Southwestern Australian Mediterranean climate regions (Cowling et al. 1996).

Fourth, annual grasslands had a mean local species richness more than five times greater than any other community type. The higher estimate was not an artifact resulting from extrapolations of small sample plots. The total number of species actually observed in those surveys ranged from 62 to 149 over sampled areas of 29 to 118.5 m^2. For the 3 data sets in which the total area sampled was >100 m^2, the total number of species found ranged from 107 to 148 and was consistent with the estimated mean local species richness based on the species-area curve. An upward bias could be caused because the plots were scattered, rather than contiguous. However, López-Pintor (2001), in a study of 16 10×10 m^2 plots in a representative annual grassland, surveyed an area of 2.25 m^2 (9 0.5×0.5 m^2 quadrats) within each and found a mean of 48.25 species (range 35-58). These values are consistent with our estimates based on more widely scattered plots.

Dwarf shrublands, which had the second highest mean local species richness, also contain many annuals. Higher local species richness in these communities can be attributed to a much higher density of individuals because the size of plants is much smaller than those in the perennial grassland, tall shrub, and forest communities (Debussche et al. 1996). For example, a study of an annual grassland community found an average of 30 individuals in plots of 10×10 cm^2 (Rebollo et al. 2001). These community-type differences appeared as precipitation effects in the environmental analyses. Nonetheless, this difference in mean local richness did not translate into differences in regional community richness. In this instance the numbers of individuals apparently operates at one scale to increase species richness, but not the other.

Intermediate environments

Intermediate environments often contain more species because more species are able to adapt to life in intermediate environments than in extreme environments (Grace 1999; VanderMuelen et al. 2001). This label refers to a complex of evolutionary mechanisms that include physiological and morphological constraints on the possible range of adaptations to extreme environments. In our data, evidence for the importance of this class of mechanisms appears in at both continental and regional scales.

First, at the continental scale we examined diversity patterns at transition zones. Transitions zones exist at the meeting of different climatic regimes, thus having an intermediate climate. In our data, transition zones had greater regional community richness representing a mingling of floras within Iberia that derive from other parts of Europe and North Africa. Increased regional community richness in transition zones is consistent with the analysis of Castro et al. (1997). They found peaks of species richness in the northern and southeastern mountain ranges, the areas that we identified as transition zones. These patterns may also be due, in part, to refugia in a land with over a millennium of varied agricultural, silvicultural, and pastoral practices, the explanation favored by Castro et al. (1997). In their analysis, areas of high species richness were also rich in endemic species. The effects of endemic species are reflected in our results by the high levels of mosaic diversity in the transition zones. Mosaic diversity increases as rare species are added to a landscape. Thus, both ecotones and refugia may contribute to the higher regional community richness and mosaic diversity of transitional zones in agreement with Cowling (1983). He found in another Mediterranean region, southern Africa, that local richness in transition zones was higher than in adjacent core zones because transition zone communities harbored species from all adjacent zones.

Second, at the regional scale we see differences among community types. Of all community types, excluding annual grasslands, dwarf shrublands had the highest mean local species richness, whereas community types did not differ in regional community richness. Dwarf shrublands are an intermediate successional stage between early-successional perennial grasslands and late-successional evergreen woodland and garrigue communities (Westman 1981). These shrublands consist of drought-tolerant and drought-resistant species that are characteristic of the Mediterranean biome. The maintenance of grassland and dwarf shrubland communities is in part the result of fire and land management practices that prevent reversion of sites to woodland or garrigue. Thus, this mechanism is similar to that proposed by the Intermediate Disturbance Hypothesis (Connell 1978; Grime 1979) that predicts a diversity peak at intermediate intensity of disturbances. Harrison (1999) also found that intermediate environments had higher levels of α and γ diversity.

Thus, our data suggest that intermediate environments affect diversity differently at different scales. At the regional scale, intermediate environments reflect temporal – successional – effects which are expressed at a local grain. At the continental scale, intermediate environments reflect spatial – climatic – effects which are manifest at a regional grain. This process is referred to as the mass effect across transition zones (Shmida & Wilson 1985) and the rescue effect among communities in a region (Brown & Kodric-Brown 1977).

Limits to adaptation

Limits to adaptation decreased mean local species richness in extreme environments, and through that, regional community richness and mosaic diversity. This label refers to the complementary outcome of the complex of evolutionary mechanisms constraining adaptation discussed in the previous section. The types of adaptations required for life in harsh conditions (e.g., extremes of drought, cold, or low nutrients) are less likely to arise (Grace 1999; VanderMeulen et al. 2001). First, greater total precipitation was associated with lower levels of mean local species richness (contra Richerson & Lum 1980; Wohlgemuth 1998). In the context of Iberia, once AET is accounted for, the highest levels of precipitation are associated with high, cold alpine areas with a surplus of available water (Rey Benayas et al. 1998). So the negative correlation between mean local species richness and total precipitation reflects limits to cold adaptation and water logging. Second, greater seasonality of precipitation, measured as the CV of precipitation, was negatively correlated to mean local species richness. This reflects limits to drought adaptation, in agreement with the analysis of Rey Benayas (2001) for Mediterranean plant communities in the entire world. Similarly, Gough et al. (1994) explained a gradient in species richness along salinity and flooding gradients in coastal marshes as limitations to stress adaptation (Grace 1999).

With respect to soil types, in many areas species numbers are lower on acidic soils than adjacent non-acidic soils. This difference is not just an effect of productivity differences, but also historical and phylogenetic effects on speciation rates (Gray et al. 1987, Grime 1979, Grime 1998). In contrast, we did not find such patterns in our study. Regional community richness did not differ among soil types. Mean local species richness differed, but the differences were not related to the soil acidity (e.g., granitic soils were richer in species than sandstone soils, the latter having a more neutral pH).

Niche variation

In the previous section we discussed limits in the optimal environment of a species. Adaptation limits also exist in the environmental breadth of a species (Lynch & Gabriel 1987;

Whitlock 1996). A species is limited to just a portion of the environmental range. We hypothesize that such limitations in the breadth of adaptation appear in our data as effects of environmental heterogeneity. As spatial heterogeneity and temperature seasonality increased, local regions contained more species and localities became less similar in terms of species composition. More heterogeneous environments allowed for the coexistence of more species. These results are consistent with other studies that found a positive correlation between environmental heterogeneity and species richness (e.g., Richerson & Lum 1980; Cowling 1990; Rescia et al. 1994; Scheiner & Rey-Benayas 1994; Hooper & Vitousek 1998; Wohlgemuth 1998).

We found a similar effect due to bedrock type. The granitic and calcareous bedrock types had higher mean local species richness than the other bedrock types. Granitic bedrock is primarily located in mountainous areas. Several calcareous-type data sets represented high elevation regions as well. These areas are less intensively used than lower elevation areas where human use tends to simplify a region. These effects are particularly important in regions such as Iberia that have been subjected to human use for millennia. Again, disturbance intensity may decrease species niche breadth. The greater diversity of annual grasslands may also be due to effects of niche variation. Smaller individuals perceive a greater spatial heterogeneity because of their highly localized use of resources (Beatty 1984).

Using a variety of diversity measures

By the combination of four diversity measures we were able to take a step in disentangling determinants of species diversity. We have attempted to pose reasonable hypotheses about complex data where direct, experimental inference is difficult to come by, although we recognize the uncertainties in making mechanistic interpretations in such a situation.

Patterns of local and regional community richness provide complementary information. We found that species richness at these two different scales was partially determined by the same environmental factor, available energy, and partially determined by different factors (Table 6). Clearly, at least a portion of local and regional species richness patterns are each determined by processes unique to that scale.

Diversity at these two scales also may reflect the size of the wider pool of available species. At dispute, currently, is whether local species richness is primarily determined by the regional species pool, or is controlled by local processes (e.g., Pärtel et al. 1996; Caley &

Schluter 1997; see review in Grace 1999). The issue of regional vs. local control of species richness is analogous to the debate over top-down vs. bottom-up control of community structure. We expect that species richness patterns are determined by both local and regional processes. Unlike the bottom-up/top-down debate, however, we are constrained by our inability to perform manipulative experiments at these scales. While our hope is that in the end we will be able to find patterns that make definitive statements about the relative importance of regional and local processes, for now we must content ourselves with identifying plausible causal factors that may be operating at each scale. In this paper we have examined this issue primarily from a local-scale viewpoint. Further analysis using a more comprehensive measure of the regional species pool is necessary before we can more definitively address the issue of regional control for Iberian communities.

The measurement of mean compositional similarity and mosaic diversity provided additional insight. Mean compositional similarity provides information on whether adding species to a local region occurs by adding entirely new communities thereby creating a patchwork, or whether it occurs by the substitution of species within existing communities. Because transition zones did not have lower mean compositional similarities, we concluded that such zones are a mingling of species within communities, not a patchwork of communities in a local region. If the transition zone was a patchwork of communities from two floras, rather than a mingling within communities, mean compositional similarity would have been lower in the transition zones.

Mosaic diversity provides information on how common and rare species are distributed in a region. Higher values of mosaic diversity indicate that species are more segregated into communities that are rich in common species or rich in rare species. For Iberia, higher mosaic diversity always was associated with factors that increased species richness, either locally or regionally. This indicates that species-rich regions have proportionally more rare species. Because of the insights gained from a multiplicity of diversity measures, we encourage their use when attempting to discover the determinants of diversity patterns.

Global change and conservation

Our results have clear implications for the effects of global change on species conservation. First, reduction of spatial environmental heterogeneity by land use will likely lead to species loss (Rescia et al. 1997). This reduction is particularly acute in mountainous regions, which are threatened by increasing recreational activities (Gómez Limón & De Lucio 1995). Second, biogeographical transition zones are of interest for *in situ* species conservation since they harbor the largest biodiversity pools. Species rarity – a diversity component included in our measure of mosaic diversity – should also be explicitly taken into account in conservation policies (Williams et al. 1991; Ojeda et al. 1995; Rey Benayas et al. 1999). Third, global climate change is expected to decrease AET and temperature seasonality, and increase precipitation seasonality (Houghton et al. 1990; Oñate & Pou 1996). These effects would result in a decrease in local and regional species richness. Anticipating and mitigating the effects of global change will require further study of the mechanisms that determine species diversity.

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Table 1. Mean ± SD for each biogeographical province and results of ANOVA for mean local species richness, regional community richness, mean compositional similarity and mosaic diversity. For mean local species richness, annual grassland communities were excluded (N in parenthesis). Only provinces with at least 4 data sets were included in the analyses; 4 provinces were thus excluded here. Provinces included are: B = Betic, C-I-L = Carpetano-Iberico-Leonesa, C-M-M = Castellano-Maestrazgo-Manchega, L-E = Luso-Extremadurense, P = Pirineos, M-A = Murciano-Almeriense, C-V-P-B = Catalano-Valencaino-Provenzano-Balear. Regional community richness and mosaic diversity differed among provinces. Provinces with statistically indistinguishable values ($\alpha < 0.05$, Tukey's test) are indicated by the same superscript. For regional community richness, because of small sample sizes, we were unable to determine which pairwise comparisons were significantly different.

Province	Mean local species richness	Regional comm. richness	Mean compositional similarity	Mosaic diversity	N
P	23.12 ± 4.11	294.84 ± 134.94	0.240 ± 0.046	5.123 ± 1.068^{A}	8
M-A	17.36 ± 5.23	237.47 ± 130.65	0.186 ± 0.067	4.114 ± 0.706^{AB}	4
C-I-L	18.34 ± 6.75	191.99 ± 98.36	0.236 ± 0.07	3.779 ± 0.829^{B}	31 (28)
C-M-M	19.09 ± 6.63	168.36 ± 78.96	0.204 ± 0.072	3.985 ± 0.667^{B}	16 (14)
L-E	17.45 ± 5.15	155.18 ± 71.41	0.259 ± 0.094	3.721 ± 0.795^{B}	16 (14)
B	23.97 ± 7.95	143.59 ± 54.09	0.191 ± 0.067	3.608 ± 0.922^{B}	8 (7)
C-V-P-B	18.17 ± 7.21	142.36 ± 31.45	0.242 ± 0.059	4.154 ± 0.679^{AB}	5 (4)
F	0.27	3.06	1.44	3.5	
P	0.9	0.009	0.2	0.004	
R^2	0.02	0.18	0.09	0.21	

Table 2. Multiple regression analyses of the effects of biogeography, environmental favorability, and environmental variation on (A) mean local species richness, (B) regional community richness, (C) mean compositional similarity, and (D) mosaic diversity. Models were determined by a stepwise procedure. Standardized regression coefficients are shown.

Effect	Coefficient	SE	P
A. Mean local species richness (N = 84, R^2 = 0.17)			
AET	0.289	0.133	0.03
Precipitation	-0.301	0.135	0.03
CV(Precipitation)	-0.298	0.104	0.005
B. Regional community richness (N = 93, R^2 = 0.24)			
AET	0.434	0.139	0.003
Precipitation	-0.434	0.136	0.002
WHC	-0.300	0.107	0.006
Altitudinal range	0.257	0.112	0.02
Transition	0.358	0.107	0.001
C. Mean compositional similarity (N = 93, R^2 = 0.21)			
Altitudinal range	-0.397	0.097	0.0001
No. of bedrock types	-0.208	0.096	0.03
Temperature SD	-0.228	0.097	0.02
D. Mosaic diversity (N = 93, R^2 = 0.24)			
AET	0.332	0.119	0.008
Precipitation	-0.324	0.133	0.01
Transition	0.388	0.098	0.0002

Table 3. Correlations among the independent variables used in the stepwise regression analysis grouped into measures of favorability (temperature, precipitation, actual evapotranspiration – AET, and water holding capacity – WHC), spatial heterogeneity (area, altitudinal range, number of bedrock types), and temporal heterogeneity (temperature SD, precipitation CV). Values in boldface are statistically significant ($\alpha < 0.05$) after Bonferonni correction for multiple tests.

	Temperature	Precipitation	AET	WHC	Area	Altitudinal range	Number of bedrock types	Temperature SD
Precipitation	**-0.52**							
AET	-0.17	**0.53**						
WHC	0.03	0.09	0.28					
Area	0.26	-0.18	-0.16	-0.04				
Altitudinal range	-0.22	0.24	-0.10	0.20	0.19			
No. of bedrock types	0.05	-0.001	0.13	0.19	0.30	0.01		
Temperature SD	-0.08	**-0.44**	**-0.36**	-0.04	-0.04	-0.11	-0.29	
Precipitation CV	**0.52**	0.06	0.06	-0.02	0.25	-0.002	0.25	**-0.52**

Table 4. Mean ± SD for each community type and results of ANOVA for mean local species richness, regional community richness, mean compositional similarity and mosaic diversity. Only mean local species richness differed among types. Types with statistically indistinguishable mean values ($\alpha < 0.05$, Tukey's test) are indicated by the same superscript.

Community type	Mean local species richness	Regional comm. richness	Mean compositional similarity	Mosaic diversity	N
Deciduous forests	22.14 ± 5.39^{A}	195.76 ± 50.79	0.229 ± 0.061	4.187 ± 0.952	15
Coniferous forests	21.15 ± 5.75^{AB}	260.83 ± 187.39	0.243 ± 0.057	4.575 ± 1.493	7
Evergreen woodlands/garrigue	18.54 ± 5.34^{AB}	152.57 ± 49.81	0.251 ± 0.073	4.057 ± 0.606	17
Tall shrublands	14.64 ± 3.89^{B}	186.83 ± 115.99	0.224 ± 0.084	3.554 ± 0.871	22
Dwarf shrublands	25.02 ± 6.94^{A}	243.47 ± 93.38	0.188 ± 0.069	4.164 ± 0.705	8
Perennial grasslands	20.89 ± 7.16^{AB}	146.31 ± 72.01	0.252 ± 0.088	3.949 ± 0.742	15
Annual grasslands*	135.16 ± 33.36	185.71 ± 49.81	0.178 ± 0.049	4.007 ± 0.965	9
F	5.96	2.18	1.69	1.62	
P	0.0001	0.053	0.13	0.15	
R^2	0.28	0.13	0.11	0.10	

*Not included in comparison of mean local species richness

Table 5. Mean ± SD for each bedrock type and results of ANOVA for mean local species richness, regional community richness, mean compositional similarity and mosaic diversity. Only data sets that had a single bedrock type were included in the analyses. For mean local species richness, annual grassland communities were excluded from the analyses (N in parentheses). Only mean local species richness and mosaic diversity differed among types. Types with statistically indistinguishable mean values ($\alpha < 0.05$, Tukey's test) are indicated by the same superscript. For mean local species richness, because of small sample sizes, none of the pair-wise comparisons were significantly different.

Bedrock type	Mean local species richness	Regional comm. richness	Mean compositional similarity	Mosaic diversity	N
Calcareous	21.36 ± 5.69	197.57 ± 97.15	0.232 ± 0.068	4.385 ± 0.911^{A}	19 (17)
Sandstone	14.25 ± 5.72	132.31 ± 65.62	0.226 ± 0.081	3.513 ± 0.456^{B}	9 (7)
Metamorphic	13.53 ± 4.07	175.99 ± 94.06	0.215 ± 0.095	3.134 ± 0.386^{B}	6 (4)
Granitic	20.39 ± 6.69	181.34 ± 127.61	0.263 ± 0.082	3.852 ± 0.774^{AB}	17 (16)
F	3.73	0.81	0.83	5.45	
P	0.02	0.5	0.5	0.003	
R^2	0.22	0.05	0.05	0.26	

Table 6. Summary of analyses of biogeographic and environmental effects on patterns of plant diversity in Iberia, showing only those variables that were statistically significant for at least one diversity measure. Statistical significance is indicated either as * for categorical variables or +/- for continuous variables. Non-significance is indicated by 0.

Effect category	Effect comm.	Mean local richness	Regional richness	Mean similarity	Mosaic diversity	Hypothesized class of causal factors
Biogeography	Transition zone	0	*	0	*	Intermediate environment
Environmental favorability	AET	+	+	0	+	Number of individuals
	Total ppt	-	-	0	-	Limits to adaptation
	WHC	0	-	0	0	Number of individuals
	Bedrock type	*	0	0	*	No. of individuals, niche variation
	Community type	*	0	0	0	No. of individuals, intermed. environ.
Temporal heterogeneity	CV(ppt)	-	0	0	0	Limits to adaptation
	SD(temp)	0	0	-	0	Niche variation
Spatial heterogeneity	Alt. range	0	+	-	0	Niche variation
	No. bedrock types	0	0	-	0	Niche variation
	Community type	*	0	0	0	Niche variation

Figure captions

Fig. 1. Locations of the 93 data sets in the Iberian Peninsula and the Balearic Islands. The dashed lines indicate borders between biogeographical provinces. The bold dashed line is the border between the Atlantic and the Mediterranean climatic zones. “T” indicates a transitional data set (see text), some T’s indicate more than one data set.

Fig. 2. Relationship between AET and (A) mean local species richness, standardized at a grain of 100 m^2, and (B) regional community richness. Closed symbols indicate non-transitional regions, open symbols indicate transitional regions. Simple regressions are shown here for illustrative purposes only. See Table 2 for statistics of the multiple regression models.

Fig. 3. Relationship between altitudinal range and (A) regional community richness and (B) compositional mean similarity. Closed symbols indicate non-transitional regions, open symbols indicate transitional regions. Simple regressions are shown here for illustrative purposes only. See Table 2 for statistics of the multiple regression models.

Appendix. Sources of the plant-by-plot data.

Data set label	Source(s)
1B	Alcaraz et al. (1989)
2B	Rivas Martínez et al. (1990)
3	Rivas Martínez et al. (1992)
4	Rivas Martínez et al. (1992)
5	Bolós & Moliner (1958)
10B	Moreno (1983); Rivas-Martínez (1968); Rivas-Martínez & Cantó (1987)
11	Fernández-González (1991); Rivas-Martínez (1963), Rivas-Martínez et al. (1987)
12	Fernández-González (1991)
13B	Fernández-González (1991); Rivas-Martínez & Cantó (1987); Rivas-Martínez (1963); Rivas-Martínez et al. (1987)
15	Rivas-Martínez et al. (1984)
16	Asensi & Rivas-Martínez (1976)
19	Pérez Chiscano (1976)
20	Pérez Chiscano (1976)
23	Lapraz (1962)
25	Rivas Goday & Borja (1961)
27	Alcaraz (1984)
28	Sánchez Gómez (1990)
29	Peralta (1992)
30	Rey Benayas (1991)
31	Rey Benayas (1991)
32	Rey Benayas (1991)
33	Rey Benayas (1991)
34	Rey Benayas (1991)
36	Sánchez-Colomer (1998)
37	Sánchez-Colomer (1998)
38	Sánchez-Colomer (1998)
39	Peralta (1992)
40	Peralta (1992)
41	Luceño & Vargas (1986)

42	Costa (1974)
43	Peralta (1992)
47	Valdés (1984)
48	Rivas-Martínez (1963); Sánchez-Colomer (1998)
49	Izco & Ortiz (1985)
50	Izco & Ortiz (1985)
51	Marcos (1985)
52	Pérez Carro (1982)
53B	Ortiz (1986)
55	Silva (1990)
56	Romero (1993)
57	Romero (1993)
58	Ortiz et al. (1991)
59	Izco et al. (1985)
61	Bellot & Casaseca (1956)
62	Fernández-González & Molina (1988)
63	Amigo (1984)
64	Amigo (1984)
65	Rivas-Martínez et al. (1991)
66	Casas & Ninot (1995)
68	Cano & Valle (1988)
69	Donated by the owner
74	de la Cruz (1994)
75	de la Cruz (1994)
76	de la Cruz (1994)
77	de la Cruz (1994)
80	Alcaraz (1984)
81	Alcaraz (1984)
82	Sánchez Gómez (1990)
83	Navarro (1986)
84	Navarro (1986)
85	Navarro (1986)
86	Navarro (1986)

88A	Ferrao de Carvlho (1988)
89	Capelo & Ferreira de Almeida (1993)
95	Ferrer (1993)
96	Montserrat (1986)
99	Martínez (1978)
100	López Vélez (1994)
101	López Vélez (1994)
102	López Vélez (1994)
103	López Vélez (1994)
104	de la Fuente (1982)
105	de la Fuente (1982)
106	de la Fuente (1982)
107	Malato (1982)
108	Tamajón et al. (1994)
109	Capelo et al. (1994)
110	Costa et al. (1994)
111	Malato Beliz (1986)
112	Malato Beliz (1990)
113	Malato Beliz (1990)
114	Capelo (1996)
115	Capelo (1996)
118	López Vélez (1994)
120	Belmonte (1986)
121	Ruiz (1986)
122	Mateo (1983)
123	Mateo (1983)
124	Álvarez (1992)
127	Data donated by the owner
129	Carreras et al. (1995)
130	Carreras et al. (1995)
131	Carreras et al. (1995)

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FIGURA 1

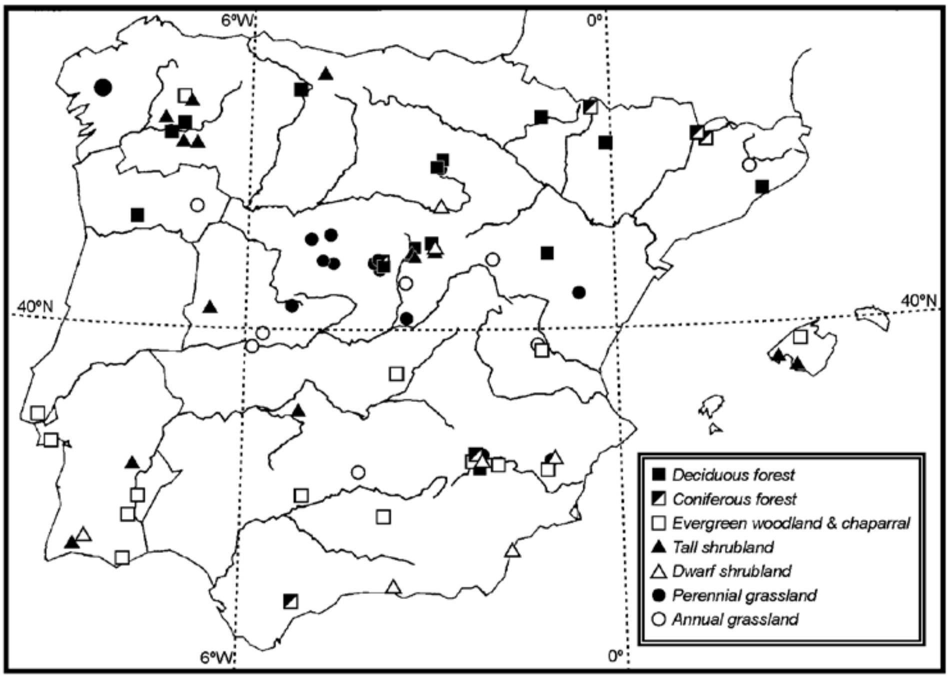

6°W
0°
40°N
40°N
6°W
0°
■ *Deciduous forest*
◪ *Coniferous forest*
□ *Evergreen woodland & chaparral*
▲ *Tall shrubland*
△ *Dwarf shrubland*
● *Perennial grassland*
○ *Annual grassland*

FIGURA 2

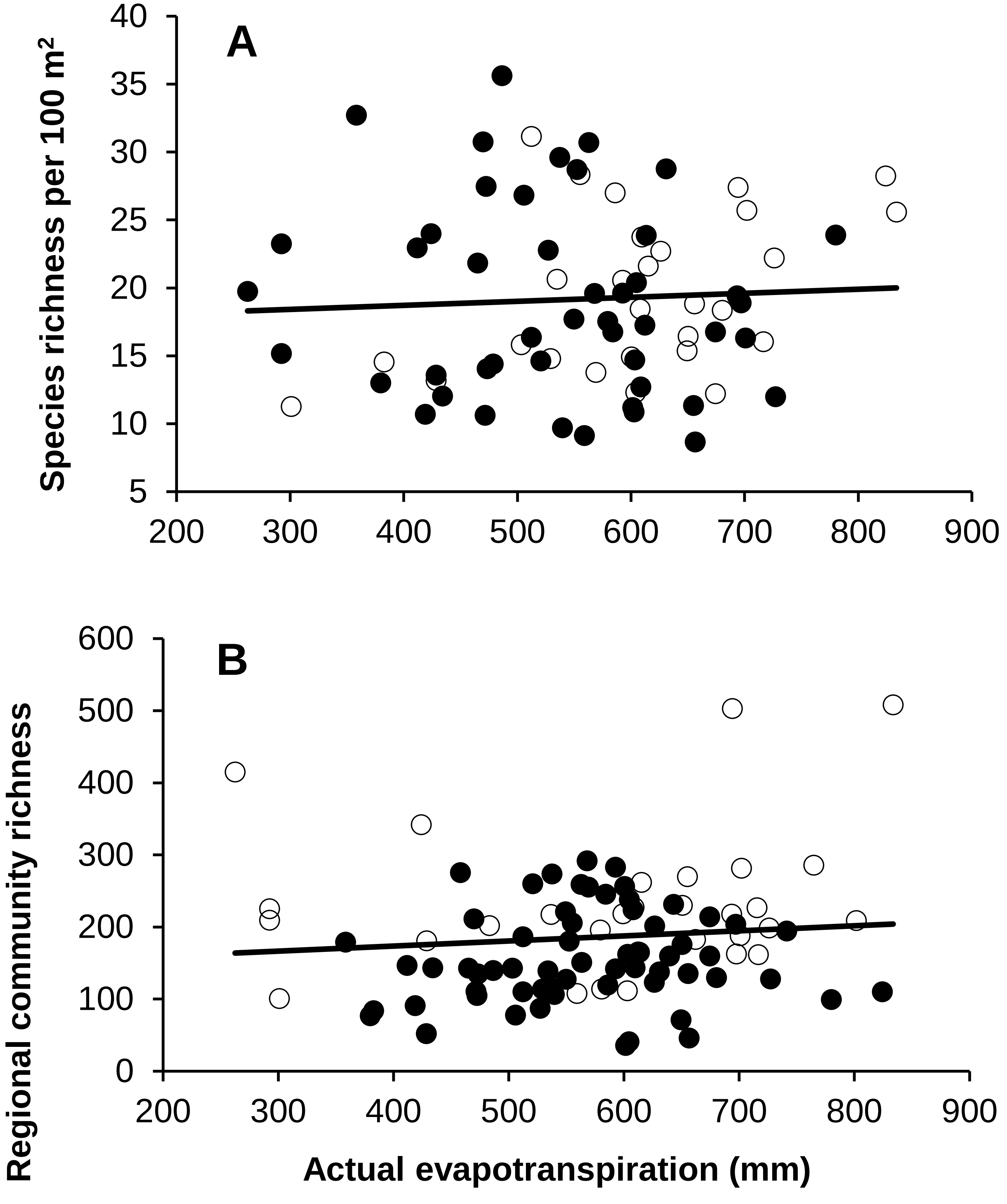
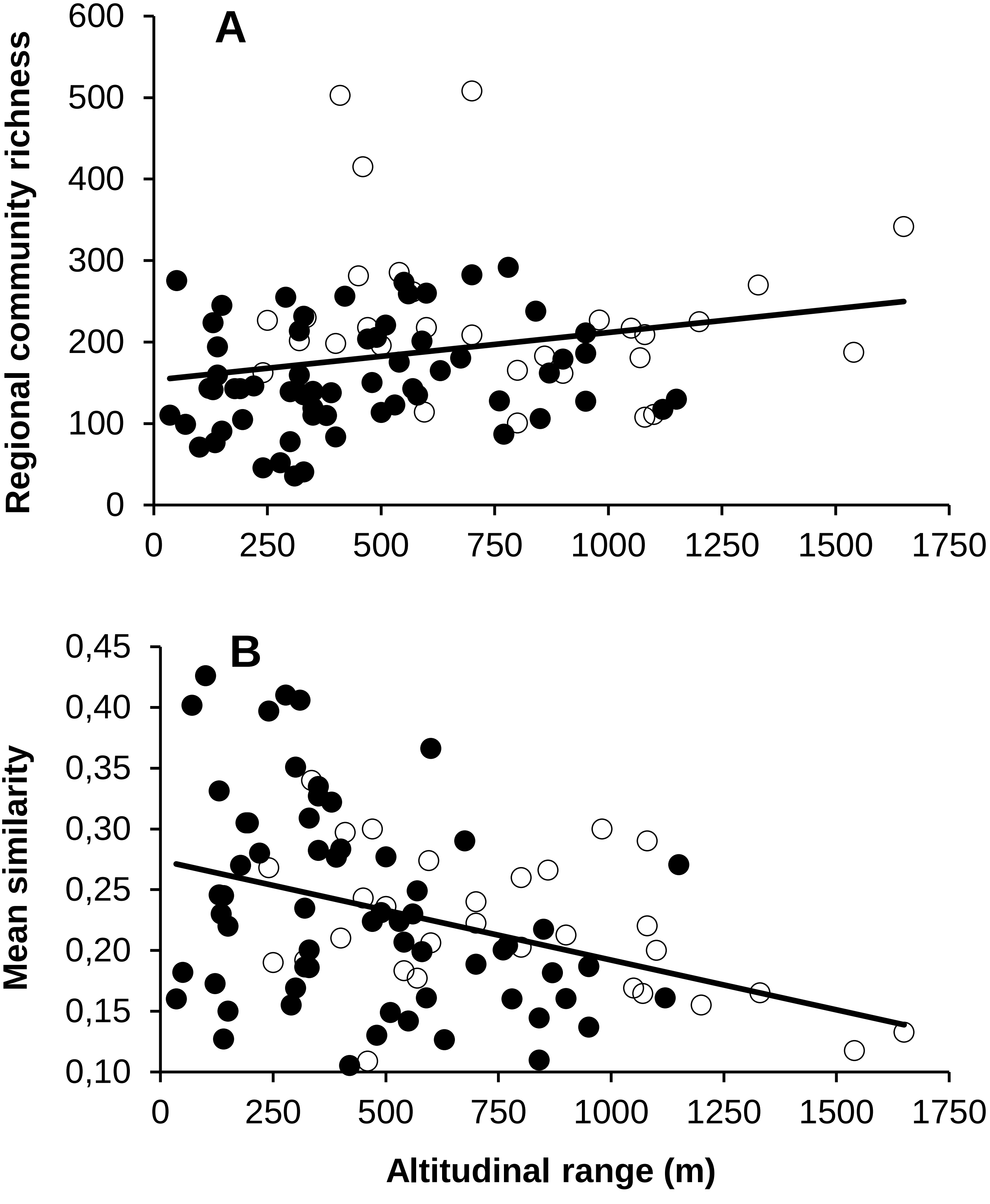

A
Species richness per 100 m²
40
35
30
25
20
15
10
5
200
300
400
500
600
700
800
900
B
Regional community richness
600
500
400
300
200
100
0
200
300
400
500
600
700
800
900
Actual evapotranspiration (mm)

FIGURA 3


A
Regional community richness
0
100
200
300
400
500
600
0
250
500
750
1000
1250
1500
1750
B
Mean similarity
0,10
0,15
0,20
0,25
0,30
0,35
0,40
0,45
0
250
500
750
1000
1250
1500
1750
Altitudinal range (m)