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Global patterns of plant diversity

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Summary

Using 94 data sets from across the globe, we explored patterns of mean community species richness, landscape species richness, mean similarity among communities and mosaic diversity. Climate affected community species richness primarily through productivity while other climatic factors were secondary. Climatic equability affected species richness only in temperate regions where richness was greatest at high levels of temperature variability and low levels of precipitation variability. Landscape species richness correlated positively with community species richness. A global gradient in mean similarity existed but was uncorrelated with community species richness. Mean similarity was least and mosaic diversity was greatest between 25 and 30° latitude. The most diverse landscapes (low mean similarity) correlated with warm temperatures, high elevations, large areas and large seasonal temperature fluctuations. The most complex landscapes (high mosaic diversity) correlated with large areas, high productivity and warm winters. We compared diversity measures among continents and found only one significant difference: Australian landscapes have greater mosaic diversity than African landscapes. Based on our analyses we propose two hypotheses: (1) for plants, biotic interactions are more important in structuring landscapes in warmer climates and (2) longer isolated landscapes have more clearly differentiated ecological subunits.

Keywords: climate; community species richness; landscape species richness; latitudinal gradient; mean similarity; mosaic diversity

Introduction

Ecologists have explored patterns and causes of species diversity from the inception of the discipline. For example, Wallace (1878) noted a gradient in species richness from the tropics to the poles. Species richness of tropical regions is often one to two orders of magnitude greater than temperate regions which in turn can be an order of magnitude greater than polar regions; this pattern extends across a wide range of taxa (see the review in Stevens (1989)).

Many causes of global patterns in species richness have been proposed (Pianka, 1966; see reviews in introductory ecology textbooks). In this paper we examine, for terrestrial vascular plant species, global relationships between species richness and three climatic factors: available energy (Preston, 1962; Connell and Orias, 1964; Currie and Paquin, 1987; Adams and Woodward, 1989; Currie, 1991), climatic mildness and climatic equability (Sanders, 1968). Most analyses of latitudinal gradients examine either community species richness or regional species richness (e.g. Currie and Paquin, 1987; Adams and Woodward, 1989). Although those species exist within communities and those communities within landscapes, no information exists on how community differentiation and landscape complexity vary on a global scale. Thus, we examine global patterns of two previously unexplored measures of landscape diversity, mean similarity among communities and mosaic diversity. By analysing global patterns of landscape diversity, we may be able to discover general rules which govern community composition.

We investigated four diversity measures: community species richness (α-diversity), landscape species richness (γ-diversity), mean similarity (β-diversity) and mosaic diversity (compositional pattern diversity). Species richness is the number of species in a community or landscape and is

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the simplest measure of inventory diversity (Whittaker, 1977). Differentiation diversity is the resemblance in species composition between two communities. At the level of the landscape it is termed β-diversity. Most commonly β-diversity is measured as species turnover along an environmental gradient (Whittaker, 1972). A second measure was proposed by Whittaker, the mean similarity among communities in a landscape. Although mean similarity was not favoured by Whittaker, we use it here because it is a general and robust measure that can be readily compared among landscapes (Scheiner, 1990). In this study we measured similarity with the Jaccard index (Jaccard, 1901) and computed mean similarity as the mean of all pairwise similarity scores of sites in a landscape.

Pattern diversity is a measure of the relative arrangement of subunits within an ecological unit (Scheiner, 1992). For example, spatial pattern diversity would measure the physical arrangement of items on a surface. Indices of clumped versus overdispersed distributions are examples. In this paper we consider communities within a landscape and a specific form of pattern diversity, compositional pattern diversity. Compositional pattern diversity is the mathematical pattern within a site-species data matrix. It is the arrangement of sites in the n-dimensional hyperspace derived from the site-species matrix where n is the number of species and individual sites are points whose coordinates are defined by their species compositions. Compositional pattern is analogous to spatial pattern, but differs in the number of dimensions. Here we measure it as mosaic diversity. Mosaic diversity measures landscape complexity and varies as a function of two properties of species patterns, the variation in species richness among communities and the variation in commonness or rarity among species (evenness). A low value of mosaic diversity indicates a simple landscape with one or a few underlying environmental gradients and which is dominated by a few species; a high value indicates a complex landscape with many environmental gradients and no ubiquitous species. Scheiner (1992) presents the details for computing mosaic diversity and an exploration of what it measures.

Materials and methods

We assembled surveys of 94 terrestrial landscapes from across the globe (Fig. 1; see the Appendix). The total latitudinal range was 43°S–81°N with 47 tropical or subtropical (0–35°), 41 temperate (36–55°) and six polar (64–81°) landscapes. The landscapes came from all continents except Antarctica: North America (30), Central America (1), South America (4), Eurasia (26), Africa (17), and Australia (16). Each data set consisted of a site-by-species matrix from which we extracted presence/absence information.

When choosing the data sets we used the following criteria. Each data set had to describe a single region and to represent a landscape of at least 10 km^2. The actual landscape size surveyed ranged from 0.5 to 740 000 km^2 (mean 755 km^2). However, the smallest samples represented a larger landscape according to the author(s) of those studies. The size of the landscape surveyed did not correlate with the latitude ($\log_{10}$ (landscape size) versus absolute latitude, $r = -0.06$, $n = 84, p < 0.5$).

Most surveys included all community types within a region although some were restricted to one type (e.g. just forests within a forest–grassland mosaic). The number of sites sampled within each landscape was generally at least 30 (mean 67.8 sampled sites, range 19–144); we chose 30 to avoid most sampling artefacts (Scheiner, 1990, 1992). The number of sites sampled did not correlate with latitude ($r = -0.13$, $n = 94$, $p < 0.5$).

Site sizes ranged from 0.5 m^2 for high arctic landscapes to 10 ha for tropical landscapes (mean 1.6 ha). We excluded surveys of sites smaller than typically used in a given biome type (e.g. <0.1 ha in temperate forests). We excluded surveys that included strongly anthropogenic determined

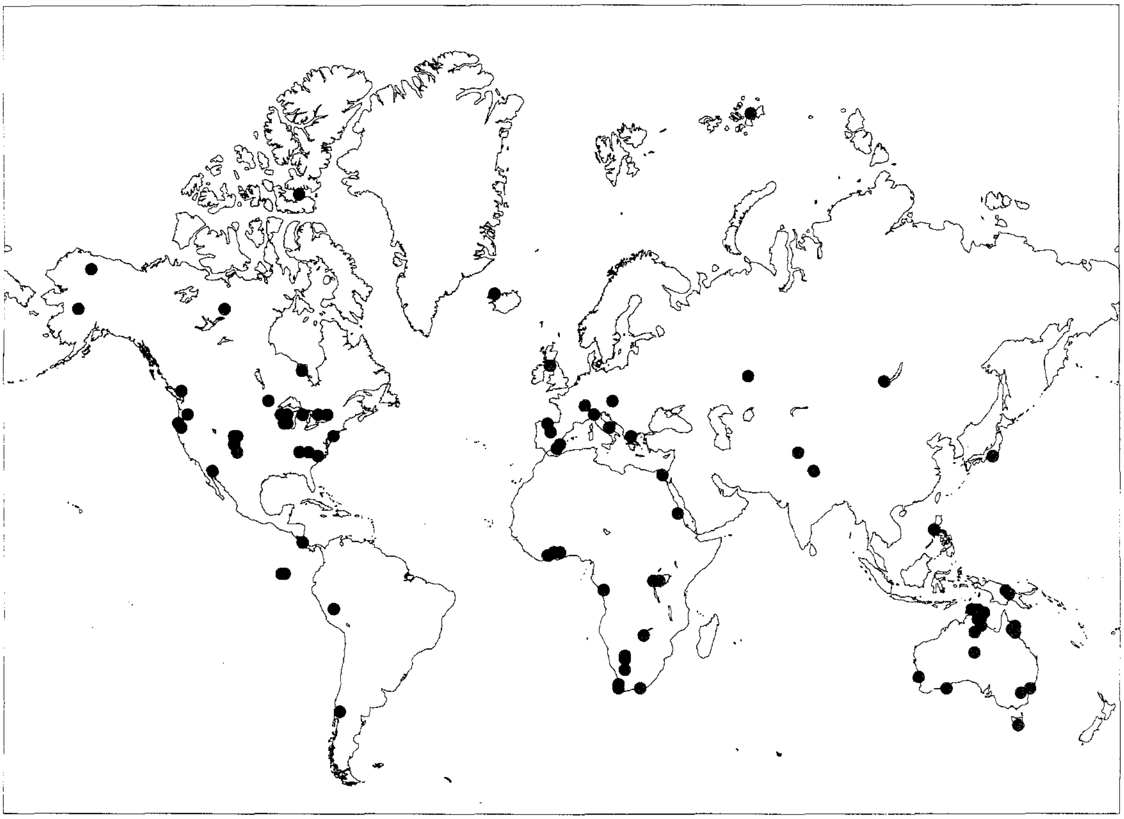

Figure 1. Distribution of sampled landscapes across the globe.

communities, although for some parts of the world (e.g. Europe and Japan) few truly 'natural' communities exist.

We tried to choose surveys that included all types of vascular plants (i.e. annuals, herbaceous perennials, shrubs and trees). We excluded those which did not include a complete sampling within indicated life-forms (e.g. studies in which rare species were not reported). Sometimes we used data sets from published sources and sometimes researchers kindly supplied them. (See the Appendix for a complete listing. All data sets from published sources are available upon request.)

For each landscape we calculated the mean number of species per site, total number of species, mean similarity among sites and mosaic diversity. We obtained climatic data from either the published paper or the nearest weather station (Rudloff, 1981; US West Optical Publishing, 1989; WeatherDisc Associates, 1989). Weather stations were, on average, within 113 km of the surveyed area; the largest distances were for high Arctic sites. We extrapolated for elevational effects as follows.

(1) For mean temperature we subtracted 6°C for every additional km of elevation (Barry, 1981).

(2) For mean annual precipitation we assigned the following surplus depending on the latitude and elevational range: latitudes between 30°S or 40°N but excluding equatorial areas were assigned a surplus of 8 mm for every additional 100 m in elevation, latitudes north of 40°N and

south of 30°S, but excluding polar areas, were assigned a surplus of 23 mm for every 100 m in elevation between 0 and 1500 m above sea level and a surplus of 53 mm for every 100 m above that (Lauscher, 1976; Barry, 1981).

For productivity values for each landscape we assigned the biome mean given in Whittaker and Likens (1973). For example, for all temperate deciduous forest landscapes we assigned a productivity of 540 gC/(m^2 year). For mixed landscapes we assigned the mean of the biomes.

We tested three hypotheses concerning the effect of climate on species richness within communities: available energy (amount of photosynthetically active radiation that can be used depending on available water), mildness and equability. For biologically usable available energy we used two measures, one direct (actual evapotranspiration) (Thornthwaite, 1948; Stephenson, 1990) and one indirect (biome productivity). We used the latter for most analyses as the information necessary to calculate the former was available for only approximately two-thirds of the landscapes. The correlation of the two measures for our data was $r = 0.64$, $n = 58$, $p < 0.0001$.

Mildness is the degree to which plant tissues are subjected to physiological stress. We tested for the effects of mild climates by looking for a negative quadratic response to mean annual temperature – intermediate temperatures being milder – or a monotonic positive response to total annual precipitation – higher precipitation being milder.

Equability is a lack of variation and indicates the degree to which plant tissues do not have to adjust to variation in climate during the year. We measured equability as its inverse, using four measures of climatic variability: the standard deviation of mean monthly temperature, the standard deviation of total monthly precipitation, the standard deviation of monthly actual evapotranspiration and the standard deviation of monthly water balance. For all analyses of species richness we used only those data sets for which the entire vascular flora was sampled.

Our ability to detect climatic effects on a global scale might be confounded by latitudinal differences in species richness, for example, by differences in continental areas or by differences in overall productivity. Thus, we also subdivided the data into tropical and subtropical landscapes (defined as those between 0 and 35° absolute latitudes) and temperate landscapes (defined as those between 35 and 55° absolute latitudes). (The small number of polar landscapes precluded separate analysis.) These designations are somewhat arbitrary but changing the boundary between subtropical and temperate landscapes to 30° absolute latitude did not substantially change our conclusions.

Our analyses included correlations, simple regressions and multiple regressions. For all of the analyses, we tested for normality and homoscedasticity and found no need to transform variables. Because we motivated most analyses with specific hypotheses using only pre-identified sets of independent variables, we did not use Bonferonni corrections for our statistical tests. In all cases we set a nominal α-value of 0.05. For all analyses we used SYSTAT (Wilkinson, 1988).

For landscape species richness, mean similarity and mosaic diversity we simply explored latitudinal gradients, comparisons among biomes and comparisons among continents. Our analyses of landscape species richness are tentative because of likely sampling artefacts. However, as this measure of diversity has been extensively studied in the past, we justify an exploratory analysis with the data at hand. Mean similarity and mosaic diversity have never been analysed on a global scale, thus we use this preliminary data to generate hypotheses for future studies. Again, in the analyses we did not use Bonferonni corrections and used stepwise multiple regressions for hypothesis generation only.

The data were limited in the following ways. First, our coverage of the globe was spotty; in particular, we had few data from South America and central Asia (Fig. 1). Second, although we tried to use only data sets which included all types of vascular plants, this was not always possible, especially for tropical forests. This constrained our analyses of species richness patterns (see below).

Third, we had to assume that the researcher(s) (1) used a sample plot large enough to capture most of the diversity within a community (or habitat) and not too much overlap between two or more communities (or habitats) and (2) adequately sampled the landscape. We found a positive correlation between $\log_{10}$ (plot size) and mean community species richness ($r = 0.64$, $n = 65$, $p < 0.0001$) (the species-area effect) and a negative correlation between $\log_{10}$ (plot size) and absolute latitude ($r = -0.33, n = 65, p < 0.01$). However, we would expect just such correlations as researchers will generally use a plot size just large enough to capture the diversity of the area under study. Our assumption is strengthened by a lack of correlation between total plant density (number of stems per m^2) and either latitude ($r = 0.28, n = 16, p < 0.5$) or plot size ($r = -0.38$, $n = 13$, $p < 0.5$). Thus, we interpret the correlation between plot size and latitude and, subsequently, some of the correlations of plot size and species richness as artefacts of ecological methodology, rather than an indication that latitudinal gradients are an artefact of sampling methods. That is, the direction of causation for the correlation is that greater species richness and larger life-forms (trees versus herbs) at low latitudes results in the use of a larger sample quadrat.

For landscape sampling adequacy we tried to minimize the problem by only choosing studies with large numbers of sites sampled and where the author(s) indicated that a representative sample of the landscape was taken. Here is one indication of the adequacy of our selection criteria. In all of the multiple regression analyses for community species richness, total landscape size sampled was never significant. Without our assumptions of sampling adequacy no global analysis is possible.

Fourth, as productivity values were not available for individual data sets, we had to use biome means. These forced us to interpolate productivity for data sets that consisted of mixed community types. More exact measures, however, would likely just strengthen our conclusions (see below). Fifth, all climatic and geographic data were not available for all data sets. Although this limited the power of some analyses, the missing data were fairly evenly distributed across the globe and are not likely to affect our conclusions.

Results

Community species richness and climate

We found that the primary determinant of species richness was biologically usable available energy, both measures correlating positively and linearly (actual evapotranspiration, $r = 0.34$, $n = 49, p < 0.01$; productivity, $r = 0.53, n = 82, p < 0.0001$). Examining the combined effects of climate and latitude we found that, for the globe as a whole, the landscapes with the greatest community species richness had high productivities, low latitudes and large seasonal temperature fluctuations (Table 1A). But, the overall model explained only 32% of the total variation. Perhaps more variation would be explained if actual productivity values for each landscape were available. Because these climatic factors do not change monotonically with latitude, a simple latitudinal gradient of community species richness does not exist (Fig. 2).

We tested hypotheses relating climatic mildness and equability to species richness performing these analyses on the entire data set and separately on tropical and temperate landscapes. Climatic equability is a lack of variation which we measured as its inverse. Variability in temperature related positively to species richness for the globe as a whole (Table 1A). Further analysis showed that this positive relationship was due to the effect of temperate landscapes, those with greater seasonality of temperature having greater community species richness ($r =$

Table 1. Multiple regression analyses of the effects of productivity and climate on community species richness

Variable	b'	SE	$p<$
A. All landscapes			
Productivity	0.531	0.099	0.0001
SD (temperature)	0.483	0.162	0.004
Latitude	−0.396	0.163	0.02
$R^2 = 0.32$	$n = 76$		
B. Temperate landscapes			
Productivity	0.638	0.121	0.0001
SD (temperature)	0.394	0.120	0.003
SD (precipitation)	−0.312	0.128	0.02
$R^2 = 0.60$	$n = 34$		

The magnitudes of the standardized regression coefficients (b') indicate the relative importance of each variable. Sample sizes differed among analyses as complete information was not available for all data sets.

0.50, $n = 37$, $p < 0.002$). This result contradicts previous hypotheses that equability correlates negatively with species richness.

When analysed by multiple regression both productivity and temperature variability positively affected species richness and, additionally, precipitation variability negatively affected it (Table 1B). This last effect agrees with the hypothesis that equability results in greater species richness. If we extended temperate landscapes to 30° absolute latitude, the effects of productivity and temperature variability were not changed, but the weak effect of precipitation variability was no longer statistically significant. Variability in temperature and variability in precipitation correlated negatively for temperate landscapes ($r = -0.36$, $n = 34$, $p < 0.05$).

Equability was not related to species richness in tropical and subtropical landscapes using either latitudinal criterion (not shown). Variability in actual evapotranspiration and water balance did not correlate with species richness for either temperate or tropical and subtropical landscapes (not shown).

Climatic mildness was not related to species richness measured either as moderate mean annual temperatures (quadratic regression coefficient: $b' = -0.085 \pm 0.172$, df = 1,68, $p < 0.62$) or as high total annual precipitation (linear regression coefficient: $b' = -0.129 \pm 0.117$, df = 1,69, $p < 0.25$). We arrived at the same conclusion in the separate analyses of tropical and temperate landscapes (not shown).

Biome types differed significantly in species richness ($F = 4.37$, df = 6,63, $p < 0.0009$) with forests, both tropical and temperate, being the most species rich and tundras and deserts being species poor (Table 2). That tropical forests were not the most species rich is somewhat misleading: we excluded the richest tropical landscapes from our analysis because they were incompletely sampled. Including incompletely sampled landscapes, mean community species richness for all tropical forests was 47.54 ± 6.48 (SE). None of the other biome types differed substantially from the values given in Table 2 when we included all landscapes.

Landscape species richness

Using an analysis of covariance model that corrected for the number of sites sampled, we found that biome types differed in landscape species richness ($F = 3.31$, df = 6,62 $p < 0.007$). The pattern among biomes followed that of community species richness (Table 2). For tropical

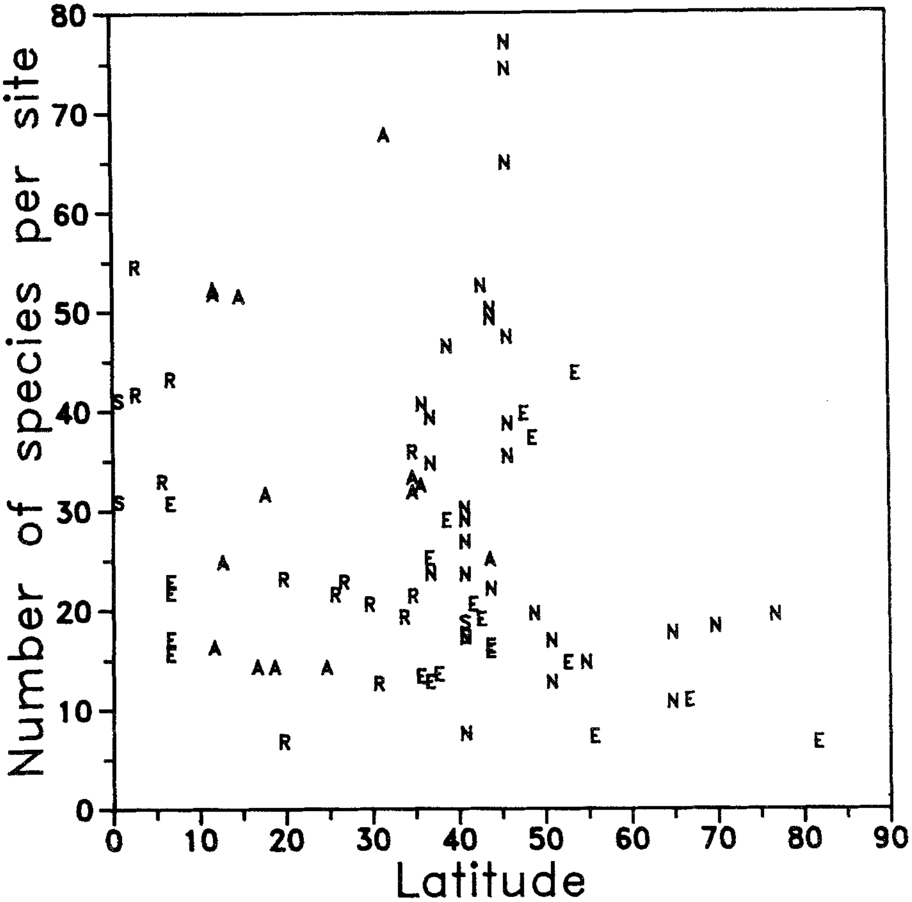

Figure 2. Number of species per site as a function of absolute value of latitude. The relationship was not significant ($n = 82, p < 0.18$). We used only those data sets for which all species were included in the survey. Symbols indicate continents: A, Australia; C, Central America; E, Eurasia; N, North America; R, Africa; S, South America.

forests, with all landscapes included, mean species richness was 452.7 ± 45.3 (SE) species per landscape.

Differentiation diversity

We found a quadratic latitudinal gradient for mean similarity with a minimum between 25 and 30° latitude (Fig. 3). Using a stepwise multiple regression procedure we found that mean similarity varied as a function of mean annual temperature, mean elevation, landscape area and the difference in temperature between the warmest and coldest months (Table 3). The most diverse landscapes (low mean similarity) had warm temperatures, high elevations, large areas and large seasonal temperature fluctuations. The latter two effects indicate that environmental variability, either spatial or temporal, increases landscape diversity. The regression of mean similarity on latitude was not statistically significant once we added the climatic variables (not shown). When added to the climatic model $\log_{10}$ (plot size) was not significant ($b' = 0.071 \pm 0.119$, df = 1,52

Table 2. Mean (± SE) diversity values by biome type

Biome	Community richness	Landscape richness	Mean similarity	Mosaic diversity	N^a	N^b
Tropical forest	37.33^{AB} ± 7.00	369.0^{A} ± 57.1	0.124^{A} ± 0.022	5.33^{A} ± 0.36	7	13
Tropical grassland	27.21^{AB} ± 4.77	268.0^{AB} ± 43.4	0.139^{A} ± 0.032	3.90^{A} ± 0.64	7	7
Shrubland	33.14^{AB} ± 5.04	315.3^{AB} ± 68.3	0.174^{A} ± 0.041	4.27^{AB} ± 0.43	9	9
Desert	17.30^{B} ± 2.72	138.3^{B} ± 17.9	0.134^{A} ± 0.012	3.61^{B} ± 0.13	6	8
Temperate broad-leaf and mixed forest	38.99^{A} ± 4.38	312.8^{AB} ± 38.8	0.180^{A} ± 0.016	3.59^{B} ± 0.19	18	17
Boreal forest	23.01^{AB} ± 4.31	195.6^{AB} ± 49.4	0.162^{A} ± 0.036	3.36^{B} ± 0.55	9	6
Tundra	17.75^{B} ± 1.82	132.2^{B} ± 24.9	0.241^{A} ± 0.036	3.22^{B} ± 0.23	14	12
Temperate grassland[c]	23.69 ± 4.71	151.5 ± 33.2	0.210 ± 0.031	3.34 ± 0.35	4	5
Temperate needle-leaf forest[c]	33.60 ± 6.70	238.3 ± 66.3	0.246 ± 0.045	3.39 ± 0.45	4	4

Means with different superscripts differ significantly at the $p < 0.05$ level based on a Tukey's test. Our analyses included only those biome types with sample sizes of six or more.

[a] Number of landscapes for which all species were recorded and used in analyses of community and landscape richness.

[b] Number of landscapes for which size of landscape sampled was recorded and used in analyses of mean similarity and mosaic diversity.

[c] Not included in the analyses due to small sample size.

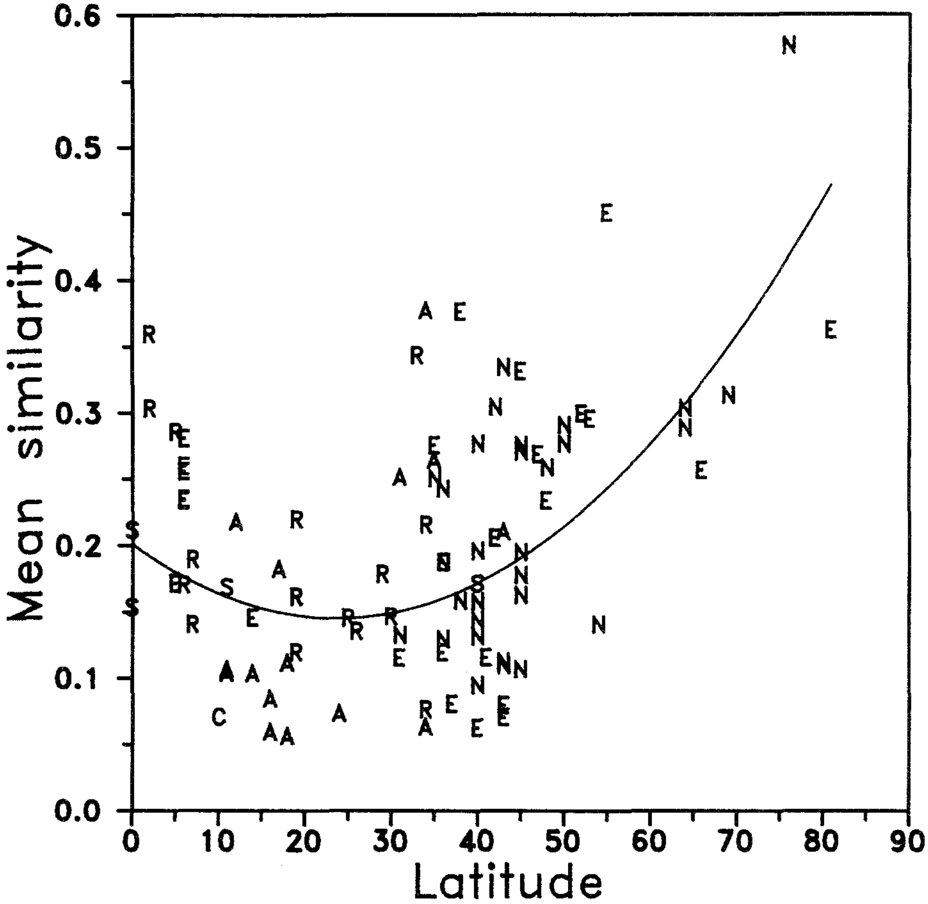

Figure 3. Mean similarity as a function of absolute value of latitude. The line is the least-squares quadratic regression; the relationship was significant (SIM = 0.20 – 0.0047 LAT + 9.9 × 10^{-5} LAT^2, $R^2 = 0.29$, $n = 94$, $p < 0.0001$), Symbols are as in Fig. 2.

Table 3. Multiple regression analysis of mean similarity

Variable	b'	SE	$p <$
Mean temperature	−0.752	0.140	0.0001
Mean elevation	−0.485	0.102	0.0001
Log_{10} (landscape size)	−0.416	0.092	0.0001
Temperature difference	−0.295	0.126	0.03
$R^2 = 0.51$	$n = 78$		

Temperature difference is the difference in mean temperatures of the warmest and coldest months.

$p < 0.6$) indicating that the latitudinal gradient was due to climatic effects rather than due to a sampling artefact. Using an analysis of covariance model that corrected for landscape size effects, we found that biome types did not differ in mean similarity ($F = 2.04$, df = 6,64 $p < 0.07$) (Table

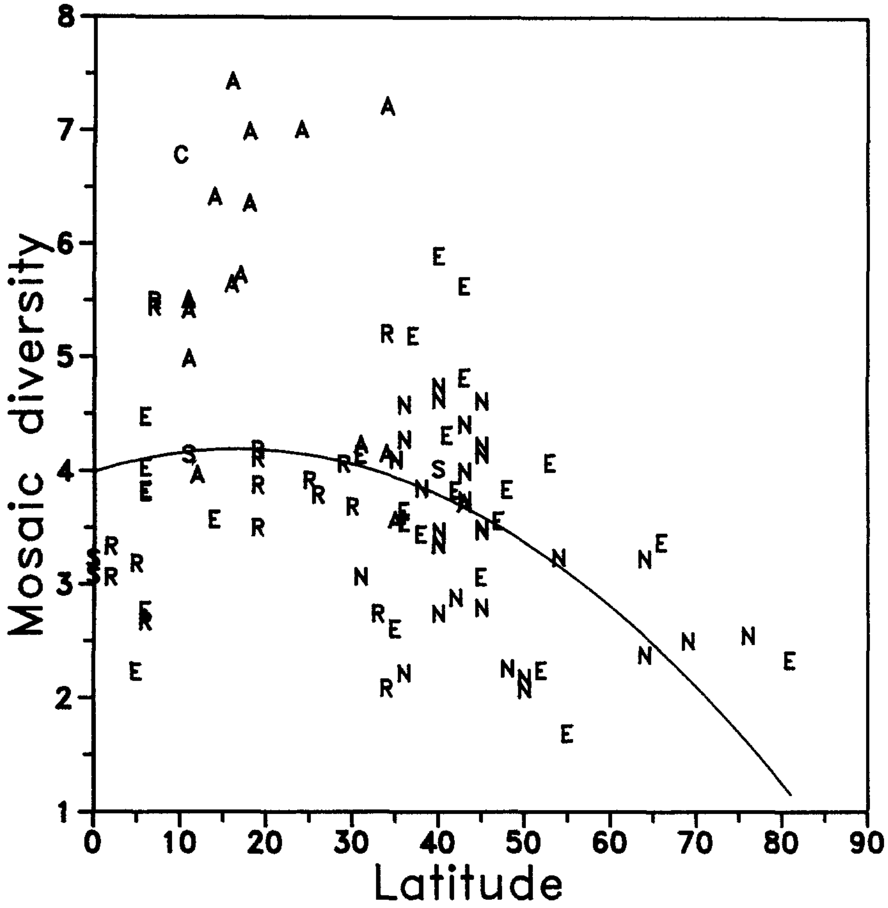

Figure 4. Mosaic diversity as a function of absolute value of latitude. The line is the least-squares quadratic regression; the relationship was significant (MOSAIC = 3.99 + 0.024 LAT -7.3×10^{-4} LAT^2, $R^2 = 0.16$, $n = 94$, $p < 0.0001$). Symbols are as in Fig. 2.

2). Community species richness and mean similarity were not correlated ($r = -0.02$, $n = 82$, $p > 0.5$).

Compositional pattern diversity

We found a quadratic latitudinal gradient for mosaic diversity (Fig. 4). Using a stepwise multiple regression we found that mosaic diversity varied as a function of landscape area, productivity and the mean temperature of the coldest month (Table 4). The most complex landscapes (high mosaic diversity) had large areas, high productivities and warm winters. Again, when added to the climatic model $\log_{10}$ (plot size) was not significant ($b' = -0.119 \pm 0.117$, df = 1,53, $p < 0.3$). Using an analysis of covariance model that corrected for landscape size effects, we found that biome types differed in mosaic diversity ($F = 4.42$, df = 6,64, $p < 0.0008$). The most complex landscapes were tropical or subtropical excluding deserts (Table 2). Community species richness and mosaic diversity were not correlated ($r = 0.19$, $n = 82$, $p = < 0.1$).

Table 4. Multiple regression analysis of mosaic diversity

Variable	b'	SE	$p <$
Log_{10} (landscape size)	0.445	0.086	0.0001
Mean temperature of the coldest month	0.346	0.088	0.001
Productivity	0.228	0.092	0.01
$R^2 = 0.49$	$n = 78$		

Continental differences

We compared community species richness, landscape species richness, mean similarity and mosaic diversity between two pairs of continents: North America versus Eurasia and Africa versus Australia. We chose these pairs because of similar latitudinal ranges and sampled biome types. To correct for geographic and climatic variables, we used an analysis of covariance model with the variables identified in the previous analyses (Tables 1A, 3 and 4). Of the eight comparisons, the only significant difference was the greater mosaic diversity in Australia (5.34 ± 0.33 (SE), $n = 16$) relative to Africa (3.60 ± 0.23 (SE), $n = 17$) ($F = 6.03$, df = 1,25, $p < 0.02$).

Discussion

We detected global patterns for all four measures of diversity: mean community species richness, landscape species richness, mean similarity and mosaic diversity, our study b eing the first such report for the latter two measures. Our analysis has obvious pitfalls due to the combination of data from so many different sources. Although different investigators undoubtedly used somewhat different methods for choosing sites and sampling the vegetation, for the patterns reported here to be artefacts would require some systematic – latitudinal or climatic – bias in sampling procedures. One systematic bias does exist, a gradient in plot sizes. However, this bias did not greatly affect our results as discussed below. The wide range of data sources argues against other such systematic biases. With regard to sampling bias, landscape species richness is the most susceptible, followed by mean community species richness, mean similarity and mosaic diversity as the least susceptible (Scheiner, 1990, 1992). In particular, for mosaic diversity, a failure to sample up to 50% of the species in a site results in only small changes in the estimated parameter (Scheiner, 1992).

One latitudinal bias clearly exists, that of plot size. The higher community species richness in the tropics could be due to the use of larger plot sizes. However, the negative correlation of total stem density with plot size suggests that, if anything, the tropical communities were under-sampled. The strongest predictor of community species richness was productivity which was uncorrelated with plot size ($r = 0.27$, $n = 16$, $p < 0.5$). Thus, although we view particular regression or correlation parameters with extreme caution, we conclude that the signs of the correlations and general patterns are likely to be robust.

We also face a potentially confounding factor in the interpretation of our results, different overall species richness levels on different continents or biogeographic regions. For example, consider the proposition (truth unknown) that North America is more species rich than Eurasia for historical reasons. This greater continental species richness might, in turn, result in greater regional and local species richness for a North American landscape than a Eurasian landscape even if the two landscapes have identical climates. Other diversity measures might be similarly affected. If these continental differences are confounded with latitude or climate – for example, North America versus Africa – then our latitudinal and climatic gradients could actually be due to these continental effects. However, two pieces of evidence suggest that our results are not so compromised. (1) In our continental comparisons, albeit of limited extent, we found no differences in species richness. (2) All latitudinal gradients were symmetrical about the equator. Thus, we saw no obvious or large-scale continental effects. A detailed comparison of diversity at a range of scales of a pair of similar continents, for example Africa and South America, is necessary to discover how diversity at one scale effects diversity at other scales.

Species richness

Species richness correlated positively with productivity. This factor was the primary determinant of landscape differences, a result consistent with previous studies (Currie and Paquin, 1987; Adams and Woodward, 1989; Currie, 1991). As our estimates of productivity were only approximate, we predict an even stronger relationship with better measures. The most important secondary effect was the greater diversity of landscapes with greater seasonal changes in temperature. We caution, however, that our conclusions are tentative because we included few tropical forests in this analysis. If included, the overall global trend or the trend among tropical and subtropical landscapes might differ. Gentry (1982), in an analysis of nine neotropical forest communities, found that species richness correlated positively with total annual precipitation, contrary to our finding of no correlation.

Of greatest interest, because it contradicts previous hypotheses, is the positive correlation of temperature variability with species richness in temperate latitudes. We believe this result means simply that seasonality allows for new life history strategies, one obvious example being spring ephemerals. Within a biogeographic province, species richness is a function of available niches. This claim finds support in the observation that forest biomes, regardless of latitude, were more species rich than shrub- or grassland-dominated biomes (Table 2). Forests contain more vertical structure and more opportunities for different successful life-history strategies.

For temperate landscapes the greatest community species richness was associated with a particular biogeographic area in North America, the Hemlock-White Pine–Northern Hardwoods Forest region, which is a transition zone between the Eastern Deciduous Forest and the Boreal Forest (Braun, 1950). Transition zones are hypothesized to have a greater species richness than adjacent areas (Shmida and Wilson, 1985) and an analysis (Scheiner and Istock, 1994) of one landscape in this region agrees with this hypothesis. Thus, it is not clear if the positive effect of temperature variability on species richness is a spurious correlation between temperature variability and the location of this transition zone or if, perhaps, the transition zone exists where it does because of the large temperature variability in this region. We favour the latter explanation by a direct examination of the data. The Hemlock-White Pine–Northern Hardwoods landscapes were not outliers but rather the end of a continuum; other non-transitional landscapes also contribute to the correlation. Additionally, Woodward (1987, Fig. 4.9) predicts the Hemlock-White Pine–Northern Hardwoods region to have a maximal leaf area index (the amount of leaf area per unit area of ground) for North America based on a climatic model incorporating temperature and precipitation. High leaf area index correlates with high species diversity (Smith and Huston, 1989).

In a study of tree species richness in North America, Currie and Paquin (1987) found results similar to ours. That analysis considered landscape species richness for 2.5° × 2.5° quadrats in relation to climatic and geographic factors. As in the present study, realized annual evapotranspiration (a measure of available energy and closely related to productivity) was most highly positively correlated with species richness. Additionally, our examination of their Currie and Paquin's (1987) Table 1 indicates that temperature variability was significantly positively correlated with species richness once the effects of productivity were accounted for. In the text, the authors state that there was no significant effect of climatic variability. However, they apparently based their conclusion on a stepwise multiple regression analysis using all variables. As they do not discuss the problem of multicollinearity among the variables, we cannot determine if their conclusion was a statistical artefact. Differences in results between the two studies may be due, in part, to our inclusion of all vascular species, not just trees. Herbaceous species may be responding to different factors than woody species and most species in most communities are herbaceous.

Landscape diversity and complexity

Landscape diversity and complexity as measured by mean similarity and mosaic diversity varied on a global scale (Figs 3 and 4). An understanding of the causes of patterns of these diversity measures leads us to two hypotheses. Both abiotic factors and biotic factors contribute to mosaic diversity. For example, mosaic diversity increases with the number of edaphic gradients (Scheiner, 1992). We reasonably assume no latitudinal gradient in the mean amount of edaphic variability within landscapes. Thus, latitudinal differences in mosaic diversity must be due to differences in biotic factors with more complex landscapes indicating greater biotic effects.

Simple landscapes, those dominated by one or a few environmental gradients and indicated by low mosaic diversity, predominate in boreal and polar regions (Fig. 4, Table 2). Interestingly, although we might expect deserts to be dominated by few environmental gradients, they were not. In structuring landscapes, environmental harshness due to cold temperatures apparently acts differently from environmental harshness due to low available moisture. Water is a resource and subject to competition while temperature is a condition. We conclude that a general trend in the processes responsible for structuring landscapes on a global scale exists. Cold regions apparently are structured primarily by abiotic conditions resulting in simple landscapes. Warm regions apparently are structured primarily by biotic interactions resulting in complex landscapes. Thus, we propose the following hypothesis: for plants, biotic interactions are more important in structuring landscapes in warmer climates.

We find curious the much higher levels of mosaic diversity in Australia than in Africa. Australia has a high percentage of endemic species with limited distributions. Such a condition may have arisen because of the continent's long isolation and extensive climate changes caused, in part, by the drifting of the continent northward to its present location. If biotic interactions lead to landscape complexity, then we predict that a long-isolated, co-evolved region would have a higher mosaic diversity, such as occurs in Australia. This greater complexity did not lead to differences in species richness or mean similarity. A greater mosaic diversity at equal levels of mean similarity indicates that species apparently are recognizing finer habitat distinctions among communities (Scheiner, 1992). Thus, we propose a second hypothesis: longer isolated landscapes have more clearly differentiated ecological subunits. Both hypotheses arise directly from the observed global patterns of mean similarity and mosaic diversity. They await testing by more detailed examinations of continental and regional floras.

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Appendix

Listing of data sets by continent indicating source. Numbers in parentheses indicate multiple data sets. Data sets listed with an asterisk are available from SMS on diskette.

Africa

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