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Diversity, productivity and scale in Wisconsin vegetation

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ABSTRACT

The relationship between diversity and productivity remains a contentious issue in ecology. Although some have asserted that the relationship is always hump-shaped, a comprehensive literature survey found no single relationship. We conducted a comprehensive examination of the components of scale (grain, focus and extent) across a geographic hierarchy (e.g. spatially defined) and two overlapping ecological hierarchies defined by formations and community types.

We examined how species richness of terrestrial vascular plants varies with net primary productivity in 901 stands scattered across the state of Wisconsin, USA. We found no single relationship between species richness and productivity. Instead, the relationship depends on the components of scale (grain, focus or extent) and hierarchy (ecological or geographic). For the state as a whole, the relationship was U-shaped. Such U-shaped relationships, while found previously, have been noted rarely and ignored completely by theory. For the geographic hierarchy, with increasing extent the relationship went from hump-shaped to negative to U-shaped. Increasing the grain resulted in the opposite pattern, the relationship going from U-shaped to negative to hump-shaped. With increasing focus, the relationship became negative. For the ecological hierarchy among community types, increasing the grain changed the relationship to negative, whereas for the among-formation hierarchy, increasing the grain eliminated any relationships. In contrast, increasing the focus among community types strengthened the U-shaped relationship, but similarly eliminated it among formations. Decreasing the extent – examining individual formations or community types – generally eliminated the relationship, although a negative relationship was found for prairies and sand barrens, a positive relationship was found for bracken grasslands, and U-shaped relationships were found for northern upland forests. These results have implications for how we study the effects of scale, its components, the effects of sampling bias, and the scale at which various causal mechanisms might be operating.

Keywords: diversity, mean similarity, productivity, scale, species richness, terrestrial vascular plants, Wisconsin.

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INTRODUCTION

The relationship between diversity and productivity remains a contentious issue in ecology. Some theories predict a unimodal or hump-shaped relationship (e.g. Grime, 1973, 1979; Huston, 1979; Tilman, 1982; Rosenzweig, 1992; Grace, 1999), and some authors have asserted that the relationship is always hump-shaped (Huston and DeAngelis, 1994). However, a comprehensive literature survey (Mittelbach *et al.*, 2001) found that no single relationship dominated. Rather, the relationship differed with scale and the taxonomic group under consideration. For terrestrial vascular plants, hump-shaped relationships predominated at geographical extents smaller than continents, although they accounted for only 40–50% of the relationships at any spatial extent. Positive monotonic relationships were equally common for plants at continental to global extents.

Scale is a multifaceted entity with multiple components that can be analysed across a variety of hierarchies. The three components are grain, focus and extent (Palmer and White, 1994; Scheiner *et al.*, 2000). Grain is the size of the common analytical unit. Focus is the sampling level or area represented by each data point, the inference space. For example, it may represent the scale at which the grains are aggregated or the scale at which a mean is calculated. Although the focus of an analysis may be larger than the grain, it can never be smaller. Extent is the scale at which the entire set of sample-units is analysed. These terms are further explained in the 'Methods' section in the context of our data analysis. Alternate hierarchies can be used to define scale; two commonly used hierarchies are geographic and ecological. A geographic hierarchy is based on spatial parameters (e.g. a total area of 100 km^2 divided into 1 km^2 quadrats), whereas an ecological hierarchy is based on species composition (e.g. within and among communities). The review by Mittelbach *et al.* (2001) only considered one aspect of scale, extent; we extend those results by also considering grain and focus.

The aims of this study were: (1) to demonstrate the need to consider multiple aspects of scale; (2) to show that, even in a limited data set, pattern varies as a function of scale; and (3) to briefly examine the implications of these data for some of those theories. An important limitation of most studies of diversity is confining analyses to a single grain and extent. Although some studies consider a range of extents, nearly all use a single grain size within a given study. However, different studies use different grain sizes, making it difficult to compare them. More fundamentally, the use of a single grain size assumes that that size is the 'correct' one. There is a strong tradition in plant ecology of determining a minimal area for sampling – the area at which the rate of increase of a species–area curve greatly slows (Mueller-Dombois and Ellenberg, 1974). The problem is that, if the area is large enough to capture most rare species, the area would be so large as to potentially include substantial environmental variation. Because environmental change is often gradual, any area is arbitrary. While a chosen grain might represent a typical minimum for a given region and community type, there is no guarantee that it is the 'correct' minimum for all samples.

A solution to this problem is to avoid assuming that any single scale is privileged. Rather, analyses should be done across a range of scales. Changes in the relationship between diversity and a third variable (such as productivity) as a function of scale can provide pointers towards the scale at which processes operate (Scheiner *et al.*, 2000). By not assuming that we know the correct scale *a priori*, we let the data speak for themselves. Our efforts here are simply the latest in a series of papers by many authors urging the use of a

multi-scale approach to ecological questions (e.g. Levin, 1992; Palmer and White, 1994; Wu and Loucks, 1995; Pastor *et al.*, 1996; Gross *et al.*, 2000; Scheiner *et al.*, 2000)

The ultimate purpose of scale analysis is to discern the mechanisms underlying ecological patterns. Mechanisms that operate on relatively small geographic scales and short timescales are amenable to experimental manipulation. Manipulation of putative causal mechanisms provides some of the clearest evidence for causal relationships. Such discernment is difficult when dealing with macroecological patterns. With mechanisms that operate at scales of time and space greater than those of typical manipulations, we must use pattern-matching to infer causal mechanisms. We observe patterns and match them to patterns generated by one or more putative mechanisms. In an ideal world, each mechanism would predict a unique pattern. In a less than ideal world, we hope that we can at least eliminate several putative mechanisms, thus narrowing further investigations.

Diversity–productivity relationships currently suffer from a surfeit of putative mechanisms, at least 24 by a recent count (e.g. Rosenzweig, 1971, 1995; Grime, 1973, 1979; Terborgh, 1973; Wollkind, 1976; Huston, 1979, 1994; Denslow, 1980; Oksanen *et al.*, 1981; Tilman, 1982, 1988; Wright, 1983; Huston and Smith, 1987; Abrams, 1988; Chesson and Huntly, 1988; Rohde, 1992, 1997; Moore *et al.*, 1993; Rosenzweig and Abramsky, 1993; Tilman and Pacala, 1993; Wright *et al.*, 1993; Colwell and Hurtt, 1994; Huston and DeAngelis, 1994; Leibold, 1996; Oksanen, 1996; Willig and Lyons, 1998; Stevens and Carson, 1999a,b; VanderMeulen *et al.*, 2001; Moore and de Ruiter, in press; for a description of many of these theories, see Gurevitch *et al.*, 2002: table 20.4). In this paper, we briefly consider four mechanisms in light of a scale-sensitive assessment of pattern. It would be wrong to consider our analyses as formal hypothesis tests. Instead, our current analyses are best considered as a hypothesis-generating activity. Because previous analyses have not comprehensively dissected scale components and hierarchies, we have no *a priori* expectations concerning the correspondence of pattern and scale. Second, and more importantly, most theories are not explicit regarding scale components and hierarchies. Typically, scale was not considered when theories were developed. A thorough examination of so many theories is a massive undertaking. Our hope is to reduce the list of theories to a manageable number by comparing the patterns found both here and in Mittelbach *et al.* (2001) with the currently available predictions of those theories and to suggest fruitful areas for subsequent analyses. We emphasize, though, that such theory testing is beyond the scope of the present paper.

To dissect the effects of scale more fully, the current paper examines a single geographic area – the state of Wisconsin, USA – using data collected in a single manner, with a comprehensive analysis of the effects of scale. Wisconsin provides a unique opportunity and challenge for investigating the effects of scale. Ecologically it is complex (Curtis, 1959). It lies at the intersection of three major biomes: the eastern deciduous forest in the southeast of the state, the tallgrass prairie in the southwest and the boreal forest in the extreme north (Fig. 1). Much of the northern half of the state consists of the western terminus of the conifer-hardwood forest (also called the hemlock-white pine-northern hardwood forest and the Great Lakes forest). This region, although considered part of the eastern deciduous forest, is a transition zone between that biome and the boreal forest biome (Greller, 1988). The climate is continental with two major gradients: (1) a wet to dry gradient running from the northeast along the Great Lakes to the southwest, and (2) a warm to cold gradient, roughly extending south to north. The temperature gradient is overlain by different east to west patterns in summer versus winter precipitation (Curtis, 1959). This interface of

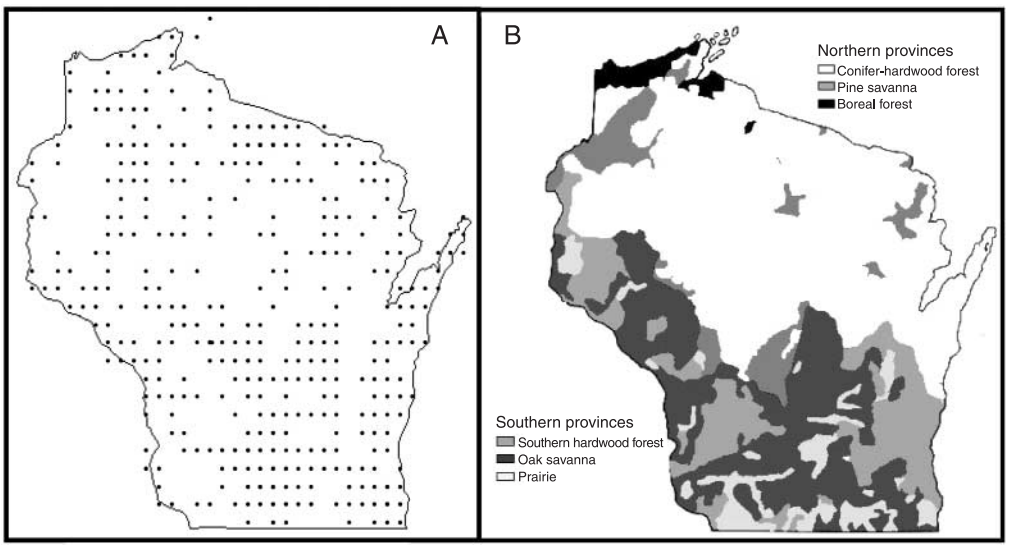

Fig. 1. The state of Wisconsin showing (A) the locations of the 901 stands used in the current analyses and (B) the formation boundaries defined by Curtis (1959).

gradients helps account for the complex vegetation, making analysis of scale effects both informative and complicated. The limits of our particular conclusions concerning productivity–diversity relationships and scale effects do not limit our general conclusion about the importance of examining the effects of scale on such relationships.

METHODS

Data sources

The measures of species richness came from John T. Curtis' Vegetation of Wisconsin study (Curtis, 1959). The data were computerized and archived in the 1980s (C.E. Umbanhower, Jr., unpublished; available from C.E.U. on request). They were obtained from of a series of stands scattered across Wisconsin (Fig. 1A). An important limitation is that the stands were neither uniformly nor randomly distributed across the state. Rather, they were intended as a survey of the breadth of community diversity in the state. Each stand was at least 15 acres on a uniform topographic site and homogeneous in composition; highly disturbed sites were avoided (Curtis, 1959). Thus, the survey is best considered as a near-equilibrial view of large-scale patterns. That is, the ecological domain of our analysis is relatively undisturbed communities. Although the survey included 19 community types, we included only 14 in our analysis (Table 1). We excluded all wetland (bog, fen and aquatic) community types, beach communities and communities on non-soil substrates (cliff faces). We also excluded any stand for which either some vascular plants were excluded (e.g. tree species only) or the location could not be determined. In particular, oak savanna stands were mostly excluded because of insufficient location information. Stand locations consisted of township and range coordinates. These were converted to latitude and

Table 1. Summary statistics for stands across the state of Wisconsin, and for various levels of the ecological hierarchy [diversity data from Curtis (1959) and productivity data from Kittle *et al.* (1995)]

	Number of stands	Species richness		Net primary productivity ($g\ C \cdot m^{-2} \cdot year^{-1}$)		Total species richness	Mean similarity
		Mean	Range	Mean	Range		
Entire state	901	49.3	15–129	639.7	405–934	1070	0.070
Northern division	414	45.0	15–112	745.0	421–901	886	0.091
Conifer-hardwood forest	307	45.2	15–98	750.9	423–901	818	0.098
Pine savanna	91	41.5	17–85	713.0	421–851	611	0.087
Boreal forest	16	60.8	28–112	812.9	789–877	309	0.175
Southern division	487	53.0	15–129	550.1	405–934	874	0.100
Southern hardwood forest	105	54.9	19–104	662.4	424–934	648	0.115
Oak savanna	260	52.0	15–129	520.7	405–794	760	0.102
Prairie	122	53.6	24–117	512.9	407–778	580	0.148
Community type							
Northern upland forest	110	55.0	19–96	722.8	445–877	397	0.230
Northern wet-mesic forest	20	65.7	32–98	814.4	721–898	238	0.327
Northern conifer swamp	80	40.2	16–86	750.3	535–898	267	0.271
Pine barrens	40	30.4	20–44	734.6	468–803	134	0.311
Boreal forest	32	65.1	23–112	792.9	692–859	295	0.298
Southern upland forest	123	71.0	27–129	540.9	413–849	527	0.252
Beech woods	35	38.8	19–65	832.1	673–934	203	0.279
Southern lowland forest	73	45.9	20–92	633.5	423–901	340	0.181
Oak savannas	10	54.2	22–77	539.9	424–762	197	0.225
Prairie	211	52.7	18–117	525.7	406–794	381	0.219
Sand barrens	44	39.0	19–79	563.9	421–827	294	0.180
Sedge meadows	78	29.8	15–48	634.8	405–934	284	0.189
Bracken grassland	27	33.1	19–54	764.0	700–862	182	0.249
Shrub carr and alder thicket	18	30.9	15–47	700.0	427–833	157	0.229

Note: Similarity, a measure of β diversity, was calculated using the Jaccard (1901) index.

longitude, estimated to the nearest 0.17°. For each stand, a complete list of all terrestrial vascular plants was compiled. The final data set included 1070 species from 901 stands.

Productivity information was estimated from the Biome-BGC model of the VEMAP Project (Kittle *et al.*, 1995; VEMAP Participants, 1995). This model predicts net primary productivity ($g\ C \cdot m^{-2} \cdot year^{-1}$) based on daily climate, vegetation and site conditions. Model output consists of productivity estimates on a $0.5° \times 0.5°$ grid across the continental USA (*c.* $37 \times 55\ km^2$ at the latitude of Wisconsin). Productivity of each stand was estimated by a linear interpolation among the four surrounding grid points. For stands adjacent to the Great Lakes, only terrestrial grid points were used. A linear interpolation is reasonable as the VEMAP estimates are based on local smoothing algorithms.

We used model predictions for three reasons. First, Curtis made no productivity estimates at the time of his survey. Second, diversity–productivity relationships are presumably the result of long-term processes. The modelled values are based on long-term climatic averages and are potentially more accurate than one-time estimates, which reflect short-term climatic variability. Third, current measures of productivity are either impossible to obtain for many sites or would be misleading. Many survey locations, especially in southern Wisconsin, have been cut down, ploughed up or paved over. In addition, estimates of productivity made 40 years after the vegetation survey could be biased by climate change. In contrast, because model estimates are based on long-term climate averages, they more accurately estimate productivity during the 1950s when the survey was done.

Data limitations

The biggest limitation is the indirect nature of the productivity estimates. In particular, the grain of the Biome-BGC productivity model was considerably larger than the size of individual stands or the nearest-neighbour distances among stands. This difference in grain means that the error of productivity estimates decreases with increasing grain or focus as the scale of analysis approaches and then exceeds the grain of the Biome-BGC model.

The second important limitation is that the sampling by Curtis and his students was neither random nor regular. Although they achieved reasonably complete coverage of the state, their intent was to sample the breadth of community diversity. Within a single area they generally sampled disparate community types (see 'Results'). For example, 25% of nearest-neighbour stands share no species. Finally, the number of stands was greater in the south than in the north, especially around the city of Madison where the University of Wisconsin campus is located.

These limitations should bias our analyses towards finding no relationship. Errors in the productivity estimates should be random with respect to productivity, thus increasing the error variance. Similarly, the sampling by Curtis was not motivated by the issues explored here, and so is unlikely to create a systematic bias in the data.

The overall data set is also limited by its ecological extent, specifically the range of productivities found within Wisconsin. The ability to observe complex, non-linear relationships can be constrained by the range of the data (Mittelbach *et al.*, 2001). For these data, the least productive stands would be considered productive on a global scale, as they do not include deserts or tundra. Thus, any conclusions about general theories of diversity (see 'Discussion') are constrained.

Data analyses

We determined whether a significant relationship existed between species richness and net primary productivity and if it was linear (positive or negative) or quadratic (hump- or U-shaped). For all analyses, we first tested whether the relationships were quadratic by examining the second-order coefficient of a quadratic regression. Only if the second-order coefficient did not differ significantly from zero, did we test for a statistically significant linear relationship. In addition, for significant second-order coefficients, we confirmed the presence of an internal maximum or minimum using the MOS-test (Mitchell-Olds and Shaw, 1987). For the bootstrap analysis of geographic extent in which determining a maximum or minimum was not possible, conclusions are based on statistically significant changes in the sign of the second-order coefficient, strongly implying changes between non-monotonic and monotonic. In addition, this bootstrap analysis is anchored by an analysis of the entire state, for which a statistically significant minimum was found (see 'Results'). Bootstrap analyses used standardized regression coefficients. Standardization corrects for differences in variances among samples; a Pearson product–moment correlation is a standardized regression coefficient for a linear regression. All statistical analyses were done using Systat (SYSTAT 6.1 for Windows, SPSS, Inc., Chicago, IL). Because we view our analyses as exploratory, we report results that were marginally non-significant by typical criteria ($0.05 < P < 0.10$); in all cases, though, we provide sufficient detail for the reader to reach independent conclusions about the biological importance and statistical significance of any results.

Scale definition and manipulation

Scale was defined geographically (spatially) and ecologically. Two ecological hierarchies were defined by Curtis (1959). The first was a semi-geographic classification consisting of two major divisions, north and south, with each further divided into three formations (Fig. 1B). These formations were called provinces by Curtis; we have renamed them to avoid confusion with biogeographic provinces using terminology that roughly follows that of the National Vegetation Classification Standard. Community types form a separate classification that overlaps formations (Table 1). For example, the prairie formation included only 83 of the 211 prairie stands and included six other community types (i.e. northern upland forest, oak savanna, sand barren, sedge meadow, southern lowland forest, southern upland forest). Community types (Table 1) were assigned during the original collection and do not correspond to those of Curtis (1959) or to those of the Wisconsin Department of Natural Resources (Finley, 1976) in all cases. Using exploratory ordination and classification analyses, we confirmed that the set of stands within a community type were a continuous unit. For example, an analysis of all the northern forest stands successfully repartitioned them into distinct upland forest, wet-mesic forest and conifer swamp groupings. The prairie stands were an exception. Some of the sand barren (sand prairie) stands were included within the prairie group in the original classification. We reclassified stands from prairie to sand barrens if their soil type was noted as 'sand' or if they clustered with the sand barren stands in a re-analysis of the prairie stands (Umbanhower, 1992).

Scale was manipulated by aggregating data in a variety of ways. Here, we briefly list the manipulations and describe them in detail in the following sections. From a geographic perspective, grain was altered by combining stands in pairs, triplets, and so on. For each

combination we calculated the total number of species and average productivity. From an ecological perspective, grain was altered by considering the total species richness of all stands within a community type or formation. Focus was altered by combining stands within a particular geographic area or within an ecological unit (e.g. community type or formation), and then averaging the number of species and productivity in the constituent stands. Thus, focus differed from grain because it was based on the average number of species per stand, rather than the total number of species in the aggregated stands. Extent was altered by analysing subsets of the state, defined geographically or ecologically.

Most analyses of scale only consider spatial hierarchies because aggregation of contiguous areas is a natural and obvious way to manipulate grain. However, an ecological domain need not be contiguous to be scaleable. For example, islands and lakes are two types of ecological domains that are not contiguous, yet the scaling properties of such domains are routinely analysed (e.g. species–area curves). An ecological domain need not be completely independent of the matrix within which it lies. For example, we study lakes as a domain even though a lake community shares members with input and output streams. What is critical is that the ecological domain of the analysis and conclusions be explicitly stated, just as the scales of those conclusions should be stated.

Extent

The effects of ecological extent were determined based on the three subsets (division, formation and community type) described previously (Fig. 1A, Table 1). The effects of geographic extent were determined by a bootstrap procedure using randomly sampled blocks of varying size (7.5×7.5 km^2 10×10 km^2, 20×20 km^2, 30×30 km^2, 40×40 km^2, 60×60 km^2, 80×80 km^2, 120×120 km^2, 160×160 km^2 and 240×240 km^2). The centre of each block was created by randomly choosing a location within an area from 42° to 47° north latitude and 87° to 93° west longitude. For each block size, 1000 bootstrapped regression coefficients were computed. To provide sufficient power in estimating quadratic coefficients, blocks were discarded if they contained fewer than four stands or if the range of net primary productivity was less than 100 g $C \cdot m^{-2} \cdot year^{-1}$. For the stands within the block, two regressions were performed, one quadratic and one linear, and standardized regression coefficients were calculated. Means and 95% confidence intervals (CI) were calculated from the bootstrapped coefficients.

Grain

The effects of ecological grain were determined by performing quadratic and linear regressions on the total number of species and mean productivities for each community type and each formation. The total number of species was estimated using a first-order jackknife estimator (Palmer, 1990) from the species–area curve procedure of PC-Ord (McCune and Mefford, 1997). Other estimators of species richness (second-order jackknife, total observed species, logistic species–area curve asymptotic value) were highly correlated, so only the results of the first-order estimator are shown.

The effects of geographic grain were determined by creating nearest-neighbour aggregations of stands. Aggregations of size 2–64 (i.e. pairs, triplets, etc.) were created by choosing a random location within the state and then finding the closest stands. The range of grain sizes was chosen both to represent the range that is found in the literature (e.g. some

continental-scale studies use $0.5° \times 0.5°$ or larger grain sizes) and to bracket the range of possible scales of ecological interest. Aggregations of a given size differed in the geographic distance they encompassed because of the non-uniform spatial distribution of stands in the state (Fig. 1A). In addition, the scale of environmental heterogeneity differs across the state, with much greater heterogeneity in the southwest than the northeast (Fig. 1A). Our method certainly resulted in the combining of different community types. However, for some types of ecological processes (e.g. metapopulation dynamics), we do not know whether species recognize the same arbitrary community definitions that we do. For a given grain size, 1000 bootstrapped aggregations were created and the total number of species and mean productivity were calculated. Each set of bootstrapped values was then subjected to quadratic and linear regressions.

Focus

The effects of ecological focus were determined by performing quadratic and linear regressions on the mean species richness and mean productivity of each community type and of each formation. The effects of geographic focus were determined by calculating mean values for all stands within blocks that differed in size (20×20 km^2, 30×30 km^2, 40×40 km^2, 60×60 km^2, 80×80 km^2, 120×120 km^2 and 240×240 km^2). For each size, blocks were arrayed in a regular fashion across the state so as to achieve complete coverage. Each set of mean values was than subjected to quadratic and linear regressions.

RESULTS

For the entire state, the relationship between species richness and productivity was U-shaped (standardized coefficient: $b'_2 = 1.23$, $n = 901$, $P = 0.001$; Fig. 2). This relationship then differed depending on attributes of scale (extent, grain and focus) and hierarchies (ecological and geographic).

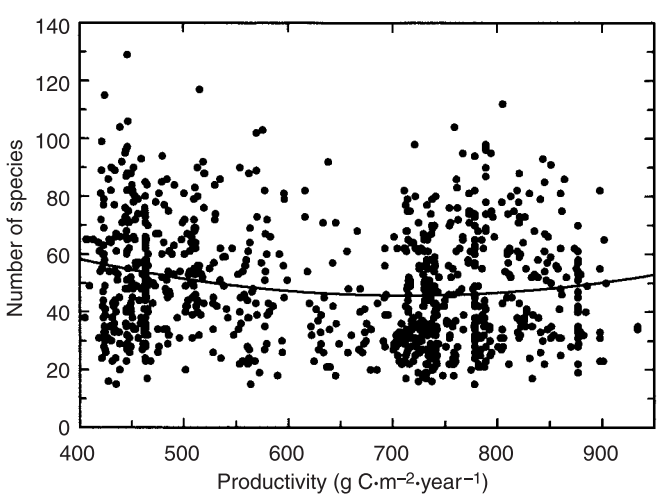

Fig. 2. The relationship between terrestrial vascular plant species richness and net primary productivity for 901 stands across the state of Wisconsin.

Extent

For all analyses of the effects of extent, the grain and focus were the individual stand. We examined the ecological hierarchy by reducing the extent to that of division, formation or community type. For each division, there was no significant quadratic or linear relationship (Fig. 3A, E). For each formation, significant relationships re-emerged. In the northern division, none of the relationships were significant. However, the conifer-hardwood forest formation showed a U-shaped relationship that approached significance ($b'_2 = 0.83$, $n = 307$, $P = 0.08$; Fig. 3B). In the southern division, the prairie formations showed a negative relationship ($b'_1 = -0.27$, $n = 122$, $P = 0.003$; Fig. 3H), whereas the southern hardwood forest formation showed a U-shaped relationship ($b'_2 = 2.54$, $n = 105$, $P = 0.02$; Fig. 3F).

Four community types showed significant relationships: northern upland forests had a U-shaped relationship ($b'_2 = 3.61$, $n = 110$, $P = 0.001$), prairies had a negative relationship ($b'_1 = -0.20$, $n = 211$, $P < 0.004$), sand barrens had a negative relationship ($b'_1 = -0.30$, $n = 44$, $P < 0.05$) and bracken grasslands had a positive relationship ($b'_1 = 0.39$, $n = 27$,

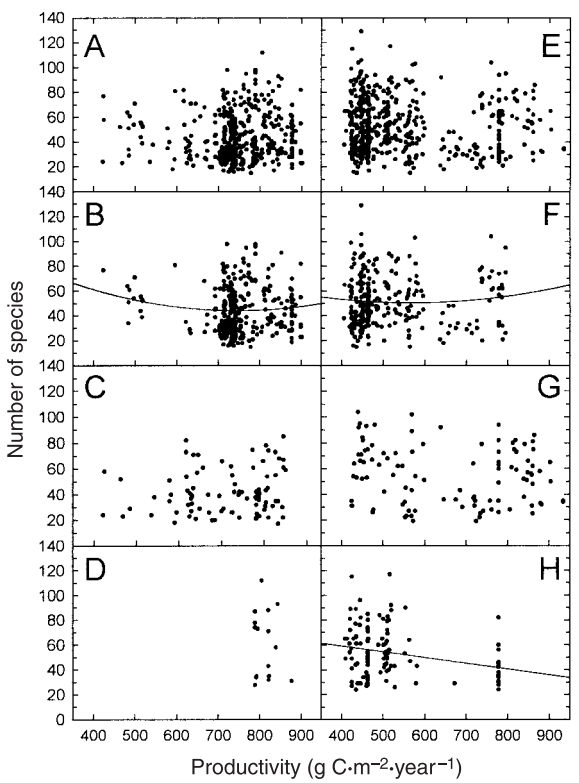

Fig. 3. Effects of changing the ecological extent on the relationship between terrestrial vascular plant species richness and net primary productivity: (A) northern division, (B) conifer-hardwood formation, (C) pine savanna formation, (D) boreal forest formation, (E) southern division, (F) southern hardwood forest formation, (G) oak savanna formation, (H) prairie formation.

$P = 0.05$). The first two relationships mirror the provincial relationships of the conifer-hardwood forest and prairie, respectively. In addition, two community types with small samples sizes had relationships that approached significance, both of which were positive (pine barrens: $b'_1 = 0.30$, $n = 40$, $P = 0.06$; oak savannas: $b'_1 = 0.58$, $n = 10$, $P = 0.08$). The chance of finding a significant relationship was not related to sample size (Table 1).

The geographic hierarchy showed an equally complex pattern (Table 2). For extents of 80×80 km^2 or smaller, the mean relationship was hump-shaped, a negative quadratic coefficient. For extents of 120×120 km^2 and 160×160 km^2, the relationship was negative. For extents of 240×240 km^2, the relationship was U-shaped, a positive quadratic coefficient, converging on the relationship for the entire state.

Grain

For all analyses of the effects of grain, the extent was the entire state and the focus equalled the grain. For one element of the ecological hierarchy (i.e. community type), the relationship was negative (Fig. 4A), although the regression coefficient was marginally not statistically different from zero ($b'_1 = -0.48$, $n = 14$, $P = 0.08$). In contrast, no relationship was found for formations (Fig. 4B). For the geographic hierarchy, single stands and pairs of stands had a U-shaped relationship (Table 3). For sets of two, three or four stands, the relationship was negative. For aggregates of eight or more stands, the relationship was always hump-shaped. The mean similarity of pairs and triplets of stands was slightly lower than for either larger aggregations or for the entire data set (0.070; see Table 1), an indication of Curtis' tendency to sample different community types located near each other.

Table 2. Effects of changes in extent on the diversity–productivity relationship

	Quadratic regression		Linear regression	
Size	Standardized coefficient	95% CI	Standardized coefficient	95% CI
7.5×7.5 km^2	−54.09	−66.14, −42.04	—	—
10×10 km^2	−70.71	−83.78, −57.64	—	—
20×20 km^2	−26.06	−33.60, −18.52	—	—
30×30 km^2	−13.34	−17.99, −8.70	—	—
40×40 km^2	−7.66	−11.15, −4.18	—	—
60×60 km^2	−3.98	−6.20, −1.76	—	—
80×80 km^2	−3.71	−5.86, −1.56	—	—
120×120 km^2	−1.61	−3.25, 0.044	−0.09	−0.10, −0.08
160×160 km^2	−0.51	−1.69, 0.67	−0.11	−0.12, −0.10
240×240 km^2	1.16	1.09, 1.22	—	—
Entire state	1.23	0.45, 2.02	—	—

Note: For each size, 1000 randomly placed blocks were created. Within each block, quadratic and linear regressions were performed. Shown are the mean and 95% confidence intervals (CI) of those bootstrapped values. For the entire state, the regression is from the original data ($n = 901$). Testing for a linear regression was restricted to cases in which the quadratic regression coefficient did not differ from 0.

Table 3. Effects of changes in grain on the diversity–productivity relationship

	Quadratic regression		Linear regression		
Aggregation size	Standardized coefficient	*P*	Standardized coefficient	*P*	Mean similarity
1	1.23	0.001	—	—	0.070
2	0.31	0.4	–0.20	0.0001	0.061
3	–0.36	0.3	–0.16	0.0001	0.067
4	–0.66	0.09	–0.09	0.006	0.072
8	–2.13	0.0001	—	—	0.069
16	–2.75	0.001	—	—	0.069
24	–2.92	0.002	—	—	0.070
32	–2.10	0.05	—	—	0.069
48	–3.43	0.01	—	—	0.070
64	–4.23	0.01	—	—	0.070

Note: For aggregations of different size, 1000 sets of nearest neighbours were created randomly. Quadratic and linear coefficients are based on regressions for the entire set of bootstrapped values. For aggregation size of 1, the regression is from the original data ($n = 901$). Testing for a linear regression was restricted to cases in which the quadratic regression coefficient did not differ from 0. Mean similarity indicates the average of the similarities of stands within each aggregation; for aggregation size 1, it is the mean similarity across the original set of 901 stands.

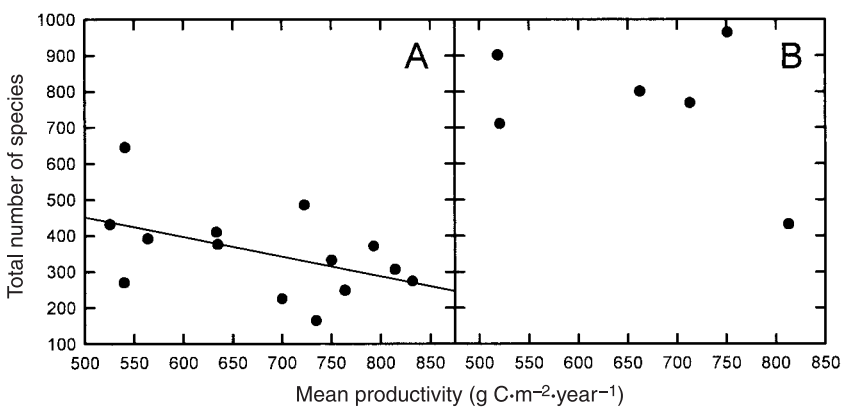

Fig. 4. Effects of changing the ecological grain on the relationship between total terrestrial vascular plant species richness and mean net primary productivity: (A) community types, (B) formations.

Focus

For all analyses of the effects of focus, the extent was the entire state and the grain was the individual stand. For one element of the ecological hierarchy (i.e. community type) the relationship was U-shaped (Fig. 5A), although the regression coefficients were marginally not statistically different from zero ($b_2' = 8.98$, $n = 14$, $P = 0.06$). In contrast, no relationship was found for formations (Fig. 5B). For geographic hierarchy, there was a negative relationship at 20×20 km^2, 30×30 km^2, 40×40 km^2 and 240×240 km^2 (Table 4). At 120×120 km^2, the relationship was U-shaped, although the regression coefficient was marginally not statistically different from zero (Table 4).

Table 4. Effects of changes in focus on the diversity–productivity relationship

Size	*n*	Quadratic regression		Linear regression	
		Standardized coefficient	*P*	Standardized coefficient	*P*
20×20 km^2	173	1.64	0.08	−0.22	0.004
30×30 km^2	104	1.28	0.29	−0.25	0.01
40×40 km^2	66	0.37	0.81	−0.44	0.0001
60×60 km^2	39	3.23	0.16	−0.28	0.09
80×80 km^2	21	−5.95	0.12	−0.26	0.26
120×120 km^2	11	8.86	0.06	−0.48	0.14
240×240 km^2	5	6.20	0.13	−0.97	0.007

Note: Grids of different sizes were distributed across Wisconsin. Within each grid square, the mean number of species per stand and the mean net primary productivity were calculated. Quadratic and linear regressions were performed using those mean values.

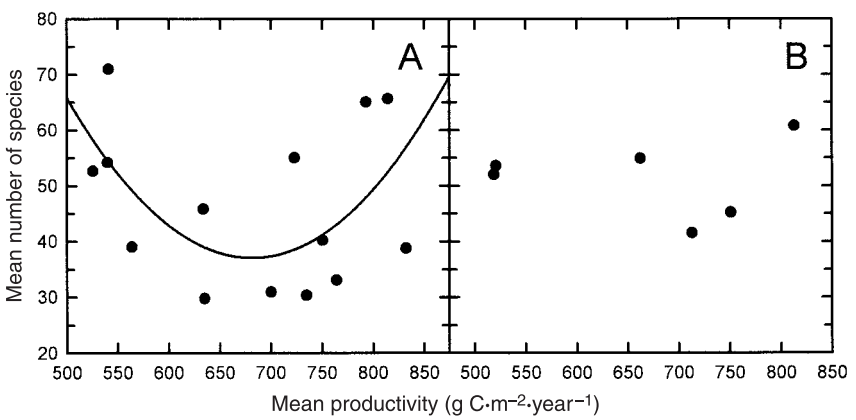

Fig. 5. Effects of changing the ecological focus on the relationship between mean terrestrial vascular plant species richness and mean net primary productivity: (A) community types, (B) formations.

DISCUSSION

Patterns observed

No single form or pattern describes the relationship between species richness and productivity. The relationship depends on the components of scale (grain, focus or extent) and hierarchy (ecological or geographic). This conclusion holds even if the marginally non-significant results are ignored. Our results mirror those of Mittelbach *et al.* (2001), in their analysis of the effects of ecological and geographic extent. Our conclusion contrasts sharply with claims that the relationship is hump-shaped at all scales (Huston and DeAngelis, 1994).

Our conclusions are probably robust given the limitations of our data because errors in the data are likely to be random rather than systematic. Where we found a statistically

significant relationship or differences in relationships as a function of scale, the result is likely to hold (e.g. Figs 2, 3H, 3F; Tables 2 and 3). In several instances (e.g. Fig. 5A), seemingly obvious relationships were not statistically significant and might become significant with more or better data.

U-shaped relationships

The discovery of U-shaped productivity–diversity relationships is surprising. No theory, as far as we are aware, previously predicted such relationships, although some can explain them in a *post-hoc* fashion. In their literature survey, Mittelbach *et al.* (2001) found that U-shaped relationships accounted for 27% of all non-monotonic relationships (17 data sets in 13 studies: Beadle, 1966: terrestrial plants; Barbour and Diaz, 1973: terrestrial plants; Whittaker and Niering, 1975: terrestrial plants; Wheeler and Giller, 1982: terrestrial plants; Owen, 1988: rodents; Owen and Dixon, 1989: salamanders; Currie, 1991: amphibians and reptiles; Wheeler and Shaw, 1991: terrestrial plants; Williams *et al.*, 1996: terrestrial plants; Cowlisha and Hacker, 1997: primates; Pearson and Carroll, 1998: birds and butterflies; Shepherd, 1998: mammals; Roy *et al.*, 1998: marine gastropods). Those authors either failed to test for a U-shaped relationship or made little note of such a result. Clearly, U-shaped relationships are not an aberration and need to be accounted for by theory.

Some of the U-shaped relationship for the state as a whole (Fig. 2) can be explained by the details of communities (Table 1). At the low end of the productivity gradient, prairies had relatively high species richness (Fig. 3H). At the other end of the productivity gradient, northern forests, especially boreal forests (Fig. 3D), also had high species richness. This high species richness may be due to the transitional nature of this region. An analysis of similar forest communities in northern lower Michigan (Scheiner and Istock, 1994) found that boreal stands were very species-rich because they contained a mixture of both northern and southern species. Prairies in Wisconsin may be enriched similarly due to their placement at an ecological transition. The combination of these two transition zones at opposite ends of the productivity gradient may thus be the cause of the U-shaped distribution. Thus, observed productivity–diversity patterns may result from the interaction of productivity-driven processes with other processes.

On the other hand, both divisions and most of the formations and community types have values for productivity and species richness that span almost the entire range of the data. So, the U-shaped relationship is not merely the result of combining three separate biomes with different species pools and productivities. This suggests that the relationship does not depend on local idiosyncrasies. As always in ecology, particularized causes must be distinguished from the more general theories that we hope to test.

Extent and productivity

The effects of spatial extent are also surprising. In our analysis, increasing the geographic extent increased the range of productivity values while decreasing the tendency towards hump-shaped relationships (Table 2), the exact opposite of the expected pattern. Previous studies (e.g. Begon *et al.*, 1990; Rosenzweig, 1992, 1995; Huston, 1994; Guo *et al.*, 1998; Grace, 1999) have claimed that the shape of a detected relationship is related to the range of productivities (i.e. a positive relationship is just the lower end of a hump). Mittelbach *et al.*

(2001) found that a hump-shaped relationship was more common in studies with a greater range of productivity.

In our data, the shape of the relationship was not related to the range of productivity (Table 1). For example, prairies had one of the largest ranges, yet showed a linear relationship, not a humped relationship. Similarly, ecological range (β diversity measured as mean similarity) could also affect the ability to detect a relationship. However, in the present data, the tendency to find a relationship was not a function of β diversity for formations or community types (Table 1) or for geographic extent (data not shown). The six community types with significant or near significant relationships spanned the range of mean similarities (Table 1).

Mittelbach *et al.* (2001) found that hump-shaped relationships were more common in studies that went across community types or at landscape to regional scales; such studies also tended to span a greater range of productivity. In our data, non-monotonic (U- and hump-shaped) relationships generally were associated with analyses across community types or formations (Figs 2, 3B, 5A). Prairies, however, are a heterogeneous mixture of dry to mesic to wet stands (Curtis, 1959; Umbanhower, 1992) and showed a negative linear relationship. It is possible that we might have found more examples of hump-shaped relationships with a greater range of productivity values, especially lower productivity. The range in our data was only 529 g $C \cdot m^{-2} \cdot year^{-1}$. For example, we might be able to extend that range by including samples farther west and northwest into the tallgrass prairie. However, studies in both Kansas (Collins and Glenn, 1995) and Minnesota (Gross *et al.*, 2000), with lower productivities than in Wisconsin, found negative – not hump-shaped – relationships. Thus, if a hump-shaped relationship exists, the hump lies at productivity values lower than those encountered on the Great Plains.

For community types with significant or near significant relationships, five of the six were monotonic. Perhaps those relationships would have been hump-shaped if the productivity range were greater. However, because the state as a whole had a U-shaped distribution, at best that relationship would have become a fourth-order curve, something that has never been observed and certainly not predicted by any theory. For the community types, based on the observed relationships, any unobserved quadratic relationship is as likely to be U-shaped as hump-shaped. Thus, we find no evidence that our general conclusions would be changed if we had been able to extend the range of productivities by extending the geographic extent of the data.

Dissecting the effects of scale

The effects of scale depended upon both the component and the hierarchy. The use of focus as an explicit component of scale is new (Scheiner *et al.*, 2000), although the notion of samples applying to an ecological inference space certainly has a long tradition. For example, ecological hierarchies go back at least as far as Clements (1916). What has rarely been done, however, is to examine how a relationship changes as a function of changing the ecological or spatial focus.

Comparing the effects of focus and grain provides information on the scale-invariance of the diversity–productivity relationship and hints about the scale of processes that determine that relationship. For the geographic hierarchy, increasing grain changed the productivity–diversity relationship from negative to hump-shaped (Table 3), whereas increasing the focus led to a negative relationship (Table 4). In contrast, for one ecological

hierarchy, increasing the grain resulted in a negative relationship (Fig. 4A), whereas increasing the focus maintained a U-shaped relationship (Fig. 5A).

These differences in the effects of grain and focus are partly due to differences in how scaling operates on different variables. Some variables are summative (e.g. species richness), whereas others are averaging (e.g. net primary productivity). The former may increase with some components of scale, while the latter probably will not. In our analysis, a hump-shaped relationship appeared with increasing geographic grain because species richness must increase, whereas productivities assume intermediate values.

In contrast to the effects of changing grain, changes in geographic focus caused both productivity and diversity to assume intermediate values. On average, high productivity regions had lower mean species richness (Fig. 2), resulting in a negative relationship. On the other hand, an increase in the ecological focus led to a U-shaped relationship. Increasing ecological focus averages values among similar stands, rather than across disparate stands, thus preserving or intensifying any pattern. Thus we need to be aware of all aspects of scale when we make comparisons across data sets. Studies may differ in more than one component of scale and be based on different types of hierarchies.

Possible causal mechanisms

Our results provide hints about the causes of productivity–diversity relationships. Many theories apply to scales not considered in our analyses (e.g. global patterns) or to trophic levels other than plants. Consequently, we limited our examination to those theories germane to our data. We find support for two theories, but only at certain scales, find mixed support for one and find no support for two others. Any conclusions must be considered tentative, however, given the limited nature of our data. A comprehensive test of these and the other theories will require both a thorough re-examination of the theories to determine what, if any, predictions they make about scale effects and the examination of many more data sets. We eschew a common practice in ecology, making general theoretical claims based on a single data set.

Two explanations for hump-shaped relationships that find support are built on assumptions about the scale of environmental variation. The first theory – environmental heterogeneity – is predicated on mechanisms that operate on within-grain environmental variation: diversity is highest at intermediate productivities because those environments are most variable (Tilman, 1982, 1988; Huston and DeAngelis, 1994). This theory can explain the appearance of humped-shaped relationships at larger geographical grains (Table 3). Increasing the grain was done by aggregating nearest-neighbour stands. For such nearest-neighbour pairs, there was a negative correlation between mean similarity and the difference in productivities ($r = -0.23$, $n = 1000$, $P < 0.001$). That is, stands that were most different in species composition tended to be most different in productivity. The aggregated unit will tend towards a high species richness (because species richness adds across stands) and an intermediate productivity (because productivity averages across stands), resulting in an interior peak in the productivity–diversity curve. Nor was the appearance of a hump at larger grain size simply an artifact of aggregates with a low mean similarity having an intermediate productivity. While such a relationship between mean similarity and productivity was found, the relationship existed at all grain sizes (results not shown). Only when grain size became large enough to capture a sufficient variety of stands did a hump appear.

Our results point to the scale at which the environmental heterogeneity process operates. The evidence suggests that the environmental heterogeneity process is more likely to operate at a large grain and a landscape to regional extent. The theory itself is agnostic about the scale of operation, although some authors have asserted that it can explain hump-shaped relationships at all scales (Huston and DeAngelis, 1994).

The second theory – available habitat – is predicated on mechanisms that operate on among-grain environmental variation: species richness is greatest at intermediate productivities because such habitats are more common (Denslow, 1980; Rosenzweig and Abramsky, 1993). In our data, density of stands was lowest at intermediate productivities (Fig. 2). Thus, an inverted version of this theory could explain the U-shaped relationships that we found. However, this theory fails to predict the change in relationship with changing grain and focus, suggesting that its domain is limited to the smallest grain examined here.

One process that could lead to non-monotonic relationships is based on changes in numbers of individuals across community types (Oksanen, 1996; Stevens and Carson, 1999a,b). There are two ways to conceptualize this effect, one driven by biological mechanisms and one driven by sampling artifacts. For our data, the biological conceptualization finds mixed support, whereas the sampling artifact finds no support.

As a biological mechanism, changes in numbers might be driven by changes in physiognomies. Such change in physiognomies is a plant-specific version of the more general inter-taxonomic competition theory: that environmental gradients result in clade replacement along them (Tilman and Pacala, 1993; Rosenzweig and Abramsky, 1993; Rosenzweig, 1995). Our results give mixed support to this proposition for both ecological and spatial hierarchies. In agreement with the proposition, non-monotonic (U- and hump-shaped) relationships generally were associated with analyses across community types or formations. Contrary to the prediction, the pine and oak savanna formations, which had the greatest mixtures of forest, shrub and grassland communities, showed no significant relationships. In support of the proposition, U-shaped relationships were more common at the largest extents; but contrary to the proposition, hump-shaped relationships were more common at the smallest extents (Fig. 2, Table 2).

As a sampling artifact, changes in numbers could also be seen as an effect of using a grain size that is too small to capture local diversity – that is, inadequate sampling (Oksanen, 1996). Contrary to this proposition, hump-shaped relationships were more common as grain size increased (Table 3).

The final theory – the intermediate productivity hypothesis – found no support in our data. This hypothesis explains hump-shaped relationships as a balance between environmental stress at low productivities and competitive exclusion at high productivities (Grime, 1973, 1979; Huston, 1979, 1994; Huston and Smith, 1987). This theory predicts that hump-shaped relationships should be most common at small grain sizes, because larger grains will combine habitats at different successional stages or with different productivities. Our results found just the opposite pattern: hump-shaped patterns appeared only at larger grain sizes (Table 3). More generally, a survey of 197 studies of the relationship between disturbance and diversity found that the most common pattern was no relationship, while humped, positive and negative relationships were all equally common (Mackey and Currie, 2001). A comprehensive test of this hypothesis is complicated because the location of hump depends on where along the productivity gradient strong competition occurs. Whether competition is greater at low or high productivity is a matter of contention. One large-scale experiment concluded that the strength of competition is independent of productivity (Reader *et al.*,

1994). However, other studies have shown that competition is greatest at high productivity (Wilson and Keddy, 1986; Sammul *et al.*, 2000; Olofsson *et al.*, 2002). On the other hand, a recent meta-analysis (Goldberg *et al.*, 1999) found that competition was greatest at low productivities, although this conclusion depended on the competition metric that was used. Again we caution that, in our data, low productivities and high environmental stress may not have been adequately represented.

Sampling bias and scale analysis

To what extent does non-random, regular or incomplete sampling affect the analysis of scale effects? Our analyses are potentially biased because habitats were sampled non-proportionally to their representation in Wisconsin. For example, prairie stands accounted for 26% of the samples, whereas only about 6% of the state is prairie (Curtis, 1959). In addition, stands were chosen within an area to represent the breadth of variation, instead of being representative.

The effects of biased sampling depend on both the scale component and the scale hierarchy. An ecological hierarchy will generally be less affected by non-proportional sampling. When examining the effects of grain and focus, data aggregations are done within each ecological sub-category (e.g. mean species richness within each community type), thereby correcting sampling differences among types. For a geographic hierarchy, analyses that involve taking averages (e.g. effects of focus) will be affected to a lesser extent than analyses that involve sums (e.g. effects of grain). For effects of extent, non-proportional sampling may actually improve the ability to discover a pattern because the power of regression analyses increases with increasing range of the independent variable (e.g. sampling to maximize the range of productivity values).

We must be cognizant of possible sampling biases. Studies of productivity–diversity relationships must be particularly sensitive to these issues because they will often involve using data collected for other purposes (e.g. Gross *et al.*, 2000) or meta-analyses of data collected using a variety of methods (e.g. Gough *et al.*, 2000; Mittelbach *et al.*, 2001).

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REFERENCES

Abrams, P.A. 1988. Resource productivity–consumer species diversity: simple models of competition in spatially heterogeneous environments. *Ecology*, **69**: 1418–1433.

Barbour, M.G. and Diaz, D.V. 1973. *Larrea* plant communities on bajada and moisture gradients in the United States and Argentina. *Vegetatio*, **28**: 335–352.

Beadle, N.C.W. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. *Ecology*, **47**: 992–1007.

Begon, M., Harper, J.L. and Townsend, C.R. 1990. *Ecology*. Boston, MA: Blackwell Scientific.

Chesson, P.L. and Huntly, N. 1988. Community consequences of life history traits in a variable environment. *Ann. Zool. Fenn.*, **25**: 5–16.

Clements, F.E. 1916. *Plant Succession*. Washington, DC: Carnegie Institute of Washington.

Collins, S.L. and Glenn, S.M. 1995. Grassland ecosystem and landscape dynamics. In *The Changing Prairie* (A. Joern and K.H. Keeler, eds), pp. 128–156. New York: Oxford University Press.

Colwell, R.K. and Hurtt, G.C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *Am. Nat.*, **144**: 570–595.

Cowlisha, G. and Hacker, J.E. 1997. Distribution, diversity, and latitude in African primates. *Am. Nat.*, **150**: 505–512.

Currie, D.J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.*, **137**: 27–49.

Curtis, J.T. 1959. *The Vegetation of Wisconsin*. Madison, WI: University of Wisconsin Press.

Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* (suppl.), **12**: 47–55.

Finley, R.W. 1976. University of Wisconsin – Extension, Madison, WI (http://www.dnr.state.wi.us/org/at/et/geo/mapgal/landcov/orgveg.htm).

Goldberg, D.E., Rajaniemi, T., Gurevitch, J. and Stewart-Oaten, A. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**: 1118–1131.

Gough, L., Osenberg, C.W., Gross, K.L. and Collins, S.L. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos*, **89**: 428–439.

Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Pers. Plant Ecol. Evol. Syst.*, **2**: 1–28.

Greller, A.M. 1988. Deciduous forest. In *North American Terrestrial Vegetation* (M.G. Barbour and W.D. Billings, eds), pp. 287–316. Cambridge: Cambridge University Press.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature*, **242**: 344–347.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. New York: Wiley.

Gross, K.L., Willig, M.R., Gough, L., Inouye, R. and Cox, S.B. 2000. Patterns of species diversity and productivity at different spatial scales in herbaceous plant communities. *Oikos*, **89**: 417–427.

Guo, Q., Brown, J.H. and Enquist, B.J. 1998. Using constraint lines to characterize plant performance. *Oikos*, **83**: 237–245.

Gurevitch, J., Scheiner, S.M. and Fox, G.A. 2002. *The Ecology of Plants*. Sunderland, MA: Sinauer Associates.

Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.*, **113**: 81–101.

Huston, M.A. 1994. *Biological Diversity: The Coexistence of Species in Changing Landscapes*. Cambridge: Cambridge University Press.

Huston, M.A. and DeAngelis, D.L. 1994. Competition and coexistence: the effects of resource transport and supply rates. *Am. Nat.*, **144**: 954–977.

Huston, M. and Smith, T. 1987. Plant succession: life history and competition. *Am. Nat.*, **130**: 168–198.

Jaccard, P. 1901. Distribution de la flore alpine dans le Bassin des Dranes et dans quelques régions voisines. *Bull. Soc. Vaud. Sci. Nat.*, **37**: 241–272.

Kittle, T.G.F., Rosenbloom, N.A., Painter, T.H., Schimel, D.S. and VEMAP Modeling Participants 1995. The VEMAP integrated database for modeling United States ecosystem/vegetation sensitivity to climate change. *J. Biogeogr.*, **22**: 857–862.

Leibold, M.A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.*, **147**: 784–812.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*, **73**: 1943–1967.

Mackey, R.L. and Currie, D.J. 2001. The diversity–disturbance relationship: is it generally strong and peaked? *Ecology*, **82**: 3479–3492.

McCune, B. and Mefford, M.J. 1997. *Multivariate Analysis of Ecological Data*, Version 3.18. Gleneden Beach, OR: MjM Software.

Mitchell-Olds, T. and Shaw, R.G. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution*, **41**: 1149–1161.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. and Gough, L. 2001. What is the observed relationship between species richness and productivity? *Ecology*, **82**: 2381–2396.

Moore, J.C. and de Ruiter, P.C. in press. Productivity, dynamic stability, and species richness. *Ecology*.

Moore, J.C., de Ruiter, P.C. and Hunt, H.W. 1993. Influence of productivity on the stability of real and model ecosystems. *Science*, **261**: 906–908.

Mueller-Dombois, D. and Ellenberg, H. 1974. *Aims and Methods of Vegetation Ecology*. New York: Wiley.

Oksanen, J. 1996. Is the humped relationship between species richness and biomass an artefact due to plot size? *J. Ecol.*, **84**: 293–295.

Oksanen, L., Fretwell, S.D., Arrunda, J. and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, **131**: 424–444.

Olofsson, J., Moen, J. and Oksanen, L. 2002. Effects of herbivory on competition intensity and species diversity in two arctic-alpine communities with different productivity. *Oikos*, **96**: 507–515.

Owen, J.G. 1988. On productivity as a predictor of rodent and carnivore density. *Ecology*, **69**: 1161–1165.

Owen, J.G. and Dixon, J.R. 1989. An ecographic analysis of the herpetofauna of Texas. *Southwest. Nat.*, **34**: 165–180.

Palmer, M.W. 1990. The estimation of species richness by extrapolation. *Ecology*, **71**: 1195–1198.

Palmer, M.W. and White, P.S. 1994. Scale dependence and the species–area relationship. *Am. Nat.*, **144**: 717–740.

Pastor, J., Downing, A. and Erickson, H.E. 1996. Species–area curves and diversity–productivity relationships in beaver meadows of Voyageurs National Park, Minnesota, USA. *Oikos*, **77**: 399–406.

Pearson, D.L. and Carroll, S.S. 1998. Global patterns of species richness: spatial models for conservation planning using bioindicator and precipitation data. *Conserv. Biol.*, **12**: 809–821.

Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, I., Keddy, P.A., Tilman, D., Morris, E.C., Grace, J.B., McGraw, J.B., Olff, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., Vanhulst, R., Johansson, M.E., Nilsson, C., Gurevitch, J., Grigulis, K. and Beisner, B.E. 1994. Plant competition in relation to neighbor biomass – an intercontinental study with *Poa pratensis*. *Ecology*, **75**: 1753–1760.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**: 514–527.

Rohde, K. 1997. The larger area of the tropics does not explain latitudinal gradients in species diversity. *Oikos*, **79**: 169–172.

Rosenzweig, M.L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, **171**: 385–387.

Rosenzweig, M.L. 1992. Species diversity gradients: we know more and less than we thought. *J. Mammol.*, **73**: 715–730.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Rosenzweig, M.L. and Abramsky, Z. 1993. How are diversity and productivity related? In *Species Diversity in Ecological Communities* (R.E. Ricklefs and D. Schulter, eds), pp. 52–65. Chicago, IL: University of Chicago Press.

Roy, K., Jablonski, D., Valentine, J.W. and Rosenberg, G. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl. Acad. Sci. USA*, **95**: 3699–3702.

Sammul, M., Kull, K., Oksanen, L. and Veromann, P. 2000. Competition intensity and its importance: results of field experiments with *Anthoxanthum oderatum*. *Oecologia*, **125**: 18–25.

Scheiner, S.M. and Istock, C.A. 1994. Species enrichment in a transitional landscape, northern lower Michigan. *Can. J. Bot.*, **72**: 217–226.

Scheiner, S.M., Cox, S.B., Willig, M.R., Mittelbach, G.G., Osenberg, C. and Kaspari, M. 2000. Species richness, species–area curves, and Simpson's paradox. *Evol. Ecol. Res.*, **2**: 791–802.

Shepherd, U.L. 1998. A comparison of species diversity and morphological diversity across the North American latitudinal gradient. *J. Biogeogr.*, **25**: 19–29.

Stevens, M.H.H. and Carson, W.P. 1999a. Plant density determines species richness along an experimental fertility gradient. *Ecology*, **80**: 455–465.

Stevens, M.H.H. and Carson, W.P. 1999b. The significance of assemblage level thinning for species richness. *J. Ecol.*, **87**: 490–502.

Terborgh, J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.*, **107**: 481–501.

Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.

Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton, NJ: Princeton University Press.

Tilman, D. and Pacala, S. 1993. The maintenance of species richness in plant communities. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (R.E. Ricklefs and D. Schluter, eds), pp. 13–25. Chicago, IL: University of Chicago Press.

Umbanhower, C.E., Jr. 1992. Reanalysis of the Wisconsin prairie continuum. *Am. Midl. Nat.*, **127**: 268–275.

VanderMeulen, M.A., Hudson, A.J. and Scheiner, S.M. 2001. Three evolutionary hypotheses for the hump-shaped productivity–diversity curve. *Evol. Ecol. Res.*, **3**: 379–392.

VEMAP Participants. 1995. Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. *Global Biogeo. Cycles*, **9**: 407–438.

Wheeler, B.D. and Giller, K.E. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk, in relation to the quantity of above-ground plant material. *J. Ecol.*, **70**: 179–200.

Wheeler, B.D. and Shaw, S.C. 1991. Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. *J. Ecol.*, **79**: 285–301.

Whittaker, R.H. and Niering, W.A. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology*, **56**: 771–790.

Williams, R.J., Duff, G.A., Bowman, D.M.J.S. and Cook, G.D. 1996. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *J. Biogeogr.*, **23**: 747–756.

Willig, M.R. and Lyons, S.K. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos*, **81**: 93–98.

Wilson, S.D. and Keddy, P.A. 1986. Species competitive ability and position along a natural stress disturbance gradient. *Ecology*, **67**: 1236–1242.

Wollkind, D.J. 1976. Exploitation in three trophic levels: an extension allowing intraspecies carnivore interaction. *Am. Nat.*, **110**: 431–447.

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

Wright, D.H., Currie, D.J. and Maurer, B.A. 1993. Energy supply and patterns of species richness on local and regional scales. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (R.E. Ricklefs and D. Schluter, eds), pp. 66–77. Chicago, IL: University of Chicago Press.

Wu, J. and Loucks, O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quart. Rev. Biol.*, **70**: 439–466.