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WHAT IS THE OBSERVED RELATIONSHIP BETWEEN SPECIES RICHNESS AND PRODUCTIVITY?

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Abstract. Understanding the relationship between species richness and productivity is fundamental to the management and preservation of biodiversity. Yet despite years of study and intense theoretical interest, this relationship remains controversial. Here, we present the results of a literature survey in which we examined the relationship between species richness and productivity in 171 published studies. We extracted the raw data from published tables and graphs and subjected these data to a standardized analysis, using ordinary least-squares (OLS) regression and generalized linear-model (GLIM) regression to test for significant positive, negative, or curvilinear relationships between productivity and species diversity. If the relationship was curvilinear, we tested whether the maximum (or minimum) of the curve occurred within the range of productivity values observed (i.e., was there evidence of a hump?).

A meta-analysis conducted on the distribution of standardized quadratic regression coefficients showed that the average quadratic coefficient was negative (i.e., the average species richness–productivity relationship was curvilinear and decelerating), and that the distribution of standardized quadratic regression coefficients was significantly heterogeneous (i.e., the studies did not sample the same underlying species richness–productivity relationship).

Looking more closely at the patterns of productivity–diversity relationships, we found that, for vascular plants at geographical scales smaller than continents, hump-shaped relationships occurred most frequently (41–45% of all studies). A positive relationship between productivity and species richness was the next most common pattern, and positive and hump-shaped relationships co-dominated at the continental scale. For animals, positive, negative, and hump-shaped patterns were common at most geographical scales, and no one pattern predominated. For both plants and animals, hump-shaped curves were relatively more common in studies that crossed community boundaries compared to studies conducted within a community type, and plant studies that crossed community types tended to span a greater range of productivity compared to studies within community types. Sample size and plot size did not affect the probability of finding a particular productivity–diversity relationship (e.g., positive, hump-shaped, etc.). However, hump-shaped curves were especially common (65%) in studies of plant diversity that used plant biomass as a measure of productivity, and in studies conducted in aquatic systems.

Key words: biodiversity; productivity; productivity–diversity relationships; scale; species diversity; species richness.

INTRODUCTION

Relationships between species richness and productivity are of long-standing interest to ecologists, and

unraveling the mechanisms driving these relationships is of fundamental importance to understanding the determinants of biodiversity. Despite the attention focused on this problem, considerable controversy remains concerning the general form of the species richness–productivity relationship, what organisms fit particular re-

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relationships, and what mechanisms produce the patterns (Abrams 1995, Waide et al. 1999).

Species richness is often hypothesized to first increase and then decrease with productivity, producing a hump-shaped or unimodal relationship (e.g., Grime 1973, 1979, Huston 1979, Tilman 1982, Rosenzweig 1992). A number of empirical examples of unimodal productivity–diversity relationships have been documented (e.g., Tilman and Pacala 1993, Huston 1994, Rosenzweig 1995, Leibold 1999, Dodson et al. 2000), and various authors have gone as far as to state that the hump-shaped curve is the “true” (Rosenzweig 1992) or “ubiquitous” (Huston and DeAngelis 1994) relationship between productivity and species richness. However, as Abrams (1995) showed, there are good theoretical reasons to expect other forms of the productivity–diversity relationship besides a hump-shaped curve. Recently, Grace (1999) surveyed the literature on productivity–diversity relationships in herbaceous plant communities and concluded that most studies relating plant species richness to plant biomass in small plots showed a hump-shaped relationship. Waide et al. (1999) examined both animal and plant studies and found that while hump-shaped relationships were common for some taxa and at some geographical and ecological scales, other patterns occurred as well.

The recent reviews of Grace (1999) and Waide et al. (1999) make valuable contributions by providing a more complete survey of the productivity–diversity literature than was previously available. However, a potential problem with the studies of both Grace (1999) and Waide et al. (1999) is that they relied primarily on published analyses to evaluate whether a productivity–diversity relationship was hump-shaped or not. Many of these original analyses suffer from methodological and statistical problems. In a few cases, the original studies provided no statistical analysis at all and the authors simply inspected the data visually to determine the form of the relationship. In most other cases, the authors used least squares regression to test for a significant positive, negative, or curvilinear relationship. Regression models that included a significant quadratic term were usually accepted as evidence of a hump-shaped relationship. However, the assumptions of ordinary least squares regression (e.g., symmetrical and normally distributed errors) are likely to be violated when dealing with count data such as species richness, and analysis using generalized linear models is preferred (Nicholls 1989, Crawley 1993). Further, evidence for a hump-shaped relationship should include a test to see whether the curve peaks within the range of productivities observed (e.g., Leibold 1999), not simply that the relationship has a significant quadratic term and is therefore curvilinear.

In this paper, we expand on the literature survey presented in Waide et al. (1999), and provide a more complete and rigorous analysis of a broader data set. We searched the literature for a 30+ year period (1968–1999) and found 257 published data sets relating pro-

ductivity and species diversity in a variety of taxa. We then subjected these published data sets to a common statistical analysis by extracting the raw data from studies with sample size ≥ 10 . Using generalized linear models (GLIM regression; Crawley 1993) and ordinary least squares regression (OLS), we tested whether productivity and species richness were related in a significantly positive, negative, or curvilinear fashion. If the relationship was curvilinear, we then used the methods of Mitchell-Olds and Shaw (1987) to determine whether the maximum (or minimum) of the curve occurred within the range of productivity values observed (i.e., whether there is evidence of a hump as opposed to simple asymptotic change). These analyses allow, for the first time, a comparison of observed productivity–diversity relationships that have been classified in a consistent and quantitative manner across all studies. Previous studies (e.g., Rosenzweig and Abramsky 1993, Wright et al. 1993, Waide et al. 1999) suggest that the form of the productivity–diversity relationship may change with scale or may be influenced by other environmental factors. Here, we examine these factors quantitatively, looking particularly at the influence of: geographical and ecological scale, productivity range, productivity measure, plot size, and study system. We also discuss how experimental manipulations of productivity (which commonly show a decrease in species richness with increased productivity), may relate to the observed patterns of productivity and species richness in natural systems.

SCALES OF STUDY

Definitions

The concepts of diversity and productivity have a rich and somewhat checkered history in ecology, and the terms have many definitions. In this study, we use species richness (i.e., the number of species present in an area) as our measure of species diversity and the rate of energy flow to a system (e.g., $\text{mg C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) as our definition of productivity. Most empirical and theoretical studies of productivity–diversity relationships have focused on these measures (Abrams 1995, Rosenzweig 1995). We note that species diversity also can be viewed as a function of both species richness and species evenness (i.e., the equitability with which individuals are distributed among species; Hurlbert 1971, Peet 1974), and this measure of species diversity may also bear interesting relationships to productivity. However, few studies report comparable measures of species evenness, so we focus our consideration on patterns of species richness.

Measuring productivity can also be problematic. Although we can define productivity as the rate of energy flow to a system (averaged over some time scale), this rate rarely is measured in nature. Instead, an indirect measure that correlates with productivity (e.g., rainfall, evapotranspiration, peak plant biomass) generally is

used. These indirect measures differ in the extent to which they correlate with productivity. Moreover, some measures estimate the potential productivity of a site (e.g., rainfall, evapotranspiration, ocean depth), whereas others (e.g., annual biomass accumulation) estimate the actual productivity of a site (which may be a function of the types of species present; see McNaughton 1993, Naeem et al. 1994, Tilman et al. 1997, Hooper 1998, Hector et al. 1999). Also, a measure of actual productivity at one trophic level (e.g., primary productivity) may in turn be an estimate of potential productivity available to higher trophic levels (e.g., herbivores). In our survey of the literature, we include studies that measured productivity directly, or measured a known or presumed correlate of productivity, and we report the measure of productivity used by the author(s) and its observed range within a study.

Finally, we note that many field studies of species diversity are constrained by time or money to examine a particular taxonomic group (e.g., rodents, trees), or (less often) a particular functional group (e.g., carnivores). Theory, on the other hand, often predicts how the diversity of an entire trophic level should change with productivity. It is important to keep this distinction in mind when interpreting the evidence for or against predicted patterns.

Scales

There are many ways to organize scales of study when examining ecological relationships, and any division of a world filled with interacting populations and interacting processes will be somewhat arbitrary. Still, there are distinctions of scale that can help us see more clearly the existing patterns between species richness and productivity, and thereby help us relate the observed patterns to current theory. We defined scales of study based upon geographical extent and ecological association. Four geographical scales were recognized: "local" (0–20 km), "landscape" (20–200 km), "regional" (200–4000 km), and "continental to global" (>4000 km). We used the greatest distance between sites within a study to measure geographical scale. We defined two scales of study based upon ecological associations: "within a community type" and "across community types." We used a shift in vegetation structure or plant physiognomy to define a change in community type (e.g., transitions from desert to grassland, or meadow to woodland). Thus, studies done within a vegetation type dominated by one life form (e.g., tallgrass prairie) were classified as within community type (even though samples may be separated in space), whereas studies conducted across vegetation types or life forms (e.g., prairie to woodland), were defined as across community type (even though they may represent contiguous samples over small areas). We excluded studies conducted at the largest spatial scale (continental to global, >4000 km) from our comparisons of within vs. across community type. For most studies, we relied on the description of sites by the authors to clas-

sify studies as within or across community types. However, we acknowledge that any classification of community types is subjective and that others might wish to group studies differently. Therefore, we provide the ecological classification we used along with the data in the Appendix.

Other researchers have recognized that species richness–productivity patterns may vary with scale. For example, Currie (1991), Wright et al. (1993), Huston (1994), and Rosenzweig (1995) have discussed patterns arising at different spatial scales. Huston (1994) and Rosenzweig (1995) also have attempted to link the spatial scale of a pattern to the ecological or evolutionary mechanisms operating at that scale. Similarly, Moore and Keddy (1989) have argued for the importance of looking at productivity–diversity relationships at different ecological scales, demonstrating that productivity–diversity patterns in wetland plants differ within and across community types. Of course, classification of patterns based on ecologically defined scales will often be associated with geographical areas (e.g., studies that traverse large geographical areas are also likely to cut across community boundaries). However, ecologically based and geographically based definitions are not equivalent. For example, it is possible to shift between community types over small geographical distances, such as up a mountainside or away from a lakeshore (e.g., Nilsson and Wilson 1991).

Finally, a number of studies have examined species richness (of various taxa) among lakes, ponds, and flowing waters that differ in nutrient input and primary productivity. In these studies, a lake or stream is usually treated as the unit of study (rather than regions or quadrats within a lake), and measures of species richness and productivity are applied to the entire water body. Variation in nutrient input and productivity among aquatic systems usually results in large differences in vegetation type and structure (both in macrophytes and phytoplankton; e.g., Watson et al. 1997). Therefore, studies of different lakes, ponds, streams, or rivers have been classified ecologically as "across community type" (or as "continental to global" if the minimal distance criterion was met). Leibold (1999) similarly argues that patterns observed among ponds should be viewed as a larger, "regional scale" pattern. Dodson et al. (2000) provide a detailed analysis of patterns of species richness and productivity in freshwater lakes.

PRODUCTIVITY–DIVERSITY PATTERNS

Assembling the patterns

We used three search algorithms to locate studies that examined relationships between productivity and species diversity. The search was designed to provide a broad survey of all ecological journals, and a more detailed search of selected journals. In our broad survey, we electronically searched the Biological Abstracts of

BIOSIS¹⁰ for articles published between January 1982 and September 1999, using the key words: species richness and productivity, species richness and biomass, species richness and rainfall, species richness and precipitation, species diversity and productivity, species diversity and biomass, species diversity and rainfall, species diversity and precipitation. Using these same keywords in JSTOR,¹¹ we electronically searched the full text of all articles published in *Ecology*, *Ecological Applications*, and *Ecological Monographs* for all years up to 1993. We manually searched all issues of these three journals published between 1994 and 1999. We conducted a detailed search of BIOSIS (Biological Abstracts) for articles published in *American Naturalist*, *Oecologia*, *Oikos*, *Holarctic Ecology/Ecography*, *Journal of Biogeography*, *Journal of Ecology*, *Journal of Vegetation Science*, and *Vegetatio (Plant Ecology)* starting in 1997 for the years 1980–1999, using the following search string: “species richness OR species diversity OR primary productivity OR production OR biomass OR rainfall OR precipitation.” These same journals were searched manually for the years 1968–1979 (pre-database). Finally, we used the old-fashioned method of going through the literature cited sections of published articles to locate papers not included in the electronic databases. Studies with sample size ≥ 4 , and that reported a statistical correlation (or presented data sufficient to calculate one) between species richness and some measure of productivity, were included in the survey and are included in the Appendix. However, to insure that a study had reasonable power to detect a pattern, we limited our analyses to studies that had a sample size ≥ 10 . Data from agricultural and intensively managed systems were excluded from the survey, as were systems subject to severe anthropogenic disturbance. We also excluded studies in which productivity was experimentally manipulated. Data from this survey, including information from each study (where available) on the taxa studied, range of species richness, productivity measure (type and range), spatial scale, and statistical analysis of productivity–diversity relationships, is available in the Appendix. Complete citations for all studies in the database also are included.

We classified studies with respect to the four geographical and two ecological scales described above. We then classified the relationship between productivity and species richness into one of five patterns: positive, negative, hump-shaped, U-shaped, or no significant relationship. Most published studies used ordinary least-squares (OLS) regression to evaluate the relationship between species richness and productivity, testing for significance and curvilinearity using linear and quadratic terms. However, because species richness can never be less than zero, the assumptions of OLS regression (e.g., symmetric and normally distributed errors) are likely to

be violated for most species richness data sets (Nicholls 1989, Crawley 1993). The preferred technique for analyzing count data such as number of species is to use a generalized linear model (GLIM) with an assumption of Poisson errors and a logarithmic link function (Nicholls 1989, Pausas 1994, Austin 1999). In contrast to OLS regression, this method uses maximum likelihood to fit model parameters.

We extracted the raw data from as many studies as possible, using either published tabular data or by digitizing published graphs. We then ran both GLIM regression (NAG Statistical Add-Ins for Excel, Release 1, NAG)¹² and OLS regression (SYSTAT version 8.0 [1998]) on the data using the equation: species richness = $a + b(\text{productivity}) + c(\text{productivity})^2$. In order to be as liberal as possible in discovering patterns, relationships were deemed significant if $P < 0.10$. The majority of relationships deemed significant had P values < 0.01 . Regressions in which the quadratic term explained a significant amount of the variance after fitting the linear term were classified as curvilinear. For these relationships, we applied the test of Mitchell-Olds and Shaw (1987; hereafter referred to as the MOS test) to determine whether the curvilinear relationship reached a maximum (or minimum) within the observed range of productivities. (See Leibold 1999, for another example using the MOS test to look for hump-shaped species richness patterns.) Curvilinear relationships that showed an internal maximum or minimum via the MOS test ($P < 0.10$) were classified as hump-shaped or U-shaped, respectively. Those without an internal maximum or minimum are equivalent to a linear regression as some transformation can be found to linearize any monotonic relationship.

We compared the results of the GLIM and OLS regressions to look for the degree of correspondence between the two analyses. For 16 of the 171 productivity–diversity relationships examined, we were unable to run GLIM regressions, because the raw or digitized data were unavailable. For those studies, we relied on the results of OLS regression to determine the form of the productivity–diversity relationship (they are coded separately in the presentation of results).

Patterns in productivity–diversity relationships

Taxonomic distribution.—The distribution of studies among taxonomic groups was uneven (Table 1). Terrestrial plants were the most commonly studied group (36%), whereas studies of aquatic plants were relatively rare (12%). For animals, studies in terrestrial systems focused on vertebrates (particularly mammals), whereas studies in aquatic systems concentrated on invertebrates (Table 1). This taxonomic distribution of studies suggests two things: (1) our understanding of productivity–diversity relationships is influenced strongly by particular taxonomic groups and therefore may be biased and

¹⁰ URL: <http://www.biosis.org>

¹¹ URL: <http://www.jstor.org>

¹² URL: <http://www.nag.com>

TABLE 1. Number of studies of productivity and species richness by taxon.

Vertebrates		Invertebrates		Plants	
Taxon	<i>n</i>	Taxon	<i>n</i>	Taxon	<i>n</i>
Terrestrial					
Amphibians	3	Insects	11	Trees, shrubs, herbs	16
Reptiles	7	Other	2	Shrubs and herbs	12
Birds	9	Total	13	Shrubs and trees	5
Mammals	22			Herbs	13
Total	41			Trees	11
				Other	5
				Total	62
Aquatic					
Fish		Zooplankton	7	Algae	6
Total	7	Macro. invert.	8	Macrophytes	2
		Corals	4	Wetland herbs	5
		Other	9	Wetland shrubs and herbs	3
		Total	28	Wetland trees, shrubs, herbs	4
				Total	20

Note: Only studies with $n \geq 10$ were included.

(2) a clear need exists for more research on underrepresented taxa (e.g., terrestrial invertebrates, fungi, bacteria).

Patterns across geographical scales.—For vascular plants, a hump-shaped relationship between productivity and species richness predominated at all scales smaller than the continental to global, and hump-shaped curves comprised 41–45% of the relationships at these geographical scales (Fig. 1). A positive relationship between productivity and species richness was the next most commonly observed pattern, and positive and hump-shaped relationships codominated at the largest spatial scale (>4000 km; Fig. 1). We used logistic regression (SYSTAT 1998) to determine whether the odds of finding a particular relationship (i.e., hump-shaped, positive, negative, U-shaped, or none) varied significantly with spatial scale. Based on this analysis, positive relationships showed a tendency to increase with spatial scale (t ratio = 1.81, $P = 0.07$, odds ratio = 2.07, $n = 59$). However, the probability of finding any of the other four patterns did not differ across spatial scales (all P 's > 0.20).

There was a pronounced shift in the way productivity was measured across a gradient of increasing spatial scales. In small-scale studies (<200 km), productivity was most often assessed by plant biomass (peak standing stock during the growing season; Fig. 1). In contrast, most of the studies at the regional scale assessed productivity gradients based on variation in rainfall, and at the continental to global scale (>4000 km), most studies estimated productivity either as actual evapotranspiration (AET) using climatic data, or net primary productivity (NPP) calculated from AET (using models of Rosenzweig 1968 or Leith 1975).

For animals, there was no dramatic change in pattern across spatial scales (Fig. 2). Positive, negative, and hump-shaped patterns were common at most spatial scales and no one pattern predominated. Logistic re-

gression showed no significant difference in the odds of finding a positive, negative, or hump-shaped pattern at different spatial scales (all P 's > 0.20). However, the odds of finding a nonsignificant relationship ("None" pattern) declined significantly with increased spatial scale (t ratio = -2.001, $P = 0.04$, odds ratio = 0.523, $n = 67$). While U-shaped relationships were more common at larger spatial scales (t ratio = 2.053, $P = 0.04$, odds ratio = 4.963, $n = 67$). Measures of productivity varied with scale in a similar fashion as for plants. At small scales (<200 km) productivity generally was measured as the standing stock biomass of the animal group being studied. At regional scales, variation in rainfall was the predominant index of productivity, and at the continental to global scale, productivity was measured as AET or NPP calculated from AET, rainfall, or indexed by latitude.

Patterns across ecological scales.—Hump-shaped curves were relatively more common for both plants and animals in studies that crossed community types compared to studies conducted within a community type (Fig. 3). A χ^2 analysis, however, showed that the overall pattern of relationships did not differ significantly between the two biotic scales (χ^2 exact test [StatXact]: $P = 0.12$ for animals; $P = 0.32$ for plants).

Patterns in aquatic and terrestrial systems.—Hump-shaped relationships predominated in aquatic systems, and they were common for terrestrial invertebrates and plants as well (Fig. 4). The difference in overall distribution of relationships between aquatic and terrestrial systems was marginally significant for plants ($P = 0.08$), but was not significant for invertebrates ($P = 0.14$), or vertebrates ($P = 0.50$) (χ^2 exact test, StatXact).

Distribution of standardized quadratic coefficients.—Although our survey of the literature turned up many significant hump-shaped relationships, the proportion may be less than expected based on current ecological thought. One possible reason is that some

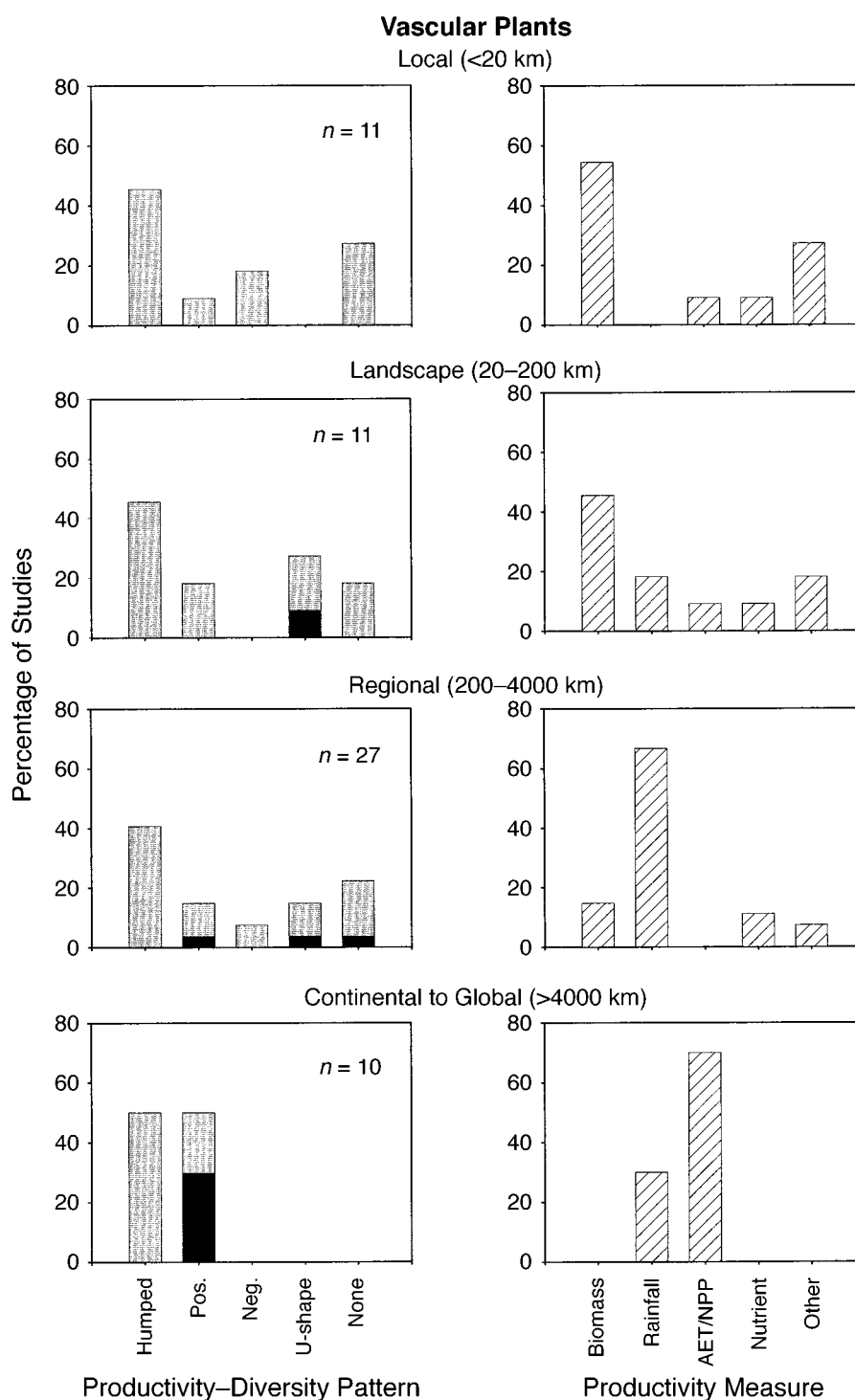


FIG. 1. Left column: percentage of published studies on vascular plants showing various patterns of species richness and productivity at four geographical scales. Solid bars (black) indicate studies for which we were unable to run generalized linear model (GLIM) regression and instead used the results of ordinary least-squares (OLS) regression. Right column: percentage of published studies using various measures of productivity. Sample sizes (n) refer to the total number of analyzed data sets in each classification and apply to both the left and right columns. Abbreviations for productivity measures are: Biomass = aboveground standing crop of plant taxa studied; Rainfall = mean annual rainfall (or mean rainfall over some other standardized period); AET/NPP = actual evapotranspiration calculated from climatic data or net primary productivity calculated from AET; Nutrient = concentration of limiting nutrient(s); Other = all other estimates of productivity.

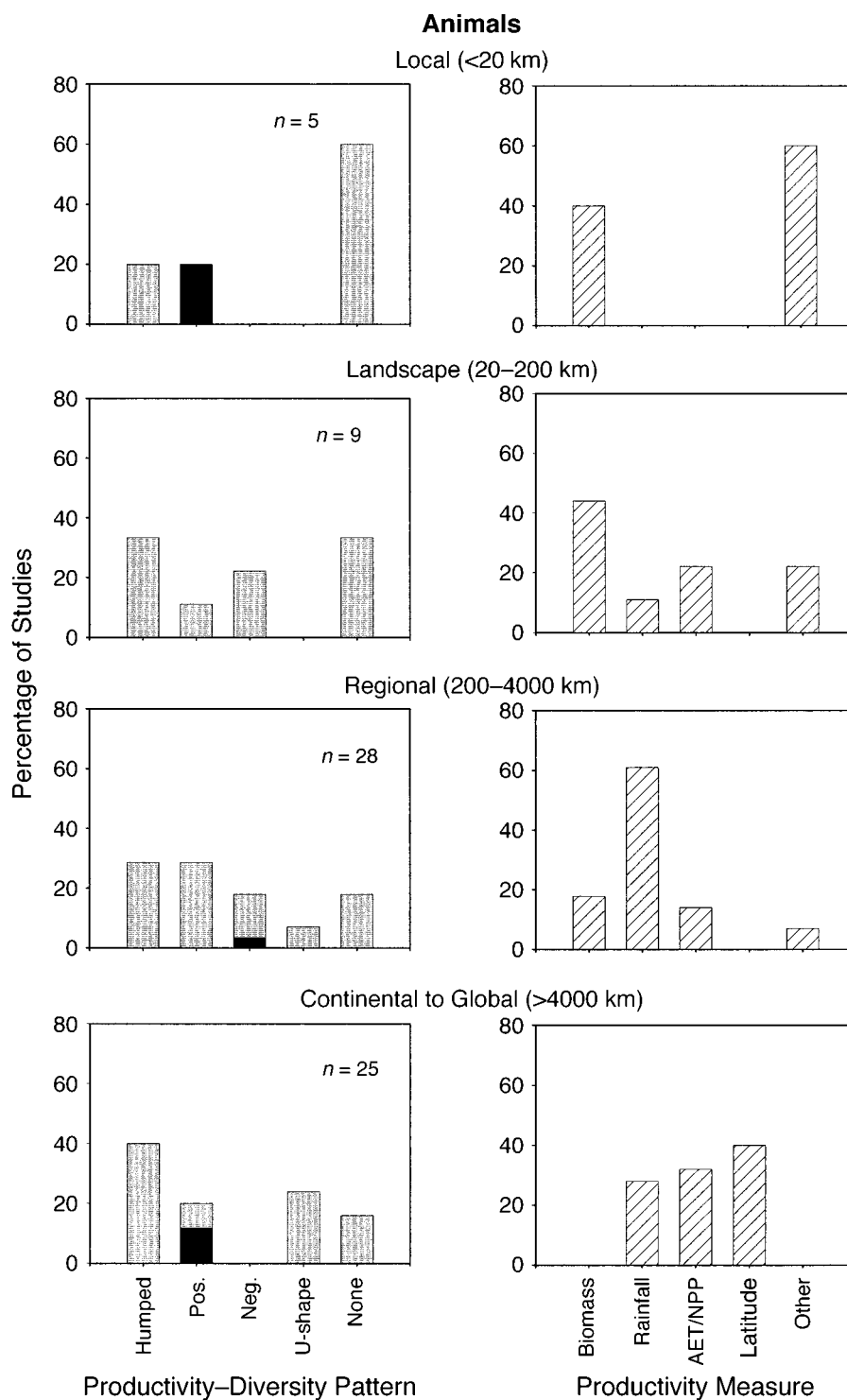


FIG. 2. Left column: percentage of published studies on animals showing various patterns of species richness and productivity at four geographical scales. Shading is as in Fig. 1. Right column: percentage of published studies using various measures of productivity. Sample sizes (n) refer to the total number of analyzed data sets in each classification and apply to both the left and right columns. Abbreviations for productivity measures are: Biomass = standing crop of animal taxa studied; Rainfall = mean annual rainfall (or mean rainfall over some other standardized period); AET/NPP = actual evapotranspiration calculated from climatic data or net primary productivity calculated from AET; Latitude = latitude; Other = all other estimates of productivity.

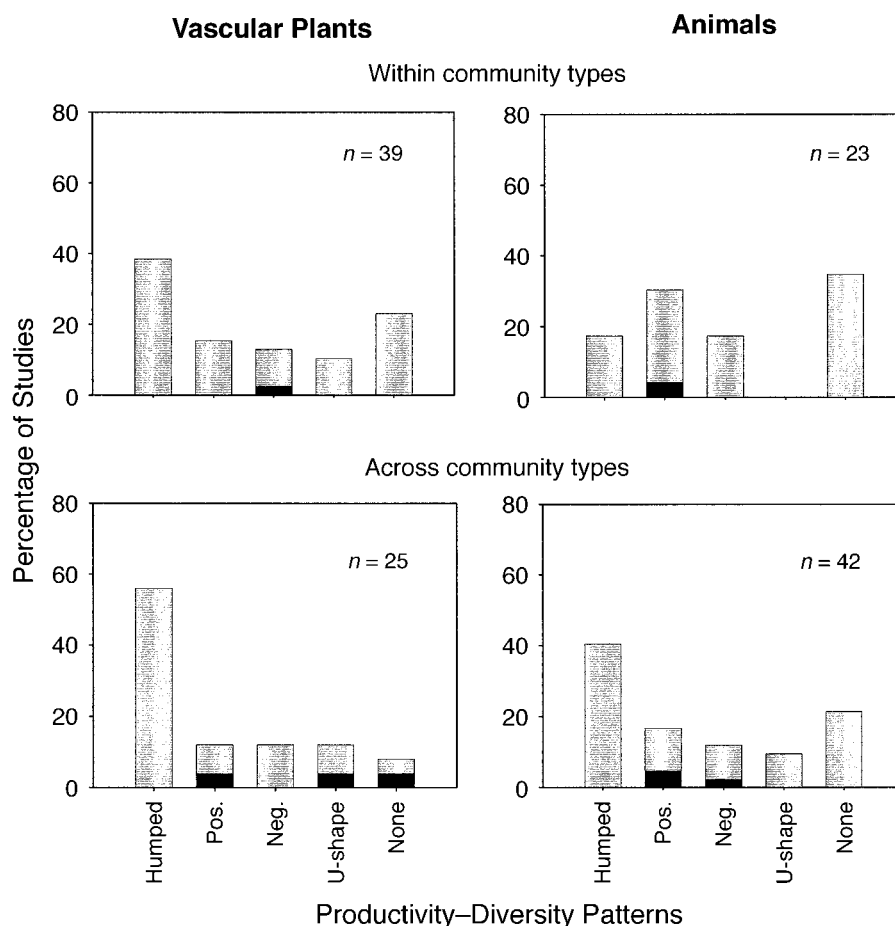


FIG. 3. Percentage of published studies showing various patterns of species richness and productivity at two scales of ecological organization. Plants and animals are illustrated separately. Sample sizes (n) refer to the total number of analyzed data sets in each classification. Shading is as in Fig. 1.

of the studies in our survey had modest sample sizes and therefore low power to detect a significant unimodal relationship ($n = 10$ was our minimum criteria for including a study in the analysis). If small sample size were the reason for failing to find more significant hump-shaped curves, we would expect to see both large and small regression coefficients associated with the studies we classified as nonsignificant. To address this issue we examined the distribution of standardized quadratic regression coefficients; the standardization accounts for scale difference among data sets. Because GLIM regression does not provide standardized regression coefficients, this examination was done using the OLS coefficients. We examined the data in two ways: graphically and in a formal meta-analysis. The graphical analysis (Fig. 5) shows that for data sets with sample sizes above 20, the significant regression coefficients had values outside the range of the nonsignificant coefficients (which ranged between -1 and 1 ; Fig. 5). In contrast, for sample sizes of 10 – 20 , both significant and nonsignificant coefficients spanned a

similar range of values (Fig. 5). Thus, conclusions might be suspect for these smaller data sets. However, the overall distribution and range of coefficients did not differ between the data sets with larger and smaller sample sizes. Therefore, our overall conclusions are likely robust. Clearly, there are a substantial number of data sets with large sample sizes and nonsignificant quadratic coefficients (i.e., no evidence of a hump-shaped curve).

We also performed a formal meta-analysis (Osenberg et al. 1999, Gurevitch and Hedges 2001) using a mixed-effects model (Rosenberg et al. 2000) to test whether the standardized quadratic regression coefficients were more heterogeneous than would be expected by chance alone. As expected, given the pattern in Fig. 5, the coefficients were significantly heterogeneous ($\chi^2_{155} = 8420$, $P < 0.00001$), and we can reject the hypothesis that they came from a single, underlying distribution. The mean quadratic coefficient was -0.632 , and the bias-corrected bootstrapped 95% CI was $(-0.905$ to $-0.362)$, which does not include zero. The fact that

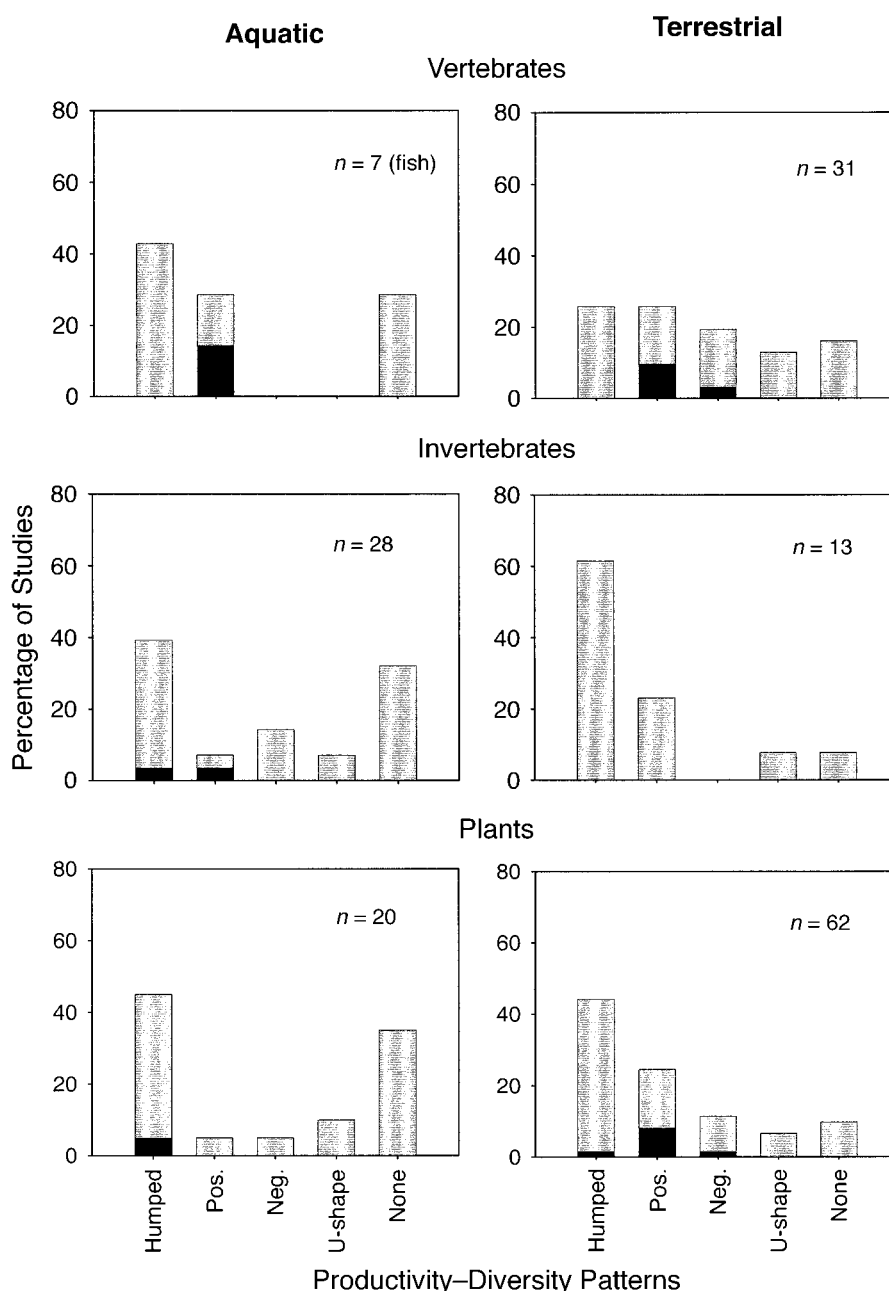


FIG. 4. Percentage of published studies showing various patterns of species richness and productivity in aquatic and terrestrial systems. Vertebrates, invertebrates, and plants are illustrated separately. Taxa that have both functional aquatic and terrestrial life stages (e.g., amphibians) were excluded. Shading is as in Fig. 1.

the mean quadratic term was significantly negative indicates that the average productivity-diversity relationship was nonlinear and decelerating. This result agrees with our previous analyses; humped-shaped distributions tend to predominate, but other relationships are common as well. A more extensive meta-analysis (e.g., testing for differences among geographic extents) is not warranted for two reasons. First, these analyses can only be done with the OLS coefficients, which are

likely biased. Second, the meta-analysis cannot distinguish between relationships with an internal minimum or maximum (U-shaped or hump-shaped) and those that are simply nonlinear.

The discovery of a substantial number of positive quadratic coefficients (U-shaped relationships; Fig. 5) was an unexpected result from this survey. Previous reviews never mention such relationships and no current theories predict them. In Fig. 5, positive quadratic

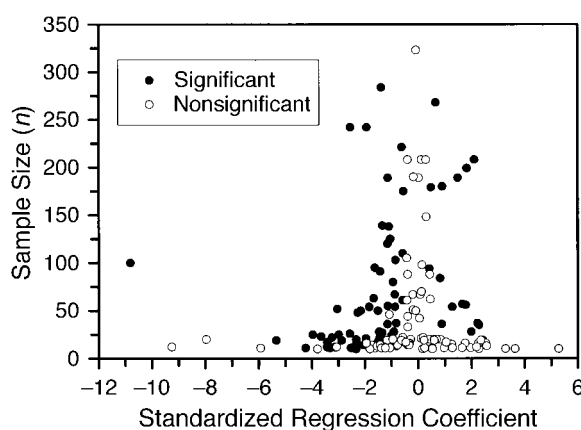


FIG. 5. Distribution of statistically significant and non-significant ordinary least-squares (OLS) standardized quadratic regression coefficients with respect to sample size. Significant coefficients included studies that the MOS test (Mitchell-Olds and Shaw 1987) determined as lacking an internal maximum or minimum.

coefficients make up 36% of the data, while negative coefficients account for 64%.

Statistical issues

Comparison of regression methods.—Because most conclusions in the literature are based on OLS regressions, rather than GLIM regression, we asked whether the two methods resulted in substantially different conclusions. For our data set, the two methods agreed 60% of the time (Table 2). GLIM was more likely to find nonmonotonic relationships (humped or U-shaped), while OLS was more likely to find monotonic relationships, especially positive ones. Otherwise, there was no particular bias between the methods. We used direct inspection to determine what features of the data resulted in the differing conclusions of GLIM and OLS analyses. Those data sets with visibly heteroscedastic residuals, in particular increasing variance with greater productivity, were most likely to be misclassified by OLS regression. Because OLS regression is currently more readily available than GLIM, it seems likely to continue to be used widely for analysis of species richness patterns. In such cases, we urge caution and careful inspection of residual plots to make sure that the assumptions of OLS regression are met.

Effects of quadrat size.—One potential problem with interpreting productivity–diversity patterns at different spatial scales is that the size of the area used to measure species richness (plot size) tends to increase with geographical scale. In our data set for terrestrial plant diversity, plot size was positively correlated with spatial extent (greatest linear distance between sample sites): log-transformed data, $n = 33$, Pearson $r = 0.62$, $P < 0.001$. Wright et al. (1993) also noted that “quadrat size was well correlated with the geographical scale of the investigation” in their review of species richness–energy patterns, although they do not report a statistical

analysis. Huston (1999) cautioned that it may be difficult to observe the impact of competition and other species interactions occurring on a relatively small spatial scale, when species richness is sampled using very large plot sizes. Also, because of the species–area relationship, the number of species sampled will generally increase with plot size. Therefore, if the probability of detecting a particular species richness–productivity pattern depends on the total number of species sampled, any effect of spatial extent on species richness–productivity relationships may be confounded by the correlation between plot size and spatial extent.

We tested for the influence of plot size on species richness–productivity patterns in terrestrial plants by using logistic regression (SYSTAT 1998) to examine whether the probability of finding a given species richness–productivity relationship changed with plot size. For none of the relationships examined (i.e., positive, negative, hump-shaped, U-shaped, or none), did the odds of finding a relationship change with plot size ($P > 0.10$, $n = 45$ in all cases). We also examined whether there was an interactive effect of plot size and spatial extent on the form of the species richness–productivity relationship by using multiple logistic regression. The results of the multiple logistic regressions show that the odds of detecting a particular species richness–productivity relationship (i.e., positive, negative, hump-shaped, U-shaped, or none) were not affected by either plot size, spatial extent, or their interaction (log-transformed data; $n = 33$, $P > 0.10$ in all cases). Therefore, although studies conducted at larger spatial scales tend to sample with larger plots and this may potentially confound the effect of spatial scale on the relationship between productivity and species richness, we found no evidence of a significant plot size effect in our data set.

INTERPRETING THE PATTERNS

Much of the current literature on productivity–diversity relationships focuses on the hump-shaped curve (Grime 1979, Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Huston 1994, Grace 1999). Our analysis supports the hypothesis that the relationship be-

TABLE 2. Comparison of regression analyses using generalized linear models (GLIM) and ordinary least-squares (OLS) methods.

GLIM analysis	OLS analysis				
	Humped	U-shaped	Positive	Negative	None
Humped	33	1	19	5	7
U-shaped	0	8	2	2	4
Positive	1	1	16	0	4
Negative	0	0	0	15	2
None	5	0	8	1	22
Total	39	10	45	23	39

Note: The table shows the number of studies classified in each of five categories.

tween species richness and productivity is often unimodal, as we found that the average quadratic term for all studies was negative. However, there is a great deal of variation in the relationship, and positive, negative, hump-shaped, and U-shaped curves occur at almost all scales of observation. Some relationships are relatively more common than others, particularly at certain scales and for certain taxa. Below, we examine in more detail some of the factors that may be responsible for the variation in productivity–diversity patterns observed at different spatial and ecological scales. We focus particularly on vascular plants, because they are the best-studied group and provide the most data.

Patterns at ecological scales

In plants, hump-shaped relationships were especially common at smaller spatial scales, and in studies that cross community boundaries (Fig. 3). Other authors have suggested that hump-shaped patterns will be detected most often when looking across community types. For example, Moore and Keddy (1989) found a significant humped-shaped pattern between species richness and standing plant biomass (a measure of primary production) when combining data from 15 wetland communities in eastern Canada. However, they found no significant relationship within a community or vegetation type. The studies of ter Heerdt et al. (1991) and Gross et al. (2000) also show hump-shaped relationships when comparing species richness across grasslands, but no hump within a grassland (but see Grytnes 2000). Moore and Keddy (1989) suggested that "... the higher level processes which structure species richness patterns among vegetation types are not the same processes which determine patterns within a vegetation type." However, it is not necessary that different processes operate at different scales to generate this pattern (Grace 1999), and there are a number of reasons why hump-shaped relationships might occur more often in studies conducted across community or vegetation types.

For example, there may be less variation in productivity within a community type than across community types, resulting in a smaller overall response in species richness. A number of authors have suggested that surveys of species richness conducted over limited productivity ranges are less likely to detect a hump-shaped relationship, than studies conducted over a broad productivity range (e.g., Begon et al. 1990, Rosenzweig 1992, 1995, Huston 1994, Guo and Berry 1998, Grace 1999).

We examined this hypothesis using the data from our literature survey. First, we compared the range of productivities observed in studies conducted within a community type to the range of productivities observed in studies conducted across community types. Second, we used logistic regression to estimate whether the probability of finding a unimodal relationship increased with the range of productivity examined. Two types of

productivity measures were used commonly enough (and measured in the same units) to allow comparisons: (1) annual rainfall and (2) plant standing crop (excluding litter). Productivity range was measured as the difference in the log values of the most productive and least productive sites, because we were interested in the proportional change in productivity observed within a study. We included all studies that reported the observed range of annual rainfall or the observed range of plant standing stock, and that were conducted at geographical scales <4000 km.

When productivity was indexed by annual rainfall, there was a greater proportional change in productivity in studies conducted across community types than in studies conducted within a community type (separate variance *t* test, *t* = 1.960, *df* = 23.6, *P* = 0.054; SYSTAT version 8.0). When productivity was measured as plant standing crop, there was no difference in the proportional change in productivity observed in studies conducted across and within community types (separate variance *t* test, *t* = 0.572, *df* = 4.8, *P* = 0.593).

In the second analysis, we used logistic regression to test whether the probability of detecting a unimodal relationship varied significantly as a function of the productivity range (annual rainfall or plant biomass) observed in a study. We also conducted a multiple logistic regression to examine the joint effects of rainfall range, sample size, and spatial extent on the probability of detecting a humped relationship. The number of studies was too small to conduct a similar multiple logistic regression for plant biomass range.

The probability of detecting a humped relationship increased significantly when studies sampled a greater proportional change in annual rainfall (*P* = 0.008, *n* = 28; Table 3). Rainfall range also had a significant effect in the multiple logistic regression including sample size and spatial extent (*P* = 0.027, *n* = 23; Table 3), while the other variables were not significant (Table 3). There was no significant effect of the difference in log plant biomass on the probability of detecting a hump-shaped relationship (*P* = 0.345, *n* = 12; Table 3).

The strength of the above analyses is somewhat limited by the number of studies available. Sample size was reasonably large for studies measuring range in annual rainfall (*n* = 28), and for these studies we found that the range of productivity sampled was greater in studies conducted across community types compared to studies conducted within community types, and that the probability of detecting a hump-shaped relationship increased with the range of productivity sampled. These same relationships were not significant for studies that measured plant standing stock as an index of productivity. However, for these comparisons, sample size was quite small. Hopefully, future analyses will readdress this issue as more studies become available.

TABLE 3. Logistic regression of the effects of productivity range (difference in log annual rainfall or difference in log plant standing stock biomass [excluding litter]) on the probability of finding a hump-shaped relationship between productivity and species richness for vascular plants. Also shown are the results of a multiple logistic regression examining the effects of the difference in log annual rainfall, spatial extent, and sample size on the probability of finding a hump-shaped relationship.

Predictor variable	Estimate	<i>t</i> ratio	<i>P</i> value	<i>n</i>
Logistic regression				
Difference in log annual rainfall	-5.381	-2.636	0.008	28
Difference in log plant biomass	-1.066	-0.945	0.345	12
Multiple logistic regression				
Difference in log annual rainfall	-7.534	-2.217	0.027	23
Spatial extent	-0.001	-0.972	0.331	23
Sample size	0.063	0.926	0.355	23

Patterns in vascular plants: geographical scales

A number of authors have suggested that on a global scale, species richness increases monotonically with productivity, and that this contrasts to the hump-shaped pattern observed at regional and smaller scales (e.g., Currie and Paquin 1987, Rosenzweig and Abramsky 1993, Wright et al. 1993, Scheiner and Rey Benayas 1994, Waide et al. 1999). Our analysis provides only limited support for this conclusion. Positive relationships were common for vascular plants at the largest spatial scale (>4000 km; Fig. 1) and the odds of finding a positive relationship tended to increase with an increase in spatial extent ($P = 0.07$). However, the number of plant studies conducted at the largest (global) scale is limited ($n = 10$ that met our criteria). For animals, there is no evidence that positive relations are more common at larger spatial scales (Fig. 2). Thus, although Waide et al. (1999) and others suggest that positive relationships predominate for plants and animals at the continental and global scale, our reanalysis of the literature shows that this is not a strong pattern (see also the previous discussion about the potential effects of increasing plot size with increasing spatial scale).

One very noticeable pattern was that the variable used to measure productivity changed with geographic scale (Figs. 1 and 2). Could these differences in the way productivity is measured influence the probability of finding a particular productivity–diversity relationship? For plants, hump-shaped curves were more commonly found when productivity was measured as standing stock biomass. Sixty-five percent of the studies that measured productivity as plant standing stock (with or without litter) found a hump-shaped relationship (compared to 6% positive, 12% negative, 12% U-shaped, and 6% nonsignificant relationships). However, the odds of finding a hump-shaped curve were not significantly higher when productivity was measured as plant standing stock vs. when productivity was measured by other factors (logistic regression: t ratio = -1.355, odds ratio = 2.30, $P = 0.17$).

Stevens and Carson (1999a, b) showed that assem-

blage-level thinning in plants (i.e., a decrease in total plant density as mean plant size increases) can generate hump-shaped relationships between plant species richness and plant standing stock. If plants differ in size in response to soil fertility, then sampling plant species richness with fixed-sized quadrats will result in relatively few individuals sampled at low plant biomass (because plants have a fixed minimum aboveground size) and relatively few individuals at high biomass (because plants are bigger at higher productivity and thus there are fewer individuals in a given-sized plot). If there is a positive relationship between the number of individuals in a plot and the number of species in a plot (a common finding), then hump-shaped patterns of species richness and plant biomass will result. Thus, Stevens and Carson's (1999a, b) theory (see also Oksanen 1996 for a similar concept) could provide an explanation for why small-scale studies of vascular plants so often found hump-shaped relationships between species richness and plant biomass (Fig. 1) (but see Grime 1997, Marañón and García 1997, Rapson et al. 1997, Zobel and Liira 1997, and Goldberg and Estabrook 1998, for views counter to those of Oksanen 1996 and Stevens and Carson 1999a, b).

Comparisons between aquatic and terrestrial systems

We found that hump-shaped relationships were particularly common in aquatic systems (Fig. 4). A compilation of data from 33 freshwater lakes by Dodson et al. (2000) also shows that unimodal relationships are the norm in lacustrine systems. Dodson et al. (2000) found that phytoplankton, macrophytes, and zooplankton all showed significant hump-shaped relationships between species richness and primary productivity, whereas the relationship for fish was curvilinear and saturating. Why are hump-shaped relationships relatively more common in aquatic systems? At this point, we know too little to provide a satisfying answer. Aquatic systems, especially lakes and ponds, are relatively closed and bounded. This may make lakes and ponds less subject to source–sink dynamics or susceptible to mass/rescue-effects (sensu Brown and Kodric-

Brown 1977, Shmida and Ellner 1984, Shmida and Wilson 1985) than terrestrial systems. High dispersal of species between sites of differing productivity can lower the probability of finding a hump-shaped relationships, because species-rich associations may act as "species sources" for "sink patches" on both the low- and high-end of the productivity gradient, effectively masking the ascending and descending portions of the hump. This effect would be heightened when species dispersal between sites of differing productivity is high.

Studies of species richness in lakes also tend to measure species richness of trophic levels (e.g., primary producers, grazers, carnivores; Dodson et al. 2000), whereas studies in terrestrial systems tend to measure species richness of taxa (e.g., trees, mammals, birds, rodents). This may contribute to the high proportion of hump-shaped relationships observed in aquatic systems, as it is generally expected that the diversity of an entire trophic level should respond to a change in productivity (Rosenzweig 1995, Leibold 1999).

Experimental and comparative approaches

Experimental manipulations of productivity through nutrient additions or manipulations of other limiting factors provide a means to test mechanisms determining productivity–diversity relationships at different scales. Experimental studies of productivity and species richness are especially common in terrestrial plants, and reviews of the literature in this area can be found in Silvertown (1980), Tilman (1982, 1987), Inouye et al. (1987), Di Tommaso and Aarssen (1989), Goldberg and Miller (1990), Schindler (1990), Huston (1994), and Gough et al. (2000). Most studies that have experimentally manipulated productivity found that species richness decreased following an experimental increase in productivity (via fertilization), although an increase or no change in species richness also has been observed (e.g., Pringle 1990, Huberty et al. 1998, Hall et al. 2000). A number of authors interpreted this decline as demonstrating the descending arm of the hump-shaped curve (e.g., Di Tommaso and Aarssen 1989). However, the meta-analysis of Gough et al. (2000) shows that the experimental addition of a limiting nutrient (nitrogen) to a number of North American plant communities (grassland, desert, and tundra) yielded the same relative magnitude of decline in species richness, regardless of the underlying productivity of the system. Fertilization reduced species richness at both high and low productivity sites.

The results of Gough et al. (2000) and others bring into question the relevance of experimental manipulations of productivity for interpreting natural patterns. Both the short-term nature and small spatial scale of most experimental manipulations are a potential problem. Short-term responses to experimental manipulations of productivity are dependent on the existing species composition (Osenberg and Mittelbach 1996, Leibold et al. 1998). Very often, one or a few species in

a community respond strongly to an increase in a limiting resource, outcompeting other species and leading to a decline in species richness (e.g., Tilman 1987). However, we do not know whether other species could potentially invade and thrive under new conditions of enhanced productivity (see Wright et al. [1993] and Rosenzweig [1995] for similar arguments). The small-scale and short-term nature of most experiments also limits the opportunity for species from higher productivity sites to disperse into the treatments, or for species to adapt to the new productivity conditions (but see Bohannan and Lenski 1997 for an example of how evolution of a novel trait can change a species' response to productivity in a microbial community). Alternatively, experiments could be conducted that simultaneously test for the effects of productivity and dispersal limitation on species richness (Cornell 2001). One such design would combine an experimental manipulation of fertility with the addition of propagules (seeds) of species found at higher fertility sites. If dispersal limitation is important in determining local diversity, we expect species richness to respond differently to combined nutrient and species addition at high and low productivity sites.

There are also many challenges to using the comparative approach to interpret patterns such as those observed in Figs. 1–3. For one, many existing theories predict similar relationships between productivity and species diversity (see recent reviews in Abrams 1995, Rosenzweig 1995, Grace 1999, Leibold 1999). Second, because unimodal curves are composed of ascending and descending portions, one can always argue that a positive or negative response of species richness to changed productivity represents only part of a hump-shaped relationship (Abrams 1995). Third, comparative studies must also deal with the issue of how existing species pools influence observed productivity–diversity relationships (Zobel 1992, Cornell 2001). For example, there may be little chance for species adapted to high productivity environments to find and colonize an area of high productivity isolated within a surrounding landscape of low productivity (D. Schluter, *personal communication*). Finally, interpretation of comparative studies must deal with the issue of cause and effect.

A number of recent papers suggest a reverse causality from that discussed here—that the realized productivity of a community may depend on the number of species present (Naeem et al. 1994, 1996, Tilman et al. 1996, 1997, Symstad et al. 1998, Hector et al. 1999). Thus far, the work in this area has been limited mostly to experimental studies of herbaceous plants (Chapin et al. 1998), and suggests that productivity is typically a decelerating function of species richness, often saturating a low species numbers (1–5 species in Naeem et al. 1996, Tilman et al. 1997, Symstad et al. 1998; but see Hector et al. 1999). Larger effects of species richness (or functional group richness) on productivity

may be observed in other types of vegetation, or when the productivity of additional trophic levels is included. It is also likely that species diversity plays an important role in determining productivity over evolutionary time scales. For example, Rohde (1998) notes that the higher productivity of coral reefs compared to the surrounding ocean is probably a consequence of greater species diversity, rather than its cause. "... there is no reason to assume that the waters in which coral reefs are found were originally more productive than the surrounding sea. Apparently, evolution of many species, such as corals and calcareous algae, facilitated evolution of other species including primary producers which gradually, over evolutionary time, led to an increase in overall productivity." Examining the ecological and evolutionary effects of species richness on productivity is an exciting and challenging area of study that is likely to see great progress in the next decade, with important applications to managing our increasing human-dominated world. Clearly, it will also be key to our general understanding of species diversity-productivity relationships.

Future study

In recent years, a number of authors have suggested that a hump-shaped curve describes the true relationship between productivity and species richness (e.g., Grime 1973, Tilman and Pacala 1993, Huston 1994, Rosenzweig 1995), and a variety of theories predict this relationship (see Rosenzweig 1995 for a review). However, Abrams (1995) has shown that models of competitive interactions between species also predict positive productivity-species richness relationships and other theories make this prediction as well (e.g., Wright et al. 1993). Our survey shows that both hump-shaped and positive productivity-species richness relationship are common in nature, and we suggest that perhaps too much attention has been focused on looking for "humps."

The argument that the true shape of the productivity-diversity curve is hump-shaped is similar to the debate that raged in the fisheries literature for years over the true form of the stock-recruitment curve. Ricker (1975) and others hypothesized that the relationship between adult fish stock and number of new recruits is hump-shaped. There are good, logical reasons to expect a humped stock-recruitment relationship. For example, when there are zero adults there can be no recruits (the relationship is anchored at the zero-zero point) and at some very high adult density all the available adult resources are likely to be used for maintenance and there will be no resources available for the production of young (Ware 1980). Therefore, at a high enough adult density the stock-recruitment curve should again bend back down to the axis (i.e., it is hump-shaped). However, while this logic is sound, it does not tell us whether the observed stock-recruitment relationship for any real population at any place or point in time is

in fact hump-shaped. What the fisheries literature shows is that the observed stock-recruitment curve can take different forms and that these observed relationships are important in understanding fish dynamics and managing fish stocks. Similarly, only empirical observation can tell us what the patterns are for productivity and species diversity in nature. We hope that this review (in combination with recent reviews of Grace 1999, Waide et al. 1999, and Dodson et al. 2000), will provide a strong empirical basis for future work examining the mechanisms that produce relationships between productivity and species diversity at different geographical and ecological scales.

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APPENDIX

The complete list of productivity–species diversity studies (196 papers) and the data extracted from them and used in our study are available in ESA's Electronic Data Archive: *Ecological Archives* E082-024.