

THE RELATIONSHIP BETWEEN PRODUCTIVITY AND SPECIES RICHNESS

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■ **Abstract** Recent overviews have suggested that the relationship between species richness and productivity (rate of conversion of resources to biomass per unit area per unit time) is unimodal (hump-shaped). Most agree that productivity affects species richness at large scales, but unanimity is less regarding underlying mechanisms. Recent studies have examined the possibility that variation in species richness within communities may influence productivity, leading to an exploration of the relative effect of alterations in species number per se as contrasted to the addition of productive species. Reviews of the literature concerning deserts, boreal forests, tropical forests, lakes, and wetlands lead to the conclusion that extant data are insufficient to conclusively resolve the relationship between diversity and productivity, or that patterns are variable with mechanisms equally varied and complex. A more comprehensive survey of the ecological literature uncovered approximately 200 relationships, of which 30% were unimodal, 26% were positive linear, 12% were negative linear, and 32% were not significant. Categorization of studies with respect to geographic extent, ecological extent, taxonomic hierarchy, or energetic basis of productivity similarly yielded a heterogeneous distribution of relationships. Theoretical and empirical approaches increasingly suggest scale-dependence in the relationship between species richness and productivity;

consequently, synthetic understanding may be contingent on explicit considerations of scale in analytical studies of productivity and diversity.

INTRODUCTION

The notion that productivity (rate of conversion of resources to biomass per unit area per unit time) affects species richness can be traced to at least the mid-1960s (45, 106, 113, 153). Nonetheless, the causal mechanisms behind the patterns between productivity and species diversity, as well as the form of the relationship, have been in dispute for almost as long (53, 193). Indeed, studies of the relationship between productivity and diversity at large spatial scales have documented linear and unimodal patterns as well as no patterns at all (see review in GG Mittelbach et al, in litt. and SI Dodson et al, 51a). Experimental manipulation of productivity via fertilization of small plots long has been known to decrease plant diversity (reviews in 48, 65, 82). Importantly, both theoretical considerations (147; SM Scheiner et al, in litt.) and empirical analyses (KL Gross et al, in litt.) suggest that patterns are likely scale dependent. Some of the disparity in perceived patterns may be a consequence of variation in the spatial scale of analyses.

Efforts to determine the relationship between number of species (or number of functional types, *sensu* 41) and the properties of ecosystems have increased as global loss of biodiversity and climate change have accelerated over the past decade. One approach to this issue has been to examine the ways ecosystem processes influence species number, community composition, or trophic structure (e.g., 84, 167, 168, 191). A separate line of inquiry has focused on the importance of the number of species, the number of functional groups, and the presence or absence of particular species (or groups) on ecosystem processes (e.g., 85, 102, 133, 134, 185, 190, 192). Field manipulations and laboratory experiments have addressed the role of these aspects of biodiversity in determining rates of ecosystem processes (e.g., primary productivity and nutrient cycling). These two lines of inquiry have been largely separate in the literature despite their conceptual linkage.

In this review, we synthesize existing knowledge of the relationship between a commonly estimated property of ecosystems (primary productivity) and one aspect of biodiversity (species richness). Most theoretical studies use net primary productivity (NPP) as the driving variable, but empirical studies often use components or surrogates of NPP. Rather than introduce confusing terminology, we use primary productivity in this paper as a general term to encompass components or surrogates of NPP. We review the literature and use case studies from terrestrial, aquatic, and wetland biomes for which detailed information is available. The work we report is an extension of research initiated at the National Center for Ecological Analysis and Synthesis that focused on the influence of primary productivity on species richness. In addition, we consider how species richness may affect ecosystem function (including productivity). This is a volatile and rapidly expanding area of study (see 1, 76, 79, 85, 107, 190). Unfortunately, the database currently is too

small and conflicting to draw conclusions with certainty. Nonetheless, we suggest that it is necessary to bridge these two approaches to achieve a better understanding of the relationship between primary productivity and the dynamics of populations and communities. We do not address the related and important issue of the relationship between diversity and stability (49, 91, 189), nor do we discuss in detail other possible biotic and abiotic controls of biodiversity.

How Does Productivity Affect Species Richness?

Most authors agree that productivity affects diversity (32, 45, 106, 113, 162); moreover, a plethora of mechanisms have been proposed to explain how species richness responds to variation in productivity (e.g., 84, 168, 167, 191). Nonetheless, no general consensus concerning the form of the pattern has emerged based on theoretical considerations or empirical findings. Some factors enhance richness as productivity increases, others diminish richness as productivity increases, and some, in and of themselves, produce unimodal patterns (see below for details). Rather than any one mechanism having hegemony, it may be the cumulative or interactive effect of all such factors that determines the empirical pattern within a particular study. Indeed, future research should identify the ecological context and spatial scale that predispose systems to evince one pattern rather than another (154).

Rosenzweig (167) provided a critical assessment of the mechanisms thought to affect patterns in the relationship between diversity and productivity. GG Mittelbach et al (in litt.) updated the summary and provided commentary on the ecological scale at which mechanisms likely operate. Theories that predict a positive relationship between productivity and species richness include the species-energy theory (44, 155, 156, 223) and theories invoking various forms of interspecific competition in heterogeneous environments (2). Mechanisms thought to diminish diversity with increasing productivity are more controversial and include evolutionary immaturity (especially with respect to anthropogenic emendations); habitat homogenization (*sensu* 187; 65, 88); dynamical instabilities and system infeasibilities (125, 160, 162, 164, 165, 222; JC Moore & PC de Ruiter, submitted); and predator-prey ratios (141, 142, 162, 163). Some mechanisms predict a unimodal pattern in their own right. Relevant theories include changes in environmental heterogeneity with productivity (87, 186), tradeoffs in competitive abilities and abilities to resist predation (105), effects of competitive exclusion and environmental stress (6, 71, 72), disturbance and productivity (82), productivity-dependent species-area relations (147), and changing competitive structure (167).

Understanding the productivity-diversity relationship will require the imposition of order on this apparently chaotic array of possible explanations. This can be achieved, at least in part, by careful attention to the spatial and ecological scales at which patterns are detected (124, 167), and by equally judicious consideration of the spatial and temporal scales over which likely mechanisms operate. JM Chase & MA Leibold (submitted) make significant headway in this regard. They develop simple conceptual models based on exploitative resource competition or keystone

predation to show that unimodal relationships emerge at local scales, whereas monotonically positive relationships emerge at regional or global scales. Empirical data for benthic animals and vascular plants in Michigan ponds corroborate the expected scale dependence in diversity-productivity relationships.

The Effect of Species Diversity on Productivity

There is general agreement that diversity of plant species is influenced by productivity (85, 192). The converse argument, that the number and kinds of species influence productivity, has been the subject of a recent series of field and laboratory experiments (79, 133, 192). These experiments have engendered a lively debate (85, 103, 211) that has yet to reach resolution. Increasing the number of species in either field (192) or laboratory (133) experiments may have positive effects on productivity and other ecosystem processes. However, the debate concerns whether these effects are the result of increased species richness per se, or the addition of different functional groups or particular species.

Theoretical approaches to this issue occur in three categories that postulate either (a) a positive, linear relationship (54, 112), (b) a positive, nonlinear relationship (52, 209), or (c) no relationship between species richness and productivity (102). MacArthur (112) hypothesized that energy flow through a trophic web would increase as the number of species, and hence pathways for energy flow, increased. Elton's (54) reformulation of MacArthur's hypothesis suggested that the relationship should be linear. If, however, species have redundant functions in ecosystems, the relationship between species number and ecosystem function may be nonlinear (52, 209). Ecosystem function changes rapidly as species representing new functional groups are added, but less rapidly when new species are redundant of existing functional groups. Lawton (102) proposed a model in which species may have strong, idiosyncratic effects on ecosystems. If this is the case, there is no predictable effect of species richness per se on ecosystem function. However, if the properties or functional traits of individual species are known, then we can predict which species will have strong effects and which will not. Such hypotheses present a useful framework for the evaluation of observations and experimental results.

Some experimental studies with herbaceous plants have shown an increase in net primary productivity with an increase in the diversity of species or functional groups (e.g., 132, 133, 185, 192). However, as Huston (85) has argued (see also 1, 190), there are at least two mechanisms by which the productivity of a trophic level may increase as the diversity (species, functional groups) of that trophic level increases.

1. Increasing the number of species initially present in a system increases the probability of encountering an exceptionally productive species (e.g., a species that is proficient in converting resources to biomass). Huston (85) has labeled this the "selection probability effect." In this scenario, the productivity of the trophic level is determined by the productivity of the most productive species.

2. Increasing the number of species initially present in a system can result in complementarity in resource use, if different species use different resources. In this case, the productivity of an assemblage of species will be greater than the productivity of any single species. Also, the total resource spectrum will be more completely used in the more species-rich system.

Empirical evidence from herbaceous plant communities (e.g., 79, 80, 85, 132, 185, 192) supports hypothesis 1. No experimental study supports hypothesis 2, despite its intuitive appeal. [data from Tilman et al (190) potentially support hypothesis 2, but no information is presented on complementarity of resource use that could be used to test this mechanism]. Complementarity in resource use is the functional basis behind intercropping and polyculture (184, 203). Although not all intercropping schemes or polycultures provide higher yields, many successful examples suggest that species complementarity may be important in determining ecosystem productivity and nutrient dynamics.

The difficulty of designing and executing field experiments to determine the effect of changing species number on productivity has resulted in a scarcity of published studies. The clearest results include field experiments conducted on communities dominated by herbaceous vegetation (79, 192) and a microcosm experiment conducted under controlled laboratory conditions (133).

In the study by Naeem et al (133), conducted in a controlled environment, a series of ecosystem processes was measured in high- and low-diversity communities. The lower diversity systems were nested subsets of the higher diversity systems. Estimates of primary productivity were greater in microcosms with higher species diversity.

Tilman & Downing (188) examined the relationship between plant species diversity and primary productivity in plots fertilized with N at the Cedar Creek Long-Term Ecological Research site in Minnesota. They reported that the productivity of more diverse plots declined less and recovered more quickly after a severe drought than did the productivity of less diverse plots. They concluded that the preservation of biodiversity is important for the maintenance of productivity in fluctuating environmental conditions. This study is not a direct test of the effects of diversity on productivity because species richness was not manipulated directly but was a product of changes in nitrogen addition, and because the study measured changes in productivity in response to disturbance.

In a different experiment, Tilman et al (192) compared productivity and nutrient-use efficiency in grassland plots seeded with different numbers of native species. Productivity was greater and soil mineral nitrogen was utilized more completely in plots with greater diversity. Measurements in nearby unmanipulated grassland showed the same pattern. This study also concluded that the preservation of biodiversity is necessary to sustain ecosystem functioning.

Huston (85) criticized the conclusions of all three of these studies, claiming that each was tainted by the lack of rigorous treatment of cause and effect. In Huston's view, appropriate tests of the effect of species richness on ecosystem processes do

not permit large variation in the size or function of species. Huston argued that one likely consequence of increasing species richness in an experiment involves the increased probability of introducing a productive species (the “selection probability effect”). If this happens, the effect of increasing species richness on productivity is attributed simply to the increased odds of encountering species particularly well adapted to the environment. If variation in productivity exists among species used for an experiment, the effect of increased species diversity cannot be distinguished from the effect of increased functional diversity or mean plant size leading to differences in total biomass among treatments.

Huston’s position, although admirable for its insistence on rigorously designed experiments, requires studies to be circumscribed to a limited range of the variability that exists in natural ecosystems. Experiments that incorporate only species of similar size and functional status, while avoiding some of the pitfalls that Huston (85) described, may not advance substantially our understanding of natural communities. Natural communities comprise species that differ in size and function; as a result, the effect of the loss of diversity is interpreted more easily through experiments that incorporate that variability. Moreover, the question of how similar species must be to achieve experimental rigor has not been addressed. Loreau (107) and Hector (76) have recently suggested mechanisms to separate the “selection probability effect” from other effects resulting from experimental manipulations of biodiversity.

Hooper (79) approached the question of complementary resource use through an experimental design that varied the number of functional groups in experimental plots. Four functional groups (early season annual forbs, late season annual forbs, perennial bunchgrasses, and nitrogen fixers) were planted in single-group treatments, as well as in two-, three-, and four-way combinations. In this experiment, no obvious relationship existed between functional diversity and productivity of the plots. The most productive treatment included only one functional group, perennial bunchgrasses. The identity of the species in the treatments was as least as important as the number of species in affecting ecosystem processes. Competition among some combinations of functional groups reduced productivity compared to single-group treatments. These results corroborate Lawton’s (102) idiosyncratic model and Huston’s (85) hypothesis 1.

For practical reasons, most experiments have focused on structurally simple ecosystems with relatively few species and have manipulated only a few species from each functional group. In general, results have shown a positive, asymptotic relationship between ecosystem processes and species richness. These results suggest that once all functional groups are present, the addition of species with redundant functions has little effect on ecosystem properties.

The conclusion that diversity is important for maintaining ecosystem function (188, 192), even if justifiable based on the few studies conducted to date, has been demonstrated only for systems in which the range of richness is from 0 to about 30 species. Conclusions about the importance of the addition or loss of species in

complex systems require further clarification (171). Structurally complex, species-rich ecosystems, in which much of the loss of biodiversity worldwide is occurring, require further study.

Questions of Spatial Scale

It generally is recognized that area and environmental heterogeneity have strong effects on diversity (84, 167). Equally important, their effects are intertwined (98) and produce scale-dependent relationships between productivity and diversity. For example, a unimodal pattern in the relationship between diversity and productivity can be a consequence of a correlation between productivity and the parameters of the power function ($S = CA^z$, where S is species richness, A is area, and C and z are fitted constants equivalent to the intercept and slope, respectively, of the log-form of the relationship (7). In meadow communities dominated by sedges and grasses, Pastor et al (147) document that C has a positive correlation with area, z has a negative correlation with area, and this tradeoff produces a unimodal form to the relation between diversity and productivity. In contrast, no scale dependence was detected in the relationship between species richness and latitude for New World bats or marsupials, even though latitude is often considered a broad-scale surrogate for productivity (111).

Moreover, two aspects of spatial scale—extent and focus—strongly affect the detection and form of the relation between richness and diversity (SM Scheiner et al, in litt.). Extent is the range of the independent variable, which in this context is productivity, whereas focus defines the inference space to which variable estimates apply (i.e., the area from which samples were obtained to estimate point values for productivity and richness). In particular, a series of studies, each with restricted extent along a gradient of productivity, may evince significant (positive and negative) linear relationships as well as no relationship between productivity and diversity, casting doubt on the hump-shaped pattern. If the slope of the relationship decreases with mean productivity, then a unimodal pattern emerges as a consequence of the accumulation of consecutive linear relationships (positive linear, decreasing to no relationship, decreasing to negative linear; pattern accumulation hypothesis). Guo & Berry (73) document an emergent hump-shaped relationship from a series of linear patterns based on an analysis of plant species richness along a grassland-shrubland transition in Arizona.

Nonetheless, a unimodal relationship may emerge that is not a consequence of the accumulation of patterns at smaller extents. A series of fields dominated by vascular plants in the mid-western United States exhibits a unimodal relationship across grasslands or across North America, but no or negative relationships when the extent of analyses were restricted to be within community types (KL Gross et al, in litt.). Moreover, the slopes within community types were not correlated with mean productivity of the communities, suggesting that the pattern accumulation hypothesis was not in effect. In summary, relationships between diversity

and productivity have been shown to be scale dependent, with the form of the scale-dependence variable from study to study, even in situations where unimodal patterns emerge at broad spatial scales.

BIOME-SPECIFIC RELATIONSHIPS

The relationship between diversity and productivity can be mediated by different control mechanisms, depending on biome. As a consequence, patterns within biomes may differ, and emergent patterns across biomes may not be the same as those within them. We explore the range of productivity and diversity in a number of major aquatic and terrestrial biomes, and we discuss the possible control mechanisms that lead to patterns between diversity and productivity. Although we have not attempted a comprehensive coverage of all biomes, it is clear that the state of knowledge is quite variable among systems. Moreover, the form of the relationship is not always clear, and understanding of the regulatory mechanisms is only rudimentary in most cases.

Aquatic Ecosystems

Lakes

Lakes are underutilized but optimal model systems for studying the relationship between species richness and primary productivity. They are well-delineated (bounded) communities in which species can be counted relatively easily, and in which primary productivity often is measured directly using standardized ^{14}C uptake methods (208). The ^{14}C method measures productivity between gross and net on a scale of minutes to hours. Annual levels of primary productivity are estimated by summing daily productivity. In lakes, the annual level of primary productivity ranges from about 1 to about $1300 \text{ g C m}^{-2} \text{ yr}^{-1}$ (51a).

Lacustrine species richness is influenced by lake primary productivity. Pure rainwater has a primary productivity of near zero because it lacks the nutrients necessary to support life. Consequently, rainwater in rock pools supports few or no species (50). The most productive lakes, such as sewage lagoons and temple tanks, are characterized by extreme conditions, such as high temperatures, no oxygen at night, and large diel shifts in pH (e.g., 61). These conditions can be endured by only a few specialized species. Lakes between these extremes of primary productivity generally have the highest species richness. Lakes of intermediate productivity, with sufficient nutrients to support photosynthesis but without extreme conditions, support the most species in virtually all groups of aquatic organisms (51a).

The size of the body of water interacts with primary productivity to determine the number of species in a lake (11, 35, 51, 81). An increase in lake area of ten orders of magnitude is associated with an increase in zooplankton species richness of about one order of magnitude (51). Indeed, over 50% of among-lake variability

in richness of crustacean zooplankton in North American lakes is the consequence of lake size. Larger lakes have more zooplankton species, regardless of other factors including primary productivity.

SI Dodson, SE Arnott, KL Cottingham (51a) investigated the relationship between the primary productivity of lake ecosystems and the number of species of lacustrine phytoplankton, rotifers, cladocerans, copepods, macrophytes and fish. In a survey of 33 well-studied lakes, species richness of all six taxa showed a significant unimodal response to annual primary productivity (^{14}C estimate, $\text{g m}^{-2} \text{yr}^{-1}$) after lake area was taken into account. Moreover, the relationship between richness and primary productivity for phytoplankton and fish was strongly dependent on lake area. The highest richness occurred in lakes with relatively low primary productivity ($\sim 100 \text{ g m}^{-2} \text{yr}^{-1}$), such as those in the northern temperate lakes area in the upper Midwest (United States) and in the Experimental Lakes Area of Ontario, Canada. When temporal and spatial scales are considered, data for lake zooplankton and macrophytes provide striking examples of unimodal relationships between species richness and primary productivity. For small lakes ($< 10 \text{ ha}$), phytoplankton species richness peaked in low-productivity lakes, whereas for larger lakes, phytoplankton species richness merely declined in more productive lakes. For lakes less than 1 ha, fish species richness peaked at low levels of primary productivity. For larger lakes, a peak was not evident, although more productive lakes had more fish species.

The relationship between species richness and productivity has been studied only for phytoplankton and zooplankton in a few other lake and marine situations. We summarize the results of those studies below.

Phytoplankton Agard et al (5) analyzed data on marine phytoplankton species richness and the primary productivity of 44 oceanographic stations in the Caribbean to test predictions of Huston's (84) dynamic equilibrium model of species richness (maximum at intermediate productivity). They argued that marine phytoplankton would likely exhibit a relationship because of the relatively large number of species and the absence of confounding factors such as spatial heterogeneity. They reported that species richness was correlated positively with primary productivity, except at high levels where the curve reached a plateau. Fishery statistics (see 84) for the region show that the diversity of harvested marine species of commercial importance mirrors the diversity of phytoplankton.

In a 4–5 year study of three productive surface mines in Pennsylvania, phytoplankton diversity was correlated inversely with primary productivity (30). These sites are within the range of productivities explored by SI Dodson, SE Arnott, KL Cottingham (51a), and the results are consistent with those of that study.

Zooplankton Microcrustacean species richness is correlated with degree days for a group of shallow Canadian and Alaskan tundra ponds (75). These low-

productivity ponds represent values along the ascending portion of the unimodal relationship reported by SI Dodson, SE Arnott, KL Cottingham (51a). Patalas (148) reported data for zooplankton and July temperature (which is an indicator of lake primary productivity) in Canadian lakes. Using these same data, Rosenzweig (167) found a unimodal relationship.

Wetlands

Coastal and inland wetlands have been the subject of much of the research on the relationship between plant species diversity and productivity. The mechanisms controlling species diversity along productivity gradients in marshes may differ from those demonstrated for terrestrial communities. In particular, selection for traits allowing survival in environments with high salinity and low soil oxygen may create low-diversity, high-productivity communities without the involvement of mechanisms such as competition.

In general, coastal marshes are some of the most productive ecosystems in the world. Tidal salt marsh plant communities are structured by salinity and flooding gradients creating distinct zonation with low plant species richness (20, 89). Primary productivity is high, up to $2500 \text{ g m}^{-2} \text{ yr}^{-1}$ (123). Mangroves replace tidal salt marshes in the tropics, with low plant species richness and highly variable productivity that depends on tidal influences, runoff, and water chemistry (123). Tidal freshwater marshes associated with rivers are more diverse because of monthly flooding and lower salinity levels (139) but are equivalently productive. Inland freshwater marshes and peatlands can be highly diverse, dependent somewhat on nutrient availability. Productivity is high, often exceeding $1000 \text{ g m}^{-2} \text{ yr}^{-1}$, and, if belowground estimates are included, can exceed $6000 \text{ g m}^{-2} \text{ yr}^{-1}$ (123).

Plant species richness in coastal marshes decreases toward the coast along natural salinity gradients (4, 37, 101, 139) and may be influenced by storm-driven salt pulses (31, 57). Flooding and soil anoxia also decrease species richness (66, 68, 117, 123). The importance of interspecific competition, disturbance, and stress tolerance in determining species distributions has been demonstrated experimentally (18, 19, 97, 151, 181). Disturbance by herbivores (14, 58, 67, 138) and wave action (178) also may affect richness.

Salt marshes may be less productive than fresh water marshes because of the metabolic cost of tolerance to salinity (70, 139). Where freshwater flows into a coastal area, bringing nutrients or reducing salinity, productivity may be higher than in areas without freshwater input (47, 123, 225). Wave exposure also may restrict productivity (97, 220, 221). In inland and coastal marshes, soil characteristics such as pH, Ca, Mg, and anoxia may correlate with productivity (e.g., 17, 62). In tidal salt marshes, sulfides rather than high salt concentrations decrease productivity (218). Mammalian and avian herbivores restrict aboveground biomass accumulation in some marshes by removing plant material (9, 14, 59, 67, 138, 202), but they may have a stimulatory effect by adding nutrients through fecal deposition (78). Based on the results of fertilization experiments in marshes, vegetation frequently is limited by nitrogen or phosphorus (67, 126, 135).

When plant species density (the number of species per unit area) and productivity (estimated by harvests of peak standing crop) are examined in concert for marshes, the relationship between them depends on the scale of measurement and other factors. When productivity is increased by fertilization, plant species richness decreases (136, 204). When herbivores are excluded, productivity usually increases, accompanied by a decrease in plant species richness (14, 58, 67). Certain abiotic variables (e.g., salinity) may have similar effects on plant species density and productivity. However, the relationship between the two is not consistent in wetlands, although it is frequently unimodal (Table 1). In most cases, data are variable, with an outer envelope of points having a peak in species density at an intermediate level of standing crop (114). In some cases, the relationship reaches an asymptote, and plant species density does not decline over an extended range of standing crops (e.g., 69, 221). Moore & Keddy (124) demonstrated a unimodal relationship across community types, although there was no relationship between plant species density and standing crop within communities.

Approximate peaks in species density are found at a range of standing crop levels from 100 to 1500 g m⁻² (Table 1). Once biomass reaches approximately 1000 g m⁻², plant species density rarely exceeds 10 species per m² and usually remains low. However, the range in plant species numbers is quite large at levels of biomass between 0 and 1000 g m⁻², suggesting that other variables affect species density at a particular level of standing crop. Stress tolerance plays an important role in survival in certain marsh habitats and may control species richness independently of other factors such as biomass (68, 69). The mechanism causing consistently low species numbers above approximately 1000 g m⁻² standing crop remains unclear but is likely a combination of abiotic stresses and biotic interactions.

Terrestrial Ecosystems

Arctic Tundra

The arctic environment restricts the presence and productivity of vascular plant species (22, 42). Because of the severity of the environment and the common origins of the flora, approximately 2200 vascular species are known in the entire arctic region (22). Many of the abiotic factors believed to control productivity also play a role in controlling diversity. In particular, low temperature, a short growing season, low rates of soil nutrient cycling, permafrost, wind exposure, and extremes of soil moisture may constrain plant productivity (reviewed in 177). Various physiological and morphological adaptations (e.g., cold hardiness, short stature, vegetative reproduction) allow arctic tundra species to survive in such an environment (22, 23). On a smaller scale, topography can dramatically influence snow cover, exposure, soil drainage, and other physical properties of the substrate that may limit or enhance accumulation of plant biomass (175, 176). Generally, the most productive arctic plant communities are those dominated by deciduous shrubs or graminoids in areas of flowing water, where nutrient availability is higher and few other vascular species are present (39, 213). Nutrient availability

TABLE 1 List of herbaceous wetlands in which the relationship between plant species density (D) and standing crop has been examined

Wetland type	Location	Standing crop range (g m ⁻²)	D range	Plot size (m ²)	Peak in D ^a	N	Relationship	R ²	p-value	Reference
Fen	England	600–4800	3–26	0.25	1000	34	Negative	^b —	—	214
Fen	England, Wales	300–4000	2–50	4	500	85	Negative	0.2 ³	0.0001	215
Freshwater lakeshore	Nova Scotia	0.4–580.8	0–23	0.25	120	121	+, unimodal	0.4 ⁰	<0.001	221
Freshwater lakeshore	Ontario	0.1–900	0–12	0.04	100	63	Unimodal	0.4 ⁸	<0.01	220
Freshwater shoreline	Ontario, Quebec	0–2600	2–24	0.25	400	224	Unimodal	0.3 ⁴	<0.0001	124
Freshwater shoreline	Quebec	12–1224	1–24	0.25	500	48	Unimodal	0.4 ¹	<0.05	178
Freshwater shoreline	Ottawa	10–1100	4–12	0.25	250	7 ^c	None	NS	NS	47
Coastal marsh	Louisiana	100–3900	1–11	1	1500	36	Negative	0.0 ²	0.01	68
Coastal marsh	Louisiana	100–700	4–12	1	350	32	None	NS	NS	66
Coastal marsh	Louisiana	0–700	1–17	1	150	180	+, unimodal	0.0 ⁹	—	69
Salt marsh	Spain	4–1280	1–25	0.25	400	50	Unimodal	0.2 ⁹	<0.001	62

+Relationship was asymptotic.

^aThe peak in D was estimated visually from figures and is approximate.^b—Indicates that regression statistics were not reported.^cOnly means were reported.

consistently limits productivity in tundra ecosystems, as demonstrated by many fertilization studies (40, 77, 94, 161, 174).

In general, the regional and local species pools in the Arctic are limited by extreme temperature, short growing season, low nutrient availability, low soil moisture, and frost disturbance (21, 27, 210, 213). Local areas of enhanced resources (e.g., animal carcasses) are occupied frequently by plants found in more productive sites, suggesting nutrient limitation of species composition as well as of productivity (118). Herbivory also may be a factor affecting arctic plant communities (12, 90), but it has been studied insufficiently (for an exception, see 13).

The relationship between productivity and diversity rarely has been addressed specifically in arctic tundra (for an exception, see 60). We present a summary of mean aboveground net primary productivity [annual net primary productivity (ANPP), $\text{g m}^{-2} \text{yr}^{-1}$] and mean species richness (S) of vascular species for each community. In the arctic, the association between S and ANPP is weak (Figure 1). To gain insight, we divided the data into two groups (High and Low Arctic) based on floristic and ecological considerations (25).

A positive linear relationship between species richness and ANPP is obvious in the High Arctic (Alexandra Fiord, Polar Desert, Polar Semidesert, Devon Island, Russia, and Barrow; $R^2 = 0.45$, $p \ll 0.001$), but no relationship characterizes the Low Arctic (Figure 1). In the High Arctic where plant cover is sparse, light competition is rarely important. When stressful conditions are ameliorated, more species inhabit more favorable areas. This is exemplified by small sites of increased moisture or temperature that are more productive and diverse than are drier or cooler sites (26, 64, 127, 128). The lack of a relationship in the Low Arctic likely is related to greater plant cover, causing both light and nutrient competition to be important in determining species richness. Perhaps as conditions become more favorable for higher plant productivity in the Low Arctic, light competition becomes more intense, countermanding the effect of productivity on species richness. The clear relationship between productivity and species richness in the extreme environment of the High Arctic suggests similar regulation of these two parameters by abiotic factors. In the Low Arctic, the relationship becomes less clear, possibly suggesting the importance of biotic regulation of species diversity in these communities.

Hot Deserts

Desert ecosystems are typically on the low end of the productivity gradient, ranging between 0 and $600 \text{ g m}^{-2} \text{yr}^{-1}$ (Table 2). Productivity in desert ecosystems generally is limited by moisture availability and is highly variable in space and time (104, 170, 182, 212, 216). When rainfall is abundant for extended periods, nutrient limitation (particularly nitrogen) may regulate primary production (55, 74, 109, 129). Seasonal timing of precipitation determines the period and duration of primary production, with some deserts exhibiting primarily single season pulses of productivity (e.g., Mojave Desert in early spring, and Chihuahuan Desert in mid- to late-summer), whereas other deserts have bimodal productivity peaks

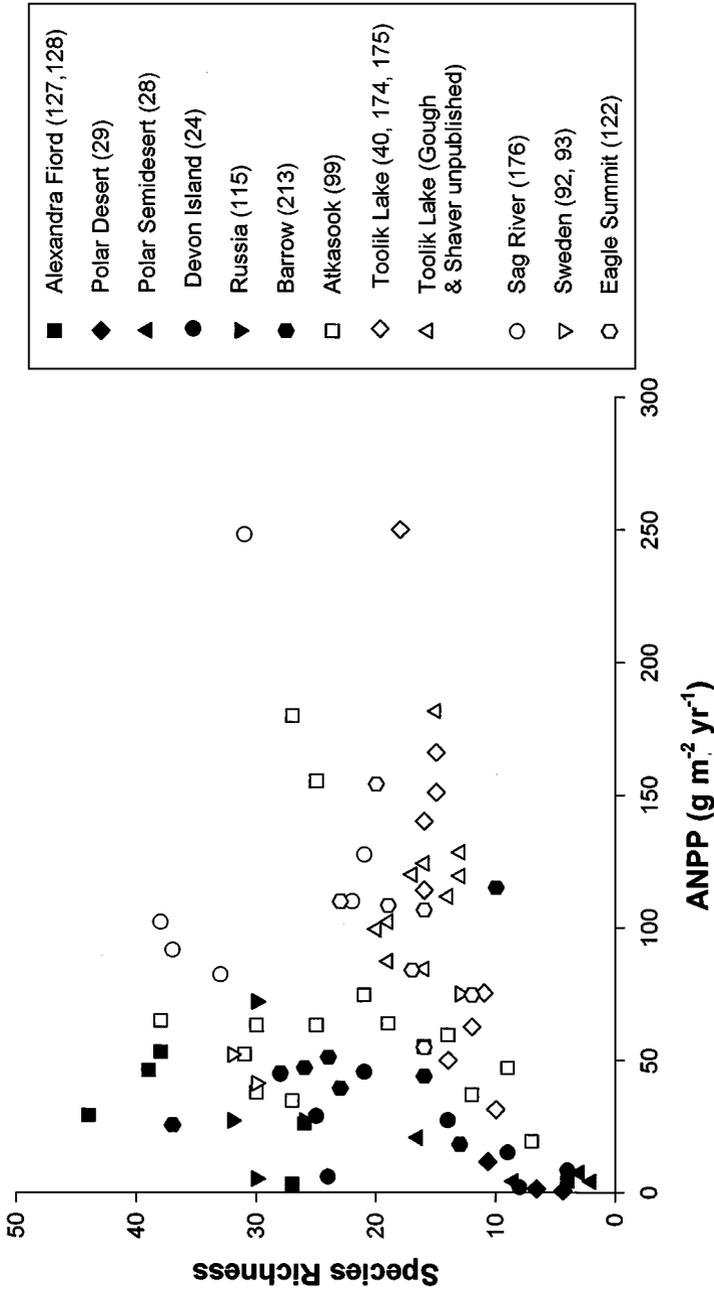


Figure 1 Scatter plot of the relationship between mean species richness and mean aboveground net primary productivity (ANPP) in arctic tundra. Site names in the insert are arranged by latitude, with Alexandria Fjord being farthest north. High Arctic sites include Alexandria Fjord through Barrow; Low Arctic sites include Atkasook through Eagle Summit.

TABLE 2 Productivity estimates of deserts

Site	Productivity/(g m ⁻² yr ⁻¹)	Reference
United States		
Great Basin Desert	125	150
Mojave Desert	0–62	15
	13–44	10
Sonoran Desert	9–95	149
	109	217
Chihuahuan Desert	50–100	43
Bajada: Alluvial fans	53–292	108
Bajada: Small arroyos	37–318	108
Bajada: Large arroyos	30–456	108
Basin: Slopes	51–179	108
Basin: Swales	292–592	108
Basin: Playa lake	52–258	108
Israel		
Negev Desert	4–43	144
India		
Rajasthan	0–126	173
Mongolia		
Gobi Desert	0–155	96
Tunisia		
Pre-Sahara Desert	22–155	56

(e.g., the Sonoran Desert in both spring and late summer). Productivity in deserts is a consequence of slower growth of woody shrubs and succulents combined, with highly variable flushes of annual and perennial grasses and forbs. Comparisons of primary production in deserts indicate that belowground productivity may be considerably greater than aboveground (108 and references therein).

Species diversity ranges widely among deserts, depending on geographic location, biogeographic history, and extremes of moisture and temperature. However, many deserts support relatively large numbers of species (Table 3) and in many cases actually exceed the numbers of species found in other ecosystems with higher productivity. At a continental scale, the arid and semiarid ecosystems of the American Southwest support greater numbers of species of numerous taxa than do other ecosystems of North America (145, 146).

Although the relationship between productivity and species diversity in arid ecosystems has not been addressed specifically, certain relationships appear when comparing large-scale and small-scale patterns among and within deserts. Comparing large-scale patterns throughout the world, deserts that have near zero

TABLE 3 Numbers of species occurring in North American Deserts

Desert	Mammals	Birds	Reptiles	Amphibians	Plants	Reference
Great Basin	86	302	18	6	929	119
Mojave	53	332	37	3	1,836	169
Sonoran*	302	366	132	14		46
Chihuahuan	74	396	55	10		120

*Includes many island endemic species from the Sea of Cortez.

productivity (e.g., the polar desert of Antarctica, and various locations within continental deserts and dune fields) have concomitantly low species diversity, whereas deserts with hundreds of plant and thousands of animal species have comparably higher productivity. However, when comparing deserts of the same region (e.g., North America), the relationship between productivity and diversity is not as clear. For example, in North America (Table 2) the Mojave Desert has the lowest and the Chihuahuan Desert has the highest productivity, yet patterns of species numbers (Table 3) do not correspond to this pattern.

At smaller scales, various sites within a desert also differ markedly in productivity and plant species diversity. Ludwig (108) showed variations among years for productivity in different habitat types within the Chihuahuan Desert of New Mexico and found that sites that benefited from additional "run-on" moisture were most productive (Table 2). These sites typically were dominated overwhelmingly by a single grass species (*Hilaria mutica*) and exhibited high productivity with low diversity as compared to more diverse, but less productive, upland bajada slopes.

Tropical Forests

Copious data on productivity and species richness of tropical forests exist in the literature. However, detecting patterns between productivity and species richness is hampered by the great variability in environmental conditions in tropical forests and the lack of standardized sampling techniques. Ecosystems ranging from savanna to cloud forest often are grouped under the rubric of tropical forest. Soil nutrient availability, precipitation, temperature, and solar radiation exhibit strong variation, even within relatively homogeneous groupings such as lowland tropical forest. Efforts to control for these variables by selecting sites with comparable conditions reduce sample sizes to the point where statistical power is jeopardized. A search of the literature encountered 168 reported values for some measure of productivity (NPP, litter fall, leaf fall) for tropical forest sites, but only 15 were associated with any kind of measure of species richness. Joint measures of net primary productivity and species richness at the same scale are infrequent and usually restricted to woody plant species.

Reviews of studies of NPP in tropical forests have reported ranges of 6–16 t ha⁻¹ yr⁻¹ for tropical dry forest (131) and somewhat higher values for tropical evergreen forests [10.3–32.1 t ha⁻¹ yr⁻¹ (130); 11–21 t ha⁻¹ yr⁻¹ (34); 10.0–22.4 t ha⁻¹ yr⁻¹

(121)]. A search of the recent literature did not encounter any more extreme values. Most, if not all, of the NPP measurements reported for tropical forests are based on increments of aboveground biomass and fail to include belowground productivity or losses to consumption of plant tissues. Partial measures of NPP are often used for comparison between sites. For example, there is an extensive database on litter fall (157) with values ranging from 1.0–27.0 t ha⁻¹ yr⁻¹. A recent effort to estimate reasonable upper and lower bounds around the total NPP at 39 tropical forest sites resulted in ranges from 3.4–6.0 and 20.1–37.0 t ha⁻¹ yr⁻¹, respectively (DA Clark, D Kicklighter, J Chambers, J Thomlinson, J Ni, E Holland, submitted).

Cumulative lists of species of plants and animals exist for diverse kinds of tropical forests, but their utility for comparison is questionable because of differences in the effort expended to construct such lists and the area upon which the lists are based. For these reasons, it is difficult to compare vertebrate species richness even in the best-studied tropical forests. Because a more standardized approach is used to count trees, it is possible to estimate the range in species richness for this group within tropical forests. For example, Phillips et al (152) reported a range of 56–283 tree species >10 cm dbh for 1 ha plots in mature tropical continental forests.

Three studies in tropical rain forest reported a positive relationship between species richness and rainfall (a surrogate for productivity). Gentry (63) interpreted positive correlations between tree species richness and annual precipitation, seasonality, and soil richness as support for a positive relationship between productivity and diversity. Huston (83) found tree-species richness positively correlated with annual precipitation and negatively correlated with soil fertility, and this was interpreted as a negative relationship between productivity and diversity. Phillips et al (152) reported positive relationships between tree species richness, climate (including increasing rainfall), and disturbance. They suggested that more dynamic systems have greater productivity, resulting in higher species richness. However, higher rainfall itself is related to increased forest disturbance and decreased soil nutrient concentrations because of leaching (83), demonstrating the tangle of cause and effect that can result when surrogates of productivity form the bases of analyses. No studies relating diversity directly to forest productivity are available to unravel this tangle.

Boreal Forests

Boreal forests occur in the coldest environments on earth in which trees survive and dominate vegetative cover. Nonetheless, a surprising diversity of climates and a wide range of ecosystem productivities are present in the boreal region. Because it controls rates of organic layer decomposition and thus the release of elements, soil temperature is a pervasive influence on productivity of boreal forests (194, 196, 197). Boreal forest productivity decreases with decreasing soil temperature, and increases with warming soil temperature (195, 197, 200), provided that moisture or other factors do not become limiting. Low soil temperatures reduce nutrient uptake particularly in higher (vascular) plants (38). In turn, soil temperatures

are influenced by inherent site factors such as slope, aspect, and topographic position with respect to cold air drainage (200) and by factors that change during succession (e.g., 206). Large-scale stand disturbances warm boreal soils, especially by removing or thinning the insulating soil organic mat (198). Advancing succession rebuilds the organic layer, causing soil cooling and the build-up of high concentrations of refractory, low-quality forest litter that depresses productivity, particularly in conifer-dominated forest types (201).

On sites underlain by permafrost soil, rooting depth is restricted to the annually thawed active layer at the surface, and ground layer vegetation is dominated by mosses. Mosses filter and sequester incoming nutrients, restricting nutrient availability and productivity for rooted vegetation (140). Sphagnum moss dominance on permafrost sites produces organic soils of such high acidity that availability of particular nutrient elements is restricted for rooted vegetation. On larger river floodplains, nitrogen addition by alder (*Alnus*) shrubs promotes a substantial increase in productivity (95, 199). On low elevation sites in semi-arid central Alaska, a soil water-balance model is well correlated with basal area growth in white spruce (224), demonstrating that moisture can limit productivity on warm, dry south slopes as well. Belowground productivity in the boreal region only recently has been measured carefully, and recent progress on methodological problems suggests that most of the previous literature may not be reliable, especially because the high turnover of fine roots makes interval measurements of productivity problematic (158). Fine root production constitutes a large part of total production in boreal forests, accounting for 32% and 49% of total production in deciduous and coniferous stands, respectively, in central Alaska (159).

An often-cited value for average boreal forest aboveground net primary production is $2,700 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (143). Productivity in the extensive larch forest and sparse larch taiga of Siberia typically ranges from $2500 \text{ kg ha}^{-1} \text{ yr}^{-1}$ to $1400 \text{ kg ha}^{-1} \text{ yr}^{-1}$ respectively (95). More recent multiyear measurements of aboveground production in boreal forests of central Alaska include $9600 \text{ kg ha}^{-1} \text{ yr}^{-1}$ on a highly productive floodplain in peak alder/balsam poplar stage of development, and a range of $3600 \text{ kg ha}^{-1} \text{ yr}^{-1}$ to $4500 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in 200 year-old floodplain and upland white spruce forest, respectively (159). Upland birch/aspen forest averaged $8100 \text{ kg ha}^{-1} \text{ yr}^{-1}$, and poorly productive black spruce on permafrost averaged $680 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (158). Long-term studies reveal a high degree of interannual variability in primary production.

Ecological studies and floristic surveys provide estimates of overall species richness in the boreal forest (Table 4). Total regional plant species richness is correlated positively with productivity, increasing from the less productive middle or northern boreal region to the more productive southern boreal region and boreal/temperate transition (adjusting for differences in intensity of sampling effort). Databases adequate for comparison of diversity and productivity with confidence at the local site and stand level do not exist, although some data are suggestive. Highly productive mature forests in the Bonanza Creek Long-Term Ecological Research Site have lower plant species density (e.g., 205), perhaps partly because

TABLE 4 List of studies in which estimates are provided for number of species of plants in boreal forests

Location	Vascular plants	Lichens	Mosses/hepatics	Total plants	Number of plots	Reference
S. Ontario & Quebec	440	—	—	—	197	36
U.S. Great Lakes, Ontario	378	—	—	—	103	8
Alaska	375	107	70	552	103	110
Canada	—	—	133	—	60	100
Ontario	162	—	—	—	228	172
Finland	1,350	1,500	810	3,660	National	137
Sweden	2,000	2,100	1,000	5,100	National	137

of more complete usurpation of resources. This suggests a negative and linear relationship.

Succession plays a major role in the relationship between diversity and productivity as well. Most boreal forests are adapted to a stand-replacement disturbance regime, so they generally lack classic climax stages and an associated specialized complement of species. Total plant species richness increases during boreal forest succession, especially during primary succession (205), whereas productivity declines in later successional stages (207), suggesting a hump-shaped relationship through successional time. Many plant species of the forest understory persist (albeit at low abundance) throughout secondary succession, during which time productivity differs greatly depending on soil cooling and other influences of the stand (207). Species richness in late succession may be underestimated systematically in most of the literature because the difficult-to-identify cryptogams can constitute a large proportion, possibly even a majority, of the autotrophic plant species in boreal regions (Table 4). Vascular plant dominance is generally at a maximum during early succession, and cryptogam diversity and abundance are usually at a maximum late in succession (207).

Summary

Integration of results from the two aquatic and three terrestrial biomes discussed above suggest that there exists no universal pattern in the relationship between primary productivity and species richness. In most cases, patterns seem to change with scale, but data within biomes are inadequate for rigorous tests of this suggestion. Unimodal patterns are found in lakes, some wetlands, and through successional time in boreal forest. In terrestrial systems, a positive relationship pertains at regional or greater scales. In no case, however, are the data adequate to examine the relationship between primary productivity and species richness across scales and taxa. To address these issues, a broader survey of the literature is necessary.

SURVEY OF PATTERNS

Biome-specific consideration of studies leads to the conclusion that, one, extant data are insufficient to conclusively resolve the relationship between diversity and productivity, and two, patterns are variable, with mechanisms equally varied and complex. This is in sharp contrast to the broad claim that the unimodal pattern is among the few valid generalizations in ecology (84, 86, 166, 167). Indeed, a unimodal pattern has been heralded as the “true productivity pattern” (166) and as the “ubiquitous” pattern (87). We surveyed the published literature in ecology to assess such claims.

Data Acquisition

We conducted a literature search to examine patterns in the relationship between diversity and productivity. Using BIOSIS[®], *Biological Abstracts*, and the search string: “species richness OR species diversity OR primary productivity OR production OR biomass OR rainfall OR precipitation,” we searched *The American Naturalist*, *Oecologia*, *Oikos*, *Holarctic Ecology/Ecography*, *The Journal of Biogeography*, *The Journal of Ecology*, and *Vegetatio* for the years 1980–1997. We also manually searched these journals for the years 1968–1979 (pre-database). We combined results of this search with those from GG Mittelbach et al (in litt.). The latter study searched all issues of *Ecology* and *Ecological Monographs* to 1993 using the JSTOR[®] database (plus a manual search of issues between 1994–1997), and electronically searched a broad-spectrum of biological journals from 1982–1997.

In all cases, we included only studies with a sample size ≥ 4 that assessed a statistical relation (or presented data sufficient to calculate one) between species richness and productivity (or its surrogates), regardless of scale, taxon, or system. Agricultural and intensively managed systems were excluded, as were systems subject to severe anthropogenic disturbance. Systems whose potential productivities were manipulated experimentally were excluded as well.

Relationships between species diversity and productivity were classified into four types: linear positive, linear negative, unimodal, or no relationship. When possible, classifications were based on original published analyses. However, when proper statistics were not available, we used raw data to perform linear and quadratic regressions. Relationships were deemed significant if $P \leq 0.10$; regressions in which the quadratic term was significantly different from zero were classified as unimodal. Two studies produced significant “U-shaped” relationships (i.e., positive quadratic in the polynomial regressions). Because these relationships are rare, we have not included them in our figures; yet they were included when calculating percentages. Hence, histograms at some scales do not sum to 100%. More than 200 relationships between diversity and productivity were found in 154 articles. A tabulation of all studies surveyed, a summary of statistical results, and information on taxon, location, and measures of productivity are available on the World Wide Web in the Supplemental Materials section of the main Annual Reviews site (<http://www.annurev.org/sup/material.htm>).

We explored patterns in the relationships between species richness and productivity via five schemes of classification. We classified studies using an ecological criterion of scale as within community, across community, or continental-to-global scales. We used a shift in the structure of vegetation or plant physiognomy to define a change in community type (e.g., transitions from desert to grassland or from meadow to woodland). For most studies, we relied on descriptions of sites by the authors to generate the classifications. In a few cases, we classified studies based on knowledge of natural history. Studies whose sites were dispersed over distances greater than 4000 km were classified as continental-to-global. All studies of non-contiguous lakes, ponds, streams, or rivers were classified as across-community or as continental-or-global if the minimum distance criterion was met. Patterns at different ecological scales were explored for animals and plants separately. Our second classification scheme was based on the greatest geographic distance between sites within a study. We recognized four geographic scales: local (0–20 km), landscape (20–200 km), regional (200–4000 km), and continental-to-global (>4000 km). The third classification distinguished studies as terrestrial or aquatic, and further subdivided them into vertebrate, invertebrate, or plant. Our fourth method of classification focused on vertebrates and separately considered fish, mammals, amphibians and reptiles, and birds. We also tallied patterns for rodents separately because the literature review generated numerous studies of rodent diversity. The final classification considered whether the quantified measure of productivity was based on energy available to a trophic level or the energy assimilated by the trophic level.

The Patterns

The relationship between productivity and diversity differs with scale (Figure 2). Considering plants at the within-community scale, unimodal relationships are about as common as positive relationships (24 and 22%, respectively); however, most studies reported no pattern at all (42%). Though the proportion of studies that show no significant relationship remains large at the across-community scale, unimodal patterns are more than three times more prevalent than positive relationships (about 39% of studies compared to 11%). At the continental-to-global scale, the pattern is dominated by positive relationships (70% compared to 10% for unimodal relationships), and negative patterns are absent.

For animals, there was a less dramatic shift in the prevalence of unimodal versus positive relationships across biotic scales. Unimodal relationships predominate at the across-community scale, whereas positive relationships occur most commonly at the within-community and continental-to-global scales. As for plants, studies showing no relationship are numerous at the within- and across-community scales, but negative relationships are a clear minority, regardless of scale of classification.

Results of a geographic scale of classification (Figure 3) contrasted with those based on ecological scale. At the local scale (<20 km), studies of plant communities exhibited mostly unimodal relationships or no relationship at all. The dominance

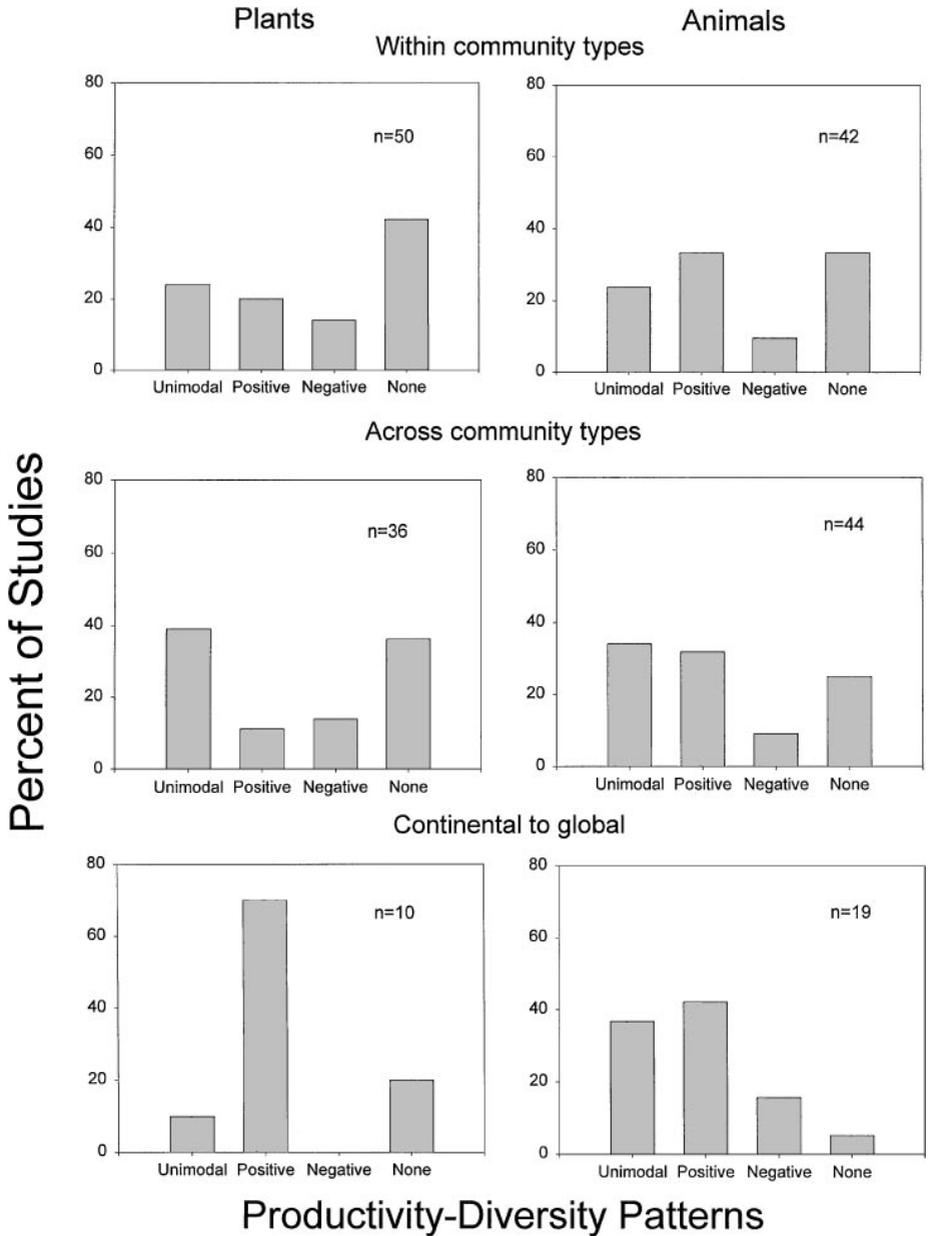


Figure 2 Percentages of published studies exhibiting particular relationships (positive linear, negative linear, unimodal, or no relationship) between species richness and productivity (or its surrogates) at each of three scales of ecological organization: within community types, among community types, and continental to global. Patterns are illustrated separately for plants and animals. Sample sizes refer to the number of analyzed data sets in each classification.

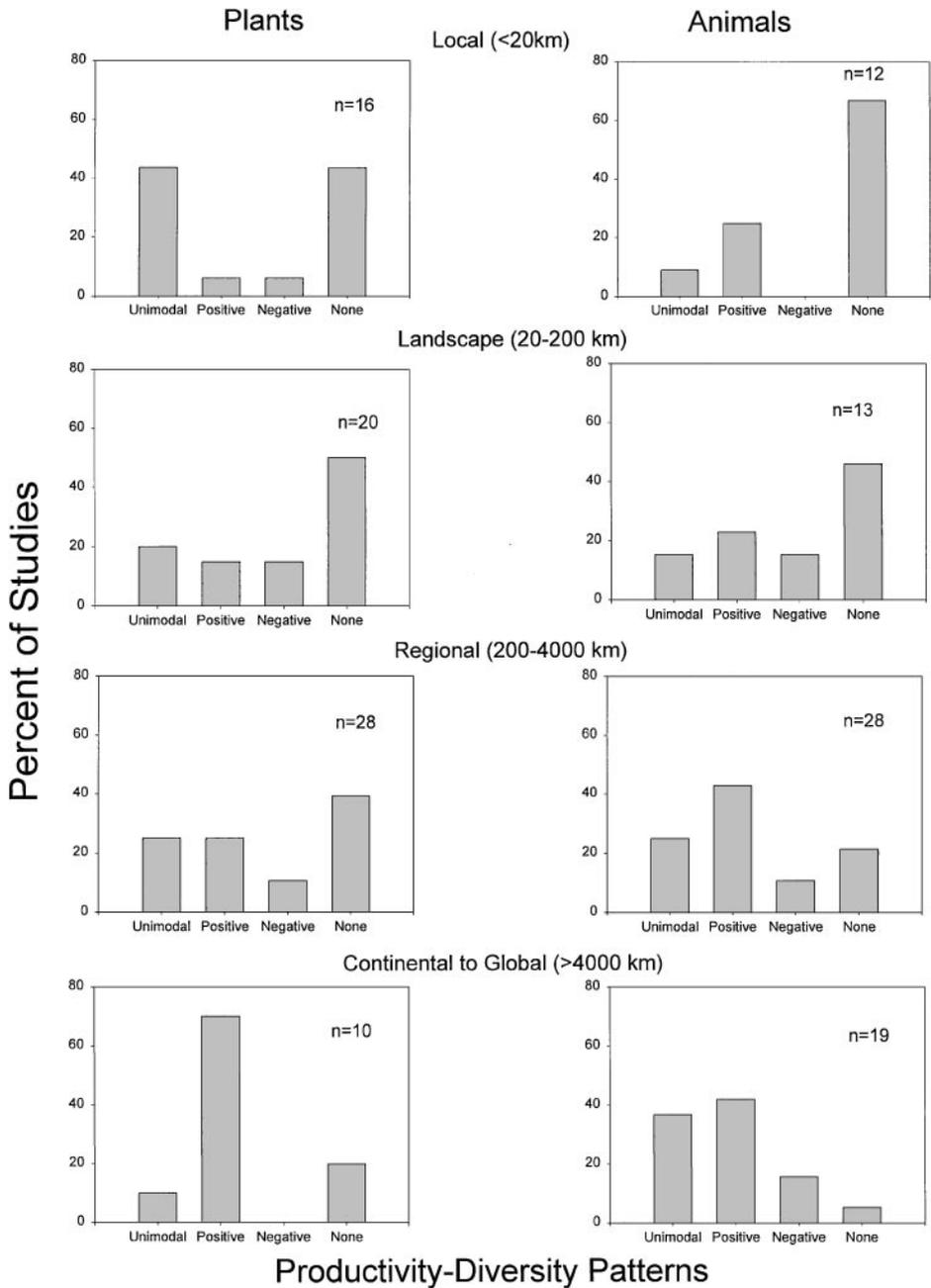


Figure 3 Percentages of published studies exhibiting particular relationships (positive linear, negative linear, unimodal, or no relationship) between species richness and productivity (or its surrogates) at each of four scales of geographic organization: local (<20 km), landscape (20–200 km), regional (200–4000 km), and continental to global (>4000 km). Patterns are illustrated separately for plants and animals. Sample sizes refer to the number of analyzed data sets in each classification.

of unimodality, relative to positive and negative relationships, declined for studies whose extents are at the level of the landscape (20–200 km) or region (200–4000 km). Again, studies showing no relationship were frequent at local to regional scales. Patterns at continental to global scales were the same as for the biotic classification; positive relationships predominated.

Studies of animals commonly exhibited no significant relationship between productivity and diversity at local to landscape scales (67% and 46%, respectively). However, when patterns occur, positive relationships between diversity and productivity were most prevalent at all geographic scales.

Our third method of classification focused on studies of vertebrates, examining productivity-diversity patterns for taxonomic groupings independent of scale. Most striking was the dominance of positive relationships for studies of birds and herpetofauna (Figure 4). In contrast, patterns were not as distinct for fish or mammals. A hump-shaped relationship was the most common pattern for fish. However, the proportions of unimodal and positive relationships were similar for fish and mammals. Most rodent diversity studies produced unimodal relationships between productivity and diversity.

When we divided studies into those concerning terrestrial and aquatic systems, striking differences became apparent. Positive relationships were more numerous in studies of terrestrial vertebrates, whereas unimodal relationships were more common in studies of aquatic vertebrates (Figure 5). Positive relationships predominated in studies of terrestrial invertebrates compared to a high percentage of unimodal relationships in studies of aquatic invertebrates. For both habitats, studies producing no relationships were numerous as well. Studies of plants in aquatic and terrestrial systems generally documented no relationship between diversity and productivity. For those studies that did show a significant relationship, a higher percentage of unimodality exists in aquatic systems.

Clearly, considerable variation characterizes the relationship between productivity and diversity, even after controlling for aspects of ecological, geographic, or taxonomic scale. Part of this variability may be a consequence of the way in which productivity was assessed for a particular site (available energy versus assimilated energy) or the power of statistical tests used to assess relationships. To assess the degree to which these factors may have affected the pattern or distribution of relationships (i.e., unimodal, positive linear, negative linear, no relationship), we conducted a hierarchical G-test (183). In general, contrasts were orthogonal and based on a priori considerations of energy, nested within habitat, nested within taxon (Figure 6). A final comparison of the pattern for all studies versus only studies with sample sizes greater than 10 was conducted for heuristic purposes (shaded portion of dendrogram in Figure 6). With one exception (aquatic animals based on all studies), the distribution of relationships was indistinguishable in contrasts between studies involving assimilated versus available energy. In addition, no significant differences in the distribution of relationships were detected for studies based on any other contrasts with respect to habitat, taxon, or data. These

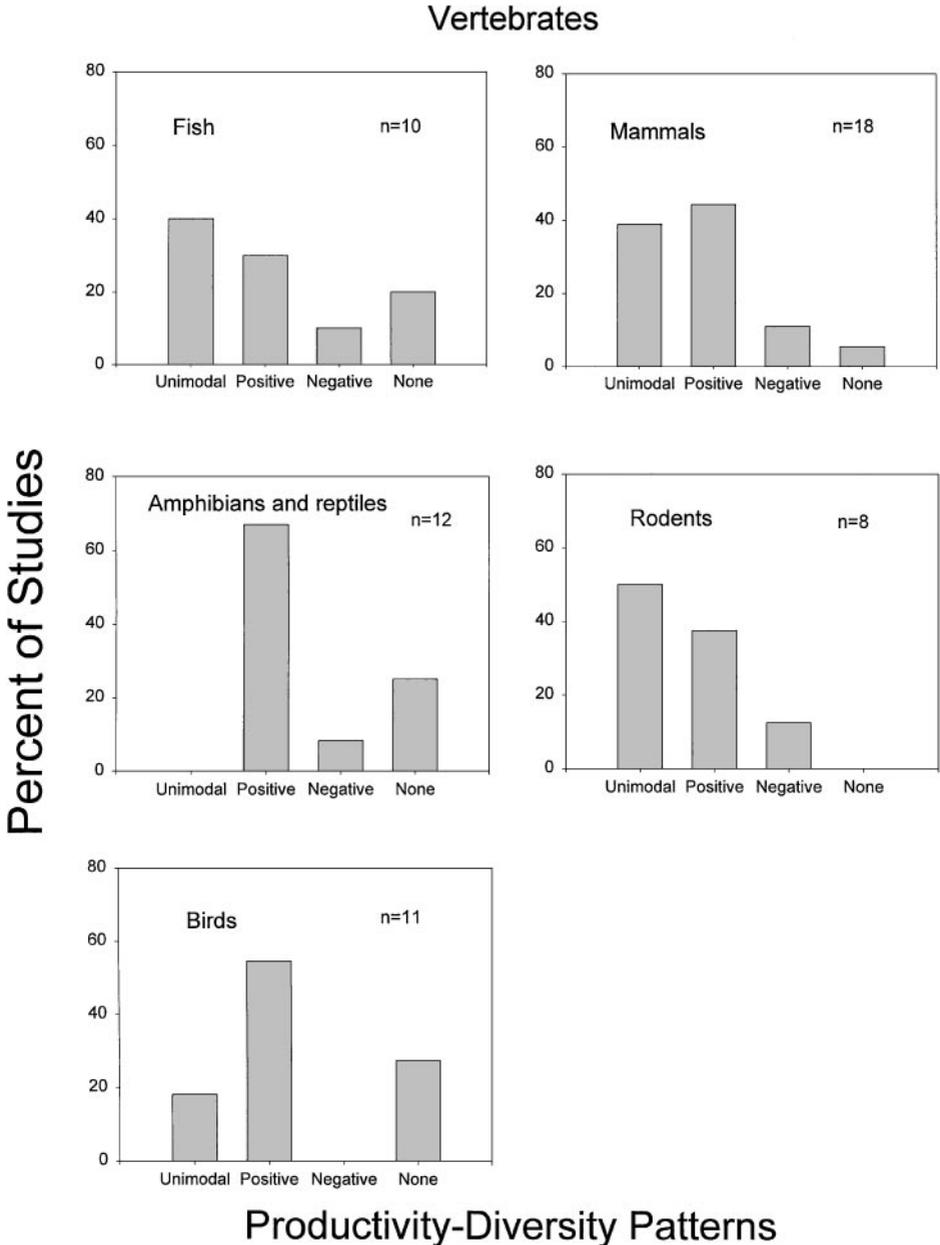


Figure 4 Percentages of published studies exhibiting particular relationships (positive linear, negative linear, unimodal, or no relationship) between species richness and productivity (or its surrogates) for each of five groups of vertebrates: fish, amphibians and reptiles, birds, mammal, and rodents. Sample sizes refer to the number of analyzed data sets in each classification.

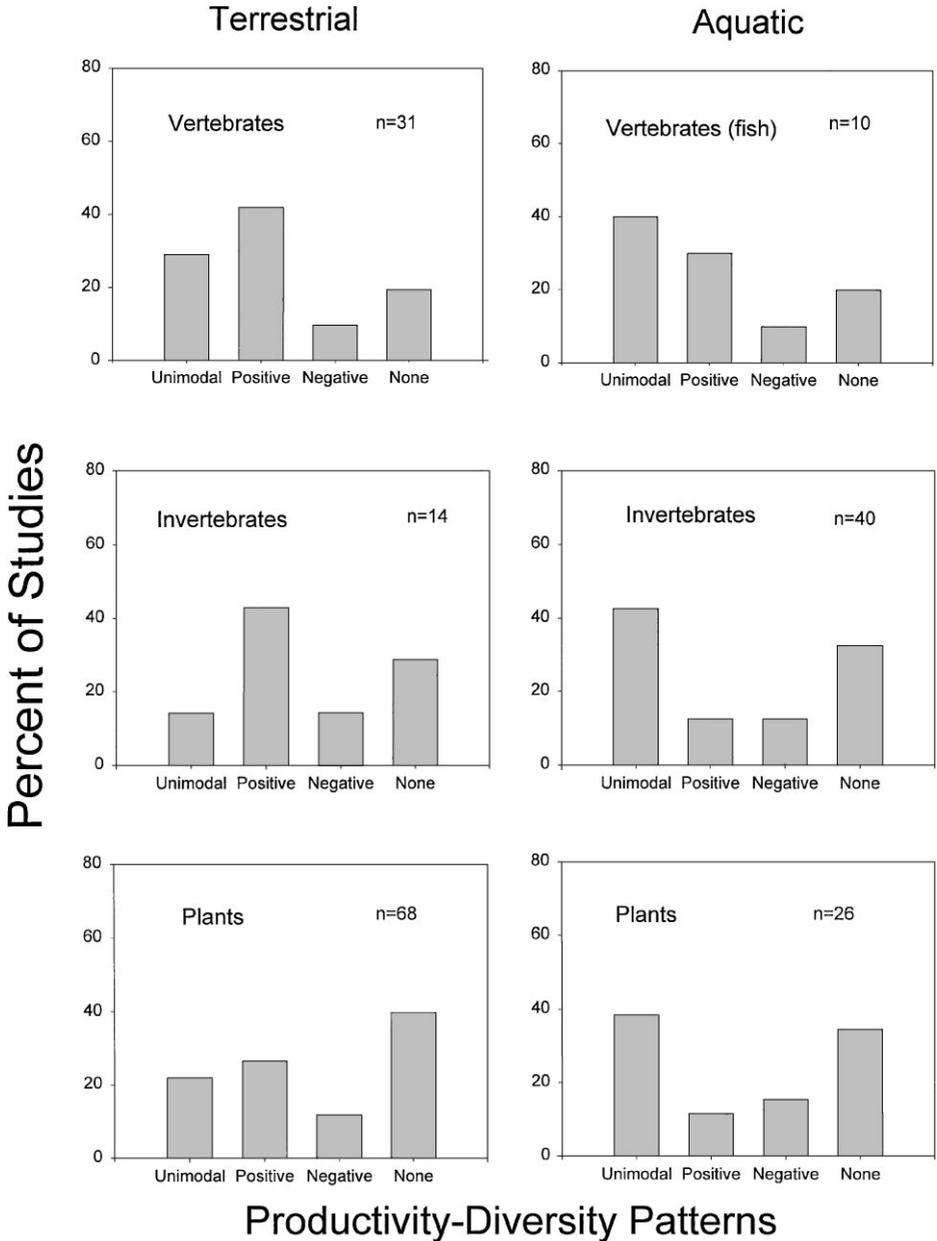


Figure 5 Percentages of published studies exhibiting particular relationships (positive linear, negative linear, unimodal, or no relationship) between species richness and productivity (or its surrogates) for each of three groups (vertebrates, invertebrates, and plants) in terrestrial and aquatic environments separately. Sample sizes refer to the number of analyzed data sets in each classification.

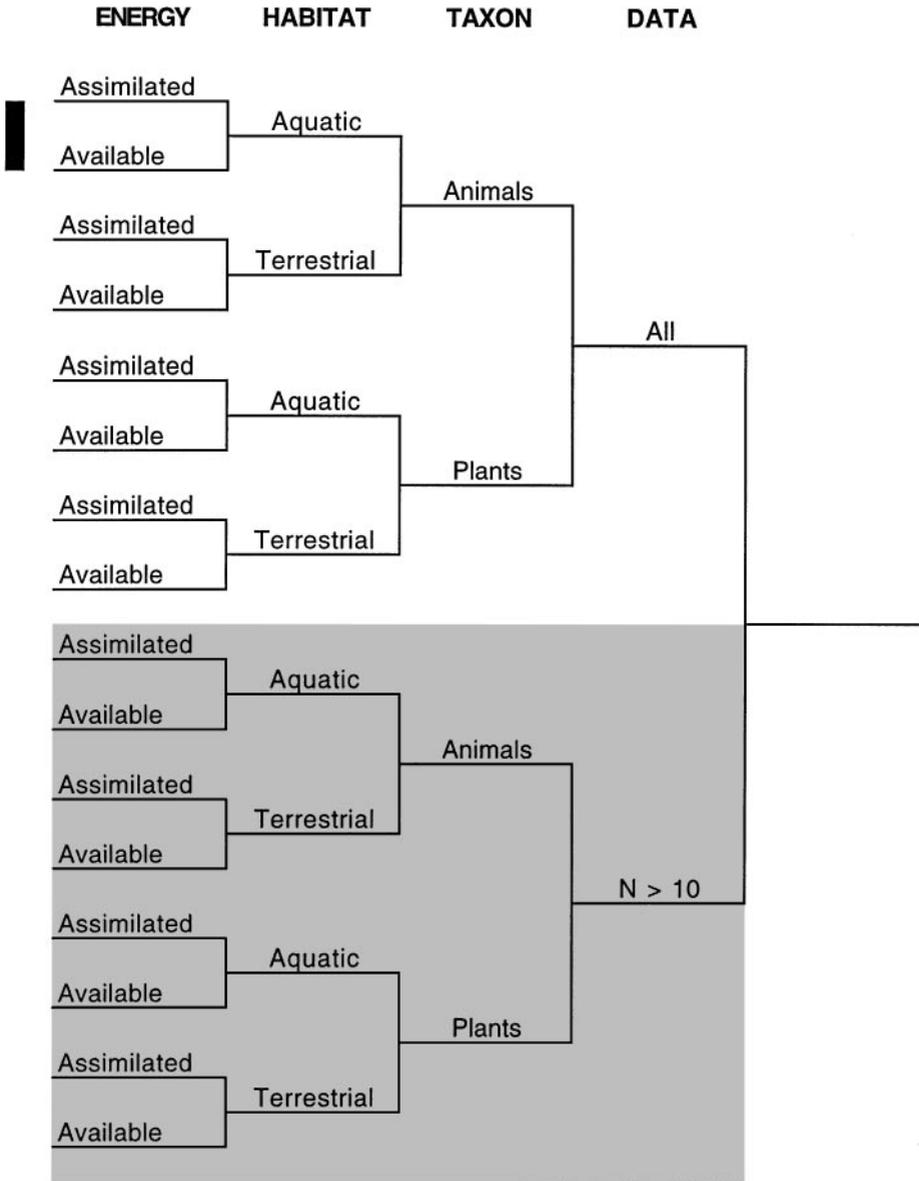


Figure 6 Dendrogram illustrating the results of a hierarchical G-test assessing differences in the distribution of relationships (positive linear, negative linear, unimodal, and no relationship) between studies classified in a nested fashion with respect to energy (available versus assimilated), habitat (aquatic versus terrestrial), taxon (animals versus plants), and data (all versus $N > 10$). Analyses conducted for heuristic purposes are shaded in gray. A statistically significant contrast ($P < 0.05$) is indicated by a black vertical bar.

results, especially when combined with those based on classifications of studies based on ecological and geographic scale, suggest that no single relationship has hegemony, and that at best, the data are insufficient to corroborate the priority of any one relationship between diversity and productivity.

Regardless of the manner of categorization, no single relationship described more than two thirds of the studies. This is surprising, given that the relationship between species richness and productivity is often characterized in the literature as unimodal (e.g., 16, 87, 167, 191). This suggests that no mechanism has a dominant role in molding patterns, that multiple mechanisms may operate simultaneously, or that confounding factors or methodological limitations (e.g., sample size or extent) conspire to produce the apparent diversity of relationships between productivity and diversity. We explore some of the factors that may be involved in producing a variety of patterns at different scales.

Conceptual Issues

Determining the manner in which productivity-diversity patterns change with scale is an important first step toward more fully understanding the applicability, limitations, and predictive power of ecological theory (111). We have benefited from several decades of experimental study of the relationship between system productivity and species richness, and a healthy body of theory complements this empirical data base. What has not been made clear is the applicability of theory to patterns at different spatial scales. The ambiguity of the proper scale of application is most obvious at the within-to-across-community scale, or at the local-to-landscape-to-regional scale. Consider as an example the graphical theories of community structure proposed by Tilman (186). When combined with resource heterogeneity, Tilman's model predicts a unimodal species diversity response to increasing nutrient supply (i.e., potential primary production). What is not clear from the model is the scale at which the pattern manifests. In fact, the theory itself can predict any type of pattern depending on range of productivity, location along a productivity gradient, heterogeneity of resources, and manner in which resource heterogeneity covaries with resource supply (2, 3, 186). Ambiguities of the scale of operation and application also may apply to alternative theories proposed to explain productivity-diversity relationships, such as the keystone predator model which also predicts hump-shaped relationships (105; for reviews of additional theories see 3, 167, 191). Determining how patterns change with scale in natural systems provides the first step in understanding the limitations and proper scales of application for theoretical frameworks.

The scale of a study may be an important factor to consider when predicting the relationship between diversity and productivity. Both geographic- and biotic-based classifications need to be considered. Unimodal patterns may emerge at relatively small spatial scales. Almost half of the studies of plant communities that reported distances between study sites of less than 20 km (local scale) produced unimodal

patterns. When studies remain within a community, patterns are almost equally divided between unimodal and positive categories for plants. This clearly changes when studies cross communities: Unimodal patterns become much more pronounced. At geographic scales greater than 20 km (landscape-to-regional scales), a larger proportion of positive patterns occurs for plants.

The range of productivities encompassed within a study may explain the decoupling of geographic and biotic classifications of scale for plants. Although we expect the two to covary (i.e., studies that are spread over large geographic ranges most likely have larger ranges of productivity), the relationship need not always hold. Investigations at small spatial scales may traverse large gradients of potential productivity, as well as multiple community boundaries, (e.g., elevational gradients from woodland to tundra). Conversely, single community types may span huge distances and several geographic scales, yet may exhibit little variation in productivity or species richness. Proponents of the unimodal pattern commonly argue that patterns without humps are a result of insufficient ranges of productivity in the study (e.g., 167, 168). Restricting studies to a single community type, from the outset, constrains them to a limited range of species compositions. If unimodal relationships occur primarily across communities, then within-community studies may be sampling only portions of the whole productivity-diversity curve. There is evidence that unimodal relationships emerge only when data from different communities along the productivity gradient are accumulated (e.g., 124, 121; KL Gross et al, in litt.). Thus, future research should consider explicitly the range of productivity sampled, which may be a major factor driving the change in plant community type.

Despite the predominance of unimodal patterns at the across-community scale, they can occur within communities (about 24% of plant and animal studies), but at this scale nonsignificant relationships are also numerous (42%). In addition to smaller productivity ranges at this scale, a number of ecological processes occur at smaller spatial and within-community scales, which may result in nonsignificant relationships. For example, dispersal between patches of high species diversity and sink patches of low diversity may mask productivity-diversity patterns. Such mass or rescue effects (33, 179, 180) likely occur at smaller spatial scales in which patches are in close proximity and immigration rates are high.

Studies of animals showed no dramatic changes in the frequency distribution of relationships across biotic or geographic scales. Positive relationships always outnumbered unimodal relationships, although the differences were small at the within- and among-community scales. Differences were more pronounced across geographic scales. Almost without exception, studies of animal diversity focused on subsets of the animal community (specific taxa such as rodents or amphibians). Most theoretical explorations of productivity-diversity phenomena deal exclusively with the species richness of whole trophic levels or guilds (e.g., 105, 186). Although models can be adapted to deal with more restricted taxonomic groups, the predictions may be very different. This is especially so because most studies of

animals not only deal with subsets of trophic levels, but also consider organisms that have different feeding ecologies (e.g., studies of aquatic macroinvertebrates can include primary and secondary consumers as well as detritivores).

Along gradients of productivity, taxonomic turnover may occur such that focal taxa within a trophic level drop out of the system, while other taxonomic groups (with the same feeding ecology) replace them. Although overall species diversity of the trophic level may show one pattern along the gradient, the focal group may exhibit a completely different one. Hence, the ability to assess the applicability of ecological theory and the influence of scale on productivity-diversity patterns for animals is limited.

The patterns and explanations presented thus far have dealt with studies at regional and smaller scales (<4000 km). Theory at this spatial scale deals primarily with communities assembled from presumably co-evolved regional species pools. Although our cut-off point of 4000 km is arbitrary, we hoped to distinguish between these types of studies and those whose communities may derive constituent species from different regional pools. This most likely occurs at the scale of whole continents or across continents (i.e., global scales). The results of our literature review indicate that species richness is primarily a positive function of productivity at this larger scale, for both animals and plants. Unimodal patterns were abundant for animals, though due perhaps to previously mentioned factors. These studies often include sites along gradients of latitude and can include species pools of different ages and evolutionary histories. Distinguishing the ecological effects of available energy from the evolutionary effects is difficult.

Despite the long history of interest in factors governing large-scale patterns of diversity, consensus remains elusive. Many potential problems accompany any literature review that gathers data from a wide variety of studies using disparate approaches, methods, and foci. Many of the caveats and shortcomings of our review provide guidance for future improvements in assembling productivity-diversity patterns. First, most of the studies we surveyed use a correlate of productivity, often an indicator of assimilated energy (such as standing crop biomass) or available energy (such as rainfall, latitude, evapotranspiration, or soil nutrients). In general, we expect these variables to be indicators of system productivity; nonetheless, correlations may be poor for some systems or at certain times of the year. Aboveground biomass is one of the most popular correlates in plant studies, but simple models of trophic regulation can predict complete decoupling of trophic-level biomass from productivity depending on the trophic structure of the system and the feeding efficiency of consumers (141). The studies included in our review use a great variety of quadrat and plot sizes, and rarely are area effects explicitly addressed or controlled.

Many different relationships between species diversity and productivity can be generated at a single biotic or geographic scale. Yet, the relative percentages of different patterns change with scale. Unimodal patterns have been described as textbook examples of productivity-diversity relationships (16). Our review is noteworthy for the lack of studies evincing a significant hump (despite our generous

criteria for detecting one). This is especially true for animals, in which positive patterns dominate at almost all scales. Our review in no way discounts the models and mechanisms that predict hump-shaped relationships, but it does attest to the potential importance of scale when applying such models and predictions. Exciting future directions include investigating why patterns change with scale; why in some systems unimodal patterns are generated at the within-community and local scales, whereas in others unimodal patterns only emerge when crossing community boundaries or large geographical distances.

FUTURE STUDIES

Two important issues facing the scientific community are the maintenance of global biodiversity and the continuance of the ecosystem services necessary to support human life. It is clear from numerous studies that these issues are inextricably entwined (41). Modeling and empirical studies demonstrate that loss of biodiversity can influence key ecosystem characteristics such as primary productivity, predictability, and resistance to invasion by exotics (41, 116). Theory and empirical studies indicate that changes in primary productivity are related to species richness at some scales but not at others. The goal of future research must be to provide mechanistic explanations for observed patterns in the relationship between primary productivity and species richness through well-designed and carefully interpreted experiments (85) that explicitly consider spatial scale as well as local and regional mechanisms.

A key strategy for improving our understanding of the interaction of biodiversity and productivity (or other ecosystem processes) considers the integration of two common experimental approaches: the manipulation of productivity and the alteration of the number of species or functional groups. A synthesis of ideas that have developed around these two approaches is a prerequisite for the advancement of a general theory that will direct the next generation of hypotheses and experiments. Conceptual models being developed by JB Grace (68a) and M Shackak (personal communication) foreshadow this synthesis. These emerging models incorporate disturbance, plant biomass (productivity), resource heterogeneity, colonization, and the available species pool as primary factors controlling species density. Consequently, they emphasize the importance of multivariate approaches to understanding patterns of species density (Figure 7).

Central to understanding the role that humans play in the present observed high extinction rate is the relationship between anthropogenic disturbance and the natural disturbance regime (219). The first attempts to explain the control of species richness had an explicit appreciation for the importance of human activities (71, 72), which led to an integration of disturbance, environmental stress, and elements of productivity in an index of factors controlling species richness (6; 68a). Future studies need to refocus on the similarities and differences between natural and anthropogenic disturbance. Incorporation of the unique nature of human

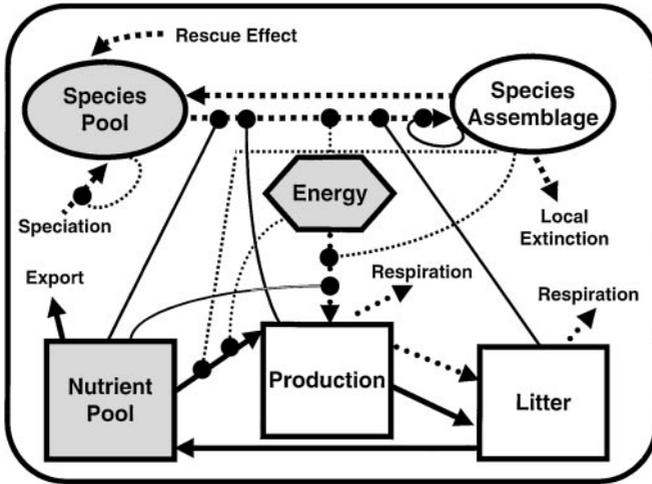


Figure 7 Conceptual model of a local ecosystem: the biota interacting with energy flow and nutrient cycling (unshaded shapes). For simplicity's sake, the model only considers the plant community. Shaded shapes represent larger-scale species pools, nutrient pools, or energy inputs. Broad arrows represent the various system currencies of species (dashed), energy (dots) or nutrients (solid); narrow lines terminating in a circle represent regulators or filters which modify the flow of species, nutrients or energy. Hence, the composition of a local assemblage is derived from a regional species pool via the action of five filters: available energy, nutrient availability, and the species already in the community, as well as structural characteristics of the production and litter. Similarly, the production of the ecosystem is affected by available energy as processed by species assemblages and constrained by nutrient availability. Because energy flow and species flow are affected by some of the same regulators, and in fact reciprocally affect each other, the relationship between them may be complex.

activities into models of the relationship between biodiversity and ecosystem processes is necessary to merge the fields of evolutionary ecology and conservation biology.

The time is appropriate for the study of the relationship between species richness and primary productivity to change focus from discerning patterns to developing mechanistic explanations, which can be tested through manipulative or observational experiments. The available evidence shows that multiple patterns exist and change with scale. The implication is also clear that multiple causal factors exist for scales, habitats, and taxa. There is reasonably strong evidence to demonstrate that productivity influences diversity at some scales, whereas functional or species diversity seems to influence productivity at other scales. Clever experiments and observations based on conceptual models of system dynamics (Figure 7) will be needed to disentangle the web of cause and effect. With this in mind, we offer in

conclusion a few general ideas concerning the characteristics of future research endeavors.

- Investigators must be careful to match the scale upon which theory operates to the scale of observation. In many cases this will require the collection of new data at the appropriate scale to test theory.
- Some standardization in operational definitions is necessary for meaningful comparison. In particular, the spatial and temporal framework for the measurement of species density and productivity must be carefully controlled. Theory that is based on net primary productivity cannot be evaluated using partial measures of NPP. Similarly, theory that is based on guilds or communities cannot be evaluated using subsets of these communities.
- Multivariate approaches are needed to separate the effects of co-varying causal factors. Investigators must recognize that different species may respond to different variables along the same geographic gradient and that changes in total species richness are the sum of these species-level responses.
- Experiments must include several trophic levels and multiple ecological scales. Without this kind of experimental approach, results will be difficult to place in context.
- Theory and experimentation need to be extended to high-diversity systems. Microcosms provide a useful approach for addressing basic questions, but issues relating to the loss of taxa from species-rich systems urgently require attention.
- More sophisticated manipulations of productivity at multiple scales will be required to determine the generality of the pattern between productivity and species richness. In particular, manipulations of limiting resources that increase heterogeneity of resource availability would provide an interesting contrast to standard fertilization experiments.

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