Species Diversity Gradients: We Know More and Less Than We Thought

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Journal of Mammalogy, Vol. 73, No. 4 (Nov., 1992), 715-730.

SPECIES DIVERSITY GRADIENTS: WE KNOW MORE AND LESS THAN WE THOUGHT

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Keynote Address, Presented at the 71st Annual Meeting of
The American Society of Mammalogists, Manhattan, KS, June 1991

Patterns in the diversity of species begin to make sense when we reduce them to well-known biological processes and take care to specify the scale of the pattern. Doing this explains why diversity declines away from the tropics (the latitudinal diversity gradient). The extensive tropical regions supply more opportunities for large geographical ranges than any other biome. Allopatric speciation feeds on such large ranges. The large regions of the tropics also probably inhibit extinction. It is a mistake to explain the richness of the tropics by noting that there are more habitats in the tropics. The global scale develops in evolutionary time. On that scale, fine habitat subdivision is a coevolved property of the species in a biome. The more species, the finer they subdivide habitats. So, it is also wrong to imagine that the tropical gradient is nothing more than a species-area curve. The species-area curve is a pattern that exists on a more local scale than the latitudinal gradient, and depends on habitat variability growing as larger areas get included in a sample. We all think that decades ago we should have understood the pattern of diversity and productivity. But the literature isn't even sure what the pattern is. Until recently, theory maintained that higher productivity should sustain more species. Evidence from poorer environments supports that theory. But most empirical evidence, including most experiments, show that diversity declines as productivity rises. Two errors confused us. First, we ecologists always assumed that the theory could not be wrong, so we refused to admit the facts, no matter how often we observed them. Second, we mixed our facts into a wild stew of scales and biomes. Diversity experiments, performed by increasing productivity on a local scale of time and space, tell us nothing about the productivity pattern at large scales. The regional pattern is unimodal. As productivity rises within a region, first diversity rises and then it falls. This pattern exists in mammals, birds, marine vertebrates and invertebrates, and some flora. We do not understand it.

Key words: biodiversity, species area curve, latitudinal gradient, productivity

Ecological patterns build ecological challenges. Wherever we find pattern, we suspect there must be rules. Can we discover them?

Ecologists long ago discovered the pattern called the latitudinal diversity gradient. Most ecologists believe we have never met the challenge of that pattern. To a great extent, they are mistaken. The literature contains not merely the clues, but the answer.

Latitudinal gradients arise because the tropics cover more area than any other zone. Their greater area stimulates speciation and inhibits extinction. I shall review and explain that answer in the first part of the paper.

Then I must make the point that the answer does not reduce the latitudinal gradient to the rank of just another species-area curve. Species-area curves exist on a much smaller scale of space and time.

Too often, ecologists studying diversity

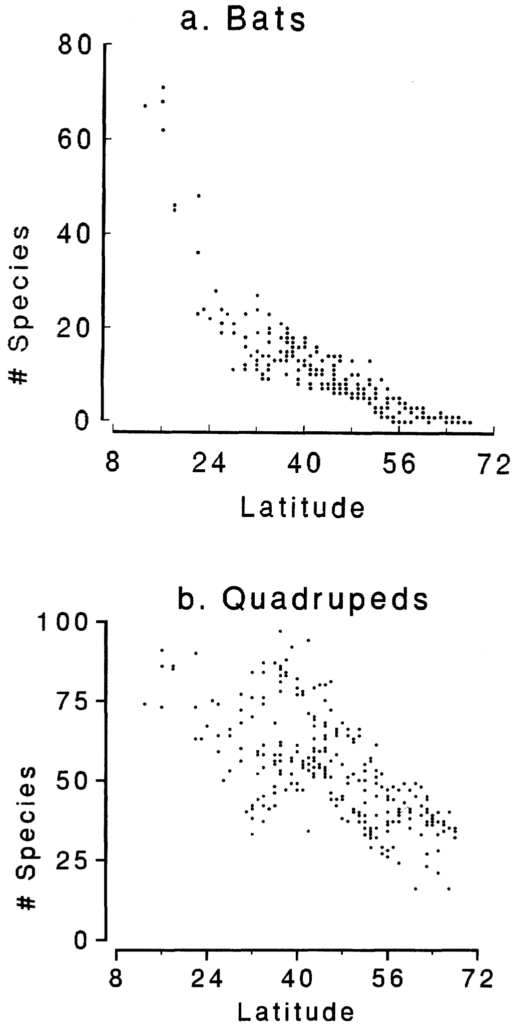


FIG. 1.—The number of mammal species declines steeply from tropics to tundra in North America. Data come from Wilson (1972). Each point gives the number of species in a rectangular block of land (150 miles × 150 miles). To eliminate the effect of unequal area, I eliminated all those blocks on coastlines that are partly occupied by water. a. Bats. b. Quadrupeds. Before exclusion of coastal blocks, the quadruped pattern cannot be seen.

patterns intermingle space-time scales with abandon. This confuses more than it clarifies. We will see more examples of it in the third part of the paper.

The third part of the paper discusses the productivity-diversity pattern. It is the opposite of the latitudinal gradient. The latitudinal gradient has been a pattern in search of a theory. But theory actually predicts the following productivity gradient: The greater the productivity, the greater the diversity. The theory is so simple, so general, so robust, that few bothered to recognize the rarity of the pattern it predicts. Too bad. If the pattern were only more common, we should have possessed the genuine article: a scientific pattern prepackaged with its own prediction-generating explanation.

But there *is* pattern in the productivity-diversity relationship. I shall review a set of nine hypotheses offered to explain it. Unfortunately, most fail, and none have yet succeeded.

That will leave us with a curiosity. The pattern we think we don't understand, we actually do. And the pattern that, decades ago, we thought we understood, still challenges us.

THE LATITUDINAL GRADIENT

Here's the issue that fills the poor boxes for ecology. The tropics are fabulously rich in species, and their destruction threatens to deplete the Earth's genetic library. Or add to global warming. Or jeopardize the very future of life on Earth.

Funny thing is, the tropics *do* harbor more species than any other latitudinal zone. And the farther you get from the Equator, the fewer species (of most taxa) you find. Mammals are no exception. Bats have a powerful latitudinal gradient (Fig. 1a). And the gradient for quadrupeds (Fig. 1b) is clear—despite the fact that the very highest diversities occur in arid areas at horse latitudes (Mares, 1992).

The latitudinal gradient is not an historical quirk of an immature post-glacial Earth. The tundra, perhaps the Earth's youngest biome, was born at least 4 my (million years) ago, and its diversity has declined since then (Matthews, 1979). Moreover, we know of latitudinal gradients that are tens if not hundreds of millions of years old. Marine fo-

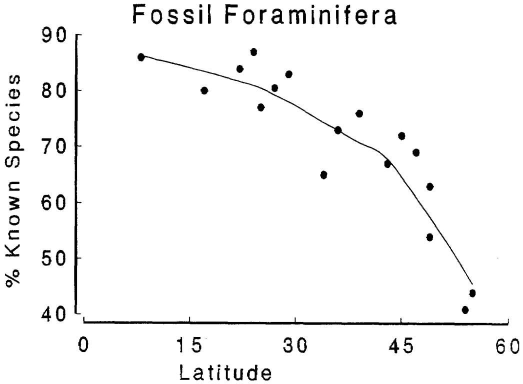


FIG. 2.—Latitudinal gradients are ancient. This one, for marine foraminifera, comes from fossil data tens of millions of years old. (Redrawn from Stehli et al., 1969.)

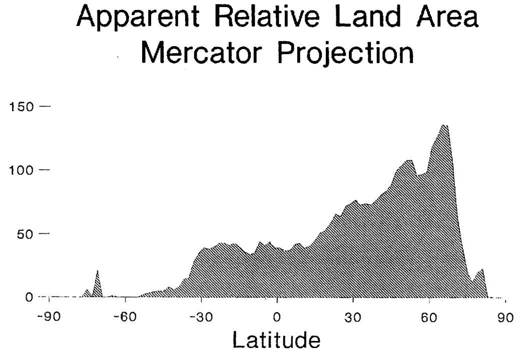


FIG. 3.—Visual impact of a Mercator map. The more northerly the area, the bigger it seems. This figure shows the exaggeration in land areas of the northern hemisphere.

raminifera have the world's most detailed and reliable fossil record—at least for the Cenozoic. And (Fig. 2) they exhibit a gradient which is some 70 million years old. Angiosperms also have ancient latitudinal diversity gradients (Crane and Lidgard, 1989). I suspect many more cases of fossil gradients will be brought to our attention as paleobiologists take advantage of their ability to measure the latitudes at which rocks were deposited.

Pianka (1966) wrote the classic list of hypotheses to explain the latitudinal gradient. He crafted it so beautifully that many still teach from his list today. (See, for example, its treatment in Begon et al., 1990).

But, when John Terborgh (1973) cut the Gordian knot, his explanation did not come from Pianka's list. Terborgh concluded that the tropics abound with life because they abound with territory. The tropics are richer because they are more extensive than any place else. Terborgh noted that those of us who carry around maps of the Earth in our heads generally carry something resembling a Mercator projection. This exaggerates the area of terrestrial features in proportion to their distance from the Equator. The farther from the Equator, the larger they appear to loom (Fig. 3).

Because the Earth is round, the distance between longitudes actually peaks at the Equator. This greatly reduces the apparent overhang of the lands of the Northern Hemisphere, and eliminates it entirely in the seas and the Southern Hemisphere (Fig. 4).

Terborgh noticed another simple thing. The northern and southern tropics abut. Thus their area is roughly double that of any other zone.

Finally, Terborgh noted (from data) that a broad belt of homogeneous temperatures, roughly 50 degrees (of latitude) wide, encircle the Earth's midsection. North or South of this belt, average annual temperature falls off linearly (Fig. 5). So, any place in the belt has the chance of being like anyplace else, but any place outside it will be rather restricted in area. Moreover, it will get more and more restricted as it centers on higher and higher latitudes (because the Earth is round).

Terborgh must be right for the seas and the Southern Hemisphere. But does his general conclusion follow for the vast north? And even if it does, how does having a huge area allow a zone to harbor more species?

I got a simple computer map of the globe that divided it into sea, land and ice. Then, I measured the actual land areas contained in several arbitrarily situated zones: tropics (±26°); subtropics (26–36°); temperate (36–

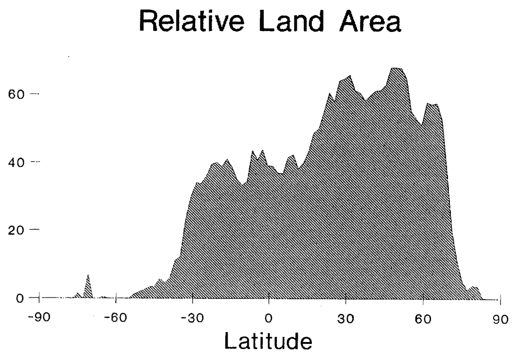


FIG. 4.—An equal area map does not exaggerate the amount of land in the northern hemisphere.

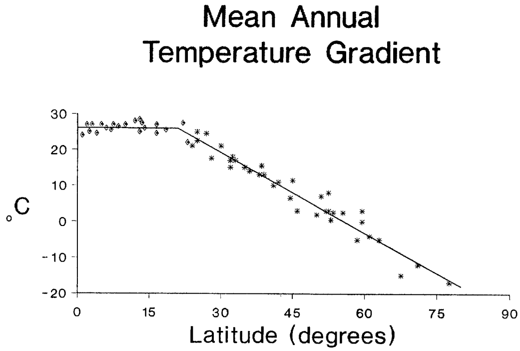


FIG. 5.—In the tropics, average annual temperature varies little with latitude, but it declines linearly outside the tropics. (Data from Terborgh, 1973.)

46°); boreal (46–56°) and tundra (>56°). Sure enough, the tropics are about four times larger than their nearest competition. Terborgh was right for northern lands too (Fig. 6).

How does area translate into diversity? We must seek the answer in comparative speciation and extinction rates because the processes that govern speciation and extinction are the processes that determine standing diversity. (I ignore immigration. For biogeographical provinces, it is a second order process.)

Let's imagine a world in which tropics and subtropics have the same diversity. We can expect the average tropical species in such a world will have a geographical range that is half an order of magnitude greater than its counterpart in the subtropics. Probably, that range difference has three consequences (Rosenzweig, 1975).

First, the greater range leads to a larger total population size (assuming densities to be about the same). Larger populations should result in smaller accidental extinction probability (because every individual must die accidentally before extinction is complete). No doubt this probability is not linear. Thus, I am not saying that a species with 10^6 individuals has 100 times the chance of accidental extinction as a species with 10^8 individuals. Just that it tends to have a higher probability.

Second, the greater range covers more niche refuges. Any weather disturbance or climatic deterioration covers a limited area. Species with big ranges are more likely to have a site or two to tide them over. So, they should again suffer lower extinction rates.

Third, larger ranges are bigger targets for geographical barriers. When a barrier hits a range so as to produce a population isolate, the process of allopatric speciation can begin. Some barriers may penetrate a range without producing isolates. But at the size of most (or all) real ranges, the probability of hitting the range tells most of the story of isolate formation. Hence we expect higher speciation rates where ranges are largest (see also Rosenzweig, 1977).

In sum, larger ranges should reduce extinction rates (for two reasons), and increase allopatric speciation rates. Our tropical regions will diversify faster than our subtropical ones, and leave them relatively poor (Fig. 7). Given what we know about speciation and extinction, we would have to be astonished if there were no latitudinal diversity gradients.

If area controls diversity, then larger provinces, regardless of their latitudes, should have more species. Flessa (1975) showed this to hold for genera of mammals (Fig. 8). Undoubtedly, it also holds for spe-

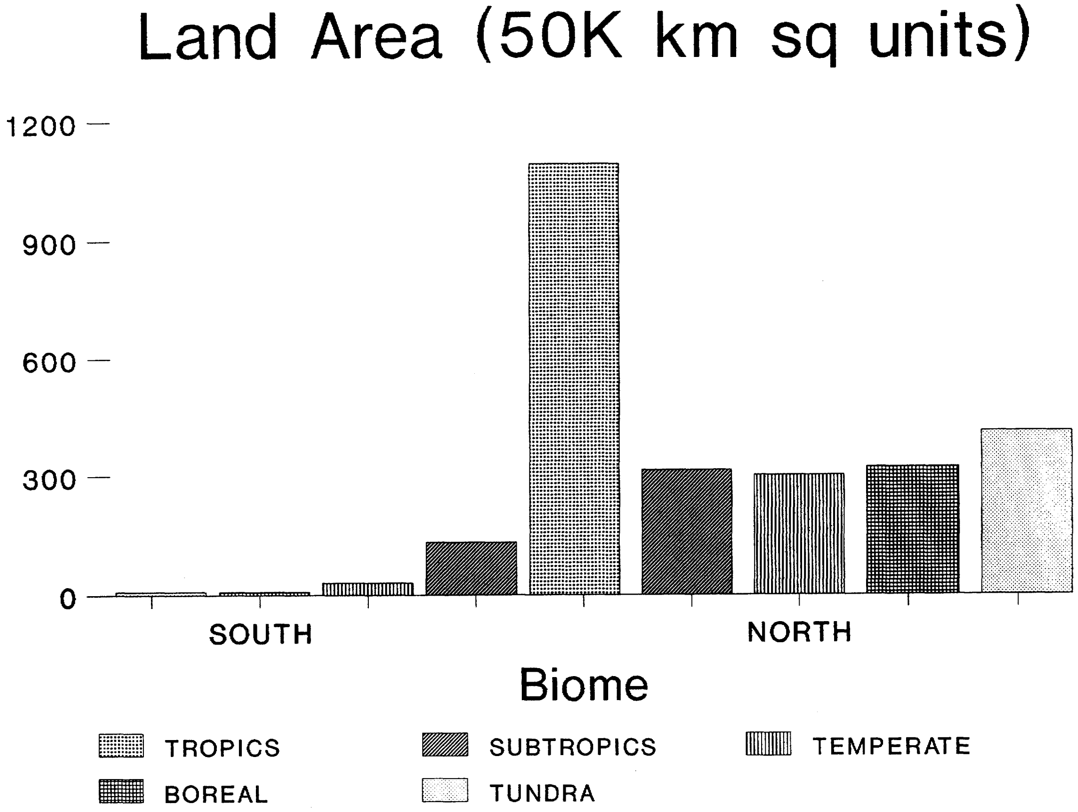


FIG. 6.—Land areas in five broad zones of the Earth. The tropics are half an order of magnitude bigger than other zones.

cies. Flessa's data span provincial areas from 0.23×10^6 km^2 (West Indies) to 52×10^6 km^2 (Eurasia).

Figure 6 shows that northern terrestrial biomes do not show much variation in area. Subtropical, temperate, boreal and tundra all have similar extents. If area is the true basis of latitudinal gradients, then why does the gradient appear within these biomes? You might expect to see a step function: higher diversity in the tropics and lower diversity north of it, but no change north of about 25°. I can think of two reasons to doubt this conclusion.

First, many species have ranges which extend over more than one zone. Many tropical species will reach northward and get counted in northern lists. (The same thing may be going on among species of other zones, but there will be far fewer of them

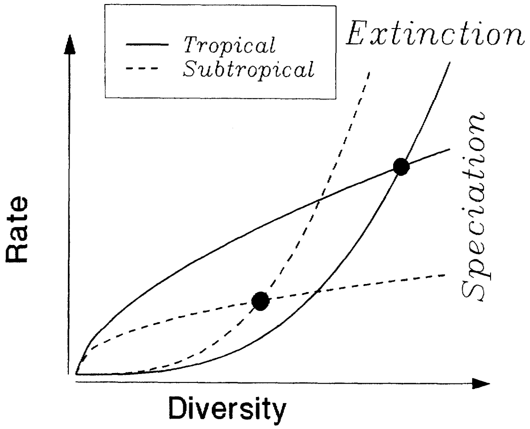


FIG. 7.—The dynamics of diversity. Owing to their larger area, the tropics have higher speciation and lower extinction rate curves. (Note that at the steady-states—the large dots—extinction rates in the tropics actually exceed those of other life zones.) (After Rosenzweig, 1975.)

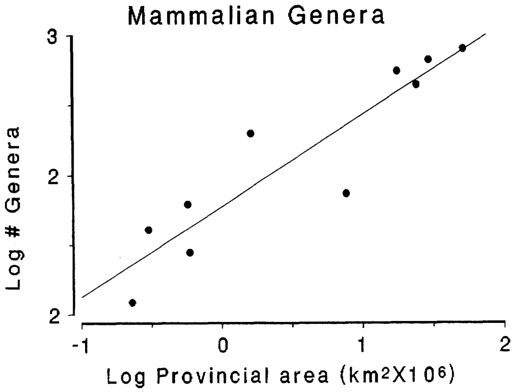


FIG. 8.—Larger biotic provinces have more mammalian genera (modified from Flessa, 1975). Flessa showed that the same relationship holds for families and orders, although their slopes are shallower. The slope for species may even be steeper.

because of the area effect.) The farther north you go, the fewer tropical species remain. The result will be a secondary diversity gradient among zones north of the tropics. This hypothesis predicts that the gradient should disappear if you remove all species with partly tropical ranges from lists of species north of the tropics. (This simple statistical experiment hasn't yet been tried.)

Second, primary productivity declines as you increase latitude. Perhaps this decline causes a similar decline in diversity. The third section of the paper deals entirely with the effects of productivity and it shows that very low productivities do indeed seem to produce very low diversities.

I think both reasons may be valid. The productivity effect and the spillover of tropical ranges into non-tropical zones may combine to produce the gradient outside the tropics in northern hemisphere lands. But notice that the spillover effect depends on the area effect; without a tropical bias in the number of species spilling over, spillover effects in different zones would cancel each other out. And, as you will see, no one has much understanding of the productivity effect. In contrast, we can rely on the area effect.

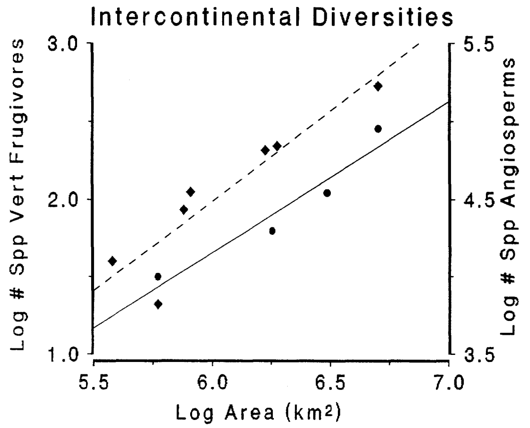


FIG. 9.—Rainforests in different biotic provinces (from Australia to Amazonia) cover vastly different amounts of land, and support vertebrate frugivores and angiosperm species accordingly. Vertebrates include frugivorous bats, birds and primates. Diamonds: vertebrates; dots: plants. (Data from Fleming et al., 1987; Prance, 1977; and my own estimate of Australian frugivores, the left most point.)

Terborgh (1973) made a straightforward prediction based on the idea that the latitudinal gradient comes from differences in the area of the different biomes. Tropical regions differ considerably in area. So the larger ones should be even richer than the smaller ones. He used this to understand the great diversity of grazing ungulates in Africa compared to the Neotropics where tropical grassland is relatively scarce. He also used it to explain why Africa has so few rainforest tree species compared to Amazonia: Africa's rainforests cover much less area.

Independently, Findley and Wilson (1983) suggested that Africa's frugivorous bats are not really depauperate; they just occupy a smaller area. They demonstrated a linear relationship between the area of a province's rain forest and the diversity of its frugivorous bats. Fleming et al. (1987) extended this result to other taxa, i.e., frugivorous birds and primates. Fig. 9 displays the data. To it I have added a point for Australian tropical rainforests. (I got the data from standard works on Australian birds and mammals.)

Figure 9 also shows the number of angiosperm species in the same rainforest regions (Prance, 1977), although sometimes the data are not available for precisely the same areas. Notice the accuracy of Terborgh's prediction. The more tropical area, the more species.

HABITAT DIVERSITY—A COEVOLVED PROPERTY OF BIOTAS

Despite the dependence of the latitudinal gradient on area, it is NOT another example of a species-area curve. Species-area curves have other causes entirely. For example, they can arise from sampling problems when more effort is put into sampling larger areas than smaller ones. But the most intriguing species-area curves deal with well-known floras and faunas. I agree with Williams (1943) that such curves depend on habitat diversity. The larger the area, the greater its variety of habitats. (Two fine overviews of species-area curves: Coleman et al., 1982; McGuinness, 1984).

Fox (1982) has shown this for mammals in southeastern Australia. They do show a species-area curve (Fig. 10a). But larger areas also include more habitat types (Fig. 10b). Moreover, the number of habitats predicts mammal diversity better than area does (Fig. 10c). The prediction is so good that area does not even help to explain the residual variance.

Many of us treat the number of habitats as if it were an inherent, objective, abiotic property of a region. But, in fact, it is a coevolved property. It depends on the number of species forcing each other to specialize on limited ranges of habitat properties. The more species, the more narrowly they specialize. The more they specialize, the more the ecologist sees different habitats.

You may imagine a hierarchy of time. First, on a grand scale, the species evolve. Then, on a somewhat smaller scale, they force each other to become habitat specialists. Finally, on an ecological time scale, they move around in search of the habitats on which they have specialized, and become extinct if those habitats have grown too scarce.

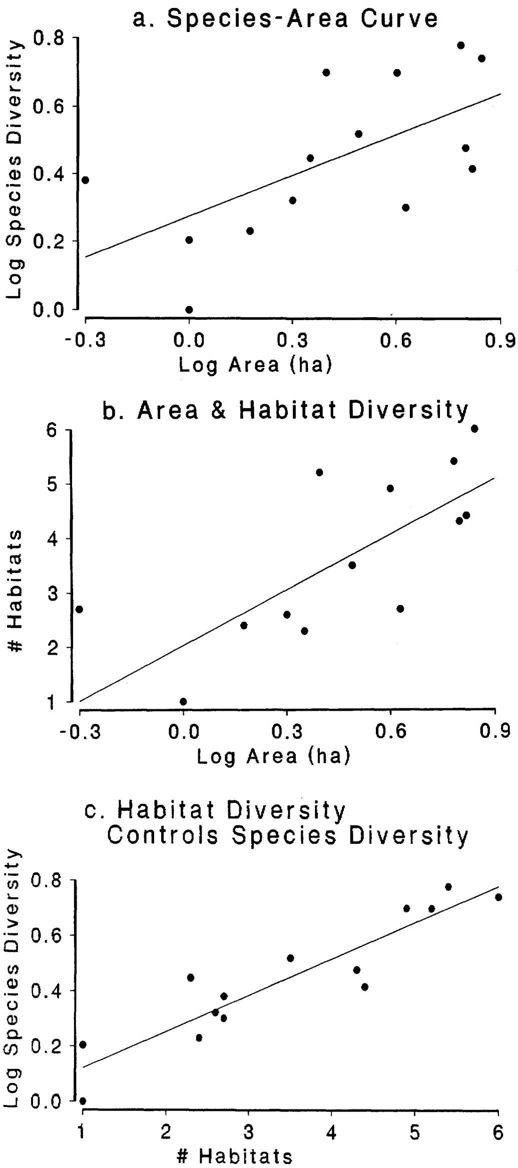
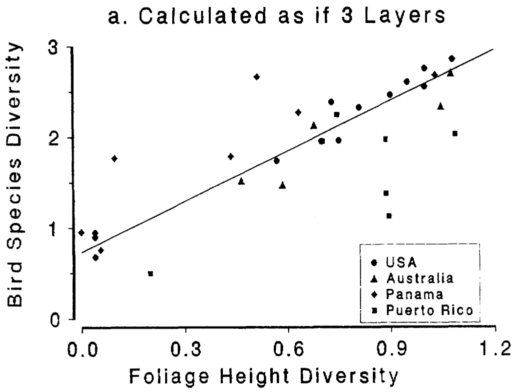


FIG. 10.—Mammal diversity in southeastern Australia fits the number of habitats better than area. (Redrawn from Fox, 1982.)

The strongest evidence for this hierarchy comes from the study of bird species diversity. In temperate North America and temperate Australia, the diversity of bird species depends on the number of habitat layers in the foliage (Recher, 1969). The best fit comes from assuming the birds recognize as many as three layers (Fig. 11a). But bird diversities in Panama routinely exceed pre-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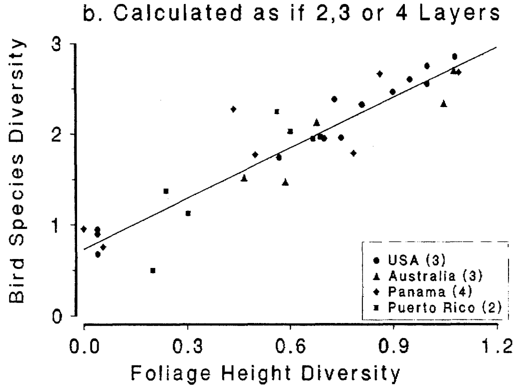
b. Calculated as if 2,3 or 4 Layers

FIG. 11.—Bird species diversity fits a measure of habitat diversity called foliage height diversity. In the USA and Australia, the measure gives a good fit to the data if we assume that birds recognize three foliage layers (the regression line in both a and b). In a we see that bird species diversities in the tropics do not fit the 3-layer assumption. Mainland Panama's avifauna tends to be more diverse than predicted (6/7 points). The island avifauna of Puerto Rico tends to be less than predicted (also 6/7 points). In b we see that tropical bird species diversities are accurately predicted if we assume birds recognize four foliage layers in Panama's rainforest but only two in Puerto Rico's. (Adapted from Recher, 1969, and MacArthur et al., 1966.)

dictions based on a three-layered forest (Fig. 11a). You might think that happens because tropical forests are more complicated and have more habitat layers. However, the tropical forests of Puerto Rico are similar in physiognomy (tree height, leaf density, etc.). Yet, you can also see in Fig. 11a that they routinely fall short of three-layer predictions.

The trick is to predict the number of birds in Panama from the assumption that they recognize four habitat layers, and to predict the number of birds in Puerto Rico from the assumption that they recognize two habitat layers. Then, both the Panamanian and the Puerto Rican results fall into line (Fig. 11b).

Puerto Rico is depauperate because it is an island, not because it lacks richly complex rainforest. Its birds need to recognize only two habitat layers. Panama's birds recognize four, not because the layers exist in some objective sense, but because avian diversity is so high that natural selection forces them to see four.

Abbott (1978) confirmed this on two series of 4 ha plots in southwestern Australia. He set up one series of 29 plots on 20 different islands. The other (12 plots) was on the nearby mainland. Mainland sites had about twice as many breeding passerine species as did island sites of the same habitat complexity. People often attribute the low species richness of islands to absence of some mainland habitats, and there is considerable truth in doing so. But Abbott, and MacArthur et al. show us that there is much more to the story. Even when the habitats are present, they do not support as many birds.

Cox and Ricklefs (1977) measured the number of habitats used by birds in Panama and four Carribean islands. The more species, the fewer habitats each used. MacArthur et al. teach us that habitats are simply not being subdivided as finely on the islands. Island birds seem to use more habitats because we transfer our experience with richer biotas and recognize too many habitat distinctions on islands. Real birds are less easily fooled.

Density-dependent habitat selection helps us to understand the cause and effect relationship between diversity and habitats. One species alone spreads out into all sorts of "habitats" (Fretwell and Lucas, 1970). Add a coexisting competitor, and somebody's niche shrinks (Rosenzweig, 1987*a*, 1991). The same principle ought to hold in evolutionary time (Rosenzweig, 1987*b*). In the most important sense, the habitats are undifferentiated until there are many competing species to treat them differently.

Speciation and extinction processes generate latitudinal gradients. So the gradients depend on that larger scale of time which determines species diversity. Habitat differentiation happens as a consequence of the diversity, so it depends on the intermediate time scale. Because species-area curves are reflections of the habitat diversity which has already evolved, they depend on the shortest time scale, and we must consider them separately from latitudinal gradients.

THE PRODUCTIVITY-DIVERSITY PATTERN

We all know how productivity ought to affect diversity. The more productivity, the more species diversity.

The argument is founded in Preston's theories of species abundance (Preston, 1962). Assume a variety of productivities and biotas in different regions. Assume all start with the same diversity. The scarcest species in the most productive region will be more abundant than in others. Therefore, scarce species of the most productive region will better resist accidental extinction. Diversity will change in all regions until the scarcest species in all regions have about the same chance of accidental extinction. Because the pie is larger in a more productive place, it must be sliced into many more pieces before its smallest are about the same size as the smallest in a poorer place. So, richer places have more species.

I do not think Preston's theories are wrong. But he intended them to deal with patterns of species' abundance distributions. Applying them to diversity may be stretching them near their limit. To do it, we must assume that distribution shapes are about the same regardless of productivity; that diversity is governed by the ability of the rarest species to survive accidental extinctions; and, most important, that the contribution of the accidental extinction rate dominates all other facets of extinction and speciation. Perhaps my pointing out all those assumptions to you, makes you unsure whether you still believe that more productivity ought always to raise diversity. I hope so, because it doesn't.

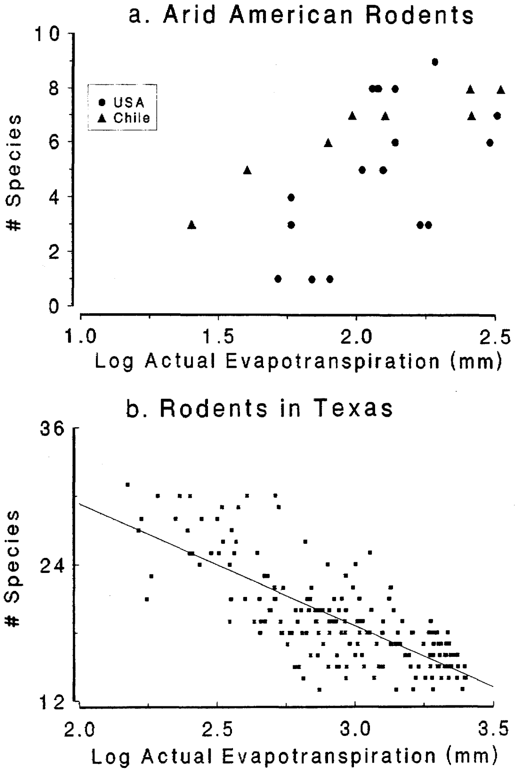

FIG. 12.—Brown (1973) and Meserve and Glanz (1978) found that rodent diversity increases with productivity in arid regions of the Americas (a). But Owen (1988) showed that it declines from semiarid shrublands to subtropical mesic forests in Texas (b). The Texas data are plotted separately because they come from larger areas.

Immature and tiny scales first suggested something was wrong. But mammal studies quickly neutralized their effect (Fig. 12*a*). For a while it seemed as if the truth would be easy to find and easy to grasp.

Then, Abramsky and I got some disturbing data on Israel's small mammals. Whether we looked at sandy or rocky communi-

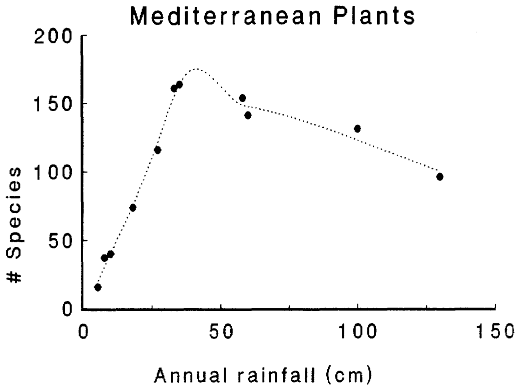

FIG. 13.—Plant diversities also sometimes peak at intermediate productivities. Most of these data come from Israel, but the rightmost comes from humid forests in Turkey and Spain. (Data from Shmida et al., 1986; and Shmida, unpub.)

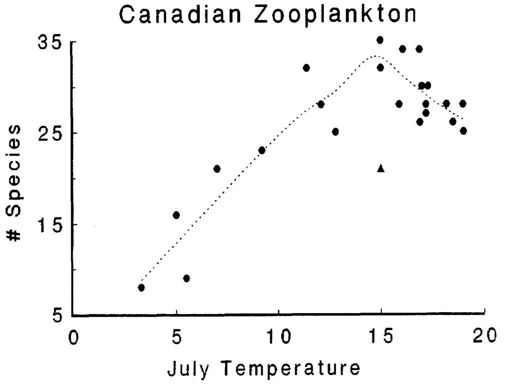

FIG. 14.—Zooplankton diversities of Canadian lake regions peak at intermediate productivities. The triangle represents the point from Newfoundland, the only island in the data set. (Redrawn from Patalas, 1990.)

ties, diversity declined after productivity grew beyond a certain point. The pattern was unimodal or "hump-shaped." It was not monotonically increasing.

About the same time, Tilman (1982) suggested that a hump-shaped curve ought to characterize plant diversity-productivity patterns. Encouraged that our data might not be a fluke, we published it as an example of Tilman's pattern (Abramsky and Rosenzweig, 1984).

Then other mammalian examples turned up. Australian tropical mammals fit the pattern (Rosenzweig and Braithwaite, in litt.). Owen (1988) showed it in Texas' carnivores (but not in bats). But most important, he showed that in Texas, rodent diversities *decline* as productivity goes up (Fig. 12b). Since Brown's data end at about the productivities where Owen's start, Brown and Owen were looking at opposite ends of the same camel. The whole pattern for U.S. rodents is hump-shaped!

The pattern exists in plants too. The data of Shmida and his colleagues (Fig. 13) show it for Mediterranean plants (censused in 0.1 ha plots).

Yet, we do not yet know how common the pattern is among plants. Currie and Paquin (1987) studied the issue in trees of Canada and the USA and found that diversity always increases with productivity.

Tilman (1982) pointed out the pattern in tropical trees in two provinces (Malesia and the Neotropics). However, Tilman used a measure of soil fertility to stand in for productivity, and no one has yet shown how tropical forest productivity can be predicted from a surrogate variable. Also, controversy surrounds the correlation of tropical forest diversity to soil fertility in Neotropical and in African rainforests. In those forests, annual precipitation correlates well with plant diversity whereas soil fertility does not (Gentry, 1988*a*, 1988*b*; Gentry and Emmons, 1987; Hall and Swaine, 1976). The more precipitation, the more species. Certainly forest diversities do not peak over intermediate soil nutrient concentrations.

High precipitation leaches the tropical soil and makes it very poor. But tropical plants have evolved a root mat that buffers the loss of nutrients from the soil itself (Jordan, 1983; Stark and Jordon, 1978). This makes it easier for us to understand how ultra-poor, sandy white tropical soils can support immense plant diversity and abundance.

All in all, we are not yet sure of the pattern relating plant diversity to productivity. It may be monotonically increasing. It may be

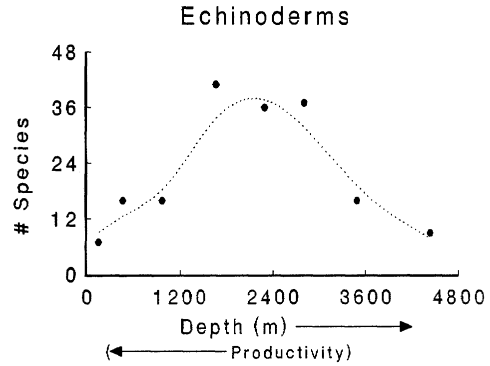

FIG. 15.—Echinoderms are one of a large number of benthic invertebrate and vertebrate taxa whose diversities peak at intermediate productivities. (The deeper the water, the less productive; data from Haedrich et al., 1980.)

unimodal. Or it may follow either pattern, depending on the continent or the latitude we study.

However, we do notice the unimodal productivity pattern in zooplankton of freshwater Canadian lakes (Fig. 16). This observation is something of a breakthrough because well-known data from Danish lakes show a negative correlation (Whiteside and Harmsworth, 1967) and were the earliest serious contradiction of Prestonian theory.

Marine biologists see the pattern in many animal taxa. Schopf (1970) noticed it among bryozoa. Haedrich et al. (1980) show it for bottom-dwelling decapods, fishes and echinoderms (Fig. 15). Rex (1981) also points it out in cumaceans, gastropods, protobranchs and polychaetes. In all these cases, ocean depth is the index of productivity. The deeper the ocean, the less light penetrates to the bottom. Rex recognized the role of productivity in supporting increased diversity from the deepest water to the depths at which we see peak diversities. But he tacitly assumes Prestonian theory must be correct. So he rejects the link with productivity as an explanation for the decline phase. Were it not for all the examples we now have, in all those taxa and for all sorts of regions, I probably also would reject the link.

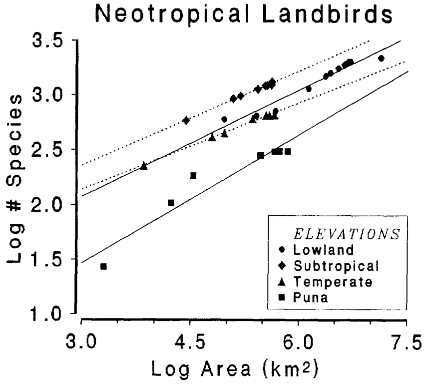

FIG. 16.—Species-area curves for neotropical birds. The life zone with the highest species-area curve has intermediate productivity (the subtropical elevations from about 1.5 to 2.5 km; data from Rahbek, unpub.; figure from Rosenzweig and Abramsky, in press).

HYPOTHESES TO EXPLAIN THE PRODUCTIVITY PATTERN

Rosenzweig and Abramsky (in press) review hypotheses to account for the hump-shaped pattern. They accept the importance of Preston's theory for the increase phase (or left side) of the pattern. In other words, for truly poor regions, abundance itself may indeed be the problem, raising extinction rates for the scarcest species and limiting diversity.

The frustration begins when they tackle the decline phase. There are nine hypotheses ranging from weak to preposterous. To give you a taste of the problem, I will summarize them here.

Perhaps the population dynamics of more productive regions are less stable?—This theory lives in ecological time (Rosenzweig, 1971). But there is no evidence for it in mature communities (by which I mean to exclude polluted, eutrophic water; fertilized agricultural land; etc.). Also, Rosenzweig and Schaffer (1978) showed that the destabilizing effect of higher productivity tends to disappear in evolutionary time.

Perhaps the decline phase is just a species-area curve?—The idea is that the most pro-

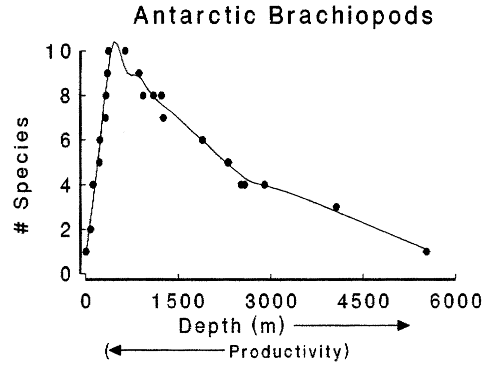

FIG. 17.—The diversity of (modern) Antarctic brachiopods peaks at intermediate productivities. (Data from Foster, 1974; figure from Rosenzweig and Abramsky, in press.)

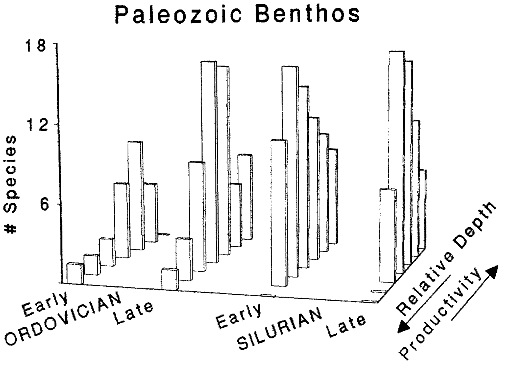

FIG. 18.—The brachiopod-dominated faunas of Paleozoic seas peaked at intermediate productivities. Depths are relative, but only within each age. Asterisks mark the bars with the largest diversity of their age. (Data from Lockley, 1983; Watkins, 1979; Ziegler et al., 1968; analysis from Rosenzweig and Abramsky, in press.)

ductive places are scarce relative to those of moderate productivity. Two things wreck this hypothesis. First, there is no reason to believe it about oceans. Second, the data contradict it. For example, the Mediterranean plant data (Fig. 13) come from equal area plots. And a comprehensive set of data on Neotropical birds (Rahbeck, unpub.) shows that the productivity pattern does not even show up until you remove the effects of area (Fig. 16). Before area is factored out, the productivity pattern looks monotonic: lowland tropics have the most species, followed by subtropical elevations, then temperate, then puna. But when you compare the species-area curves of these four zones, you see that at equal areas, subtropical diversities exceed those of the lowlands.

Perhaps the most productive places are younger and haven't had enough time to realize their potential?—Notice that this hypothesis stands the usual "time hypothesis" on its head. That one says the tropics are rich because they are old. But a more compelling problem—empirical data—scuttles the time hypothesis as the cause of the productivity pattern.

Modern brachiopods exhibit the productivity pattern nicely (Fig. 17). But so do the brachiopod-dominated faunas of the Upper Silurian, Lower Silurian, Upper Ordovician (Caradoc) and Lower Ordovician (pre-Caradoc) (Fig. 18). That little expanse covers some 75 million years. You'd think 75 million years would be long enough for the richest shallows to mature. Notice also that during the Ordovician there was plenty of time for a major increase in marine diversity (Bambach, 1977). So there must also have been enough time for the pattern to become Prestonian. It just didn't.

Three more hypotheses should not be taken seriously—at least not yet. One ascribes the decline phase to *a decline in the prevalence of interference competition.* Another to *a decline in the covariance of the densities of different species.* The third to *an increase in the predator/victim ratio.* There is no evidence for any of them. In fact, predator/victim ratios do not seem to vary much with diversity (Mithen and Lawton, 1986). And the covariance hypothesis (Rosenzweig, 1979) hasn't even been well explored theoretically.

Three other hypotheses each deserve considerable attention, although I firmly believe that two of them are false and the third is inadequately developed and tested.

Perhaps too much productivity reduces the number of habitats?—This hypothesis has the greatest appeal. It combines theory and data. Its theory actually predicts the entire hump, not just the decline phase. And it treats my favorite ecological variable, habitat diversity. I wish I did not think it was wrong.

Tilman (1987) imagines that each species specializes along some habitat gradient. Areas of poor productivity contain little of the gradient, so they have few species. Rich areas also contain little of it, so they too have few species. Intermediate productivity areas contain a wide variety of habitats and harbor the most species.

Consider all the myriads of data that show the importance of habitat diversity to species coexistence. It all favors this hypothesis. Moreover, if you take a close look at specific cases, you become even more convinced. For example, desert rodents in southeastern Arizona are sitting right on the North American rodent peak. Increase the productivity a bit and their desert becomes a semi-arid grassland. The shrubs and open patches which support so much of the desert's diversity disappear. The grass spreads out and minimizes just the aspects of habitat heterogeneity that seem so useful in supporting many small mammal species.

I could relate similar stories about Israel's rodents (Rosenzweig and Abramsky, in press), and about nutrient-enrichment experiments which drive plant diversity down (Goldberg and Miller, 1990). But none of these convince me of the hypothesis.

The problem is that the hypothesis assumes habitats are inelastic and pre-defined. But we saw (above) that they are a coevolved property of their biota. Load up a region with species and they define more habitats for themselves.

No places better exemplify the folly of believing that habitat differences are objective than do the fynbos of South Africa and the kwangan (southwestern Australian heath). These plant communities grow on extremely impoverished soil, but are among the world's most speciose (Lamont et al., 1977; Naveh and Whittaker, 1979; Rice and Westoby, 1983). The plant cover looks monotonous, because there are few growth forms (Adamson, 1927). Nevertheless these plants have subdivided time quite finely. Some flower now, some later. The continuum of the year—no more extensive or discrete there than anywhere—has become a cornucopia of distinct habitats.

Why can't the lowland (0–1.5 km) tropics of South America evolve more habitats than the subtropical uplands? What prevents small grassland mammals from subdividing their world as finely as those of the desert? The answer, I believe, is that they don't because they don't need to. Processes of extinction and speciation have set their diversities lower, and they respond by recognizing fewer habitat differences. If natural selection compels species to define more habitats when there are more species, then we cannot say—except at very local scales of space and time—that there are more species because there are more habitats.

Perhaps high productivity is associated with unusual disturbance regimes (both high and low regimes reducing diversity)?—This hypothesis comes directly from Connell (1978), who suggested it for intertidal and subtidal patches. Theory supports it (Levin and Paine, 1974; Paine and Levin, 1981) and experiments confirm it (Lubchenco, 1978; Petraitis et al., 1989; Sousa, 1979), but only for relatively small scale patches. It cannot explain the productivity pattern, because that pattern exists at much larger scales of space and time.

The disturbance pattern depends on a pool of species settling small patches, growing and being removed by local catastrophes. Patches that are quickly disturbed don't have time to collect a full complement from the pool. Patches that are rarely disturbed allow some of the species to overgrow and eliminate others.

We should not be tempted to replace "settlement" with "speciation" and "local competitive exclusion" with "extinction." If we do, we have to explain how the disturbance hypothesis can account for the decrease phase. On an evolutionary time-scale, the lower the rate of extinction-causing disturbances, the more species we expect.

Rosenzweig and Abramsky (in press) discuss many other problems of applying the disturbance hypothesis to the productivity pattern. Now, however, I come to the last hypothesis.

Perhaps each taxon is best suited to a particular productivity and, at higher productivities, more often loses out in competition to other taxa?—We know intertaxonomic competition exists (e.g., Davidson et al., 1984). Ants even appear to reduce mammal diversity along one series of locations forming a productivity gradient (Brown and Davidson, 1977). Since the competitive ability of species often differs along a productivity gradient (Keddy, 1990; Rosenzweig, 1991), why shouldn't that of higher taxa?

In support of this hypothesis, I note that different taxa have their peak diversities over different productivities. Rodents peak in southeastern Arizona, carnivores in eastern Texas. The marine taxa of Haedrich et al. (1980) and of Rex (1981) peak over very different ocean depths. What makes a place remarkably diverse in one taxon does not make it remarkably diverse in another.

However, if the hypothesis of intertaxonomic competition is correct, then some taxa should "peak" at the highest productivities. We have not yet found one that does. Another weakness of this hypothesis? It has no theory to formalize it and enrich its set of predictions. As yet, we cannot place much confidence in it.

I am acutely aware that the hypothesis of intertaxonomic competition may be the best of a bad lot. I also remember that the explanation for tropical gradients—so simple, yet so profound—was not even included in Pianka's (1966) much more elegant list of hypotheses. But at least we can see the true productivity pattern now, and eliminate most of the hypotheses that might have tempted us. Someday I hope we explain it as simply and powerfully as the vastness of the tropics explains the latitudinal gradient.

ACKNOWLEDGMENTS

Thanks to the mammalogists who attended the 1991 meetings at Kansas State University for their careful and valuable comments. Zvika Abramsky has been a constant source of inspiration, noticing the similarity of terrestrial and marine patterns and pushing ahead with the Israel mammal work when I was perplexed and disheartened by our results. Ed Maly brought the Canadian lake data to my attention. David Jablonski encouraged me to dig out the fossil patterns, and Sam Scheiner prodded me into seeing all sides of the controversy about forest diversity. Kasimierz Patalas and Martin Lockley helped me interpret their important papers. Jim Brown, Mike Mares, Peter Meserve and Bruce Patterson all helped with the New World mammal patterns. Dick Braithwaite, Carsten Rahbeck and Avi Shmida were generous in allowing me to use their data. Pat Behling found and gave me the perfect set of global area data for my needs. I am particularly grateful for the hospitality of Warren Porter and the Zoology Department of the University of Wisconsin–Madison. The research was supported by NSF grant BSR-8905728 (to me), Warren Porter's DOE grant DE-FG02-88ER60633 through OHER and a Brittingham Fellowship at the University of Wisconsin.

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Submitted 24 June 1991. Accepted 3 July 1992.