

Bird-Nutrient Lit.

# Species diversity in space and time

**Michael L. Rosenzweig**

Professor  
Department of Ecology and Evolutionary Biology  
University of Arizona

&

Brittingham Fellow  
Department of Zoology  
University of Wisconsin



**CAMBRIDGE**  
UNIVERSITY PRESS

574.524  
R

Published by the Press Syndicate of the University of Cambridge  
The Pitt Building, Trumpington Street, Cambridge CB2 1RP  
40 West 20th Street, New York, NY 10011-4211, USA  
10 Stamford Road, Oakleigh, Melbourne 3166, Australia

© Cambridge University Press 1995

First published 1995

Printed in Great Britain at the University Press, Cambridge

A catalogue record for this book is available from the British Library

Library of Congress cataloguing in publication data

Rosenzweig, Michael L.  
Species diversity in space and time/Michael L. Rosenzweig.  
p. cm.

Includes bibliographical references and index.  
ISBN 0 521 49618 7 (hc). – ISBN 0 521 49952 6 (pb)

1. Species diversity. 2. Biogeography. I. Title.

QH541.15.S64R67 1995

574.5'24-dc20 94-43750 CIP

ISBN 0 521 49618 7 hardback  
0 521 49952 6 paperback

## Chapter 12

# *Energy flow and diversity<sup>1</sup>*

Many ecologists believe that productivity is one of the most pervasive influences on diversity. But, as I completed this book, I realized that I hardly understood that influence. Yes, diversity exhibits spatial patterns that seem related to productivity. And, as you will see, we understand the pattern that occurs at small spatial scales. We even think we understand a part of the larger-scale pattern. Yet, unlike the other spatial patterns, the productivity pattern remains somewhat mysterious. Not that people have ignored it. They have caused a river of ink to flow in its name. We just aren't sure where the river is headed.

We have two patterns to account for. First, when experimental ecologists increase productivity to small patches of plants, plant diversity declines. Second, as productivity rises on a regional scale (c.  $10^6$  km<sup>2</sup>), animal diversity first increases, then it declines.

### **Experimental increase of productivity**

Correlations help us search for patterns. However, patterns may not reflect causes. They may instead reflect phantom correlations, correlations of one of our variables with another variable, a variable we may not even have thought about, let alone measured. That caution applies to no variable more strongly than to productivity since productivity correlates with many other important ecological variables. So, once we find a productivity pattern, we must investigate it further, preferably by experiment.

Proper control of ecological experiments requires a small scale. So all productivity experiments have been done at small scales. Each comes with a ready-made set of species already provided by evolution. And, by design, each produces small patches of super-rich environment that do not exist naturally anywhere nearby. The species that might be able to live in them may live thousands of kilometers away. Or they may not yet exist. How can

<sup>1</sup> Much of this chapter appeared in an earlier edition as Rosenzweig and Abramsky (1993). The preface contains special acknowledgements for it.

snails too, the density of snails is a good inverse index of the time since last disturbance. Yet, algal colonists arrive so rapidly that they almost obliterate the increasing part of the disturbance pattern (Figure 11.7).

You can see that each of these local diversity patterns will follow its local circumstances. Yet we can understand them all by paying attention to the rates at which species enter local patches and to the rates at which they disappear by competition, predation or disturbance.

Recently, Caswell and Cohen (1993) produced a pair of models that join the disturbance pattern to species-area curves. The models depend on a fixed species pool, and are thus not meant to handle evolutionary time as well as space. The world is composed of a large number of patches, all of the same size. Species colonize patches, and patches suffer disturbances thus losing all their species. One model allows no competition. The other assumes that all but one species will go extinct owing to competition if disturbance is long enough delayed.

With or without strong competition, the models produce diversities which rise monotonically as area grows. This work suggests a new way to collect and analyze diversity data: census an increasingly large set of similar patches with a similar disturbance regime, and determine whether the set's diversity grows according to the theory.

On the other hand, the results of the models must not be compared to the species-area curves we already have. Elements crucial to known species-area curves do not appear in these models. In particular, they lack both habitat variability and evolutionary processes (i.e. speciation and global extinction). So, even if the models match real data, we will know that the known curves get their shape from other processes.

In fact, the models differ from known curves in several substantive properties. The models predict convex-upward curves that glide to an asymptote (the species pool). The data show curves that are straight or even concave-upward. The models predict considerable variation (about an order of magnitude) in  $z$ -values depending on disturbance frequency: the higher the disturbance frequency, the steeper the slope. Real  $z$ -values, taken at scales for which disturbance can possibly govern diversity, cluster tightly in the range 0.1–0.2.

But those discrepancies should not cause us to reject the models. They must be tested with new data sets collected with the models especially in mind. We should not re-use sets that incorporate evolutionary events. Nor should we reuse sets in which habitat-absence (rather than disturbance) is the usual reason a species is not found.

diversity not fall? Maybe evolutionary immaturity is all that accounts for the experimental pattern?

Yet, those who do these experiments see a general mechanism at work. Usually, instead of a subset of the plants dying of nitrate burns, or of some other malady brought on by unfamiliar good conditions, the plants that die get overgrown by aggressive competitors.

Tilman (1987) reports the results of systematic experiments to study the effects of nutrient enrichment in various successional stages from new field to woods. Increasing the productivity drives diversity down. In three years, more than 60% of the species disappeared from high nitrogen treatments. He believes 'that nutrient addition makes plots more homogeneous spatially, forcing more species to compete for the same limiting resource.'

Certainly, the natural history survey data taken in the area of Tilman's experiments support his hypothesis (Inouye *et al.*, 1987). The older a field, the more nitrogen and the fewer species it has. Goldberg and Miller (1990) also support Tilman's interpretation.

On the theoretical side, Rosenzweig (1971) and Wollkind (1976) showed that enrichment can destabilize predator-victim interactions. Riebesell (1974) did the same for competition. I still believe that loss of stability most probably accounts for the loss of species in polluted aquatic systems. But I know of no field experiments to test this prediction.

Competitive displacement and community immaturity may combine to explain the experimental pattern in terrestrial plants. Suppose most communities contain a mixture of competitive types. Some are aggressive competitors able to take advantage of richer circumstances, but are badly hurt by suboptimal conditions. And some are subordinate species not badly harmed by poorer conditions and thus dependent on them for their existence. I believe that mixture to be common, and to reflect a common kind of community organization called 'shared preferences' or 'tolerance differences' (Rosenzweig, 1987a, 1991a). The competitively subordinate species tolerate a wider range of habitats.

Natural selection cannot outfit a species for environments that the species never use. So, you would also expect the range of conditions to which the whole set of plants is adapted to reflect the range ordinarily available to them. Hence, when you enrich the system experimentally, you greatly help the aggressors and remove the poorer microenvironments that the subordinates actually depend on.

But if you were to maintain the enrichment for a longer time, say a million years, the plant community's norm would increase. Species would evolve that were able to take even better advantage of the very rich environment you provide. By comparison, today's dominants would be tomorrow's lambs. And diversity might very well rise again.

Maybe you don't agree with that. Maybe you believe that plant biology is too rigid to allow it. Maybe you believe that a rich environment will always be rich, and a poor one always poor. If so, consider this. Using a variety of adaptations, the shrubs growing luxuriantly on Australia's heathlands manage on nutrient concentrations low enough to kill most anything else (Lamont, 1984). Yet, if you supplement their nutrient supply, you do them no favor (Specht, 1981). They do grow faster, but die in as little as half the usual time. Moreover, their seedlings suffer from phosphorus toxicity after fire and usually fail to survive. If they do survive, they are particularly susceptible to attack by root-rotting soil fungi.

A similar combination of interactive forces and immaturity could also produce the loss of species from aquatic systems. Rosenzweig and Schaffer (1978) showed that natural selection, given enough time, would indeed tend to restore the stability of enriched predatory systems.

Consequently, the experimental results now available cast little or no light on patterns at larger scales of time and space. None of these experimental results takes evolution into account, but the evolution of species to take advantage of higher productivity must constitute an important part of the response of a region to higher productivity. Some experiments fail to allow even enough time for succession, although we know how important that can be.

We must not be tempted to extrapolate the results of smaller time scales to larger ones. Huston (1993) provides a worrying example of the results of such extrapolation. It leads – quite erroneously I believe – to the conclusion that intense agricultural use will rarely depress species diversity providing that only free market forces are allowed to control which hectares get cleared and plowed. Try telling that to a conservation officer charged with saving the flora and fauna of Australia's rich wheatbelts.

Before enrichment experiments learn how to compensate for lack of time, their relevance will remain restricted. We should use them solely to understand and predict the short-term consequences of local enrichments. For that purpose, they are ideal.

### The unimodal pattern in regions

Theoreticians and empiricists have long agreed that productivity must affect diversity (e.g. Connell and Orias, 1964; Leigh, 1965; MacArthur and Pianka, 1966; Pianka, 1966; Rosenzweig, 1971; Brown, 1973; Tappan and Loeblich, 1973). But they have disagreed about the mechanism that underlies it. They have even disagreed about the direction of the correlation (Valentine, 1976; Elseth and Baumgardner, 1981). Some – typically those studying aquatic systems or enriched plant systems – found fewer species at higher productivities. Others – especially those studying terrestrial vertebrates – found the opposite.

We now know that within regions about the size of small to medium-sized nations, animal species diversity is often – perhaps usually – a unimodal function of productivity (or some well-accepted index of it like rainfall in arid regions). To remind you of the pattern, here are more examples. Figure 12.1 comes from benthic megafauna (vertebrates and invertebrates) in the North Atlantic. Figure 12.2 provides yet another mammal case, this one from the Gobi Desert of Mongolia. So does Figure 12.3, which tracks

### North Atlantic Megafauna

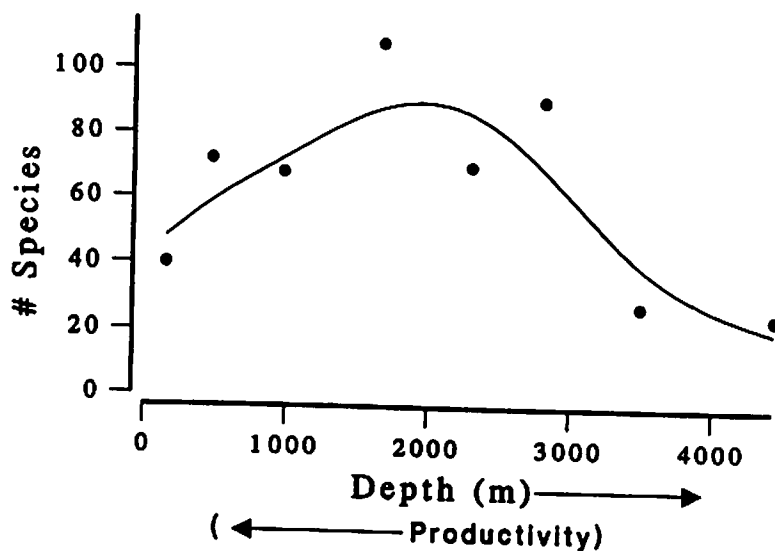


Figure 12.1. Benthic megafauna in the North Atlantic follow the unimodal productivity pattern. Most species are fish, echinoderms or decapod crustacea. Depths are the midrange points of series of samples. Data from Haedrich *et al.* (1980).

### Gobi Desert Rodents

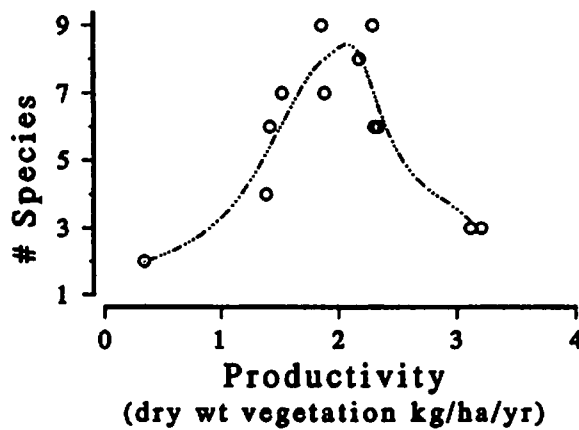


Figure 12.2. Rodents of gravel and rocky plains habitats of the Gobi Desert peak in diversity at intermediate productivities. Konstantin Rogovin supplied the data from Kazantseva (1986) and Rogovin *et al.* (1986). Productivities are averages of data taken from 1978 to 1984. The regression line is lowess.

### African Herbivorous Mammals Larger than 10kg

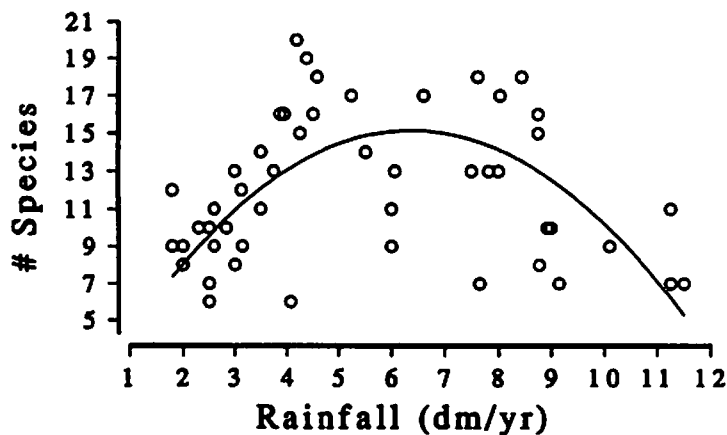


Figure 12.3. Large herbivorous mammal diversity peaks over intermediate rainfall in African ecosystems. Herbivores must weigh at least 10 kg to be included. The systems come from all over Africa. Redrawn from an idea in Western (1991); data supplied by David Western.



the number of species of large herbivorous mammals in a wide variety of African ecosystems.

We can easily see how a unimodal pattern could cause confusion. Scientists reached opposite conclusions about the direction of the relationship because they were looking at opposite ends of the camel. Brown (1975) for example, was looking at the increase phase (over the poor end of the productivity spectrum) (see also Bramlette, 1965; Tappan, 1966; Meserve and Glanz, 1978). Students of eutrophication (e.g. Sawyer, 1966; Whiteside and Harmsworth, 1967; Lipps, 1970; Hessler and Jumars, 1974) usually focused on the rich end (the decrease phase). Take two steps backward, however, and you see the whole hump.

The data of Schoenly *et al.* (1991) allow us a new perspective. It abandons taxonomically based data sets and looks at all species. The intertaxonomic pattern is also unimodal (Figure 12.4). Peak diversity lies in the second trophic level. If species of the first trophic level followed the straight regression line of Figure 4.7, they would be about an order of magnitude more diverse. If they followed the regression slope of Figure 11.2 they would be almost two orders of magnitude more diverse.

### Insect Food Webs

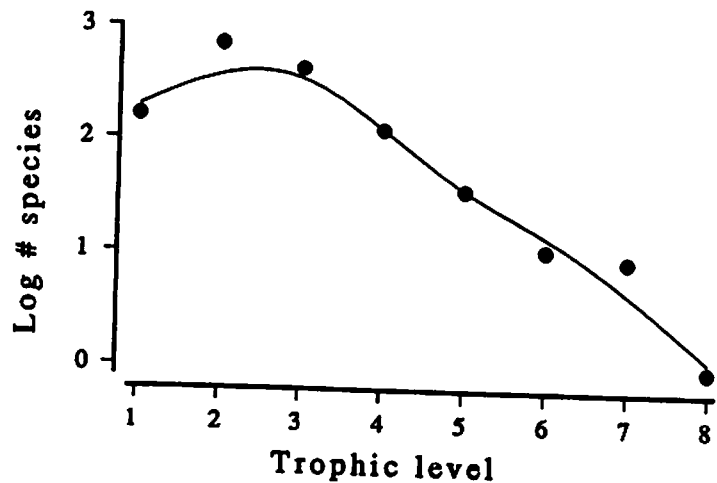


Figure 12.4. Diversity in the first trophic level is less than that of the second. Community food web data of Schoenly *et al.* (1991), but the trend is confirmed by the small number of plant species in the world (relative to insects). Lowess regression.

Perhaps the unimodality is false? Perhaps the one point, from the first trophic level, that produces the unimodality does not reflect the true diversity of primary producers relative to their consumers? After all, Schoenly *et al.* assure us that their animals are much more finely identified than their plants. Many plants and other level 1 species are lumped together. Does that explain the dearth of plant species? I doubt it. Remember – from Chapter 1 – that insects are the Earth's most diverse taxon. They probably have tens of millions of species. Plants have fewer than 250 000 worldwide. So, the diversity of level 1 must be less than that of its consumers. The intertaxonomic productivity pattern is also unimodal.

Knowing what the pattern is, we can begin to progress in explaining it. For convenience, let us address the problem as two separate patterns: the increase phase and the decrease phase.

### *The increase phase*

*As productivity rises from very low to moderate levels, diversity also rises.* That is the increase phase of the productivity-diversity pattern.

An interesting example of this part of the pattern allows us to factor out the effect of time. That is worth doing because until fairly recently, many of the least productive places were covered by glaciers. Thus, it is possible that their low diversity comes from their immaturity.

Hebert and Hann (1986) amassed the diversities of shallow tundra ponds in 11 regions of the Canadian Arctic. These were all glaciated until about 7000 years ago. Assuming that the number of degree days (above 0 °C) provides a reasonable surrogate for productivity, these regions have diversities of microcrustaceans proportional to productivity (Figure 12.5;  $R^2 = 0.54$ ;  $p = 0.006$ ). Are warmer, richer regions also younger? Is it immaterial that they also happen to be warmer and more productive? Is age the real actor here?

Luckily, Hebert and Hann had a comparable data set available from northern Alaska. This area, unlike the Canadian areas, had not been glaciated during Wisconsin times. Yet, it too shows the increase (the three Alaskan points in Figure 12.5 are insufficient for regression, but they come from 251 different ponds and the trend is clear). True, the Alaskan locations have many more species than the Canadian ones. That reveals the effect of age. But the positive relationship between productivity and diversity characterizes them both.

Actually, the increase phase of the relationship troubles no one. Ecologists who have thought about it, consider it to sit on a solid theoretic-

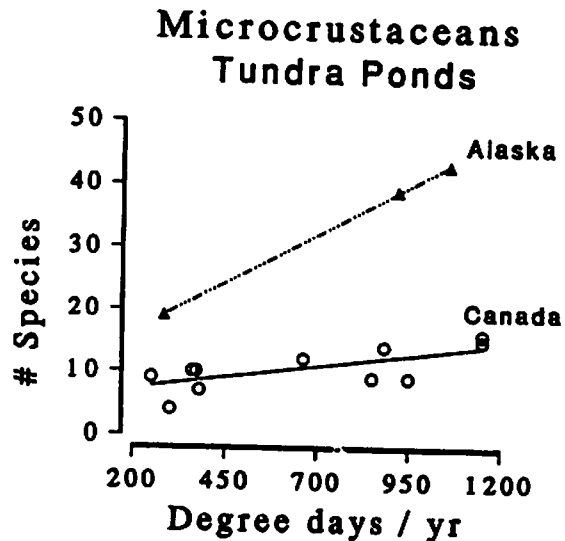


Figure 12.5. Shallow Canadian tundra ponds are only 7000 years old, but both they and their much older counterparts in northern Alaska show the increase phase of the productivity pattern. However, the older system does have more species for a given productivity. Warmth is the surrogate for productivity in these systems. Redrawn from Hebert and Hann (1986). See text for more details.

cal base. A poor environment supplies too meager a resource supply for its would-be rarest species, and they become extinct.

Preston (1962a, b) developed the theory behind this hypothesis. He proposed that the abundances of species in a region fit a distribution called the lognormal (see Chapter 9). The abundance of a species is all its individuals. So, if the area of a region is small, then the sparsest species of the lognormal distribution will have insufficient abundance to survive.

Preston used the metaphor of the 'veil line' to describe the effect of rarity. A small area veils the existence of all the species whose total abundance falls below a critical minimum. The critical minimum is the veil line. Today, we call the veil line, 'the minimum viable population' (see Chapter 6).

Wright *et al.* (1993) have been extending Preston's theory to the variable of productivity. They call it 'species-energy theory'. It notes that the species of an unproductive region will be relatively rare for their abundance rank. So, the region's veil line should occur at a fairly high abundance rank and all lower-ranking species will be veiled (i.e. non-existent).

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 similar chances 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 theory is wrong. In fact, I believe Prestonian theory rightly permeates ecological thinking (see Chapters 2, 3, 8, 9 and 10). It does much more than explain the increase phase of the productivity-diversity pattern. If rarity does not raise extinction rates, then the whole foundation of conservation ecology crumbles. If rarity does not raise extinction rates, then we must reinvent the basic dynamic theories of both island (MacArthur and Wilson, 1963) and continental (Rosenzweig, 1975) diversity. If rarity does not raise extinction rates, then we all have a lot of work to do. We will have to rethink a host of ecological processes and applications we've come to rely on. We generally use Frank Preston's theory the way we use aspirin: often, without much thought, and without credit to its inventor.

But, just as we overuse aspirin, sometimes we overuse Preston. Preston intended his theory to deal with the relationship of diversity to species' abundance distributions. Applying it to the productivity-diversity pattern all by itself may be stretching it near its limit. To do it, we must assume that diversity is entirely governed by the ability of the rarest species to survive accidental extinctions. And we must assume that the contribution of the accidental extinction rate dominates all other facets of extinction and speciation. Perhaps my pointing out those assumptions to you, makes you unsure whether you still believe that more productivity ought always to raise diversity. I hope so, because as you learned in Chapter 2, it doesn't.

Yet, I suspect that Preston's theory, as extended by Wright, explains a good part of the productivity pattern. In fact, at very low productivities, the consequences to the extinction rate of having a tiny population may well dominate all other influences on extinction. Diversity will rise as populations are freed from this constraint. Thus, to me, the decrease phase presents the real puzzle: why, past a certain point, does enhanced productivity tend to reduce the number of species?

### *Hypotheses to explain the decrease phase*

The literature contains nine different hypotheses to explain the decrease phase. Although losers do emerge from the list of hypotheses, I am not sure whether there are any winners. So, I present you all of them.

To maintain discipline and a parallel format, I treat each hypothesis under three subheadings. First I state it briefly. Then I explain why it might be true. Then I evaluate it. Please understand that this format requires me to play devil's advocate on behalf of several hypotheses. That is, although I do not believe them, I begin by arguing for them as well as I can. But, in the evaluations, I write my own opinions and the reasons for them.

#### *1. Environmental heterogeneity*

**HYPOTHESIS:** Under conditions of extreme low productivity, there is not much habitat or resource heterogeneity. The landscape is uniformly barren. An average location will not sustain any species. As productivity rises, the average variety of micronutrient combinations in fertile sites increases. Alternatively, some fertile spots have more light with sparser nutrients while others have less light with richer nutrients. In either case, plant diversity increases and plant physiognomies diversify, allowing animal diversity to increase also.

Past a certain point, more productivity has the opposite effect. It reduces heterogeneity of micronutrient combinations and habitats. Productivity tends to be spread more evenly within and between years, reducing the variety of viable temporal specializations. Diversity declines.

Notice that this hypothesis explains both the increase and decrease phases of the productivity pattern. It does not require low productivity to cause rarity and thus higher extinction rates. So it predicts the entire hump-shaped pattern with no help from any other hypothesis.

**REASONING:** The variety of habitats in space and time underlies much of the specialization that supports diversity (Rosenzweig 1987a). Most ecologists would agree that relatively barren areas offer only a few kinds of habitable times and places. The mean habitat is inhospitable, but some unusually favorable times or places cross the line and support niches. Moderately productive areas have excellent mean habitats. But also, their variance encompasses a wealth of different sorts of exploitable niche opportunities. Very productive areas also have excellent mean habitats. But their variance rarely presents significant challenges to life. A productive

patch that falls to half its mean productivity from one year to the next is still very productive. Similarly, a patch 0.5 km away with half the productivity is still very productive.

Tilman (1982), using micronutrient combinations as the measure of habitat specialization, argues persuasively for this hypothesis. Recently, Tilman (1987) and Tilman and Pacala (1993) have been exploring a similar model. Newman (1973) noted that as nutrients increase, light becomes more and more a problem for competing plants. This sets up a gradient along which Tilman posits a specialty for each plant species. Regions of poor productivity will include little of the whole gradient and, therefore, few of the plant species that specialize along it. Regions of high productivity will also support few of the species because they include little of the gradient. Most of our sites will cause intense competition for light.

Abrams (1988) developed this model formally. He discovered that it could also lead to a monotonic rise in diversity as productivity grows. But, are the assumptions necessary for monotonicity ever be satisfied? Tilman and Pacala (1993) doubt it. Abrams (personal communication) does not. Once the plant pattern appears, a similar animal pattern will evolve. Dozens of studies recognize the importance of plant diversity (in physiology as well as species) to the maintenance of animal diversity.

EVALUATION: Study after study shows the importance of habitat diversity to species coexistence. All such studies favor 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 on the North American rodent peak. Increase the productivity a bit and their desert becomes a semi-arid grassland. We lose the shrubs and the patches that support so much of the desert's diversity. The grass grows out and minimizes just those aspects of habitat heterogeneity that many small mammal species depend on (Rosenzweig, 1977a; Lemen and Rosenzweig, 1978; Brown, et al., 1979; Kotler, 1985; Kotler and Brown, 1985). Both Rosenzweig (1973a) and Whitford et al. (1978) showed experimentally that simplifying the structure of the plant community decreases rodent diversity.

Connell's sand-dwelling rodents also seem to fit. Areas with intermediate productivity have patchy ground cover exploitable both by species usually found in denser cover and by those often found where there is little cover (Rosenzweig et al., 1984; Abramsky et al., 1985; Rosenzweig and Abramsky, 1985, 1986).

However, most of the evidence cited by others in favor of this hypothesis deals with the results of short-term experiments. As I have already pointed out, these results do not bear on patterns present in evolutionarily mature associations.

The heterogeneity hypothesis also leaves us a nagging logical question. Is it tautology? Recall that habitat and resource heterogeneity are co-evolved responses of organisms (Chapter 7). We expect that life will subdivide any particular variance into as many niches as natural selection forces it to. In particular, more species means more selection for finer habitat discrimination.

- That is why birds in Puerto Rican rainforest recognize only two foliage levels while birds in Panamanian rainforest recognize four (Figure 7.7) (MacArthur *et al.*, 1966). That is why birds of southwestern Australian islands have far fewer species for any level of foliage diversity than their mainland counterparts (Figure 7.9). And that is why birds of Caribbean islands use a wider variety of habitats when their island has fewer species (Figure 7.10).
- That is why some of the world's richest floras grow on the impoverished soils of southwestern Australia and South Africa (Figure 7.5).
- That is why there is 'such exuberant biological diversity in (the deep sea), an environment apparently lacking in ... habitat complexity' (Gage and May, 1993).
- That is why similar-sized areas of wet tropical forest in different biological provinces have different diversities of plants, of fish and of vertebrate frugivores (Figure 9.1).
- That is why similar-sized areas of similar environments in Australia usually differ substantially in diversity compared to other continents (Morton, 1993).

Where provincial origination and extinction processes yield many species, life recognizes many habitats. Where they yield few species, life recognizes few habitats.

If species are forced to recognize more habitats when there are more species, then we chase our tails to say that the reason there are so many species is that there are so many habitats. We need an independent model. It must start with a habitat continuum. It must show that speciation and extinction rates vary with productivity in such a way that we finish with more species (and thus more recognized habitats) at intermediate productivity levels.

We cannot start with an effect (habitat diversity). Then, notice that the effect correlates closely with its cause (species diversity). And then conclude that the effect is the cause of the cause.

## 2. Dynamical instability

**HYPOTHESIS:** More productivity reduces dynamical stability. The loss of dynamical stability increases extinction rates, reducing diversity.

**REASONING:** I invented this hypothesis in a theory of eutrophication (Rosenzweig, 1971). Higher productivity reduces the negative feedback of competition within species, and increases the positive feedback that predatory control produces (Rosenzweig, 1977b). There is a net loss of dynamical stability at higher productivities.

Wollkind (1976) extended the theory to three-level food chains. Riebesell (1974) extended it to competition between species.

**EVALUATION:** This hypothesis breaks down when natural selection has enough time to do its job. Rosenzweig and Schaffer (1978) showed that natural selection tends to restore the dynamical stability of enriched systems. That is how some extremely productive biomes like coral reefs and tropical forests can be extraordinarily diverse. Moreover, I cannot explain the intertrophic level pattern with this hypothesis (Figure 12.4). All trophic levels join to produce the dynamics of a food web. We cannot say that the dynamics of a web are stable for consumers but not for their food plants.

Yet, many have reported that diversity does decline after nutrient enrichment. In addition to the plant examples, which I mentioned in connection with the previous hypothesis, there are several aquatic examples (e.g. Swingle, 1946; Yount, 1956; Schindler, 1990). I cannot easily explain all these cases as the result of increasing competition for light, or homogenization of habitat. So perhaps the hypothesis of dynamical instability does apply to some recently enriched environments, especially the aquatic ones like eutrophic lakes. At least the stability hypothesis makes a field-testable prediction that could someday convince us to accept it: enrichment should be accompanied by an increase in oscillatory dynamics and a decline in return times (Pimm, 1982).

## *Changes in ratio of predators to victims*

**HYPOTHESIS:** As productivity increases, predators absorb much more than a proportional share, and reduce the diversity of consumers.



**REASONING:** Predators can absorb most or all of any increase in standing crop caused by higher productivities (Rosenzweig, 1971, 1972). Moreover Oksanen *et al.* (1981, 1992, in press) determined theoretically that increase in productivity adds controlling levels in a food chain. A new higher trophic level should considerably reduce the standing crops of the species beneath it. Case and Bolger (1991) demonstrated that predators of lizards do reduce total populations of all lizard species on islands. Smaller standing crop should produce higher extinction rates and diminished diversity.

**EVALUATION:** Predator-victim diversity ratios are a topic of debate (see Chapter 4). Yet all data do agree in one particular. All data show that more victim species are associated with more predators (Pimm, 1991). This contradicts the prediction of the hypothesis. The hypothesis requires that victim diversities decrease in the presence of more predators.

Even if I did not know about the predator-victim ratios, I would distrust the hypothesis. The theory on which it is based depends on the presence of weak interaction coefficients among predator individuals. Individuals that form dominance hierarchies or steal each other's territories don't fit the theory. But such animals (e.g. Texas carnivores) do exhibit the hump-shaped pattern.

Furthermore, a lot of work has demonstrated that predators can add to the sustainable diversity of their victims. Much of this work consists of incontrovertible field experiments done in all sorts of biomes on various taxa (e.g. Summerhayes, 1941; Paine, 1966; Hay, 1985). More recently, theoretical studies have explained how this can happen as apparent competition or competition for predator-free space (Holt, 1977, 1984; Jeffries and Lawton, 1984).

The predator-victim ratio hypothesis fails.

#### 4. Intertaxonomic competition

**HYPOTHESIS:** Once a critical productivity is reached, a taxon cannot absorb any more. All further increases go to a competing taxon. In fact, the competing taxon takes even more than the increase. It actually reduces the productivity going to the first taxon. So the first taxon declines in diversity.

Notice that this hypothesis claims there is only one relationship between diversity and productivity: The more productivity, the more diversity. The twist is – according to this hypothesis – that higher system productivities sometimes mean lower productivities to some taxa. (The predator-victim

ratio hypothesis shares this twist, but otherwise it is too weak to consider further.)

**REASONING:** Intertaxonomic competition exists. For instance, granivorous rodents do compete with ants (Brown *et al.* 1979a; Davidson *et al.*, 1984). Brown and Davidson (1977) detected a likely suppression of rodent diversity by ants in their east-west productivity transect. Possibly, each type (*bauplan*) of organism competes best at a restricted set of productivities and is largely defeated at others.

**EVALUATION:** Competitive abilities among species often do differ along a richness gradient (Rosenzweig 1987a, 1991a; Keddy, 1990). Why shouldn't the same be true among higher taxa?

Also, taxa differ in the productivities at which their diversities peak, just as you would expect from this hypothesis. Rodents peak in southeastern Arizona, carnivores in eastern Texas. Various marine taxa (Haedrich *et al.*, 1980; Rex, 1981) peak over very different ocean depths. What makes a place remarkably diverse in one taxon does not always make it remarkably diverse in another.

Nevertheless, this hypothesis needs much more work. By definition, it cannot explain the vertical intertaxonomic pattern (Figure 12.4). It also needs a coherent theoretical treatment to formalize it and enrich its set of predictions. More predictions would make it easier to test. One untested prediction: the broader the taxonomic grouping, the weaker the decrease phase.

Finally, some taxa should exist that do not decline at higher productivities. Where are they? As Tilman and Pacala (1993) point out, we know of no group whose diversity rises monotonically with productivity.

### 5. Change in competitive structure

**HYPOTHESIS:** Interference competition prevails at intermediate productivities and adds considerably to the diversity maintainable at them.

Notice that this hypothesis also requires no other to predict the entire hump-shaped pattern.

**REASONING:** Territoriality appears commonly in asymmetrical competitive systems and can help to promote competitive coexistence in them (e.g. Pimm *et al.*, 1985). But, Brown (1971b) showed that territoriality depends

on productivity. Among chipmunks, it first increases and then declines as productivity increases. Brown argues cogently that this pattern makes sense. Productivity should influence territoriality. Poor situations are not worth defending. Rich ones are too costly to defend because they support so many individuals that excluding them would take too much time.

Perhaps species are less diverse in richer places because they cannot therein ameliorate the effects of competition by being territorial. In the terminology of Nicholson (1954), perhaps high productivity forces species from contest competition into scramble competition.

We may be able to extend this reasoning to plants. Perhaps plants in poorer places cannot afford the costs of chemical defense. And perhaps plants in very rich places cannot preserve the areas around themselves for their own seedlings because, if they did, they would encourage too many herbivores.

The plant argument uses herbivory to understand how interference competition could wane at high productivity. The animal argument uses the time cost of active territoriality. Nevertheless, I join them into one hypothesis because they make the same broad prediction: interference competition should peak at intermediate levels of productivity.

**EVALUATION:** This hypothesis has three problems. They stem from the fact that a rich place has plenty of levels of productivity on which to specialize.

- Interference (especially as exemplified by territoriality) is a well-documented phenomenon in some of the Earth's most productive places (e.g. coral reefs and tropical rainforests). Any successful hypothesis concerning interference will have to predict that where productivity is high, interference should decline, but not very much.
- All species in an ecosystem do not experience its productivity to the same extent. In a richer one, some species specialize on wealth while others can also use the sparser times and places that an environment offers. Even in a region of high productivity, species may specialize on moderate habitats, and so escape the pressure to forgo territoriality. A good example is the bee community of the Santa Catalina Mountains (Schaffer *et al.*, 1979). During each day, honeybees forage first, when nectar supplies are most plentiful. Then come bumblebees, and finally carpenter bees. Another case is the system of pond fish in Michigan (Werner and Hall, 1979). There, the near-shore tangle of aquatic vegetation provides the richest

habitat. All three fish species prefer it, but once fish grow past the tiny stages of their life, only one species uses it much. Arizona hummingbirds give us a third example (Pimm *et al.*, 1985). One species lives exclusively in the rich riparian forest along the canyon bottom. The other two also prefer that habitat, but usually forage in poorer woods, arid slopes or higher elevations.

- Species may indeed stake out a range of habitat richnesses for their niche. But, although they may do so by interference, they need not (Brown 1986, 1989a, b). Various sorts of morphological or physiological adaptations can take the place of interference if that gets to be an impractical strategy. But only interference can reduce diversity. Other means of subdividing a habitat-richness axis add to diversity.

For example, some species of desert rodents forage during the poorer months of the year, or in poorer patches of seeds. Others actually require the richer times and places that all prefer. But among heteromyid species, only the largest kangaroo rats use interspecific territoriality to protect their end of the habitat spectrum (the richest) (Frye, 1983; Brown and Munger, 1985). The niches of the others are determined by their position in a trade-off continuum: the more efficiently a rodent deals with food (once found), the less efficiently it travels in space and/or time to find it. (Hibernation – and torpor in general – provides the efficient way of traveling between times of food abundance.) Efficient travelers tend to discover the rich patches first and tend to monopolize them. But, usually because they are larger, efficient travelers are too inefficient at food use to exploit the poorer patches at all (Brown, 1986, 1989a; Kotler and Brown, 1988).

Someone needs to produce a quantitative model predicting the predominance of interference and its effects on diversity. Otherwise, I cannot believe this hypothesis will help us understand the diversity-productivity pattern.

### Time

**HYPOTHESIS:** Richer patches have been around a shorter time than poorer patches. They have not reached equilibrium and are producing new species faster than they are losing them. The decrease phase is temporary.

**REASONING:** Speciation takes time. Considering the upheavals of the Pliocene, many habitats and taxa may not have reached equilibrium. If

the most productive habitats are also the newest or were hardest hit, they should be most depressed below equilibrium.

EVALUATION: I know of no evidence to support the hypothesis. It depends on richer patches being considerably younger than the time it takes evolution to fill them. It also depends on richer patches being considerably younger than poorer patches. Does anyone think this is generally true? Even if it is, are plants younger than their consumers? If not, how does this hypothesis explain Figure 12.4?

The greatest damage to this hypothesis comes from the fossil record. We now know that the unimodal pattern goes back at least to Paleozoic times.

The breakthrough came when Ziegler (1965) noted the good correlation of sediment type and relative ocean depth. The finer the sediment, the deeper the water in which it was deposited. So, sediment type becomes an index of relative productivity. Ziegler and other paleobiologists began to use that correlation to describe ancient environments and their communities.

We now have estimates of invertebrate diversity over depth gradients for several epochs in the Ordovician and the Silurian Periods. All show the hump-shaped pattern. I could find no summary data on diversity in Llandovery time of the Lower Silurian. Yet it, too, shows the pattern (Rosenzweig and Abramsky, 1993).

In Figure 12.6 I plot the pattern in four fossil transects. Were any of these to stand alone, it might not convince you. But the pattern occurs repeatedly. The combined Silurian and Ordovician investigations represent some 75 Myr of fossil history. And each graph incorporates a very large amount of data. For example, each point of the Ludlow series (Watkins, 1979) of six communities (Figure 12.6: early Silurian Period) is the mean diversity per 50 individuals per sample. There are 200 samples and no Ludlow point comprises fewer than 11. The Ordovician bars synthesize 'about 2000 samples collected through about 5 km of strata representing about 200 000 individual identifications' (Lockley, 1983).

How can the time hypothesis explain the pattern's existence and persistence for 75 million years during the Ordovician and Silurian Periods? I mention the time hypothesis, but I also reject it.

## 7. Disturbance

HYPOTHESIS: Productivity itself is not a cause. It is just a correlate of disturbance rate. So, the productivity-diversity pattern is the disturbance-

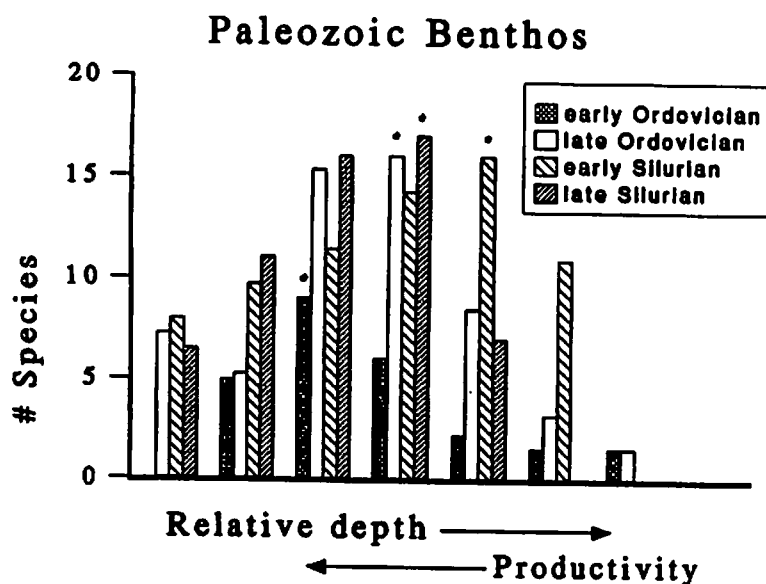


Figure 12.6. Brachiopod-dominated faunas of the Paleozoic Era show the productivity pattern. The stars indicate the peak diversity of each period. Ordovician data from Lockley (1983). Lower Silurian data from Watkins (1979). Upper Silurian data from Hancock *et al.* (1974). For more details, see Rosenzweig and Abramsky (1993).

diversity pattern (Chapters 2, 11). As disturbance rate falls, diversity first rises then falls (Grime, 1973, 1979; Levin and Paine, 1974; Connell, 1978; Lubchenco, 1978; Paine and Levin, 1981; Petraitis *et al.*, 1989). Varying disturbance rates cause the productivity-diversity pattern.

The connection between productivity and disturbance depends on the system. But regardless of the system, there is a strong connection.

- Terrestrial relationship: the higher the productivity, the less frequent the disturbances.
- Marine relationship: the higher the productivity, the more frequent the disturbances.

In a sense, this hypothesis also predicts the entire hump-shaped pattern. But remember that the disturbance hypothesis itself requires two mechanisms: local extinction from disturbance and local extinction from competition. So it is not inherently simpler than others.

REASONING: On land, as rainfall increases, its coefficient of variation certainly does decline. Rainfall, necessary for actual evapotranspiration, helps set productivity (Rosenzweig 1968). Moreover, even in tropical biomes some ecologists believe that the wettest, warmest habitats are the most stable.

In the sea, shallow water allows violent waves to reach down to the bottom and destroy life on it. The deeper the water, the more protected its benthic inhabitants from storms. But shallow water allows more productivity (see Chapter 2; Sanders, 1968; and many others).

The marine paleoecologist sees the same pattern in the rocks. Mikulic and Watkins (1979) for instance, make it clear that the shallow, productive community is most storm-influenced and unstable.

Why use two variables (disturbance and productivity) to do the work of one? Let's keep disturbance – we have experimental proof of its role – and forget about productivity.

EVALUATION: You should suspect part of the reasoning. Few ecologists accept uncritical, undefined statements about stability any more. Few believe they know how to rank biomes, let alone habitats, as to their stability or freedom from disturbance. Take a walk in a Neotropical lowland rainforest. That popping and crashing you will hear all the time is the sound of falling vegetation creating new open spaces. How is that open space so different from a patch of intertidal substrate newly opened by a violent wave?

All right, maybe it is far too soon to be sure that productivity and disturbance correlate well at middle and higher productivities. But there is no question that they do at lower productivities. From the most extreme deserts to semi-arid grasslands to mesic forests, productivity and lack of disturbance surely go together.

However, the disturbance–diversity pattern comes from a well-understood theory that makes several collateral predictions. As diversity grows from extreme deserts to richer places, do those predictions come true? If it turns out that the richest places really do have the lowest frequencies of disturbance, do those collateral predictions fit the data of tropical mammals or trees?

What are the collateral predictions?

- The species found in the least disturbed patches should be a subset of those in the most diverse patches. No species will be restricted to the least disturbed patches.

- Once it does get disturbed, the recuperation history of one of the least disturbed patches should follow a course much like the pattern of the combined patches. It should begin by accumulating species, reach a diversity like that of a patch with intermediate disturbance, and then decline in diversity owing to loss of species already present. In other words, patches with little disturbance should recapitulate in their own histories the entire diversity-disturbance pattern.

The diversity-productivity graphs themselves offer no information to help us decide if they match the collateral predictions. But I know enough the details of the mammal patterns to believe that they do not.

Points with low diversity and high productivity do not contain a small subset of the species from peak diversity points. The species lists from east Texas (high productivity) and from lowland rainforests in tropical Australia (high productivity) contain many species not found at all in peak diversity places. This is glaringly so in Texas: only a few species of the rich, Trans-Pecos rodent fauna also live in east Texas. And in east Texas they make up a small proportion of its low diversities.

The fossil data also do not fit this collateral prediction of the disturbance hypothesis. For instance, Mikulic and Watkins (1979) report that all three species of trilobite that lived in the shallowest community (most productive) of the Upper Silurian, lived nowhere else.

The second collateral prediction also fails, at least for the mammals of northern Arizona. There is no apparent historical pattern. Occasionally, I have seen the most species-rich patches devastated by a predator (such as a cougar). But soon (less than a year later), the same species that were wiped out, recolonized. And no one has ever seen an Arizona short grass patch (of slightly higher productivity, considerably lower diversity) at an 'intermediate stage of history' with lots of the species generally found in mixed desert shrub patches (of highest diversity and lower productivity). An army of students of mammals has sampled so many short grass patches for so many decades that by now someone should have reported such a high diversity assemblage in a short grass patch. Reported one, that is, if they exist. No one has.

The theoretical flaw in the disturbance hypothesis would kill it even without any other problem. The flaw lies in assuming that processes operating on one scale will operate much the same way at all scales. Those who suggest the disturbance hypothesis, forget that its mechanisms operate at very different time scales and very local spatial scales. Species do not evolve to fill



empty patches. They come from a pre-existing local pool, and disperse to empty patches.

Despite this, paleobiologists and marine biologists have appealed to the disturbance relationship for explanations of the patterns they find (e.g. Watkins, 1979; Rex, 1981). But Rex *et al.* (1993) have recently made clear that explanations of larger-scale patterns of diversity should not be sought in disturbance regimes. No one knows if the rate of brief, local disturbances like wave scouring, indicates anything about the sorts of disturbances that drive whole species extinct.

Moreover, even if whole species extinction and local extinction correlate closely, the disturbance hypothesis cannot generate the decrease phase in terrestrial regions. On an evolutionary time scale, the higher the rate of extinction, the fewer the species. So, terrestrial locales with high-productivity and low-disturbance should have the most species. They do not.

In an address to the August, 1994 meeting of the Ecological Society of America, Warren Allmon introduced a most promising suggestion for rescuing the disturbance hypothesis as an explanation for the unimodal productivity-diversity curve. Allmon focused on disturbance's effects on speciation rates. In doing so, he has left the domain of the scouring wave and the wildfire. These he has replaced with the sort of climatological and geological disturbances that fragment gene pools and begin the process of geographical speciation.

Allmon notes that where large-scale disturbances are rare, speciation rates ought to be low. On the other hand, if they are too common, then budding species will be interrupted before they achieve taxonomic independence. It is the intermediate disturbance rate, he concludes, that ought to maximize speciation rates. If so, it is quite possible that diversity will peak over intermediate rates of large-scale disturbance. I hope that Allmon's idea will attract a serious modeling effort over the next several years. But even if it turns out to be likely, it may have nothing to do with the productivity pattern. We know that small-scale disturbances correlate with productivity. However, no one has suggested that large-scale disturbances do. If they do not, then the disturbance pattern – even at large scales – will stand apart from the productivity pattern.

In sum, small-scale disturbances cannot explain the productivity pattern, because the disturbance pattern talked about in textbooks exists at much smaller scales of space and time than the productivity pattern. The disturbance pattern depends on a pool of species settling small patches, growing, and being removed by local catastrophes. Patches that are quickly dis-

turbed 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.

It will take a lot of work before we can replace 'settlement' with 'speciation' and 'local competitive exclusion' with 'extinction'. To succeed, we have to explain how the disturbance hypothesis can account for the decrease phase. On an evolutionary time scale, when extinction-causing disturbances occur at a lower rate, we should always expect more species. The sole hope appears to be that intermediate rates of disturbance may promote the highest rates of speciation and somehow be connected to intermediate productivities.

#### *8. Reduction in the covariance of population densities*

**HYPOTHESIS:** High temporal covariance of population sizes among species leads to higher diversity. As productivity increases, the covariance diminishes. So the decrease phase of the productivity pattern is due to decreasing covariance, not increasing productivity. For example, this covariance would be high if species A tends to have about 185% of its long-term average whenever species B has about 185% of its average; and A tends to have about 30% whenever B has about 30%.

**REASONING:** Population sizes fluctuate. The covariance statistic of this hypothesis summarizes the tendency for different species to experience above average populations simultaneously, and – at other times – to experience below average populations simultaneously.

Density-dependent optimal foraging theory predicts that individuals of competing species should restrict themselves to their special habitat(s) only when they and their competitors (of other species) are similarly common relative to their respective averages (Rosenzweig, 1979, 1987a). When species do restrict themselves to their special habitat(s), they compete minimally. That gives them the best chance to coexist. If their population sizes do have high covariance, then they will usually find themselves similarly common or similarly scarce, and minimizing their competition. On the other hand, when one species is very common and another is very rare, then the common one must use the rare one's special habitat, and they compete intensely (Rosenzweig, 1981; Pimm and Rosenzweig, 1981; Brown and Rosenzweig, 1986). In sum, according to optimal habitat selection, high temporal covariance leads to dissimilar behavior, reduced competition and

lower extinction rates; low covariance to similar behavior, increased competition, and higher extinction rates.

In terrestrial biomes, covariance and productivity probably do correlate negatively (Rosenzweig, 1979). In a truly harsh, unproductive place, some master variable (like water availability in deserts) should govern the fate of all (or most) species. A good year for one is likely to be good for all. Once productivities increase, other, more diverse variables should exert more control, thus reducing covariances.

**EVALUATION:** This mechanism is too restricted. It applies only to unstable environments. It requires species to have true habitat specialties (not shared preferences). And it applies only if individuals cannot sense a patch's quality except by taking resources from it (Brown and Rosenzweig, 1986).

Desert rodents, for example, do not conform to these requirements. They can sense seed quantities in their immediate vicinity (Brown, 1989a) – probably by olfaction. And they do not have true habitat specializations. Some species merely get to the best places first (Brown, 1989a) or are capable of defending them better (Frye, 1983). But all prefer areas with the highest seed abundances. Such a relationship among the niches in a guild is called 'shared preferences' or 'tolerance differences'. Field ecologists discover shared preference relationships more than any other kind of community organization (Rosenzweig, 1991). The hypothesis of covariance reduction can govern none of them.

Another deficiency: the fundamental assumption of this hypothesis has not been tested. No one has good evidence for the connection between productivity and covariance. True, several field experiments do support the isolog models that make the optimal foraging predictions underlying this hypothesis (Pimm *et al.*, 1985; Rosenzweig, 1986; Abramsky *et al.*, 1990, 1991, 1992, 1994). But only theory says that higher covariance leads to lower extinction rates.

I include this hypothesis because I want to emphasize covariance relationships. But the hypothesis may need so much revision that it becomes unrecognizable before it becomes very useful. Nevertheless, I guess we will need to test a better hypothesis based on covariance before we can settle the question of the productivity pattern. The models of Chesson may supply the improvements (Chesson and Huntly, 1988).

## 9. Area

**HYPOTHESIS:** High productivity habitat is scarce compared to intermediate habitat. Small areas harbor few species. The productivity pattern is just the species–area curve on different coordinate axes.

If the productivity of very large patches is distributed with a central tendency (say, normally or log-normally), then this hypothesis also predicts the entire humped pattern. Both rich and poor patches will be relatively scarce and relatively depauperate.

**REASONING:** Like all variables, productivity should have a central tendency. Deviations in each direction should be less and less probable as they depart from the mean. The rest is just the species–area curve in action.

**EVALUATION:** Much suggests that the area hypothesis does not account for the productivity pattern. First, only one productivity can represent the most common habitat. So, if area is the answer, all taxa should peak over productivities similar to it. But they don't. Compared to plants, desert rodents in Israel peak at half the productivity. Compared to carnivores, rodents in Texas peak at about one-tenth the productivity (Owen, 1988).

Second, the area hypothesis cannot apply to USA rodents. They peak in the semi-desert and fall to much lower diversities in grasslands. Who will defend the idea that grasslands are relatively scarce in North America compared to semi-deserts?

Finally, and most distressingly, the productivity–diversity pattern remains in data even after analysts take out the unequal-area effects. Abramsky and Rosenzweig (1984) discovered this in their Israel rodent data set. But there is a second example which is truly spectacular.

Every birdwatcher, every fan of natural history television shows, and certainly every ecologist knows that bird species fairly ooze from the lowland tropics. Nobody has ever found another place that comes close. Who would have guessed that higher productivities depress tropical bird diversities?

Yet, Rahbek (personal communication) showed that the highest productivities are associated with lower diversities. He did it by removing the effect of area. Compared with the less productive higher elevations, the lowlands are depauperate! (As you read the following summary of his findings, keep in mind that elevation is a good inverse index of productivity in the wet tropics.)

Rahbek found that, in the Neotropics, the area of lowland far exceeds that of any other elevation. But, in similar-sized areas, the more productive lowlands have fewer bird species than subtropical elevations. For example, a lowland area of  $10^5$  km<sup>2</sup> has about 526 species, but at subtropical elevations, an area of that size has 855 (Figure 2.4).

The temperate elevation bird species-area curve is like the lowland's: a  $10^5$  km<sup>2</sup> region at temperate elevation has 461 species. The high elevation curve is the lowest of the four: its  $10^5$  km<sup>2</sup> region has only 176 species. Thus, from high elevations down to subtropical elevations, the more productivity, the more bird diversity.

But the even greater productivity at low elevations does not add to diversity. It decreases diversity. We see so many more birds in the lowlands merely because the lowlands are so extensive. The tropics would be even richer if we could make them somewhat less productive for several million years.

The literature points out that ecologists often confound area and productivity (Wright, 1983; Turner *et al.*, 1987). But some have tried to separate them (Abramsky and Rosenzweig 1984; Owen 1988; Turner *et al.*, 1988). Rahbek's work teaches us how astonishing and rewarding it is to disentangle them.

### The global scale

So far I have avoided the big picture. What is the productivity-diversity relationship amongst biogeographical provinces? Is it monotonically positive? I am not sure.

Wright (1983), realizing that a barren hectare has no species, extended the concept of species-area studies. He created a new variable by multiplying area times productivity. The result is gratifying. Diversity does increase with this variable. Of that there is no doubt.

Doesn't that monotonic relationship contradict the unimodal relationship? No. Wright *et al.* (1993) agree that the pattern at the regional scale is unimodal. The monotonic pattern appears at the global scale.

But Wright's new variable is not productivity. It is a combination of productivity and area. Because of the combination, Wright relinquishes the ability to determine the influence of area and productivity separately.

I am no reductionist, but if a mechanism exists which tells us that one of two variables has a separate and powerful influence on diversity, then I pre-

r to treat it separately. Area exerts such an influence. It influences allopatric speciation rates and extinction rates. Through that influence, it sets up diversity differences among biogeographic provinces. Through that influence, it produces latitudinal gradients. And, through its influence on extinction rates, it produces patterns of island diversity.

Now you can appreciate why I am unsure of the global relationship of productivity and diversity. Diversity does increase monotonically with Wright's variable. But that result could easily stem from its area component rather than its energy flow component. On a global scale the area component may be so important as to overwhelm and mask the influence of productivity.

### Prospects

The connection between productivity and diversity – long thought to be intimate – remains murky. All the nine hypotheses to explain the decrease phase have noteworthy weaknesses. Not a single hypothesis successfully explains the pattern (yet).

The two most attractive hypotheses are covariance of population densities and intertaxonomic competition. However, at present, the covariance hypothesis relies entirely on theory. And even those theories need fuller treatment.

The other strong hypothesis, intertaxonomic competition, fits most of the facts we have. It predicts great variety from taxon to taxon in the position of the peak diversity on the productivity axis. Certainly, we see this. But the hypothesis of intertaxonomic competition lacks a mechanistic model and is therefore poor in predictions.

The intertaxon hypothesis needs adequate explanation. Why should taxa have optima along a productivity gradient? When that optimum is exceeded, why can't they at least defend the share of the productivity that they have already acquired? And which are the taxa succeeding at the high-productivities? And why are primary producers less diverse than their consumers?

Maybe there will never be a hypothesis that fully explains all known instances of the decline phase. Maybe that hypothesis is a fantasy. Suppose, instead, that the increase phase comes from the relationship of productivity and population size (as most believe it does). Suppose that once a system passes a critical point, further increases in population size bring insignifi-

cant returns in reduced extinction rates. Then, beyond that point, the diversity of any taxon may be little more than a balloon waiting for a pin. Any number of environmental changes associated with increased productivity would deflate the diversity.

But do not surrender hope yet. Just because the matter is still perplexing, do not conclude that the unimodal curve has no unified explanation. It fits too many animal taxa. It fits in too many habitats and on too many continents. Something so pervasive ought to have a simple explanation.

*Div*

My friend  
the first 12  
Where is t  
forever do  
for that? I  
Although

As Art l  
zles and s  
their puzz  
another bo  
squares wi  
Or they or  
they have  
supplies the

System b  
pour the u  
puzzle or g  
building ru  
judge. I wo  
in the worl

But may  
who like to  
answer for  
Besides, eco  
puzzles or ji

First, we  
nomenon at  
with respect