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Michael L. Rosenzweig
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Chapter 1

The road ahead

How many rooms in Noah's Ark?

Noah, the first appointed steward of life on Earth, would have been proud of Robert Burns' passionate concern for a humble harvest mouse. But even Burns, living as he did in the Age of Enlightenment, could not have suspected the ominous truth of his poem's last line. We have indeed done dreary things to our splendid world. And we are coming to understand the future terrible cost of our greed and our selfishness.

I believe that the more reasonable our fears, the more potent our voice will be. So this book explores what we know about the science of species diversity.

Steward or not, no one could spend much time working on the mechanics of diversity without being fascinated by it for its own sake. You are about to invest some of your own time in such an effort, so I guess you share that fascination with me. Welcome.

What is it that concerns us? Just how miraculous (or, if you prefer, incredible) is it that Noah got all the world's species onto one boat?

A famous story circulates among biologists about an encounter between two famous intellectual foes. J.B.S. Haldane – a genius of evolutionary biology and a renowned public atheist – was seated next to the Archbishop of Canterbury at one of those formal British dinners known for their civility and sparkling conversation. God knows who put them together like that.

The archbishop broke the ice with a question. What do your studies tell you, professor, about the nature of the Creator?

Haldane's answer has echoed for decades: 'He must have an inordinate fondness for beetles.'

Indeed, generations of biologists have kept an unlovely little secret. The answer to the question, 'How many species?', is essentially the answer to the question, 'How many insect species?' There are but 4004 species of mammals and about 9020 species of birds. There are 18 818 fish species (Nelson, 1984). Roughly 255 000 species belong to the great plant taxon Embryobionta (bryophytes to angiosperms) (Parker, 1982). And even the most ardent champion of fungi (Hawksworth, 1991) proposes that we will one day know of 1.6 million fungus species. (We now know fewer than 70 000.) But there are probably tens of millions of insect species. And a very large fraction of these are beetles.

Stork (1988), relying on data of Collins, divides the 1.82 million species named by the beginning of 1988 into a pie chart. At the time, insects comprised about 57% of all named species. Beetles comprised 25%. But, as Stork points out, even those percentages don't do justice to the dominance of insects on planet Earth. Most non-insects have probably been discovered and described. Most insects never will be.

In the late 1970s, entomologists began to use knockdown insecticides to collect insects from the canopy of tropical rainforests. Previously, we had thought this layer of the forest to be rich, but we had no way to take reasonably inclusive samples in it. The knockdown methods use a fan to spray insecticide up into the low canopy, or sideways within a layer of the canopy. Or else they use the exhaust of a motor to fog it up to the very top. The insects die and fall into collecting devices (Stork, 1988).

Using the knockdown method, Erwin (1982) electrified the ecological world with his estimate of just how many insects do live in the tropical rainforest. Working in the Neotropics, Erwin fogged 19 individuals of a leguminous tree, *Luehea seemannii*, at different seasons. He collected 9000 beetles belonging to more than 1200 beetle species. Let us pause briefly to emphasize that number. The rest of Erwin's estimate extrapolates from it, perhaps accurately, perhaps not. But that number is data: 1200 species of beetle from only 19 trees of one species. And, as Stork (1988) points out, Erwin presents no evidence that his trees were running out of beetle species for him to find. Even more work might have doubled, tripled or done who-knows-what to the figure of 1200. But it could not have reduced that number. That's 1200 species of beetle from only 19 trees of one species.

Moreover, we believe such numbers may be ordinary. Stork (1988) reports 2800 species of arthropod from the canopies of ten trees belonging to five species in the Bornean rainforest. Kitching (personal communication) sampled the canopies of smaller, liana-free trees of Australia's tropical Green Mountains; he found 465 beetle species among 2238 individuals.

Now come the extrapolations. Erwin estimates that 13.5% of those beetles – about 162 species – live only on *Luehea seemannii*. Roughly 50 000

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species of tree live in tropical rainforests around the world. So, if *Luehea seemannii* represents an average tropical tree, there must be about 8.1 million beetle species specializing on single species of tree.

Erwin now adds beetles that live on more than one tree species. He believes there are about 2.7 million of them. No one thinks that number will long stand as research information accumulates. Nevertheless, it is as good as any other estimate just now, and Erwin repeated it as recently as a carefully prepared symposium talk to the Sixth International Congress of Ecology (Manchester, August 1994). Thus he estimates about 10.8 million species of canopy beetles.

Now Erwin guesses that such beetles represent about 40% of all tropical arthropod species. This figure may be the most debatable in the string of estimates. Stork says that in Borneo, they make up only 22.9% – less in temperate forests. Yet, Erwin's figure has some merit. Stork's pie chart listed beetles at 25% of species and all insects at 57%. That is 25/57 or 44% of insects. Beetles constitute 36% or 37% of all arthropods in the chart. So Erwin may be close to the mark. In fact, the biggest potential error I can see might lead Erwin to an underestimate of diversity!

If beetles are 40% of tropical arthropod species, then about 27 million arthropod species live in the tropics. Add to that the estimated 3 million temperate species. Then about 30 million arthropod species live in the world today.

Most of the serious problems in Erwin's estimate seem to me to err on the side of caution. By supposing that two thirds of beetle species live in the canopy, Erwin may have produced an estimate that is too small by 10 million. Stork actually guesses the truth may be closer to a 50–50 split, i.e. about the same number of species live in each of the two layers. Then of course, we are talking about 40 million arthropod species. Remember, too, that Erwin shows us no reason to believe that *Luehea seemannii* was running out of beetles when he stopped sampling.

What could make Erwin's estimate too high? Suppose *Luehea seemannii* has an unusually large set of insect specialists. Suppose the average tropical tree has only 10 specialized insects to contribute to the total. Then the proper estimate of global arthropod diversity would drop below 10 million.

So we have to admit we cannot yet be sure how many species live in the world. Not even about the order of magnitude. Yet, 2 million are already in the bag. And even 100 million may not be unrealistic. You can read more about this controversy if it fascinates you (e.g. Gaston, 1991;

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Hodkinson and Casson, 1991; Hammond, 1992; May, 1990). But Erwin contributed greatly by bringing it up in the first place. It's really not so important if better estimates show that his estimate of 30 million is off by a factor of five. Noah may have needed to know the exact truth, but the rest of us will simply have to admit, with Stork, that there are more insects than we can keep track of in all the world's museums. And that's assuming we have found them all, named them and properly deposited specimens of them in at least one collection.

One day soon, however, we shall know the order of magnitude – and probably even a significant digit – for the number of living species. Erwin has shown us a way to get those, and his way suggests others.

The structure of this book

Patterns

Although we ecologists cannot yet say how many species inhabit the Earth, we have found various regularities about diversity. These patterns are too common for anyone to say they are accidents. They occur repeatedly in different taxa, on different continents and in different geological eras.

Because the patterns happen again and again, we believe that knowable mechanical processes must control the diversity of species. In fact, by studying the patterns closely, we've made considerable progress in understanding some aspects of this control.

In Chapters 2–4, I am going to lay out some of the best known patterns of species diversity. I cannot cover all diversity patterns, but I want you to see some that I consider fundamental and others that appear often in current journals. We can describe some of these patterns very well. For instance, the latitudinal gradient – the decrease in diversity as we move from the Equator to the poles – recurs in all sorts of taxa and has been a feature of diversity for more than 100 million years (Myr.).

But we are much less sure about other patterns. For instance, how does diversity behave as ecosystem energy flow varies? Many believe diversity and energy flow are directly proportional. But others believe they are inversely proportional. Recently, a lot of evidence has appeared that suggests they may be both: directly proportional over low flow rates and inversely proportional over high rates (Rosenzweig and Abramsky, 1993).

The species–area curve is the pattern longest known to science. The larger the area studied, the more species you find in it. But we shall discover that this pattern consists of four different patterns. Each has its own scale of space and time. But they will grade into one another as we begin to understand how they come to exist.

Patterns of diversity with time fall along a scale axis that runs from one year to hundreds of millions of years. Nine orders of magnitude! In Chapter 3, I shall treat time patterns in scale order, from longest to shortest.

Chapter 4 treats patterns that you may never have considered in the context of a diversity book. They are dimensionless, involving regularities of diversity not directly connected to space or time. For example, the higher the trophic level, the fewer the species that use it. These patterns are among the least well defined and most controversial in existence.

In this book, I do not discuss the diversity of microorganisms at all. From the point of view of diversity, they are probably the most poorly known of taxa. Perhaps their diversity shows many patterns, but I am unaware of them.

Processes

We find out how many species there are by counting them somehow. That is not a statement to be tested, but to be implemented. Similarly, we can say that the species got there by speciating or immigrating. And that they are lost by extinction. The rates at which speciation, immigration and extinction operate, now and in the past, determine the diversity of species. Any satisfactory explanation of diversity must be rooted in those rates. Chapters 5 and 6 describe the basic processes that add to or subtract from diversity.

But, I do not intend Chapters 5 and 6 to be a textbook on either speciation or extinction. Others have written those. Instead, I intend them as a summary of certain features of these processes, features that you need to have handy in Chapters 8–12. That is when we get down to the business of explaining some of the patterns we saw in Chapters 2–4.

Explanations

I tried to make the explanations of the rest of the book both theoretical and empirical. No doubt this combination has the ultimate power to convince us of scientific reality. Nevertheless, I could not always achieve it.

When only theory is available, I present it. If the theory is a true piece of deductive logic – and not just a guess – then theory in advance of data has the power to help us collect and use data efficiently.

The reverse of this coin? Data are treacherous when offered in support of explanations free of theory. Do not trust such explanations, no matter how much data seems to support them. Without the theory, it is too easy to confuse scales and to be unaware of what variables need to be measured. For example, you will see that theory claims disturbance has a qualitatively different effect on diversity at different scales of space and time. Yet people unabashedly offer data in support of '*the* disturbance hypothesis', whether or not their data come from the same scales as the theory they cite. Because of this, I avoid explanations based solely on data.

You may now flip through Chapters 7–12 expecting the worst – a text dense with equations and subscripts. You will not find it.

When I was a graduate student, my mentor Robert MacArthur rejected a model I worked up because it was too complex. His advice? Don't try to build everything you know into a model. Make it as simple as you can. Find the intensive variables – the ones that really make the system behave. Join them into the simplest of formal structures. Say only what you know about them. Then what you learn will be robust. If you can reach a conclusion from the signs of a few first or second derivatives, you won't have to wonder whether linearity or additivity is responsible for your result. What you have not included cannot be responsible.

Both Levins (1966) and Slobodkin (1965) offer similar sage advice, and we should listen to them. Levins tells us that precision has a cost. Precise models need to be dense with coefficients and their complex relationships. As a result, they make predictions that apply in only very limited circumstances. Or else, some of the relationships get modeled erroneously but the errors hide in the model's thicket of equations. Then the model never makes valid predictions. Slobodkin, on the other hand, warns us not even to seek such precision. In the real ecological world so full of noise and change and chaos, what good would a coefficient with four significant digits do? If we did an experiment and found the second, third and fourth digit wrong, would we reject the principles underlying the theory?

Like all of us, MacArthur did not always follow his own rules. In one case, the result (limiting similarity) was quicksand that trapped the energies of community ecologists for more than ten years and nearly killed the subdiscipline. Maybe MacArthur was teaching us the hard lesson: even he couldn't get away with an over complex model.

Ecological systems do seem thick, however. It may take decades to pare a problem down to its core. Meanwhile, restricted theory is better than none. And theory that comes from the circuits of a microchip will do for a start. At least it sometimes tells you what might be going on. When I cannot find better theory to write about, I do resort to such theories in this book (and in my own research). A prime example is the pioneering computer work done by Pimm and Lawton that attempts to explain food web patterns as the outcome of dynamical stability filters (Chapter 11). Nevertheless, you should always remember that such simulation theories – not the more general theories – are the ones that need expansion and improvement.

Unpacking. That's what general theories do need (Rosenzweig, 1991a). Unpacking means partly decomposing intensive variables to make them easier to measure. It also can mean building specific equations to fit specific instances. Unpacking prepares theories for testing or for specific use. A wildlife manager charged with setting bag limits for a pheasant population needs a detailed equation for its population dynamics. It will look very different from an equation for algal blooms, although both flow from the same general theory. Too few of us appreciate the strategy of unpacking; examples of it rarely occur in the literature (or this book).

The guidelines for the explanation chapters are easy to summarize. Use theory and data to test explanations whenever possible. Make the theory as general and robust as it can be. Avoid explanations based only on data and lacking any theoretical framework.

In Chapters 7–12, we'll not always succeed in explaining the patterns of Chapters 2–4. But often we will. And the very existence of so many patterns tells us that diversity is a predictable variable, susceptible to scientific analysis. We must try to discover scientific explanations for as many diversity patterns as we can.

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Chapter 2

Patterns in space

The job of this chapter is to present some spatial diversity patterns. It is not to judge them or explain them. That part of my agenda comes much later in the book, i.e. Chapters 7, 8, 9 and 12. So read this chapter (and the next two also) as if it were merely an attempt to define what it is that needs explaining.

Species–area curves

You will find more species if you sample a larger area. That rule has more evidence to support it than any other about species diversity. Ecologists noticed it before any other diversity pattern. Williams (1964) credits H. C. Watson with its discovery in 1859 (Figure 2.1). Dony (1963) credits him with the discovery in 1835. I have also seen de Candolle cited as its originator a few years before 1859.

But, as Williams (1943) pointed out, it is not one pattern. Williams detected three. There are actually four:

1. Species–area curves among tiny pieces of single biotas.
2. Species–area curves among larger pieces of single biotas.
3. Species–area curves among islands of one archipelago.
4. Species–area curves among areas that have had separate evolutionary histories.

Williams did not distinguish between the second and third patterns. Preston (1962a, b) did. Despite that, Williams led his generation (and most of ours) in recognizing that different processes are responsible for the different curves. I shall describe those processes in Chapters 8 and 9. In fact, to explain the first and fourth patterns I need merely to reiterate Williams' position about them.

But in this chapter I simply want to present the patterns themselves. I

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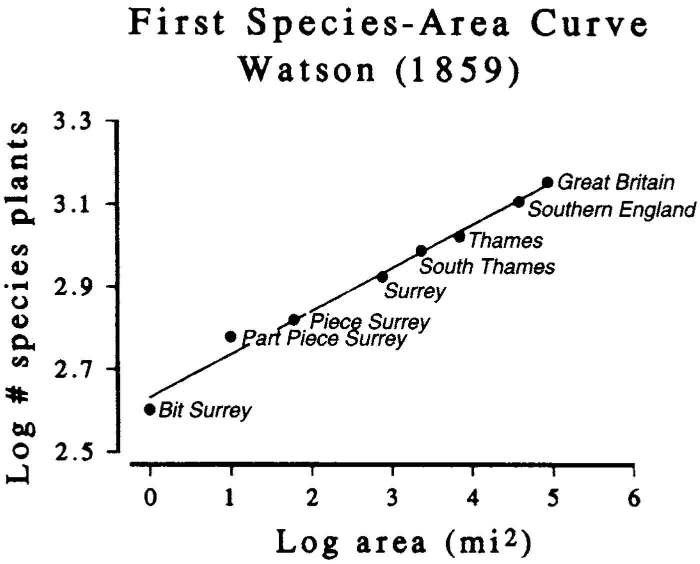

Figure 2.1. This plant species–area curve begins with a bit of Britain's richest county, Surrey, and then builds up to the whole island. It is the world's oldest known empirical example of an ecological pattern.

begin with the two intermediate scale patterns that Williams lumped together. They may already be familiar to you. Then I will describe the smallest and the largest patterns, 1 and 4.

Pattern 2 – among large pieces of a biota

Imagine you know every plant species living on Great Britain and exactly where it lives. Such a degree of comprehensive knowledge comes close to describing what British botanists and plant ecologists know collectively about their flora. The botanical societies of the British Isles work continually to refine their knowledge of plant distribution in that country.

Having the benefit of that knowledge, you now divide Britain into ten equal-area segments. Each will have fewer plant species than the entire island. You write down their diversities, perhaps reducing them statistically to a mean and variance.

You repeat the procedure on areas one-tenth as large as before, that is, on areas each 0.01 as large as the entire island. Probably, you do not use all such areas, but sample them in some justifiable way. Again you note your results.

Now you sample areas 0.001 the size of Great Britain. You keep reducing area one order of magnitude at a time until you begin to worry that the area is too small to house enough individuals for an adequate sample. When you reach that point, you stop and plot your data.

The *x*-axis is area. The *y*-axis is the number (or mean number) of species. The result is a species–area scattergram. To make it a species–area curve, you apply some reasonable statistical technique, like regression, to fit a line through the points.

Using data in Dony (1963), I plotted the actual species–area curve for the plants of all the British isles (Figure 2.2). These data begin with the county of Hertfordshire. Curves beginning with other counties such as Surrey (Figure 2.1) differ in their exact slopes. The richer the county, the more gentle its slope. But they do not differ fundamentally. They all show that if area increases, so does diversity.

In determining species–area curves, you must remember to keep your sub-plots contiguous when you group them to measure the diversity of larger areas. This is called the nested design. If you do not keep them contiguous, but amass them from scattered subplots, the result will have a steeper slope. Figure 2.3 presents an example of this effect from the classic work of Gleason, (1922). The species surveyed are plants in 240 m^2 of

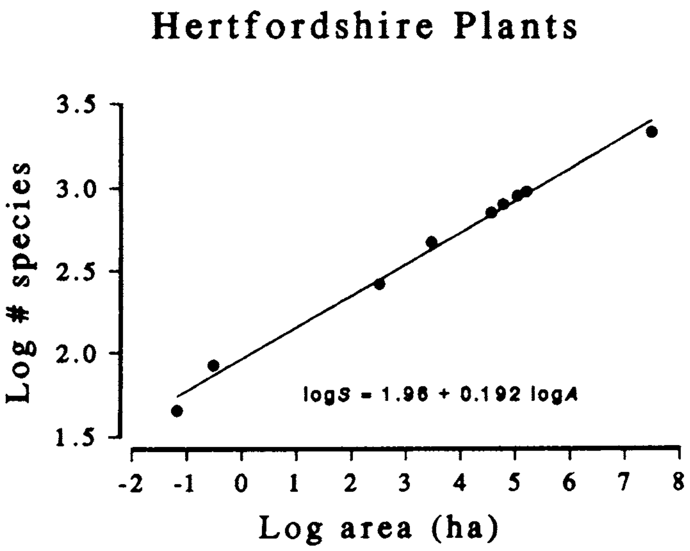

Figure 2.2. A second species–area curve for British plants. This one centers on a county that is not as rich as Surrey. Thus its slope is higher than that of Figure 2.1. Data from Dony (1963).