Why do larger areas have more species? What makes diversity so high near the Equator? Has the number of species grown during the past 600 million years? Does habitat diversity support species diversity, or is it the other way around? What reduces diversity in ecologically productive places? At what scales of space and time do diversity patterns hold? Do the mechanisms that produce them vary with scale?

Species diversity in space and time examines these questions and many others, the author employing both theory and data in his search for answers. Perhaps surprisingly, many of the questions have reasonably likely answers. By identifying these, attention can be turned towards life's many, still unexplained diversity patterns.

As evolutionary ecologists race to understand biodiversity before it is too late, this book will help set the agenda for diversity research into the next century.

Species diversity in space and time

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DEDICATION

To the memory of my teacher,

ROBERT H. MACARTHUR

Hic situs est Phaëton
currus auriga paterni
Quem si non tenuit
magnis tamen excidit ausis.
Ovid

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Preface

People love a good dinosaur story. Surely, after all these years, the ecological question of the number of species ought to qualify as a dinosaur. Yet, no one has ever taken the trouble to write up the glory days of species diversity work, the era of the 1960s and 1970s.

It was a time of great excitement, of elegant theories and huge promise. Modern graduate students must be curious about it. Having played a small role in it myself, I decided to have a go at it. At least, I thought, I won't have to nag my graduate students to read **that** primary literature anymore; I'll give them a little map of it.

I'm not sure when I realized the dinosaur was still alive. There had been a stirring here and there as I poked over the old bones and fitted a few together into an occasional new sub-assembly. But then I heard a roaring. As if attracted by an improved portrait of its progenitors, a living being reared up and spat challenges. By the time I finished this book, the dinosaur was breathing honest fire. At first, only I could hear it; after you read the book, I hope you can too.

Having a living dinosaur to contend with, I had to change my original plan for the book. What I had envisioned as a six-month sabbatical diversion, became a four-year obsession. The book took on a combination of duties.

- Its first function – no, its primary function – remains to tell today's students the story of species diversity in the voices that so delighted ecology in the 1960s and 1970s. Since I have students uppermost in my mind, I mention things, define things and explain things that established ecologists take for granted. I hope those of you who do not require discussion of such basic ideas as negative feedback will forgive me for taking the time to go over them in a book on species diversity.
- Its second is to bring out some things that have been locked up in the data all along, things that help us understand the diversity patterns around us.
- Its third points out the reasons for the successes of a quarter century ago, and thus encourages new students to emulate the kind

of thinking and analysis that led to them. Here again, I beg the indulgence of established ecologists.

- Its fourth is to present some novel analyses. These practically insisted to me that I do them when, to make text figures, I was loading old data into a modern, flexible computer graphics program (all credit to AXUM by Trimetrix, Seattle, Washington).

Thus, the book runs the gamut from history to textbook to monograph. Most of the work is not mine and not new, but some is both.

I will devote some of the text itself to the third function of the book – how to do diversity work. Look for it especially in the first and last chapters. However, I do want to mention five of the book's novelties here. That way you may be especially alert and critical when you notice them.

1. I have tried to combine scales of space and time. The most important consequence of that is the work on the species–area curve. From already published data, I was able to discern a set of nested relationships that carry this curve from scales of a hectare (and less) to those of the whole biosphere.
2. Until working on this book, I thought that Frank Preston's canonical log-normal analyses of species abundances gave us a solid understanding of species–area curves. Now, I believe that Preston's work explains only a fraction of what we see in nature. By the time you finish Chapter 9, I hope you agree with me that Preston just opened the door.
3. Looking at large spatio-temporal scales brought out a surprising conclusion. At the province-wide scale, the scale of evolutionary time, habitats are not causes, but effects. The more species, the more habitats. I've tried especially hard to make the reasons for that proposition clear. I think I did so because I myself was surprised by it and wanted to gain more confidence in it.
4. I also believe that area's effects at large scales are strong enough to cause latitudinal gradients, and I do not hedge in saying so. That does not mean they act alone in all cases. In fact, I suspect that variation in average productivity from latitude to latitude is another important part of the story. But I do not have enough evidence for that conclusion.
5. Wherever possible, I tried to investigate diversity with data from the fossil record. These data constitute a prime source of tests for our hypotheses, but neontological ecologists keep themselves too

> distant from them. You will notice that there is no chapter headed 'Information from Paleobiology.' If there were, you might skip it. Besides, that would not make my point. We need to learn about, understand and integrate the information that comes from fossils. We must use it side by side with modern data to help form our hypotheses and test them.

Like most scientists, I write with difficulty or even pain. Audubon apparently was like the rest of us. He wrote the following gem to fellow ornithologist, J. Bachman, in 1834 (quoted by Alice Ford, 1957, *The Bird Biographies of John James Audubon*, Macmillan, NY, pp. vii, viii):

> God...save you the trouble of ever publishing books on natural science... I would rather go without a shirt...through the whole of the Florida swamps in mosquito time than labor as I have...with the pen.

Today, however, we know that writing, at least science writing, is partly a skill. And skills can be improved. The pain can be reduced.

If you have read anything I wrote more than a few years ago, you will notice a marked change in my style. My writing talent still lies at the abysmal end of the scale, but I did deliberately change my style. It may startle you. It may even repel you. It will sound – if I have learned my lessons – offhand, conversational, light and unstudied. You may marvel at my gall in simply dictating a first draft and than abandoning it to the printer.

The paragraphs are shorter. The sentences are shorter.

And the sentences sometimes start with 'but'. Paragraphs, too.

You will rarely find the passive voice. Short, common, even coarse Germanic verbs abound at the expense of more delicate, refined Romance verbs.

Except for the verb 'to be'. My masters have taught me to hate that verb and to view it as an enemy of comprehension.

Though you may disapprove, you will understand what I write with less trouble than before. This book presents enough difficulties. I did not want to make it even harder to understand by using standard, 19th century, scientific, Prusso-Victorian prose. You would not have been amused.

In addition to hoping that you will get excited about the science in this book, I hope you will enjoy reading it. We enjoy doing science; why shouldn't we enjoy reading it? Reading about the work we love ought not be an unpleasant chore. If you want to write in simple prose yourself, you can.

Get a copy of a standard modern style book. I use Flesch (1974) and Gowers (1977) and Bernstein (1971). Many computer-based style-checking programs use these authorities too.

But be warned. Writing more clearly takes hard work. The more effortless it seems, the more effort it took. It all depends on whether you have something you want to say. If you do, you'll care to work hard to get it across.

Here's another warning. Clear writing brings a grave danger: **People may begin to understand you!** Then they will probably disagree with you. For example, if I have done my job, you will probably not agree with everything I wrote in this book. I am prepared for that. Not happy, but resigned. Science works that way. I'll give you ten years to change your mind. But then, I may have changed mine.

Meanwhile, I've signed the book. So, you know just where to take any disagreements. Fuzzing up my conclusions in hedge words would obfuscate them. Hedges are for hiding things. I want to be exposed. I want you to argue about and improve my conclusions. I don't want you to wonder what they are.

Papers about species diversity – particularly most of those from the 1980s and 1990s – rarely reach conclusions. They perpetuate controversies. They list as many published hypotheses as they can find, and generally conclude with a call for more research. Hang on, folks! Do you believe that science boils down to a continual poll on an ever-lengthening questionnaire? I have tried to include various sides of controversies if I believe they should still be mined. But there's no sense perpetuating old, well-investigated controversies when we've plenty of new ones. There's plenty of reason to call for more research without insisting we've learned nothing so far.

Besides, why would anybody want to give us more support if we never reach any conclusions? Published papers count as end products only in academia, not the real world. The real world wants conclusions from us, even if they are provisional. Nevertheless, I feel certain the book will be criticized for omitting some hypotheses. I just hope that few are ones I am ignorant of.

I honestly do believe the study of species diversity overflows with results. Not trivial ones, either. We must learn to admit it. Our science has produced fundamental conclusions that bear on great issues of environmental quality and conservation. Please don't think that if we admit it, the world will decide our work is done, and cut us off. On the contrary, it will say hurrah and onward!

Yet, 'life speaks with a voice ... that brings you answers to the questions you continually ask of it (Adams, 1985, p. 98).' Ecological research, in particular, takes patience. Consider the long, multi-laboratory investigations that this book summarizes. They bear witness that good ecology takes a long time. Lots of clues suggest that ecologists know that. For one thing, they say it a lot. Also, they establish long-term ecological research programs. Nevertheless, we ecologists can be terribly faddish.

A typical fad seems to follow a five to ten year course. First, someone comes up with a novel and attractive way to organize a variety of research projects. That someone may be a theoretician, as in the case of optimal foraging. Or the someone may be an empiricist, as in plant–animal interactions. The idea smolders for a year or two and then bursts into flame. Proposals get written, and a few get funded. The fire becomes a conflagration. Almost nothing else gets talked about. Projects generate some data and statistical analyses. Then it is over. We go on to the next hot question and pretend either that the old one got settled, or failed to help us enough.

I have seen that scenario in action many times during the past three decades. For instance, ten years ago, plant–animal interactions got declared passé. Yes. And that, despite the potential invigoration of a stimulating paper by one of its originators (Rhoades, 1985). I guess everyone had expected all the original hypotheses to be either perfectly right or totally wrong. Of course, the initial results disappointed them. And then they showed their real interest in the question by abandoning it at the first sign of scientific reality.

Optimal foraging fared no better. Here is a fundamental research program (Mitchell and Valone, 1990) originally suggested by no less than Charles Elton (1927). It is linking up behavior, natural selection and ecology. Yet, its critics, taking no time to understand its mathematical substance, and confusing 'optimal' with 'perfect', consider it dead because ... Well, I really don't know why they think it is dead. Students of optimality know that 'constraints' prevent perfect outcomes in the real world. But 'constraints' are not foreign to optimality theory. They form one of its central features. Optimalists know that, work with it, and have produced some of the most exciting ecology of the 1980s by sticking to their rusty old guns. I depend heavily on their results in Chapter 7.

Yes, ecology really does take a long time to do. Discerning the patterns takes a long time. Testing hypotheses takes a long time. And going through the process repeatedly takes a long time. But if the question is weighty, like 'How many species should there be?', the time will be well spent. And if it is not, perhaps we should just ignore it in the first place.

I wish I could start the acknowledgements now. If I could, I would begin by thanking my teacher, the late Robert H. MacArthur. This book is an extension of his work. That's the meaning of the dedication: 'Here lies Phaeton, driver of his father's chariot. If he did not handle it, at least he fell in a great enterprise.' This book is *MacArthur's Chariot*. If it were a novel, that's what I would have called it.

Two friends, respected reviewers of the manuscript, wondered about the dedication and my obvious admiration for the work that Robert MacArthur did. I am sorry I made them uncomfortable, but I have not diluted my praise. He earned the praise. And I believe I have earned the right to praise him. I am his student, for one thing, and I come from a culture in which students praise their teachers. In addition, I am hardly the apostle type. When it needed it, I have criticized his work (Schroder and Rosenzweig, 1975). And I did it when others were scraping and bowing. MacArthur set the course for much of what good ecologists still do, and the time has come to admit it.

But MacArthur knew that he was part of a cooperating army, and I do not want to leave you with the impression that we should all have retired when he stopped working. Most of the work reported in this book came after his death. In particular, many scientists helped me in my efforts. Quite a few let me use their valuable data. These include Ian Abbott, Sara and Peter Bretsky, Richard Cowling, Bill Mitchell, Jim Owen, Kasimir Patalas, Carsten Rahbek, Konstantin Rogovin, Jeffery A. Smallwood, Max Specht, Elizabeth Sandlin and David Western. Paul A. Johnson, Laurie Oksanen, Tom Nudds, Wayte Thomas, Bruce Walsh and Tom Whitham showed me crucial unpublished works and let me incorporate them.

The work with Colin Clark was done especially for the book, and I was lost before he showed me the way. Phil Rutter took a valuable day and spent it giving me a field seminar on the American Chestnut. Ian Abbott and Norm McKenzie guided my wanderings in Western Australia and saw to it – though it was mid-winter – that I learned something about that special corner of a spectacular continent. Verne Grant helped me get the polyploid data for Chapters 2 and 11. Bill Heed discussed some of the recent papers on Hawaiian *Drosophila* with me. Peter Yodzis and John Moore led me to understand and appreciate their views of food webs. Greg Adler sorted through his work on birds of tropical archipelagos and gave me an unbiased, informed opinion on which species are endemics. Bert Leigh rescued me from some of my mistakes about tropical plant productivity. Rich Strauss gave me a copy of a digitization program he had written, and

taught me how to use it. Rob Robichaux tutored me in the fundamentals of how plant cells respond to variation in light regimes; I hope my rendition in Chapter 7 does not embarrass him. Suggestions from Bob Baker, Ted Fleming, Paul Hebert, Len Milich, Jane Lubchenco, Bob Ricklefs, Bill Schaffer, Don Thomson, Larry Venable, Geraat Vermeij and Pat Webber all added immensely to the book. Michael Canning helped with technical support.

Three hapless groups of guinea pigs (two at Arizona and one at Wisconsin) suffered through trial runs of the course that tested material for this book. One even had to beta-test a flawed preliminary version. They were brave and mostly uncomplaining. I hope their experiences had a positive side.

But Carole Rosenzweig had more to complain about than anyone else. Oy vey, it's not always a joy being married to a zealot. I'll try to find ways to make it up.

Others who suffered include my coauthors on several hibernating papers: Zvika Abramsky, Dick Braithwaite, Goggy Davidowitz, Wade Leitner, Marc Mangel, Debby Rosko, Gareth Russell, Elizabeth Sandlin, Moshe Shahak, Susan Wethington. Please excuse me. I have always been too single-minded.

Stuart Pimm deserves some of the credit for the very existence of this book. Talk about single-minded! After I edited his first book, he spent eight years telling me that now it was my turn to write one. OK, already.

The friends who did me the signal honor of actually reading and commenting on the manuscript have my sincerest gratitude. I know they aren't likely to have the stomach to reread the book and see how much I valued and used their advice. But they were the key. I could not have completed the project without their help and encouragement. Ian Abbott, Zvika Abramsky, Eric Charnov, Andy Cohen, Alan Crowden, Mike Kaspari, Mark Lomolino, Stuart Pimm, Art Shapiro, Larry Slobodkin and Yaron Ziv, I love you all. You straightened me up with deep and fair criticism. You picked my nits. You bucked me up when I felt I'd failed. I tried my best to learn from what you said. Please forgive my obstinacy and pity my denseness.

Mrs Jane Bulleid did an extraordinary job editing the ms. for Cambridge University Press. She was quick, and unbelievably perceptive. And she brought her knowledge of the biology to help me correct some of my mistakes. The ones that remain are just more examples of my obstinacy.

Chapter 12 and some of Chapter 2 was written for this book, but also contributed to Schluter and Ricklefs (1993) with the understanding that it

would appear here. I thank the editors for their willingness to follow that plan and for the great work they themselves accomplished in their own book. For a similar courtesy, I also thank the *Journal of Mammalogy*, in particular, Bob Baker, Mike Mares and Jim Brown. A preview of part of Chapters 7 and 9 appeared in their pages (Rosenzweig, 1992).

Owing to a production oversight, the first printing of Schluter and Ricklefs (1993) did not contain its acknowledgements section. Here are mine and Zvika Abramsky's (they will also appear in future reprintings of Schluter and Ricklefs):

> We thank Bob Ricklefs, Dolph Schluter and David Wright for their careful and valuable comments. David Jablonski encouraged us to dig out the fossil patterns, and Martin Lockley helped us interpret his important paper. 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 us to use their data.

NSF grant BSR-8905728, a Brittingham Fellowship in zoology at the University of Wisconsin–Madison, and Warren Porter's DOE grant DE-FG02-88ER60633 thru OHER supported the research and writing. I am particularly grateful for the sabbatical hospitality of Warren Porter and the Zoology Department of the University of Wisconsin–Madison.

To a mouse

On turning her up in her nest with the plough, November 1785

1
Wee, sleekit, cowrin, tim'rous beastie
O, what a panic's in thy breastie!
Thou need na start awa sae hasty,
Wi' bickering brattle!
I wad be laith to rin an' chase thee,
Wi' murd'ring pattle!

2
I'm truly sorry man's dominion,
Has broken nature's social union,
An' justifies that ill opinion,
Which makes thee startle
At me, thy poor, earth-born companion,
An' fellow-mortal!

3
I doubt na, whiles, but thou may thieve;
What then? poor beastie, thou maun live!
A daimen icker in a thrave
'S a sma' request;
I'll get a blessin' wi' the lave,
An' never miss't!

4
Thy wee bit housie, too, in ruin!
It's silly wa's the win's are strewin!
An' naething, now, to big a new ane,
O' foggage green!
An' bleak December's winds ensuin,
Baith snell an' keen!

5
Thou saw the fields laid bare an' waste,
An' weary winter comin fast,
An' cozie here, beneath the blast,
Thou thought to dwell —
Till crash! the cruel coulter past
Out thro' thy cell.

6
That wee bit heap o' leaves an' stibble,
Has cost thee many a weary nibble!
Now thou's turn'd out for a' thy trouble,
But house or hald,
To thole the winter's sleety dribble,
An' cranreuch cauld!

7
But Mousie, thou art no thy lane,
In proving foresight may be vain;
The best-laid schemes o' mice an' men
Gang aft agley,
An' lea'e us nought but grief an' pain
For promis'd joy!

8
Still thou art blest, compar'd wi' me:
The present only toucheth thee:
But och! I backward cast my e'e,
On prospects drear,
An' forward, tho' I canna see,
I guess an' fear!

Robert Burns

Glossary: *agley:* askew; *bicker:* move with a rapidly repeated noise; *brattle:* noisy rush; *coulter:* plow; *cranreuch:* hoarfrost; *daimen:* occasional: *foggage:* pasture; *icker:* ear of grain; *lave:* remainder; *maun:* must; *pattle:* spade; *snell:* fast; *thole:* endure; *thrave:* bundle; *whiles:* at times.

The scottish spelling and pronunciation I lae'e to thee.