



Gary G. Mittelbach  
& Brian J. McGill

# COMMUNITY ECOLOGY

SECOND EDITION

## **Community Ecology**



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# Community Ecology

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*Second edition*

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# Preface to 2nd Edition

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The first edition of this book was published in 2012 and since that time there have been major advancements in the field of community ecology. Many of these advances are centered on the ever-expanding knowledge of how local and regional processes interact to shape ecological communities, as well as the growing recognition that ecological and evolutionary processes are inexorably linked in structuring communities on both short and long time scales. Our goal in producing this second edition was to highlight these and other exciting new developments in the study of community ecology (e.g., trait-based analyses, modern coexistence theory). In addition, we have worked hard to incorporate the many suggestions from instructors and students who used the first edition of *Community Ecology* in their courses and who have generously provided us with their feedback. Finally, up-to-date coverage of the literature was central to the success of the first edition. In this edition, we have done our best to update all the topics covered in the first edition. Even the most foundational topics in ecology (e.g., population regulation) continue to see advancements in both ideas, data and synthesis.

I (Mittelbach) imagine that writing the second edition of a book is a little like childbirth—you have to let the pain of the first experience wear off before thinking about doing it again. The biggest factor for me in minimizing the pain and making the experience profoundly rewarding was having Brian McGill join in writing this second edition. And for me (McGill) being asked to be involved in a book that Gary had already done so well on his own was a bit intimidating, but also a very exciting opportunity. We bring different approaches and expertise to the study of community ecology, but

share a common love for this area of ecology that straddles the boundary between populations and ecosystems, and that focuses squarely on questions related to the generation, maintenance, distribution, and preservation of Earth's biodiversity. Michael Rosenzweig (Brian's PhD advisor and Gary's friend) once wrote that "I am not ashamed to be a puzzle solver". Neither are we! Together, we hope that this second edition both highlights the "puzzles" that abound in the study of ecological communities and the ways that ecologists have marshalled theory, experiments, and observations to solve many of ecology's puzzles, while (of course) generating new ones.

The field of scientific publishing continues to change at a rapid pace and a major change affecting the second edition of *Community Ecology* was the acquisition of Sinauer Associates (first edition publisher) by Oxford University Press. The wisdom and good-natured advice of Andy Sinauer and Ian Sherman (Oxford Press), both with years of publishing experience under their belts, made the transition as smooth as possible and resulted in a book that we can all be proud of. We hope that you, the readers, find it interesting and useful, and we welcome your feedback. Another change in publishing has been the increasing use of online supplements to provide a more dynamic interaction than a book can provide. We are excited to incorporate a website that has dynamic versions of several of the mathematical models and associated figures described in this book. Each model allows the viewer to change parameters and observe how the model outcomes change. To access a model use the URLs found in the figure legend, or visit the website <http://communityecologybook.org>



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# Preface to 1st Edition

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The community is... the hierarchical level where the basic characteristics of life—its diversity, complexity and historical nature—are perhaps most daunting and challenging.

**Michel Loreau, 2010: 50**

For communities... the task of choosing which topics to emphasize and which to elide [omit]... is necessarily quirky.

**Robert M. May et al., 2007: 111**

Well those drifter's days are past me now  
I've got so much more to think about  
Deadlines and commitments  
What to leave in, what to leave out

**Bob Seger, Against the Wind**

“What to leave in, what to leave out”? Much of writing well about any subject comes down to this simple question. (I sometimes think much of life comes down to this simple question.) But, as Robert May notes, the task of choosing which topics to emphasize in community ecology is “necessarily quirky.” Our discipline is broad and there is no clear roadmap. The organizational path I have chosen for this book is the one that works best for me when teaching this subject to graduate students. I begin with an exploration of patterns of biodiversity—that is, how does the diversity of life vary across space and time? Documenting and understanding spatial and temporal patterns of biodiversity are key components of community ecology, and recent advances in remote sensing, GIS mapping, and spatial analysis allow ecologists to examine these patterns as never before. Next, with species disappearing from the Earth today at a rate unprecedented since the extinction of the dinosaurs, what are the consequences of species loss to the functioning of communities and ecosystems? This question drives the very active research area of biodiversity and ecosystem functioning discussed in Chapter 2.

With the patterns of biodiversity at local and regional scales firmly in mind and with an appreci-

ation for the potential consequences of species loss, I next shift gears to focus on what I call the “nitty-gritty” of community ecology: population regulation and species interactions, including predation, competition, mutualism, and facilitation. The goal here is to understand in some detail the mechanics of species interactions by focusing on consumers and resources in modules of a few interacting species. From these simple building blocks we can assemble more complex ecological networks, such as food webs and mutualistic networks, which involves exploring the importance of indirect effects, trophic cascades, top-down and bottom-up regulation, alternative stable states, diversity–stability relationships, and much more. In the section on spatial ecology, I focus on the processes that link populations and communities across space (metapopulations and metacommunities) and on the consequences of these local and regional links for species diversity.

The interplay between local and regional processes is a prominent theme throughout the book. Likewise, the interplay between ecology and evolution—what is termed “eco-evolutionary dynamics” or, more broadly, evolutionary community ecology—is an important new area of research. I explore



evolutionary community ecology, along with the impacts of variable environments on species interactions, in the book's final section on changing environments and changing species. Applied aspects of community ecology (e.g., resource management and harvesting, invasive species, diseases and parasites, and community restoration) are treated throughout the book as natural extensions of basic theoretical and empirical work. The emphasis, however, is on the basic science. Theoretical concepts are developed using simple equations, with an emphasis on the graphical presentation of ideas.

This is a book for graduate students, advanced undergraduates, and researchers seeking a broad coverage of ecological concepts at the community level. As a textbook for advanced courses in ecology, it is not meant to replace reading and discussing the primary literature. Rather, this book is designed to give students a common background in the principles of community ecology at a conceptually advanced level. At Michigan State University, our graduate community ecology course draws students from many departments (zoology, plant biology, fisheries and wildlife, micro-biology, computer science, entomology, and more) and students come into the course with vastly different exposures to ecology. I hope this book helps students from varied academic backgrounds fill in the gaps in their ecological understanding, approach a new topic more easily, and find an entry point into the primary literature. I'd be doubly pleased if it can do the same for practicing ecologists.

When teaching community ecology, I try to show students how seemingly differently ideas in ecology have developed over time and are linked together. This is important and hopefully useful to students who are just beginning to sink their teeth deeply into the study of ecology. At least, I believe it is useful. An early reviewer of this book wrote, "It is obvious that Mittelbach has a deep understanding and respect for the literature." I take this as a great compliment. We do, after all, stand on the shoulders of giants, and it's important to acknowledge where ideas come from. Moreover, an appreciation for the historical development of ideas and for how concepts are linked together helps deter us from recycling old ideas under new guises. However, another early reviewer suggested that students today aren't all

that interested in the history of ideas and that a modern textbook on community ecology should focus on what's new, particularly on how community ecology can inform and guide conservation biology and the preservation of biodiversity. I appreciate this advice as well. I have worked to include cutting edge ideas and to provide case studies from the most recent literature, along with some of the classics. Hopefully, the balance between old and new contained herein is one that works. I recognize, however, that more could be done to illuminate the links between community ecology and conservation biology. Perhaps someone else will take up this call.

Finally, I want to say a few words about the use of mathematical models and theory in this book. Robert May (2010: viii) wrote that "mathematics is ultimately no more, although no less, than a way of thinking clearly." May also pointed out that one of the most celebrated theories in all of biology, Darwin's theory of evolution by natural selection, is a verbal theory. In most cases, however, the ability to express an idea mathematically makes crystal clear the assumptions and processes that underlie an explanation. I have used mathematical models here as a way to "think more clearly" about ecological processes and the theories put forth to explain them. The mathematical models in this book are simple, heuristic tools that, combined with graphical analyses, can help guide our thinking. Readers with limited mathematical skills should not be anxious when they see equations. I am a mathematical lightweight myself, and if I can follow the models presented here, so can you. On the other hand, readers with a strong background in mathematics and modeling will quickly recognize that I have stuck to the very basics and that much more sophisticated mathematical treatments of these topics abound. I have tried to point the way to these treatments in the references cited.

This book is a labor of love that has stretched out for over five years. I always knew that the ecological literature was vast, but I never truly appreciated its scale until I started this project. OMG! It's humbling to spend weeks reviewing the literature on a topic, only to stumble across a key paper later (and purely by accident). I know that I have missed much. I apologize in advance to those scientists whose excellent work I passed by (or simply missed in my

ignorance) in favor of studies that were better known to me. Please don't be shy in telling me what I missed.

The first ecology textbook I purchased as an undergraduate in the early 1970s (at the hardcover price of \$7.00!) was Larry Slobodkin's *Growth and Regulation of Animal Populations*. In his preface to this marvelous little book, Slobodkin wrote, "Every reader will find some material in this book that appears trivially obvious to him. I doubt,

however, that all of it will appear obvious to any one person or that any two readers will be in agreement as to which parts are obvious. Bear with me when I repeat, in a naïve-sounding way, things you already know" (Slobodkin 1961: page v). Ditto.

**Gary G. Mittelbach**  
*March, 2012*



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# Acknowledgments to 2nd Edition

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I once read an interview with a professional bull rider. The interviewer asked, “How do you get ready to ride the bull?” To which the rider replied, “You’re never really ready, it just becomes your turn.” This simple answer applies to many things—you put the wheels in motion and then you see what happens. Producing the second edition of *Community Ecology* was like that for me. The first step was to ask Andy Sinauer if he would be interested in publishing a second edition and he said “YES” (thankfully). I owe Andy a great debt for his encouragement and support with the first edition of *Community Ecology* and with this edition as well, even though Sinauer Publishing became part of Oxford University Press just as we were getting rolling and Andy has now retired. At Oxford Press, Ian Sherman and Bethany Kershaw were instrumental in guiding us through the production process and in smoothing the transition from Sinauer to Oxford. We gratefully acknowledge their always-cheerful help and support.

For the second edition, I wanted to enlist a co-author as I felt there were many aspects of community ecology where I lacked expertise. I also hoped to find someone interested in carrying the book forward after I retired. Brian McGill was my first choice, hands down. Fortunately, he agreed, jumping

in with both feet, even though he was busy writing his own book on macroecology and doing a million other things. Writing this book with Brian was my great pleasure and the product is much richer and broader in scope because of his efforts. Thank you, Brian, for your friendship, your smarts, and for your deep commitment to the field of ecology.

I thank all those who used the first edition of *Community Ecology* in their classes and who sent me their comments and feedback, especially Saara DeWalt, Kyle Harms, Bob Holt, Craig Osenberg, Todd Palmer, Rob Pringle, and others who I know I am forgetting. To every graduate student who has thanked me for writing a book that helped them study for their comprehensive exams, thank you—your kind words often made my day. As always, I am grateful to my colleagues at KBS/MSU for reading chapters and sharing ideas, especially Jen Lau and the Lau Lab, Chris Klausmeir and Elena Litchman, and their post-docs and students, and to my own graduate students, especially Pat Hanly. Doug Schemske has been a wonderful friend and colleague at MSU, and his unseen hand is on many parts of this second edition.

Finally, I thank my family and especially my wife Kay, for everything.

**Gary G. Mittelbach**

I am extremely grateful to Gary for inviting me to be involved in the 2nd edition of *Community Ecology*. I have been teaching a graduate community ecology class using the 1st edition, and it has been one of my all-time favorite academic books. Not only because community ecology is one of my favorite topics, but because it was so well executed. Even though there were a lot of good reasons to say no (there always are for writing a book), the opportunity to contribute in some small ways to a book that was starting already from such a strong, elevated position was way too good an opportunity to pass up. So was the opportunity to work again with Gary who has been a wonderful mix of mentor, colleague, and friend all the way back to my postdoc days. It has been more fun than I can describe to bounce ideas about the state of community ecology around with Gary.

I would second Gary's appreciation for the partnership with Ian Sherman and Bethany Kershaw at Oxford University Press. This is the second of what I hope will soon be three books for me with Ian. He has a wonderful way of humanizing the increasingly corporate world of publishing. I am also very grateful to two locations where I did a lot of my writing. The Monteverde Institute provided a wonderful place to write while on sabbatical (my "office" was a rocking chair on a porch in front of the library looking out across a tropical rain forest). The Orono Public Library has always been welcoming, even when I have ducked over there many hundreds of afternoons to find a quiet place for focused work. The University of Maine Library has also been ace at tracking down obscure references for me. Libraries and librarians are just plain awesome, and they don't get the appreciation they deserve!

I could not begin to list all of the colleagues that have taught me so much about community ecology through our conversations and co-authored papers, but thank you all. Finally, a great debt of gratitude to my wife, Sarah, and two sons, Eli and Jasper, for just smiling and saying "that's nice" when I told them I had started working on two books simultaneously. Living with an author is not always easy!

**Brian J. McGill**

We are very grateful to Mark McPeck who generously shared with us computer code from his book *Evolutionary Community Ecology*, allowing us to add a website with dynamic models and figures to this second edition of *Community Ecology*.

Finally, Gary and Brian would both like to dedicate this book to Michael Rosenzweig. Mike was Brian's PhD adviser, and Gary's friend and colleague. Mike recently retired and over his five decades of work, he has had a broad and deep impact on community ecology. The Rosenzweig–MacArthur predator–prey equation covered in Chapter 5 was co-invented by him. He has also done important work on optimal choice (especially habitat choice), biodiversity measurement, the species–area relationship and the latitudinal diversity gradient (Chapter 2), the interface of ecology and macroevolution (Chapter 15), and founded two key journals in the field of evolutionary ecology. He is also a wonderful teacher. It is hard to have a conversation with Mike without learning something new about science and how scientists think. Mike is also a wonderful human being and a generous scientist. Community ecology will be less rich without him, but we both wish Mike a happy retirement.

**Gary G. Mittelbach & Brian J. McGill**

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# Acknowledgments to 1st Edition

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I have had the privilege of teaching a graduate course in population and community ecology at Michigan State University for 25 years. At some point it occurred to me that I should take what I have learned from teaching this course and put it in a book. No doubt the thought of leaving something behind drives many an author to write a book, for as Peter Atkins notes, textbooks capture a mode of thinking. I have focused on that part of ecology that I find most exciting—community ecology. It was only after I was well into the writing that I realized how woefully ignorant I was about my chosen field. I still am ignorant, but less so now. Writing this book has made me a better student of ecology and a better teacher. I will count myself lucky if it helps others in the same way.

I am fortunate to have had five excellent co-instructors in our “Pop and Com” course at MSU over the years: Don Hall, Katherine Gross, Doug Schemske, Elena Litchman, and Kyle Edwards. I thank you all for helping make teaching a fun and rewarding experience. Thanks also to our students (500+ and counting). You listened and challenged, and I hope you will recognize your many contributions in these pages.

Special thanks to the many people who read and commented on early drafts of chapters: Peter Abrams, Andrea Bowling, Stephen Burton, Peter Chesson, Ryan Chisholm, Kristy Deiner, Jim Estes, Emily Grman, Jim Grover, Sally Hacker, Patrick Hanly, Allen Hurlbert, Sonia Kéfi, Jen Lau, Mathew Leibold, Jonathan Levine, Nancy McIntyre, Brian McGill, Mark McPeck, Carlos Melián, Sabrina Russo, Dov Sax, Oz Schmitz, Jon Shurin, Chris Steiner, Steve Stephenson, Katie Suding, Casey terHorst, Mark Vellend, Tim Wootton, and Justin

Wright. I owe a particularly large debt to Peter Abrams, who piloted an early draft of this book in his graduate course at the University of Toronto and who provided many insightful comments in his usual, no-holds-barred style.

Interactions with Doug Schemske, Kaustuv Roy, Howard Cornell, Jay Sobel, David Currie, Brad Hawkins, and Mark McPeck have been instrumental in helping me think about broad-scale patterns of biodiversity. Likewise, conversations with Kevin Gross, Armand Kirus, Chris Klausmeier, Kevin Lafferty, Jonathan Levine, Ed McCauley, Craig Osenberg, Josh Tewksbury, Earl Werner, and the “2010–2011 cohort” of postdocs at the National Center for Ecological Analysis and Synthesis (NCEAS) had a significant impact on the book. Thanks to my former graduate students for so many things and to my current graduate students for putting up with an advisor far too preoccupied with writing a book. Thanks also to Colin Kremer and Mark Mittelbach for their mathematical help. I gratefully acknowledge colleagues and staff at the Kellogg Biological Station for many years of support and friendship. I don’t dare start naming names now, because there are too many people to thank. You know who you are and you know why you make KBS such a special place and that’s enough. How was I ever so lucky to land here and somehow make it stick for a career?

This book has had a long gestation. When I first approached Andy Sinauer with a book proposal, my one request was that he not put time constraints on me, because I knew this would take awhile (and, secretly, I questioned whether I could pull it off at all). Andy graciously agreed, and he and the staff at Sinauer have been extraordinarily encouraging and

helpful in every step of the processes. In particular, I thank my terrific editors, Carol Wigg and Norma Sims Roche, as well as art and production director Chris Small. I appreciate that Michigan State University granted me sabbatical leaves in 2001–2002 and 2010–2011, the first of which helped inspire this book; the second allowed me to finish it (almost).

Large parts of both sabbaticals were spent at the National Center for Ecological Analysis and Synthesis (NCEAS), a center funded by the National Science Foundation, the University of California at Santa Barbara, and the State of California. NCEAS provided the ideal environment for thinking and

writing. This book would never have happened without its support. I am particularly grateful to Jim Reichman, Ed McCauley, Stephanie Hampton, and the wonderful NCEAS staff for their friendship and support. In spring 2011, Kay and I spent a short but magical time at EAWAG research institute on the shores of Lake Lucerne, Switzerland, where I worked on the final chapters of this book. I thank Ole Seehausen, Carlos Melián, and the scientists and staff at EAWAG Kastenienbaum for their hospitality and for making our brief stay productive and memorable.

I have enjoyed writing this book. My fond hope is that you enjoy reading it and will find it useful.

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# Contents

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<b>1 Community ecology's roots</b>	<b>1</b>
What is a community?	1
The ecological niche	3
Whither competition theory?	6
New directions	7
<hr/>	
<b>Part I The Big Picture: Patterns, Causes, and Consequences of Biodiversity</b>	<b>9</b>
<b>2 Patterns of biological diversity</b>	<b>11</b>
Assessing biological diversity	13
Alpha, beta, and gamma diversity	14
Patterns of biological diversity	18
Area and species richness	18
The distribution of species abundance	21
Productivity and species richness	25
The latitudinal diversity gradient	27
A null model: geometric constraints and the "mid-domain effect"	27
Ecological hypotheses: climate and species richness	29
Historical hypotheses: the time-integrated area hypothesis and the concept of tropical niche conservatism	31
Evolutionary hypotheses: do rates of diversification differ across latitude?	33
Conclusion	36
Summary	36
<b>3 Biodiversity and ecosystem functioning</b>	<b>38</b>
Diversity and productivity	40
Mechanisms underlying the diversity–productivity relationship	41
Diversity, nutrient cycling, and nutrient retention	45
Diversity and stability	46
Temporal stability	47
Diversity and invasibility	49
Biodiversity and ecosystem multifunctionality	51



Unanswered questions (revisited)	52
Multiple trophic levels	52
Community assembly or species loss?	52
Global extinction and local ecosystem functioning: is there a mismatch of spatial scales?	54
The invasion paradox	55
How important are diversity effects in nature?	56
The two sides of diversity and productivity	58
Conclusion	59
Summary	59

---

## **Part II The Nitty-Gritty: Species Interactions in Simple Modules** **61**

### **4 Population growth and density dependence** **63**

Exponential population growth	64
Logistic population growth	65
The debate over density dependence	68
Evidence for density dependence in nature	69
Bottom-up or top-down density dependence? and other questions	72
Positive density dependence and Allee effects	73
Community-level regulation of abundance and richness	74
Density dependence, rarity, and species richness	77
Conclusion	79
Summary	79

### **5 The fundamentals of predator–prey interactions** **81**

Predator functional responses	82
The Lotka–Volterra model	85
Isocline analysis	86
Adding more realism to the Lotka–Volterra model	88
The Rosenzweig–MacArthur model	89
The suppression–stability trade-off	90
Density-dependent predators	91
Herbivory and parasitism	92
Herbivory	93
Parasitism and disease	94
Summary	95

### **6 Selective predators and responsive prey** **96**

Predator preference	96
Optimal foraging theory leads to a model of predator diet choice	98
Consequences of selective predation for species coexistence	104
Predator movement and habitat choice	104
The non-consumptive effects of predators	107
Habitat use and habitat shifts	107
Life history evolution	110

Activity levels and vigilance	111
Morphology	113
The relative importance of consumptive and non-consumptive effects	114
Looking ahead	116
Summary	116
<b>7 The fundamentals of competitive interactions</b>	<b>118</b>
Defining interspecific competition	118
The Lotka–Volterra competition model	119
Another way to look at the Lotka–Volterra competition model	120
Modification to the Lotka–Volterra competition model	122
Consumer–resource models of competition	123
What are resources?	123
One consumer and one resource: the concept of $R^*$	124
Two consumers competing for one resource	124
Coexistence on a single, fluctuating resource	127
Competition for multiple resources	127
Competition for two essential resources	128
Competition for two substitutable resources	131
Spatial heterogeneity and the coexistence of multiple consumers	132
Testing the predictions of resource competition theory	133
Apparent competition	136
Conclusion	138
Summary	139
<b>8 Species coexistence and niche theory</b>	<b>141</b>
Revisiting the origins of the notion of competitive exclusion	141
How are the assumptions of simple theory violated in nature?	142
Spatial variation in the environment can promote species coexistence	142
Temporal variation in the environment can also promote species coexistence	144
Ways in which dispersal and immigration can promote species coexistence	144
How do we tell if the strength of intraspecific competition is greater than interspecific competition ( $\alpha_{jj} > \alpha_{ji}$ )?	145
Predation and coexistence	153
Conclusion	154
Summary	156
<b>9 Beneficial interactions in communities: mutualism and facilitation</b>	<b>158</b>
Mutualism and facilitation: definitions	159
A brief look at the evolution of mutualism and facilitation	161
Incorporating beneficial interactions into community theory	163
Mutualisms may be context-dependent	165
Interactions may change from positive to negative across life stages	167
Combining positive and negative effects	169
The stress gradient hypothesis for plant facilitation	171
Looking ahead	173
Summary	174

---

<b>Part III Putting the Pieces Together: Food Webs, Ecological Networks and Community Assembly</b>	<b>177</b>
<b>10 Species interactions in ecological networks</b>	<b>179</b>
Food webs	180
Connectedness webs	181
Energy flow webs	184
Functional webs	185
Keystone species	187
Body size, foraging models, and food web structure	189
Species traits and the structure of ecological networks	193
Indirect effects	193
Other types of ecological networks	196
Mutualistic networks	196
Parasites and parasitoids	199
Complexity and stability	202
Conclusion	203
Summary	204
<b>11 Food chains and food webs: controlling factors and cascading effects</b>	<b>206</b>
Why is the World Green?	206
What determines abundance at different trophic levels?	207
A simple thought experiment illustrates the duality of top-down and bottom-up control	211
Some conclusions	211
Testing the predictions	211
Effects of productivity on trophic-level abundances	212
Food chains with parallel pathways of energy flow	220
Trophic cascades and the relative importance of predator and resource limitation	222
How common are trophic cascades in different ecosystems?	225
Trophic cascades and non-consumptive (trait-mediated) effects	226
What determines food-chain length?	227
Conclusion	229
Summary	230
<b>12 Community assembly and species traits</b>	<b>231</b>
Species pools	231
Three assembly processes limit membership in the local community	232
Pattern-based assembly rules	233
Comparisons between local and regional species richness	235
Trait-based community assembly	236
A focus on species traits	236
Traits and limited community membership	236
Traits and abiotic processes	237
Traits and biotic processes	239
Assessment and prospectus of trait-based assembly research	241

Functional diversity	242
Phylogeny as a proxy for functional traits	244
Regional pool processes	244
Community assembly as an organizing framework for ecological theory	245
Conclusions	245
Summary	245

---

## **Part IV Spatial Ecology: Metapopulations and Metacommunities** **247**

### **13 Patchy environments, metapopulations, and fugitive species** **249**

Metapopulations	249
The classic Levins metapopulation model	249
Implications of the metapopulation model for conservation biology	250
Parallels between metapopulation models and epidemiology	254
Empirical examples of metapopulation dynamics	254
Fugitive species: competition and coexistence in a patchy environment	257
The competition/colonization trade-off	258
Consequences of patch heterogeneity	261
Conclusion	264
Summary	264

### **14 Metacommunities** **266**

Metacommunities in homogeneous environments	268
The patch dynamics perspective	268
The neutral perspective	268
Metacommunities in heterogeneous environments	268
The species sorting perspective: “Traditional” community ecology in a metacommunity framework	269
The mass effects perspective: diversity patterns in source–sink metacommunities	270
Measuring dispersal in metacommunities	273
The neutral perspective	274
Assumptions of the neutral theory	274
Testing the predictions of the neutral theory	276
The value of the neutral theory	279
Niche-based and neutral processes in communities	279
Conclusion	283
Summary	283

---

## **Part V Species in Changing Environments: Ecology and Evolution** **285**

### **15 Species in variable environments** **287**

Ecological succession	289
The intermediate disturbance hypothesis	291
Fluctuation-dependent mechanisms of species coexistence	292

The storage effect	293
Regime shifts and alternative stable states	297
Conclusion	305
Summary	306
<b>16 Evolutionary community ecology</b>	<b>307</b>
Rapid evolution and eco-evolutionary dynamics	308
Rapid evolution, and its consequences for population dynamics and species interactions	308
Eco-evolutionary feedbacks and predator–prey cycles	310
Eco-evolutionary feedbacks in nature	311
Quantifying the ecological consequences of rapid evolution	312
Eco-evolutionary dynamics in diverse communities	314
Evolutionary rescue	314
Community phylogenetics	315
Assumption #2A: are closely related species stronger competitors?	319
Patterns of phylogenetic structure in communities	320
Phylogenetic niche conservatism (assumption #1)	322
Evolutionary processes that structure regional species pools	325
Speciation and community assembly in island-like systems	325
Building a mainland regional species pool	328
Conclusions	331
Summary	332
<b>17 Some concluding remarks and a look ahead</b>	<b>334</b>
Looking ahead: issues to ponder	335
Metacommunities and the integration of local and regional processes	335
Drivers of regional biodiversity	336
Community assembly and functional traits	337
Pathogens, parasites, and natural enemies	337
Biodiversity and ecosystem functioning	337
Changing technology will change how we collect data	338
Eco-evolutionary feedbacks and regional pool processes	338
Climate change, and its effects on species distributions and species interactions	339
The role of time	339
In closing, we would like to say...	339
Literature cited	341
Author index	389
Subject index	397

# Community ecology's roots

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Every genuine worker in science is an explorer, who is continually meeting fresh things and fresh situations, to which he has to adapt his material and mental equipment. This is conspicuously true of our subject, and is one of the greatest attractions of ecology to the student who is at once eager, imaginative, and determined. To the lover of prescribed routine methods with the certainty of “safe” results, the study of ecology is not to be recommended. **Arthur Tansley, 1923: 97**

If we knew what we were doing, it wouldn't be called research.

**Albert Einstein**

The diversity of life on our planet is remarkable. Indeed, among the biggest questions in all of biology are: How did such a variety of life arise? How is it maintained? What would happen if it were lost? Community ecology is that branch of science focused squarely on understanding Earth's biodiversity, including the generation, maintenance, and distribution of the diversity of life in space and time. It is a fascinating subject, but not an easy one. Species interact with their environment and with one another. As we will see in the pages that follow, these interactions underlie the processes that determine biodiversity. Yet, unlike the interacting particles studied by physicists, species also change through time—they evolve. This continual change makes the study of interacting species perhaps even more challenging than the study of interacting particles.

In his 1959 address to the American Society of Naturalists, G. Evelyn Hutchinson posed a simple question: “Why are there so many kinds [species] of animals?” Hutchinson's question remains as fresh and relevant today as it was half a century ago. This book will explore what ecologists understand about the processes that drive the distribution of animal and plant diversity across different spatial and temporal

scales. In order to appreciate the current state of community ecology it is important to know something about its history, particularly the development of ideas. This first chapter provides a brief summary of that history. Those of you familiar with the field may skip ahead, while those of you interested in learning more should consult the books and papers by Hutchinson (1978), Colwell (1985), Kingsland (1985), May and Seger (1986), McIntosh (1980, 1985, 1987), and Ricklefs (1987, 2004). Many of these “histories” were written by ecologists actively involved in the field's development, for community ecology is a relatively young science.

## What is a community?

A **community** is a group of species that occur together in space and time (Begon et al. 2006). This definition is an operational one. Any limits on space and time are arbitrary, as are any limits on the number of species in a community. For example, the study of “bird communities” or “fish communities” might be referred to, in order to delimit the assemblage of interest, recognizing that it is impossible to study all the species that occur together in the same

place at the same time. Although most ecologists would be happy with this definition, the concept of what a community is and how it is organized has changed widely through time (Elton 1927; Fauth et al. 1996).

The first community ecologists were botanists who noted what appeared to be repeated associations between plant species in response to spatial and temporal variation in the environment. Frederic Clements, the pioneer of North American plant ecology, viewed these plant associations as a coherent unit—a kind of superorganism—and he presumed that plant communities followed a pattern of succession to some stable climax community (Clements 1916; see discussion of ecological succession in Chapter 15). Limnology, the study of lakes, also adopted a superorganism view of communities. In 1887, the limnologist Stephen Forbes published a famous paper entitled “The lake as a microcosm,” in which he stated that all organisms in a lake tend to function in harmony to create a system in balance. Thus, these early ecologists tended to view communities as unique entities, and they became preoccupied with classifying plant and lake communities into specific “types.”

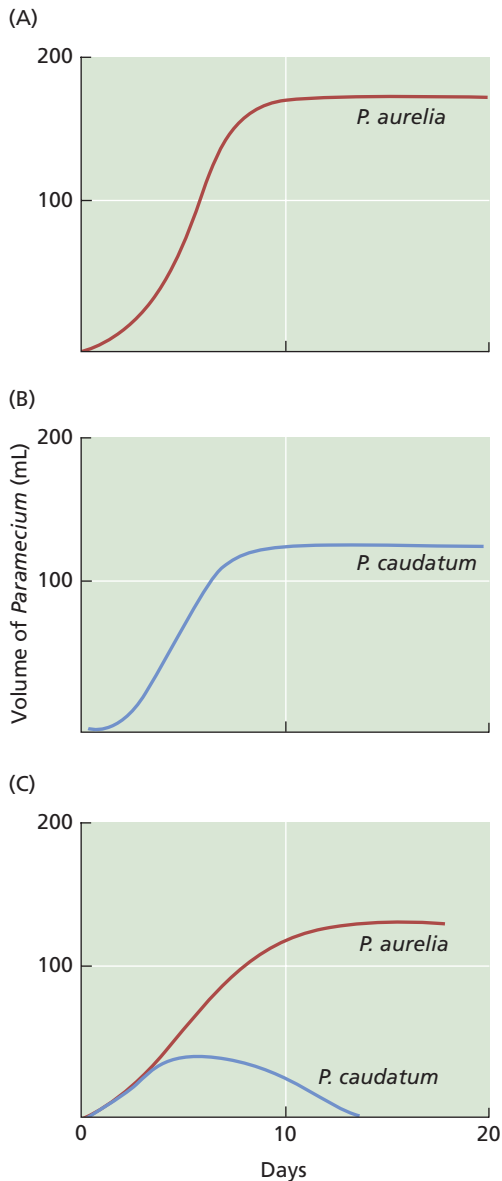
This superorganism concept of communities did not sit well with everyone. It was soon questioned by a number of plant ecologists, most notably Henry Gleason (1926) and Arthur Tansley (1939). Gleason asserted that species have distinct ecological characteristics, and that what appear to be tightly knit associations of species on a local scale are, in fact, the responses of individual species to environmental gradients. Gleason’s individualistic concept of communities was ignored at first, but later asserted itself, and led to a rejection of Clements’s hypotheses in favor of a continuum or gradient theory of plant distributions (Whittaker 1956).

The debate between Clements and Gleason over the nature of communities may seem like a historical footnote today, but at its core is a question that is very much alive: To what extent are local communities—the collections of species occurring together at a site—real entities? Ricklefs (2004) suggested that “ecologists should abandon circumscribed concepts of local communities. Except in cases of highly discrete resources or environments with sharp ecological boundaries, local communities do not exist. What ecologists have called communities in the

past should be thought of as point estimates of overlapping regional species distributions.” This focus on the interplay between local and regional processes in determining species associations is a theme that we will return to often in this book.

In contrast to plant ecology, the study of animal communities grew out of laboratory and field studies of populations. Animal population biologists, resource managers, and human demographers were concerned with the factors that regulate the abundance of individuals over time (birth, death, migration). Charles Elton, one of the pioneers of animal community ecology, worked for a time as a consultant for the Hudson’s Bay Company, and his thinking was strongly influenced by the fluctuations he observed in the abundance of Arctic animals. Elton was opposed to the “balance of nature” concept espoused by Forbes and others, and in a book entitled *Animal Ecology* (1927), he discussed such important ideas as food webs, community diversity and community invasibility, and the niche. In another book, *The Ecology of Animals*, Elton (1950, p. 22) proposed that communities have limited membership, stating that in any prescribed area, “only a fraction of the forms that could theoretically do so actually form a community at any one time.” Elton went on to note that, for animals as well as humans, it appears that “many are called, but few are chosen.”

Elton’s idea of limited membership was a significant insight, and it meshed well with the concurrent development of mathematical theories of population growth and species interactions. In the 1920s, mathematical ecologists Alfred Lotka (1925) and Vito Volterra (1926) independently developed the now famous equations that bear their names, which describe competition and predation between two or more species. These mathematical models showed that two species competing for a single resource cannot coexist. Gause (1934) experimentally tested this theory with protozoan populations growing in small bottles on a single resource. He found that species grown separately achieved stable densities, but that when pairs of species were grown together in a simple environment, one species always won out and the other species became extinct (Figure 1.1). Other “bottle experiments” with fruit flies, flour beetles, and annual plants produced similar results. The apparent generality of these results led to the formulation of what became known as Gause’s **competitive**



**Figure 1.1** Results of Gause's competition experiments with two *Paramecium* spp. (*P. aurelia* and *P. caudatum*) grown separately and together in small containers in the laboratory. (A, B) Each species reached a stable population size (carrying capacity) when grown in isolation. (C) When grown together, however, one species always outcompeted and eliminated the other. After Gause (1934).

**exclusion principle**, which can be stated as “two species cannot coexist on one limiting resource.” The competitive exclusion principle had a profound effect on animal ecology at the time and, in a modified

form, became a cornerstone of the developing field of community ecology.

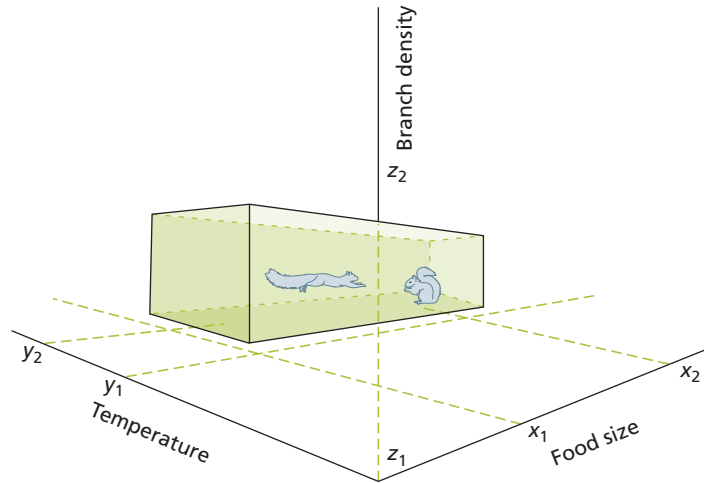
In the 1940s and 1950s, there was vigorous debate over the competitive exclusion principle and whether populations were regulated by density-dependent or density-independent factors. Important figures in this debate were Elton, Lack, and Nicholson on the side of competition and density-dependent regulation, and Andrewartha and Birch on the side of density independence. In 1957, a number of ecologists and human demographers met at the Cold Spring Harbor Institute in Long Island, New York, to debate the issues of population regulation, with little consensus. However, this symposium did lead to one remarkable result. At the end of the published conference proceedings is a paper by G. E. Hutchinson (1957), modestly entitled “Concluding Remarks.” In this paper, Hutchinson formalized the concept of the niche and ushered in what might well be considered the modern age of community ecology.

### The ecological niche

The concept of the **niche** has a long history in ecology (see Chase and Leibold 2003a for an excellent summary). Grinnell (1917) defined the niche of an organism as the habitat or environment it is capable of occupying. Elton (1927) independently defined the niche as the role a species plays in the community. Gause (1934) made the connection between the degree to which the niches of two species overlap and the intensity of competition between them. Each of these concepts of the niche was incorporated into Hutchinson's thinking when he formalized the niche concept and connected it to the problem of species diversity and coexistence (Hutchinson 1957, 1959). In his “Concluding Remarks,” Hutchinson showed how we might quantify an organism's niche, including both biotic and abiotic dimensions of the environment, as axes of an *n*-dimensional hypervolume (Figure 1.2).

Hutchinson (1957) went on to distinguish between an organism's **fundamental** (or *pre-interactive*) **niche** and its **realized** (or *post-interactive*) **niche**. The fundamental niche encompasses those parts of the environment that a species could occupy in the absence of interactions with other species, whereas the realized niche encompasses those parts of the environment that a species actually occupies in the





**Figure 1.2** Hutchinson's visualization of the niche as an  $n$ -dimensional hypervolume. In this hypothetical example, the fundamental niche of a squirrel species is shown along three environmental dimensions. One axis (here labeled  $y$ ) might define the range of temperatures tolerated by the species, another dimension ( $x$ ) might describe the range of seed sizes (e.g., acorns) eaten, and a third axis ( $z$ ) the range of tree branch densities (diameter, volume) that support this squirrel species. Subscripts 1 and 2 represent the lower and upper limits for each niche dimension. After Hutchinson (1978).

presence of interacting species (e.g., competitors and predators). In Hutchinson's view, a species' realized niche was smaller than its fundamental niche, due to negative interspecific interactions. However, positive interactions between species (mutualisms, commensalisms) can result in a species occupying portions of the environment that were previously unsuitable; in other words, it is possible for the realized niche to be *larger* than the fundamental niche (Bruno et al. 2003). The fact that positive interactions were not explicitly considered in Hutchinson's niche concept shows how completely the ideas of competition and predation permeated ecological thinking at the time.

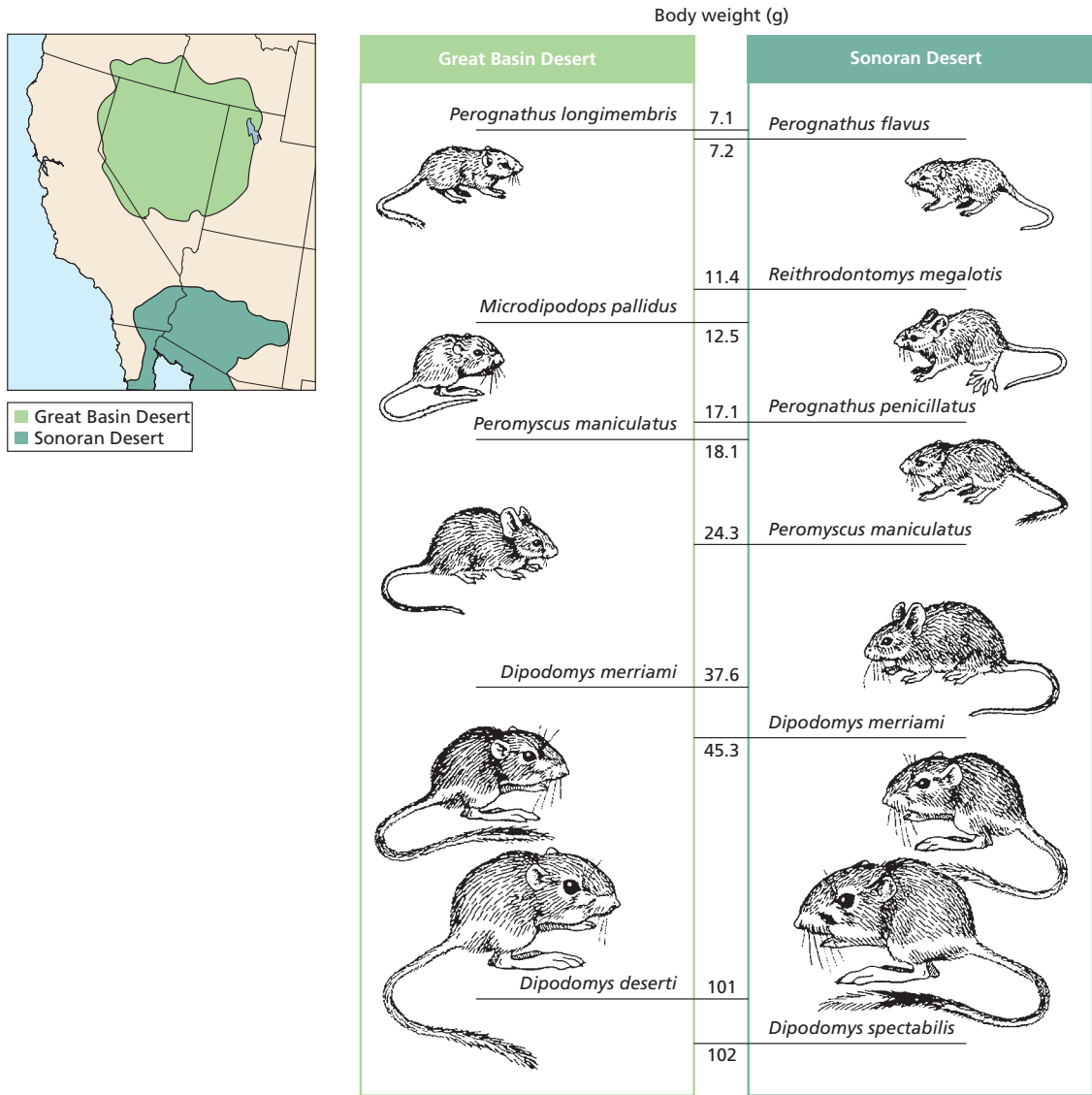
Hutchinson's definition of the niche provided the framework on which ecologists would build a theory of community organization, based on interspecific competition. First, however, they needed to make Hutchinson's concept more workable. An " $n$ -dimensional niche" is fine in the abstract, but empirically, it is impossible to measure an undefined number of niche dimensions. It took one of Hutchinson's students, Robert MacArthur, to make the concept operational. MacArthur's approach (1969) was to focus on only a few critical niche axes—those for which competition occurs. If, for example,

interspecific competition for seeds limits the number of seed-eating birds in a community, then we should focus our study on some measure of seed availability to define a species' niche (e.g., seed size). Thus, it became possible to examine the distribution of species in "niche space" within a community (see Figures 8.3 and 8.4). More importantly, MacArthur's approach showed how we might quantitatively link overlap in niche space to the process of competitive exclusion (MacArthur 1972). We discuss the modern extension of this approach to the study of species coexistence in Chapter 8.

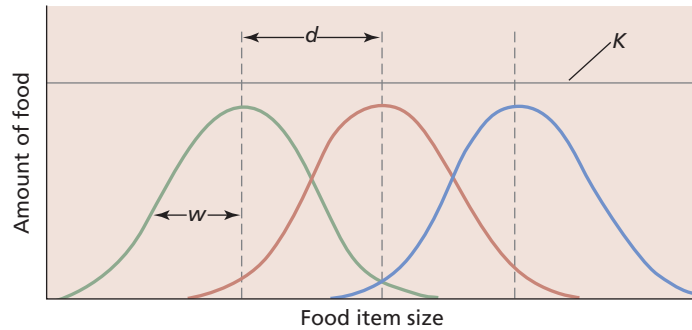
Shortly after the publication of his "Concluding Remarks" in 1957, Hutchinson (1959) provided another key insight in his published presidential address to the American Society of Naturalists, entitled "Homage to Santa Rosalia, or why are there so many kinds of animals?" Here, Hutchinson pondered a question that goes a step beyond Gause's competitive exclusion principle: If the competitive exclusion principle is true and interspecific competition limits the coexistence of species within the same niche, then how dissimilar must species be in their niches in order to coexist? Hutchinson suggested that the answer might be found in the seemingly regular patterns of difference in body size

among members of an **ecological guild**—co-occurring species that use the same types of resources. He noted that species that were similar in most ways, except the sizes of prey eaten, tended to differ by a constant size ratio: a factor of about 1.3 in

length and 2.0 in body mass. Such regular differences in size among coexisting species were found in many ecological guilds (one example is shown in Figure 1.3) and became known as **Hutchinsonian ratios**.



**Figure 1.3** Hutchinsonian ratios among desert rodents found in the Great Basin and Sonoran Deserts of the western USA. Differences in body size reflect differences in diet and habitat use (niche differences) between these species. The pattern of body-size spacing observed in these two desert rodent ecological guilds is more regular than would be expected by chance. From Brown (1975).



**Figure 1.4** The concept of limiting similarity illustrated for three species utilizing a continuum of food resources.  $K$  represents a resource continuum (for example, the amount of food as a function of food size). Each species' niche is represented by the mean and the standard deviation ( $w$ ) of its resource utilization curve, and  $d$  is the distance between the mean resource uses of the closest pair of species. MacArthur and Levins (1967), and May and MacArthur (1972) showed that the minimal niche separation required for the coexistence of competing species (under very specific conditions) is  $d/w \approx 1$ . After May and MacArthur (1972).

MacArthur and Levins (1967) built on these ideas and introduced the concept of **limiting similarity**, which specified the minimal niche difference between two competing species that would allow them to coexist. In MacArthur and Levins's theory, species are arrayed linearly along a resource (niche) axis, and each species' resource use is represented by a normal (bell-shaped) utilization curve (Figure 1.4). The overlap between adjacent utilization curves can be used (under specific assumptions) as a measure of the competition coefficients ( $\alpha$ 's) in the Lotka–Volterra model of interspecific competition (described in Chapter 7). Using this model of competition, MacArthur and Levins (1967) were able to specify the minimum niche difference required for two species to coexist. Later, May and MacArthur (1972) and May (1973b) used a different approach, based on species in fluctuating environments, to arrive at a very similar outcome: the limiting similarity between two competing species is reached when  $d/w \approx 1$ , where  $d$  is the separation in mean resource use between species and  $w$  is the standard deviation in resource use (see Figure 1.4).

### Whither competition theory?

In less than 50 years, animal community ecology progressed from the simple recognition that species too similar in their niches cannot coexist to the development of a theoretical framework, poised to

predict the number and types of species found in natural communities based on a functional limit to the similarity of competing species. This was an enormous leap forward, and community ecology seemed well on its way to becoming a more quantitative and predictive science. The heady optimism of the times is reflected in Robert May's (1977a, p. 195) comment that "the question of the limits to similarity among coexisting competitors is ultimately as deep as the origin of species itself: although undoubtedly modified by prey–predator and mutualistic relations, such limits to similarity are probably the major factor determining how many species there are." In the end, however, the theory of limiting similarity failed to achieve its promise. What happened?

First, there were strong challenges to the idea that interspecific competition is the only, or even the primary, factor structuring communities. Much of the evidence for the importance of interspecific competition in communities was based on descriptive patterns, such as regularly spaced patterns of body size among coexisting species (see Figure 1.3) or "checkerboard" distributions of species on islands (Diamond 1973, 1975). When examined more closely, however, many of these patterns turned out to be indistinguishable from those predicted by models that did *not* include interspecific competition as an organizing force—that is, by null models (Strong et al. 1979; Simberloff and Conner 1981; Gotelli and

Graves 1996). Secondly, predictions of limiting similarity between species turned out to be model-dependent (Abrams 1975, 1983b). That is, even though most mathematical models of interspecific competition predict some limit to how similar species may be in their resource use and still coexist, that limit varies widely depending on the assumptions and structure of the model. We now know there are no universal (or “hard”) limits to similarity as originally envisioned by MacArthur and Levins (1967). However, recent work has shown that, while there are no formal limits to similarity, the more tightly packed a community is in terms of niche space, the more fragile is species coexistence (Meszena et al. 2006; Barabas et al. 2012, 2013). The extreme fragility of tightly packed communities suggests a reinterpretation of the limiting similarity principle, rather than its complete abandonment.

These and other challenges caused ecologists to look beyond interspecific competition, and to consider the plurality of factors that might determine species diversity. In contrast to the unbridled optimism that characterized community ecology in the 1960s and early 1970s, the next decade was a period of soul-searching, as ecologists struggled to find a conceptual framework to replace what had seemingly been lost (McIntosh 1987). In the end, however, the idea that communities are organized around strong interspecific interactions was not so much wrong as it was overly simplistic.

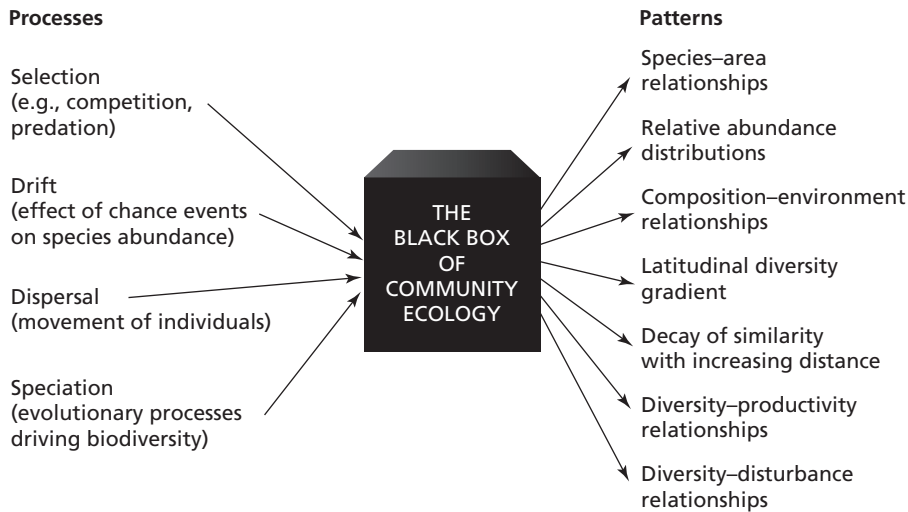
## New directions

The “failure” of simple competition-based models to explain community diversity led to important new directions in community ecology, and many of these directions continue to influence how we study ecology. For example, the “null model debate” of the 1970s led directly to an increased emphasis on using field experiments to test ecological hypotheses. Many of these field experiments focused on studying interspecific competition. However, pioneering experiments by Paine (1966), Dayton (1971), and Lubchenco (1978), all working in the marine intertidal zone, also showed that the presence or absence of predators could have dramatic effects on species diversity. These experiments set the stage for a wealth of future work on food webs, trophic

cascades, and top-down effects. We will consider these topics in detail in subsequent chapters, as well as more recent approaches to characterizing food webs and other types of ecological networks (see Chapters 10 and 11).

The experimental studies cited above demonstrated how competition and predation may interact to affect species diversity and composition (for example, diversity is increased when predators feed preferentially on a competitive dominant), again setting the stage for subsequent empirical and theoretical work on keystone predation and competition–predation trade-offs. Over time, the accumulation of results from multiple field experiments fostered the application of **meta-analysis** in ecology, in which the outcomes of many experiments are combined and synthesized to arrive at general conclusions (Gurevitch et al. 1992; Borenstein et al. 2009; Schwarzer et al. 2015). Today, ecologists rely heavily on meta-analysis, and there will be many times in this book when the authors will look to the results of meta-analyses to evaluate the importance of a process in ecology.

The “failure” of a single process (interspecific competition) to account for many of the patterns in species diversity observed in the 1960s and 1970s led ecologists to take a more pluralistic approach to their science (Schoener 1986; McIntosh 1987). A pluralistic ecology recognizes that multiple factors may interact to determine the distribution and abundance of species. The difficulty with pluralism, however, is that it can quickly lead us into a morass. In his thought-provoking article, Vellend (2010, p. 183) suggested that “despite the overwhelmingly large number of mechanisms thought to underpin patterns in ecological communities, all such mechanisms involve only four distinct kinds of processes—selection, drift, speciation, and dispersal.” In Vellend’s framework, “selection” encompasses the processes that determine the relative success of species within a local community (e.g., competition, predation, disease), whereas “drift” refers to changes in species’ relative abundances due to chance or other random effects, and “dispersal” is the movement of individuals and species, into and out of local communities. “Speciation” operates over spatial scales larger than the local community, and it is the process that ultimately generates diversity in regional species



**Figure 1.5** A conceptual view of the functioning of community ecology, in which four basic processes (selection, drift, speciation, and dispersal) combine to determine the biodiversity patterns listed on the right. The “black box of community ecology” refers to the fact that there are many ways in which the four processes listed at the left may combine to produce the patterns listed at the right. After Vellend (2010).

pools. Vellend (2010, 2016) suggests that conceptual synthesis in community ecology can be achieved by focusing on these four major drivers of species diversity patterns at different spatial and temporal scales (Figure 1.5). We agree with Vellend’s suggestion. Moreover, we believe that community ecologists are further challenged to illuminate the interior of the “black box” in Figure 1.5, and to better understand how the four basic processes of community ecology interact to determine patterns of biodiversity.

The recognition that local communities bear the footprint of historical and regional processes (Ricklefs and Schluter 1993) is an important insight that grew out of the narrow, local community focus of the 1960s and 1970s. Interestingly, MacArthur (1972) anticipated this paradigm shift, but he died too young to be a part of it (see discussion in McIntosh 1987). Simply put, few communities exist in isolation. Instead, the diversity of species within a community is a product of their biotic and abiotic interactions (i.e., species sorting or “selection,” together with drift), the dispersal of species between communities, and the composition of the regional species pool (a function of biogeography and evolutionary history). Therefore, it is necessary to consider the

processes that regulate diversity on a local scale, as well as the processes that link populations and communities into metapopulations and metacommunities, and the processes that ultimately generate diversity at regional levels. This is a tall order. Chapter 2 will use broad-scale diversity gradients, particularly the latitudinal diversity gradient, as a vehicle to begin to think about the processes that generate regional diversity. At geographic scales of regions or continents, biodiversity is a function of evolutionary processes that may play out over millions of years. In addition, chance events in Earth’s history can influence a region’s size, geomorphology, climate, and the amount of time available for speciation. These historical factors conspire to make the study of the processes that determine regional biodiversity challenging. Of course, there is also little opportunity to do experiments at such vast scales of time and space. However, as we will see, recent advances in molecular biology, phylogenetics, paleontology, and biogeography have greatly facilitated the study of broad-scale diversity patterns, and these new tools are providing the key to understanding the factors that generate biodiversity at regional scales.

PART I

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**The Big Picture: Patterns, Causes, and  
Consequences of Biodiversity**

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