

## ● Introduction

### What Is Tropical Ecology?

Asking the question, What is tropical ecology? may seem akin to asking questions such as, Who is buried in Grant's tomb? *Tropical ecology* is the study of the ecology of tropical regions. But so what? Consider these questions: First, what is ecology? What are its paradigms, what are its principles, and what is its place in the biological sciences? What unique insights has ecology added to biology? Second and perhaps more important, is tropical ecology unique within the study of ecology? In other words, if you studied the ecology of the eastern deciduous forest, the arctic tundra, the Mojave Desert, or the seas that surround Antarctica, what paradigms and principles might you miss because none of these ecosystems are tropical? Take a few minutes to think about these questions, and then read on.

Readers of this book should be familiar with ecology and thus need little coaching as to what *ecology* is. It is, in a nutshell, the study of how organisms exist, adapt, and interact within their environments within the context of both abiotic and biotic factors. It is studied at widely different spatial and temporal scales. Ecologists reveal and attempt to explain patterns of species richness and explore how top-down and bottom-up forces influence the structure and stability of food webs, structuring whole ecological communities. Ecologists use experimental techniques and mathematical models to study competition, predation, mutualism, and the assembly, persistence, and stability of ecological communities. Ecology has matured in that disciplines such as landscape ecology, restoration ecology, and conservation ecology all use theory from basic ecology. Each of these areas of applied ecology has made an impact on issues in tropical ecology.

The various topics cited in the previous paragraph are the grist for ecological study and make up the "usual suspects" in ecology texts. Once one understands these topics, one is considered proficient in ecology. Do these topics form the paradigms of ecology? Not really. They are best considered *principles*, areas of study around which the discipline is organized. Ecology arguably has no paradigms. (I argue this point throughout my book *The Balance of Nature: Ecology's Enduring Myth*.) On close inspection, ecology is a prominent branch of evolutionary biology. Not much of what ecologists study makes sense without placing the data firmly within evolutionary context. This reality will become apparent in the study of tropical rain forest ecology, especially regarding species' origins, interactions, and interdependencies. The paradigm within which ecology is included is *organic evolution*, and it, along with *cell theory*, are the only real paradigms of biology. Cell theory and evolution are what biology is. All the rest is detail.

Where does this leave tropical ecology? What will you learn by going to Panama, or Ecuador, or Indonesia, or Queensland, Australia, that could not be learned

by going to central Spain, or Norway, or Japan, or New Jersey? Yes, the species are different, but what of it? The pattern of seasonality is different; precipitation patterns are different; lots of things are different. What of it?

This “what of it?” is the subject of this book. By the conclusion of your study, you should be competent to voice an educated opinion regarding the question of just how unique tropical ecology is. Learn and enjoy the journey.

## Overview

When Charles Darwin was fresh out of college, he visited a tropical rain forest in eastern Brazil as part of his famous voyage aboard the HMS *Beagle*. Like others who came before and since, his first impressions were vivid. He wrote of this experience in the tropical rain forest:

When quietly walking along the shady pathways, and admiring each successive view, I wished to find language to express my ideas. Epithet after epithet was found too weak to convey to those who have not visited the intertropical regions the sensation of delight which the mind experiences. (Darwin 1845)

In other words, Darwin was pretty overwhelmed by what he saw, felt, heard, even what he smelled. He commented on the hazy air within the forest, evidence of the high humidity. A tropical rain forest does leave you with a vivid “first impression.” It gets your attention both rationally and emotionally. But years later, a much older Charles Darwin had a different perspective when he was composing his autobiography:

In my journal I wrote that whilst standing in the midst of the grandeur of a Brazilian forest, “it is not possible to give an adequate idea of the higher feelings of wonder, admiration, and devotion which fill and elevate the mind.” I well remember my conviction that there is more in man than the mere breath of his body. But now the grandest scenes would not cause any such convictions and feelings to rise in my mind. (Darwin 1887)

What changed Darwin was, of course, evolution. When Darwin returned from the *Beagle* voyage, he

quickly became convinced of the truth of organic evolution. All present species have arisen from previous species and were not specially created. This was soon followed by his discovery of the mechanism for evolutionary change, *natural selection*, and so he began to view the world differently. Of course, not everyone agreed with Darwin. Some rejected his theory outright; others agreed that evolution might be true but did not agree that a blind mechanism called natural selection caused species to evolve into different forms. From 1859, when *On the Origin of Species* was published, until Darwin’s death at the age of 73 in 1882, he was strongly attacked in speeches and in print over his assertions concerning evolution.

What does all this Darwinian history have to do with tropical ecology? The great twentieth-century evolutionary biologist Theodosius Dobzhansky, who spent a fair amount of time collecting fruit flies in the tropics, said “Nothing in biology makes sense except in the light of evolution” (Dobzhansky 1973, p. 449). Darwin’s big idea has become the most important paradigm in biology, and without it, the immense complexities that characterize a tropical rain forest or any other ecosystem would seem hopelessly beyond rational explanation.

Therefore, much of this book will be about evolution as it is evident in the tropics, and in rain forests in particular. There is nothing unique about this approach, as I fail to see how it could be otherwise for any kind of ecological study. If this book were about the ecology of Antarctica, evolution would still be the organizing paradigm. The noted ecologist G. Evelyn Hutchinson once titled a book about general ecology *The Ecological Theater and the Evolutionary Play*. I doubt that many who visit a rain forest or any other tropical ecosystem today need fear losing their sense of awe (as Darwin apparently did) simply because of acquiring an understanding of how the process of evolution is manifest in the multitudes of morphologies and interactions that characterize the ecological community. Darwin, when elderly, apparently lost his awe of nature, perhaps embittered by all the criticism directed toward him. You need not worry, however. Learning the science behind the landscape really adds to awe—it does not detract from it. This book aims to teach the science behind the landscape.

As author of the book you hold, I am in a unique position. It’s my book, and I wrote it my way. Other books about the tropics take different approaches from what you will read within this volume. This book reflects my views from study and field experience (particularly

in ornithology) over my four decades as an ecologist. Let me explain something of how the book came to be.

In 1989, Princeton University Press published my book titled *A Neotropical Companion*. The book was modest in size and had a bright green cover, which led to its nickname, the “Little Green Book.” It amazed me while writing that book how much wonderful information ecologists had garnered in their collective research efforts and how little of this really cool stuff was finding its way to more popular-based audiences, including into the hands and minds of students. My goal was to be selective and make some of that amazing information available.

The success of the Little Green Book led to a major revision and expansion of *A Neotropical Companion* that appeared in 1997, again published by Princeton University Press. This volume was bigger, had new illustrations and some color photographs, and, most importantly, covered more topics in greater detail, with much additional treatment of South America.

Eager to learn from my readers, I included my e-mail address in the revised volume, and many responded. I have had a few errors of both omission and commission pointed out to me, as well as many comments as to how the book could be improved. Some want more maps; some want more illustrations; some want greater emphasis on particular topics. But the most-repeated comment (the title of the book notwithstanding) is that the book is too narrow, as it covers only the Neotropics and omits the Old World tropics of Africa, Southeast Asia, and Australia/New Guinea. How does the Neotropics compare with other tropical regions of Earth? How are these regions biogeographically distinct, one from another? Are the ecological processes that characterize Neotropical ecosystems the same as those in other regions?

Thus, it seemed both to me and to my editors at Princeton University Press that it was time for yet another revision and expansion, this time going “the full Monty” toward a more comprehensive book covering the ecology of the global tropics. And that is how *Tropical Ecology* came to be.

Ah, but as always, the devil is in the details. My previous book was specifically about the Neotropics, and the vast majority of my field experience has been in that region. True, I have visited Africa (Tanzania), Southeast Asia (Indonesia), as well as the Australian tropics in Queensland and Darwin, but most of my reading and field study is from Central and South America and the Caribbean. And, I dare say, much if not most of the published literature continues to be

from studies in the Neotropics. So I cannot pretend to take an “even-handed” approach to the global tropics. This book will expose my bias, as it reflects my confidence level in my expertise—and that bias remains clearly toward the Neotropics and, in particular, birds. But such a bias has a pragmatic component in that many students will likely use this text in conjunction with an actual field experience, a college course that includes a trip to experience a tropical region. And most North American college courses in tropical ecology visit some area within the Neotropics. My continued emphasis on that region will benefit such courses.

The organization of the work is mine, my way to tell the story of tropical ecology. But the information contained herein is largely the work of others, the thousands of researchers in the field and lab whose work, often repetitive and always exacting, deals with some aspect of tropical ecology. For the most part, I rely on primary source material, papers from journals—some of which, like *Biotropica*, publish only papers about tropical ecology, and some of which, like *Ecology* and *American Naturalist*, publish many papers that deal with the tropics. I also include many citations from *Science* and *Nature*, both of which publish numerous major papers on various aspects of tropical biology. Each topic covered is illustrated by selected examples, so obviously many worthy papers are not cited. My apologies to these authors, but this book is not meant as a comprehensive review of all topics tropical. It is nice to have an embarrassment of riches when it comes to information about the tropics, and I have had to carefully pick and choose. Examples were by and large chosen for their overall interest, potential significance, clarity, and robustness. And, since researching the second edition of *A Neotropical Companion*, I am amazed by the remarkable increase in the number of tropical studies represented in professional publications of all kinds. Another point worth emphasizing is that my area of expertise is in *ornithology*, the study of birds, so whoever reads my text will encounter quite a few examples that involve birds. But consider that birds are fairly easy to observe in the field, and thus much data about species interactions in the tropics does, indeed, focus on birds.

The first question any author faces is, Who is the audience for this book? This work is aimed at students and others who take a serious interest in learning about tropical ecology. It assumes a basic knowledge of introductory biology, including ecology and the tenets of evolutionary biology. I present an overview of each topic and then note where information gaps exist

and where controversies have arisen. The book is meant to be provocative and poses many questions, the answers to which are still to be revealed or are presently being hotly debated. Some of the studies I describe come to different conclusions about the same topic. Science is always a work in progress, and this book strongly takes that approach.

All science books should be subject to peer review, and this book certainly has enjoyed that advantage (see the Acknowledgments). Others, expert in various areas of tropical biology, have read chapter drafts and made numerous critical comments. I have taken many of these suggestions, but I have also chosen not to take some. No two tropical biologists would ever write the “same” book. Our views are influenced by our biases, varied interests, and experiences, to say nothing of our intellectual outlooks. We make judgments, and we often have to agree to disagree on various points. Any problems identified with this text should be directed to me (jkricher@wheatonma.edu), and I take sole responsibility for any errors that may be detected.

Some material that has remained robust has been taken and often updated from *A Neotropical Companion*, but most of the material is new to this book. That said, any book such as this is old before it is published. Right now, any number of good studies are occurring or have occurred that alter some of what is written on these pages. That is the nature of science, the strength of science, the very essence of science. Science is cumulative, and anyone entering into the study of a field of science profits from acquiring a firm foundation from which to begin critical study. I hope this book will serve that purpose for its readers.

## Organization of This Book

This book consists of 15 chapters, a challenge for a one-semester course, but hopefully the writing is sufficiently engaging that the task of moving through the chapters will prove to be relatively pleasant. There are numerous figures, maps, tables, and color photographs throughout to add to the clarity of the text.

I begin (Chapter 1) with a broad overview of what and where the tropics are. This provides some information about how tropical ecology emerged from global exploration into the realm of scientific study. It also describes something of the climatic variables that

are the overarching determinants of tropical ecosystem characteristics, and it sets the stage for what is to come throughout the book.

Next (Chapter 2) I discuss biogeography and evolution in the tropics. For those already well versed in these topics, this chapter may serve as a helpful review. But for many, and I expect most students, it will be essential in explaining how and why tropical regions differ, as well as in clarifying basic evolutionary principles, particularly speciation.

Then it is time to enter a rain forest (Chapter 3) and examine the physical structure of this unique ecosystem. This chapter discusses the various characteristics of rain forest vegetation, from tree shapes to buttressed roots. It should be the primer that will allow any student to see the many details and general characteristics common to all rain forests.

Chapters 4 and 5 both explore ideas as to why tropical regions and rain forests in particular are so rich in their numbers of species. *Biodiversity* is one of the most significant areas of tropical research, and thus two chapters are devoted to research focused on this complex topic. Chapter 4 discusses how diversity is partitioned within and between habitats and considers whether the high diversity of tropical regions is an example of high rates of speciation (or low rates of extinction). What factors allow the continued existence of such complex communities? Chapter 5 looks at the range of hypotheses attempting to explain the uniquely high tree species richness in tropical forests, one of the most difficult theoretical problems in tropical ecology.

The effect of disturbance is explored next (Chapter 6). Periodic natural disturbance may result in a shifting mosaic of different aged patches of forest such that high species richness is maintained over large areas. This chapter deals in part with *gap phase dynamics*. Gaps in a forest are created by forces ranging from single fallen trees to major blowdowns caused by storms or fire. Gaps are exposed to high levels of sunlight and thus have a different ecology from closed rain forest, where canopy trees strongly attenuate the light striking the forest floor. Last, this chapter considers the topic of *secondary succession*, which is of major importance in assessing how rain forest regrows following disturbance.

The richness of species in tropical forests results in numerous complex forms of interactions among species—some rather casual, some sufficiently complex that the species are evolutionarily interdependent. Chapter 7 presents examples of some of the

most striking biotic interactions involving such topics as fruit consumption as it relates to seed dispersal and the propensity of many tropical species to evolve mutualistic interactions. This chapter includes a focus on *coevolution*, when two or more species become mutually interdependent.

*Food webs* and the adaptations associated with them form the core of Chapter 8. This chapter looks at various top-down and bottom-up interactions that contribute to structuring food webs and trophic dynamics in rain forests. Topics include the evolution of characteristics such as cryptic and warning coloration.

The high rate of photosynthesis evident in tropical rain forests results in high rates of *primary productivity*, and this is the subject of Chapter 9. How much carbon do lush tropical forests take in and how much do they emit (as carbon dioxide)? The *carbon flux* of tropical forests is an important area of research. As current climate change continues due to ongoing addition of atmospheric carbon dioxide, what is the potential of tropical forests to act as carbon sinks, absorbing and storing excess carbon? This chapter explores some of the sometimes contradictory research about how tropical forests might act to mitigate the effects of increasing atmospheric carbon dioxide.

Rich tropical forests often occur on poor soils. Chapter 10 examines nutrient cycling and tropical soils. It describes how vital nutrients such as phosphorus, nitrogen, and calcium cycle in tropical ecosystems and the essential function of decomposer organisms. This chapter includes discussion of various kinds of tropical soils and contrasts forests on *floodplains*, where annual flooding renews soil fertility, with those on *terre firme*, off floodplains.

Chapters 3 through 10 all focus on the ecology of the tropical rain forest. The remaining five chapters sur-

vey other tropical ecosystems and also examine topics having to do with conservation science in the tropics.

Areas of grassland with scattered trees are called *savanna*. Chapter 11 discusses tropical savannas and dry forest ecosystems. This discussion examines two views of how savannas and dry forests coexist in the tropics. One is that grassland, savanna, and dry forest represent a *moisture gradient effect* (where grassland is found in the most arid areas, and dry forest where there is more annual precipitation), and the other views them as *alternative stable states* dependent on local conditions. The importance of fire and grazing are also discussed.

Chapter 12 surveys other major tropical ecosystems, beginning with montane ecosystems and continuing to riverine forests and coastal mangrove forest. This chapter also considers the connectivity between montane and lowland ecosystems from the standpoint of biodiversity maintenance.

Humans evolved in tropical Africa, and Chapter 13 discusses human ecology in the tropics. Topics include hunter-gatherer communities, simple agriculture in the tropics, and some of the traditional ways that humans have affected the overall ecology of the tropics.

The last two chapters deal with conservation issues in the tropics. Chapter 14 focuses on forest fragmentation and biodiversity. Chapter 15 discusses deforestation and forest degradation, as well as the effects of fire on tropical forests. It also examines emergent pathogens and invasive species and concludes with an overview of a current debate among ecologists about the likely future of tropical forests. While not meant to be comprehensive, these two chapters taken together cover the most fundamental issues and questions facing tropical conservation science.