

TROPICAL FOREST COMMUNITY ECOLOGY

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CONTENTS

| | |
|--|------------|
| <i>Preface</i> | x |
| <i>Walter P. Carson and Stefan A. Schnitzer</i> | |
| <i>Foreword</i> | xi |
| <i>S. Joseph Wright</i> | |
| <i>List of Contributors</i> | xiii |
| SECTION 1 INTRODUCTION | 1 |
| 1 Scope of the Book and Key Contributions | 3 |
| <i>Stefan A. Schnitzer and Walter P. Carson</i> | |
| SECTION 2 LARGE-SCALE PATTERNS IN TROPICAL COMMUNITIES | 9 |
| 2 Spatial Variation in Tree Species Composition Across Tropical Forests: Pattern and Process | 11 |
| <i>Jérôme Chave</i> | |
| 3 The Disparity in Tree Species Richness among Tropical, Temperate, and Boreal Biomes: The Geographic Area and Age Hypothesis | 31 |
| <i>Paul V.A. Fine, Richard H. Ree, and Robyn J. Burnham</i> | |
| 4 Explaining Geographic Range Size by Species Age: A Test Using Neotropical <i>Piper</i> Species | 46 |
| <i>John R. Paul and Stephen J. Tonsor</i> | |
| 5 Patterns of Herbivory and Defense in Tropical Dry and Rain Forests | 63 |
| <i>Rodolfo Dirzo and Karina Boege</i> | |
| 6 Ecological Organization, Biogeography, and the Phylogenetic Structure of Tropical Forest Tree Communities | 79 |
| <i>Campbell O. Webb, Charles H. Cannon, and Stuart J. Davies</i> | |
| 7 Large Tropical Forest Dynamics Plots: Testing Explanations for the Maintenance of Species Diversity | 98 |
| <i>Jess K. Zimmerman, Jill Thompson, and Nicholas Brokaw</i> | |
| SECTION 3 TESTING THEORIES OF FOREST REGENERATION AND THE MAINTENANCE OF SPECIES DIVERSITY | 119 |
| 8 Tropical Forest Ecology: Sterile or Virgin for Theoreticians? | 121 |
| <i>Egbert G. Leigh, Jr</i> | |
| 9 Approaching Ecological Complexity from the Perspective of Symmetric Neutral Theory | 143 |
| <i>Stephen P. Hubbell</i> | |

| | | |
|--|---|-----|
| 10 | Functional Basis for Resource Niche Partitioning by Tropical Trees <i>Kaoru Kitajima and Lourens Poorter</i> | 160 |
| 11 | Colonization-related Trade-offs in Tropical Forests and Their Role in the Maintenance of Plant Species Diversity <i>Helene C. Muller-Landau</i> | 182 |
| 12 | Treefall Gaps and the Maintenance of Plant Species Diversity in Tropical Forests <i>Stefan A. Schnitzer, Joseph Mascaro, and Walter P. Carson</i> | 196 |
| 13 | Challenges Associated with Testing and Falsifying the Janzen–Connell Hypothesis: A Review and Critique <i>Walter P. Carson, Jill T. Anderson, Egbert G. Leigh, Jr, and Stefan A. Schnitzer</i> | 210 |
| 14 | Seed Limitation and the Coexistence of Pioneer Tree Species <i>James W. Dalling and Robert John</i> | 242 |
| 15 | Endophytic Fungi: Hidden Components of Tropical Community Ecology <i>A. Elizabeth Arnold</i> | 254 |
| SECTION 4 ANIMAL COMMUNITY ECOLOGY AND TROPHIC INTERACTIONS | | 273 |
| 16 | Tropical Tritrophic Interactions: Nasty Hosts and Ubiquitous Cascades <i>Lee A. Dyer</i> | 275 |
| 17 | Variation in Tree Seedling and Arbuscular Mycorrhizal Fungal Spore Responses to the Exclusion of Terrestrial Vertebrates: Implications for How Vertebrates Structure Tropical Communities <i>Tad C. Theimer and Catherine A. Gehring</i> | 294 |
| 18 | Ecosystem Decay in Closed Forest Fragments <i>John Terborgh and Kenneth Feeley</i> | 308 |
| 19 | Resource Limitation of Insular Animals: Causes and Consequences <i>Gregory H. Adler</i> | 322 |
| 20 | Tropical Arboreal Ants: Linking Nutrition to Roles in Rainforest Ecosystems <i>Diane W. Davidson and Steven C. Cook</i> | 334 |
| 21 | Soil Fertility and Arboreal Mammal Biomass in Tropical Forests <i>Carlos A. Peres</i> | 349 |
| SECTION 5 SECONDARY FOREST SUCCESSION, DYNAMICS, AND INVASION | | 365 |
| 22 | Processes Constraining Woody Species Succession on Abandoned Pastures in the Tropics: On the Relevance of Temperate Models of Succession <i>Chris J. Peterson and Walter P. Carson</i> | 367 |
| 23 | Chance and Determinism in Tropical Forest Succession <i>Robin L. Chazdon</i> | 384 |
| 24 | Exotic Plant Invasions in Tropical Forests: Patterns and Hypotheses <i>Julie S. Denslow and Saara J. DeWalt</i> | 409 |

| | |
|--|-----|
| SECTION 6 TROPICAL FOREST CONSERVATION | 427 |
| 25 Linking Insights from Ecological Research with Bioprospecting to Promote Conservation, Enhance Research Capacity, and Provide Economic Uses of Biodiversity <i>Thomas A. Kursar, Todd L. Capson, Luis Cubilla-Rios, Daniel A. Emmen, William Gerwick, Mahabir P. Gupta, Maria V. Heller, Kerry McPhail, Eduardo Ortega-Barría, Dora I. Quiros, Luz I. Romero, Pablo N. Solis, and Phyllis D. Coley</i> | 429 |
| 26 Tropical Rainforest Conservation: A Global Perspective <i>Richard T. Corlett and Richard B. Primack</i> | 442 |
| 27 Environmental Promise and Peril in the Amazon <i>William E. Laurance</i> | 458 |
| 28 Contributions of Ecologists to Tropical Forest Conservation <i>Francis E. Putz and Pieter A. Zuidema</i> | 474 |
| <i>Index</i> | 491 |

PREFACE

It is not hyperbole to say that there has been an explosion of research on tropical forest ecology over the past few decades. The establishment of large forest dynamics plots in tropical forests worldwide, in and of itself, has led to a near revolution in our understanding of forest change. In addition, there has been a substantial increase in the use of models and experiments to test longstanding theories developed to explain the striking patterns found in tropical forests and the putative mechanisms that underlie these patterns. When we started this project, we felt that a comprehensive synthesis of tropical forest community ecology was necessary in order to help the field move forward. Of course, no single volume could do this. Nonetheless, this book is our attempt to make a significant contribution to the field, and to ask anew: What are the main theories in tropical ecology, and which ones are supported or refuted by empirical data? Thus, we have attempted to assemble a volume that describes the most up-to-date findings on the important theories of tropical forest community ecology. We hope that this book accomplishes this goal to the degree possible, while at the same time providing a road map of what we know, what we think we know, and where future research is most needed.

The focus of the chapters in the volume is at the community level because this is where some of the most fundamental questions in tropical ecology exist. Indeed, perhaps the greatest challenge to community ecologist is to explain what processes account for the maintenance of the staggering diversity of plants and animals common in tropical forests around the globe. Still, our emphasis on communities definitely reflects our bias as community ecologists. While we have focused on communities, we certainly recognize the important contributions to tropical ecology that have come from those who study different levels of

ecological organization. Indeed, it is difficult to understand communities without understanding the ecology of populations and individuals. We decided to focus on forest communities because, to date, that is where the bulk of research on tropical community ecology has been conducted. We acknowledge that our focus has forced us to omit many important studies. Nonetheless, the emphasis on tropical forest community ecology provides enough material to fill multiple edited volumes, and thus we have attempted to focus on the areas that have received the most empirical attention, along with some topics that are currently nascent, but are rapidly becoming key areas in tropical ecology.

Each chapter in this book was reviewed by at least two relevant experts. We thank these reviewers for their efforts and we are indebted to all of them. We will not list them by name, thus allowing them to remain anonymous. We also thank the production team at Newgen Imaging Systems, and our editors at Blackwell for guiding us through the publication process.

This book, as with all edited volumes, would not have been possible without the dedicated contributions of the authors, each of whom is an expert in his or her respective area of study. For their hard work, truly top-notch contributions, and their patience throughout this process, we owe them a great deal of gratitude. This book is a tribute to their research, along with the research of all of the other scientists whose work is cited in this volume.

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FOREWORD

The present volume captures the excitement generated by an explosion in tropical forest research. When I was a graduate student in the late 1970s, it seemed to be possible to read every new article published on tropical forests. The ISI Web of Science[®] confirms this schoolboy memory. Just 289 articles published between 1975 and 1979 included the words “forest*” (for forest, forested or forests) and the name of a tropical country (or tropic*) in their titles. By reading just one or two articles a week, I was able to keep abreast of the entire literature on tropical forests. This would be nearly impossible today. Between 2002 and 2006, 2593 articles met the criteria described above reflecting a nine-fold increase in the rate of publication of tropical forest articles since the late 1970s. This explosion has been driven by new discovery; new theory; new technology; new challenges posed by global change, deforestation and other threats to tropical biodiversity; and ongoing interest in theory posed in the 1970s and earlier. This volume illustrates each of these developments.

In the 1970s, we all “knew” that ants were predatory with the exception of an insignificant few observed at extrafloral nectaries. No one guessed that plant exudates supported most of the great biomass of ants (Chapter 6). Likewise, no one guessed that plants consisted of a mosaic of plant plus endophytic fungi and that the endophytic fungi were hyperdiverse with tens to hundreds of species inhabiting each leaf in the forest (Chapter 15). The roles of herbivorous ants and endophytic fungi are only beginning to be explored, and their implications for forest biology are potentially profound. New theories of chance, dispersal and seed limitation (Chapters 2, 8 and 14) and new tradeoffs postulated between fecundity and habitat tolerance (Chapter 11) also hold the potential to change our understanding of how tropical

forest communities are structured and are only now beginning to be explored.

In the 1970s, we would have been mystified by functional (Chapter 10) and phylogenetic (Chapter 20) approaches to plant community ecology and the knowledge base in physiology, morphology and molecular genetics that makes these approaches possible today. Both approaches have the potential to reduce the immense number of species of tropical forest plants to a manageable number of ecologically distinct groups or crucial relationships among species' traits. Today, we are striving to bring functional, phylogenetic and ecological approaches together for 6000 plus tropical tree species found in the network of large Forest Dynamics Plots maintained by the Center for Tropical Forest Science (Chapter 7).

A graduate student in the late 1970s would have been familiar with the plant favorableness (Chapters 3 and 4), regeneration niche (Chapter 6), Janzen–Connell (Chapter 13) and bottom-up versus top-down hypotheses (Chapters 16–19 and 21) addressed by one third of the chapters in this volume and would be delighted to read the progress summarized here. I was also familiar with the potential of large forest plots – Robin Foster and Steve Hubbell were busy generating excitement for a grand new plot when I was a graduate student on Barro Colorado Island – and it is also a delight to see that potential realized (Chapter 7). Likewise, Phyllis Coley and I were contemporaries as graduate students on BCI as she revolutionized the study of herbivory (and I muddled about with island communities of birds and lizards), and it is a delight to see many of her ideas extended to a new framework to explain herbivory gradients across tropical rainfall gradients (Chapter 5) and to bioprospecting for new pharmaceuticals (Chapter 25).

The final section of this volume (Chapters 22–28) would shock a 1970s graduate student. A potential tropical deforestation crisis was only first publicized in the early 1970s (Gómez-Pompa *et al.* 1972 *Science* 177, 762–765). The severity of deforestation in 2007 and the many exacerbating problems (Chapters 24, 26 and 27) would be entirely unexpected. The potential for solutions through natural secondary succession on abandoned agricultural land (Chapters 22 and 23) and conservation action (Chapter 25) proposed, in some cases, by my peers from the late 1970s on BCI would be equally surprising and heartening.

Where do we go from here? What might a graduate student do in 2007 to have the greatest future impact? There are many answers. Spectacular new data sets are being made available by the Angiosperm Phylogeny Group, by several new efforts to assemble global plant and animal trait data, and by the new remote sensing technologies mobilized in global change research. Those trained to capitalize on these and other similar data sets will make many important contributions.

Simultaneously, we are still in the age of discovery in tropical forest ecology. No one suspected that there might be millions of species of endophytic fungi in tropical leaves until Elizabeth Arnold looked starting in 1996. We are equally ignorant of the roles of myriad other organisms. Even the local point diversity of herbivorous insects remains an unknown. Basic discovery will

continue to make many crucial contributions to tropical forest ecology.

Finally, I will return to the nine-fold explosion in tropical forest publication rates mentioned in the first paragraph. The publication rate for extra-tropical forests increased just 4.3-fold over the same time interval. This latitudinal difference has been driven by a 15-fold increase in publication rates for authors from tropical countries. The increase in tropical forest publication rates falls to 5.8-fold when authors with tropical addresses and unknown addresses are excluded. The rapid increase in publication rates for authors from tropical countries is very uneven. Scientists from Brazilian and Mexican institutions increased their rate of tropical forest publications by 71-fold between 1975–1979 and 2002–2006 (from just 9 to 644 articles). Perhaps not surprisingly the authors of this volume include one Brazilian (Chapter 21) and two Mexicans (Chapter 5). Increasingly, scientists from Brazil, Mexico, and other tropical countries will formulate the tropical forest research agenda and determine what research has the greatest future impact. This is a positive development.

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Chapter 23

CHANCE AND DETERMINISM IN TROPICAL FOREST SUCCESSION

Robin L. Chazdon

OVERVIEW

Based on chronosequence studies and permanent plot studies, I describe successional changes in vegetation structure, population dynamics, species richness, and species composition in tropical forests. Tropical secondary forests initially increase rapidly in structural complexity and species richness, but the return to pre-disturbance species composition may take centuries or longer – or may never occur. Vegetation dynamics during secondary tropical forest succession reflect a complex interplay between deterministic and stochastic processes. As more studies of succession are carried out, the importance of stochastic factors is becoming more evident. Features of the local landscape, such as proximity to forest fragments or large areas of diverse, mature forest, strongly impact the nature and timing of species colonization. Disturbance history and previous land use strongly determine the extent to which resprouts or remnant mature-forest vegetation dominate during secondary forest regeneration and, together with soil fertility, strongly influence the composition of dominant pioneer species. Community assembly processes during succession appear to be strongly affected by dispersal limitation at all stages. Initial community composition, often dominated by long-lived pioneer species, changes extremely slowly over time. Tree seedlings that colonize only after the stem exclusion stage of succession may take decades or longer to recruit as trees, thus contributing to a slow rate of change in tree species composition. Long-term studies within individual sites do not support the notion that secondary succession in tropical forests leads to convergence in species composition, as suggested by some chronosequence studies. Predictable, directional changes do occur in vegetation during tropical forest succession, but convergent trends are more apparent for structural features, life-forms, and functional groups than for species composition. Although relay floristics may well describe changes in species dominance early in succession, there is little evidence to support this model during later phases of succession. Clearly, there is much more work to be done, with a particular need to avoid biasing initial site selection and to use experimental approaches in combination with long-term studies. Through these research approaches, we will be better able to identify the effects of deterministic versus stochastic processes in tropical forest succession.

INTRODUCTION: SUCCESSIONAL THEMES AND VARIATIONS

Secondary succession is the long-term directional change in community composition following a disturbance event, often at a large (>1 ha) spatial scale. Hurricanes, floods, landslides, windstorms, cyclones, and fires are examples of major natural disturbances that can initiate the successional process (Waide and Lugo 1992, Whitmore and Burslem 1998, Chazdon 2003). Human impacts

are responsible for most of the world's secondary forests, however (Brown and Lugo 1990, Guariguata and Ostertag 2001). The relationship between land use and forest succession is complex; the type and intensity of land use, soil fertility, and the surrounding landscape matrix all strongly influence the nature and rate of successional processes (Purata 1986, Hughes *et al.* 1999, Johnson *et al.* 2000, Moran *et al.* 2000, Pascarella *et al.* 2000, Silver *et al.* 2000, Ceccon *et al.* 2003, Ferguson *et al.* 2003, Myster 2004).

A major challenge in studies of tropical forest successional dynamics is to reveal the relative importance of deterministic versus stochastic processes affecting species composition, spatial distributions, and their rates of change. Niche-based processes, such as the competition–colonization trade-off and successional niche theory, generate predictable transitions between early and late successional species with distinct sets of life-history traits (Rees *et al.* 2001). But the rate of these transitions and the particular species involved can vary widely across forests within the same region and climate. Although these theoretical predictions reflect an underlying theme of successional change observed in many temperate and tropical forests, the overall importance of stochastic factors during vegetation succession remains poorly understood. Deterministic successional processes are defined as orderly and predictable changes in species abundance determined by climate, soils, and species life history (Clements 1904, 1916), whereas stochastic processes are influenced by random events that are not predictable in nature.

The most direct way to study succession is to follow changes in structure and composition over time. Yet in tropical forests, few studies have examined changes in vegetation structure and composition over time for more than a few years (Chazdon *et al.* 2007). Consequently, our knowledge of successional processes derives almost exclusively from chronosequence studies (Pickett 1989, Guariguata and Ostertag 2001). Space-for-time substitutions make (often) unrealistic assumptions, such as similar environmental conditions, site history, and seed availability across sites as well as over time. Moreover, sites are often carefully selected to minimize variation in abiotic conditions, and site selection may favor stands that conform to preconceived models of successional development of vegetation. Successional areas available for study may also represent a biased sample of the landscape due to underlying differences in soil fertility, slope, elevation, or drainage – these environmental factors often influence patterns of land use and abandonment. Ideally, chronosequence studies should be based on a series of replicated plots of different ages selected using objective criteria (land-use records,

soil type). Ruiz *et al.* (2005), for example, randomly selected 59 forests in six age classes (based on aerial photographs and satellite imagery) in a 56-year tropical dry forest chronosequence on Providencia Island, Colombia. Long-term studies within individual sites, however, are more effective in providing a mechanistic understanding of succession, population dynamics, and effects of local site factors on recruitment, growth, and mortality of different growth forms and size classes (Foster and Tilman 2000, Sheil 2001). These aspects are poorly understood for most tropical secondary forests, but are essential for a complete understanding of successional dynamics and their local, regional, or geographic variations. Knowledge of successional processes is also critically needed to develop ecologically sound tropical forest management and restoration programs.

Successional studies in tropical forests have generally emphasized the tree component, ignoring the community dynamics of tree seedlings and saplings and non-tree life-forms. Moreover, few studies have examined non-arboreal life-forms, such as herbs, shrubs, and lianas (Dewalt *et al.* 2000, Martin *et al.* 2004, Capers *et al.* 2005). Thus, we have a limited understanding of how the plant community as a whole is changing during succession within forests of known history. Successional forests are embedded within a dynamic regional landscape that determines the pool of species available for colonization, the genetic diversity of seed sources, the availability of pollinators, herbivores, seeds, dispersal agents, and pathogens, and the likelihood of repeated human perturbations. Finally, within successional as well as mature tropical forests, climate fluctuations and human-induced environmental changes simultaneously exert pressure on a wide range of ecological processes (Ramakrishnan 1988, Clark 2004, Laurance *et al.* 2004, Malhi and Phillips 2004). All of these factors lead to a highly complex set of interactions that ultimately drive community dynamics, and thus seriously challenge our ability to distinguish the relative importance of niche-based versus neutral processes (Vandermeer 1996).

In this chapter, I examine patterns and processes of vegetation dynamics during secondary tropical forest succession. First, I present a brief

discussion of successional theory, as it applies to forest succession. I then describe the basic framework of tropical forest succession, based on chronosequence studies in wet, dry, and montane tropical forests. I discuss the few long-term studies that describe successional change in vegetation structure, population dynamics, composition, and species richness within individual forests. Finally, I consider the question of whether secondary tropical forests ever reach a stable climax community. Throughout, I re-examine the role of deterministic versus stochastic processes during different phases of tropical forest succession and across different types of landscapes.

THEORETICAL BACKGROUND

Successional theory has a long history, originating at the beginning of the twentieth century with studies by Cowles (1899), Clements (1904, 1916), Gleason (1926), and Tansley (1935). Clements viewed succession as a highly orderly, deterministic process in which the community acts as an integrated unit, analogous to the development of an individual organism. The endpoint of succession is a stable climax community (homeostasis), which exists in equilibrium with the contemporary climatic conditions. This deterministic view was later emphasized by Odum (1969) in his pioneering studies of ecosystem development.

Critics challenged this view of communities as highly integrated units and stressed the importance of chance events and the role of individualistic behavior of species during succession. Gleason (1926) viewed succession as a largely stochastic process with communities reflecting individualistic behavior of component species, whereas Tansley (1935) argued that regional climate alone does not determine the characteristics of climax vegetation. Watt (1919, 1947) examined successional processes in small-scale disturbances within forests, emphasizing the unstable spatial mosaic created by patch dynamics. Egler (1954) maintained that the initial floristic composition of an area was a strong determinant of later vegetation composition, emphasizing the role of site pre-emption and the long-term legacy of chance colonization events.

During the 1970s, ecologists replaced equilibrium paradigms with alternative non-equilibrium theories and began to emphasize the mechanistic basis of ecological processes. Vegetation dynamics during succession were viewed as emerging from properties of component species (*sensu* Gleason 1926), rather than from a holistic, organismal concept of community development (Pickett *et al.* 1987). The mechanistic approach of Drury and Nisbet (1973), Pickett (1976), Connell and Slatyer (1977), Bazzaz (1979), and Noble and Slatyer (1980) emphasized changes in resource availability during succession in relation to the life-history characteristics of dominant species. These works led to the predominant contemporary view that vegetation change emerges from the interactions of component populations as they ebb and flow in response to changing environmental conditions (Rees *et al.* 2001). The intermediate disturbance hypothesis (Connell 1978, 1979) also grew out of this non-equilibrium thinking, and predicted that species diversity would reach a peak during intermediate phases of succession and would decrease to low levels (approaching monodominance) in a late successional community in the absence of disturbance. The notion that competitive exclusion is prevented by disturbance events, thus permitting more species to coexist, has now become well accepted (Huston 1979, Wilkinson 1999, Sheil and Burslem 2003).

Early studies of tropical vegetation showed strong evidence of non-equilibrium viewpoints. In his studies of forests of Ivory Coast, Aubréville (1938) questioned the concept of stable "climax" vegetation, replacing it with a concept of gap-phase dynamics that Richards (1952) termed the "mosaic theory" and Watt (1947) termed the "cyclical theory of regeneration" (Burslem and Swaine 2002). Studies by Eggeling (1947) and Jones (1956) on old secondary forests of Uganda and Nigeria, respectively, were used to provide detailed empirical support for Connell's non-equilibrium theory. Webb *et al.* (1972), in one of the first experimental studies of tropical forest regeneration, emphasized the importance of chance dispersal events and highly patchy spatial distributions in early phases of secondary succession.

Three conceptual frameworks have been applied to studies of vegetation dynamics during tropical forest succession. The first framework examines the role of deterministic (predictable) versus stochastic (unpredictable) factors in vegetation dynamics. If deterministic forces predominate (as viewed by Clements), successional communities that share the same climate should exhibit predictable convergence in community composition over time, regardless of differences in initial composition (Christensen and Peet 1984). This view also holds that mature forests within a region should maintain stable and similar species composition (Terborgh *et al.* 1996). Environmental variation across sites, among other factors, can create divergence in species composition during succession, rather than convergence (Leps and Rejmánek 1991).

A second framework is based on the timing of colonization of species during succession and contrasts the models of initial floristic composition versus relay floristics (Egler 1954). Relay floristics involves colonization by later successional species well after the initial disturbance, whereas initial floristic composition applies when species from all stages colonize early following disturbance but reach peak abundances at different times according to their growth rates and longevity (Gómez-Pompa and Vázquez-Yanes 1974, Bazzaz and Pickett 1980, Finegan 1996).

A third framework focuses on the relative importance of species life-history traits and species interactions in determining the balance among mechanisms of tolerance, inhibition, and facilitation during succession (Connell and Slatyer 1977, Rees *et al.* 2001). Later successional species may establish due to facilitation or release from inhibition by earlier successional species, or due to intrinsic life-history characteristics such as arrival time, growth rate, and longevity with no direct interaction with early species.

These conceptual frameworks also apply to community assembly processes in mature forests (Young *et al.* 2001), in the study of gap-phase dynamics (Whitmore 1978), in assessing the role of random drift versus environment in determining spatial variation in species composition (Hubbell and Foster 1986), and in developing neutral models of community composition based

on source pools and dispersal limitation (Hubbell *et al.* 1999). Moreover, the relative importance of successional processes may change over time (Connell and Slatyer 1977, Walker and Chapin 1987).

AN OVERVIEW OF TROPICAL SECONDARY FOREST SUCCESSION

Phases of succession

In its general outline, tropical forest succession is similar to temperate forest succession (Oliver and Larson 1990), but the recovery of forest structure can be particularly rapid in tropical wet climates (Ewel 1980). The sequence and duration of successional phases may vary substantially among tropical forests, depending upon the nature of the initializing disturbance and the potential for tree colonization and forest structural development. Vegetation succession following hurricanes follows a different trajectory than post-agricultural succession in the same region (Boucher *et al.* 2001, Chazdon 2003). Similarly, post-extraction secondary forests follow different successional trajectories than swidden fallows (Riswan *et al.* 1985, Chokkalingam and de Jong 2001, Chazdon 2003).

The first phase of secondary succession is often dominated by herbaceous species (grasses or ferns in abandoned pastures), vines, shrubs, and woody lianas (Budowski 1965, Kellman 1970, Gómez-Pompa and Vázquez-Yanes 1981, Ewel 1983, Toky and Ramakrishnan 1983, Finegan 1996). This building phase is termed the "stand initiation stage" by Oliver and Larson (1990). Dramatic changes in vegetation structure and composition occur during the first decade of succession in tropical regions, as woody species rapidly colonize abandoned fields (see reviews by Brown and Lugo 1990 and Guariguata and Ostertag 2001). Rapid growth of early colonizing trees ("pioneers") can bring about canopy closure in only 5–10 years after abandonment. Early woody regeneration consists of new seedling recruits from seed rain and the seed bank (Benitez-Malvido *et al.* 2001) as well as resprouts; the latter often dominate the early woody community (Uhl *et al.* 1981,

Kammesheidt 1998). Resprouting is the most common form of early plant establishment in swidden fallows (Uhl *et al.* 1981, Kammesheidt 1998, Perera 2001, Schmidt-Vogt 2001), and may lead to the development of uneven cover and clumped tree distributions during the first phase of regrowth (Schmidt-Vogt 2001).

Following hurricanes, logging, and superficial fires, resprouting residual trees dominate early regenerating woody vegetation, often bypassing the stand initiation phase. Studies of forest regeneration following Hurricane Joan in southeastern Nicaragua provide a detailed description of this “direct regeneration” process, where the post-hurricane forest composition was similar to that of the mature, pre-disturbance forest due to extensive resprouting of damaged stems (Yih *et al.* 1991, Vandermeer *et al.* 1995, 1996, Boucher *et al.* 2001).

Following abandonment of intensive agriculture, such as cattle pastures, the first seedling shrub and tree recruits emerge from the seed bank or newly dispersed seed and tend to be wind-, bird-, or bat-dispersed species with small seeds that require direct light or high temperatures to germinate (Uhl and Jordan 1984, Vázquez-Yanes and Orozco-Segovia 1984). Rotting logs (Peterson and Haines 2000) and remnant trees (Elmqvist *et al.* 2001, Slocum 2001, Guevara *et al.* 2004) facilitate colonization of bird- and bat-dispersed tree species in abandoned pastures, whereas the aggressive growth and clonal spread of shrubs, vines, and lianas can inhibit seedling recruitment of light-demanding tree species (Schnitzer *et al.* 2000, Schnitzer and Bongers 2002). In Sri Lanka, dense growth of bamboo can suppress tree regeneration during early succession following swidden agriculture (Perera 2001).

The stand initiation phase of succession is the most vulnerable to invasion by exotic species (Fine 2002). In many tropical regions, particularly on islands, exotic pioneer species form dense, monospecific stands in early phases of succession, such as *Lantana camara* in Australia, *Piper aduncum* in eastern Malesia, and *Leucaena leucocephala* in Vanuatu (Whitmore 1991). Invasive plant species can have long-lasting effects on tropical forest succession. Invasive grasses such as *Saccharum spontaneum* in Panama and

Imperata cylindrica in Indonesia can inhibit regeneration of woody species (D’Antonio and Vitousek 1992, Otsamo *et al.* 1995, Hooper *et al.* 2004). Young secondary forests in the Caribbean islands of Puerto Rico and the Dominican Republic are often dominated by exotic species (Rivera and Aide 1998, Aide *et al.* 2000, Lugo 2004, Lugo and Helmer 2004, Martin *et al.* 2004). In moist forests of Madagascar that were logged (50 years earlier) or cleared for subsistence agriculture (150 years earlier), populations of invasive species persisted throughout the successional trajectory, with a lasting effect on woody species richness and composition (Brown and Gurevitch 2004). Inhibitory effects of invasive species are not limited to tropical islands, however. In subtropical northwestern Argentina, native tree recruitment in 5–50-year-old secondary forests was negatively related to the dominance (% basal area) of the invasive tree *Ligustrum lucidum* (Oleaceae; Lichstein *et al.* 2004).

Canopy closure signals the beginning of the second phase, termed the “stem exclusion phase” by Oliver and Larson (1990). As early colonizing trees increase rapidly in basal area and height, understory light availability decreases dramatically. These changes are associated with decreasing woody seedling density and high seedling mortality of shade-intolerant species of shrubs, lianas, and canopy trees (Capers *et al.* 2005). Low light availability in the understory favors establishment of shade-tolerant tree and palm species that are dispersed into the site from surrounding vegetation by birds and mammals (particularly bats). By 10–20 years after abandonment, the stage is set for a shift in the abundance and composition of tree species that gradually plays out over decades, if not centuries. This constitutes the third and longest phase of forest succession.

This third phase of forest succession corresponds to the “understory reinitiation stage” of Oliver and Larson (1990) and is characterized by a gradual turnover of species composition in canopy and subcanopy layers. The advance regeneration in the understory often contains species characteristic of mature old-growth forests (Guariguata *et al.* 1997, Chazdon *et al.* 1998, Denslow and Guzman 2000). Eventually, the

death of canopy trees creates gaps, increasing resource availability for new recruits. Over long periods of time, perhaps several hundred years, the canopy will consist of mixed cohorts of tree species that were not present early in succession, thus initiating the “old-growth stage” of forest dynamics (Oliver and Larson 1990). Old-growth forests are characterized by a complex vertical and horizontal structure, presence of large, living, old trees, large woody debris, and highly diverse canopy and understory vegetation (Budowski 1970).

Ecological processes affecting vegetation dynamics and species composition vary among successional phases. During the stand initiation phase of succession, stochastic processes of dispersal and colonization are likely to influence community composition most strongly, whereas later in succession, deterministic processes, such as species

fidelity to environment, may become more powerful factors (Walker and Chapin 1987). Thus, processes of dispersal, seed germination, resprouting, and rapid growth of shade-intolerant species determine early species composition (Table 23.1). Some studies show that rates of seed predation are highest during this stage of tropical forest succession (Hammond 1995, Peña-Claros and de Boo 2002, Andresen *et al.* 2005), but these patterns may be species- and site-specific (Holl and Lulow 1997). After canopy closure, forest dynamics in the stem exclusion phase (phase 2) reflect high mortality of shade-intolerant shrubs and lianas, suppression and mortality of shade-intolerant tree species within the subcanopy, and high recruitment of shade-tolerant species that are primarily dispersed by birds and bats (Table 23.1). These processes have been described in detail by Chazdon *et al.* (2005) and Capers *et al.* (2005)

Table 23.1 Vegetation dynamics processes across successional phases in tropical forests.

| |
|---|
| <p><i>Phase 1: Stand initiation phase (0–10 years)</i></p> <ul style="list-style-type: none"> Germination of seed-bank and newly dispersed seeds Resprouting of remnant trees Colonization by shade-intolerant and shade-tolerant pioneer trees Rapid height and diameter growth of woody species High mortality of herbaceous old-field colonizing species High rates of seed predation Seedling establishment of bird- and bat-dispersed, shade-tolerant tree species <p><i>Phase 2: Stem exclusion phase (10–25 years)</i></p> <ul style="list-style-type: none"> Canopy closure High mortality of lianas and shrubs Recruitment of shade-tolerant seedlings, saplings, and trees Growth suppression of shade-intolerant trees in understory and subcanopy High mortality of short-lived, shade-intolerant pioneer trees Development of canopy and understory tree strata Seedling establishment of bird- and bat-dispersed, shade-tolerant tree species Recruitment of early colonizing, shade-tolerant tree and palm species into the subcanopy <p><i>Phase 3: Understory reinitiation stage (25–200 years)</i></p> <ul style="list-style-type: none"> Mortality of long-lived, shade-intolerant pioneer trees Formation of canopy gaps Canopy recruitment and reproductive maturity of shade-tolerant canopy and subcanopy tree and palm species Increased heterogeneity in understory light availability Development of spatial aggregations of tree seedlings |
|---|

Notes: Names of phases are derived from Oliver and Larson (1990). Dispersal remains a key process throughout, but shifts from predominantly long-distance dispersal initially to predominantly local dispersal towards the end of phase 3. Ages reflect approximate rates of succession as observed in the Caribbean lowlands of Costa Rica.

for secondary forests in northeastern Costa Rica. Over time, these processes lead to the long understory reinitiation phase, characterized by mortality of long-lived pioneer tree species, formation of canopy gaps, and reproductive maturity of shade-tolerant tree species and their continued recruitment into the canopy. The relatively homogeneous, low light conditions in the understory of phase 2 forests act as a strong filter for recruitment of the shade-tolerant tree species that will later recruit in the canopy. Understory light conditions become more heterogeneous during later stages of succession and create more diverse opportunities for seedling and sapling recruitment than in phase 2 forests (Nicotra *et al.* 1999). Thus, the understory reinitiation phase (phase 3) is associated with increasing species richness and evenness in all vegetation size classes. Successional phases do not correspond strictly with age classes, however, as actual rates of succession are known to vary widely with climate, soils, previous land use, and landscape configuration (Arroyo-Mora *et al.* 2005).

Successional patterns of tree colonization

Studies of vegetation dynamics in mature tropical forests emphasize two divergent life-history modes of trees: pioneer and shade-tolerant species (Swaine and Whitmore 1988). Yet studies of successional forests clearly suggest a far greater complexity in regeneration modes and life histories. For example, Budowski (1965, 1970), Knight (1975), and Finegan (1996) noted the distinction between short- and long-lived pioneer tree species in lowland forests of Mesoamerica. Secondary forest in phase 2 (stem exclusion phase) in northeastern Costa Rica is actually composed of three groups of pioneer tree species: (1) short-lived shade-intolerant species, (2) long-lived shade-intolerant species, and (3) long-lived shade-tolerant species. All of these species colonize early, but the “short-lived” species (which tend to be smaller in stature as well) generally do not persist in the canopy beyond the first 10–15 years (Budowski 1965, 1970). The inheritors of the canopy are two groups of “long-lived”

trees that grow to large stature and persist for many decades or longer. One group of these secondary forest trees lacks seedling or sapling recruits in older secondary forests (Figure 23.1a), whereas a second group shows abundant recruitment of seedlings and saplings (Figure 23.1b). This second group of “shade-tolerant pioneers” has been recognized in only one previous study (Dalling *et al.* 2000), but plays an important role in wet forest succession, at least in northeastern Costa Rica. These species are common or dominant species in mature forests of the region, such as *Pentaclethra macroloba*, *Hernandia didymantha*, and *Inga thibaudiana* (Figure 23.1). Canopy individuals of these species appear to reach reproductive maturity within 15–20 years during secondary forest succession (personal observation).

Although many shade-tolerant tree species (and canopy palm species) colonize during the stand initiation phase (e.g., Kenoyer 1929, Knight 1975, Peña-Claros 2003), other species do not appear in the seedling community until decades have passed, and these tend to occur in low abundance and frequency. Finegan (1984) maintained that forest species generally do not colonize during the stand initiation phase of succession and that some facilitation is required for their establishment. He proposed a composite mechanism of succession, whereby short- and long-lived pioneers establish early and forest species colonize later, during the stem exclusion and understory reinitiation phases (phases 2 and 3). Later establishment could reflect limited seed dispersal, differences in abundance of mature trees in surrounding communities, or specific regeneration requirements that are met only during later stages of succession. We have little detailed information on patterns of tree colonization within individual sites in the second and third phases of succession, as most studies have emphasized vegetation dynamics during the stand initiation phase (Finegan 1996, Myster 2004).

Gómez-Pompa and Vásquez-Yanes (1981) first proposed that tropical forest succession follows a relay floristics model (*sensu* Egler 1954), where species achieve their greatest abundance at different times, such that dominant species shift temporally across a successional sere. A study

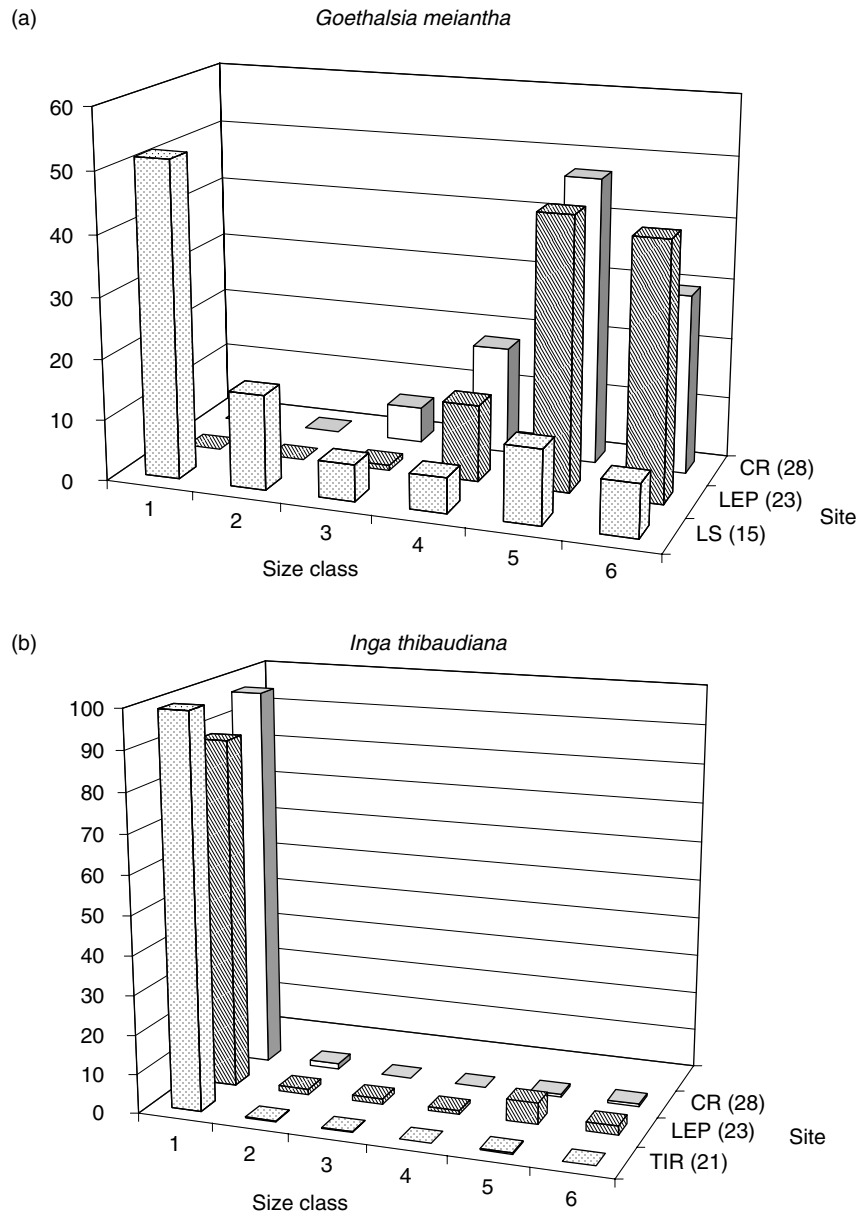


Figure 23.1 Size distributions of (a) a shade-intolerant pioneer (*Goethalsia meiantha*) and (b) a shade-tolerant pioneer (*Inga thibaudiana*) in three secondary forests of different age since abandonment in northeastern Costa Rica. Forest sites are abbreviated as follows: CR = Cuatro Rios, LEP = Lindero el Peje; LS = Lindero Sur; TIR = Tirimbina. Site ages are in parentheses. Size classes are defined as follows: 20 cm ht > class 1 < 1 cm dbh ≤ class 2 < 2.5 cm dbh ≤ class 3 < 5 cm dbh ≤ class 4 < 10 cm dbh ≤ class 5 < 25 cm dbh ≤ class 6.

of forest succession in the Bolivian Amazon, based on two chronosequences following shifting cultivation, generally supported this model. Peña-Claros (2003) distinguished four different groups of tree species: (1) species that reach maximum abundance during phase 1 of succession; (2) species that dominate in phase 2; (3) species that reach their peak abundance in phase 3 or old-growth forests; and (4) mid-successional species that showed no trend in abundance with stand age. Species in the third group varied in their period of first colonization; some species were present in 2–3-year-old stands, whereas others first appeared in stands 20 years old (Peña-Claros 2003). Few data are available to test this model during the late phases of succession.

Forest structure

The most striking changes that occur during tropical forest succession are structural changes, such as the increase in canopy height, density of trees ≥ 10 cm diameter at breast height (dbh), basal area, and above-ground biomass. In wet lowland areas of northeastern Costa Rica, these structural changes cause a reduction of understory light availability to below 1% transmittance of diffuse photosynthetically active radiation within 15–20 years after abandonment (Nicotra *et al.* 1999). Leaf area index increases rapidly and often reaches a peak before other components of forest structure (Brown and Lugo 1990). Mean photosynthetic light availability near the forest floor was not significantly different between young secondary forest (15–20 years old) and mature forest stands in wet tropical regions of Costa Rica (Nicotra *et al.* 1999). Light availability in young secondary forests, however, is more spatially homogeneous than in mature forests due to even-aged canopy cover and absence of treefall gaps (Nicotra *et al.* 1999). Structural changes during tropical forest succession are well documented in reviews by Brown and Lugo (1990), Guariguata and Ostertag (2001), Chazdon (2003), and Chazdon *et al.* (2007). Tropical secondary forests often show rapid structural convergence with mature forests (Saldarriaga *et al.* 1988, Guariguata *et al.*

1997, Ferreira and Prance 1999, Aide *et al.* 2000, Denslow and Guzman 2000, Kennard 2002, Peña-Claros 2003, Read and Lawrence 2003). Rates of structural convergence depend strongly on soil fertility (Moran *et al.* 2000), soil texture (Johnson *et al.* 2000, Zarin *et al.* 2001), and the duration and intensity of land use prior to abandonment (Uhl *et al.* 1988, Nepstad *et al.* 1996, Hughes *et al.* 1999, Steininger 2000, Gehring *et al.* 2005).

Species richness and diversity

Many chronosequence studies have also documented rapid recovery of species richness and species diversity during tropical succession, but these trends are strongly influenced by soil fertility and land-use history (Brown and Lugo 1990, Guariguata and Ostertag 2001, Chazdon 2003, Chazdon *et al.* 2007). Inconsistent methods, use of different stem size classes, and presentation of biased diversity measures confound accurate comparisons of species abundance and richness across study plots. Moreover, many chronosequence studies lack replication of age classes and use small plots 0.1 ha or less in size. Finally, the ability to identify and locate forest areas that have remained undisturbed for over a century has proven challenging in many tropical areas (Clark 1996, Willis *et al.* 2004). These problems help to explain the inconsistent patterns in species diversity found across chronosequence studies.

Species richness and stem density are positively correlated in virtually all vegetation samples (Denslow 1995, Condit *et al.* 1996, Chazdon *et al.* 1998, Sheil 2001, Howard and Lee 2003), confounding comparisons of species number among sites that differ in overall stem density or area sampled (Gotelli and Colwell 2001). Thus, the best way to compare species richness among sites is to use rarefaction techniques to compare the accumulation of species within a site as a function of the cumulative number of individuals sampled (Chazdon *et al.* 1998). It is not appropriate to use sample data to compare species per stem, because species accumulation is a non-linear function of the number of individuals

in a sample (Chazdon *et al.* 1999, Gotelli and Colwell 2001). Indices of species diversity, such as Shannon–Weiner or Simpson indices, that emphasize evenness or dominance, respectively, are less biased by density than simple species counts per unit area (species density). Species richness estimation techniques can also be useful in correcting for sample-size bias (Colwell and Coddington 1994, Chazdon *et al.* 1998), although no method (including Fisher’s α ; Condit *et al.* 1996) can overcome limitations of sparse data due to small sample areas or small numbers of stems. Here, I restrict my comparisons to studies based on diversity indices or that have incorporated rarefaction techniques or species richness estimators to compare species richness across stands within a chronosequence.

A variety of temporal patterns have been observed in successional studies of tropical forests. Eggeing (1947) conducted the first study of species composition across a tropical forest chronosequence, based on a series of 10 plots in Budongo Forest, Uganda. He concluded that there was an initial rise in species numbers (species density) during succession, reaching a peak at intermediate phases of succession, followed by a decline during late succession. His analysis, however, did not take into account differences in tree density among the plots. Sheil (2001) applied the rarefaction method of Hurlbert (1971) to these data, and confirmed that the plots of intermediate age indeed had the highest species richness of trees ≥ 10 cm dbh, whereas late successional plots had the lowest species richness. In a comparison of early, intermediate, and late successional tropical dry forests in Costa Rica, Kalacska *et al.* (2004) also found higher species richness of trees ≥ 5 cm dbh in sites of intermediate age. This trend was further supported by the Shannon diversity index and an incidence-based, non-parametric species richness estimator (Kalacska *et al.* 2004). In northwest Guyana, 60-year-old secondary forest had higher species richness (Fisher’s α) of trees ≥ 10 cm dbh than mature forests (van Andel 2001).

Other studies have documented continuously increasing species diversity with stand age, but these studies often lack comparative data for older secondary forests or “primary” forests. In swidden

fallow succession in northeastern India, Toky and Ramakrishnan (1983) found a linear increase in species diversity (Shannon index) with fallow age during the first 15–20 years. Chinaea (2002) found that the Shannon diversity index for trees ≥ 2.5 cm dbh increased with age since abandonment in sites from 1 to 45 years old in eastern Puerto Rico. In a 56-year chronosequence in tropical dry forest on Providencia Island, Colombia, Ruiz *et al.* (2005) found that species richness, based on rarefaction of stems ≥ 2.5 cm dbh, increased steadily with increasing age of abandonment; abundance-based, non-parametric species richness estimators confirmed this trend. Peña-Claros (2003) found a similar pattern for two 40-year chronosequences in Bolivian Amazon forest; Shannon diversity index increased with stand age for understory, subcanopy, and canopy vegetation layers. Along a chronosequence in Argentinian subtropical montane forests, Grau *et al.* (1997) also found that Shannon diversity of trees ≥ 10 cm dbh increased in young stands and by 45–50 years reached values similar to mature forests in the region. In the upper Rio Negro of Colombia and Venezuela, Saldarriaga *et al.* (1988) found similar values of Shannon and Simpson’s indices for stems ≥ 1 cm dbh between 40-year-old stands and mature forests.

Several studies in the Old World tropics suggest that species richness recovers very slowly, even in older secondary forests. Shannon diversity for trees ≥ 10 cm dbh in a 55-year-old secondary rainforest in central Kalimantan, Indonesia was significantly lower compared with adjacent mature forest (Brearley *et al.* 2004). In Singapore, Turner *et al.* (1997) also found significantly lower Shannon diversity for trees ≥ 30 cm dbh in approximately 100-year-old secondary forest compared with primary forest. Even after 150 year of recovery following clearing for subsistence agriculture, moist forests of Ranomafana National Park, Madagascar showed significantly lower species richness (estimated number of species/250 stems) than uncleared forests (Brown and Gurevitch 2004).

In general, canopy trees (≥ 30 cm dbh) show slower recovery of species richness during succession compared with seedlings and saplings due to the longer time required for shade-tolerant

species to reach these size classes. Using sample-based rarefaction curves, Guariguata *et al.* (1997) found that species richness of trees ≥ 10 cm dbh was consistently lower in young secondary stands (15–20 years) compared with mature forest stands in wet lowland forest of Costa Rica, but these differences were less pronounced or absent for woody seedlings and saplings. Similarly, Denslow and Guzman (2000) found that estimates and indices of seedling species richness did not vary with stand age across a 70-year tropical moist forest chronosequence in Panama.

Species composition

Species composition appears to vary independently of species richness across a chronosequence (Finegan 1996, Guariguata and Ostertag 2001, Chazdon 2003). Even where species richness and forest structure of secondary forests are not significantly different from those of mature forests, species composition remains quite distinct in secondary forests for periods up to centuries (Finegan 1996). Early differences in colonizing vegetation and land use can impact the successional trajectory of a particular site (Janzen 1988, Mesquita *et al.* 2001). In 6–10-year-old forest of the Brazilian Amazon, *Cecropia*-dominated logging clear-cuts were considerably more diverse than *Vismia*-dominated stands on abandoned pastures (Mesquita *et al.* 2001), reflecting facilitation of recruitment by residual vegetation following logging (Chazdon 2003). Variation in species composition due to site history and environmental heterogeneity creates a major challenge in comparing floristic composition of secondary forests with mature forests within a single landscape (Whitmore 1973, 1974, Ashton 1976, Duivenvoorden 1996, Swaine 1996, Clark *et al.* 1998). First, this variability makes it difficult to select representative mature forest areas for robust comparisons of species composition between secondary and mature forests. Second, land-use history may interact with environmental conditions, such as elevation, soil fertility, slope, and drainage. Third, in many instances, remaining mature forest areas have been exposed to human and natural disturbances of variable spatial and temporal impact

(Whitmore and Burslem 1998) or may continue to be influenced by disturbances that occurred centuries ago or longer (Denevan 1992, Brown and Gurevitch 2004, Wardle *et al.* 2004, Willis *et al.* 2004). Consequently, the use of nearby mature forests as a benchmark can be problematic.

Tropical dry forests tend to exhibit fewer successional stages and faster recovery of species composition compared with wet forests (Ewel 1980, Murphy and Lugo 1986, Perera 2001, Kennard 2002). In tropical dry forests, late successional species are tolerant of hot and dry conditions, resprouting is common (Denslow 1996), and wind dispersal is more common than in wet forests. Furthermore, due to the higher frequency of large-scale fire, even the oldest, least disturbed dry forests in the landscape may be undergoing late stages of secondary succession (Kennard 2002). Most of the present closed-canopy mature forests in dry regions of Sri Lanka, for example, are secondary forests on abandoned formerly irrigated cultivated land (Perera 2001). Fire tends to damage small stems more than large stems, and frequent fires may therefore retard succession (Goldammer and Seibert 1990, Cochrane and Schulze 1999).

Although we do not yet know what processes influence the rate of change of species richness during tropical wet forest succession, three factors are probably involved. First, long-lived pioneer species persist well into the understory reinitiation stage, pre-empting space and slowing the rate of species turnover. Second, low light availability in young and intermediate aged second-growth forests and the rarity or absence of canopy gaps may restrict establishment and recruitment of gap-requiring tree species (Nicotra *et al.* 1999, Dupuy and Chazdon 2006). Third, low seed availability may limit colonization of tree species. Dispersal limitation is high in recently abandoned clearings and in secondary as well as mature tropical forests (Dalling *et al.* 1988, Holl 1999, Wijdeven and Kuzee 2000, Muller-Landau *et al.* 2002, Hooper *et al.* 2004, Svenning and Wright 2005). The extent of dispersal limitation may be greatest for species with animal-dispersed seeds. Following logging in lowland rainforests of eastern Borneo, seed addition increased seedling recruitment for five

animal-dispersed species, but not for two wind-dispersed species (Howlett and Davidson 2003). Even when secondary forests are close to mature forests, seed dispersal can be a major limitation (Gorchov *et al.* 1983, Corlett 1992, Turner *et al.* 1997, Wunderle 1997, Duncan and Chapman 1999, Holl 1999, Ingle 2003). Martinez-Garza and Gonzalez-Montagut (1999) found that dispersal limitation of forest interior species resulted in pioneer dominance for 30–70 years in abandoned pastures of lowland tropical regions of Mexico.

Under ideal conditions, the early arrival and establishment of some shade-tolerant canopy tree species (including palms) can increase the rate of succession, as these species often grow rapidly in height and reach reproductive maturity within 20–30 years, when they begin to produce their own seedling cohorts (Sezen *et al.* 2005). Many of these species are capable of recruitment into canopy tree size classes (≥ 25 cm dbh) in the absence of gaps (Chazdon unpublished data). If seedlings of shade-tolerant and slow-growing species colonize later, during the stem exclusion or understory reinitiation phase, their recruitment to the canopy may require several decades or longer (Finegan and Chazdon unpublished data).

Few studies have statistically compared species composition across a tropical forest chronosequence. Terborgh *et al.* (1996) compared species composition in early, middle, and late successional floodplain vegetation with mature floodplain forests of the Manu River in Peru. In this study, cluster analysis showed that the five mature floodplain forests were most similar to each other in species composition and that they differed considerably from successional forests. A detrended correspondence analysis suggested a clear directionality to species compositional changes during floodplain succession in this region. A similar approach was used by Sheil (1999) to compare canopy tree species composition for the 10 sites in Eggleing's (1947) study of forests in Budongo, Uganda. This analysis indicated a consistent compositional progression across the plot series, with the ranking of plots conforming precisely to Eggleing's original successional sequence. Within this set of plots, there was strong evidence

for compositional convergence towards a species-poor forest dominated by *Cynometra alexandri* (ironwood; Sheil 1999). An alternative interpretation, suggested by Sheil (1999), is that Eggleing originally selected the plots to fit his preconceived model of an ordered developmental successional series in Budongo Forest.

Life-forms, functional groups, and life-history traits

During succession, life-form composition shifts dramatically, particularly during the stand initiation phase. During the first 5 years of post slash-and-burn succession, Ewel and Bigelow (1996) documented decreases in herbaceous vines, increases in shrubs and trees, and a dramatic increase in epiphytes between 30 and 36 months. Grass and forb dominance peaked after 3 years in an abandoned pasture in Puerto Rico (Myer 2003). Vines, ferns, and persistent grasses can impede establishment and growth of woody shrubs and trees in abandoned pastures (Holl *et al.* 2000, Hooper *et al.* 2004). More often, however, early dominance of large-leaved herbaceous species facilitates establishment of shade-tolerant woody species (Denslow 1978, Ewel 1983). Across a sequence of stands from 20 to over 100 years old in Barro Colorado Island and surrounding areas, liana abundance decreased as a function of stand age (Dewalt *et al.* 2000). Liana size increased during succession, however, resulting in a lack of correspondence between stand age and liana basal area. Liana diversity (as measured by Fisher's α) was higher in young stands than in older stands, up to 70 years in age (Dewalt *et al.* 2000).

Considering only woody life-forms in wet tropical forests of northeastern Costa Rica, Guariguata *et al.* (1997) found that shrub abundance was significantly higher whereas understory palm abundance was significantly lower in young secondary stands (15–20 years old) compared with old-growth stands. Mature canopy palms (stems ≥ 10 cm dbh) were also significantly more abundant in old-growth stands. Woody seedlings in second-growth permanent plots in this region

showed decreasing abundance of shrubs and lianas and increasing abundance of canopy and understory palms over a 5-year period, mirroring chronosequence trends (Capers *et al.* 2005).

Several studies have documented successional changes in leaf phenology and wood characteristics. Tropical dry forests are a mix of deciduous and evergreen species, but early successional communities tend to be dominated by deciduous species, with increasing abundance of evergreen species later in succession. A trend towards increasing leaf lifespan with succession is well established for tropical wet and seasonal forests (Reich *et al.* 1992). Another well-established trend is that of increasing wood density from early to late succession (Whitmore 1998, Suzuki 1999, Muller-Landau 2004).

Successional trends have also been observed in seed dispersal modes and other reproductive traits. During the first few months of succession following clear-cutting in northeastern Costa Rica, nearly all newly establishing plants were of wind-dispersed species (Opler *et al.* 1977). This fraction decreased over time, while the percentage of fleshy-fruited species increased. Within 3 years, animal-dispersed species composed 80% of the species, similar to values in mature forest. Self-compatibility is more prevalent among species in early successional stages, whereas out-crossing is more common in later stages as dioecy and self-incompatibility increase (Opler *et al.* 1980). Chazdon *et al.* (2003) compared the distribution of reproductive traits in woody vegetation in relation to successional stage in forests of northeastern Costa Rica. In second-growth trees, relative abundance of species with explosive seed dispersal, hermaphroditic flowers, and insect pollination was higher, whereas relative abundance of species with animal dispersal and mammal pollination was lower compared with old-growth forests (Chazdon *et al.* 2003). In the same study area, Kang and Bawa (2003) examined variation in flowering time, duration, and frequency in relation to successional status. Supra-annual flowering was proportionately less common in early successional species than in species of later successional stages, but flowering time did not vary consistently with successional status (Kang and Bawa 2003).

SUCCESSIONAL DYNAMICS WITHIN INDIVIDUAL FORESTS

Few studies have examined successional dynamics within individual tropical forests over time. Here, I highlight these studies and examine whether the trends observed within individual forests are similar to those trends described from chronosequence studies. This topic is discussed in more detail by Chazdon *et al.* (2007), based on case studies from northeastern Costa Rica and Chiapas, México. Sheil (1999, 2001) and Sheil *et al.* (2000), examined long-term changes in species richness and composition in five plots (1.5–1.9 ha) originally studied by Eggeling (1947) in Budongo, a semi-deciduous forest in Uganda. In plot 15, a former grassland at the forest margin, the number of tree species more than 10 cm dbh increased from 25 to 74 over 48 years and rarefaction revealed an increase in species per 200 individuals from 22 to 45 (Sheil 2001). But few shade-tolerant stems or species were present over these years (Sheil *et al.* 2000), suggesting a strong influence of savanna species. In plot 7, which was a late successional stand in the 1940s, species richness increased and the number of smaller stems increased. Over 54 years, there was a relative increase in shade-tolerant stems, but a decrease in the proportion of shade-tolerant species (Sheil *et al.* 2000). Larger stems in this plot showed lower average mortality rates (1% per year) than those reported for other tropical forests. Considering all of the plots in Eggeling's study that were also monitored over 54 years (several had silvicultural interventions), Sheil (2001) found that each plot showed increases in species richness, exceeding the richness found within Eggeling's original chronosequence. The peak in species richness observed for intermediate successional sites in Eggeling's original series was not observed in the time series data, however. Using a size-structured approach, Sheil (1999) compared temporal trends in species composition within plots. In the time series analysis, only one plot supported Eggeling's model, but overall the temporal changes within plots did not support the model of convergent vegetation composition during succession or a mid-successional peak in species richness.

Vandermeer *et al.* (2000) monitored annual changes in species richness of forests severely damaged by Hurricane Joan in eastern Nicaragua. Over a 10-year period, species richness of stems ≥ 3.2 cm dbh increased two- to three-fold. After only 10 years of recovery, the hurricane-damaged forests had higher species richness than undisturbed forests within the region (Vandermeer *et al.* 2000). These same six hurricane-damaged forests were subjected to an analysis of species compositional trajectories, including 12 years of data (Vandermeer *et al.* 2004). Analyses of multidimensional distance were used to assess whether these sites were becoming more similar over time, as predicted by deterministic (Clementsian) models of succession. Results indicated that three of these six pairwise comparisons showed increasingly divergent vegetation, two showed increasingly similar vegetation, and one showed no significant trend. Thus, Vandermeer *et al.* (2004) concluded that successional pathways were not convergent among these different plots, perhaps due to differences in initial conditions or to later successional dynamics.

Lang and Knight (1983) followed changes in tree growth and dynamics over a 10-year period in a 60-year-old secondary forest on Barro Colorado Island, Panama. All species ≥ 2.5 cm dbh were followed in a single 1.5 ha plot. During this period, mortality exceeded recruitment and net tree density declined by 11%. Trees above 10 cm dbh increased in density and stand basal area and biomass increased accordingly. Species varied widely in mortality rates and in diameter growth rates. The overall turnover rate of stems in the plot was 7.3%, with pioneer species showing overall declines in abundance and species typical of older forest recruiting into the canopy (Lang and Knight 1983).

Few studies have monitored vegetation dynamics of second-growth forests on an annual basis (Breugel *et al.* 2006, Chazdon *et al.* 2007). Chazdon *et al.* (2005) monitored mortality and recruitment annually for 6 years for trees ≥ 5 cm dbh in four 1 ha plots in wet second-growth, lowland rainforests in northeastern Costa Rica. In 12–15-year-old stands, abundance decreased 10–20% in the small size class (5–10 cm dbh), but increased 49–100% in the

large size class (≥ 25 cm dbh) over 6 years. Common species changed dramatically in abundance over 6 years within plots, reflecting high mortality of early colonizing tree species and high rates of recruitment of shade-tolerant tree and canopy palm species. Mortality rates of small trees (5–9.9 cm dbh) were higher in younger than in older stands, but large trees (≥ 25 cm dbh) showed low rates of mortality, averaging 0.89% per year across stands and years. Most tree mortality occurred in overtopped individuals and therefore did not lead to the formation of canopy gaps. Tree mortality in these young secondary forests (particularly for trees ≥ 25 cm dbh) was highly sensitive to dry season rainfall, even during non-El Niño Southern Oscillation years (Chazdon *et al.* 2005). Woody seedling density in these four secondary forest plots declined over 5 years, whereas Shannon diversity and the proportion of rare species increased (Capers *et al.* 2005). Among plots, seedling species composition showed no tendency towards convergence over this period.

These studies support the hypothesis that successional dynamics are being driven by high mortality of light-demanding species (mainly in small size classes) and simultaneous recruitment of shade-tolerant trees into the canopy (Rees *et al.* 2001), with low mortality of long-lived pioneer species in the canopy. Vandermeer *et al.* (2004) documented high rates of mortality of suppressed trees beneath the canopy in 10–14-year-old forests recovering from hurricane damage. In secondary forests developing after pasture abandonment in Costa Rica, mortality rates of large trees appear to be lower compared with mature tropical forests, whereas recruitment of trees into canopy size classes is high (Chazdon *et al.* 2005). Thus, trees recruit to canopy positions in the absence of canopy gaps in these second-growth forests. Whereas canopy gaps are thought to drive much of the dynamics of canopy tree recruitment in mature tropical forests, the *absence* of canopy gaps seems to drive species turnover in secondary forests during the transition from phase 2 to phase 3.

The few studies conducted to date suggest that rates of recruitment, mortality, growth, and species turnover are particularly high within

smaller size classes (<10 cm dbh) during the stand initiation phase and decrease as stands enter the understory reinitiation phase of succession (Breugel *et al.* 2006). The decreased rates of change in species and stem turnover over time reflect an increased relative abundance of slow-growing, shade-tolerant species overall, but particularly in smaller size classes (Chazdon *et al.* 2007).

RECRUITMENT LIMITATION DURING SUCCESSION

Many studies have examined the relative importance of biotic and abiotic factors that affect seedling establishment and recruitment during tropical forest succession. These factors, such as light availability, seed predation, and non-local seed dispersal, vary in importance across successional stages (Figure 23.2). During early stages of succession in abandoned fields and pastures, for example, seedling recruits originate from the seed bank and from non-local seed rain, and these factors assume high importance in controlling seedling establishment (Young *et al.* 1987, Dupuy and Chazdon 1998, Benitez-Malvido *et al.* 2001). Seed predation rates are initially high in abandoned fields (Uhl 1987), and several

studies suggest that rates of mammalian seed predation (post-dispersal) decrease during succession (Hammond 1995, Notman and Gorchoff 2001).

Light availability is uniformly high in abandoned fields, but becomes increasingly limiting for seedling recruitment as forest cover increases during succession. Gaps are small and relatively uncommon in young secondary forests (Yavitt *et al.* 1995, Nicotra *et al.* 1999, Denslow and Guzman 2000), but increase in size and frequency in later stages of succession. In a 1.5 ha plot, Lang and Knight (1983) documented 13 new canopy gaps created by treefalls during a 10-year observation period in a 60-year-old secondary forest on Barro Colorado Island, whereas no gaps had been observed in this site previously. Gap creation in young secondary forests (phase 2) resulted in increased abundance and species richness of woody seedlings (Dupuy and Chazdon 2006). It is therefore likely that canopy gaps are associated with increased abundance and species richness of regenerating seedlings during the understory reinitiation phase of secondary forest succession as well as during the old-growth phase (Nicotra *et al.* 1999; Figure 23.2). Canopy gaps promote increases in tree species richness through increasing overall levels of recruitment as well as permitting establishment and

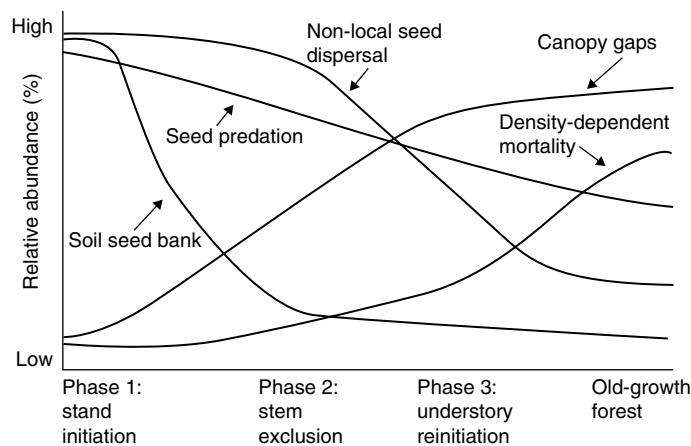


Figure 23.2 Shifting relative importance of biotic and abiotic factors that affect seedling recruitment and mortality across tropical forest secondary succession following abandonment of cultivated fields or pastures.

recruitment of light-demanding species (Denslow 1987, Hubbell *et al.* 1999, Brokaw and Busing 2000).

During early stages of succession, shade-tolerant tree species are not yet reproductively mature and therefore seeds must be dispersed from nearby or distant mature forests or forest fragments, if remnant trees are not present (Guevara *et al.* 1986). As shade-tolerant species recruit to canopy positions and become reproductively mature, local seed shadows increase the potential for density-dependent effects on seedling recruitment and growth (Janzen 1970, Connell 1971; Figure 23. 2). Mean seed dispersal distances also are expected to decrease. Ultimately, these successional trends in seedling recruitment and spatial distribution of reproductive trees influence the abundance, species composition, and genetic composition of saplings and trees (Sezen *et al.* 2005).

During the end of the stand initiation phase of succession, when the forest canopy begins to close, fast-growing, shade-intolerant colonizing tree species are present as canopy trees and are also found as smaller individuals in the understory, as seedlings and saplings. As time progresses and the understory becomes more shaded, however, these shade-intolerant tree species are eliminated from the seedling and sapling pool and shade-tolerant species not present in the canopy colonize these small size classes (Guariguata *et al.* 1997). Chao *et al.* (2005) predicted that, as secondary forests mature, compositional similarity between tree species and seedlings or saplings would initially be high (phase 1), but would quickly decline to a minimum during intermediate stages of succession (phase 2) followed by an increase later in succession as shade-tolerant trees reach reproductive maturity and produce seedlings that can establish, grow, and survive (phase 3). Using an abundance-based estimator of the Jaccard index, Chao *et al.* (2005) found that compositional similarity between seedling and tree assemblages and between sapling and tree assemblages was, indeed, initially high in the youngest (12-year-old) stand, as predicted. As the forest matures, tree seedling and sapling pools gradually become enriched by shade-tolerant species not represented as canopy trees, resulting

in a decrease in compositional similarity that reached a minimum in the 23-year-old stand. This minimum similarity represents a point in forest succession of maximum recruitment limitation for both seedlings and saplings. In the 28-year-old second-growth plot, the abundance-based Jaccard index increased, reflecting recruitment of shade-tolerant species in all three size classes. The similarity index continued to increase and stabilized at 0.4–0.5 in two old-growth stands.

IS THERE AN ENDPOINT TO SUCCESSION?

The distinction between old secondary forests and mature forests is often blurry. Budowski (1970) pointed out several features that distinguish “climax” from old secondary forests in the Neotropics, including abundant regeneration of dominant shade-tolerant canopy tree species, slow-growing species, trees with dense wood and large gravity- or animal-dispersed seeds, lower abundance of shrubs, highly diverse and abundant epiphytes, and abundant large woody lianas.

Does succession ever reach a stable climax? This is a difficult question to address because the process of succession can occur over broad spatial scales. The successional framework described here applies to large-scale disturbances that lead to relatively homogeneous regenerating stands. As stands develop and spatial heterogeneity increases due to canopy gaps or other disturbances, small-scale patch dynamics and dispersal limitation begin to exert a strong influence on community composition and organization. Thus, different late successional forest stands are likely to show divergence in species composition due to exogenous disturbances or endogenous heterogeneity, even if they shared a similar early successional trajectory. For tropical forests, there is much reason to question the notion of a stable climax (Clark 1996).

Just as responses to disturbance can move forests off a late successional trajectory, historical legacies of human disturbance can influence long-term patterns of species composition in forests that are not visibly disturbed at present. In Central Africa, the dominant tree species in

many old-growth forests recruit poorly, even in canopy gaps (Aubréville 1938, Jones 1956). More than 20% of the tree species in old-growth forests of southern Cameroon showed a preference for recruitment in shifting cultivation fields. The presence of charcoal in almost a third of the areas sampled supports the view that these forests are currently undergoing late stages of succession (van Gemerden *et al.* 2003). Evidence from other studies confirms that large-scale disturbances in rainforest areas throughout the world have been caused by widespread historical human impact (Denevan 1992, White and Oates 1999, Bayliss-Smith *et al.* 2003, Willis *et al.* 2004).

If there is no stable endpoint to the successional process, we are forced to view all forests as points along a successional continuum. We must also recognize that we may never be able to reconstruct the initial (pre-disturbance) species composition of a successional forest. The challenge is then to identify how biotic and abiotic factors at a range of spatial scales influence the successional trajectory of particular forests. This task may ultimately require experimental approaches at the scale of entire communities and landscapes, but such large-scale experiments will be challenging to execute and manage over long time periods. A mixed approach involves conducting experimental studies combined with monitoring of long-term changes in vegetation dynamics in sets of replicated stands that initially span a range of successional ages but share similar abiotic conditions.

SUCCESSION IN RELATION TO LANDSCAPE PATTERN

Forest succession occurs within the context of the surrounding landscape. As tropical landscapes become more deforested and fragmented over time, these landscape patterns will influence both the pattern and the processes of secondary forest succession. In shifting cultivation fields of Belize, composition of woody and herbaceous species was significantly influenced by distance to older forest, but species richness and evenness were not significantly affected (Kupfer *et al.*

2004). Abandoned fields close to intact forest had greater densities of successional woody taxa that are common in seasonally dry, subtropical forests.

Landscape-level studies clearly show that secondary forests more frequently develop in areas close to or bordering existing forest patches and that species diversity and composition recover more quickly in areas close to large forest patches (Tomlinson *et al.* 1996). Although comparative studies are greatly needed, these trends may be more representative of neotropical regions than in East Asian forests, where mature forest species often fail to recruit, even in adjacent second-growth forests (Turner *et al.* 1997). In this case, recruitment failure may be due, at least in part, to the extinction or rarity of large frugivores, which are important dispersal agents for large-seeded mature forest species (Turner *et al.* 1997). In montane Costa Rica, secondary forests were more likely to occur near old-growth forests, at increased elevation, on steeper slopes, further from roads, in areas of lower population density, and within forest reserves (Helmer 2000). Distance to older forest was a key predictor of species richness and diversity in a landscape-scale study of secondary forests in Puerto Rico (Chinae 2002). Chinae and Helmer (2003) examined the effect of landscape pattern on species composition in secondary forests in Puerto Rico, based on a series of 167 forest inventory plots (each approximately 120 m²) that varied in climate, land-use history, and landscape structure. Canonical correspondence analysis based on nine variables explained only 16% of the total variance in species abundances. Land use covaried with elevation and substrate, so variation in species composition of secondary forests was generated by interactions between biophysical and socioeconomic forces (Chinae and Helmer 2003). Species composition of abandoned coffee plantations (at higher elevations) remained distinct from that of abandoned pastures (at lower elevations). Distance to large forest patches (at least 3800 ha) was also a significant factor explaining variation in total and native species richness, although the effect was small in this large-scale study (Chinae and Helmer 2003).

Tropical forests are among the most complex and diverse ecosystems in the world. It should

be no surprise, therefore, that the process of transformation from a massively disturbed forest or an abandoned agricultural field or pasture to a community resembling the original structure, species richness, life-form composition, and species composition is prolonged, often idiosyncratic, and strongly contingent upon history and chance events.

Clearly, there is much more work to be done, with a particular need to avoid biasing initial site selection and to use experimental approaches in combination with long-term studies. Through these research approaches, we will be better able to identify the effects of deterministic versus stochastic processes in tropical forest succession.

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