



Tropical Rainforests

Past, Present, and Future

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Overview:
The History and Ecology of
Tropical Rainforest Communities

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The biologists and natural historians of the nineteenth century had a prescient fascination with the species richness of lowland tropical forests (Bates 1864; Belt 1874; Wallace 1878). More than a hundred years later, we remain fascinated, yet not sufficiently close to understanding the origins and long-term maintenance of high species diversity in the tropical forest biome. Thus, a principal aim of this volume is to accelerate the understanding of tropical rainforests through increased recognition that evolutionary processes, in addition to ecological ones, strongly influence the species composition of local communities. As we will see in the chapters of part I, questions regarding the relative roles that ecology and evolution play in the assembly and persistence of tropical forest communities are deeply intertwined, and at a time when biodiversity is being lost at an unprecedented rate, they are among the most important questions in biology.

Although attitudes are changing rapidly, many ecologists have argued that history can be safely ignored. Simply put, because species interactions—principally competition—have rapid dynamics relative to climatic or geologic change, communities reach local equilibria fast enough to overwrite the trace of history (MacArthur 1965; Ricklefs 1989). However, diversity differences among communities occupying similar habitats in different regions (so-called diversity anomalies) provide a strong indication that history has a lasting effect on the species richness of local communities. For example, diversity anomalies between local tree communities in the rainforests of Africa and the Neotropics indicate that regional differences in species richness translate into differences in local species richness. As Richards (1952) noted, “whatever the true explanation for the poverty of the African rain forest, it can hardly be due to any ecological factor operating at the present day.”

Diversity anomalies indicate that historical factors reach down through time, interacting with ecological processes to determine patterns of local diversity. But a strong role for historical/regional processes is difficult to reconcile with local

processes operating on time scales several orders of magnitude shorter in duration. Ricklefs (1989) pointed out that the putatively weak force of historical/regional processes might be reconciled with their apparent imprint on local diversity if the outcomes of competitive exclusion were prolonged to evolutionary time scales. The experiments of Gause (1934) and others notwithstanding, it may be rare in nature that one species excludes another in ecological time. The competitive equivalence of species is a principal assumption of Stephen Hubbell's neutral theory of biodiversity and biogeography (2001; Hubbell, chap. 4 in this volume). Under the neutral theory, species characterized by even modest population sizes persist for long periods of evolutionary history. Furthermore, even a small increase in the time course of competitive exclusion beyond the tens of generations often considered by ecologists (Ricklefs 1989, table 3) brings this local community process into temporal register with the regional process of dispersal, and even with speciation under Hubbell's (2001) point mutation mode of species formation.

Ricklefs (1987, 1989; Ricklefs and Schluter 1993b) has long argued that a major synthesis of ecology and evolution is necessary to adequately interpret the development of biological communities. Although we are still a long way from the desired synthesis, part I of this volume fosters a more dualistic approach to the investigation of tropical rainforest assembly, maintenance, and conservation. It is fitting that Ricklefs leads off part I, and the book, with a chapter presenting two phylogenetic methods aimed at providing insight into the role that historical factors have played in establishing regional and local differences in species richness. Phylogenetic analysis of species production, dispersal, ecological adaptation, and extinction in relation to geologic, geographic, and environmental history is key to understanding regional differences in diversity and, in turn, local diversity anomalies. Sister-taxon phylogenetic analysis provides one profitable direction of investigation because differences in the contemporary species richness of sister clades located in different regions must have resulted from differences in the net rate of diversification (speciation minus extinction). Thus, sister-taxon phylogenetic comparison provides a means for identifying differences in morphology, ecology, or geographic distribution that set regional differences in species number. The second method advocated by Ricklefs is increased use of phylogenetic analysis to separate the contributions of time and speciation rate to species diversity in order to determine the relative ages of clades constituting regional species pools or local ecological communities.

Phylogeny and species identification (taxonomy) also play a role in assessing the relative importance of ecological drift in establishing species richness and relative abundance. According to Hubbell's neutral theory (2001), described

in chapter 4, local diversity is controlled by the rate of speciation and by the size of the regional biogeographic unit within which evolutionary lifetimes" (Hubbell 2001) particularly to the degree that species are of similar abundance mode, thus yielding species that are more likely to be recognizable. The evolution of species is controlled by assigned probabilities of speciation and extinction. Models of phylogenetic reconstruction (Mooers, and Harvey 1992; Nee, 1992) of speciating or going extinct is controlled by the age, leading to the prediction that common species, compared with rare species, and common species. Thus, the loss of species is much more rapid than the gain of species. These processes might occur on regional scales. Simplified model systems or microcosms

Because ecological drift is a stochastic process, separated in time (or space) should lead to different compositions. In the absence of speciation rate, local species richness is not a genuine steady state between speciation and extinction. Changes in species richness based on the fossil record are often used to infer speciation rates. In chapter 5, John Flenley presents a simple test using pollen and spore fossil data by establishing a relationship between species diversity with decline in latitudinal diversity gradient. The reliability from the arboreal pollen record is a good quality, given that the latitudinal diversity gradient is a prominent feature of earth history because of the latitudinal diversity gradient (species, genera, and families). However, the latitudinal diversity gradient is a reasonable proxy for species richness. The latitudinal diversity gradient in rainforest tree species diversity has been used to test for a positive or negative change in species richness since the Cretaceous. Such a test can falsify diversity change in species richness.

Pollen records from only two sites are used as primary and chronological criteria for testing species number over time. The Borneo site is used to test species number over time, and the pollen taxa

in chapter 4, local diversity is controlled primarily by rates of species diversification and by the size of the metacommunity, defined as the "evolutionary-biogeographic unit within which most member species spend their entire evolutionary lifetimes" (Hubbell 2003). But this is a challenging area of inquiry, particularly to the degree that species form according to the point mutation mode, thus yielding species that are not sufficiently divergent from their parent to be recognizable. The evolutionary unit is the individual, and lineages have no assigned probabilities of speciating or going extinct, as in conventional neutral models of phylogenetic reconstruction (Raup et al. 1973; Gould et al. 1977; Nee, Mooers, and Harvey 1992; Nee, May, and Harvey 1994). Rather, the probability of speciating or going extinct is determined by the relative abundance of a lineage, leading to the prediction that most regionally abundant species are old compared with rare species, and are far more likely to have produced daughter species. Thus, the loss of species through competitive exclusion might not occur much more rapidly than the gain of new species in a community, and both of these processes might occur on much longer time scales than apparent in simplified model systems or microcosms.

Because ecological drift is a stochastic process, samples of local communities separated in time (or space) should have low correlations between their species compositions. In the absence of changes in metacommunity size or in the speciation rate, local species richness should stay the same and should represent a genuine steady state between speciation and extinction (Hubbell 2003). Assessments of temporal changes in species diversity and community membership based on the fossil record are often faulted owing to holes in the record. In chapter 5, John Flenley presents a simple but useful test of the quality of plant pollen and spore fossil data by establishing that the well-documented increase in tree species diversity with decline in latitude can be recovered with a high degree of reliability from the arboreal pollen record. This is a fair test of palynological data quality, given that the latitudinal diversity gradient must be a relatively persistent feature of earth history because it is expressed at multiple taxonomic levels (species, genera, and families). Having verified that the pollen record provides a reasonable proxy for species richness, Flenley sets out to test whether tropical rainforest tree species diversity has increased or decreased during the Pleistocene. Such a test can falsify diversification hypotheses predicting either positive or negative change in species diversity due to climatic fluctuations.

Pollen records from only two sites, Borneo and Amazonia, meet the sedimentary and chronological criteria necessary to assess changes in local species number over time. The Borneo site showed virtually no change in species number over time, and the pollen taxa in the Miocene and Holocene pollen records

were almost identical, whereas the Amazonian site revealed that palynological richness was approximately halved in the Holocene compared with the Miocene. Keeping in mind caveats regarding taxonomic resolution and sample quality between time intervals, the apparent lack of species turnover between the Miocene and Holocene records at the Borneo site falsifies ecological drift and suggests that non-stochastic processes (e.g., niche assembly) have stabilized community composition. A similar pattern of community stability for a temperate forest was observed across a 10,000-year pollen record of red maple, birch, beech, ash, oak, hemlock, and elm trees from cores of lake sediments in southern Ontario (Clark and McLachlan 2003). If the time scale of species turnover through ecological drift is generally longer than the time scale of environmental change at a particular location (Ricklefs 2003), it follows that the palynological record can more easily be used to reject the neutral theory than to support it. Thus, the decline in species number at the Amazonian site documented by Flenley could be considered evidence of ecological drift only in the absence of environmental change over the time interval assessed by the pollen record.

In chapter 6, Paul Colinvaux holds our focus on the Amazon basin during a period of dynamic environmental change and marshes pollen, temperature, CO₂, and geomorphological evidence to advance two important points. The first is that the lowland South American rainforest was a stable formation in the face of Pleistocene climate change. In other words, the forest was never fragmented into the refugia envisioned by Haffer (1969). Second, both species composition and species population sizes varied with climate in Amazonian rainforests. The Amazon pollen record demonstrates the penetration of some montane tree species into the lowland rainforest and hints at changes in the relative abundances of lowland species. Thus, the detailed species composition of Neotropical lowland plant communities varied, but there was no community-level replacement, and what is forested now was forested during the Pleistocene glacial periods. The evidence of changes in species composition and relative abundance presented by Colinvaux is consistent with the species turnover predicted by Hubbell's ecological drift model, but environmental fluctuations can produce the same patterns.

In any event, Colinvaux's stated objective was to write the requiem for Haffer's (1969) extraordinarily resilient refuge theory. A growing body of evidence, including a number of molecular systematic studies (reviewed in Moritz et al. 2000), discounts the importance of forest refugia in increasing the rate of speciation across the Pleistocene ice ages (Bermingham and Dick 2001). Of course, palynological studies, such as those presented here and in part II of this

volume (chapters 18 and 19), take a broad brush; finer brushstrokes are the history of tropical forest evolution. Palynology profits from the integration of pollen and species data, and thus provides well-dated sedimentary records and a clarification at present, however, across tropical environments. The dynamics of the tropics are being reconstructed of relationships between geographic populations. The genetic approach suffers from molecular clocks and the consideration of genetic information to periodize (Bermingham 2001), but the pollen record carried in the genetic diversity of fauna and flora.

The advantage of being able to study has promoted a growing body of work that not only establishes a refined understanding of their distributions, but also provides a framework for any given group of organisms. This approach is epitomized by the work of Colinvaux, which enriched our understanding of the patterns of Neotropical forest evolution and to tease population history and speciation models. In chapter 6, a synthesis of the phylogeographic evidence, which discount the importance of refugia, and relatively high levels of genetic diversity in Amazonian mammals support the Pleistocene, and thus also support the hypothesis that increased rates of Pleistocene forest history that is concordant with tectonic uplift and changes in paleoecology. The temporal dimension of this study is mainly because the basic design of the study incorporates molecular systematics.

volume (chapters 18 and 19) and by Morley (2000), paint history with a very broad brush; finer brushstrokes will undoubtedly be required to represent the history of tropical forests that cover regions as large and complex as Amazonia.

Palynology profits from reliable dating techniques and the long-term integration of pollen and spores into the sedimentary records of catchment basins, and thus provides well-dated snapshots of species richness. The small number of sedimentary records and the coarse taxonomic scale of palynomorph identification at present, however, permit only a first impression of historical change across tropical environments. Second impressions of the evolutionary dynamics of the tropics are being formed, at an increasing pace, from the phylogenetic reconstruction of relationships—most often based on DNA molecules—between geographic populations, species, and higher taxa. The molecular phylogenetic approach suffers from uncertain dating techniques based on molecular clocks and the considerable effort required to accumulate sufficient phylogenetic information to permit integration at the community level (Ricklefs and Bermingham 2001), but gains considerably from the accessibility of a historical record carried in the genome of every member of the contemporary tropical fauna and flora.

The advantage of being able to choose both organisms and locations for study has promoted a growing body of phylogenetic data and analysis that not only establishes a refined evolutionary understanding of tropical species and their distributions, but also permits alternative models of speciation to be tested for any given group of organisms and for any specific geographic region. This approach is epitomized by the studies of Jim Patton and his students, who have enriched our understanding of the species relationships and distribution patterns of Neotropical forest mammals while utilizing explicit analytical methods to tease population history from population structure in order to adequately test speciation models. In chapter 7, Patton and da Silva present an overview and synthesis of the phylogeographic patterns exhibited by Amazonian mammals, which discount the importance of Wallace's (1852) riverine hypothesis. The relatively high levels of genetic divergence documented between populations of Amazonian mammals suggest that these population divergences precede the Pleistocene, and thus also cast doubt on theories such as Haffer's (1969) that posit increased rates of Pleistocene speciation. Rather, the data suggest a deep history that is concordant with, and may have resulted from, episodes of Andean uplift and changes in paleodrainages.

The temporal dimension of regional biodiversity assessment is possible mainly because the basic description of the tropical flora and fauna increasingly incorporates molecular systematic analysis alongside natural history observa-

tion. In turn, molecular divergence, particularly accumulated changes in DNA sequences among contemporary members of the tropical community, provides considerable insight into the ages of species and the timing of their expansions across tropical landscapes (Bermingham and Martin 1998; Perdices et al. 2002; Dick, Abdul-Salim, and Bermingham 2003). As we learn more about the temporal and geographic origins of species, it becomes possible to design conservation strategies that steward not only the biodiversity of today, but also the evolutionary processes that have generated it.

This point is clearly demonstrated in chapter 8 by Fjelds  and coauthors' molecular study of greenbuls, common African forest birds, and galagos, nocturnal African forest and savanna mammals. The study found that in both groups the oldest taxa were widespread in lowland rainforests, while more recently diverged taxa inhabited ecotonal montane habitats in eastern Africa, suggesting a species source/sink relationship between tropical mountains and lowland rainforests. In the framework of conservation strategy, this result indicates that altitudinal habitat gradients represent an important cradle of diversification that needs to be protected.

Ecotonal speciation, the idea that divergent natural selection across environmental transitions might drive phenotypic change and diversification (Endler 1977), presumably results in sufficient character differentiation to permit sympatry of sister species and thus elevated levels of alpha diversity. However, natural selection is usually assumed to be too weak to cause morphological change in the absence of barriers to gene flow. In chapter 9, Smith and co-workers focus attention on the vast African forest-savanna mosaic between contiguous rainforest and savanna, suggesting that the ecotonal speciation model might explain the widespread occurrence of ecotonal populations that are phenotypically differentiated from their central forest relatives. For many rainforest bird species, food quality and habitat structure differ dramatically between ecotones and the central forest, suggesting that selection might explain the observed phenotypic divergence. Smith and colleagues set out to test this hypothesis by estimating levels of gene flow and divergent selection in populations of black-bellied seedcrackers, olive sunbirds, and little greenbuls existing in ecotonal forest patches and in central rainforest areas. Their results provide a tantalizing suggestion that phenotypic diversification can occur in the face of significant gene flow, but they have yet to document the reproductive isolation necessary to support the ecotonal speciation model. But they lay out methods—one intraspecific assay of reproductive divergence and one sister-species test based on distribution patterns—to more generally assess the role that ecotonal speciation has played in the dramatic diversification of tropical species.

Several chapters in this volume, especially high during the Pleistocene, regarding the existence of refugia (chapter 6) rejects the very notion of refugia. A healthy skepticism about the patterns of endemism and the hypothesis still require exploration. A survey of the geographic distribution presented in support of the *refugia hypothesis* (1982a), subspecies endemism, and the refugia proposed on the African continent (1990) pointed to ensure that endemism and species richness is highest in these areas because these areas are in different refugia. Under the refugia would suggest elevated

Owing to the rich species diversity, approaches to understanding the mechanisms of speciation simulations that mimic natural selection and dispersal are needed to decipher contemporary patterns of diversity. Su (chap. 11) provide suggestions for which phenomena such as speciation occur. But even at very limited scales, the task is formidable, and, the data required before dynamic models can be applied to rainforest systems. If such models can guide exploration of the mechanisms (chance) and deterministic processes that influence richness and relative abundance, they would be a valuable heuristic models for landscape-level diversity.

A single contentious issue is the relative importance of chance and deterministic processes in explaining species richness and diversity. Rubinoff, in chapter 12, discusses the role of chance events, life history trade-offs, and other factors in explaining ecologically complex patterns of diversity. The role of ecological interactions as

Several chapters in this book discount the idea that speciation rates were especially high during the Pleistocene, although these authors remain neutral regarding the existence of rainforest refugia during that time. Colinvaux (chapter 6) rejects the very notion of rainforest refugia in the Amazon. We support a healthy skepticism about their existence. Nevertheless, we also recognize that the patterns of endemism that initially swayed biologists to the side of the refuge hypothesis still require explanation. In chapter 10, Keith Brown expands his survey of the geographic distribution of Neotropical butterflies, a pivotal data set presented in support of the refuge hypothesis in Prance's *Biological Diversification in the Tropics* (1982a). The new data suggest at least forty-seven regions of subspecies endemism, many of which strongly overlap with paleoecological forest refugia proposed on the basis of geologic and climatic data. As Nelson and colleagues (1990) pointed out with regard to Amazon refugia, caution is required to ensure that endemism and collecting intensity are not conflated. In addition, species richness is highest at the peripheries of the areas of endemism, presumably because these areas represent zones of contact between species originating in different refugia. Under a refuge model, the lower species richness within refugia would suggest elevated extinction rates during the Pleistocene.

Owing to the rich species diversity of tropical landscapes, empirical approaches to understanding distribution patterns are painstaking. Computer simulations that mimic natural landscape dynamics provide one means for deciphering contemporary distribution patterns of forest organisms. Mackey and Su (chap. 11) provide such a model in order to predict the spatial scales over which phenomena such as disturbance responses are more or less likely to occur. But even at very limited spatial scales, the challenge for meaningful simulations is formidable, and, as the authors note, considerable development is required before dynamic landscape models can be routinely applied to tropical rainforest systems. If successful, however, such models have the potential to guide exploration of the relative roles of stochastic (e.g., ecological drift, disturbance) and deterministic (e.g., niche assembly) processes in establishing species richness and relative abundances at different spatial scales, as well as to provide heuristic models for land managers.

A single contentious assumption of the neutral theory—competitive equivalence among species—raises the hackles of many biologists who strive to explain species richness and coexistence with reference to adaptation. Leigh and Rubinoff, in chapter 12, provide a sweeping overview of the ecological interactions, life history trade-offs, and population regulatory mechanisms that underpin ecologically complex rainforests. The authors consider the dynamics of ecological interactions as the species composition of local communities passes

through climatic oscillations, continental drift, and mass extinctions. In contrast to the neutral theory of chapter 4, Leigh and Rubinoﬀ emphasize the life histories of species, and their ecological interactions with mutualists and pests, as fundamental forces underlying the structure of local rainforest (and coral reef) communities.

The need to gain improved knowledge of the roles that the regional driving force of species production and the local constraining force of competition play in tropical diversity points to increased study of beta diversity, or the turnover in species between communities. Ruokolainen, Tuomisto, and Kalliola (chap. 13) discuss an intriguing paradox from western Amazonia; namely, the discrepancy between high local and low regional species diversity. Western Amazonia harbors some of the most species-rich tropical forests in the world, with over 900 vascular plant species documented in a single hectare of Ecuadorian forest (Balslev et al. 1998). Yet its regional diversity is unremarkable. Renner, Balslev, and Holm-Nielsen (1990) documented a total of 3,100 flowering plant species in the lowlands of Ecuador and estimated that a total of 4,000 might be expected for the entire area (71,000 km²). This implies that a single 1 ha plot harbors nearly a quarter of all the species known for an area 7 million times larger. Ruokolainen and colleagues evaluate this paradox in a detailed spatial analysis of ferns and small trees in the family Melastomataceae in sample sites spanning Ecuador and Peru, and conclude that the anomaly merely reflects our incomplete taxonomic description of tropical plant diversity, rather than a true pattern of low species turnover across the western Amazon. Widespread, common, and easily recognized species in tropical rainforests are typically the first to be named, either because the investigator is already familiar with them or because they are abundantly represented in herbaria and therefore easy to match. Rare and more cryptic species may be identified eventually, but, as the authors suggest, a high percentage (20%–30% of tree species) are likely to remain unidentified. The authors conclude that our current knowledge of Amazonian plant taxonomy, ecology, and biogeography is inadequate for answering even rudimentary questions regarding the spatial scale of species turnover in tropical forests, a point that, taken more generally, resonates across many of the book's chapters.

Condit and colleagues (chap. 14) have had the good fortune to study the less diverse but much better described flora of central Panama. Using inventory plots scattered along the drainage system of the Panama Canal, the authors examine the tree species composition of Panamanian forests along soil substrate and climatic gradients. The authors document high levels of species turnover among plots and little correlation in species assemblages across habitats marked

by similar rainfall or soils. This is not based on habitat selection, but rather on the debate about using environmental variables to explain patterns of species in different groups.

As we saw in chapter 6 by Paulsen, the species composition of tropical rainforests varies at different spatial scales. Climatic dynamics that affect the demographic success of tropical rainforests are important in community structure. Models predict that increased CO₂ emissions and regional warming, increased temperatures, and more frequent droughts (Wright observes in chapter 15, El Niño) will provide a window on the future for many tropical rainforests.

The El Niño Southern Oscillation (ENSO) affects temperature in ways that directly affect the ability for reproduction. Climatic changes affect plant guilds and growth form. The ability to drought is greatest among shallow-rooted herbs and shrubs, and less so for deep-rooted trees. Changes in temperature and rainfall length, appear to act as proximate factors in tree performance (Ashton, Givnish, and Ashton). That tree performance is enhanced during very strong El Niño events, leading to a reduction of seed set, radial growth, and mortality in the community. The ecological effects of ENSO on the community we face the prospect of managing the effects of drought, fire, and flooding (Laurance 2002). This study further suggests that tropical rainforests should be expected to be affected by global climate change.

The chapters in part I are focused on the biogeography of members of regional rainforests and establishing the temporal scale of species extinction. These diverse chapters provide a subject matter sets the stage for a detailed analysis of the Australian Wet Tropics and an assessment of tropical rainforests.

by similar rainfall or soils. This result implies that conservation planning cannot be based on habitat selection alone. Condit and colleagues liken this problem to the debate about using "indicator" groups to designate conservation areas, since many studies find poor correlations between the distribution patterns of species in different groups of higher taxa (Moritz et al. 2001).

As we saw in chapter 6 by Paul Colinvaux, climate change can measurably alter the species composition of rainforest tree communities over geologic time scales. Climatic dynamics that act over ecological time scales can regulate the demographic success of tropical rainforest trees and thereby contribute to changes in community structure. Models of anthropogenic climate change stemming from CO₂ emissions and regional deforestation predict decreased precipitation, increased temperatures, and more intense seasonality in the tropics. As Joe Wright observes in chapter 15, El Niño events share these attributes and provide a window on the future for many tropical rainforests.

The El Niño Southern Oscillation (ENSO) alters cloud cover, rainfall, and temperature in ways that directly limit plant function and the resources available for reproduction. Climatic anomalies may have different effects on different plant guilds and growth forms within a single forest. For example, susceptibility to drought is greatest among epiphytes, intermediate among shallowly rooted herbs and shrubs, and least among deeply rooted trees and lianas. Some changes in temperature and moisture availability, as well as changes in day length, appear to act as proximate cues to initiate reproduction in rainforest trees (Ashton, Givnish, and Appanah 1988). Wright evaluates the hypothesis that tree performance is enhanced during mild El Niño events and reduced during very strong El Niño events, and he finds supporting evidence in his examination of seed set, radial growth, and mortality in the Barro Colorado Island tree community. The ecological effects of El Niño events have broad implications as we face the prospect of managing remnant tropical forests that are subject to drought, fire, and flooding (Laurance, Williamson et al. 2001; Cochrane and Laurance 2002). This study further indicates that even the best-protected rainforests should be expected to experience profound ecological changes resulting from global climate change.

The chapters in part I are first steps toward characterizing the history and geography of members of regional tropical species pools and local communities and establishing the temporal and spatial dimensions of species production and extinction. These diverse chapters cover every major tropical rainforest biome. Their subject matter sets the stage for the integrated historical and ecological analysis of the Australian Wet Tropics rainforests presented in part II and for the assessment of tropical rainforest futures in part III.