Biotic Interactions in the Tropics
Their Role in the Maintenance of Species Diversity

Tropical ecosystems house a significant proportion of global biodiversity. To understand how these ecosystems function we need to appreciate not only what plants, animals and microbes they contain, but also how they interact with each other. This volume synthesizes the current state of knowledge in this area, with chapters providing reviews or case studies drawn from research conducted in both Old and New World tropics and including biotic interactions among taxa at all trophic levels. In most chapters plants (typically trees) are the starting point, but, taken together, the chapters consider interactions of plants with other plants, with micro-organisms and with animals, and the inter-relationships of human-induced disturbance with interactions among species. An underlying theme of the volume is the attempt to understand the maintenance of high diversity in tropical regions, which remains one of the most significant unexplained observations in ecological studies.

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Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity
Edited by David F. R. P. Burslem, Michelle A. Pinard and Sue E. Hartley

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Biotic Interactions in the Tropics
Their Role in the Maintenance of Species Diversity

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Editors’ Preface

It is well known that tropical forests and savannas house a significant proportion of global biodiversity. However, an appreciation of the diversity of interactions among organisms in tropical ecosystems is only just emerging. Interactions among species are important because they affect the growth, survival and reproduction of individuals, but also because they have a key role in structuring communities and in the functioning of ecosystems. A sound knowledge of these interactions is therefore fundamental to understanding how tropical ecosystems work, as well as informing important practical concerns such as conservation, management and carbon sequestration. The aim of this book, and the meeting from which it derives, is to synthesize the current state of knowledge of biotic interactions in terrestrial communities in the tropics. Each of the 22 chapters of this volume provides a review or a case study of interactions among organisms from tropical ecosystems, with a perspective drawn from the organisms and sites with which the individual authors work. Our aim was to draw on research conducted in both Old and New World tropics and to include biotic interactions among taxa at all trophic levels. Most authors have taken plants (typically trees) as their starting point, but taken together the chapters consider interactions of plants with other plants, with micro-organisms and with animals, and the inter-relationships of human-induced disturbance with interactions among species. An underlying theme of the volume is the attempt to explain the maintenance of high diversity in tropical regions, which remains one of the most significant unsolved problems in ecology.

This new synthesis of biotic interactions is particularly timely because current empirical and theoretical advances, as well as technical developments, are yielding important and novel insights into the biology of tropical organisms. These insights result both from a ‘scaling up’ of empirical studies of tropical communities (e.g. the expansion of long-term censuses of tropical forest plots and recent large-scale field experiments), and from more in-depth experimental manipulations (e.g. detailed case studies of interactions across multiple trophic layers). These exciting new data, together with theoretical developments (see, for example, The Unified Neutral Theory of Biodiversity and Biogeography, by S. P. Hubbell;
(Princeton University Press, 2001), have collectively stimulated renewed debate on the relative importance of niche-assembly and dispersal-assembly processes as drivers of species coexistence in tropical forests. Interactions among organisms provide the mechanistic basis for both these sets of processes, and any theoretical reconciliation of alternative views can only emerge from a sound review of the empirical evidence. New evidence is also coming from the application of the techniques of molecular biology to studies of dispersal, population structure and less ‘visible’ taxa such as fungal symbionts and pathogens.

In July 2003, a symposium of the British Ecological Society was convened at Aberdeen University to review these developments in tropical forest ecology and to summarize the recent advances in our understanding of the role of biotic interactions in tropical ecosystem function. The symposium was a joint meeting with the Association for Tropical Biology and Conservation, and attracted a participation of about 500 delegates who made a total of 420 oral and poster contributions. Some chapters of this volume were presented as oral contributions to the plenary sessions at that symposium, while others were commissioned from specialists working in areas that were under-represented among existing contributions. Authors were asked to review their own research in the context of related research in the field.

The chapters of this book are grouped in four sections of unequal length. The variation in the length of the sections parallels, in part, an imbalance in the distribution of research activity by tropical biologists among different taxa, trophic levels and interactions. Part I concerns interactions among plants and their consequences for ecosystem function and theories of species coexistence in tropical forests. In this section, the assumptions that underpin niche-assembly and dispersal-assembly models of species coexistence are explored, and a theoretical reconciliation of these views is presented in the final chapter. Other chapters of this section consider resource use and partitioning and the extent to which trade-offs among life-history traits contribute to ecosystem function and the maintenance of plant species richness. Part II provides an overview of the diversity of interactions among plants and fungi, both as pathogens and as symbionts. It opens with chapters that explore the ecological importance of fungal pathogens and mycorrhizas, particularly in relation to their roles in the maintenance of plant species diversity. Plant-host specificity and environmental variability emerge as key issues affecting patterns of disease and plant response to mycorrhizal infection. The study of plant–microbe interactions has been constrained by the difficulty of species identifications, and is being revolutionized by developments in molecular techniques. The chapters of this section illustrate the application of these new methods and highlight the opportunities and the pitfalls. Plant–animal interactions receive the greatest emphasis in this volume and form the subject of Part III. They are considered from the perspective of animals as pollinators, predators and dispersers. This section also
presents some important reviews and case studies of multi-trophic and complex interactions from the tropics, many of them involving ants, one of the most abundant, diverse and ecologically significant animal groups in the tropics. Finally, Part IV presents a series of case-study reviews of biotic interactions in human-dominated landscapes. In these papers, the impacts of habitat fragmentation, invasive species, human-induced fires and timber management highlight the importance of biotic interactions to the response of communities to human-induced disturbance. The authors consider the evidence for the disruption of biotic interactions and the influence of land-use history and forest history on the outcomes of biotic interactions. The implications of changes in biotic interactions for ecosystem function and management are discussed.

The book emphasizes the richness and diversity of new research on interactions among organisms in the tropics, but, despite this, a small number of unifying themes can be distinguished that cut across groups of related contributions. First, it is evident that no single mechanism will be sufficient to explain the maintenance of tropical forest diversity. There is abundant evidence in this volume for an important role for niche differentiation driven by plant-plant competition, density-dependent recruitment resulting from biotic factors (pathogenic fungi, and seed and seedling predators), dispersal limitation and ecological equivalence. Several contributors thus conclude that the question of whether niche assembly or dispersal-assembly processes are predominant is a quantitative one that is likely to be sensitive to site and species differences. Second, the popular perception that communities of tropical organisms are highly coevolved assemblages with complex trophic structures is supported by studies described in this volume. These chapters provide evidence for direct and indirect interactions across several trophic layers. For example, a case study of Piper–ant interactions spans four trophic levels, whilst myrmecophytes in Cameroon are at the centre of an interlocking set of mutualisms involving ants, plants, bacteria and phloem-feeding insects. These sorts of interactions have important implications for the structure and functioning of food webs in tropical communities since their effects cascade well beyond the two immediate mutualistic partners. The high frequency of ants as model species for this research reflects the importance of this group to a wide variety of interactions and processes in the tropics, particularly mutualistic ones, as illustrated by their key roles in seed dispersal, plant nutrition and plant protection. Third, the book highlights the importance of large-scale data-intensive studies to future progress in understanding tropical ecosystems because they bring together practitioners across disciplinary boundaries. The Center for Tropical Forest Science through its network of large-scale forest-dynamics plots has pioneered the consortium approach to collection of large-scale, long-term and spatially explicit data on trees that has stimulated so many developments in tropical forest ecology. A similar scale of research funding and research effort is now required to catalogue
other taxa and to describe and interpret the highly complex interactions that link them as ecological communities. Finally, several authors emphasize the importance of temporal and spatial variability to particular interactions, and how the outcomes can vary greatly for different scales of investigation. For example, interactions between plants may shift between competitive and complementary during succession. This change is associated with a shift in the dominance hierarchy within the community and results from the differential effectiveness of species to capture light, nutrients and water. Spatial and temporal variability is also a feature of interactions among animals, for example when the outcome of interactions between peccaries and beetles depends on the stage of the peccary population cycle. These considerations have important consequences for the design and interpretation of studies of biotic interactions.

The book illustrates many of the ongoing debates in tropical forest biology, and highlights the opportunities for future research. The extent to which coexisting trees are ecological equivalents or niche-differentiated habitat specialists is not yet resolved, although evidence supporting both perspectives is provided. In particular, the role of trade-offs in determining acquisition of resources, plant-plant competition and niche differentiation is emphasized, but different authors clearly view different traits as most important. For example, in the case of trees, the role of canopy gaps in the maintenance of species richness is still widely debated, despite the fact that this question has stimulated more research than any other in tropical forest ecology. Debate over the importance of herbivory in controlling growth and survival of tropical forest plants has been reactivated by recent research and this issue is reflected in a number of contributions to this volume. Resolution of this question will be contingent on application of new statistical procedures for deriving robust estimates of tissue loss to herbivores from leaf-census data. New statistical and molecular tools are also helping to resolve old questions concerning the importance of long- versus short-distance dispersal of plants, although practitioners of molecular techniques will need to heed the warning provided here that DNA extracted from ‘plants’ is very often mixed with that of fungal associates such as mycorrhizas and endophytes.

Although we have attempted to be as wide-ranging as possible, the book nonetheless contains some significant gaps in its coverage. We regret, in particular, the relative lack of studies centred on tropical African ecosystems and by African researchers. There is also a bias towards research in wetter terrestrial (forest) ecosystems rather than arid ecosystems or semi-deserts, and we have made no attempt to consider biotic interactions in freshwater aquatic or marine ecosystems. We believe that the lack of African-authored and arid-ecosystem studies reflects a genuine imbalance in the literature that was available to authors for review, and we hope that future research will fill these gaps, perhaps in part stimulated by the contributions to this volume.
We are deeply grateful to the many individuals and organizations that have contributed to the production of this volume. Most importantly, we thank the contributing authors and the reviewers of their papers for their tremendous commitment of expertise and time. We acknowledge the generous financial and logistical support of the British Ecological Society and the Association for Tropical Biology and Conservation, and we thank the officers and councillors of both societies for supporting our concept for the meeting. We are especially grateful to Hefin Jones, Hazel Norman and Richard English for their help and advice implementing the symposium.