Wesley Dáttilo · Victor Rico-Gray *Editors*

Ecological Networks in the Tropics

An Integrative Overview of Species Interactions from Some of the Most Species-Rich Habitats on Earth

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Wesley Dáttilo dedicates this book to all his mentors who supported him throughout his academic career on ecological interaction networks, especially Thiago Izzo, Victor Rico-Gray, Paulo Guimarães, Kléber Del-Claro, and Pedro Jordano.

Victor Rico-Gray dedicates this book to Alex Rico Palacios, Carmelo Rico Belestá, Thomasina Gray Wilkinson, and Leonard B. Thien.

Foreword

The astonishing diversity of life is simultaneously a source of wonder and a challenge for those trying to understand how the earth's millions of species are organized across continents and oceans. One approach is to study how each species has adapted to its physical environment and its interactions with other species. Another approach, at the other extreme, is to describe how local or regional ecosystems are organized into broader biogeographic patterns. The study of ecological networks has provided a way of bridging the gap between these extremes. By analyzing who interacts with whom within communities, studies of ecological networks—that is, webs of interacting species—have provided a way to probe how webs assemble as new species arrive, how they dis-assemble as species go locally extinct, and how webs change as species continue to evolve and coevolve.

Ecological Networks in the Tropics provides a thoughtful and forward-looking set of insights into what we have learned from analyses of ecological networks in general and, more particularly, from studies of some of the most species-rich habitats on earth. Finding patterns within these webs requires an ecological understanding of the direct and indirect ecological links among species. The question addressed in these chapters is why use the mathematics and metrics of network theory to find the patterns and infer some of the processes that shape them. The first two chapters consider how and why network approaches have become so useful. *Ings and Hawes* (Chap. 1) weave the historical pathways by which network approaches entered ecological studies, and *Andresen et al*. (Chap. 2) highlight why the great diversity of some tropical communities offers special challenges to our understanding of webs of interacting species. Network approaches cannot answer all the important questions about the diversity of life, but the chapters by *Dehling* (Chap. 3) and *Raimundo et al.* (Chap. 4) show convincingly how these approaches provide a systematic way for ecologists to compare similarities and differences in ecological networks under different ecological conditions.

Network approaches have been applied unevenly to studies of the web of life, but that is changing quickly. So far, they have proven especially insightful for evaluating how plants interact with particular animal lineages such as ants (*Del-Claro et al.,* Chap. 5) or with many other taxa in particular ways, such as with pollinators

(*Vizentin-Bugoni et al.*, Chap. 6), seed dispersers (*Escribano-Avila et al.,* Chap. 7), or herbivores (*López-Carretero et al.*, Chap. 8). These studies have been particularly useful in identifying common patterns in how plants interact mutualistically with other taxa. Even broader insights into patterns of network assembly are becoming possible as other forms of interaction are analyzed using network approaches, including studies of animals and their parasites (*Bellay et al.*, Chap. 9) and analyses of interactions among tropical reef fish (*Cantor et al.*, Chap. 10). Initially, many network studies were based on patterns observed within a single year or a small number of years, but as the number of longer-term studies has increased, so have the opportunities to search for patterns in how networks change over time (*Moreira et al.*, Chap. 11)

There remains much to learn about the ecological, evolutionary, and coevolutionary conditions that shape similarities and dissimilarities among networks of interacting species. Just keeping up on the range of innovative approaches to the study of networks is becoming a challenge in itself (*Antoniazzi et al.*, Chap. 13). The insights gained so far, though, have produced yet more questions about why some aspects of network structure are similar among different forms of interaction, even as other aspects vary. And these studies are motivating the application of yet other ecological and molecular approaches that will allow even deeper and broader insights into the structure and dynamics of interaction networks (*Cagnolo*, Chap. 12). It should not surprise us that these studies of species interactions continue to produce novel questions about the web of life. Species interactions are perhaps the major driver of ongoing evolution and the diversity of life itself.

The greatest current challenges in studies of the organization of biodiversity are to understand how complex networks form among mutualistic, antagonistic, and communalistic species, how local networks assemble into broader regional networks, and how ongoing coevolution among species contributes to the continual reorganization of networks. Tropical communities are those in which Darwin's "entangled bank" is the most entangled. These enlightening chapters on ecological networks show that we have learned much in recent years, that we still have much to learn, and that the study of tropical networks is rapidly expanding our appreciation of the diversity of ways in which the diversity of life is organized.

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Contents

List of Abbreviations

DNA	Deoxyribonucleic acid
EFN	Extrafloral nectaries
J-C	Janzen-Connell effect
URL	Uniform resource locator

Chapter 1
Tropical Biodiversity: The Importance of Biotic Interactions for Its Origin, Maintenance, Function, and Conservation

Ellen Andresen, Víctor Arroyo-Rodríguez, and Federico Escobar

Abstract Most of the Earth's terrestrial biodiversity is found in tropical forests, a fact that fascinates us today as it did the early naturalists of past centuries. It is in this biome where a tremendously high number of coexisting species weave themselves into the most complex web of life, linked together through biotic interactions. These interactions are not only the threads that give structure to biotic communities, but they are also responsible for their evolution and function. In this chapter, we try to render a brief account of the roles that biotic interactions play in (1) the origin of tropical diversity, (2) the maintenance of such diversity through facilitating species coexistence, and (3) the functioning of tropical forest ecosystems. Our fascination with tropical biodiversity is only matched by our fear of losing it. We finish this chapter by stating the undeniable facts, showing how the threads in the web of life are being severed by our own actions. Yet as long as we have some understanding of how the threads of biotic interactions assemble, and if we succeed in conveying the urgency of applying this information, we may be able to keep the web from falling apart.

1.1 Introduction

If one had to mention one common feature among all people ever interested in life on Earth, it would be a fascination with the complexity of living forms and of their intertwining relationships; something that today, we call biodiversity. Biodiversity has many facets, and while the one that has received the most attention is taxonomic diversity, we now recognize the existence and importance of many other components of biodiversity, such as genetic, phenotypic, functional, phylogenetic, and interaction

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diversity. The latter has received increasing attention in the last few decades, particularly in the face of nature's degradation. Every species on Earth interacts directly and indirectly with many other species such that biotic interactions are at the core of most ecological and evolutionary processes. Thus, biotic interactions play fundamental roles in the evolution of biodiversity, the assembly and dynamics of biotic communities, and the functioning of ecosystems (Fig. 1.1; Thompson 1999; Tylianakis et al. 2008; Mittelbach 2012; Vellend 2016).

Nowhere in the world is the complexity of life, in its forms, functions, and interactions, more ubiquitous than in the warm and humid tropics. Tropical forests contain the vast majority of the Earth's terrestrial biodiversity, and most taxa (with notable exceptions) have peak diversities in the tropics (Corlett and Primack 2011). Yet since Humboldt, Darwin, and Wallace, we have not stopped wondering how is it possible that more than 40,000 tree species exist in tropical forests of the world, while fewer than 130 are found in temperate Europe (Slik et al. 2015)? How can 500 ha in a tropical forest harbor over 670 species of butterflies (DeVries 2001)? How can it be that a single species of tropical tree may interact with over 250 different species of herbivorous insects (Novotny et al. 2010)? Questions like these have driven countless scientific publications and will undoubtedly continue to move our research agendas for a long time to come. Over the decades, an increasing number of hypotheses have been proposed for explaining the origin and/or maintenance of the seemingly impossible numbers of species occurring in tropical regional biotas and coexisting in local tropical forest communities (reviewed, among others, by Wright 2002; Brown 2014; Fine 2015). In many of these hypotheses, biotic interactions play a prominent role.

More recently, and motivated by the current global biodiversity crisis that is largely caused by the loss and degradation of tropical forests (Lewis et al. 2015), two additional questions also occupy our research agendas: (1) How does biodiversity affect ecosystem function? and (2) How do we conserve biodiversity? Extensive research has shown strong influences of biodiversity on key aspects of the functioning of both natural and anthropogenic ecosystems, such as productivity, temporal stability, nutrient cycling, and resistance to invasion (Cardinale et al. 2012; Hooper et al. 2012). While traditionally studies on ecosystem function and conservation have focused on the taxonomic component of biodiversity, the need to focus efforts on the diversity of biotic interactions, although already indicated by Janzen (1974) more than 40 years ago, has become a prominent theme since the beginning of the new millennium (Tylianakis et al. 2008, 2010; Cardinale et al. 2012; Valiente-Banuet et al. 2015).

It is not within the scope of this chapter to review the hypotheses proposed for explaining the origin and maintenance of biodiversity in tropical forests or to present a comprehensive account of the key roles that biodiversity plays in ecosystem function, nor of the challenges that we face in conserving it. Rather it is the aim of this chapter to highlight the prominent roles that biotic interactions play in the origin, maintenance, and functioning of tropical forest biodiversity (Fig. 1.1), indicating some implications for the conservation of this unique but vanishing biome.

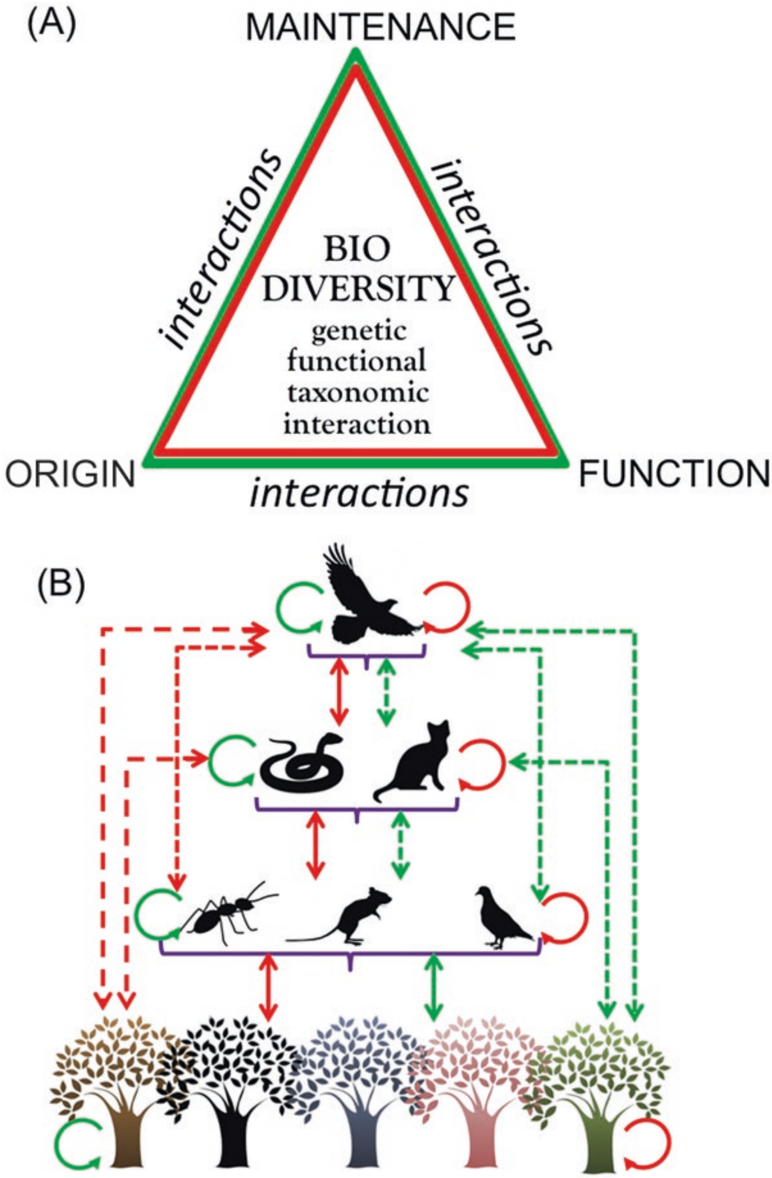

Fig. 1.1 Biotic interactions in tropical forests (**a**) seen as both a component of biodiversity (internal surface of the *triangle*; together with other components such as taxonomic, genetic, and functional diversity), and as a process (*edges* of the *triangle*) responsible for the origin (e.g., speciation due to coevolution and/or specialization), maintenance (e.g., species coexistence due to stabilizing and equalizing mechanisms), and function of biodiversity (e.g., flows of matter and energy between trophic levels and complementarity effect within trophic levels). The two colors of the *triangle* represent both antagonistic (*red*) and mutualistic (*green*) biotic interactions. Any biome can be represented by a similar *triangle*, with *triangle* surface varying according to the biome's biodiversity, which in turn will depend on the amount of biotic interactions (*edges*). Highly simplified schematic representation of the web of life (**b**), depicting

1.2 Biotic Interactions and the Origin of Tropical Forest Biodiversity

New species arise through speciation. A combination of dispersal, drift, and selection then determines the coterie of species coexisting in a given space, at a given time, at any scale (Vellend 2016). Biotic interactions play a role in all these processes, except drift, although the relative importance of drift can certainly be influenced indirectly by biotic interactions, for example, antagonistic interactions that maintain species' populations at low numbers may increase the occurrence of local chance extinction. The central role of biotic interactions in determining the origin of tropical forest biodiversity must already have been quite clear to Wallace when he wrote that "equatorial lands must […] have been unintermittingly subject to those complex influences of organism upon organism, which seem the main agents in developing the greatest variety of forms and filling up every vacant place in nature" (Wallace 1878).

To explain why tropical forests have more species than other biomes, some hypotheses argue that net diversification rates in the tropics must be higher because of either increased speciation and/or decreased extinction rates. Phylogenetic and paleontological evidence exists in favor of both ideas (see Mittelbach 2012 and references therein); however, how do biotic interactions favor higher diversification rates in the tropics? To answer this question, let us first consider how biotic interactions may affect speciation and extinction. Regarding extinction, biotic interactions play a central role in favoring the coexistence of species through different mechanisms, such as facilitating niche differentiation or promoting negative density-dependent mortality, ultimately preventing or slowing down competitive exclusion (see next section). In addition, when biotic interactions involve the movement of gametes or individuals (e.g., pollination and seed dispersal by animals), they can decrease extinction through facilitating patch recolonization, which is a crucial process in avoiding local and regional extinction in today's fragmented tropical landscapes (Arroyo-Rodríguez et al. 2017).

In terms of speciation, while extensive evidence exists on the role that biotic interactions play in microevolution, linking interactions to patterns of macroevolutionary diversification, still remains a challenge, though one that is quickly being

Fig. 1.1 (continued) how the interaction-component of diversity (20 *arrows*) is necessarily much higher than the number of interacting groups of organisms (11 *silhouettes*). Each *silhouette* represents a taxonomic/functional group, which are in turn grouped into four trophic levels: plants, herbivores, carnivores, and apex carnivores. *Straight-line arrows* represent some of the possible biotic interactions between trophic levels, and *loop arrows* some of the interactions within levels; *red arrows* represent antagonistic interactions (competition and consumer–prey interactions), whereas *green arrows* represent mutualistic relationships (symbiosis, free-living mutualisms, facilitation); *solid arrows* indicate direct interactions, while *dashed arrows* indicate indirect or higher-order interactions (e.g., trophic cascades, indirect mutualisms, apparent competition, predator-mediated coexistence). Most terrestrial biomes could be represented by this diagram; the main difference between biomes would be accounted for by the number of species within each trophic level, reaching maximum numbers in tropical forests, with an associated exponential increase of biotic interactions within and between trophic levels. Images in (**b**) used with permission from Microsoft surmounted with advances in community phylogenetics (Weber et al. 2017). Total geographic isolation of populations is not necessary for new species to arise, and two non-exclusive mechanisms that often involve biotic interactions play a central role in promoting parapatric or sympatric speciation: specialization and coevolution (Fine 2015; Fig. 1.1). Specialization along abiotic gradients (e.g., differences in soil nutrients) or biotic gradients (e.g., differences in mutualistic species) can cause divergence among individuals, which may ultimately lead to the origin of a new species (Fleming and Kress 2013; Galetti et al. 2013). Furthermore, in the case of abiotic gradients, biotic interactions may accentuate the gradient's strength, thus promoting habitat specialization, as clearly shown by Fine et al. (2013). In their studies in Amazonia, they have found strong evidence that insect herbivory interacts with a gradient in soil fertility, strengthening the process of plant specialization for either nutrient-rich or nutrient-poor soil, which likely facilitates parapatric plant lineage divergence.

The interaction between plants and herbivorous insects has also figured prominently in the coevolution literature since Ehrlich and Raven (1964) proposed the idea that an arms race between insect herbivores and their host plants might cause an escalating process of specialization and lineage divergence. They further proposed that because insects are not limited by low temperatures in the tropics the above process ought to be faster in the tropics, thus explaining geographic patterns of species diversity. Ehrlich and Raven, however, did not propose specific mechanisms through which herbivores might influence plant diversification (Marquis et al. 2016). Thus, despite the central role of the arms race paradigm in theories about plant and insect diversification, strong evidence validating some of its key assumptions have only recently become available. Results of these studies (see Marquis et al. 2016 and references therein) show that (1) the diversity and complexity of chemical plant defenses increase in a plant lineage as it diverges over evolutionary time, (2) the diversity of plant defenses is positively correlated with both the diversity of herbivorous insects and their degree of specialization, and (3) herbivore specialization promotes plant species richness. Marquis et al. (2016) have proposed two mechanisms through which insect herbivory might promote plant speciation, suggesting that these mechanisms are more likely to occur in the tropics and inviting further research to rigorously test these hypotheses.

Coevolution has many types of outcomes in space and time (Thompson 1999, 2006). Arms race dynamics (e.g., herbivorous insects and host plants), directional selection toward extreme morphologies (e.g., floral spurs and the proboscis of probing pollinators), and extremely specialized interactions (e.g., figs and fig wasps) might depict coevolution quite vividly, but they are not its most common outcomes. Most often coevolution involves the continuous shaping of interacting populations of groups of species (Thompson 1999, 2006), an apparently more "modest" process, but nonetheless pervasive. This is the case of the relationships between plants and their animal pollinators and seed dispersers, which assemble into networks rather than obligate pair-wise mutualisms. According to Thompson (2006), as more species are added to these networks, the possibilities for evolution also increase, creating a "vortex" that promotes biodiversity, i.e., diversity begets diversity.

Recent studies on mutualistic networks strongly suggest that coevolution does indeed shape species characteristics in these networks, resulting in higher rates of evolution (Guimarães et al. 2011). In addition, recent tests support the long-held, though controversial, hypothesis that biotic interactions, in particular pollination, are associated with the macroevolutionary diversification of some angiosperm families and their vertebrate pollinators (Fleming and Kress 2013). On the other hand, while the most important groups of modern frugivorous vertebrates originated after the first appearance of the fleshy-fruited families they consume, major radiations in some plant taxa could have occurred in temporal concordance with radiations of specialized frugivorous animals (Fleming and Kress 2013). For example, the diversification of exceptionally species-rich genera of Neotropical plants, such as *Piper* and *Miconia* (each with over 50 species), could have been caused by the appearance of their highly specialized frugivores: *Carollia* bats and manakins, respectively (Fleming and Kress 2013). While the role of animal seed dispersal in promoting plant speciation may still not be clear, recent studies have shown that the loss of certain frugivores can cause rapid evolutionary changes in important plant traits such as seed size (e.g., Galetti et al. 2013).

Thus, we come back to the question posed above: How do biotic interactions favor higher diversification rates in the tropics? There is little doubt that biotic interactions affect the diversification of lineages (Weber et al. 2017), but for these effects to be stronger in tropical forests, the interactions themselves would need to be more intense and/or frequent in these biomes. The same logic holds in the case of biotic interactions favoring species coexistence in tropical forests (next section). Yet the existence of a latitudinal gradient in the strength of species interactions is still a controversial and unresolved issue (but see Roslin et al. 2017). While some studies present seemingly strong evidence in favor of higher interaction intensity in the tropics (Schemske et al. 2009) or a positive relationship between temperature and rates of ecological interactions (Brown 2014), others do not (Moles and Ollerton 2016). More studies will be needed to determine in which cases and to what extent stronger biotic interactions are responsible for originating and/or maintaining higher biodiversity in tropical forests, in comparison to other biomes.

1.3 Biotic Interactions and the Maintenance of Tropical Biodiversity

Diversity maintenance—the coexistence of species in the same time and space—depends, among other factors, on the outcome of biotic interactions (Fig. 1.1). While traditionally negative interactions such as competition and predator–prey relationships were thought to be the main drivers of community structure, today we know that positive interactions, such as mutualism and facilitation, can also have a tremendous effect on species' presence and abundance (Bronstein 2015). Furthermore, there is a growing realization that the outcomes of particular pair-wise interactions often depend not only on abiotic factors but also on other species, and that these indirect or higher-order interactions play a crucial role in determining diversity (Bairey et al. 2016). Because of the very high species richness in tropical forests, interaction networks in this biome are complex systems, and we are still far from identifying the most important mechanisms for the maintenance of tropical biodiversity though some strong candidates have emerged.

The mystery of species coexistence is that based on the competitive exclusion principle any biome, including tropical forests, should be composed of a few, strongly competitive species in each guild. How then can tropical forests maintain such high species richness? For many years, the idea of niche packing, caused by either the existence of more niches and/or narrower niches, has been a popular hypothesis for explaining the maintenance of biodiversity in the tropics. For example, Metz (2012) found that 90% of 136 tree seedling species in an Ecuadorian rainforest specialized in recruiting, growing, and/or surviving in specific topographic conditions, thus contributing to the maintenance of plant diversity. Niche packing is the consequence of specialization, which can be an important process not only for the maintenance but also for the origin of diversity (see previous section). While some types of biotic interactions in tropical forests have a high degree of specialization (e.g., interactions between plants and herbivorous insects, Becerra 2015; symbiotic interactions between ants and myrmecophytes, Dáttilo et al. 2013), others have been found to have lower specialization in tropical regions compared to temperate biomes (e.g., pollination and seed dispersal networks, Schleuning et al. 2012).

Although for a period of time the niche concept lost much popularity, two important and complementary conceptual frameworks ("modern coexistence theory" and "contemporary niche theory") have revived the niche and its role in species coexistence (Letten et al. 2017 and references therein). Coexistence theory focuses on high-order processes (sensu Vellend 2016), distinguishing two general types of mechanisms that prevent or slow down competitive exclusion: (1) stabilizing mechanisms, which reduce niche overlap and increase negative frequency dependence, and (2) equalizing mechanisms, which reduce fitness differences among competing species. Niche theory, on the other hand, focuses on low-level processes and aims at determining the specific mechanisms underlying species' coexistence (e.g., predation vs. competition vs. facilitation). Yet regardless of the theoretical framework chosen (see Letten et al. 2017 for a comprehensive review and integration of both frameworks), species interactions play crucial roles in many of the mechanisms proposed for the maintenance of tropical diversity.

A well-known example of how biotic interactions may maintain diversity in tropical forests is the Janzen-Connell (J-C) effect, which is in turn an example of the classical idea of predator-mediated coexistence. According to the J-C model, plant enemies such as seed predators, seedling/sapling herbivores, and pathogens acting in a distance-dependent fashion prevent replacement of a plant by a conspecific, thus promoting species diversity (Terborgh 2012). There is now sufficient empirical evidence validating the J-C effect (Terborgh 2013), but whether this effect is stronger or more prevalent in tropical forests compared to other biomes still remains to be tested (Fine 2015). Other mechanisms facilitating species coexistence are those that involve ecological tradeoffs, usually associated with temporal and/or spatial fluctuations in biotic and abiotic resources. Ecological tradeoffs may increase niche differences (i.e., coexistence facilitated by niche partitioning) or decrease fitness differences (i.e., coexistence facilitated by competitive equivalence) among species (Burslem et al. 2005). Well-known among tropical forest plants are the survival/colonization and defense/growth tradeoffs. For example, large-seeded species are often better survivors in the shaded tropical understory, while small-seeded species are better colonizers of suitable sites for recruitment such as canopy gaps (Wright 2002). On the other hand, the defense/growth tradeoff posits that species that invest more in tissue growth do so at the cost of lower production of defenses against herbivores (Viola et al. 2010). This tradeoff allows plants to specialize along abiotic resource gradients (e.g., light, nutrients, moisture) such that species with high growth rates but low defenses are dominant where resources are high, while species with low growth but high defenses are dominant where resources are low. This tradeoff facilitates species coexistence and can also promote the formation of new species (Fine et al. 2013; see previous section).

Finally, the observation in tropical forests that understory plants are generally found in low densities has given rise to the hypothesis that the coexistence of many plant species is accomplished through recruitment limitation (i.e., failure of a plant to recruit in an available site) and the consequent lack of interspecific competition (Schupp et al. 2002; Wright 2002). Lack of competition, however, does not mean that biotic interactions do not influence recruitment limitation. For example, plant–animal interactions can cause recruitment limitation through three general mechanisms (Schupp et al. 2002): (1) source limitation, when pollination by animals is low and/or pre-dispersal seed predation is high; (2) dissemination limitation, when frugivores disperse seeds in low quantities, or to limited distances and/or produce spatially aggregated seed depositions; and (3) establishment limitation, when post-dispersal seed predation and/or seedling herbivory are high.

In summary, the coexistence of a high number of species in tropical forests, and thus the maintenance of biodiversity, most likely depends on a combination of many mechanisms acting simultaneously, most of which involve species interactions. The network approach to the study of biotic interactions is yielding promising advances in this area, as recent studies have shown that structural characteristics of mutualistic networks, such as nestedness and asymmetry, seem to play crucial roles in facilitating species coexistence (Bascompte et al. 2006; Bastolla et al. 2009).

1.4 Biotic Interactions and Ecosystem Functioning

It is undeniable that the functioning of tropical forests relies on biotic interactions (Fig. 1.1). For example, a typical tropical tree may require animals for its pollination and seed dispersal; it may frequently have close mutualistic relationships with ants and other organisms for protection against herbivores, and with mycorrhizal fungi for efficient nutrient uptake, just to mention the direct positive interactions. The network of mutualistic plant–pollinator interactions alone involves about 90% of tropical angiosperms, more than a million species of insects, at least 1000 species of birds, and approximately 100 species of mammals (Ollerton et al. 2011). Moreover, in many tropical forests >80% of woody plants are dispersed by animals, most of which are highly dependent on fruit for their survival (Fleming and Kress 2013).

Biotic interactions, being the basis of all trophic relationships among living organisms, are the drivers of matter and energy flows in ecosystems (Thompson et al. 2012). Non-trophic interactions also affect many important ecosystem processes, for example nutrient cycling through the mutualistic interactions of plants with nitrogen-fixing bacteria and mycorrhizal fungi (Burslem et al. 2005). These interactions produce a positive feedback with direct effects on the nutrient cycle, as well as indirect effects through microbial activity and consumption by herbivores, which in turn are important avenues for carbon and nutrient transfer from plants to soils (Metcalfe et al. 2014).

A topic that has received considerable attention and fostered much debate in the last 30 years is the relationship between biodiversity and ecosystem functioning (Loreau et al. 2002). Assessing this relationship is crucial for understanding the processes underlying ecosystem dynamics, stability, and productivity (Hooper et al. 2005). Several hypotheses have been proposed to explain the relationship between biodiversity and ecosystem function (reviewed by Hart et al. 2001). Empirical evidence, however, comes mostly from controlled experiments testing the effects of species diversity on a limited set of ecosystem functions (e.g., productivity). Yet natural ecosystems are defined by many interdependent ecological processes, modulated largely by biotic interactions such that multi-function and whole-ecosystem approaches are urgently needed (Thompson et al. 2012; Fayle et al. 2015; Lefcheck et al. 2015).

Most hypotheses proposed to explain the positive relationship between biodiversity and ecosystem function emphasize one of two main types of mechanisms: the complementarity effect and the selection effect. According to the complementarity effect, as species are added, the productivity of the ecosystem will increase because of the effective partitioning of resources (Tilman et al. 1997). Therefore, if coexisting species are able to avoid competitive exclusion by occupying different niches (often mediated through biotic interactions; see previous section), then productivity and stability in the ecosystem will increase (Turnbull et al. 2013). Complementarity-effect models also consider facilitation, i.e., biotic interactions in which the presence of one or more species may enhance the capacity of other species to survive and reproduce (Valladares et al. 2015). In contrast, the selection effect posits that the relationship between biodiversity and ecosystem function merely occurs because highly competitive species play the greatest roles in ecosystem functioning. According to this idea, as diversity increases, there is a greater likelihood of high-functioning species being present and driving ecosystem function (Hooper et al. 2005). Recent studies in tropical forests suggest that both mechanisms, complementarity and selection, are not mutually exclusive and that both can operate simultaneously to affect productivity (Fargione et al. 2007) although their relative importance may be context- and scale-dependent. For example, Cavanaugh et al. (2014) found that aboveground carbon storage in tropical forests increased with both taxonomic diversity and functional dominance, while another study showed that dominance was more important than species traits in determining a species' contribution to ecosystem functions (Lohbeck et al. 2016).

Biodiversity can be visualized as a complex ecological network, and the next step in studies addressing the relationship between diversity and ecosystem function will benefit hugely from using a network approach. Recent studies show that interactions networks tend to be highly structured, and that some structural attributes not only promote the coexistence of species (Bascompte et al. 2006; Bastolla et al. 2009), but may also facilitate resilience and stability in the face of disturbance (Thébault and Fontaine 2010; Tylianakis et al. 2010). Nonetheless, depending on what species are affected by disturbance, their loss from biotic networks can cause cascading effects, altering both the structure and functioning of communities and reducing ecosystem stability. For example, when species that are particularly important in structuring interaction networks (e.g., highly interacting species) are also particularly sensitive to disturbance, then the network's ability to withstand changes and maintain ecosystem functions will be low (Tylianakis et al. 2008, 2010). In addition, it has been shown that certain functional traits of species (e.g., animal body size) are often related to its importance in structuring interaction networks (Eklöf et al. 2013). Unfortunately, there is also often a positive correlation between the amount of function associated with particular functional traits and the risk of extinction of species with those traits (e.g., Vidal et al. 2014).

A greater number of species interacting is a form of insurance for long-term ecosystem functioning, and represents a buffer against environmental variation, including climate change (Thébault and Fontaine 2010). Yet, we are barely beginning to understand how the structural patterns of biotic interaction networks can influence ecosystem function and stability (Tylianakis et al. 2010), which in turn affect the supply of ecosystem goods and services of vital importance for human well-being. The development of a network approach for assessing what the effects of losing species interactions might be on ecosystem function is an emerging challenge that will improve our capacity for predicting and mitigating the effects of global changes on our planet.

1.5 Management and Conservation Implications

Human activities have caused dramatic global impact on the environment, particularly in tropical forests, including deforestation, forest fragmentation, logging, and defaunation (Dirzo et al. 2014; Lewis et al. 2015). Predicting, preventing, and reverting such impact require a much better understanding of biotic interactions and ecological networks than we currently have, as human impact not only affects individual species, but also alters complex ecological relationships often even before species are lost (Valiente-Banuet et al. 2015). As described in more detail in the Chap. 11 of this book, altered ecological relationships are increasingly common in human-modified tropical landscapes, and both top-down and bottom-up effects of disturbances have repercussions through ecological networks negatively affecting ecosystem integrity.