

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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Springer

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Wesley Dátilo 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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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.

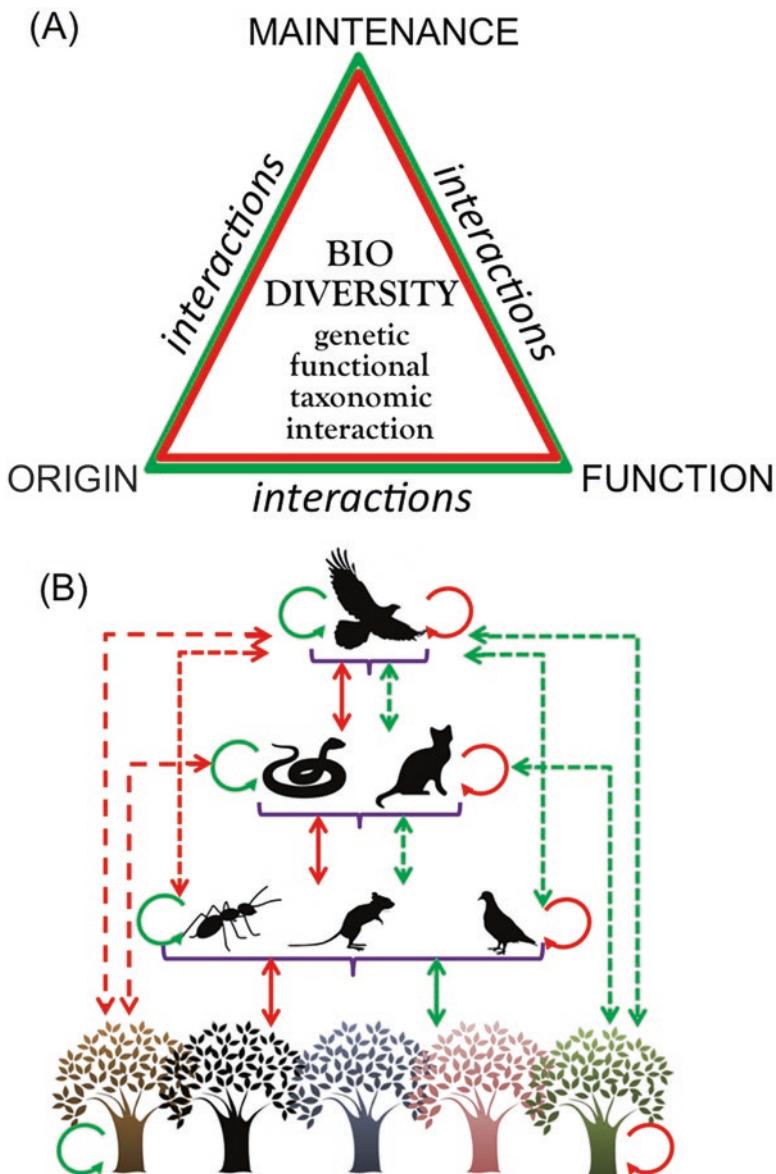


Fig. 1.1 Biotic interactions in tropical forests (a) seen as both a component of biodiversity (internal surface of the *triangle*; together with other components such as taxonomic, genetic, and functional diversity), and as a process (*edges of the triangle*) responsible for the origin (e.g., speciation 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 uninterruptedly 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

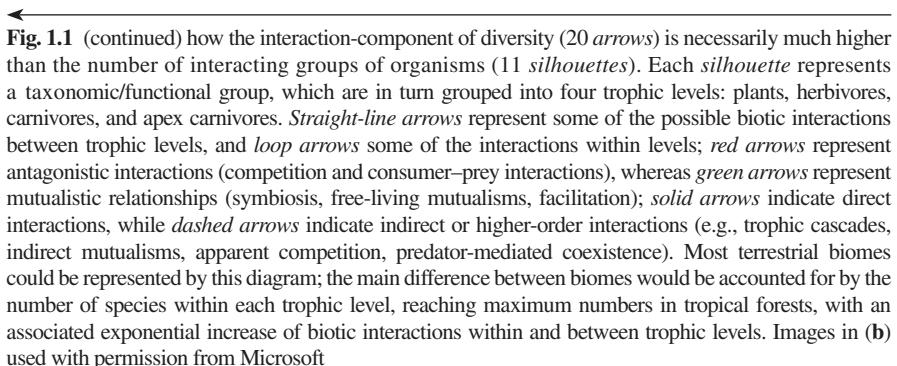
A diagram showing the interaction-component of diversity between 11 taxonomic groups across four trophic levels. The diagram consists of 11 silhouettes representing different taxonomic groups, arranged in a grid-like pattern. Arrows connect the silhouettes, representing various types of interactions. Some arrows are straight lines connecting different silhouettes, while others are dashed lines connecting the same silhouette to itself or to nearby ones. The colors of the arrows vary, with some being red, green, or black. The overall pattern shows a dense web of interactions between the different groups, with more interactions occurring within the same trophic level than between different levels.

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, Dátillo 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.

For instance, the disappearance of top predators causes many types of top-down cascading effects, altering the abundance and/or behavior of mammalian seed predators and herbivores, which may in turn cause changes in tree seedling and sapling assemblages (e.g., Martínez-Ramos et al. 2016). Yet while the loss and decline of large predators and other large animals may be more conspicuous, defaunation is as pervasive in smaller animal taxa, with probably greater consequences for ecosystem functions (Dirzo et al. 2014). The overall effects of defaunation and other disturbances may be hard to predict as not only top-down, but also bottom-up effects cascade through the network of interacting organisms. For example, insect leaf damage can be higher in deforested tropical forest landscapes, where the simplification of vegetation structure associated with edge effects undermines the bottom-up control. In other words, plant anti-herbivore defenses are reduced in forests dominated by fast-growing pioneer plant species, thus improving the conditions for herbivore proliferation (Morante-Filho et al. 2016).

In summary, forest resilience and biodiversity conservation in human-modified tropical landscapes depend on the impact that human disturbances have on key ecological processes, many of which involve biotic interactions, such as seed dispersal, predation, and herbivory (Arroyo-Rodríguez et al. 2017). A take-home message from this brief essay is that additional studies on biotic interactions and ecological networks are urgently needed if we are to attain a better understanding on the origin, maintenance, functioning, and management of tropical biodiversity. We also want to stress the importance of focusing conservation strategies on preserving ecological interactions, in addition to the traditional focus on key taxa (Tylianakis et al. 2010; Valiente-Banuet et al. 2015). We cannot finish this chapter without remembering Janzen's almost prescient assertion: "What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions" (Janzen 1974). As long as ecological interactions are preserved, species diversity, evolutionary processes, and ecosystem functioning will be maintained in tropical forests, and all other biomes on Earth.

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Chapter 2

The History of Ecological Networks

Thomas C. Ings and Joseph E. Hawes

Abstract The complex web of inter-relationships observed in nature that confronted early natural historians on their voyages to the tropics, inspired not only the theory of evolution by natural selection but also the development of ecology as a scientific discipline and set the foundation for the study of ecological networks. Modern network analyses owe much to these early observations of species interactions but also to pioneering advances in the fields of mathematics and social sciences. In this chapter, we review the history of ecological network studies, documenting their background in the fields of natural history, mathematics and social sciences, along with the most influential players and the ideas that they introduced. We continue the story up to the present day, documenting developments within ecology including food web models and mutualistic networks, and emerging concepts such as individual-based, trait-based and multi-layer networks. Following generations of detailed observations and theoretical development, modern network ecologists now have both the data and the analytical techniques to advance our understanding of nature's interdependencies, particularly in the diverse tropical environments that so captivated early naturalists.

2.1 Introduction

The network of interactions that exists between different organisms, and between organisms and their environment, are the focus of ecology as a science. While its roots can be found in early natural history observations, many fundamental principles of network analyses were initiated first by mathematicians (Box 2.1) and social scientists (Box 2.2). The conceptual leap in applying mathematical models to the study of species interactions was in large part due to the wonder inspired in the minds of temperate naturalists on their first exposure to the incredible diversity of organisms and interactions to be found in the tropics (Chap. 1). Even then, it has taken the cumulative effort of many generations of researchers to reach the point

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Box 2.1 Interactions with Mathematics

The ideas of Malthus on the positive checks to population growth, which were so influential in developing the theory of evolution by natural selection, also had a direct influence on the derivation of the logistic equation (Verhulst 1845) and on the mathematical models of predator–prey relationships later developed independently by Alfred Lotka and Vito Volterra (Lotka 1925; Volterra 1926). These simple trophic interactions, representing minimum length food chains, can be viewed as the first ecological networks to be modelled mathematically, opening the possibilities for a quantitative approach to ecology.

The background for more realistic, complex food webs stems from the earlier seminal work by mathematician Leonard Euler in solving the Königsberg bridges problem (Euler 1736). This problem, which may seem trivial, and indeed did at first to Euler, concerned how to walk in a circuit through the city today known as Kaliningrad, by crossing each of the city's seven bridges only once and returning to the starting point. Euler generalised his solution to cover any number of landmasses and bridges, giving rise to the new mathematical field of graph theory (Tutte 2001) which led, in turn, to network theory (Newman 2003).

Further pioneering work in this field was provided by mathematicians Paul Erdős and Alfred Rényi, with their construction of random graphs (Erdős and Renyi 1959). These ideas were later developed to relate to complex networks (Barabási and Albert 1999) and adapted from theoretical physics to apply to ecological networks (Cohen et al. 1990; Margalef 1991). Physics also delivered the background for the many contributions of Robert May to theoretical ecology. May notably challenged the concept that diverse systems are more stable (May 1972), stimulating further examination of the complexity–stability debate that continues to the present day (McCann 2000; Allesina and Tang 2015; Jacquet et al. 2016). Mathematics continued to underpin key developments in ecology, from multi-species Lotka–Volterra models (May 1973; Pimm and Lawton 1978), metabolic theory (Brown et al. 2004) and optimal foraging (Petchey et al. 2008). This integration between mathematics and ecology is exemplified in network researchers such as Joel Cohen, who was the first to collate and analyse collections of food webs from the literature using niche-overlap graphs (Cohen 1978; Cohen et al. 1990).

today where we are able to more precisely explore the complexities of tropical interaction networks.

Recognising the importance of appreciating past literature (Belovsky et al. 2004), we review the history of ecological network studies, documenting their background in the fields of natural history, mathematics and social sciences, along with influential

Box 2.2 Interactions with Social Sciences

In addition to the contribution by Malthus (1798), another critical input from the social sciences towards modern network analyses came from the ‘small world’ experiments of social psychologist Stanley Milgram (Kleinfeld 2002). These experiments recorded the number of first-name contacts a posted letter had to pass through to reach a target individual, in order to explore the distribution of path lengths in a network. The results were the source of the popular phrase ‘six degrees of separation’, subsequently adapted to form the basis of Bacon numbers (connections to the actor Kevin Bacon in the film industry; Collins and Chow 1998) and Erdős numbers (co-authorships with the mathematician Paul Erdős; Castro and Grossman 1999).

The small world experiments and mathematical advances (Box 2.1) such as graph theory stimulated a network-based approach across the social sciences (Borgatti et al. 2009), paralleling progress in ecology. Exchange of ideas and tools for network analysis continued between fields, into areas as diverse as computing (Lazer et al. 2009), finance (May et al. 2008), epidemiology (Klov Dahl et al. 1994), neurology (Bullmore and Sporns 2009) and security (Dupont 2004).

players and the ideas that they introduced (Fig. 2.1). Considering the large number of contributions, this is necessarily a series of selective highlights, focussing on the principal hubs within the vast network of network proponents. Additional details may be found in other reviews (Newman 2003; Bersier 2007; Egerton 2007a; Ings et al. 2009; Layman et al. 2015).

2.2 Pioneering Natural Historians

Pioneers in the succession of ecological networks include Hippocrates, Aristotle and Theophrastus, who made the first documented natural history observations in Ancient Greece (Fig. 2.1). Herodotus recorded one of the earliest accounts of mutualism in his (unconfirmed) observation of plovers removing leeches from crocodiles (Bronstein 2015), before accounts of pollination and seed dispersal by Aristotle and Theophrastus (Thanos 1994). These ideas were later taken forward by Arab scholars, notably Al-Jāḥīz in ‘*Kitāb al-Hayawān*’ (*The Book of the Animals*), who introduced the concept of food chains (Palacios 1930).

Many of these earliest observations of species interactions focussed on trophic interactions but (with the contribution by Al-Jāḥīz often overlooked) it was not until the eighteenth century that individual interactions were combined into a

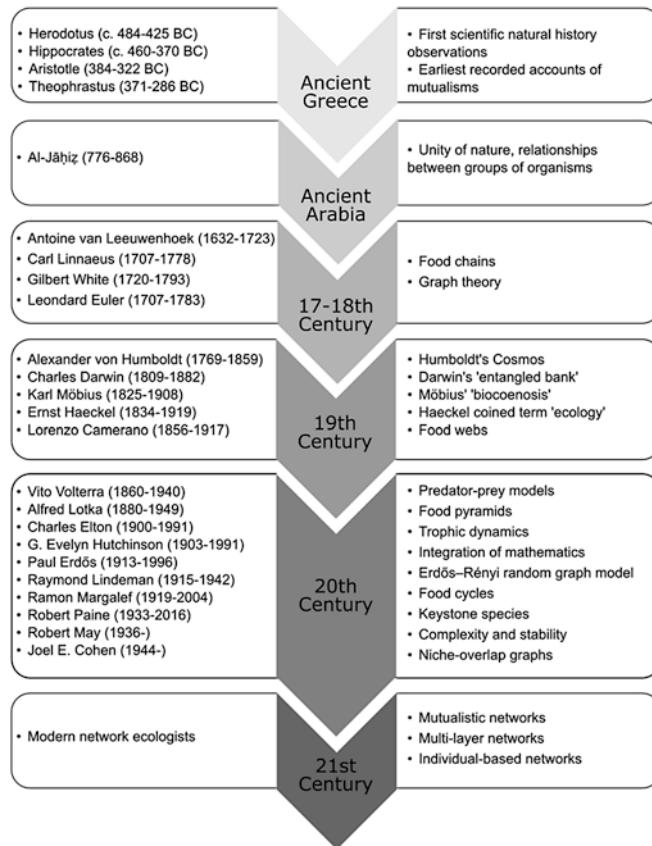


Fig. 2.1 Timeline showing progression in ecological network concepts over history

series by the founding microbiologist Antoine van Leeuwenhoek to produce what is usually recognised as the first described food chain (Egerton 1968). This development was also clearly present in the thinking of the naturalist Gilbert White (White 1789; Egerton 2007c) and the father of modern taxonomy Carl Linnaeus (Egerton 2007b), particularly in his essay '*The Economy of Nature*', where he outlined the sequential steps of both a terrestrial and an aquatic food chain (Linnaeus 1775).

Recognising that the simple food-chain model did not fully reflect the more complex interdependencies present in nature is often credited to Darwin's image of an 'entangled bank' (Darwin 1859). However, much as with his ideas on natural selection, these thoughts were shared by relatively neglected contemporaries such as Alfred Russell Wallace, whose descriptions of tropical fruit-eating birds (Wallace 1853), for example, accurately illustrate the diffuse, generalist networks whose prevalence have only recently confirmed by modern analyses (Bascompte and Jordano 2007). Even more important is the critical role of Alexander von

Humboldt, whose influence on Darwin, amongst others, cannot be underestimated (Wulf 2015). Humboldt's concept of *Naturgemälde* showed emphatically how 'nature is a living whole'; in describing the web of life, he emphasised both relationships between species, and those between living organisms and the natural environment (Humboldt and Bonpland 1814; Humboldt 1851).

Humboldt's *Personal Narrative* was read and highlighted by Darwin on the *Beagle*, with particular passages clearly inspiring subsequent sections in *On the Origin of Species* (Wulf 2015). Compare, for example, Humboldt's imagery of beasts and birds in forest thickets with Darwin's 'entangled bank', or Humboldt's recognition of the importance of *Mauritia* palms in the Llanos of Venezuela with Darwin's comparable description of kelp forests off the coast of Chile. Wulf illustrates how Darwin himself credited Humboldt as his primary influence, with his earlier accounts of the tropics providing stimulation for Darwin's voyage, and helping him to see that all plants and animals 'are bound together by a web of complex relations' (Darwin 1859).

Many others also stood on the shoulders of Humboldt. Amongst those inspired by his thoughts were Karl Möbius, who introduced the term 'biocoenosis' to describe the biotic community (Möbius 1877), and Ernst Haeckel, who coined the term 'ecology' to describe 'the total science of the connections of the organism to the surrounding external world' (Haeckel 1866; Egerton 2013). Man was certainly already included within these concepts at this stage, with Humboldt, Darwin, Haeckel and Möbius all appreciating the interdependence of humans on the natural environment and the destructive role that their actions could potentially have in unravelling the web of interactions. With borders between disciplines yet to become so established, it is also interesting to note how the thinking of both Darwin and Wallace was influenced by the ideas on population checks put forward by the political economist Thomas Malthus (Malthus 1798). Humboldt had earlier remarked upon the role of predators in checking the population growth of capybaras and turtles along the Orinoco but it was the reflections of Malthus' on the logarithmic growth he observed in populations, compared to the arithmetic growth in food supply, that provided the theoretical framework needed for Darwin's ideas on the 'struggle for existence', in terms of both inter- and intra-specific competition (Bowler 1976).

2.3 Early Ecologists

As Darwin famously continued to focus on competition, many of the other pioneers in the field of ecology, such as Stephen Alfred Forbes (1887) and Eugen Warming (1895), remained more interested in trophic interactions and relationships with the abiotic environment. Warming's research in Denmark was supplemented by expeditions to tropical sites in Brazil, Venezuela and Trinidad, while Forbes focussed on temperate environments, notably in the lake systems of North America. The prominent position of limnology in the history of ecological network development was reinforced by the work of August Thienemann in lake communities of northern

Germany (Thienemann 1926) and of G. Evelyn Hutchinson in North American lakes, notably Linsey Pond (Hutchinson 1957). This in turn influenced Roman Margalef's work founded on aquatic and marine ecosystems in Spain (Margalef 1991), and inspired Raymond Lindeman to produce his famous food cycle figure showing the relationships between producers, consumers and decomposers in Cedar Bog Lake (Lindeman 1942).

Before Lindeman and Thienemann, trophic links had rarely been visualised in this way. Perhaps the first diagrammatic representation of an ecological network was created by Lorenzo Camerano (Camerano 1880), when combining multiple food chains into an integrated web. However, Camerano's contribution was seemingly long overlooked and this shift from food chains to food webs, together with the leap from verbal to visual descriptions, was slow to be adopted more widely, with the next examples not provided until the twentieth century (e.g. Pierce et al. 1912; Shelford 1937). Lindeman's diagram was particularly important in its inclusion of bacteria and other decomposers to loop the food chain back on itself and demonstrate the continuous cycling of nutrients within the system. At this point, food webs or food cycles were mainly still generalised although both Lindeman and Thienemann now had the underlying species specific data that Camerano had previously lacked.

Charles Elton played a major role in popularising the use of diagrams to represent networks through his book *Animal Ecology* (Elton 1927), which was also responsible for introducing the terms 'food chain' and 'food cycle', and promoting the concepts of ecological niches and the food pyramid. As more field data were collected, it became clear that some food webs were more complex than others, and ecological niche partitioning (Elton 1927; MacArthur 1958) provided a crucial approach for interpreting how species were distributed within webs. Complexity, however, did not mean randomness, and the growing number of detailed cases eventually allowed patterns to be recognised within and between networks.

For example, Elton observed the progressive decrease in abundance from the base of the food chain to the top predator, the pinnacle of his 'pyramid of numbers' (Elton 1927). Lower abundance, however, did not imply less importance, as demonstrated by Paine's renowned experiments of predator removal, which cemented the concept of 'keystone species' (Paine 1966). The cascade effects that rippled through trophic levels clearly demonstrated the varying influence that species had on community stability. While Paine explained the limits to food chain length by top-down control, Lindeman's inclusion of decomposers and parasites added bottom-up control. What a species did within the ecosystem was important, and the characteristics of a network appeared to be important for how they responded to disturbance, supporting the idea that structure affected function, just as in other areas of biology (Pimm 1982).

Both Elton and Robert MacArthur proposed the notion that 'complexity begets stability' (MacArthur 1955; Elton 1958), predicting that complex tropical systems were more stable than simple temperate ones. This hypothesis required testing but, since complexity was difficult to assess by eye alone, it was necessary to introduce simple metrics that allowed comparison across networks (Chaps. 3 and 13). Connectance, the number of links between nodes, was adopted as a common measure of complexity. This began the use of quantitative metrics but, at this point, analytical tools were still lacking to test many of the hypotheses that Elton and oth-

ers were forming. The Odum brothers, Eugene and Howard, recognised that ecology needed a stronger mathematical foundation, e.g. in their consideration of energy flow between trophic levels (Odum and Odum 1959). Eugene Odum was also an early advocate for expanding traditional food webs that comprise antagonistic trophic links to include mutualistic interactions. More generally though, this cohort encouraged a more mathematical attitude towards investigating ecosystem networks, including a modelling approach that paved the way for modern analyses.

2.4 Food Web Models

With solid mathematical foundations, and a rapidly increasing amount of data available on ecological interactions, more sophisticated models could be produced and tested. Stouffer (2010), in their excellent review of food web models, proposed two broad modelling approaches used in the context of ecological networks: (1) phenomenological models, where rules are used to describe foraging behaviour, and (2) population-level models, where observed emergent properties of food webs are based upon decisions of individuals, i.e. they are mechanistic. The key phenomenological models used to date are the cascade (Cohen and Newman 1985), niche (Williams and Martinez 2000) and nested-hierarchy (Cattin et al. 2004) models, as well as a number of their derivatives (e.g. Warren et al. 2010). They are used to generate model networks whose properties can then be compared with those of empirical networks (Stouffer 2010).

In essence, the cascade model assumes that species in the network are ordered along a single dimension, e.g. trophic level, body size or metabolism, and that predators choose prey randomly from those with a lower rank along that dimension (Cohen and Newman 1985). The main problem with this model is that it does not allow for cannibalism or feeding cycles (Allesina and Pascual 2009), aspects often found in empirical food webs (e.g. Denno et al. 2004).

The niche model (Williams and Martinez 2000) allows for feeding cycles because it includes a niche range, i.e. a limited selection of lower ranked species that a predator can consume. This leads to the so-called interval networks, where the diets of predators are contiguous when prey are ordered along a single niche dimension. While there has been some debate as to whether empirical food webs are interval or not, by measuring the degree of diet contiguity rather than using binary measures for detecting interval networks, we find that many food webs are significantly interval (Allesina et al. 2008; Petchey et al. 2008).

The nested-hierarchy model proposed by Cattin et al. (2004) uses phylogenetic constraints and adaptation as its rules for prey selection, and thereby allows for non-contiguous diets. Despite very different rules, its performance is similar to that of the niche model. This is believed to be due to the fact that both models satisfy two conditions that allow them to predict empirical food web properties: (1) species values along the single niche dimension form a completely ordered set, and (2) the probability that a species preys on a fraction of species with lower values on the niche dimension decays exponentially (Stouffer et al. 2005).

The validity of comparing models based on their ability to reproduce structural properties of networks has been questioned (Allesina et al. 2008). Arguing that network metrics are not independent and that some models do well for certain metrics while others do better for a different set of metrics, Allesina et al. (2008) propose that models should be compared by their ability to predict all feeding links, i.e. the structure of the whole network. As none of the earlier models are able to predict both cannibalism and feeding cycles, Allesina et al. (2008) decomposed networks into reproducible and irreproducible links allowing them to calculate the total likelihood for the models. As models based on a single niche dimension were not sufficient to accurately replicate empirical food webs, Allesina et al. (2008) generated a new general model using a minimum niche range, whereby species at the extent of the range are always preyed upon and other species in the range are preyed upon at a probability constrained by forbidden links (i.e. cannot occur due to the constraints of other traits). This allows for gaps (non-intervallity) in the food web and is based on simple parameters, the number of species, density of links and probability of forbidden links, all of which are available from empirical data.

In contrast to phenomenological models, population-level models start with processes operating at the individual level, which lead to interaction patterns emerging at the level of the whole community. Another important distinction is that phenomenological models use emergent properties of networks as their parameters, whereas population models use lower level processes such as adaptation, speciation and foraging behaviour (Loeuille and Loreau 2005; Beckerman et al. 2006). The population model by Beckerman et al. (2006) is based on foraging theory and uses diet breadth to predict interactions between species. The predictive power of the diet breadth model was further increased by including body size allometry (Petchey et al. 2008). This type of population model allows specific hypotheses about mechanisms determining interactions to be tested and also identifies trophic interactions which may be determined by alternative processes. A recent extension of this model, parameterised with individual level body size data, accurately predicts twice as many links (83%) as the model based on species averaged body size data (Woodward et al. 2010). This theme of using individual-based data to improve our understanding of the mechanisms driving species interactions in complex communities will be taken up below.

2.5 Modern Developments in Ecological Network Analysis

During the last three decades, there has been a rapid development of new approaches to understanding ecological complexity, which have been well documented in several key works (Hall and Raffaelli 1993; Dunne 2005; May 2006). As well as new analytical approaches, there is a growing catalogue of highly resolved networks constructed using quantified interaction data rather than just binary information (Ings et al. 2009). This shift in focus, combined with parallel developments in other fields of network theory, and increasingly powerful computers, is allowing us to

address more detailed questions. As these developments represent a large body of work, our intention here is to give only a brief overview of earlier advances in ecological network studies.

Most of the early work on ecological networks was dominated by trophic interactions, i.e. food webs, perhaps because the foundation of ecological network modelling was the Lotka-Volterra predator-prey models. Indeed, food web studies still dominate, but there has been a rapid increase in studies of other interaction types since the 1990s (Ings et al. 2009), including symbiotic networks: plant-ant (Chap. 5), plant-pollinator (Chap. 6), plant-frugivore (Chap. 7), host-parasitoid, and host-parasite networks (Chap. 9). Even more recently, we have seen the emergence of studies that are beginning to break down the traditional separation into different network types, but rather to consider them as multiple layers of an integrated whole (Pocock et al. 2012; Sauve et al. 2014; Dátilo et al. 2016; Genrich et al. 2017).

Key developments in ecological network studies that have increased our understanding of complexity are the relationship between complexity and stability (May 1972; Allesina and Tang 2015; Jacquet et al. 2016), the non-random nature of real networks (Albert et al. 1999; Dunne et al. 2002; Montoya et al. 2006), and the shift from just considering the magnitude of complexity (Cohen 1978; Pimm 1982) to understanding the configuration of complexity (Solé and Montoya 2001; Dunne et al. 2002; Montoya et al. 2006). Important components of network topology that have been studied to date are: distribution of links amongst species, nestedness, modularity, and small world properties (reviewed in Ings et al. 2009 and Chaps. 3 and 13).

May (1972) proposed that for (randomly assembled) ecological networks to be stable they must meet the condition $i(SC)^{1/2} < 1$, where i is the mean interaction strength between species, S is the number of species, and C is connectance. This implied that complex networks would be unstable, seemingly at odds with the fact that real (ecological and non-biological) networks tend to be complex. However, this disparity was partially explained when Albert et al. (1999) showed that real networks are ‘scale-free’ (new nodes attach to highly connected nodes), non-random networks (reviewed in Barabási 2009). Consequent analysis of degree distributions in biological food webs showed that while they were not generally small world, scale-free networks, they were non-random and had similar topology to other network types (Dunne et al. 2002). Shortly after, mutualistic networks were also shown to be non-random, and again they had similar topology to other network types (Bascompte et al. 2003), although they have truncated power law distributions compared to non-biological networks (Montoya et al. 2006).

Comparative studies on the topology of different network types have revealed some commonality, but also interesting differences. For example, food webs tend to have strong hierarchical structure, often related to body size distributions, and a high degree of generalism (Ings et al. 2009). Mutualistic networks (reviewed in Bascompte and Jordano 2007), on the other hand, are typically nested (i.e., specialists interact with a subset of the species which generalists interact with), heterogeneous (where a few species are more highly connected than expected while the majority of species have few links) and asymmetric (e.g. specialist pollinators tend to interact with

generalist plants and vice versa in plant-pollinator networks) (Bascompte and Jordano 2007). The dissimilarities in topology possibly reflect different mechanisms operating in different interaction types. Phylogenetic constraints are believed to be a major driver of nestedness in mutualistic networks (Cattin et al. 2004), whereas body size constraints are implicated in food webs, where the diets of small predators are a subset of prey consumed by larger predators (Woodward and Warren 2007). Furthermore, topology is believed to affect stability in different ways in different network types (Thébaud and Fontaine 2010): in food webs it is related to compartmentalised structure with weak links, whereas in mutualistic networks high levels of connectance and nestedness promote stability. While there is no doubt that studies on network topology have provided important insights into community structure, caution is required when interpreting topological patterns. Some patterns, such as nestedness, could be the result of neutral processes such as abundance (Lewinsohn et al. 2006), or could just be ‘evolutionary spandrels’ (Valverde et al. 2016).

2.6 Concluding Remarks

The foundation of ecological network history came from early observations of natural history. As these observations accrued the first simple models (food chains) were created, which gradually increased in complexity (food webs). The founding ecologists, often using relatively simple systems in temperate environments as the breeding ground for ideas, started to think about general rules that could be understood through mathematical principles, and quantified using metrics. In turn, these models generated predictions and formed hypotheses that, at that point, lacked both the large well-resolved datasets and tools with which to analyse them. With increasing computing power, more complex models, and a global academic network that allows the compilation of meta-datasets on an unprecedented scale, we are now entering a new phase.

Food webs were at first generalised (e.g. Camerano) before being gradually refined to species level. The species focus from population biology helped established the species as the traditional unit for network analyses. Modern analyses, extending beyond food webs to combine layers of antagonistic and mutualistic interaction types, now also appear to be advancing in both directions by (1) increasing resolution to the level of individuals and (2) adopting trait-based approaches that focus on ecosystem function and may no longer require species identification.

Ecology, now armed with the mathematical and computational tools to quantify interaction strengths and compare network metrics, is maturing as a field and yet the latest sophisticated statistics and simulations still need to be fed with detailed observational data. This is particularly relevant as efforts return to focus on the diverse tropical habitats that inspired early natural historians. The following chapters describe the exiting opportunities that tropical environments provide to explore this variety of species interactions and ecological networks.

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Chapter 3

The Structure of Ecological Networks

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Abstract Ecological networks describe species interactions in ecological processes. There is a growing number of methods for describing and analysing the interaction patterns between species in these networks. The most commonly used network-level indices, such as connectance, degree distribution, nestedness, and modularity, describe the diversity and organization of species interactions within the entire network. These indices can provide insight into the rules underlying the organization of ecological processes, but also about the robustness of ecological networks to changes and perturbations. Species-level indices, such as centrality, dependence, species strength, module roles, and different indices for species specialization, describe the roles of species in the network and the importance of species, both for their direct interaction partners and for the cohesion of the entire network. These indices can be used to identify species with important roles which is useful for the conservation of ecological processes. Both network-level and species-level indices are influenced by various factors, such as species' local abundances, traits, and phylogenetic relationships, as well as environmental conditions.

3.1 Introduction

Ecological networks describe the interactions between species in different ecological processes, such as predation and parasitism, competition and facilitation, or mutualistic interactions like seed-dispersal and pollination. While—due to the complexity of ecological networks and the lack of suitable quantitative methods—studies of species interactions were until recently limited to the analysis of interactions between species pairs or small subsets of networks, advances in the available methods—often borrowed from physics and the social sciences—and increased computational power now allow studying ecological networks in the context of entire species communities (Bascompte and Jordano 2014).

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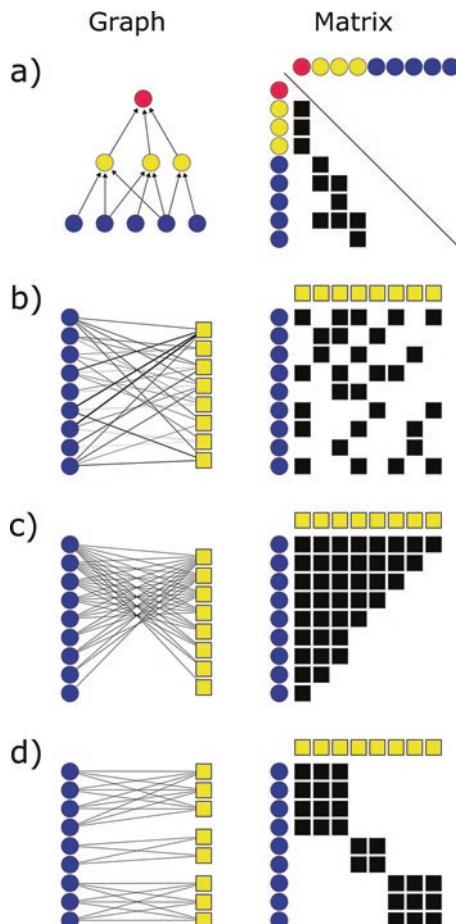


Fig. 3.1 Ecological networks can be depicted as graphs (left-hand side) and matrices. Nodes are shown as *coloured symbols* and can represent species or individuals of a species. Edges (i.e. interactions) are shown as *lines* between nodes in graphs, and as *black squares* in the matrices. **(a)** Unipartite network (simple food web). Species from three trophic levels are indicated by different colours, edges are shown as *arrows* that go from the lower trophic level (prey) to the higher trophic level (predator). In the matrix, entries in each column show the prey species per predator. **(b)** Simple bipartite network. *Blue circles* and *yellow squares* show species from two trophic levels. In the matrix, *black squares* indicate only the presence of an interaction, whereas in the graph, the width of the *lines* indicate the interaction frequencies. **(c)** Strongly nested network. Species with a lower degree interact with a subset of the species with which species with a higher degree interact. **(d)** Strongly modular network. Species from two trophic levels interact in three distinct modules. Species within a module interact exclusively with species from the same module

Networks are commonly depicted as *graphs* that consist of *nodes* and *edges* (Fig. 3.1). In ecological networks, nodes usually represent species, while the edges describe the relationships or *links* between the species in a given ecological process. There are two main types of ecological networks. *Unipartite networks* show the

relationships between all species that can (potentially) interact with each other both across and within trophic levels, e.g. a food web between all predator and prey species in a community (Fig. 3.1a). Bipartite networks show the relationships between species from two distinct groups—often two trophic levels, e.g. mutualistic interactions between animals and plants—but not between the species of the same group (Fig. 3.1b). Both unipartite and bipartite networks can also be visualized by an adjacency matrix (Fig. 3.1a, b) in which columns and rows represent interacting species, and the matrix entries indicate the presence of an interaction (in unweighted, binary networks) or the strength of the interaction (in weighted networks) between two species. In addition, networks can be divided into directed and undirected networks, depending on the effect that species have on their interaction partners. Unipartite networks are usually directed because they illustrate the flow of energy in an ecosystem often across several trophic levels, and there is usually a clear direction of the effect. For instance, describing the negative effect of a species on another as “A eats B, B eats C, etc.” is the same as describing the positive effect in the opposite direction: “C is prey for B, B is prey for A.” Bipartite networks are undirected networks because the effect of the interaction goes in both directions; in a mutualistic pollination network, for instance, a plant has a positive effect on the animal by providing a resource, and at the same time the animal has a positive effect on the plant by serving as a pollinator.

Ecological networks present a simplified model of the actual ecological processes with a trade-off between the feasibility of data collection and the level of complexity. They are most commonly sampled either by direct observation of the interaction (often with a focal species or a plot) or indirectly via clues, such as pollen deposited on the body of a pollinator or prey species found in the gut of a predator. The sampling method can affect the analyses. Bosch et al. (2009) showed that focal plant observations lead to lower estimates for the number of interaction partners per pollinator than when pollen was collected directly from pollinators. There are limited ways to estimate the quality of the sampling, for instance, using richness estimators to compare the number of species and interactions sampled with the expected maximum numbers (e.g. Dehling et al. 2014; Falcão et al. 2016). When analysing networks, one should keep in mind that all sampling methods, and hence the subsequent analyses that depend on the quality of the sampled data, are subject to different biases, as it is virtually impossible to sample all interactions between all species in a network (Jordano 2016).

3.2 Indices to Describe the Topology of Ecological Networks

The simplest measures to describe an interaction network are the number of species (S) and the number of links observed between the species (L). The ratio between the two measures L/S is the *linkage density* (Bartomeus 2013) and provides an estimate for the mean *degree*, i.e. the mean number of links per species in the network. This is a coarse indicator for linkage patterns, as it does not inform about differences

between species. Similarly, *connectance* describes the ratio between the total number of realized links in a network and the theoretical maximum number of possible links (Jordano 1987). While in other fields of network science it is appropriate to calculate the number of possible links simply by multiplying the number of species in the network (in unipartite networks) or the number of species in the different trophic levels (bipartite networks), in ecological networks it is unrealistic to assume that all interactions are possible, and it was therefore proposed that connectance should be calculated relative to the number of biologically possible interactions (Jordano 2016). A different measure for the connectivity of a network is the *diameter*, the number of steps that are necessary to connect each pair of species in the network (Albert and Barabasi 2002). It is determined as the maximum value found when measuring the shortest distance between any two species in the network and provides an estimate for how quickly perturbations could spread through a network.

The distribution of links between the species in the network can be analysed in more detail via the *degree distribution*, which describes how often a species with a certain number of interaction partners occurs in a network. In ecological networks, this distribution usually has the form of a power-law or truncated power-law distribution, which means that most species tend to have few interaction partners, whereas only a small number of species—called *hubs* or *supergeneralists*—has many interaction partners (Jordano et al. 2003; Vázquez and Aizen 2004; Bascompte and Jordano 2014). In mutualistic networks, the degree distribution seems to be similar across ecosystems and independent of species composition (Jordano et al. 2003). Furthermore, the maximum number of links per species tends to be limited due to *forbidden links*, i.e. morphological or phenological mismatches that prevent an interaction between two species (Jordano et al. 2003; Olesen et al. 2010). Despite its simplicity, degree distribution has been used to identify keystone species—the most influential species—in interaction networks (Solé and Montoya 2001; Dunne et al. 2002).

In a further step, one can analyse the overlap in the interaction partners of low-degree vs. high-degree species, which is described by the *nestedness* of a network. The concept of nestedness was introduced in the field of Island Biogeography to analyse overlap in species assemblages on islands (Patterson and Atmar 1986). It was first applied to ecological networks by Bascompte et al. (2003), and it describes the extent to which the interaction partners of one species present a subset of the interaction partners of another species. A network is perfectly nested when species with low degree interact with the same interaction partners with which high-degree species interact, i.e. if all links of the lesser-connected species are *nested* within the links of the species with a higher degree (Fig. 3.1c). Plant-animal networks tend to be highly nested; low-degree species (also called *specialists*) interact with subsets of the species with which high-degree species (*generalists*) interact. In bipartite networks, this has an important implication as it leads to an asymmetry in the specialization of interaction partners; a core of generalist species interacts with both the generalists and the specialists from the other trophic level, whereas the specialists from each trophic level interact with the generalists from the other trophic level

(Fig. 3.1c). This asymmetry hence suggests that—contrary to expectation—mutualistic interaction networks do not always consist of reciprocally specialized pairwise interactions (Bascompte et al. 2003; Vázquez and Aizen 2004; Joppa et al. 2009, but see Dehling et al. 2016 for functional specialization). The nested structure of mutualistic networks increases the stability of networks (Bastolla et al. 2009; Thébault and Fontaine 2010) as it leads to a higher resistance to extinction for the well-connected generalist species (Aizen et al. 2012), but at the same time increases the endurance of the often rare specialist species (Bascompte et al. 2003). In addition, it can reduce competition between species from the same trophic level (Bastolla et al. 2009).

Another measure for the organization of species interactions in the network is *modularity* (Fig. 3.1d). It describes the propensity of different subsets of species in the network to interact more frequently with each other than with the rest of the species in the network (Guimerà and Amaral 2005a, b; Thébault 2013). Depending on the strength of this propensity, this can lead to a division of the network into distinct compartments, or *modules*. A perfectly modular interaction network comprises several sets of species that exclusively interact with each other (Fig. 3.1d). Such cases are, however, rare in nature (if they exist at all), and most modular networks include species that preferably interact with species from one module as well as species that interact with species from different modules. There are different methods to define modules in networks (e.g. Guimerà and Amaral 2005b; Barber 2007; Guimerà et al. 2007; Dormann and Strauß 2014). These methods aim to assign interacting species pairs to modules in such a way that the number of interactions within modules is maximized, and the number of interactions between modules is minimized. The modularity of networks increases its robustness to disturbances because these initially only affect modules and are not easily spread to other modules (Stouffer and Bascompte 2011). However, highly modular networks inevitably also show a lower overall connectance, and hence lower overall redundancy which could arguably lower the robustness against secondary extinctions.

The compartmentalization of networks led to the view of modules as functional units or “basic building blocks of mutualistic networks” (Bascompte and Jordano 2014). Modularity has been related to phylogenetic relationships (Krasnov et al. 2012), climatic seasonality (Dalsgaard et al. 2013; Trøjelsgaard and Olesen 2013; Schleuning et al. 2014), as well as pollination and dispersal syndromes, that is sets of plant species that share a certain combination of traits that attract, e.g., a certain set of pollinator species or a certain set of seed dispersers (Stebbins 1970). Differences in the degree of modularity in mutualistic networks could be related to different requirements of species in different ecological processes. For instance, during pollination, a plant species might profit more if all individuals are visited by a subset of specialized pollinators because this increases the chance that pollen is transported between individuals of the same species (Pellmyr 2002), whereas during seed-dispersal, it might be more advantageous for a plant to attract as many potential dispersers as possible to increase the chance that one of its fruits is deposited in a site that is favourable for the growth of new plant individual (Howe 1993). In addition, sampling of seed-dispersal networks is commonly restricted to

one taxon, for instance birds, whereas pollination networks are usually sampled across a wider range of taxa, for instance several insect orders, which makes it more likely to include species pairs from different syndromes into the network. Not least, the probability of finding modules increases with increasing size of the network (Olesen et al. 2007); one of the most diverse seed-dispersal networks sampled to date, collected by Donatti et al. (2011) in the Brazilian Pantanal across several vertebrate taxa, was found to be highly modular, and modules could be related to the different animal taxa (one module each for fish, birds, and tortoises, another module included mammals and large terrestrial birds). Analyses of modularity should hence be interpreted with care if they involve small networks and/or are focussed on only a distinct subset of species because those networks likely represent only a module of a larger network.

3.3 Indices to Describe the Roles of Individual Species

There are several measures to assess the role and possible importance of a species in a network. As was introduced above, the simplest measure to describe how a species is connected with other species in the network is its *degree*, the number of interaction partners (Freeman 1977). In directed networks, such as food webs, degree can be divided into in-degree (e.g. the number of prey species) and out-degree (the number of predators of a species), whereas in undirected networks, for instance bipartite mutualistic networks, it is not possible to differentiate between the two because a species can only be resource or consumer. Degree is one measure for the *centrality* of a species, i.e. its influence on other species in the network (Freeman 1977). The higher the degree of a species, the more potential influence it has on other species in the network.

In quantitative networks, the importance of one species for another can be calculated as *dependence*: the number of interaction events between a species and one of its interaction partners relative to the number of interaction events between that species and all of its interaction partners (Jordano 1987; Bascompte et al. 2006). The dependence between two species is often asymmetric; if a species depends strongly on a certain interaction partner, the interaction partner usually does not depend much on that species (Bascompte et al. 2006). While dependence is a measure for a species' importance for one other species, the importance of a species for the entire network can be expressed as *species strength*, i.e. the sum of the dependencies of all interaction partners on that species (Barrat et al. 2004).

While degree, dependence, and strength are all (largely) based on a species' direct interaction partners, other measures of centrality also consider how a species is embedded in the interactions between all species in the network (Jordán et al. 2007). For example, *betweenness centrality* (Freeman 1977) assesses for each species how often it occurs in a connection between every pair of species. *Closeness centrality* (Freeman 1978) measures the shortest connections between a species and every other species in the network. As already mentioned for degree distribution above, centrality measures can be used to identify keystone species in networks (Jordán et al. 2006; Mello et al. 2015).

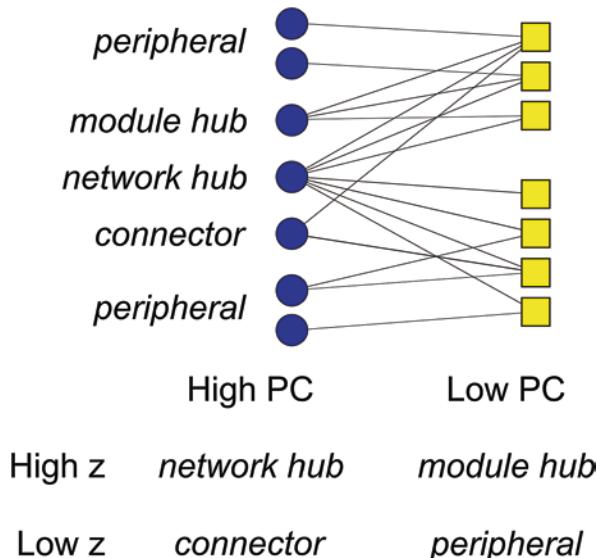


Fig. 3.2 Module roles of species in a simple bipartite network with two modules. Roles are shown for the upper trophic level (*blue circles*). The *z*-score describes whether a species has a lower (low *z*) or higher-than-average (high *z*) number of interaction partners in a module. The participation coefficient (PC) describes the degree to which a species only interacts with species from one module (low PC) or with species across all modules (high PC). The table shows the combinations of *z*-score and participation coefficient that describe the different module roles of species in the network

Centrality measures can also serve to identify species with different roles in modular networks (Fig. 3.2). Based on a *z*-score that assesses whether a species has a higher or lower-than-average number of links within a module (i.e. its in-module degree), Guimerà and Amaral (2005a) identified species that serve as *hubs* (high *z*-score) in the network. Together with the *participation coefficient* (PC) which ranges from 0 (if a species only interacts with species from one module) to 1 (if a species has links evenly spread across all modules), hubs can be divided into *module hubs* (high *z*, low PC) and *network hubs* (high *z*, high PC), both of which are important for the cohesion and robustness of the network (Guimerà and Amaral 2005a; Olesen et al. 2007). Species with low *z*/low PC are considered *peripheral species* that neither connect strongly with a module nor serve as module connectors, whereas species low *z*/high PC serve as *connectors* between modules and are therefore also important for the cohesion of the network (Guimerà and Amaral 2005a; Olesen et al. 2007). The module roles of species tend to be phylogenetically conserved (Poulin et al. 2013; Schleuning et al. 2014).

Species can be separated into specialists and generalists according to their interaction patterns. In the simplest way, the classification is based on the number of interaction partners because this arguably provides a measure for the range of resources used and, hence, the possible size of a species' niche. Accordingly, low-degree species are considered specialists, and high-degree species are considered generalists.

From early on, this terminology has been criticized because it can be misleading. Networks are usually sampling the resource use in only one ecological process, and it is not uncommon to find that network ‘specialists’ are in fact omnivores that opportunistically participate in the process sampled in the network, whereas true resource specialists tend to be the network ‘generalists’ (see also Dalsgaard et al. 2017). Degree does not provide information regarding the niche overlap, and hence the possible redundancy or complementarity of species (Blüthgen and Klein 2011). Blüthgen et al. (2006) therefore proposed a standardized specialization index, d' (‘d prime’), which assesses the specialization of a species (ranging from 0 to 1) by comparing the realized links between a species and its interaction partners to the link pattern expected based on the abundances of all available interaction partners (measured from occurrence frequencies in the network, not from external abundances). A species that exclusively interacts with an abundant species has a lower d' value and is hence less specialized than a species that exclusively interacts with a rare species. On the network level, d' is extended by the complementary specialization index, H'_2 (Blüthgen et al. 2006), which relates the observed interaction frequencies between species to the interaction frequencies expected based on species abundances (i.e. occurrence frequencies), and presents a measure for the complementarity of species’ interaction patterns.

The specialization indices presented above are based on species numbers and identities but do not take into account the similarity between species’ interaction partners, such as their morphology and chemical contents, which is relevant to describe species’ niche differences and their different roles in the network. Dehling et al. (2016) determined the specialization of species’ roles as the differences in the functional traits of species’ interaction partners. This approach to measuring specialization is based on differences in species’ functional roles and the concept of the Eltonian niche (Elton 1927; Dehling et al. 2016), and it has the advantage that it is independent of species identities. Differences between species are expressed as functional originality—the degree to which the traits of a species’ interaction partners differ from the traits of the interaction partners of all other species—and functional uniqueness—the degree to which the traits of a species’ interaction partners differ from the traits of the interaction partners of the functionally most similar species (Dehling et al. 2016). Even though functional originality and uniqueness are determined relative to other species and the range of available resource can change seasonally, the functional specialization of species is similar throughout the year (Bender et al. 2017).

3.4 Factors That Influence the Structure of Ecological Networks

Different interacting factors might underly the structure of ecological networks and the interactions between species. Several studies addressed the question of whether interactions between species occur at random (or according to species’ abundances,

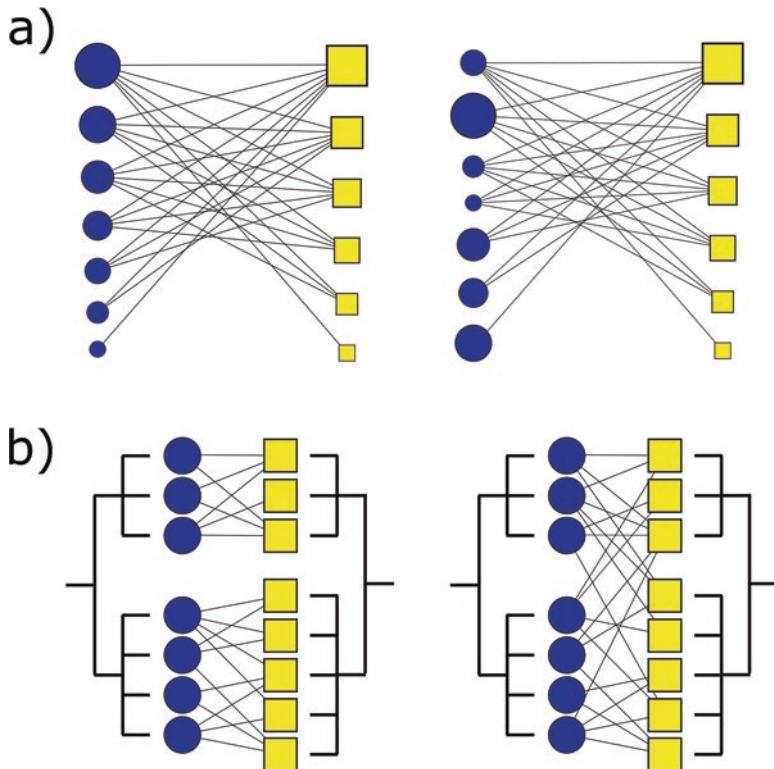


Fig. 3.3 Factors that influence the structure of ecological networks. (a) Influence of local abundance (indicated by the size of the symbols) on species interactions in two bipartite networks. In the network on the *left*, species with high local abundance have a higher number of interaction partners; in the network on the *right*, the number of interaction partners is independent of species' local abundance. (b) Influence of phylogenetic relationships on species interactions. In the network on the *left*, closely related species have similar interaction partners; in the network on the *right*, interaction patterns are independent of species' phylogenetic relationships

Fig. 3.3a) or whether they are determined by ecological factors. Abundance can influence network structure and the interactions between species (Jordano 1987; Jordano et al. 2003; Vázquez and Aizen 2004, but see Blüthgen et al. 2006; Stang et al. 2006; Krishna et al. 2008; Vázquez et al. 2009) but there is also strong support for the influence of species traits in determining species interactions and especially their role in determining “forbidden links” (Jordano et al. 2003; Olesen et al. 2010). Forbidden links are constraints that prevent some species from interacting with each other (Jordano et al. 2003), for instance due to differences in species’ phenology (Olesen et al. 2010), or size mismatches between the resource and consumer species (Jordano et al. 2003; Stang et al. 2006). These forbidden links can make up a large percentage of all the theoretically possible links in a network (Jordano et al. 2003; Olesen et al. 2010), but the challenge is to tell apart forbidden links from

unobserved links, especially in under-sampled networks (Jordano 2016). Controlling for independently sampled local species abundances (instead of the common practice of using network occurrences as proxies for local abundances), Vizentin-Bugoni et al. (2014) showed that the influence of forbidden links is much stronger than that of abundance.

Current studies on the influence of species traits on species interactions focus on the identification of matching traits in interaction partners (Stang et al. 2009; Eklöf et al. 2013; Junker et al. 2013; Dehling et al. 2014; Magliaenesi et al. 2014; Morales-Castilla et al. 2015; Bartomeus et al. 2016) and the relationship between functional traits and functional roles (Eklöf et al. 2013; Dehling et al. 2016; Bartomeus et al. 2016). Single traits can sometimes be used to explain interactions between species, for instance in food webs where body mass alone can often to a large extent determine species' positions in the food web (Williams and Martinez 2000; Petchey et al. 2008; Stouffer et al. 2011). However, in most networks a larger number of traits is necessary to explain all interactions (Eklöf et al. 2013). So far, the insights from trait relationships are not sufficient to predict species interactions from traits alone, which would be extremely valuable, for instance for assessing the potential of species to form new interactions in species assemblages with altered species composition due to disturbances or range shifts. However, the methodology in this field is developing rapidly with many promising approaches (e.g. Morales-Castilla et al. 2015; Bartomeus et al. 2016; Dehling et al. 2016).

Network structure can also be influenced by phylogeny (Cattin et al. 2004; Rezende et al. 2007; Peralta et al. 2015) (Fig. 3.3b). However, when studying phylogenetic signal in ecological networks, an important question is always whether the signal is due to ecological events in the past and the subsequent conservation of the resulting interaction patterns in species' phylogenies, or whether current ecological factors determine interactions and a phylogenetic signal is found because closely related species have similar ecologies and traits (Thompson 2005; Vázquez et al. 2009). For instance, nestedness could be influenced by species' phylogeny (Rezende et al. 2007), or mostly result from trait complementarity and trait convergence (Thompson 2006). Similarly, while modules often contain phylogenetically closely related species (Dupont and Olesen 2009; Donatti et al. 2011; Mello et al. 2011; Poulin et al. 2013), species in modules also tend to have similar traits (Corbet 2000; Donatti et al. 2011; Montoya et al. 2015). In a study across 18 seed-dispersal networks (Schleuning et al. 2014), modularity was only weakly related to phylogeny and best predicted by climatic seasonality. Module roles of species, however, tend to be phylogenetically conserved (Schleuning et al. 2014; Nogales et al. 2015). Related to that, phylogenetically closely related species in mutualistic networks tend to have similar degree values, but differ in their interaction strength (Rezende et al. 2007). The disentangling of the influence of phylogeny and other ecological factors, especially species traits, on species interactions and the question how phylogeny can be used as proxy for ecological factors, is an exciting field for future research.

3.5 Conclusions

In this chapter, I presented several indices for the analysis of ecological network (please also see Chap. 13). As discussed above, some of these indices are easier to interpret regarding their biological meaning than others. Network indices should therefore always be chosen according to their relevance for the particular research question because without an ecological meaning all of these indices are of little use. Ecological networks are usually limited in space, time, and with respect to the ecological processes and the species group studied, and they are sensitive to sampling effort and biases in the sampling methods. Nevertheless, keeping in mind these shortcomings, ecological networks can be powerful tools to study the mechanisms underlying ecological processes.

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Chapter 4

Ecology and Evolution of Species-Rich Interaction Networks

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Abstract The perception that the complexity of tropical ecological interactions is both a product of evolutionary processes and a feedstock for evolution lies at the origin of Evolutionary Ecology. We now have the opportunity to revisit this foundational perception to gain insight into the processes shaping biodiversity structure and ecosystem functioning. Such an opportunity arises from the ongoing theoretical integration between ecological and evolutionary theories, alongside with the application of the network approach to characterize the structure and dynamics of multi-species communities. In this chapter, we focus on the fundamental aspects of ecological, evolutionary, and eco-evolutionary theories underlying the network approach to the study of multi-species systems, such as megadiverse tropical communities. Together, these perspectives illustrate the challenges we shall face in the decades to come in order to take advantage of ongoing theoretical integration, the gradual accumulation of data on tropical interactions, and the availability of robust analytical and computational tools to enlighten the processes shaping biodiversity.

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4.1 Introduction

Tropical ecological interactions provided empirical foundations for evolutionary theory (Darwin and Wallace 1858) and for the first mathematical approaches to evolutionary ecology (Müller 1879). During the 1700s and 1800s, naturalists unraveled novel interaction types across the tropics. That age of discoveries inspired the pioneers of biodiversity research to identify general questions regarding the origin and persistence of species-rich assemblages. For instance, Darwin (1859) forged the analogy of the “entangled bank,” synthesizing the insight that universal processes shape biodiversity in every single site on Earth. Indeed, the concluding sentences of the *Origins* (Darwin 1859) compare the role of evolution as a driver of biodiversity to the law of gravity in Physics:

“... Thus, from the war of nature, from famine and death, the most exalted object of which we are capable of conceiving, namely, the production of the higher animals directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.”

More than 150 years later, understanding general mechanisms whereby ecological interactions and evolution feedback with each other to drive biodiversity remains as a major scientific problem (Thompson 2009; Losos et al. 2013). For decades, the paradigm that ecological and evolutionary processes occur at different timescales (Hutchinson 1965) supported theoretical development, but constrained integrative approaches to biodiversity dynamics (Thompson 1998, 2013). Recently, theory and growing evidence converged to support the view that ecological interactions are both the product and a driving force of selection, implying that adaptive evolution and ecological processes reciprocally affect each other across levels of biological organization (Urban and Skelly 2006; Grant and Grant 2014; Koch et al. 2014).

Rapid evolution refers to genetic changes that are fast enough to influence ecological processes (Hairston et al. 2005). As rapid evolution pervades taxa and biomes (Carroll et al. 2007; Ellner et al. 2011), it is a candidate mechanism to explain biodiversity patterns (Thompson 1998; Koch et al. 2014). The extent to which eco-evolutionary dynamics influence species-rich assemblages is an open issue (Fussmann et al. 2007; Strauss 2014). Evolution of ecologically relevant traits, such as plant flowering time (Franks et al. 2007) or floral display (Gómez et al. 2009), can change interaction patterns and species abundances. In turn, ecological changes can redefine selective regimes and trigger eco-evolutionary feedbacks (Post and Palkovacs 2009). In this scenario, the network approach to species interactions appears as a promising tool to investigate the ecological and evolutionary dynamics of multi-species communities.

Variation in network structure relates to natural history attributes of ecological interactions. For example, biological intimacy, the degree of physiological dependence and phenotypic integration between interacting individuals (see Ollerton 2006; Guimarães et al. 2016) correlates to network structure in mutualisms and

antagonisms (Fontaine et al. 2011). The following examples illustrate the relationship between biological intimacy and network structure in mutualisms (Guimarães et al. 2007), but similar patterns hold for antagonisms, such as parasite–host and predator–prey interactions (Fontaine et al. 2011; Pires and Guimarães 2013).

In high-intimacy mutualisms, individuals are highly dependent on interactions, which occur with one or a few interspecific individuals (Fonseca and Ganade 1996). High-intimacy mutualistic networks are strongly modular, i.e., they form clusters of species more connected among themselves than with the rest of the network (Olesen et al. 2007), as interactions occur between myrmecophytes and ants (Fonseca and Ganade 1996) and between seed parasites and their host plants (Hembry 2012). Conversely, in low-intimacy mutualisms, species interact with several partners without depending on particular mutualist individuals. Low-intimacy networks are usually nested, such as in networks formed by plants and ants visiting extrafloral nectaries (Dátilo et al. 2014a, b) and by pollinators and flowering plants (Bascompte et al. 2003). In nested networks, generalist species (i.e., those with the most interactions) form an interaction core, whereas specialist species (i.e., those with fewer interactions) are peripheral and interact mostly with generalists (Bascompte et al. 2003).

Data scarcity constrains the understanding of how network structure influences ecological and evolutionary dynamics in tropical communities. However, novel molecular technologies will soon provide information on ecological networks in unprecedented ways (Evans et al. 2016). To take advantage of increasing data availability in the decades to come, we can benefit from a number of theoretical and methodological frameworks aimed to unravel the dynamics of large networks. As a contribution in this sense, we here discuss current network approaches to ecological, evolutionary, and eco-evolutionary dynamics of multi-species communities, such as those recurrently found in the tropics.

4.2 Ecological Dynamics

The two fundamental questions of network studies are (1) how ecological and evolutionary processes organize the interaction structure of communities and (2) how network structure shapes ecological dynamics and ecosystem functioning (Dunne 2006)? *Ecological dynamics* refers to disparate aspects of community functioning, including rates of energy or biomass flow, effectiveness of ecosystem functions, and variations in species composition and populations abundances over time. Theoretical population ecology has shown that pairwise species interactions affect species abundances in multiple ways (Lotka 1920; Volterra 1926; Gause 1932). Even interactions within a single population can generate complex dynamics, such as chaotic behavior (May 1973). Therefore, it is not a surprise that an enormous suite of dynamics, often characterized by multiple alternative stable states (Kang and Wedekind 2013), challenges our ability to predict how species abundances vary in species-rich networks.

Differential equations are often used to explore the ecological dynamics of multi-specific networks (May 1973; Allesina and Tang 2012). Modeling a species-rich networks with S species requires an S -dimensional system of differential equations (Box 4.1). Each equation has p parameters that quantify rates of population increase, per capita interaction rates, and carrying capacities. For the entire community, there are pS parameters whose values and ranges are often unknown. Yodzis and Innes (1992) proposed a parameterization of dynamical models based on energetics and empirical allometries, exploring the dynamics emerging over a range of resource-consumer body mass ratios. Similar models, generalized to S species, explored how body size structure and phenotypic evolution affect community dynamics (Weitz and Levin 2006). These models can help us to understand ecological dynamics in tropical networks since the complexity of tropical interactions frequently hamper experimental and even observational studies.

In a similar way, theoretical studies on community stability (Box 4.1) can explore relationships between network structure and ecological dynamics, including the role of weak interactions (McCann et al. 1998), how topologies and interaction types influence stability (Thébaud and Fontaine 2010; Allesina and Tang 2012), conditions for species coexistence under alternative topologies (Rohr et al. 2014), and effects of evolution on ecological dynamics (Loeuille 2010). Contrasting model assumptions constrain the generality of insights arising from stability analyses. Some models support that higher connectance and nestedness increase community persistence by minimizing co-extinctions (Thébaud and Fontaine 2010) and interspecific competition (Bastolla et al. 2009). However, decreases in stability have also been attributed to nestedness (Allesina and Tang 2012; Suweis et al. 2013). Similarly, modularity and low connectance may increase stability by constraining the spread of perturbations (Kolchinsky et al. 2015), but may also increase the likelihood of co-extinctions (Dátilo 2012). Generalized models are an alternative to investigate species-rich networks under variable assumptions, for example, by modeling their dynamics under different functional responses (Yeakel et al. 2011).

Box 4.1 Stability Analysis

In analyses of dynamic behavior, the equation \vec{f} represents the rate of density change in each one of the m species forming the multi-specific system \mathbf{M} . The system *stability* informs the ability of \mathbf{M} to recover from small perturbations that impose changes in species densities. Early studies on the stability of species-rich systems (May 1973) established theoretical expectations for the relationship between species richness, complexity (connectance), and stability. Qualitative stability analyses rely on the eigenvalues of the linearized system, i.e., the Jacobian Matrix of the system at the equilibrium x^* (also known as the community matrix). The Jacobian is the matrix of all first-order partial derivatives of the functions that define the system. When the Jacobian matrix J_M is evaluated at equilibrium \vec{x}^* ($J_M|_{\vec{x}^*}$, i.e., at the point at which the system

does not change over time) the real parts of its eigenvalues inform how the system should respond to small perturbations. If all real parts of the eigenvalues are negative, the system is stable and should return to the original equilibrium following a perturbation. On the other hand, if one or more eigenvalues have positive real part(s), the system is unstable and perturbations should drive the system away from the equilibrium and, probably, to another equilibrium.

<i>Equations of the dynamical system</i>	$\mathbf{M} = \begin{bmatrix} f_1(x_1, \dots, x_n) \\ \vdots \\ f_m(x_1, \dots, x_n) \end{bmatrix}$
<i>Jacobian matrix</i>	$\mathbf{J}_M = \begin{bmatrix} \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_n} \end{bmatrix}$
<i>Community matrix</i>	$\mathbf{J}_M _{\bar{x}^*} = \begin{bmatrix} \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_n} \end{bmatrix} _{\bar{x}^*}$

Network models capturing ecological dynamics can support the conservation of tropical communities. For example, network approaches can identify which species we should track abundances to detect the collapse of communities (Pires et al. 2017) or whether ecological restoration improves resilience (Kaiser-Bunbury et al. 2017). Simulations suggest that different network types, including food webs and bipartite mutualistic networks, are robust to random extinctions, but fragile to extinctions of highly connected species (Dunne et al. 2002; Memmott et al. 2004) (Fig. 4.1). The loss of highly connected species is harmful to network structure even if models incorporate interaction rewiring (see Sect. 4.3 for details), which improves overall network resilience (Kaiser-Bunbury et al. 2010). Network theory can also support conservation by unraveling drivers of ecological dynamics, including the combination of interaction types, such as mutualisms and antagonisms (Mougi and Kondoh 2012), the distributions of interaction strengths (Grilli et al. 2016), and spatial

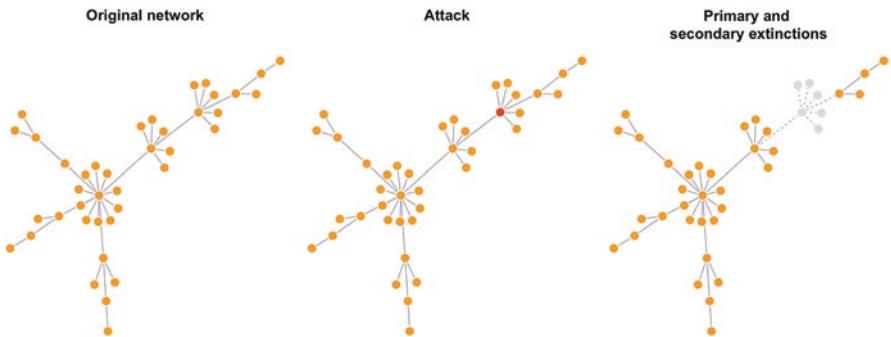


Fig. 4.1 Nodes represent species and links show interspecific interactions. If a species is attacked and lost (extinction), as in the case of the *red node*, other species interacting only with the attacked node can also be lost. *Robust* networks are less susceptible to primary and secondary losses after a species dies out

processes (Gravel et al. 2016; Lurgi et al. 2016). Despite these exciting perspectives to bridge network theory and conservation, we still are in the early stages of understanding how interaction structure shape the dynamics of multi-specific systems and how these dynamical properties feed evolutionary patterns.

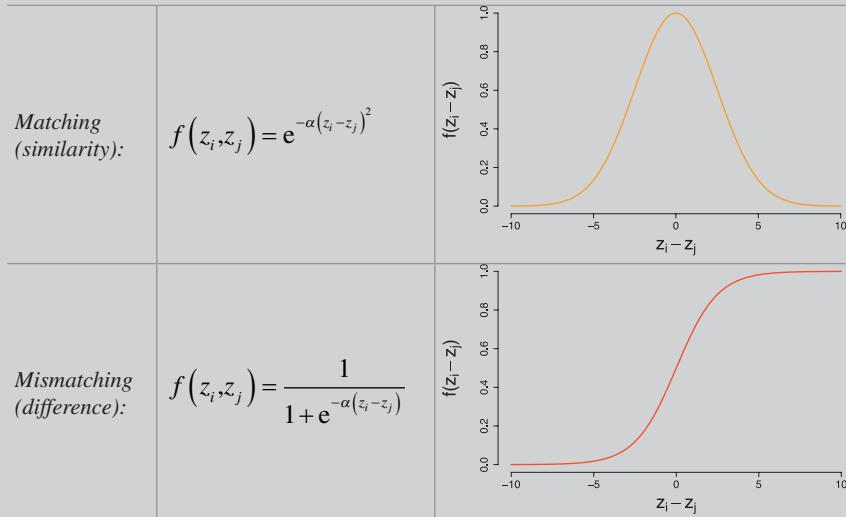
4.3 Evolutionary Dynamics

Any organism is embedded within a variety of intra- and interspecific interactions that impose diverse and often conflicting selection on ecological traits (Schoener 2011; Strauss 2014). The outcomes of directional trait evolution that would result from each pairwise interaction alone are thus expected to change according to network structure (Thompson 2013). Deepening our knowledge on the evolutionary dynamics of multi-species networks thus requires that we understand not only how selection shapes ecological traits that define local interaction structures (Siepielski and Benkman 2009), but also how adaptive changes in interaction patterns reshape the structure of selection (Thompson 2005; Haloin and Strauss 2008).

To understand trait evolution in multi-species networks, we can depart from evolutionary dynamics in pairwise interactions (Box 4.2). Pairwise interaction models predict contrasting evolutionary dynamics for mutualisms and antagonisms. Selection favors trait matching enhancing mutualism effectiveness, such as in interactions between long-tongued animals and long-tubed flowers (Sazatornil et al. 2016) because mutualists showing higher phenotypic complementarity in relation to their partners acquire greater benefits (Box 4.2). Contrasting to mutualisms, trait mismatches are fundamental adaptive responses for organisms exploited or consumed by antagonist species. In seed predation by weevils, for example, the difference between the seed thickness and the beetle's rostrum length allow plants to escape from weevils, but trait matching between seeds and weevils positively correlates with the weevil success (Toju and Sota 2006).

Box 4.2 Trait Evolution Models

Effects of traits on a pairwise interaction can be expressed by mathematical functions. In this case, one can assume that z_i and z_j represent a continuous trait for species i and j . These traits express how the interaction between individuals of the different species affects their fitness. In the equations below, α modulates the sensitivity of interaction to the difference between species traits.



When the interaction with all possible j partners is coupled with environmental effects, we can express the average fitness W_i of individuals of a given species i :

$$W_i(z_i, z_j) = e^{-\gamma_i(z_i - \theta_i)^2} \sum_j f(z_i, z_j),$$

where θ_i is the optimum trait favored by the abiotic environment and γ_i modulates the sensitivity of such abiotic optimum (Nuismer et al. 2010). Using quantitative genetic approaches, we may express how the trait changes (Δz_i) depending on the genetic additive variance, G_i , and on interactions with other species and the environmental pressure included in the fitness (W_i) (Lush 1943; Lande 1976) using the notion of selection gradients:

$$\Delta z_i = G_i \frac{1}{W_i} \frac{\partial W_i}{\partial z_i}$$

A first step to gain insight into evolutionary dynamics beyond pairwise interactions is to relate the structure and strength of selection shaping ecological traits to the emergence of network patterns. For example, theory suggests that: (1) reciprocal specialization arising from coevolutionary selection favoring trait matching can split an initially generalized mutualistic network into several compartments, each of which with variable species richness and, conversely, (2) when phenotype differences drive ecological interactions, coevolution is expected to reshape interaction patterns in a way that nested structures become more generalized architectures in which specialists are rare (Nuismer et al. 2013). Recent theoretical work on antagonistic networks suggests that modularity emerges if selection is stronger on exploiters, such as parasites or predators, whereas nestedness will arise if selection is stronger on hosts (Andreazzi et al. 2017). Network structures are not static, but will often change as a consequence of diverse adaptive processes that reshape interaction patterns over time.

Adaptive changes in network structure can occur when natural selection favors the rewiring of interactions (Suweis et al. 2013). A diversity of biological mechanisms underlies the adaptive rewiring of ecological interactions. For example, high- and low-intimacy mutualisms show strong variation in the dependence, liability, and specificity of interactions (Bronstein 2009), which in turn affect the patterns of selection in these ecological interactions (Fonseca and Ganade 1996). In low-intimacy mutualisms, interaction switches seldom require further morphological, physiological, or behavioral adaptations (Bascompte and Jordano 2014). Indeed, rewiring events related to adaptive resource tracking (Agosta and Klemens 2008) commonly occur at ecological timescales in these systems (Olesen et al. 2008; Díaz-Castelazo et al. 2013). On the other hand, rewiring is expected to be less frequent in specialized, high-intimacy mutualisms (Cook and Rasplus 2003) because coevolution shapes complex phenotypes that mediate these interactions, filtering out potential partners (Thompson 2005). The recurrence of phylogenetic constraints on interaction rewiring has been invoked to explain the modularity of high-intimacy mutualistic networks (Fonseca and Ganade 1996).

Another major cause of adaptive changes in network structure is the addition of new species to a community (Abrams 1996), which can have strong consequences for network structure (Russo et al. 2014). The addition of new species to local biotas, either via cladogenesis or biological invasions, reorganize network structure because these new species change costs and benefits of interactions for multiple co-occurring species. Such changes in interaction payoffs are expected to lead to the reorganization of biotic dimensions of ecological niches over time. The reorganization of ecological interactions arising from species additions affects both ecological and evolutionary processes, as it has consequences for per capita growth rates as well as for trait evolution across the community (Abrams 1996).

4.4 Eco-evolutionary Dynamics

By creating feedback loops between ecological and evolutionary processes, rapid evolution can trigger eco-evolutionary dynamics (Fussmann et al. 2007; Post and Palkovacs 2009). For instance, evolution of body and beak sizes feedback has been shown to contribute with population growth in a population of Darwin's finches (Hairston et al. 2005). In the same population, changes in ecological conditions impacted interaction patterns and the strength, direction, and outcomes of selection (Grant and Grant 2002). Darwin finches illustrate the extent to which ecological and evolutionary dynamics are intertwined (Schoener 2011). Knowledge on eco-evolutionary dynamics can benefit from complementary research frameworks (Abrams 2005), particularly as we change the focus from systems comprising a few species to species-rich communities, in which effects often propagate in indirect and unexpected ways (Strauss 2014).

Three common approaches to model eco-evolutionary dynamics (Fussmann et al. 2007) include: (1) single-locus genetic models in which genotypic fitness is used to compute mean population fitness as a proxy for the population growth rate; (2) multiple-loci genetic models in which quantitative models describe the evolution of a continuous trait affecting population dynamics, which is under selection and modeled as a function proportional to the fitness gradient and; (3) adaptive dynamic models, in which the trait value characterizes individuals of a population, but mutants bearing alleles that enhance fitness may invade that population and affect the equilibrium of ecological dynamics, closing the feedback loop (Dieckmann and Law 1996). Adaptive dynamics works suggest that the interplay between the evolution of interactions and population dynamics may be a key mechanism driving ecological networks (Pacheco et al. 2006; McQuaid and Britton 2013). However, understanding how eco-evolutionary processes feedback with network structure under diverse topologies remains an open question. Therefore, network-based approaches addressing the interplay among trait evolution, interaction rewiring, and demography within species-rich networks can help us to explore this major research frontier.

Adaptive networks represent a promising tool that has been used to model trait-interaction-abundance feedbacks that drive long-term community dynamics (Poisot et al. 2015). Adaptive ecological networks can be defined as dynamic graphs in which changes in interaction structure feedback with species properties, such as traits and abundances (Gross and Blasius 2008). In simulations that depart from random networks, natural selection favoring interaction switches that maximize species abundances lead to the emergence of nested structures similar to the architecture of empirical mutualistic networks (Suweis et al. 2013). The strength of the adaptive network approach is founded on the integrative investigation of trait- and abundance-based processes in the course of network assembly. Adaptive network models can easily incorporate biological constraints on interactions, which may

play a key role in tropical networks (Vizentin-Bugoni et al. 2014). Such constraints refer to morphological, behavioral, or phenological traits that impose restrictions to interactions, leading to “forbidden links” that cannot occur due to biological incompatibilities between species (Jordano et al. 2003; Olesen et al. 2011).

Eco-evolutionary dynamics may have pervasive effects on the structure and dynamics of natural communities (Strauss 2014; Hendry 2016). Community composition rapidly responds to evolution, as shown by changes in arthropod diversity and abundances after experimental selection on plant biomass, life history, and resistance to herbivory (Johnson and Agrawal 2005). Adaptive evolution will often change interaction structure and interaction strengths, affecting per capita growth rates of multiple species (Post and Palkovacs 2009; Abrams 2010; Becks et al. 2010). For this reason, network models that incorporate eco-evolutionary dynamics are promising tools to enlighten mechanisms subjacent to the dynamical properties of ecological communities (Suweis et al. 2013; Valdovinos et al. 2010; Andreazzi et al. 2017).

Eco-evolutionary feedbacks that lead to the stability of traits and population densities are known as cryptic eco-evolutionary dynamics (Kinnison et al. 2015). Such cryptic dynamics may explain why species-rich communities are more resilient to perturbations (Strauss 2014). The dynamical outcomes of eco-evolutionary feedbacks vary with the type of ecological interaction considered. Evolution often stabilizes antagonistic consumer–resource interactions, such as predator–prey, herbivore–plant, and parasite–host (Fussmann et al. 2007; Strauss 2014; Hendry 2016), particularly when consumers switch among alternative resources (Yamauchi and Yamamura 2005; Valdovinos et al. 2016). In competitive interactions, eco-evolutionary feedbacks may favor ecological character displacement, drive evolutionary divergence in resource, and promote coexistence (Vasseur and Fox 2011; Pfennig and Pfennig 2012; Abrams and Cortez 2015). Alternatively, evolutionary convergence in resource use may arise from competitive interactions, especially if resources are non-replaceable (Fox and Vasseur 2008; Vasseur and Fox 2011; Abrams and Cortez 2015). Coexistence among competing species may also be maintained by negative frequency-dependent selection associated to cycles (Vasseur et al. 2011). Model mutualistic networks that incorporate drift, dispersal limitation, and forbidden links suggest that trait convergence and complementarity can emerge from the interplay between fundamental genetic and ecological processes (Encinas-Viso et al. 2014). Eco-evolutionary dynamics of mutualisms may also be affected by cheaters, which are species whose individuals take advantage of mutualist species without providing any type of return (Jones et al. 2009).

The combination of eco-evolutionary theory and network models open exciting perspectives for future studies addressing fundamental question on the processes that shape community structure, including: the joint action of neutral and trait-based mechanisms as drivers of network structure (Vázquez et al. 2009), population, and community-level consequences of species additions and deletions (Abrams 1996; Valdovinos et al. 2009; Russo et al. 2014), the roles of competition in mutualistic assemblages (Jones et al. 2012; Dátilo et al. 2014a, b), the multiple mechanisms by

which species rewire their interactions (Ramos-Jiliberto et al. 2012), and the dynamics of networks encompassing several types of interactions (Fontaine et al. 2011; Dátilo et al. 2016).

4.5 The Challenge Ahead: Eco-evolutionary Dynamics in Tropical, Species-Rich Networks

The challenge ahead for the evolutionary ecologists interested in tropical networks is to test predictions of eco-evolutionary theory with empirical work. Recent empirical findings on rapid evolution in tropical systems provide a first step in this direction. For example, in Atlantic Forest fragments where large-gaped birds (Fig. 4.2) have been absent for several decades, the palm *Euterpe edulis* now show smaller seed sizes. The fruits of this palm are key resources for frugivores (Galetti et al. 2013). Small seed sizes lead to changes in plant population structure via differential recruitment (Moles et al. 2005) and may also affect interactions. For instance, smaller seeds of *E. edulis* are subject to higher seedling mortality under drier conditions and also generate smaller seedlings (Galetti et al. 2013). By changing population structure and dynamics, these demographic consequences of rapid evolution may reshape local selective regimes, completing the eco-evolutionary loop (Hendry 2016). Eco-evolutionary effects have the potential to spread via species interactions and influence community organization and dynamics (Barraclough 2015). For example, because *E. edulis* provides resources for multiple animal species and because the loss of large seed dispersers may affect multiple plant species (Hansen and Galetti 2009), the evolution of smaller seed sizes could generate community-level changes in morphological or behavioral attributes of seed dispersers, which in turn may reshape abundance and interaction patterns (Abrams 1996; Poisot et al. 2015). In addition, spatial variation in biotic interactions can lead to divergent

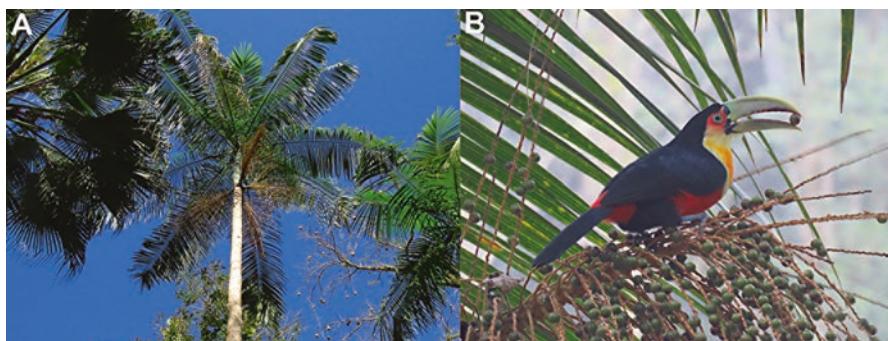


Fig. 4.2 (a) Individual of the palm tree *Euterpe edulis*, whose fruits are key resources for frugivores in the Brazilian Atlantic Forest. (b) The green-billed toucan, *Ramphastos dicolorous*, has a large-gape beak, which allows it to disperse larger seeds of *E. edulis* at the Brazilian Atlantic Forest. Photos: M. M. Pires

natural selection and drive genetic and species-level diversification between populations (Nosil 2012). Therefore, allopatric divergence of seed sizes of *E. edulis* between Atlantic Forest fragments with and without large-bodied frugivores can increase in the future. We used this example to explore the potential that the continuous, reciprocal feedback between rapid evolution and ecological dynamics has to drive ecological networks. It is reasonable to expect that such eco-evolutionary effects will also have consequences at the meta-community because they are likely to change the structure of selection mosaics that shape the diversification of traits and species (see Thompson 2005). However, the extent to which eco-evolutionary effects in species-rich communities and meta-communities are predictable, and thus useful to support theory and applications, remains to be understood.

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Chapter 5

The Complex Ant–Plant Relationship Within Tropical Ecological Networks

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Abstract The tools involved in the study of ecological networks are relatively new and very useful to improve the knowledge about communities, biodiversity, and their conservation. In many tropical habitats, ants form the major part of the arthropod fauna found on vegetation and, therefore, it is extremely common to observe ants establishing ecological interactions with the host plants, where they find and use nectar, oils, pollen, arils, and seeds as food resources. In this chapter, we show that ant–plant interactions are dynamic, diverse, worldwide spread, and very manipulative which fit perfectly as models in studies dealing with interaction networks. For this, we have conducted global review in the distribution of studies on ant–plant networks and highlighted the most recurrent structural patterns observed in ant–plant networks and the main mechanisms and process behind this structure. Finally, we pointed out the limitations and new directions for the study of ant–plant networks in tropical environments.

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5.1 Introduction

As a focus for conservation efforts, biodiversity has received increased attention in the last four decades (Wilson and Peter 1988; Pearson 1994). Searching for patterns in biodiversity, researchers have suggested various units of study including ecological communities (Hunter et al. 1988), cladistics classifications (Vane-Wright et al. 1991), hierarchical composite of different levels of organization (Noss 1990), and groups of taxonomically related species (Holloway and Jardine 1968). The majority of programs for conservation of natural systems have been concerned primarily with the maintenance of species diversity, ecosystem function, and the preservation of genetic variation within populations (Thompson 1997). Thus, a broader view of biodiversity has prevailed (Thompson 2013). However, in a more recent and realistic perspective, biodiversity should be viewed and evaluated in ways that also embraces the extreme richness inherent in biotic interactions, including not only trophic relationships (Price 2002), but also aspects of life histories, biology, and behavior of related species (Del-Claro et al. 2013). In this still new promising pathway to really understand the mechanisms involved in our amazing biodiversity dawn the studies of ecological networks (Bascompte 2009; Bastolla et al. 2009; Bascompte and Jordano 2013; Dátilo et al. 2016—see the other chapters of this book for a general review). In this sense, to add ecological networks studies to our knowledge of aspects of life histories, biology, and behavior of related species, we need to search for useful tools and biological systems to achieve success in a so complex scientific field.

Ant–plant systems can be pointed out as excellent models for gaining a better understanding of biodiversity through the ways of interactions or “interaction biodiversity” (Thompson 1997; Del-Claro et al. 2016). Why ants? Well... in many habitats ants present a particularly remarkable abundance and diversity of associations with plants in the tropical region (Rico-Gray 1993; Blüthgen et al. 2000; Rico-Gray and Oliveira 2007; Lange and Del-Claro 2014; Del-Claro et al. 2016). In fact, it is very common to see ants foraging on plants, mainly due to the availability of food and nesting sites on and within plant tissues (Rico-Gray and Oliveira 2007). In general, we can score an ant species foraging on a plant species as an ant–plant interaction. This approach encompasses different types of ecological interactions, including: mutualisms (e.g., protective ant–plant system, seed-dispersal, and pollination); neutralisms (e.g., ants using plants only as substrate); antagonisms (e.g., leaf-cutting ants or repelling pollinators); and more complex indirect interactions that are both positive and negative (Rico-Gray and Oliveira 2007; Dátilo and Dyer 2014) (Fig. 5.1). Within a natural environment different ant and plant species can interact with each other and generate complex ecological networks. In the last decade, researchers have increasingly used tools derived from the network theory to study the relationships between ants and plants in tropical regions, which have allowed us to understand the origin and maintenance of structural patterns in ant–plant networks.



Fig. 5.1 Examples of ecological interactions involving ants on plants. *PROTECTIVE MUTUALISMS:* (a) a worker of *Neoponera villosa* feeding on an extrafloral nectar of *Senna* sp. (Fabaceae); (b) a worker of *Camponotus crassus* tending *Achenophora* sp. (Membracidae) on *Peixotoa tomentosa* (Malpighiaceae) (c) a worker of *Camponotus* sp. tending a lycaenid butterfly larva. *ANTAGONISMS:* (d) leaf-cutting ants; (e) a worker of *Camponotus* sp. repelling the visitation of *Centris (Ptilotopus)* sp. (Apidae) on the flowers of *Byrsonima intermedia* (Malpighiaceae). *NEUTRALISMS:* (f) a worker of *Ectatomma tuberculatum* using leafs of *Plathymenia reticulata* (Fabaceae) only as a foraging substrate

In this chapter, we present a global overview in the use of network theory to study ant–plant interactions in the tropics. Specifically, our goals were to: (1) review the global distribution of studies on ant–plant networks; (2) describe the most recurrent structural patterns observed in ant–plant networks and highlight the main mechanisms and process structuring them and; (3) point out the limitations and new directions for the study of ant–plant networks in tropical environments.

5.2 Ant–Plant Interactions in a Network Perspective

The advent of the use of tools derived from graph theory to investigate the structure and shape of ecological interactions around the world is drastically modifying the manner we look to the tree of life. Several metrics have been used to enable conclusions to be drawn about structure, specialization, stability, and robustness of interaction networks. Such metrics are useful descriptors of ecological systems that can show the composition of the interactions between multiple and complex elements of a system (Bascompte 2009), by forming an essential ingredient in studies of natural communities (Hagen et al. 2012).

When compared to other systems (e.g., pollination and seed-dispersal), ant–plant interaction networks have received less attention in literature. To date, we have knowledge of about 35 published articles (searched in the database of Web of Science and Scopus) on ant–plant networks (Fig. 5.2). The first study dealing with the relationships between ants and plants within interaction networks was conducted by Guimarães et al. (2006), but only in the last 5 years (from the year 2012) there has been a remarkable growth in the literature on the subject. In the seminal study of Guimarães et al. (2006), the authors showed for the first time that nestedness is a pattern that emerges also from ant–plant networks, which had been considered only for other types of mutualisms (pollination and seed-dispersal). Most of these studies (62%) dealing with ant–plant networks have focused on the interactions between ants and plants with extrafloral nectaries (EFN-bearing plants), where ants have a sugary food resource from plants in exchange of plant protection against potential herbivores. However, little is known about other types of ant–plant interaction networks, such as: ant–myrmecophyte networks (20%), ant–flower networks (11%), and ant–seed networks (6%). In addition, most of the studies involving ant–plant networks have been conducted in the Neotropical region (80%), basically in three specific regions: Amazon and Neotropical Savanna both in Brazil, and on the coast of the Gulf of Mexico. Thus, there is a bias in the number of studies dealing with ant–plant networks (mainly involving EFN-bearing plants) limited to a few regions, which makes it difficult to compare studies between types of ant–plant interactions and large spatial scales.

5.3 Origin and Maintenance of Structural Patterns in Ant–Plant Networks

Using a network approach several studies have described the structure of interactions between ants and EFN-bearing plants (Guimarães et al. 2006, 2007; Díaz-Castelazo et al. 2010; Sugiura 2010; Dátillo et al. 2013a, 2014a, b, 2016; Lange et al. 2013; Lange and Del-Claro 2014; Fagundes et al. 2016). Nestedness is the most common nonrandom pattern found in these ant–plant networks, it predicts that within these interaction networks there is a central core of highly interacting species

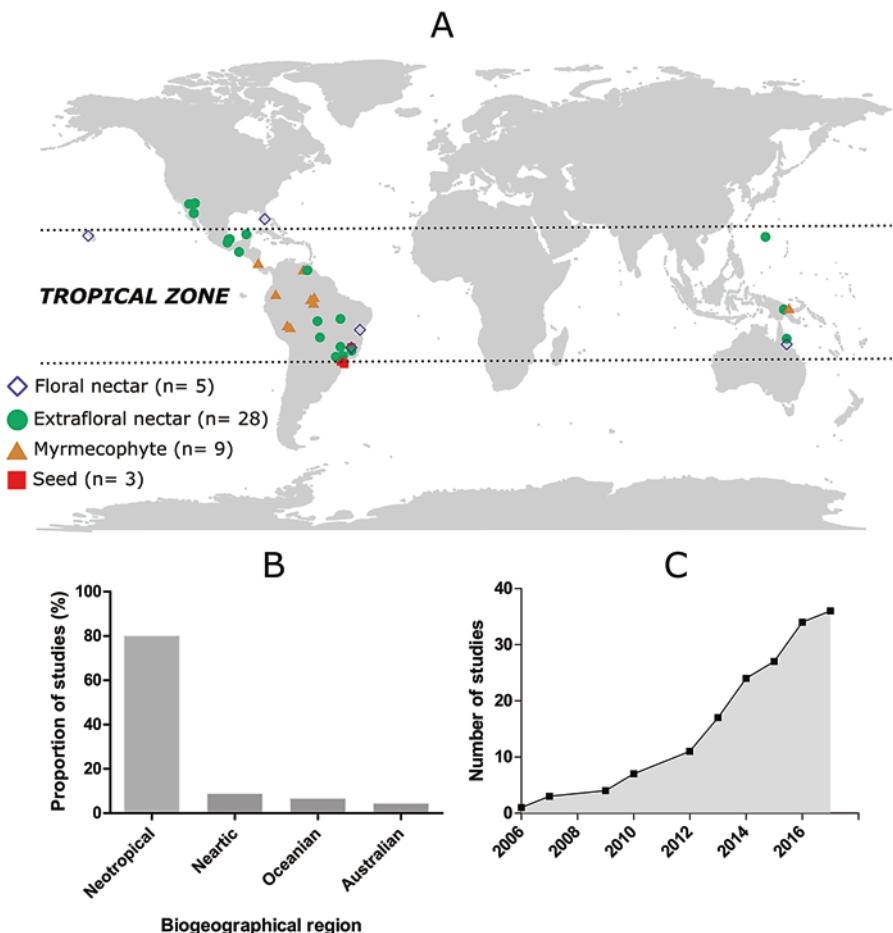


Fig. 5.2 (a) Distribution of ant–plant networks around the world representing different relationships between ants and plants (floral nectar, extrafloral nectar, myrmecophyte, and seeds/fruits). (b) Proportion of ant–plant networks published in different biogeographical regions. (c) Cumulative number of published studies on ant–plant networks from 2006 to 2017. Note that the number of published studies and the number of networks recorded are different among them because within one study there may be more than one network available

with many interactions among themselves, and peripheral species with few interactions interact with a proper subset of the central core of generalists with the most interactions (Bascompte et al. 2003). Díaz-Castelazo et al. (2013) showed that, despite the variation in ant and plant species over time, the nested pattern remained in ants–EFN-bearing plant network in a tropical Mexican forest, even after 20 years. Similar results were observed by Lange and Del-Claro (2014) with the same system but in a Neotropical Savanna. Both studies when added to several other studies of short period suggest that this network descriptor is persistent and relatively constant over time.

Several factors have been proposed to explain the origin and maintenance of structural patterns in ant–plant networks including both abiotic and biotic factors, such as temperature and precipitation (Rico-Gray et al. 2012), soil and vegetation features (Dátilo et al. 2013b), body size of ant species (Chamberlain and Holland 2008), and ant dominance hierarchy (Dátilo et al. 2014a, b). Nevertheless, we yet know (Anjos et al. unpubl. data) that morphological features like seed and ant mandible size are enough to shape ant–plant interactions. All these factors influence somehow the structure of ant–plant networks, but plant phenology is a remarkable one (Lange et al. 2013; Vilela et al. 2014). Specifically for interactions between ants and EFN-bearing plants, EFN secretion is directly related to specific phenological stages of the plant, such as leaf expansion and flowering (Korndörfer and Del-Claro 2006; Calixto et al. 2015). It is known that abiotic factors directly influence the ant–plant interaction (e.g., through EFNs-productivity), as well as the phenology of plants. Thus, sequential events may directly affect ant–plant interactions and the resulting ecological networks over time. Vilela et al. (2014) showed that the sequential flowering of a community of Malpighiaceae shrubs, which possess EFNs and are tended by protective ants (Torezan-Silingardi 2011; Ferreira and Torezan-Silingardi 2013; Alves-Silva et al. 2014), resulted in the share of an entire herbivores community and also the associated ant species among plant species. There was a transferring of the biotic protection by ants from one plant species to other over time, following the plant phenology and the movement of herbivores among plant species.

Independent of the local and landscape environmental factors, the nonrandom pattern of the assemblages involved in ant–plant networks does not change, and therefore, this cohesive structure appears to be the key for the maintenance of biodiversity in these and other communities (Díaz-Castelazo et al. 2013). Recent studies show that the central core of highly interacting ant species is stable over long time (Lange et al. 2013) and spatial scales (Dátilo et al. 2013a) and interact among them more than expected under the assumption of an abundance-based, random mixing of individuals (Dátilo et al. 2014c). This central core of ant species is stable because the ant species found in the generalist core are competitively superior, showing massive recruitment and resource domination, compared with peripheral species with fewer interactions (Dátilo et al. 2014a). A possible biological consequence of the generalist core formed by competitively superior species is that most plant species found within ant–plant networks could be better protected against herbivory by these dominant ant species since the number of ants on the host plant is associated with effectiveness in defense against herbivores (Del-Claro and Marquis 2015).

The variation in outcomes of mutualisms between ants and EFN-bearing plants is widely recognized (see Rico-Gray and Oliveira 2007; Rosumek et al. 2009). In ecological networks, knowing the outcomes of interactions among pairwise associates is imperative to draw valid conclusions about the functionality of these networks. In this sense, a recent study conducted by Lange and Del-Claro (2014) evaluated the ants–EFN-bearing plants interaction using two tools: network analysis and experimental manipulation. This study showed that the general structure of

the network was maintained over time, but internal changes (species degree, connectance, and ant abundance) influenced the protection effectiveness of plants by ants. This study also shows that the dynamic of ant–plant interaction affected both the network and the outcomes of the mutualisms. Beyond the use two tools of interactive studies, Lange and Del-Claro (2014) also presented the original and complete list of related (ants and plants) species, what is basic to studies of biodiversity distribution. This type of data contributes to more general studies (e.g., meta-analysis) (see also Díaz-Castelazo et al. 2010, 2013; Chamberlain and Holland 2008; Lange et al. 2013; Dátilo et al. 2014a, b).

Although nestedness has been a pattern commonly found in ant–plant networks (Del-Claro et al. 2016) and in several other mutualistic interactions (e.g., pollination) (Burgos et al. 2007; Bascompte and Jordano 2013), it is not a pattern that emerges from all ant–plant relationships. For instance, Guimarães et al. (2007) characterized a very specialized mutualism between ants and myrmecophytes, less common than ant–EFN-bearing plants, the ant–myrmecophyte interactions produce nets clearly divided with isolated groups, a compartmentalized pattern (see also Blüthgen et al. 2006, 2007). Therefore, networks involving ants and EFN-bearing plants tend to be more nested and less modular compared to ant–myrmecophyte networks, which tend to be highly specialized and phylogenetically structured (Cagnolo and Tavella 2015).

5.4 The Robustness of Ant–Plant Networks

We have already seen that patterns found in ant–plant interaction networks are constant throughout space and time, but how are they robust to perturbations? Following these steps, Dátilo (2012) compared the tolerances of symbiotic (myrmecophyte) and nonsymbiotic (EFN-bearing plants) ant–plant networks to species extinctions. The author showed that symbiotic networks were less robust for both ants and plants species extinction compared to nonsymbiotic networks. Therefore, the intimacy level of interactions directly influences the pattern of the network as a result of coevolution among related organisms where the change in one species affects its partner in more closed relationships, for example, in ant–myrmecophytes interactions. In facultative interactions like ants–EFN-bearing plants, could evolutionary changes in one species affect multiple partners? (e.g., Guimarães et al. 2007). On the other hand, the resistance and stability of ant–plant networks have been causing some preoccupation in terms of biological conservation. Passmore et al. (2012) showed that, although less robust to species extinction, ant–myrmecophyte plants interactions in the Amazonian forest fragments presented the same pattern observed in continuous and preserved forest. Similar results were found by Dátilo et al. (2013a, b), where the authors demonstrate that these highly specialized associations between ants and myrmecophytes result in cohesive associations within modules, regardless of the type of habitat (primary and secondary forests) and, therefore, the ecological conditions where the associations occur. Moreover, there is other

evidence that ant–plant networks are robust to different types of disturbances, such as: changes in land use (Falcão et al. 2015), removal of abundant seed disperser through rewiring (Timóteo et al. 2016) or after the passage of a tropical hurricane (Sánchez-Galván et al. 2012). Thus, it seems that in general terms ant–plant networks tend to be robust to different types of disturbance.

Recent studies evidenced that these ecological networks are so successful that can cause an “invasive collapse” (Eichhorn et al. 2011; Green et al. 2011) at community level in case of ant species and its associated plants being introduced in a new environment. Only two studies considered the impact of exotic species on ant–plant networks. The first one, the author shows that interactions involving exotic species can represent up to 82.5% from all ant–plant interactions observed on islands in the Pacific Ocean (Sugiura 2010). More recently, Falcão et al. (2017) observed that tramp and invasive ant species have little direct impact on the structure of ant–plant interactions in a tropical coastal environment in Mexico. However, there is still little knowledge available in the literature to draw conclusions about the effect of invasive species on ant–plant networks.

5.5 Limitations and Recommendations for the Study of Ant–Plant Networks

Due to the fact that ants are eusocial organisms and generally recruit many workers in the same plant, it generates a problem in the quantification the frequency of interaction for a quantitative network. Thus, in order to avoid overestimating the ant species with more efficient systems for recruiting, we suggest to use the frequency of ant–plant interactions based on the number of times in which an ant species was recorded interacting with a plant species in the plot/transect, not the number of workers on a plant (Dátillo et al. 2014b). Therefore, we should at least consider these artifacts when comparing studies involving ant–plant networks, which have not been done so far.

Another limitation in the study of ant–plant networks is the methodology for sampling the ants on the plants. There are a wide variety of methods for collecting ants on plants (e.g., active collection, entomological umbrella, baits, and arboreal pitfall traps), as well as climbing techniques for canopy ants, which could lead to studies that are not comparable among them. In order to avoid misleading conclusions about the role of species and the structure of ant–plant networks, we suggest using complementary methods to sampling ant–plant interaction networks (Dátillo et al. 2014c). In addition, we also suggest using both daytime and nighttime sampling, mainly because the role of species in ant–plant interaction networks seems to change between different times of the day (Dátillo et al. 2014b, 2015). But what is the size of the plot/transect needed to sample ant–plant networks? Well... one of the most persisting challenges in ecology is the definition of spatial scales to describe an ecological system. Since the effects of spatial variation and scale on the patterns observed in ant–plant networks remains poorly understood, we recommend the use

of accumulation curves of distinct pairwise of interactions to assess if we have a well-sampled community or if we recorded enough species and interactions to describe our ant–plant network, as recently proposed by Falcão et al. (2016).

The bias in the number and concentration of ant–plant network studies in a few regions and the lack of standardization of collection methods generates a difficulty when comparing ant–plant networks and consequently, the knowledge about large patterns of interactions networks. Therefore, there is no information available in the literature on the macroecological knowledge (e.g., continental patterns of interactions and altitudinal and latitudinal gradients) of ant–plant interaction networks. Based on the recent policy of data sharing that has been growing in most scientific journals, we have called the attention of researchers to make their databases available in the supplementary material of their articles. Also, working in more effective networks of scientific collaboration may increase the understanding about the organization of ant–plant interaction networks studies on the Earth.

5.6 Future Directions in the Study of Ant–Plant Networks

It is incontestable that graph theory brings enormous advances to the knowledge of ecological interactions, especially to ant–plant interactions, but there are many topics to discuss in relation to existent metrics and about the methodology to collect field data. There is a clear lack of standardization and common protocols that produces great variation and little confidence to establish general patterns. The production of common protocols, considering also data of natural history, biology, and distribution of related species (e.g., Del-Claro and Torezan-Silingardi 2009), added to graph theory tools could amplify our knowledge about the pinnacles that sustain ecosystems. We need, specially to ant–plant ecological networks, more studies considering the: cost versus benefit and variation over space (large scales) and time (plant phenology and seasonality); added to data of identity and natural history of species to produce a more clear scenario of the history behind these evolved/coevolved pool of species. It is still a considerable challenge and remains an open question about the structure of interaction networks involving plants, trophobiont herbivores, and ants within natural environments (Fagundes et al. 2016).

Traditionally, studies on ant–plant networks have considered only one type of ecological interaction (e.g., ant-flower, ant-seed, and ant-nectaries) within bipartite sub-networks. However, in ecological communities, ants and plants are involved in multiple kinds of interactions. In fact, ants are one of the few organisms that can have multiple roles in interacting with plants within an ecosystem, as for example: pollinator, disperser, protector, and neuter. In this way, ants and plants can have all their interactions within an environment merged to generate multi-networks of species interactions, and involving different trophic levels (e.g., predators and parasitoids) (Fig. 5.3). Trying to unravel these multiple interactions involving ants, some studies have recently showed that interactions networks involving different resource types (e.g., nectaries and flowers) and hemipterans are connected by a few central

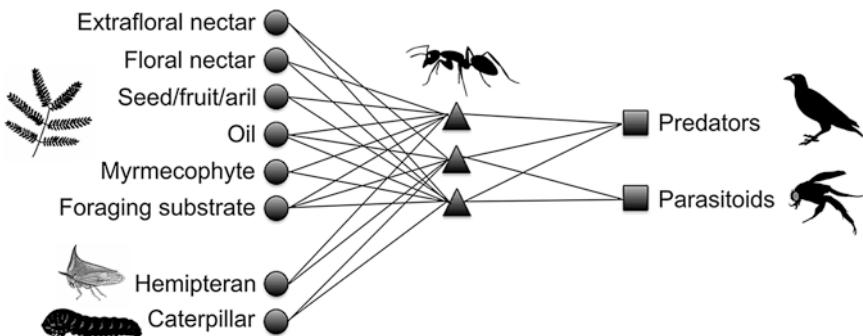


Fig. 5.3 A schematic multi-network of coupled interactions involving ants, plants, hemipteran, Lepidoptera caterpillar secretion, predator, and parasitoid

ant species (Costa et al. 2016; Fagundes et al. 2016). However, we still have little empirical evidence on how the organization of interlinked mutualistic networks may be essential for the maintenance of ecological communities rich in species. The next steps pass by an evaluation on the role of each partner within these multi-trophic networks. This preoccupation is not new, and some studies yet do that (see Díaz-Castelazo et al. 2010, 2013; Lange et al. 2013; Dátilo et al. 2014a, b; Lange and Del-Claro 2014). Therefore, a more clear comprehension of functional organization of the interactions involving ants and plants is fundamental to our understanding of the ecological and evolutionary dynamics of the complex relationships involving these organisms in tropical environments.

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Chapter 6

Plant-Pollinator Networks in the Tropics: A Review

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Abstract Most tropical plants rely on animals for pollination, thus engaging in complex interaction networks. Here, we present a global overview of pollination networks and point out research gaps and emerging differences between tropical and non-tropical areas. Our review highlights an uneven global distribution of studies biased towards non-tropical areas. Moreover, within the tropics, there is a bias towards the Neotropical region where partial networks represent 70.1% of the published studies. Additionally, most networks sampled so far (95.6%) were assembled by inferring interactions by surveying plants (a phytocentric approach). These biases may limit accurate global comparisons of the structure and dynamics of tropical and non-tropical pollination networks. Noteworthy differences of tropical networks (in comparison to the non-tropical ones) include higher species richness which, in turn, promotes lower connectance but higher modularity due to both the higher diversity as well as the integration of more vertebrate pollinators. These interaction patterns are influenced by several ecological, evolutionary, and historical processes, and also sampling artifacts. We propose a neutral–niche *continuum* model for interactions in pollination systems. This is, arguably, supported by

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evidence that a high diversity of functional traits promotes greater importance of niche-based processes (i.e., forbidden links caused by morphological mismatching and phenological non-overlap) in determining which interactions occur, rather than random chance of encounter based on abundances (neutralism). We conclude by discussing the possible existence and direction of a latitudinal gradient of specialization in pollination networks.

6.1 Introduction

Naturalists have long been amazed by the diversity and complexity of life in the tropics (e.g., Darwin 1859; Wallace 1869). In tropical ecosystems, a high proportion of species rely on mutualistic interactions to complete their life cycles. Pollination by animals is one of these processes and occurs when animals transfer pollen grains among flowers while visiting them, hence promoting seed set. Despite the occurrence of self-fertilization and abiotic pollination by wind and water, most angiosperms (at least 300,000 species) rely on animals for pollination (Ollerton et al. 2011), while as many as 350,000 described vertebrate and invertebrate animal species are estimated to engage in this interaction (Ollerton 2017). The proportion of animal-pollinated plants is widely variable around the planet, with some tropical communities having as much as 100% of the plants partially or entirely dependent on animals (Ollerton et al. 2011; Rech et al. 2016).

Classically, plant-pollinator studies have considered a few focal species of plants or functional pollinator groups (Burkle and Alarcón 2011; next section in this chapter). However, coexisting assemblages of plants and pollinators engage in complex interaction networks encompassing sometimes hundreds of species (Jordano 1987). Studying plant-pollinator systems as *ecological networks* allows the investigation of the structure and dynamics of these complex interactive assemblages and facilitates the understanding of system-level phenomena that cannot be inferred by looking at the components of a community in isolation (Memmott 1999; Bascompte 2009). In doing so, network analysis offers possibilities to explore novel and long lasting questions in ecology (Bascompte 2009). Importantly, network thinking has been integrated into conservation, restoration, and management (Tylianakis et al. 2010; Falcão et al. 2015). This integration offers promising tools to cope with the urgent challenge to understand and mitigate the effects of environmental changes, biological invasions, and species loss on crucial ecological processes such as pollination (Tylianakis et al. 2010; Burkle and Alarcón 2011; Maruyama et al. 2016, Biella et al. 2017).

Indeed, network analyses have thus promoted several advances including the description of consistent structural patterns of mutualistic assemblages and the underlying processes (reviewed in Vázquez et al. 2009a, Trøjelsgaard and Olesen 2016). Furthermore, it has stimulated research using plant-pollinator interactions as a study system to elucidate challenging questions in ecology and evolution, such as how coevolution takes place within communities (Bascompte 2009; Guimarães

et al. 2011) and whether there is a latitudinal gradient in specialization (Schleuning et al. 2012; Pauw and Stanway 2015).

Here, we present an overview of the contribution of the network approach to pollination ecology, with particular focus on the understanding of plant-pollinator interactions in the tropics. Specifically, our goals are (1) to review the global distribution of studies on pollination networks; (2) to describe the most recurrent structural patterns and the main underlying mechanisms, discussing peculiarities of tropical pollination networks; and (3) to discuss the evidence, or the lack thereof, of a latitudinal gradient of specialization in pollination networks.

6.2 A Profile of Pollination Network Studies

To investigate the global distribution of research on pollination networks, we compiled the published articles on the topic searching on Web of Science, Scopus, and Google Scholar, using the following search terms: “plant-pollinator network,” “pollination network,” and “floral visitation network.” After filtering these papers for redundancies (e.g., the same networks used in different studies), we extracted the following metadata: coordinates, altitude, country, ecosystem type, and sampling methods (Online appendix at: doi.org/10.6084/m9.figshare.4758646.v1; Vizentin-Bugoni et al. 2017). For simplicity, here we defined “tropical region” as the region located between the Tropics of Cancer ($23^{\circ}26'13.4''$ N) and Capricorn ($23^{\circ}26'13.4''$ S). We also considered *comprehensive networks* those interaction matrices encompassing all plants and pollinators in a given site without any a priori cut-off, and *partial networks* those assembled considering a subset of interacting species from a larger pollination network within the entire community (e.g., bee-pollinated plants). We also classified networks assembled in *forest* or predominantly in *open areas* (e.g., tundra, scrubland, and savanna).

6.3 Global Distribution of the Studies

We found 206 published papers on pollination networks (last search: 2 October 2016) which included 325 distinct networks sampled. Considering the localities of these studies (Fig. 6.1A), an uneven distribution around the globe becomes evident. Indeed, most studies are from non-tropical areas ($n = 178$ vs. 147 tropical networks), especially Europe ($n = 103$) and North America ($n = 34$). In the tropical region, the great majority comes from the Neotropics ($n = 137$) especially from Central America and the Atlantic Coast of South America, with a notable gap in the Amazon and Central Neotropical Savanna areas. Studies are even more scarce in the Paleotropics, with only a few networks from tropical Africa, Asia, and Indian Ocean Islands, e.g., Mauritius and Seychelles ($n = 11$). Temperate networks in the Southern hemisphere and Asia are also comparatively few in number ($n = 35$). From this, a bias towards

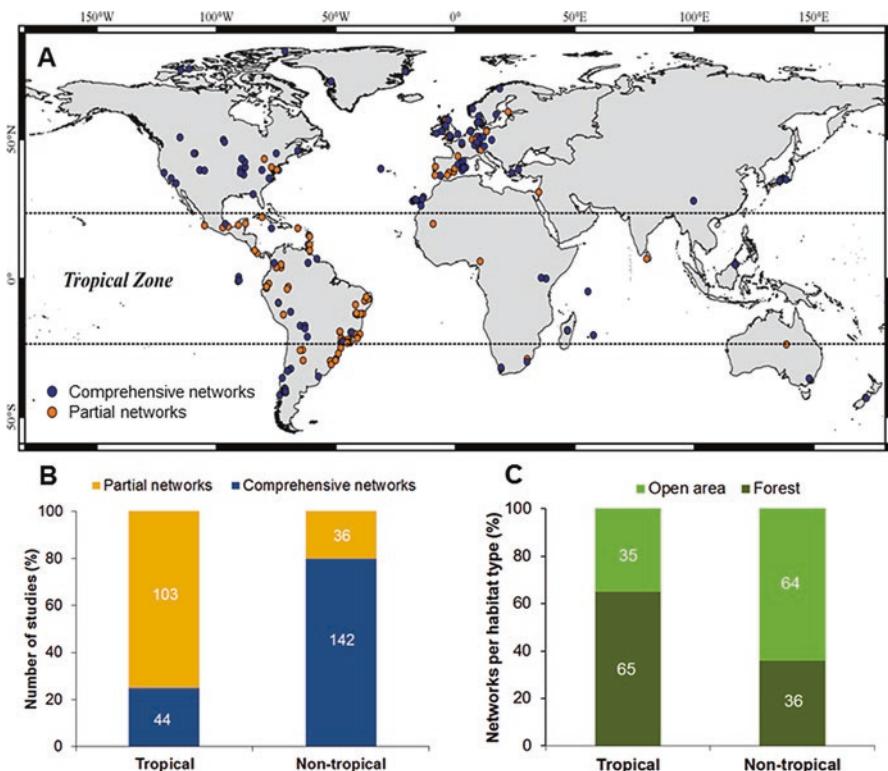


Fig. 6.1 (A) Distribution of pollination networks around the world. Comprehensive networks, i.e., including entire assemblages of plants and pollinators in a site, encompass 79.8% and 29.9% of the networks assembled in non-tropical and tropical studies, respectively. (B) Proportions of pollination networks assembled based on interactions of a subset of species (partial networks; orange) or comprehensive networks (blue) in tropical and non-tropical areas. (C) Proportions of networks assembled in open areas (light green) or forests (dark green) in tropical and non-tropical areas. In (B) and (C), number of networks in each category is indicated

Northern hemisphere temperate areas and a few well sampled Neotropical areas became evident. The geographical gaps indicate places where future studies should be considered in order to have a more complete understanding of spatial variation in pollination networks. We consider that several historical and political reasons—more than proper biological reasons—are likely the causes of this bias, such as scarce or non-existent financial support for basic research programs in some regions, lack of tradition on the study of pollination in other places, or logistical difficulties to access and sample in remote sites. Consequently, the knowledge accumulated so far on tropical pollination networks is inherently biased towards well-sampled Neotropical areas, suggesting that generalizations have to be drawn carefully when comparing tropical and temperate regions.

Most tropical networks to date were collected at elevations between 297 and 1350 m a.s.l. (25–75% percentiles) ranging from 5 to 4200 m a.s.l. while in non-tropical regions

elevations are mostly between 100 and 1300 m a.s.l. (25–75% percentiles), ranging from 5 to 3600 m a.s.l. (Online Appendix, see above). Overall, this suggests that lower coastal (<100 m) and higher mountain top (>2000 m a.s.l.) areas have been relatively poorly sampled. Therefore, under-sampled areas for pollination networks coincide with areas under particular threat by climatic change (IPCC 2014).

6.4 Comprehensive Versus Partial Networks and Habitats Sampled

Overall, we found 186 comprehensive and 139 partial networks. Despite the more integrative nature of the network approach (Memmott 1999), obvious limitations to understand system-level phenomena arise when subsets of species are considered. The definition of the species included in partial networks usually follows functional or taxonomic criteria, such as all hummingbird-pollinated flowers (e.g., Maruyama et al. 2014) or oil-producing flowers (Bezerra et al. 2009). Even though partial networks have been studied from both tropical and non-tropical areas (Fig. 6.1A), there is a much higher proportion of partial networks in the tropics (70.1%; $n = 103$) than outside the tropics (20.2%; $n = 36$) (Fig. 6.1B). This is likely a consequence of the challenge associated with sampling entire communities in the tropics arising from higher species diversity. Moreover, not only species richness is higher, but functional groups of both plants and pollinators (e.g., nocturnal *versus* diurnal behavior of floral visitors, numerous animal-pollinated epiphytes) and the range of pollination systems encountered is more diverse in the tropics (see Ollerton et al. 2006). In addition, the greater structural complexity in tropical vegetation is challenging, e.g., canopy in tropical forest such as the Amazon is sometimes 60 m above the ground. Therefore, it is simpler to produce comprehensive networks for temperate grasslands or tundra ecosystems, for instance, than most tropical forests. In this sense, the few tropical comprehensive networks are generally restricted to structurally simpler ecosystems such as high-altitude or rocky outcrop grasslands (Danieli-Silva et al. 2012, Carstensen et al. 2016, but see Watts et al. 2016). Hopefully, with new technologies for sampling interactions, such as automated monitoring by cameras coupled with motion video detection (Weinstein 2015) and DNA sequencing techniques (Evans et al. 2016), this challenge may be overcome in the future.

Importantly, there is a need to recognize that pollination networks themselves are merged into larger, more complex networks which include other types of positive, negative, and neutral interactions, such as seed dispersal, mycorrhizae, herbivory, predation, and epiphytism. However, few studies to date have undertaken such an integrative approach. This is one of the main avenues for study that is just starting to be investigated in tropical environments (e.g., Dátillo et al. 2016). There are also plant and pollinator species that are not connected to the wider interaction web because they are largely mutually specialized, for example, fig trees and their fig wasps (but see Machado et al. 2005). Not surprisingly, these have mainly been ignored in plant-pollinator studies focused on networks, but nonetheless they are an

important component of these assemblages as “satellite” species or taxonomic/functional groups standing apart from the rest of the community.

Lastly, most tropical networks were assembled in forests (65% vs. 35% in open areas; $n = 115$), while open areas were predominantly sampled in non-tropical areas (36% vs. 64% in forests; $n = 138$) (Fig. 6.1C). Hence, knowledge on tropical pollination networks is based on partial networks mainly sampled in forests. This imbalance in the type of habitats sampled and sampling methods in tropics and non-tropics may also limit direct comparisons of networks between regions.

6.5 Sampling Methods

Pollination networks can be assembled by two major sampling approaches. The *phytocentric* approach consists of identifying and quantifying interactions by observing flowering plants, i.e., “focal observation” or observation in spatially delimited areas. Alternatively, the *zoocentric* perspective consists of inferring interactions via identification of pollen grains attached to the pollinators’ body (Bosch et al. 2009; Jordano et al. 2009; Freitas et al. 2014).

Our survey indicates a clear bias towards phytocentric sampling ($n = 311$ out of 325 networks) as only ten studies used a zoocentric approach and four studies used both methods. Both approaches have their merits and limitations: while phytocentric sampling is simpler and straightforward to apply in the field with few demands of later lab work, plant species can be sometimes overlooked if they are rare or occur in inaccessible spots. In contrast, the zoocentric approach is more comprehensive as it virtually encompasses pollen of all plants where anthers were contacted by the pollinator. However, pollen identification tends to be time-consuming, and it is especially difficult in highly diverse tropical communities, demanding comparisons with a reference collection of pollen or genetic sequencing. Furthermore, pollinators such as bees can sometimes clean their bodies, or collect pollen without facilitating pollination. In addition, as individuals have distinct home ranges, the spatial scale of zoocentric studies is often unknown, in contrast to phytocentric sampling (Freitas et al. 2014; Jordano 2016b). Regarding network metrics, studies suggest that phytocentric approaches tend to overestimate specialization in tropical bird-plant networks (Ramirez-Burbano et al. 2017, Zanata et al. 2017). This fact, together with the observed over-representation of phytocentric approaches, indicates that the higher specialization detected in pollination networks may be to some extent a methodological consequence. However, how the prevalence of phytocentric approaches influences other network patterns remains poorly investigated. Ideally, the combination of both approaches would result in a more accurate description of the pollination networks (Bosch et al. 2009) although it may be challenging in practice owing to the difficulty of sorting pollen samples to species in some plant groups, e.g., Ericaceae (Ramirez-Burbano et al. 2017). Finally, a recent study counting pollen deposition on stigmas after single visits of each visitor revealed higher specialization of networks when compared to a network based on visitation frequency

only (Ballantyne et al. 2015), suggesting better accuracy in inferring the consequences related to network structure for plant reproduction (as suggested by Ollerton et al. 2003). However, although ground-breaking, Ballantyne et al. (2015) worked in a low-diversity community that included only five plants and 16 species (or groups) of flower visitors. Applying single visit pollen deposition to build networks would be far more challenging in species rich communities in the tropics.

It is also important to consider the difference between pollination networks and floral visitation networks. In phytocentric sampling, pollinators are usually defined as those species observed touching anthers and stigmas, while a number of other visitors may extract floral resources without carrying pollen, for instance, when an animal extracts nectar by holes in the base of the flower. These illegitimate visits may potentially have negative effects on the plant, such as those carried out by nectar-thieves and pollen or nectar robbers; therefore, networks including these interactions are not properly mutualistic. Importantly, illegitimate floral visitors may be as frequent as 75% of the species in some cases (Genini et al. 2010) which may lead to dramatic structural differences between visitation networks including such interactions and pollination networks that exclude them (Ollerton et al. 2003; Genini et al. 2010; Maruyama et al. 2015), highlighting the importance of considering the visitor behavior to generate biologically meaningful networks.

6.6 Structure and Drivers of Pollination Networks

Emerging structural patterns in plant-pollinator networks are relatively well documented and similar to other mutualistic networks, such as seed dispersal webs (reviewed in Vázquez et al. 2009a, Trøjelsgaard and Olesen 2016). Despite the recurrence of these patterns, few of these networks are tropical and the ones from the tropics are mostly Neotropical partial networks. Importantly, the existing geographical and sampling biases hinder accurate comparisons of network structure between tropical and non-tropical areas, and even generalization for the tropical areas is hampered. Nevertheless, studies accumulated to date do not suggest dramatic structural differences between tropical and non-tropical network structures (Trøjelsgaard and Olesen 2016). Here, we will describe the main patterns and later discuss peculiarities found (or predicted) for tropical plant-pollinator networks.

6.7 General Network Patterns

6.7.1 Low Connectance

Pollination networks usually possess low connectance, i.e., only a small proportion of potential links actually occur (Jordano 1987). Connectance is sensitive to network size and, indeed, it is known to decrease with species richness, even in partial

networks (Jordano 1987); thus tropical hyper-diverse communities are expected to possess less connected networks. This is likely due to morphological mismatches or spatio-temporal non-overlap which constrains interactions. Indeed, the role of these mechanisms as barriers to some interactions has been increasingly supported (e.g., Vizentin-Bugoni et al. 2014; Jordano 2016a) and will be detailed in Sect. 6.8.

6.7.2 Uneven Degree Distribution and Interaction Strength

Degree is the number of partners a given species interacts with. In a pollination network, many species have few partners while few species have many partners (Waser et al. 1996, Jordano et al. 2003). Thus, extremely low or high specialization are ends of a *continuum*. Despite the recognized influence of sampling effort on network structure (e.g., Vizentin-Bugoni et al. 2016), this pattern was found to be relatively robust to sampling effort for a database including 18 networks, of which three were tropical (Vázquez and Aizen 2006). Also, when some measure of interaction strength is considered (quantitative networks), it becomes evident that few interactions are strong while most are weak (Bascompte et al. 2006; Vázquez et al. 2007). These uneven patterns imply that most species exhibit some degree of specialization, while only a few hyper-generalists are present in the network (Jordano et al. 2006; Vázquez et al. 2009a). However, relatively low sampling intensity, often concentrated over a single season, is still commonplace and hampers our efforts to truly understand how specialized or generalized species are. Importantly, species-level data may hide potential individual differences in specialization within populations; this aspect, however, remains poorly investigated.

6.7.3 Asymmetric Interactions

This feature refers to both the degree and the interaction strength, i.e., an estimate of the impact of one species on another. Respectively, this means that species with many partners tend to interact with specialized partners, and that if species A is strongly dependent on a species B, then B tends to be less dependent on A (Vázquez et al. 2009a). However, it is important to notice that asymmetric interactions do not necessarily mean asymmetric dependencies, as some plant species can set seed without pollinators, i.e., by spontaneous self-pollination or apomixy, or have few ovules which may be all pollinated even under low visitation rates, ensuring maximum seed set. Even though asymmetric interactions have been suggested to be pervasive, few tropical networks have been analyzed in this regard (one tropical network out of 18 pollination networks in Vázquez and Aizen 2004).

6.7.4 Nestedness

As with other plant-animal mutualistic interactions, pollination networks are often nested, i.e., specialists (both pollinators and plants) interacting with generalist partners, while generalists interact also with other generalist partners (Bascompte et al. 2003). Nestedness in tropical pollination networks has been comparatively less explored, but three out of the five tropical networks included in a global analysis were found to be significantly nested (Bascompte et al. 2003). On the other hand, several flower–visitor networks from high tropical mountain forests were non-nested (Cuartas-Hernández and Medel 2015) as well as a plant–hummingbird partial network (Vizentin-Bugoni et al. 2014). Nestedness notably implies that specialization only occurs on generalist partners while specialists almost never specialize on specialist partners. In this sense, nestedness can be seen as a consequence of the interaction asymmetries and uneven distribution of interactions among partners described above. Importantly, nestedness supports the idea that plant-pollinator co-evolution is mainly a diffuse process (Ehrlich and Raven 1964) and it is partially determined by species abundances and phenologies (Vázquez et al. 2009b).

6.7.5 Modularity

Modularity is the presence of subsets of species interacting more frequently among themselves than with other species in the network, which seems pervasive in pollination networks (Dicks et al. 2002; Olesen et al. 2007; Carstensen et al. 2016; Watts et al. 2016) and even in partial networks (Maruyama et al. 2014). For plant–hummingbird partial networks, modularity tends to increase with species richness, suggesting that competition in species rich communities generates finer niche partitioning and ultimately produces modules (Martín González et al. 2015). Accordingly, a larger analysis showed that networks containing more than 150 plants and pollinators were always modular. In addition, the number of modules and the size of each module increases with species richness (Olesen et al. 2007). However, only seven out of 51 networks were from tropical areas. Also, low sampling effort was shown to overestimate modularity and the number of modules in a tropical plant–hummingbird partial network (Vizentin-Bugoni et al. 2016).

It is important to recognize that more robust conceptual and analytical frameworks to test significance of nestedness (Almeida-Neto and Ulrich 2011) and modularity (Dormann and Strauss 2014) for quantitative matrices were developed only recently. Taken together, this calls for the need to revisit both patterns using more robust tools and larger comprehensive datasets including more numerous tropical networks. In sum, despite the fact that pollination networks have been generally less studied in the tropics, most structural properties seem similar between tropical and non-tropical regions. Some fundamental differences detected (or expected)

include the lower connectance but higher modularity in the tropical networks due to the higher species richness and integration of a greater number of functional pollinator groups (Ollerton et al. 2006).

6.8 Drivers of Network Structure and a Niche–Neutral Continuum Model for Interactions

A number of ecological, evolutionary, and historical processes, as well as sampling artifacts, influence detected patterns in pollination networks (Vázquez et al. 2009a, b) and their relative importance is still under debate. Overall, pollination networks present many non-observed links. To understand why these “zeros” occur is essential to explain virtually all of the patterns described above. A combination of factors contributes to “zeros” in the interaction matrix, including biological constraints, neutrality, and sampling as outlined below.

6.8.1 Contemporary Mechanisms

If the link occurs in nature but was not observed due to sampling, then the absence of an interaction in the matrix is a “missing link.” However, if any biological phenomenon prevents a pair of species from interacting, then this is a “structural zero” in the matrix. To make a distinction of true missing links and structural zeros is challenging and may demand deep natural history knowledge to determine their causes (Olesen et al. 2011; Jordano et al. 2006; Jordano 2016b). These structural zeros may be explained by three main hypotheses.

First of all, the *forbidden links hypothesis* postulates that inherent biological features of species define the occurrence (or not) of an interaction. Several mechanisms may cause forbidden links, for example, spatial or temporal non-overlap in species distribution or activity are some of the most obvious causes, but factors such as morphological barriers are also frequent (Jordano et al. 2006). For instance, a plant–hummingbird partial network in the Neotropical savanna has an entire module dictated by bill-corolla matching, while other modules are mainly defined by non-overlapping distribution of potential partners among habitats (Maruyama et al. 2014). Therefore, these modules emerge from the impossibility of some interactions to occur due to biological constraints, i.e., niche-based processes. In other words, species may interact only when they are in the same place at the same time and have compatible phenotypes.

Alternatively, a *neutral hypothesis* postulates that interactions may be defined by random (stochastic) encounters of individuals. Therefore, species abundances are expected to have an important role. If this is the case, abundant species should interact with more partners and more frequently than the rarer ones. On the other hand, when rare species match in their biological traits they may be too rare to find each

other and then interact (Canard et al. 2012). Indeed, species abundances have been shown to predict interactions in several networks, e.g., plant-insect [in general] (Vázquez et al. 2009b) and some temperate plant-hawkmoth partial networks (Sazatornil et al. 2016). Although we refer to this as “neutral,” it is important to note that the relative abundance of a species may be driven also by niche-based processes (Vizentin-Bugoni et al. 2014) and the elaboration of a mechanistic framework of processes structuring interactions deserves further attention (Bartomeus et al. 2016).

A third mechanism called the *morphological matching hypothesis* has been shown to better predict interactions in some cases. It postulates that—among the interactions that are not forbidden links—pollinators are expected to preferentially explore flowers whose morphology fits closely to pollinator mouthparts, and some plants that could potentially be accessed are not, for instance, due to competition with other pollinators (Santamaría & Rodríguez-Gironés 2007, Maglianese et al. 2015). Indeed, this mechanism has been shown to determine interactions in some plant-hawkmoth networks from the tropics (Sazatornil et al. 2016). The influence of trait matching highlights that interactions may be determined also by (1) evolutionary adjustment of morphologies in sets of interaction partners, (2) species preferences, and (3) avoidance of easier-to-access resources, which presumably implies more intense competition.

6.8.2 A “Neutral–Niche Continuum Model” for Species Interactions

Importantly, the three hypothetical mechanisms outlined above are not mutually exclusive and all can (potentially) be occurring in every network, though their relative importance remains debated (Vázquez et al. 2009a, b; Vizentin-Bugoni et al. 2014). In this sense, the existence of a *continuum* of importance from niche-based processes, i.e., forbidden links and matching hypotheses, to neutrality structuring interactions has been hypothesized (Canard et al. 2014), as for competitive systems (Gravel et al. 2006). For pollination networks, the relative importance of a process will depend on the diversity of functional traits, i.e., the extent in which traits vary in the assemblage. In an extreme of this *continuum*, where plants and pollinators present highly variable traits, niche-based processes such as forbidden links and morphological matching are expected to be dominant drivers of interactions, such as in highly diverse tropical areas (Fig. 6.2; right tip of the dashed line). In the opposite extreme of this *continuum*, random chance of encounter driven by species abundances is expected to matter more where traits are not very variable, i.e., low diversity of functional traits (Fig. 6.2; left tip of the solid line). As an example of high trait diversity, one may consider the corolla tube length, with discrepancies between shorter and longer corollas producing opportunities for forbidden links. Similarly, some floral colors act as a filter for specific visitor groups (Lunau et al. 2011), such that high floral color diversity would also likely translate to more constraints to interactions.

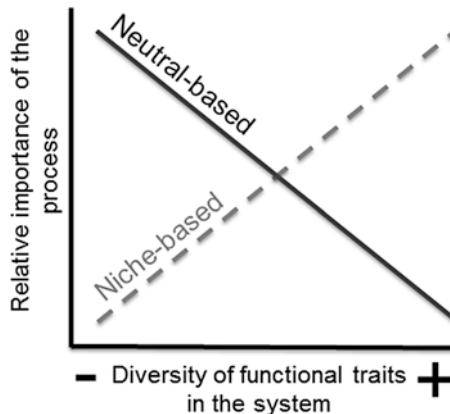


Fig. 6.2 Neutral–niche *continuum* model for interactions in pollination networks. In this model, species interactions are expected to be mainly structured by forbidden links and morphological matching (niche-based processes) when associated with high functional diversity, while random chance of encounter based on species abundances (neutral-based process) are expected to matter more under low functional diversity. See Sect 6.8 for examples

Indeed, for pollination networks, evidence accumulated so far arguably supports the expectations of this simple “neutral–niche *continuum* model” for species interactions. Niche-based processes were shown to matter more than neutrality in systems with high trait variation from tropical areas, such as plant–hummingbird (Maruyama et al. 2014; Vizentin-Bugoni et al. 2014) and tropical plant–hawkmoth pollination systems (Sazatornil et al. 2016). On the other hand, neutral processes were found to be important in some non-tropical networks (e.g., Vázquez et al. 2009b, Olito and Fox 2015). As seasonal climate may shape species phenologies in some communities, niche-based processes related to phenology can also play a role along with species abundances to structure interactions. Indeed, phenological overlap was shown to be an important driver of interactions—along with abundances—in some non-tropical pollination networks (Vázquez et al. 2009b; Olito and Fox 2015). The *continuum* hypothesis we develop here does not exclude the potential existence of a hierarchy of importance among distinct mechanisms determining interactions in a system (Junker et al. 2015; Bartomeus et al. 2016), but suggests that the order in this hierarchy may depend on the diversity of functional traits. Despite the predictions of the “neutral–niche *continuum* model,” a proper test of this hypothesis is still missing and must directly relate the importance of distinct niche and neutral processes along a gradient of networks differing in (functional) trait diversity.

Importantly, it is necessary to highlight that the niche- and neutral-based processes outlined above originate from a number of other causal processes. Such processes underlie community composition and structure, i.e., species richness and relative abundances, and species distributions in time and space, which ultimately influence network structure (Vázquez et al. 2009a; Trøjelsgaard and Olesen 2016; Bartomeus et al. 2016). Some other processes include, for example, dispersal limitation, demographic processes, adaptation, local extinction, and competition (Vázquez et al. 2009a).

6.8.3 *Evolutionary History May Shape Interactions by Its Influence on Species Traits*

One of the few attempts to describe a complete pollination network in a tropical high-altitude grassland found around 69% of interactions correctly predicted by the combination of floral traits (Danieli-Silva et al. 2012), as was found also for a temperate study (Dicks et al. 2002). Hence, modules of taxonomic (presumably also functional) pollinator groups interact with plants which are adapted (phenotypically convergent) to these pollinators. In other words, closely related pollinators tend to interact with a functionally similar array of flowers and, in several cases drive convergent floral evolution. An implication of these findings is that partial networks assembled by considering particular pollination systems (or pollination syndromes) may not be just an artifact, and correspond to reasonably independent modules within a larger and more complete pollination network, especially in the tropics (Danieli-Silva et al. 2012; Carstensen et al. 2016; Watts et al. 2016).

6.8.4 *Historical Drivers of Interactions*

If species coexistence is crucial for interactions, phenomena promoting speciation or extinction must also be important for contemporary network structure. These phenomena may include catastrophic events (e.g., local extinctions by hurricanes; Sánchez-Galván et al. 2012) or gradual events such as historical climate change. In this sense, environmental (climatic) stability is expected to promote structurally more complex networks, by offering more opportunities for coexistence, co-adaptation, and the evolution of narrower niches, i.e., specialization, as shown for plant-hummingbird partial networks (Sonne et al. 2016). Indeed, pollination networks present higher modularity in areas of higher historical climate stability, such as some tropical areas, both in mainland and on islands (Dalsgaard et al. 2013) which is an indication of higher specialization in these areas. Accordingly, modularity increases with contemporary precipitation while nestedness decreases (Dalsgaard et al. 2013), which suggests that climatic conditions operating on more recent time-scales are also influencing the structure of pollination networks (see also Rech et al. 2016).

6.9 Is There a Latitudinal Gradient of Specialization in Pollination Networks?

The general latitudinal trend of rising species richness as one moves from the poles to the tropics has long been recognized (Pianka 1966; Hillebrand 2004; Willig et al. 2003). There are around 25 tentative explanations to this latitudinal gradient (Brown and Lomolino 1998). Considering this higher diversity in the tropics, ecologists have proposed that species in the tropics are more often specialized in their

interactions with other species because their niche breadths evolve to be narrower in communities that are more densely packed with species (MacArthur 1972; but see Vázquez and Stevens 2004). However, there have been rather few tests of this assumption with plant-pollinator interactions, and their findings have been mixed. Olesen and Jordano (2002) initially suggested that plant-pollinator networks were more specialized in the tropics; however, Ollerton and Cranmer (2002) showed that any apparent increase in plant specialization in the tropics disappeared when sampling effort was considered, a pattern that was consistent over two large, independent datasets. Schleuning et al. (2012) later showed plant-pollinator networks to actually be less ecologically specialized in the tropics compared to other regions. More recently, Pauw and Stanway (2015) have further demonstrated that there may be differences between the northern and southern hemispheres. The “opposite” latitudinal trend found by Schleuning et al. (2012) was both theoretically and intuitively unpredicted, and (controversially) suggests that ecological functions such as mutualistic seed dispersal and pollination may be most sensitive to the extinction of species in temperate ecosystems, rather than those in the tropics, as is often assumed.

Importantly, as evidenced here (Sect. 2), most tropical networks are actually partial networks, mostly including (or restricted to) vertebrates, while non-tropical networks are comprehensive but encompass only insects. Moreover, there is evidence that some partial networks may be more specialized in the tropics, e.g., New World hummingbird-flower assemblages, where specialization seems to be related mostly to precipitation (Martín González et al. 2015). This could indicate that tropical specialization may be encountered in only some partial networks, but it is unclear why, and there is much scope for further research. What is certain, however, is that suggestions that tropical species, and the interaction networks in which they are embedded, are always more specialized is a huge over-simplification (Moles & Ollerton 2016).

It is worth mentioning that biodiversity gradients are strongly dependent upon spatial scale and sampling effort (Willig et al. 2003, see also Dalsgaard et al. 2017). Hence, considering that tropical studies are often less intensively sampled than temperate ones, it is plausible to suggest that we are still far from a proper test of whether specialization is higher in tropical pollination interactions. Even though the pattern of species increase from the poles to the equator is far more common than the opposite (or the absence of pattern) and holds true for terrestrial plants (Cowling and Samways 1995; Gentry 1988), some important groups of pollinators such as bees show their highest diversity at intermediate latitudes (Ollerton et al. 2006; Michener 2007). Indeed, Trøjelsgaard and Olesen (2013) found the number of pollinators per plant species peaking at mid-latitudes. Also, among the groups showing a negative correlation to latitude, not all of them increase in species at the same rate. Bats, for example, show the steepest equatorward species increment among mammals (Willig et al. 2003). Therefore, considering that different pollinator groups may show contrasting local diversities along the latitudinal gradient, it will also be interesting to go deeper into how their relative importance as pollinators and the plants relying upon each pollinator group will behave over space (Ollerton et al. 2006).

6.10 Concluding Remarks

Our review suggests that pollination networks are structurally similar in the tropical and non-tropical areas. In tropical regions where species diversity (and presumably also functional diversity) is high, however, niche-based processes which impose barriers to species interactions via forbidden links and trait matching among partners are expected to be more important than neutral-based processes in structuring interaction networks. Importantly, the influence of sampling artifacts on pollination networks has been poorly investigated so far, especially in the tropics. Here, we show that there are some important biases which potentially limits accurate generalizations, notably, geographical and sampling biases in the distribution of pollination networks worldwide. Thus, we highlight that further advances in the understanding of plant-pollinator networks demand increasing research effort covering the Paleotropical region, consideration of the multiple functional groups and their roles (e.g., true pollinators *vs.* other floral visitors) interacting with flowers and sampling of more complete networks. Such studies are needed to better understand differences among tropical and non-tropical areas and whether the latitudinal gradient in species richness affects the structure of pollination networks, which may have important implications on our ability to predict and manage interactions under scenarios of increasing environmental change.

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Chapter 7

Tropical Seed Dispersal Networks: Emerging Patterns, Biases, and Keystone Species Traits

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Ruben Heleno, and Anna Traveset**

Abstract Seed dispersal mediated by animals is a pivotal ecological interaction in the tropics. Despite a long tradition of tropical seed dispersal studies, only recently the drivers of the structure of seed dispersal networks are beginning to be uncovered at macroecological scales. The knowledge on tropical seed dispersal comes mainly from avian dispersal studies in the Neotropics while other frugivores and tropical regions are strongly understudied. The networks sampled with a combination of visitation census and seed recovery from feces seem more reliable of the number of detected links and web asymmetry than networks based on a single method. Our review reveals that keystone species in most networks share a set of functional traits likely influenced by species phylogeny. Woody plants bearing small berries (in the Melastomataceae, Myrtaceae, Moraceae, and Urticaceae families) were the most frequent keystone plants whereas two groups of keystone animals could be identified, namely: small obligate frugivores (Pipridae and Thraupidae) and large animals including a variety of taxonomic groups such as cracids, rodents, monkeys, and megafauna. Large keystone species tend to face a higher extinction risk leading to a concern on the sustainability of the dispersal services they provide, mainly to large-seeded plant species that are essential to ecosystem functioning.

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7.1 Introduction

In the tropics, the majority of seeds are contained in fleshy fruits of different shapes and colours, adapted to endozoochory (Wheelwright 1988). When feeding upon fruits, the animals remove the pulp and free the seed that is frequently moved away from its parent' crown, escaping strong competition with siblings and high pressure from shared natural enemies (Janzen 1970; Connell 1971, but see Hyatt et al. 2003). This interaction between frugivorous animals and fleshy-fruited plants is the most relevant mode of seed dispersal in tropical forests and promotes local regeneration and colonization of vacant habitats (Howe and Smallwood 1982). However, it has been identified as one of the biological interactions related to forest dynamics that is most vulnerable to human disturbance (Neuschulz et al. 2016). Seed dispersal mediated by animals contributes to genetic diversity and gene flow at local and regional scales (Jordano et al. 2007) and it also functions as a relevant driver of evolutionary dynamics for fleshy-fruited plants (Jordano et al. 2007; Lomáscolo et al. 2010; Galetti et al. 2013). A large proportion of vertebrates rely on fruits for a living, especially in tropical forests where the extraordinary bird and mammal richness is partly explained by the evolutionary relationship of such species with fleshy-fruited plants (Fleming et al. 1987).

Strictly speaking, seed dispersal events usually involve two individuals: a plant and an animal. Yet, the fruits of each plant are usually dispersed by an array of frugivorous, which in turn consume the fruits and disperse the seeds of many other plants, and consequently seed dispersal is intrinsically a community-level process. Hence, to fully understand the ecological and evolutionary consequences of seed dispersal, it is crucial to consider the inherent complexity of interactions at the level of entire biological communities (Vázquez et al. 2009a). The analytical network approach is the most valuable tool to accomplish such task by providing a holistic viewpoint from where each pairwise plant–disperser interaction can be considered simultaneously and at the same time account for the biological context of the entire community (Bascompte and Jordano 2007).

Some of the classic studies on seed dispersal already embraced such a community-wide understanding for the study of seed dispersal (Snow and Snow 1971); Crome 1975; Wheelwright et al. 1984). However, only with the advent of modern ecological networks analysis, communities started being considered as interaction networks, progressively moving from qualitative to quantitative networks (Heleno et al. 2014). Recent work has already detected some emerging macroecological patterns from tropical seed dispersal networks (Schleuning et al. 2011, 2012, 2014; Sebastián-González et al. 2015; Sakai et al. 2016). For instance, tropical dispersal networks show to be less specialized than temperate ones, which has been attributed to the greater plant diversity and lower relative abundance of resource plants in the former (Schleuning et al. 2012; Chama et al. 2013). Tropical networks also appear to be less modular than temperate ones, which might be due to a lower preponderance of seasonal effects structuring tropical interactions (Schleuning et al. 2014). Yet, such a relationship between modularity and latitude was absent once accounting for spatial autocorrelation, and a nested pattern with latitude was not found either (Sebastián-González et al. 2015).

Probably, the next challenge for researchers working on seed dispersal networks is to build more functional networks, i.e., networks that inform us on how their composition and structure translate into ecosystem functioning. To accomplish such task, it is necessary to move from seed dispersal to recruitment networks (Schleuning et al. 2015) and also from community to intra-population level. Yet, only recently has seed fate begun being incorporated in networks by quantifying the proportion of intact seeds present in animal droppings (Heleno et al. 2013). Studies that quantify seed dispersal effectiveness (*sensu* Schupp et al. 2010) and estimate seedling recruitment are still very rare (González-Castro et al. 2015; Donoso et al. 2016) with only some attempts in tropical ecosystems (Muñoz et al. 2016; Pigot et al. 2016).

Despite the progress made over the last decades, our understanding of tropical seed dispersal networks is still in its infancy and is currently limited by the quality, quantity, and distribution of available datasets. Here, our aim was to perform a review to characterize the state of the art, to detect potential biases affecting current understanding of tropical seed dispersal networks, and to identify emerging patterns related to the identity and functional traits of the keystone dispersers and plants and discuss their implications for conservation, something not previously tackled by previous revisions. For these purposes, we searched for articles published up to 2016 on seed dispersal networks in the tropics using the following search terms in *Web of Science* and *Scopus*: “seed dispersal network” OR “frugivory* dispersal network” OR “plant-frugivory* network” OR (“mutualistic interaction network” AND dispersal) in the title, keywords or abstract. This search resulted in 58 articles. An additional search was performed in *Google Scholar* with the same keywords for papers published in 2015–2016 to detect articles accepted for publication but still not available in *Web of Science*. Additional studies were compiled from two specialized databases: *Interaction Web Data Base* (<https://www.nceas.ucsb.edu/interactionweb>) and *Web of Life* (<http://www.web-of-life.es/2.0/index.php>). After processing all publications, we selected 43 studies that provided information on seed dispersal or frugivory networks at the community level within tropical latitudes (23.5°N and S). From each study, we compiled the following information: location (latitude and longitude, country and biogeographic region), main habitat type, and level of disturbance (Table 7.1). Regarding the taxonomic groups, we recorded the number of animal taxa included in each network, and the class of each animal (e.g., bird, mammal, reptile); for mammals, we further classified them according to the order to which they belong (e.g., ungulate, rodent, primate). Moreover, we obtained (1) the total number of plant species in the network and the number of links, (2) whether the network was qualitative (binary) or quantitative (weighted), (3) the sampling method implemented (e.g., visitation census or fecal analyses), and (4) whether extinction simulations were performed (Table 7.1). When the studies highlighted the role of particular species owing to their contribution to network structure, this information was also extracted and the main traits of these species were compiled.

Table 7.1 Information of the networks included in this review

Country, Region	Lat	Long	Habitat	Sampling method	P	A	Guilds	Authors	Year
Trinidad, N	10.7	61.3	DF*	V, W	50	14	B	Snow and Snow	1971
Australia, Au	-17.8	-146	RF	V, B	72	7	B	Crome	1975
Mexico, N	18.5	89.4	EDF	V, B	5	27	B	Kantak	1979
New Guinea, Oc	-7.3	-146.7	MF	VF, W	31	9	B	Beehler	1983
Costa Rica, N	10.3	84.4	MF	VF, B	169	40	B	Wheelwright et al.	1984
Malaysia, Or	3.7	102.2	RF	V, B	24	61	B	Lambert	1989
Brazil, N	-22.8	-47.1	DF*	NA, W	7	18	NA	Galetti and Pizzo	1996
Brazil, N	-22.8	-47.1	DF*	V, W	35	29	B	Galetti and Pizzo	1996
Papua, N. Guinea, Oc	-6.7	-145.1	RF	V, B	29	32	B	March and Wheelwright	1996
C. Philippine, Or	10.7	123.2	MF*	F, B	36	19	B, Ba, M	Hamman and Curio	1999
Gabon, A	0.16	11.6	EDF	F, B	16	8	M	Tutin et al.	1997
Panama, N	9.1	79.6	DF	F, W	67	32	B	Poulin et al.	1999
Brazil, N	-24.3	48.4	AF*	VF, B	207	110	NA	Silva et al.	2002
Puerto Rico, N	18.3	66.8	EDF	V, W	25	16	B	Carlo et al.	2003
Puerto Rico, N	18.3	66.5	EDF*	V, W	34	20	B	Carlo et al.	2003
Puerto Rico, N	18.2	66.6	EDF	V, W	25	13	B	Carlo et al.	2003
Puerto Rico, N	18.3	66.6	EDF*	V, W	21	15	B	Carlo et al.	2003
Brazil, N	-24.2	-48.2	AF*	VF, B	207	110	B, Ba, M	Silva et al	2007
Brazil, N	-19.3	-56.1	DF	VF, B	46	46	B, R, F, M	Donatti et al	2011
Regional, N	NA	NA	NA	NA, B	85	18	B, Ba	Mello et al.	2011a
Regional, N	NA	NA	NA	F, W	NA	NA	B	Mello et al.	2011b
Thailand, Or	14.3	101.2	RF	VF, B	17	41	B	Sankamethawee et al.	2011
Kenya, A	0.1	34.5	RF*	V, W	33	88	B, M	Schleuning et al.	2011
Mexico, N	21.5	99.2	EDF*	F, B	16	7	Ba	Garcia-Morales et al.	2012
Kenya, A	0.1	34.5	RF*	V, W	8	54	BM	Menke et al.	2012

Ecuador, N	-0.4	-89.6	DF	F, W	58	18	B, R,	Heleno et al.	2013
Bolivia, N	-16.2	-67.3	MF*	V, W	40	47	B	Saavedra et al.	2014
Brazil, N	-8.6	-36.3	AF*	F, B	56	20	B, Ba	Sarmento et al.	2014
Brazil, N	-23.5	-47.2	RF	V, B	88	59	B	Vidal et al	2014
Regional, N	-4.5	-56.3	FPF*	F, NA	234	69	NA	Correa et al.	2015
Mexico, N	19.3	96.6	MF	F, W	30	16	Ba	Hernández-Montero et al.	2015
Regional, N	NA	NA	NA	VF, B	NA	NA	B, Ba	Mello et al.	2015
Ecuador, N	-0.4	-89.6	EDF	F, B	34	28	B, R, M	Nogales et al.	2016
Brazil, N	-22	-47	AF*	NA, NA	51	39	B	da Silva et al.	2015
Colombia, N	2.4	74.1	RF	V, W	73	68	B, M	Stevenson et al.	2015
Brazil, N	-20	-42	AF	NA, B	234	4	M	Bufalo et al.	2016
Mozambique, A	-18.6	-34.2	DF*	F, W	43	17	M	Correia et al.	2016
Brazil, N	-19.6	-43.6	AF	F, W	34	9	M	Genrich et al.	2016
Colombia, N	3.3	76.4	MF*	V, B	75	60	B	Palacio et al.	2016
Mexico, N	19.4	96.2	DF*	VF, W	42	44	B	Ramos-Robles et al.	2016
Argentina, N	-23.5	-64.5	MF	VF, W	69	52	B	Ruggera et al.	2016
Brazil, N	-18.5	-47.5	DF	V, W	12	66	B	Silva et al.	2016
Panama, N	9.1	-79.1	DF	F, W	12	66	B	Silva et al.	2016

N neotropical, *A* afrotropical, *O* oriental, *Oc* Oceanian; *Au* Australian. Animals: *B* mammals, *M* birds, *V* bats, *R* reptiles, *F* fish. Habitat types: *RF* rain forest, *MF* montane forest, *AF* Atlantic forest, *EDF* evergreen dry forest, *DF* deciduous forest, *FPF* flood plain forest. Anthropogenic disturbed habitats are denoted with a star (*). *V* visitation censuses, *F* fecal analyses, *W* weighted; or *B* binary. A full list of the references is available at CSIC-Repository-Pending code assignment

7.2 Temporal and Spatial Distribution of Tropical Seed Dispersal Networks

The gathered studies range from 1971 to 2016, although 56% of them were performed in the last 5 years, denoting the growing interested in the subject. More recent networks tend to include more animal guilds and to quantify interactions based on the identification of dispersed seeds (Table 7.1). The vast majority of tropical seed dispersal networks have been collected in the Neotropics (77%, $n = 33$), particularly in Brazil (36% $n = 12$), Mexico (12% $n = 4$), and Puerto Rico (12% $n = 4$) (see Fig. 7.1). This bias had already been detected by Corlett (1998) who pointed out the lack of studies in certain areas, such as tropical Asia, despite the great proportion of tree species adapted to seed dispersal by frugivores. Given the low proportion of studies outside the Neotropics (23%), our analyses will only distinguish between studies from the Neotropics and the Paleotropics, including Oceania.

The 43 selected studies encompassed five main habitat types: deciduous and evergreen forests, rain forests, montane forests, and Atlantic forest, all being evenly represented in the dataset (Table 7.1). Similarly, these studies included both habitats with low anthropogenic disturbance ($n = 22$) and highly humanized habitats ($n = 18$), these last ones including secondary forests (44%, $n = 8$), fragmented habitats (33%, $n = 6$), and shade plantations of coffee and cocoa (22%, $n = 4$).

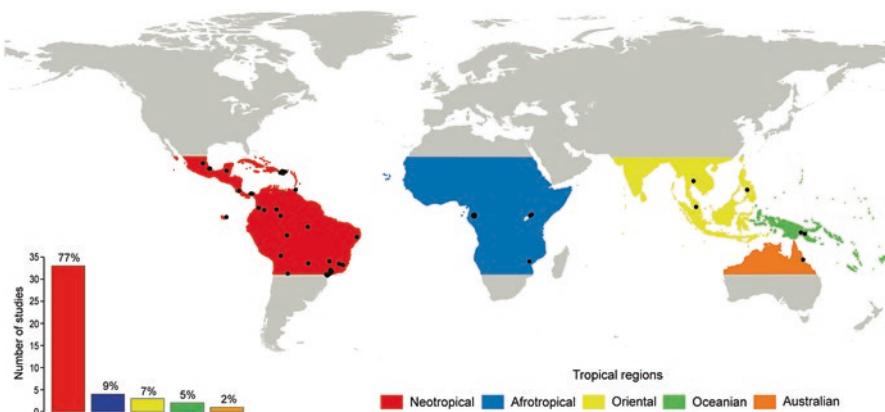


Fig. 7.1 World map representing the tropical regions on different colors. Black dots represent the locations of the studies included in this review. The barplot on the lower left handside indicates the number and percentage of studies in each tropical region. Differences on the number of studies between regions were significant ($\chi^2 = 87.12$, $df = 4$, $P < 0.001$)

7.3 Basic Network Descriptors and Methodological Bias

On average, seed dispersal networks in the tropics involved 60 plant species and 37 animal species. The average number of plants was greater for the Neotropics than the Paleotropics, the former ranging from 5 to 234 plant species and the latter from 8 to 72 plant species (Table 7.2). Animal richness, in contrast, did not follow this trend and no differences were found between the two regions. The overall species richness was greater for the Neotropics than for Paleotropics (Table 7.2) and, accordingly, Neotropical networks were less connected than Paleotropical ones (Table 7.2). Web asymmetry was consistently negative in the two regions, in agreement with the greater abundance of plants compared to animals (Table 7.2). Network robustness to species extinction (R) is defined as the network resistance to species loss (Bascompte and Jordano 2007) and can be quantified by the area below the extinction curve generated by secondary extinctions (Dormann et al. 2009). Only 14% ($n = 6$) of the studies evaluated network robustness by means of extinction simulation analyses. Such studies showed robustness values ranging from 0.50 to 0.87 with the lowest values found in fragmented rainforests (Menke et al. 2012; Stevenson et al. 2015; Palacio et al. 2016). Overall, thus, seed dispersal networks seem to be quite robust to random extinctions (Stevenson et al. 2015; Palacio et al. 2016). However, when keystone species (species with high linkage level and betweenness) are removed first, rapid secondary extinctions occur and the network collapses much sooner (Stevenson et al. 2015; Palacio et al. 2016).

7.4 Methodological Bias

Forty six percent of the networks in our dataset were binary whereas 54% were weighted (Table 7.1). Methods based on visitation census or on fecal content analyses were evenly used (43 vs. 33%), whereas the combination of both was less frequent (23%).

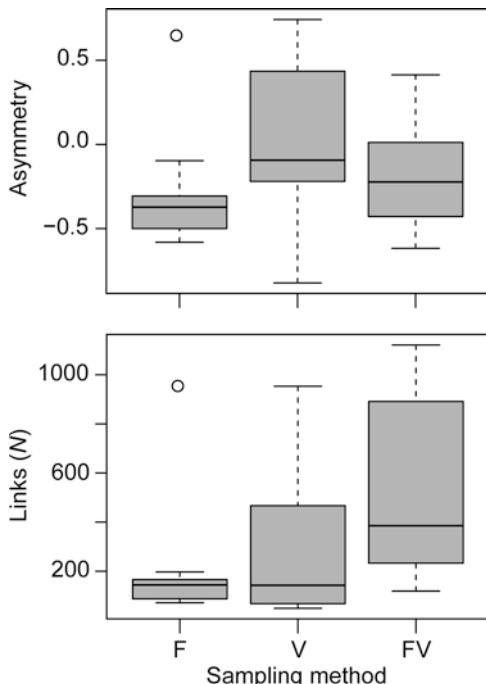
Table 7.2 Number of plants, animals and overall species, links, connectance, and web asymmetry (mean \pm SE) for the Neotropics and Paleotropics

	Neotropics	Paleotropics	Test statistic (t/χ^2)	df	P-value	N
Plants	69 ± 11.6	31 ± 5.4	2.06	25	0.049	31, 10
Animals	38.1 ± 4.8	33.6 ± 8.6	0.58	14	0.567	31, 10
Species	107.13 ± 15.1	64.5 ± 8.3	3.94	13	0.003	31, 10
Links	356 ± 72.5	182 ± 48.4	1.12	21	0.275	24, 8
Connectance	0.19 ± 0.03	0.31 ± 0.1	2.27	14	0.039	24, 8
Web asymmetry	-0.18 ± 0.07	-0.035 ± 0.2	0.33	1	0.564	31, 10

Number of studies used for each variable are shown in the last column for Neo and Paleotropics, respectively. Mean differences were evaluated with a t -test in all cases except for Web asymmetry, which was compared with a Kruskal-Wallis test as it violated the assumptions of normality

It has been previously shown that the method used to collect plant–animal interaction data can influence the number of plants, animals, or links detected in a network (Bosch et al. 2009; Gibson et al. 2011). We thus evaluated whether the methodology used in each study influenced web asymmetry and the number of links detected. We found that networks sampled through visitation census tended to be more symmetrical than those sampled via seed recovery from feces; however, these results were not statistically significant ($F_{2,34} = 2.51, P = 0.095$; see Fig. 7.2). The number of links, by contrast, was affected by the type of sampling method ($F_{2,27} = 2.67, P = 0.05$), with those networks based on a combination of the two methods encompassing on average more links than those based either on only visits or only feces (Fig. 7.2). This pattern has been previously found for pollination networks (Bosch et al. 2009) and may be explained by the underestimation of interactions with rare plants or with those outside the boundaries of the study area when methods are only based on visits. By recovering the seeds that frugivores consumed, such interactions are more likely to be detected. In addition, seed recovery also offers the possibility of obtaining information on seed dispersal quality, such as seed viability after dispersal, germination capacity, or microhabitat suitability (Schupp et al. 2010). As previously mentioned, such information allows moving forward towards seed dispersal effectiveness networks, providing data on recruitment dynamics and effective ecosystem service (Schleuning et al. 2015). Accordingly, the inclusion of methods based on seed recovery is strongly recommended.

Fig. 7.2 Effects of interaction sampling method on Web asymmetry and Links number. The method did not affect web asymmetry ($F_{2,34} = 2.51, P = 0.095$) whereas a higher number of links was detected in the networks based on a combined method of visit census (V) and fecal analyses (F), ($F_{2,27} = 2.67, P = 0.05$)



7.5 Taxonomical and Functional Composition of Seed Dispersal Networks

7.5.1 *Dispersers' Guilds*

Among the 43 studies, most (74%, $n = 32$) have focused on a single disperser guild, 13% ($n = 6$) and 9% ($n = 4$) of studies included two and three animal guilds, respectively, and only 2% ($n = 1$) of the studies have considered all relevant disperser guilds (Table 7.1). A strong bias was detected on the frequency of animal taxa studied in seed dispersal networks ($\chi^2 = 60.45$, $df = 4$, $N = 57$, $P < 0.001$) with birds being the most frequently studied seed dispersers. Seventy nine percent of the studies ($n = 34$) included birds while terrestrial mammals, the second group most frequently studied, appeared in 25% of the studies ($n = 11$) followed by bats (12%, $n = 7$); reptiles and fish were accounted for in only 5% ($n = 3$) and 3.5% ($n = 1$) of the studies, respectively. Within the group of terrestrial mammals, primates were the most frequently studied followed by ungulates and rodents.

7.5.2 *Keystone Species in Tropical Seed Dispersal Networks*

Only 11 (25%) of the 43 revised studies identified the most important species based on their contribution to network structure, yet using different methods for such purpose. Some works used the contribution to network modularity (Olesen et al. 2007), namely the within-module degree (z) and among module connectivity (c) values (e.g., Donatti et al. 2011; Nogales et al. 2016); da Silva et al. 2015). Other studies used the topological position of species within the network, i.e., centrality, with the indexes betweenness centrality (BC), closeness centrality (CC), and degree centrality or standardized degree (k_r) among others (González et al. 2010; Mello et al. 2015; Genrich et al. 2016). The third most frequently used method was the ad hoc categorization of species as being part of the core or the periphery of the network (Palacio et al. 2016; Ramos-Robles et al. 2016). Still, other studies followed an integrated approach combining several methods (Sarmento et al. 2014; Vidal et al. 2014; Ruggera et al. 2016). According to all those metrics, 70 species played disproportionately important roles in these tropical seed dispersal networks. Of those 70 species, 26 were plants and 44 animals with one bird species (*Cathartes ustulatus*) appearing in two studies performed in Argentina and Panama as a “relevant species.” Hereafter, all these species performing a relevant role (i.e., being network or module hubs or connectors, belonging to the central core, or with high standardized degrees) will be referred to as “keystone species” regardless of the metric used to determine such role. Nonetheless, the coherence and matching of keystone species according to different methodologies is poorly understood and warrants further research (Jordán et al. 2009; Stevenson et al. 2015).

7.5.3 Keystone Dispersers

Animal keystone species belonged to 19 families, with uneven representations ($\chi^2 = 34.8$, $df = 18$, $N = 45$, $P = 0.01$). The Paleotropical families Pycnonotidae and Lybiidae (bulbuls and barbets) and the Neotropical Pipridae and Thraupidae (manakins and tanagers) were expected to be more relevant than other families for seed dispersal given their higher number of interactions, both at the network level and also as connectors of different modules (Schleuning et al. 2014). The most frequent families in the networks were Thraupidae (15%) and Turdidae (15%) followed by Pipridae (11%), Cotingidae, Cracidae, Ramphastidae, and Tyrannidae (6% each), with all other families represented by a single species, except the bat family Phyllostomidae with two species (4%). These findings add to previous evidence supporting the relevant role of Neotropical manakins and tanagers, both typical understory species (Fleming et al. 1987). Neither bulbuls nor barbets were identified as keystone families, probably due to the scarcity of data from the Paleotropics (Schleuning et al. 2014). Interestingly, our results revealed other groups of keystone dispersers including megafauna, monkeys, canopy specialist birds such as chachalacas, guans (Cracidae), and toucanets (Ramphastidae), temperate migrants (e.g., thrushes; Turdidae), and also phyllostomid bats.

7.5.4 Keystone Plants

A total of 34 plant species belonging to 16 families were identified as keystone in their networks. The most frequently represented families were Melastomataceae and Myrtaceae, which together represented 32% of all plants in the dataset. Moraceae and Urticaceae represented 24% of the species (12% each) followed by Rubiaceae (8%) and Solanaceae (6%), being the rest of the families represented only by one species. However, these differences were not significant probably owing to the scarcity of data ($\chi^2 = 20.58$, $df = 15$, $N = 34$, $P = 0.15$). All these plant families have been previously highlighted as relevant for frugivores (Snow 1981; Wheelwright et al. 1984). Other important plant families for tropical frugivores, such as Lauraceae and Palmae (Crome 1975; Snow 1981; Wheelwright et al. 1984) are, however, missing from the dataset analysed here. These families typically bear large fleshy fruits, having a mastozoochory dispersal syndrome (Snow 1981; Kuhlmann and Ribeiro 2016); thus, a possible explanation for the absence of these families on the identified keystone species group may be the difficulty of detecting the large animals that typically disperse large fruits and seeds. In contrast, the plant species identified as keystone tend to bear small fruits usually preferred by small birds. This is the case of *Miconia* (Melastomataceae), the most frequently detected genus among the keystone plants, as well as many Rubiaceae species. The typical fruits of these species are small juicy berries containing many tiny seeds. Plants with these fruit types on the mentioned families are typical of early successional stages with high colonization ability, thereby frequently appearing in cleared areas and edges (Snow 1981; Saavedra et al. 2015; Silva et al. 2016).

Some studies found ecological conditions such as species abundance, and its spatiotemporal variation, and morphological constraints as key drivers of network roles (Vázquez et al. 2009b; Silva et al. 2016). Our results reveal a strong phylogenetic component on the identity of keystone species, which does not only result of ecological contingency but is also determined by inherited characteristics shaped by evolutionary history (Vázquez et al. 2009b). The identification of keystone species and their effects on community stability are strongly relevant to understand evolutionary patterns and ecosystem services delivery (Sakai et al. 2016). Therefore, the interplay between drivers of keystone species, such as species abundance, functional traits, and phylogeny needs to be further explored (Vázquez et al. 2009b).

7.6 Functional Traits of Keystone Species of Tropical Seed Dispersal Networks

Previous attempts to explain why some species play a more relevant role in seed dispersal networks have evaluated several morphological and behavioral traits, of which the most common are dietary specialization, body size, and migratory behavior (Donatti et al. 2011; Sarmento et al. 2014; Schleuning et al. 2014; Vidal et al. 2014; Mello et al. 2015; Palacio et al. 2016). In the case of plants, most frequently studied traits were fruit size, seed burden, fruit type, and life form (Donatti et al. 2011; Vidal et al. 2014; Palacio et al. 2016; Ruggera et al. 2016). Accordingly, we compiled this information for the 70 species recorded as keystone in our database, as well as their IUCN conservation status (www.iucnred.list.org). When trait information was not available in source articles, in addition to scientific literature, specialized databases were used (www.hbw.com, animaldiversity.org, www.tropicos.org). The categories assigned owing to dietary specialization were obligate, partial, or opportunistic frugivores. A species was considered an obligate or partial frugivore when fruit constitutes the majority (>50%) or a relevant (20–30%) component of its diet, respectively, whereas frugivores that consume fruits only occasionally were classified as opportunistic (Mello et al. 2015; Palacio et al. 2016). Animals up to 74 g of weight were classified as small sized, those in the range 75 to 250 g as medium, whereas large animals were those over 250 g and up to 40 kg (Dirzo et al. 2014; Silva et al. 2016; Mello et al. 2015). Over such weight, species were considered as megafrugivores (Dirzo et al. 2014). According to fruit diameter, plant species were classified as small (<5 mm), medium (5–10 mm), large (11–50 mm), or mega (>51 mm) and in multi- or single-seeded species according to seed number (Wheelwright et al. 1984; Saavedra et al. 2015).

7.7 Keystone Dispersers' Functional Traits

We found that most animal species identified as keystone were either obligate (62.2%) or partial frugivores (24.4%), with less than 15% being opportunistic frugivores ($\chi^2 = 17.733$, df = 2, $P > 0.001$). Interestingly, two thirds of the keystone species

(64%) were small frugivores, around 30% where either medium or large sized and only 6% were megafrugivores ($\chi^2 = 38.11$, df = 3, $P > 0.001$). Only 14% of the key-stone species were classified with higher risk of extinction (i.e., Near threatened, Vulnerable) relative to 86% that were classified as Least Concern ($\chi^2 = 24.2$, df = 1, $P > 0.001$). We detected that the categories of these three variables were not randomly distributed; for instance, most obligate frugivores were small sized whereas mega and large keystone species were most frequently partial frugivores ($\chi^2 = 19.48$, df = 6, $P > 0.005$). Also, larger species tended to be in higher extinction risk ($\chi^2 = 16.04$, df = 3, $P = 0.001$). In contrast, dietary specialization and extinction risk were not correlated ($\chi^2 = 1.17$, df = 2, $P = 0.57$). To classify frugivores according to the four variables studied (dietary specialization, body size, conservation status, and migratory behavior) a Non-metric Multidimensional scaling analysis (NMDS) was performed using the packages (*vegan* and *FD* in the R platform 3.2 (Dixon 2003; Laliberté and Legendre 2010). We found an ordination of keystone species on several groups coherent with previous analyses on trait distribution frequency. The group gathering most species was that of small obligate frugivores; several species of tanagers, manakins, and phyllostomid bats were the most frequently represented (Fig. 7.3). Another group was that of medium to large partial frugivores of low conservation concern including several species of tucanets, chachalacas, guans, and terrestrial and arboreal mammals such as opossums and howler monkeys. Most keystone species were not threatened; however, we detected two specific groups of keystone dispersers that face an higher extinction risk, namely: some small and medium-sized obligate frugivores such as tucanets and cotingas on one side, and two mega dispersers, the Galapagos giant tortoise (*Chelonoidis nigra*) and the lowland tapir (*Tapirus terrestris*) (Fig. 7.3).

7.8 Keystone Plants Functional Traits

Keystone plants differed much in fruit size ($\chi^2 = 9.6$, df = 3, $N = 27$, $P = 0.022$). Most frequent keystone species (78%) bore medium (5–10 mm) and small fruits (>5 mm) while plants with larger fruits played more rarely such a role (Large: 11–50 mm, 18% and Mega: >51 mm, 4%). Most keystone plants produced berries (52%) followed by drupes (18%) and achenes (11%). Keystone species were typically multi-seeded, with only 20% being single-seeded ($\chi^2 = 9.14$, df = 1, $N = 28$, $P = 0.002$). Trees (55%) and shrubs (38%) were the most frequent life forms, whereas herbs (3.5%) and lianas (3.5%) were scarcely represented ($X^2 = 23.27$, df = 3, $N = 29$, $P < 0.001$). In contrast to animal functional traits, there was not interdependency of different plant traits and thus no further analyses were performed. The threatened category is not shown as most species were classified as non-evaluated.

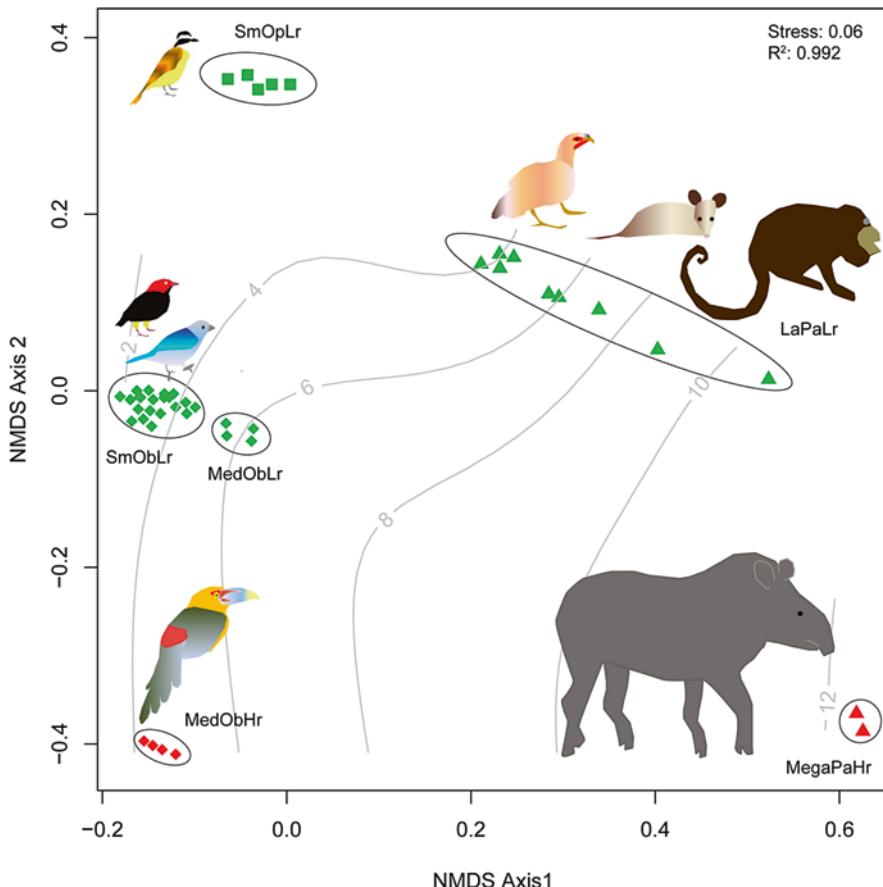


Fig. 7.3 Keystone species Non-metric Multidimensional scaling (NMDS). Representation of key-stone dispersers based on log transformed body size (showed in the isolines), dietary specialization (diamonds: obligate frugivores, triangles: partial frugivores; squares: opportunistic frugivores), and conservation status (Red: species at higher risk of extinction, green: low risk of extinction). Ellipses denote dispersers with similar traits: *SmOpLr* Small, Opportunistic frugivores at Low risk of extinction (tyranid), *SmObLr* Small, Obligate frugivores at Low risk (manakin and tanager), *SmObHr* Small, Obligate frugivores at High risk (tucanet), *MedObLr*, *MeObHr* Medium Obligate frugivores at Lower and Higher risk of extinction, respectively (tucanets), *LaPaLr* Large, Partial frugivores at Low risk (cracid, opossum, howler monkey), *MegaPaHr* Megafauna, Partial frugivores at High risk (tapir). Species inside brackets are representative of each group

7.9 Trait-Based Niche Complementarity Among Network Keystone Species

There is rather low consistency among previous studies on the role of animal species traits to determine their relevance in seed dispersal networks. Some works did not find a relationship between body size and species importance in network structure

(Schleuning et al. 2014, Vidal et al. 2014, Mello et al. 2015) while others suggested that large animals tend to be the most relevant in the network (Donatti et al. 2011). Dietary specialization has been pointed out as a pivotal trait with obligate and partial frugivores playing the role of keystone species (Sarmento et al. 2014; Schleuning et al. 2014; Mello et al. 2015; Pigot et al. 2016) other studies find that the only relevant characteristic determining animal species contribution to dispersal network was the threatened category, being keystone species those that are at higher risk of extinction (Vidal et al. 2014).

Our approach based on multivariate analyses allowed the determination of keystone frugivores integrating all relevant traits. Dietary specialization and body size seem thus the pivotal variables determining the role of keystone species in tropical seed dispersal networks (see also Pigot et al. 2016). Small-sized species of obligate frugivores were the most frequent keystone group though with the condition of being obligate frugivores (Schleuning et al. 2014; Mello et al. 2015). However, medium- to large- and mega-sized frugivores functioned as keystone species, even when they have more generalized diets. These groups of keystone species seem to provide functional complementarity to tropical dispersal networks. Namely, (1) small specialized frugivores forming the core of the keystone species and likely responsible for a large quantity of local seed dispersal of small- to medium-sized seed species; and (2) large and mega-sized animals with a more generalized diet, that may consume an array of fruits and seed types mobilized over long distances (Jordano et al. 2007; Donatti et al. 2011; Escribano-Avila et al. 2014). This pattern resembles a trait-based niche complementarity according to which closely related species (in our case tanagers, manakins and thrushes) tend to share functional traits (small-sized, obligate frugivores) and to disperse similar plants (Dehling et al. 2016; Pigot et al. 2016). Conversely, unrelated species (cracids, toucanets, opossums, howler monkeys, giant tortoises, and mega herbivores) exhibit obvious heterogeneous functional traits on size, behavior, and diet that may lead to wider arrays of dispersed species likely related to plants and animals trait matching (Dehling et al. 2016; Pigot et al. 2016).

7.10 Conservation Implications

There is a growing concern that seed dispersal services might be compromised in the future due to the decline and eventual extinction of frugivores populations (Galetti et al. 2013). Large animals, which tend to play a preponderant role as dispersers of many fleshy-fruited plant species (Muñoz et al. 2016; Pigot et al. 2016) are particularly threatened in many ecosystems due to hunting and poaching (Dirzo et al. 2014), further threatening seed dispersal services (Galetti et al. 2013; Vidal et al. 2013). Owing to a strong non-random matching in the morphologies of dispersers and fruits (Dehling et al. 2016), large-fruited and seeded plants are dispersed by the larger frugivores in the community (Hamann and Curio 1999). Thus, larger-fruited plants exhibit a scarcer coterie of frugivore partners than smaller-fruited

species (Crome 1975; Wheelwright et al. 1984; Donatti et al. 2011; Vidal et al. 2014; Muñoz et al. 2016; Palacio et al. 2016) and are more vulnerable to the loss of their seed dispersers, eventually truncating their reproductive capacity (Wotton and Kelly 2011). Large fruited and seeded plants are typically late-successional species that play a unique role in ecosystems (Bello et al. 2015). Therefore, further attention should be paid to the conservation status and the regeneration capacity of these species in a world depauperated of large frugivores.

7.11 Conclusions

The last decades have seen substantial advances in our understanding of the structure and function of seed dispersal interactions and how they might shape tropical ecosystems. Here, we identify two main functional groups of seed dispersers: one homogeneous group of small, specialized, and abundant dispersers moving many small seeds at the local scale, and another more heterogeneous group formed by larger dispersers with lower abundances and dispersing both small- and large-seeded fruits at larger regional scales. The recent advent of highly resolved, comprehensive, and quantitative seed dispersal networks encompassing whole communities will surely pave the road to further advances in the near future. Such new studies are vital to clarify global patterns on seed dispersal networks, characterize the role of large herbivores and megafauna (including extinct species) in seed dispersal, and further advance ecological network theory by incorporating temporal, spatial, and evolutionary changes into this key ecosystem service.

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Chapter 8

Plant-Herbivore Networks in the Tropics

Antonio López-Carretero, Ek del-Val, and Karina Boege

Abstract Understanding the patterns and processes behind the high biological diversity of tropical ecosystems has been one of the most important issues in modern ecology. Plant-herbivore interactions constitute an important percentage of biodiversity in the tropics, and their ecological and evolutionary importance has been demonstrated in a large number of studies. However, it is only very recently that plant-herbivore antagonistic interactions are being addressed from the perspective of complex networks to evaluate how different factors influence their interaction patterns. In this chapter, we provide a summary of the processes that have been reported shaping the specialization and structuring of tropical plant-herbivore networks. From the limited availability of studies in such habitats we suggest that plant-herbivore networks are spatiotemporally dynamic and are the result of multiple non-exclusive processes where seasonality, variation in resource availability, habitat type, disturbance regime and species-specific attributes contribute to structuring these highly diverse and specialized antagonistic networks.

8.1 Introduction

Trophic interactions involving plants and their herbivores account for approximately 40% of global terrestrial biodiversity (Price 2002), which is mainly concentrated in tropical ecosystems (Novotny and Basset 2005; Lewinsohn et al. 2006; Beck and Khen 2007), and also represent one of the major conduits of energy flow to higher trophic levels (Futuyma and Agrawal 2009). The diversification of

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herbivorous insects in the tropics is evolutionarily associated with plants (Futuyma and Agrawal 2009; Forister et al. 2015), and the high diversity and specificity of insect-plant interactions renders herbivory as one of the processes determinant in the distribution and composition of plant species (Bagchi et al. 2014; Kempel et al. 2015). Therefore, studying the different ecological and evolutionary processes that influence the structure of plant-herbivore ecological networks is an important step in understanding patterns of tropical biodiversity (Lewinsohn et al. 2005; Becerra 2015).

In biological communities, herbivorous species and plants interact with many other species, originating an intricate network of trophic interactions. Network analyses have been a useful tool to describe plant-animal interactions and to analyze their role in the organization and dynamics of biodiversity in tropical ecosystems (Bascompte and Jordano 2007). Furthermore, complex network analyses can be informative to assess if the evolution of plants and their consumers occurs through one-to-one coevolutionary processes or are the outcome of diffuse coevolution, where the assemblage of multiple species play an important role. In particular, different metrics used to describe the structure of plant-herbivore networks can be useful to identify evolutionary interaction units, defined by the species influencing fitness of target species under diffuse coevolution (Thompson 1982). In spite of the ecological and evolutionary importance of antagonistic plant-herbivore interactions, just a few studies have examined these interactions from a network perspective in the tropics.

In general, plant-herbivore networks are highly specialized mainly due to the evolution of physical and chemical defenses of host plants and, in turn, the adaptation of herbivores to such defenses (Wardhaugh et al. 2014; Becerra 2015; Forister et al. 2015). Given this context, the preference of herbivores to feed on closely related plants (Funk et al. 1995; Janz et al. 2001; Weiblen et al. 2006; Benítez-Malvido and Dátilo 2015) or those with similar leaf attributes (Becerra 1997; Agrawal 2007) has been found to be one of the most important factors promoting modularity in antagonistic networks (Thompson 1994; Prado and Lewinsohn 2004). Furthermore, the ecological and phylogenetic mechanisms that originate the structural patterns of antagonistic networks have only recently begun to be explored despite important prior advances in the identification and description of the structure of different plant-herbivore networks. Research from temperate ecosystems has shown how specialization and structural attributes of plant-herbivore networks are influenced by phylogenetic signals (Volf et al. 2017), intraspecific genetic variation of plants (Barbour et al. 2016; Lau et al. 2016), habitat restrictions, and species attributes (Cagnolo et al. 2011) in addition to habitat disturbances (Valladares et al. 2012).

In tropical ecosystems, patterns of plant-herbivore networks can vary with respect to habitat disturbance (Villa-Galaviz et al. 2012; de Araújo et al. 2015; Benítez-Malvido et al. 2014, 2016) and spatiotemporal variation in plant availability (López-Carretero et al. 2016), host plant resistance (López-Carretero et al. 2016), herbivores specificity, and the degree of intimacy of interactions (Novotny et al. 2010; Pires and Guimarães 2012). Even so, the study of processes influencing

the specificity and structural patterns of plant-herbivore networks is still under development. Therefore, the objective of this chapter is to provide an update on these processes, particularly in tropical ecosystems. We first characterize the structural patterns of tropical plant-herbivore networks in relation to other types of networks in non-tropical habitats. In addition, we review how antagonistic networks vary spatially and temporally, and the biotic and abiotic factors influencing this variation. Then, we address how habitat disturbance and the species-specific attributes of plants and their herbivores affect the structure and resilience of antagonistic networks. Finally, we provide a conclusion with future directions for the study of plant-herbivore networks in the tropics.

8.2 Structure of Plant-Herbivore Interaction Networks

In contrast with mutualistic networks that tend towards generalization, antagonistic networks are more specialized, less nested, and have greater modularity (Lewinsohn et al. 2006; Thébaud and Fontaine 2010; Sauve et al. 2014). Nevertheless, within antagonistic networks, the degree of compartmentalization depends on the interacting trophic guilds, the type of ecosystem, and even latitude. In the case of plant-herbivore networks, specialization and hence modularity can vary as a function of herbivore guilds, being highly specialized in the case of herbivores living inside the plants (e.g., miners and galling insects), but less specialized in the case of free living herbivores (e.g., suckers and chewers, Novotny et al. 2010, Pires and Guimarães 2012). Although there are not enough studies to perform formal analyses to compare between temperate vs. tropical networks, a marked latitudinal gradient towards a greater diversity (Novotny and Miller 2014), and specialization (Dyer et al. 2007, Forister et al. 2015, but see Novotny et al. 2006, Stork 2007) of herbivores in the tropics has been reported. From the available empirical evidence cited in this chapter, we detected larger networks with greater specialization and a higher number of rare herbivore species in tropical ecosystems. Other parameters, such as connectance, modularity, and nestedness, seem to be equivalent between tropical and temperate forests. However, more studies on plant-herbivore networks are needed across large latitudinal gradients and among different ecosystems to assess significant differences between temperate and tropical ecosystems.

8.3 Plant-Herbivore Interaction Networks in the Tropics

Tropical plant-herbivore interactions have been studied since long time ago (Janzen 1970; Coley 1983; Coley and Barone 1996); however, only recently the interaction network approach has been considered in this area. The studies comprise evaluations of different herbivore guilds, including leaf chewers (lepidopteran, orthopteran, and coleopteran), leaf miners (dipteran and lepidopteran), and sapsuckers

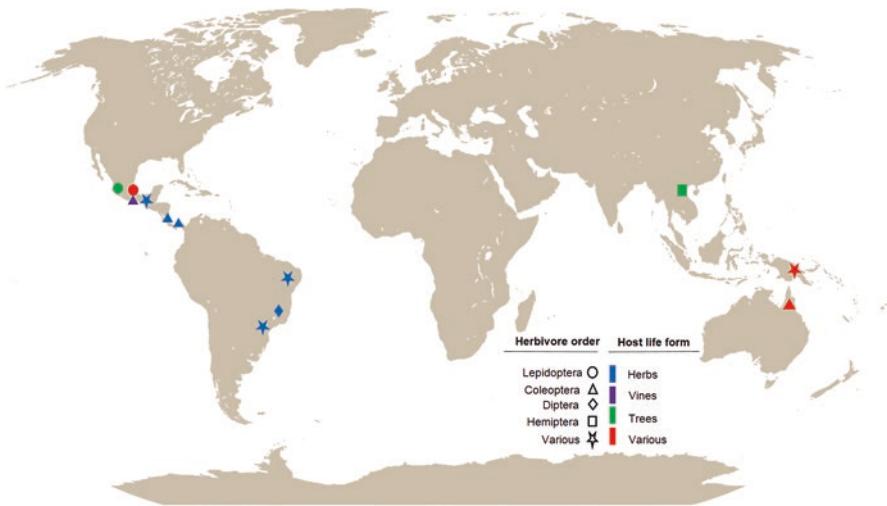


Fig. 8.1 Distribution of studies of plant-herbivorous networks in the tropical regions of the planet. Each symbol represents the locations of the studies reviewed in this chapter. Symbol forms indicate different orders of herbivorous insects (circles = Lepidoptera larvae, triangles = adult Coleoptera, diamonds = dipteran larvae, square = Hemiptera, and stars = studies that include more than one insect order). Colors represent the different life forms of the herbivorous host plants studied (blue = herbs, purple = vines, green = trees, red = more than one plant life form)

(hemipteran), which are concentrated in the Neotropical region, mainly focused on plant herb hosts (Fig. 8.1 and Table 8.1). There is a lack of studies that incorporate different orders of herbivores associated with host plants of different life forms. In addition, there are some regions where plant-herbivore networks have not been explored, in particular studies in tropical Africa are unknown (Fig. 8.1 and Table 8.1).

In general, studies have reported that tropical plant-herbivore networks have high levels of specialization coinciding with other studies reporting diet breadth of herbivores being narrower in lower latitudes (Erwin 1991; Novotny et al. 2004, 2006; Forister et al. 2015). Network size (i.e., species richness and number of interactions) is quite variable as a function of the taxonomical level of different groups of herbivores. In terms of network parameters, most studies in the tropics have found a modular structure (Meskens et al. 2011; Villa-Galaviz et al. 2012; López-Carretero et al. 2014; Wardhaugh et al. 2014; Bergamini et al. 2016) with the exception of work by Eben and Espinosa de los Monteros (2015), in which they report a plant-Chrysomelid network without a modular structure, in spite of being very specialized. A study in Australian rainforest reports similar levels of specialization in plant-herbivore and flower visitor networks although the herbivore network was modular and the flower visitor was nested (Wardhaugh et al. 2014). Thus, in this case, the topology of interaction networks appears to be independent of the level of specificity. Interestingly, some tropical food webs, although are extremely complex, seem to be dominated by relatively few interactions (Novotny and Miller 2014).

Table 8.1 Information of the plant-herbivore networks studies included in this review

Factor evaluated	NP	L/A	Order	PF	PS	HF	HS	Region	Habitat type	Source
Phylogenetic signal	M	L	C DL	1	22	6	55	Neo Bra	Cerrado Savanna	Bergaminini et al. (2016)
Phylogenetic signal	C H M	A	C	8	Ns	1	43	Ame	Several tropical, subtropical and temperate habitats	Eben and Espinosa de los Monteros (2015)
Host taxonomy and phenotype	C G H M N NO	A	C	5	17	1	30	Neo Pan	Rain forest	Meskens et al. (2011)
Forest canopy	H	A	C	13	23	5	88	Aus Aus	Rain forest	Wardhaugh et al. (2014)
Plant diversity	G	A	H	5	16	8	33	Ori Chi	Evergreen subtropical forest	Staab et al. (2015)
Habitat type and resource availability	C G H IE M V	L	L	20	56	12	176	Neo Mex	Different coastal seasonal habitats	López-Carretero et al. (2014)
Anti-herbivore defenses	d ss	L	L	16	29	9	104	Neo Mex	Different coastal seasonal habitats	López-Carretero et al. (2016)
Habitat disturbance	C D H L D VR	AL	CDHL	1	2	ns	ns	Neo Mex	Rain forest	Benítez-Malvido et al. (2014)
Secondary succession	C N M E C R H R	L	L	36	140	21	471	Neo Mex	Dry forest	Villa-Galaviz et al. (2012)
DNA barcodes use	-	A	C	5	33	1	20	Neo CR	Rain forest	García-Robledo et al. (2013)
Forest fragmentation	DI N	AL	CHL	1	1	9	29	Neo Mex	Rain forest	Benítez-Malvido et al. (2016)
Interaction intimacy	C H N ID M NO	AL	AHHyL	ns	24	1	9	Neo Bra	Cultivars and other habitats	Benítez-Malvido et al. (2015)
Herbivore guild	ES HI	AL	CDHLOP	38	88	44	399	Oce PNG	Rain forest	Novotny et al. (2010)

NP network parameter evaluated, *M* modularity, *c* connectance, *H* network-level specialization, *G* generality, *N* nestedness, *NO* Niche overlap, *IE* interaction evenness, *V* vulnerability, *d* species-level specialization, *ss* species strength, *ES* effective specialization, *HF* host plant isolation, *LD* linkage density, *VR* variance ratio, *EC* extinction curve, *R* robustness, *DI* diversity of interactions, *NO* niche overlap. Herbivore developmental stage: *L* larval, *A* adult. Herbivore order: *C* Coleoptera, *D* Diptera, *H* Hemiptera, *Fy* Hymenoptera, *L* Lepidoptera, *O* Orthoptera, *P* Phasmidae, *A* Acari. *PF* number of plant families, *PH* number of plant species, *HF* number of herbivore families, *HS* number of herbivore species. Region: *Ame* several habitats types throughout the Americas, *Neo* neotropical, *Aus* Australian, *Ori* oriental, *Oce* oceanian, *Mex* México, *Bra* Brazil, *Chi* China, *CR* Costa Rica, *PNG* Papua New Guinea, *ns* not specified

8.4 Spatiotemporal Variation of Plant-Herbivore Networks

In some tropical and non-tropical ecosystems where seasonality and climatic conditions are not widely variable, specialization, and structure of plant-herbivore networks remain stable over time and space (Wardhaugh et al. 2014; Kemp et al. 2016). However, the contrasting monthly and seasonal climatic variation (mainly in precipitation and temperature) of some deciduous and sub-deciduous tropical ecosystems affect the availability and quality of host plants (Janzen 1993; Coley 1998; Pearse and Hipp 2012) and therefore can promote important changes in herbivore composition (Janzen 1993; Coley and Barone 1996), diet breadth (Scherrer et al. 2016), specialization, and structural patterns of plant-herbivore networks (López-Carretero et al. 2014, 2016). For example, environments that provide high richness and abundance of host plants (i.e., habitats rich in host species with different life histories or rainy season) promote specialization, modularity, and interaction evenness of plant-lepidopteran herbivore networks, as observed in Mexican (López-Carretero et al. 2014) (Fig. 8.2b, c) and Brazilian tropical forests (Scherrer et al. 2016). In contrast, in environments where resource availability for herbivores is restricted (i.e., poorly structured habitats and/or marked dry season), selectivity and modularity of plant-herbivore networks decrease due to the dominance of generalist herbivores (López-Carretero et al. 2014) that are capable of expanding their host preferences in face of adverse conditions (Scherrer et al. 2016, Fig. 8.2b, c).

The temporal increase in the availability and structural complexity of plant species in the warmest and rainy months promote a great variety of microhabitats and host plant richness, which in turn reduce niche overlap and promote a more equitable distribution of food resources (i.e., interaction evenness) among herbivores in the network (López-Carretero et al. unpublished data) (Fig. 8.2d). This pattern is consistent with the notion that specialization of herbivores allows for the coexistence of species through a fine distribution of trophic niches (Futuyma and Moreno 1988; Dyer et al. 2007; Lewinsohn and Roslin 2008). In this context, comparative studies of plant-herbivore interaction networks in tropical wet vs. dry forests would be revealing, and comparisons between seasonal temperate and tropical forests could help to disentangle the influence of species diversity vs. seasonality on plant-herbivore interaction networks (Dirzo and Boege 2008).

In addition, tropical plant communities show a marked vertical stratification, as does the assembly of associated herbivores. For example, herbivore diversity is greater in the canopy than in the understory, and consequently the faunistic similarity between the two strata is low (Basset et al. 2003; Ribeiro and Basset 2007). This is likely promoted by differences in abiotic conditions, the availability of good quality foliage and predation risk between these strata (Van Bael et al. 2003; Boege and Marquis 2006; Neves et al. 2014). Nevertheless, the ways in which the structure of herbivore networks varies with respect to vertical stratification are still largely unknown.

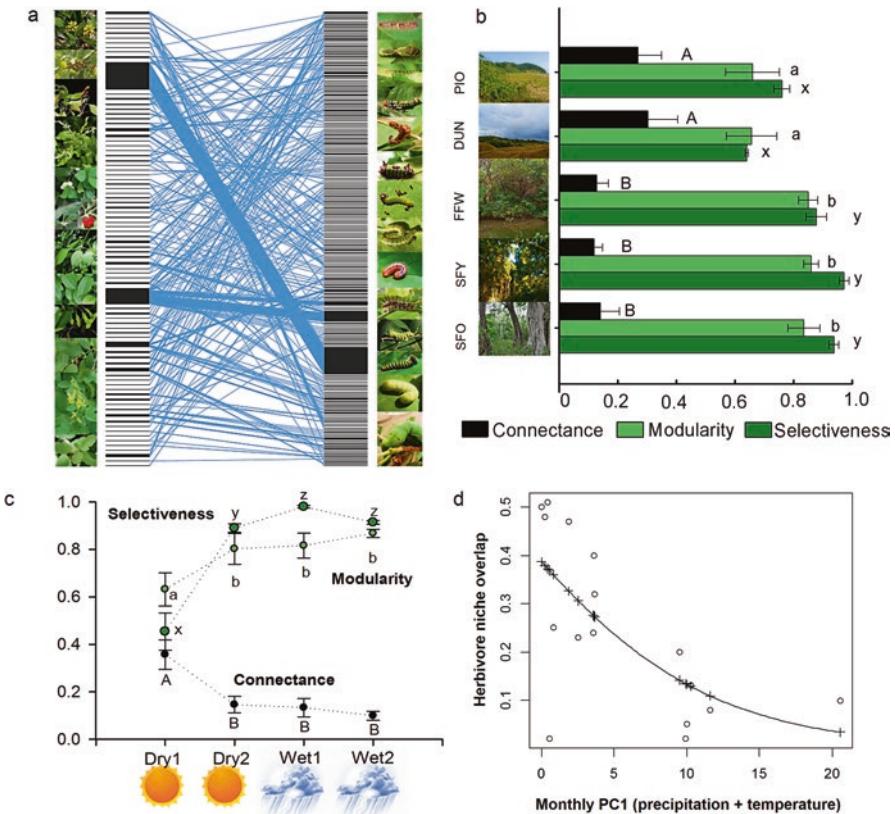


Fig. 8.2 Spatiotemporal variation in selectiveness and structural patterns of plant-lepidoptera network in a seasonal tropical ecosystem of México. **(a)** Weighted bipartite network between 176 caterpillar species (right nodes) and 56 plant species (left nodes) with different life history. Linkage width indicates the frequency of each herbivory interaction. **(b)** Variation of macroscopic network parameters in different habitats types that vary in their complexity (*PIO* pioneer dune vegetation, *DUN* coastal dune scrub, *FFW* tropical lowland floodplain forest with a wetland ecotone, *SFY* recently established tropical lowland sub-deciduous forest, *SFO* lowland sub-deciduous forest in advanced stage of succession) (López-Carretero et al. 2014). **(c)** Variation in network parameters across seasonality in year 2011: Dry1 (April–March), Dry2 (May–June), Wet1 (July–August), Wet2 (September–October) (Dry = Dry season, Wet = Rainy season). Different letters represent significant differences ($P < 0.05$); and **(d)** Significant negative relation between monthly PC1 values (precipitation + temperature) and herbivore niche overlap ($P < 0.05$). PC1 is a synthetic variable that describe the simultaneous variation of precipitation and temperature, greater values of PC1 corresponded to greater precipitation and temperature (López-Carretero et al., unpublished data)

8.5 Influence of Phylogeny, Species, and Genetic Diversity on Plant-Herbivore Networks

Antagonistic plant-herbivore interactions are highly specialized as a result of different ecological factors, including plant diversity, the biochemistry of host plants, and historical factors (Ehrlich and Raven 1964; Weiblen et al. 2006; Futuyma and

Agrawal 2009; Richards et al. 2015). In particular, evolutionary history often plays an important role in determining both community assemblages and species interaction networks (Peralta 2016, Volf et al. 2017 but see Novotny et al. 2010). This influence can be detected through phylogenetic signals found in the properties of plant-herbivore interaction networks. In general, studies have shown that phylogenetic distances influence interacting species, modularity, and network nestedness (Peralta 2016). For example, in a leaf beetle-plant interaction network in Panamá, Meskens et al. (2011) found that plant phylogeny constrains herbivore modules and therefore determines network parameters. However, Bergamini et al. (2016) reported a strong phylogenetic signal for flower-head herbivores but a mild signal for interacting plants. Other studies on tropical herbivore communities in New Guinea have found that host phylogenetic distance explains a significant fraction of the variance in herbivore community similarity for some herbivore guilds (Novotny et al. 2010). In particular, caterpillar species show higher phylogenetic clustering than coleopterans and orthopteroids (Weiblen et al. 2006). However, recent studies from temperate forest showed that not all levels of host plant phylogeny are equal in their effect on structuring plant-herbivore food web, which depends on the specialization of insect guild considered (Volf et al. 2017).

In some cases, plant defensive traits do not correlate with plant phylogeny (Becerra 1997; Novotny et al. 2010) but are determined by local environmental and ecological factors. For example, although the interactions between Diabroticina beetles (Chrysomelidae) and their host plants (Cucurbitaceae) have been considered to be the product of a coevolutionary process directed by the secondary metabolites of hosts (Metcalf 1986); recently, Eben and Espinosa de los Monteros (2015) showed that the structural patterns of plant-chrysomelid networks do not correspond with plant phylogeny but are rather related to the chemical and morphological similarity of the host plants.

8.5.1 Plant Diversity

Although plant diversity has been found to influence the stability of food webs (Haddad et al. 2011), its effects on plant-herbivore network parameters has been scarcely studied. Staab et al. (2015) investigated a plant-hemipteran network in a gradient of plant diversity in subtropical China, and concluded that the number and abundance of host species was not determinant for network structure as modularity and specialization remained constant across the gradient. This could be due to the specific feeding behavior and particular morphological structures characteristic of sap-sucker insects, which feed only on plant taxa to which they are adapted (Walling 2008). In the case of caterpillars, for example, levels of specific selectivity and species strength in plant-lepidopteran networks seem to be better explained by foliar host plant traits than their relative abundance (López-Carretero et al. 2016).

8.5.2 Genetic Diversity

Intraspecific genotypic variation in plant traits can also have an important influence in herbivore communities (Whitham et al. 2006), food web complexity (Barbour et al. 2016), and hence in plant-herbivore interaction networks in general. For example, an analysis of genotype-species network has revealed that genotypic variation in *Populus angustifolia* influences modularity, nestedness, centralization, and species co-occurrence of the assemblages of associated herbivores (Lau et al. 2016). The influence of genotypic variation in plant-herbivore networks, however, has not been assessed in tropical systems and requires further attention. Incorporating the evolutionary history and genetic variation of species into the study of plant-herbivore interaction networks can greatly contribute with our understanding of community assembly rules and processes, community dynamics, and resilience.

8.6 How Host Plant and Herbivorous Traits Can Affect Plant-Herbivore Networks

8.6.1 Host Defensive Traits

Foliar damage inflicted by herbivores strongly affects plant growth and reproduction (Rausher and Feeny 1980; Marquis 1984; Maron and Kauffman 2006). Therefore, this antagonistic interaction results in continuous evolutionary processes influenced by reciprocal selection. During these processes, plants express defensive traits that reduce herbivore damage and in turn, herbivores adapt to the defensive strategies of plants (Ehrlich and Raven 1964; Thompson 2005). In the tropics, reciprocal selection can be so intense that dissimilarity in plant defensive traits is positively associated with herbivore diversity and specialization (Novotny et al. 2002; Weiblen et al. 2006; Forister et al. 2015). For example, in tropical plant genera that maintain enormous herbivore richness, such as *Inga* (Kursar et al. 2009), *Bursera* (Becerra 1997, 2007, 2015), and *Piper* (Richards et al. 2015), the diversity of defensive metabolites is positively related with the diversification and specialization of herbivores, both at ecological and geological scales (Gentry 1982, 1989; Richards et al. 2015).

Although coevolutionary processes involving the continuous defense and counter-defense of plants and their herbivores have been referenced to explain the high specificity of plant-herbivore interactions (Thompson 1994; Coley and Barone 1996; Prado and Lewinsohn 2004) the influence of specific physical and chemical defensive plant traits on the specialization and structuring of plant-herbivore networks has been practically unexplored. A recent study in a Mexican tropical forests showed that the simultaneous expression of foliar toughness, trichome density, and phenolic content in different host species influences the selectivity of caterpillars and the strength of plant

species (trophic importance; López-Carretero et al. 2016). In particular, host species with high foliar toughness and low contents of foliar phenolic compounds were related to high species strength and selectiveness, which suggest that plants with this combination of attributes represent an important food resource for the assemblage of specialist herbivores in the network. On the other hand, during the dry season, host species with high trichome density and leaf phenolic content were consumed by a small number of highly selective herbivorous species capable of feeding on this combination of leaf attributes (López-Carretero et al. 2016).

Leaf morphology can also play an important role in the structure of plant-herbivore networks. For example, in a Chrysomelinae-plant network in Barro Colorado Island, Panama, the architecture of immature leaves forming standing pools in some host families (Zingiberales) but not in others (Arecales and Poales) have influenced the adaptive zones for different hispine beetles influencing as a consequence the modularity within this interaction network (Meskens et al. 2011).

8.6.2 *Herbivore Feeding Behavior*

The specificity and intimacy (i.e., physiological dependence) of plant-herbivore interactions, which transcend the general structure of herbivory networks, vary as a function of the different herbivore guilds, plant developmental stage, and/or organs consumed (Novotny et al. 2010). In the tropics, the degree of specialization of different insect guilds that consume plants varies enormously, and the percentages of specialization of different guilds is granivorous (99%), leaf miners (96%), frugivores (83%), leaf chewers (56%), sap suckers (56%), xylophages (24%), and root feeders (10%) (Novotny and Basset 2005). In general, herbivorous guilds with low mobility that consume highly defended plants (e.g., lepidopteran leaf chewers) or those with high physiological dependence on their hosts (e.g., leaf miners and gall-inducing insects) have highly specialized and modular interaction networks, in comparison with more generalist herbivorous guilds (e.g., phloem suckers, root eaters, borers). However, because most studies on plant-herbivore networks have focused on external leaf eaters guilds (particularly on caterpillars and chewing beetles) for practical reasons, these studies may not be ecologically representative of all plant-herbivore networks (Novotny et al. 2010). In fact, studies of herbivore networks including endophagous herbivores or root feeders are nonexistent (Fig. 8.1).

8.7 Habitat Disturbance and Plant-Herbivore Interaction Network Resilience

Ecosystems are in constant change due to natural and anthropogenic disturbances and as a consequence, species interactions are modified after perturbation. Natural disturbance in forests is generally associated with changes in tree canopy, increased light availability, and drier conditions. These sudden changes imply the disappearance

of some plant species and their associated specialist herbivores, but also facilitate the production of fresh leaves on the remaining plants representing an increase in resource availability for different herbivore species. Some studies have reported that canopy openness is a determinant factor for lepidopteran richness and abundance after disturbance (Barlow et al. 2007; Hawes et al. 2009) but hemipterans have shown differential impacts depending on the species (Osborn 1935; Wolcott 1941). More recently, Grimmbacher and Stork (2009) investigated changes in beetle assemblages in a fragmented tropical forest in Australia, following the passage of tropical cyclone Larry finding that communities were similar to their pre-hurricane condition since only 5% of the species was found to have changed.

A logical prediction after the empirical evidence on the impacts of disturbance on herbivore communities is that plant-herbivore network parameters should also be affected by such perturbations. However, there are only a handful of studies addressing this prediction. Valladares et al. (2006, 2012) investigated changes in a plant-herbivore network in the Argentinean Chaco forest after forest fragmentation and found that species richness, network size, and connectance diminished as the forest area decreased as a function of the area of forest remnants. Benítez-Malvido et al. (2014, 2016) assessed anthropogenic perturbation on a plant-arthropod network comparing forest gaps and forest edges finding that the network properties were not affected by disturbance. Villa-Galaviz et al. (2012) investigated if plant-lepidopteran network structure was recovered during forest succession and found that indeed, after few years of land abandonment all network parameters are indistinguishable from those found in mature undisturbed forests. Therefore, with the available information, it appears that plant-herbivore network attributes in the tropics are resilient to natural and anthropogenic perturbations (as long as the disturbed area is surrounded by sources of the original biodiversity), but further investigations are needed. In fact, a recently published global analysis of the effect of land-use intensity on plant-herbivore networks compared 72 individual networks and found that some parameters are affected by land-use change. In particular, the most susceptible parameter is network connectance, which increases under high levels of anthropogenic alteration due to a decrease in specialization. This suggests that specialist herbivores are more susceptible to disturbance (de Araújo et al. 2015).

8.8 Concluding Remarks and Future Directions

Records of plant-herbivore interactions for used in network analyses have been based on small geographic areas. Hence, recorded trophic interactions have only included a small fraction of local floristic diversity and often considering only common plant species or plants of the same taxonomic group or life story (Fig. 8.1). Because the estimation of herbivore specificity and the emergent network structural patterns depend on the diversity, composition, and life history of the plants considered (Novotny et al. 2006; Weiblen et al. 2006), estimates of network-level and species-level specialization in tropical forests are still elusive. This demonstrates the

importance of including greater ecological and taxonomic amplitude in studies on tropical plant-herbivore networks (Novotny et al. 2010).

Furthermore, the vast majority of studies on herbivory networks have focused on characterizing and evaluating variation of metrics that aim to capture the overall structure of a network, considering macroscopic parameters such as modularity, interaction evenness, robustness, and network-level specialization. Very few studies have included species-level metrics (i.e., species-level specialization, species strength, role of species, and food preferences). In solely focusing on macroscopic network parameters, important information on the dynamics of specific entities that constitute a network (of species) may be missing. This is of obvious importance considering that plant-herbivore interactions are highly specie-specific and are finely regulated according to the attributes of plant and herbivore species. Additionally, given the importance of anti-herbivore defenses in patterns of tropical plant-herbivore interactions, the role of different chemical (i.e., saponins, alkaloids, and/or cyanogens compounds), and biotic defenses (i.e., ants associated with extra-floral nectaries) should also be considered in the study of process that influences the configuration of herbivory networks.

Until recent years, a handicap for the study of plant-herbivore networks in the tropics was the vast undescribed diversity, particularly for insect groups (Novotny and Miller 2014). Accessible molecular tools such as DNA barcoding represent today a viable opportunity to improve our knowledge on plant-herbivore networks and make network comparisons across regions and ecosystems possible. For example, García-Robledo et al. (2013) evaluated a plant-leaf-roller beetle interaction network through DNA barcoding and demonstrated that host plant identifications at the species level are accurate providing a sample size of four individuals per herbivore and per plant. Because this methodology is a cost-effective strategy for reconstructing plant-herbivore interactions we expect to see more studies in tropical systems using this approach in the coming years, which will enhance our understanding of the ecology and evolution of species assemblages in the tropics.

In addition, new statistical methods proposed to estimate diet breath may allow to incorporate plant traits to the metrics and increase our understanding of the factors influencing plant-herbivore interaction networks. For example, Fordyne et al. (2016) have recently proposed an ordination methodology to quantify diet breath, based not only in the associations of plants and herbivores, but also including the multivariate distances among plants in ordination space.

Finally, incorporating the other trophic levels can be revealing as well. Some authors are starting to test whether observed patterns in plant-herbivore networks constructed from field data are related with herbivore preferences or other factors such as predation and competition and have experimentally demonstrated that herbivore preference can explain the modular structure in their leafhopper-plant network (Augustyn et al. 2016).

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Chapter 9

Host-Parasite Networks: An Integrative Overview with Tropical Examples

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Abstract The lack of ecological studies on parasite species is contradictory with their high diversity. In this context, the ecological network approach has drawn attention to patterns of tropical host-parasite interactions; however, it is still very restricted to a few taxonomic groups. In tropical regions, studies on host-parasite networks have encompassed specially fish, amphibian hosts, and malaria parasite communities of birds. High specificity is peculiar to parasites, either considering the host species or the site of infection. Variations in specificity indicate differentiated structural patterns between ecto- and endoparasites networks, as well as larval and adult stages of parasites, influencing the values of connectivity, nestedness, and modularity. Host characteristics also influence the structure of networks, including phylogenetic relationships and diet. Similarly to free-living species in ecosystems suffering the influences of environmental change, parasite species may also be extinct due to primary extinctions of hosts or possibly present new patterns of interaction due to the arrival of invasive species in the environment. New studies should

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explore network patterns between tropic and non-tropic environments, in addition to the use of molecular tools to identify especially cryptic parasites, which may provide better-supported results.

9.1 Introduction

Parasites are hidden components of ecological communities, comprising approximately 40% of the species described worldwide (Dobson et al. 2008)—a scope in which the tropics retain a large number of species yet to be described. These “invisible” organisms play an important role in ecosystems (Holt and Boulinier 2005) for their ability to directly or indirectly affect host species at different levels of organization (i.e., individual, population, and community levels) (Poulin 1999; Wood and Johnson 2015). Lafferty and Kuris (1999) stated that the complexity and ubiquity of host-parasite interactions are good arguments when considering parasitism to assess anthropogenic impacts on aquatic systems. Nevertheless, parasites have been neglected in the scope of conservation or management strategies (Gómez and Nichols 2013; Dougherty et al. 2015).

Each parasite species exhibits a degree of specialization by its resource (e.g., host species or available microhabitat). Ecto- and endoparasites are exposed to different selection pressures and outcomes (see Thompson 1994) when exploring the host, which creates differentiated patterns in the organization of the communities. In addition, a wide variation occurs in the distribution and intensity of their interactions with the host species (Thompson 1994; Poulin 2007). These variations are usually related to biological, ecological, and/or phylogenetic aspects (Poulin et al. 2013).

Over the past few years, a remarkable number of studies have used network analysis to assess the biodiversity, ecological processes, and relationships between community structure and functioning in tropic and non-tropic environments (Hagen et al. 2012; Heleno et al. 2014). In ecological parasitology, the network approach has been used seeking to understand a wide variety of issues, for example, (1) the role of parasitic biodiversity in ecosystem functioning, the transmission of parasitic diseases via social or sexual contacts, (2) influence of structural attributes of host species and their dynamics regarding food webs, (3) effect of species interaction on the structure of networks, (4) coevolutionary components within a larger system, and (5) community response to disturbances such as migration, extinction, or biologic invasion (Vázquez et al. 2005; Chen et al. 2008; Dallas and Cornelius 2015; Strona and Lafferty 2016). In a review synthesizing the findings from network analyses of host-parasite interactions and food webs, Poulin (2010) concluded that the benefits of this approach far outweigh its disadvantages.

Even though many interactions between parasites and vertebrate hosts are known, this chapter provides an approach of ecological networks on the interactions between fish and amphibians along with their parasites, in addition to malaria parasite communities of birds in the tropics. Furthermore, we also demonstrate other examples of interactions, such as host-bat fly networks.

9.2 Environments and Host Characteristics with Possible Implications in Networks

By analyzing the data available in Bellay et al. (2015a), we observe that the patterns of fish-parasite networks, such as connectivity and nestedness, differ between tropical and temperate environments (Fig. 9.1), having resulted from more specialized interactions in the tropics, reducing connectivity and nestedness; even though both the modularity and species richness showed no differences between environments. Specialization did not differ between the tropical and temperate sites from the parasite perspective in multihost malaria parasite communities of birds (Svensson-Coelho et al. 2014). Furthermore, studies on lizards suggest that possible relationships between latitude and parasitic load occur due to the host's life history (Salkeld et al. 2008). Parasite-host interactions are expected to present different patterns in relation to the taxonomic groups involved, with greater evidence than between latitudes.

It is expected that the composition of the host community influences parasite richness since a higher diversity of hosts represents a wider range of resources for

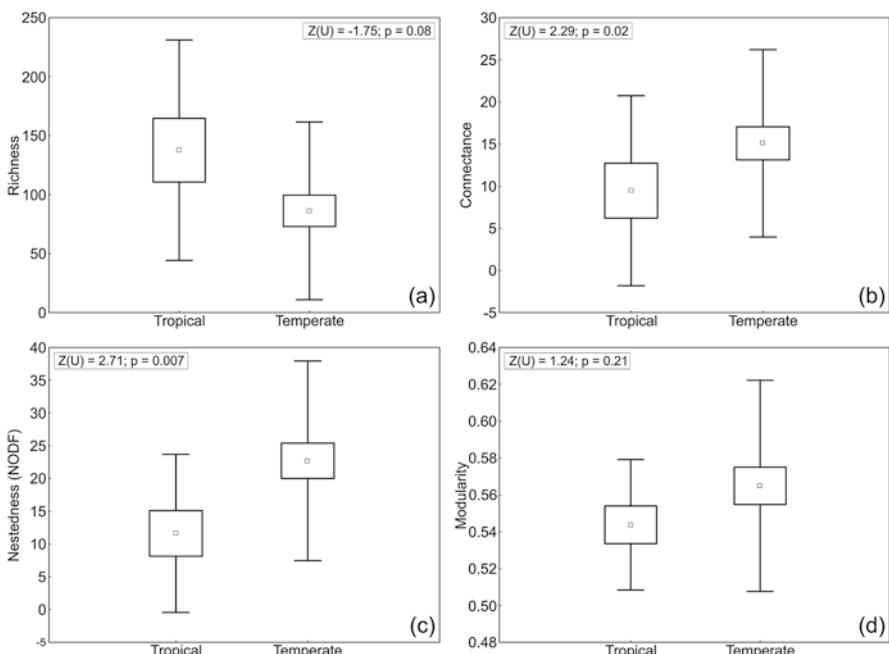


Fig. 9.1 Comparison between tropical and temperate environments regarding four parameters from 44 fish-parasite networks. (a) Species richness corresponds to the total number of species in the network (parasites + hosts); (b) Connectance; (c) Nestedness; (d) Modularity. Middle point: Mean; Box: Standard Error; Whisker: Standard deviation. The significance of the Mann-Whitney test was $p < 0.05$. Data available in Bellay et al. (2015a)

parasites (Hudson et al. 2006). Similarly, host and parasite abundance play an important role at determining network structure. If trait matching underlies potential interactions between species, abundance would determine their dynamic (Canard et al. 2014). Empirical evidence indicates the occurrence of a few host traits, such as abundance, body size, and diet, mostly contributing to the maintenance of parasite diversity and network structure (Dallas and Cornelius 2015).

9.2.1 Host Specificity and Phylogenetic History

The combination of varying levels of host specificity and abundance contributes to the high asymmetry observed in host-parasite networks. Specialist parasites tend to interact with hosts presenting high parasite richness, whereas generalist parasites tend to interact mainly with hosts containing low parasite richness (Fortuna et al. 2010). This nested pattern, which is more evident in host-parasite networks from temperate latitudes (Fig. 9.1c), may be related to host abundance. High host abundance may contribute to harboring richer parasite faunas, with higher proportion of rare specialists (Vázquez et al. 2005). Understanding the mechanisms beneath the nested pattern in host-parasite networks might also contribute to quantify the importance of neutrality in ecological interactions (Krishna et al. 2008; Canard et al. 2014).

The interaction of hosts and parasites encompasses a high degree of intimacy and adaptation between species (Fortuna et al. 2010). When different host species share dietary, behavioral or habit preferences, the formation of modules in the network is enhanced (Bellay et al. 2011; Lima-Junior et al. 2012; Bellay et al. 2013). Therefore, sharing ecological traits favors parasite sharing, which in turn favors the formation of modules. Ecological and phylogenetic groups of related host species can promote modularity in a way that the similarity (e.g., phylogenetic, ecological, or functional) is higher among species within the same module (Fortuna et al. 2010; Bellay et al. 2011; Lima-Junior et al. 2012; Bellay et al. 2013). This has been observed in several networks, including fish (Fortuna et al. 2010; Bellay et al. 2011; Lima-Junior et al. 2012) and reptile (Brito et al. 2014) hosts along with their parasites, highlighting the importance of historical and ecological processes to network structure.

9.2.2 Host Body Size

Host body size has a positive relation to parasite species richness for a broad spectrum of host taxa (Kamiya et al. 2014; Campião et al. 2015b). Nonetheless, it is expected that such influential trait played an important role in the architecture of

host-parasite networks. Indeed, it has been demonstrated that body size is an important trait determining network structure and stability in ecological networks (Woodward et al. 2005). Dallas and Cornelius (2015) found that fish biomass is important predicting nestedness, which is influenced by host body size. These findings suggest that species in antagonistic networks may be defined by host traits, such as body mass.

9.2.3 Host Diet

For many parasite taxonomic groups of fish of a tropical floodplain, host diet is an important factor affecting host-parasite interaction although weaker and less conserved than phylogeny (Lima et al. 2016). For endoparasites, hosts that share food items are also more likely to share parasites (Benesh et al. 2014). Consequently, hosts that consume a wide variety of food items harbor a higher amount of parasite species (Chen et al. 2008; Locke et al. 2014). An intriguing finding is a host with the highest amount of shared parasites belonging to low trophic level species (i.e., they are preyed upon by other species of fish or birds) and with omnivorous diets (Lima et al. 2016). A possible explanation would be associated with feeding behavioral, exposing it to infection by free-living parasites, eggs, or cysts.

Many parasites trophically transmitted are able to furnish ecological information on the links between their host and other organisms in a given environment, where parasites may indicate long-term feeding information and ontogenetic changes in the host's diet (Marcogliese 2005). During ontogeny, the host may undergo niche shifts and display feeding specialization; for instance, adults often use different resources other than larvae or juveniles, thus affecting the host-parasite network. Changes in the parasitic community of *Prochilodus lineatus* (Characiformes, Prochilodontidae) during its ontogenetic shifts were also supported by Lizama et al. (2005). Juvenile individuals of this host species live in lagoons until 2 years, subsequently living in river channels (Fig. 9.2). Such changes in transition and adaptation expose the adult host to a higher degree of parasitism.

Obviously, throughout all life stages, the resources are substitutable for the most of host species; even though it may occur a certain degree of overlap in resource use among stages. A host species with a broad diet can be less vulnerable to secondary extinction; however, it could be an ontogenetic specialist (with several stages, each consuming a different resource) (Rudolf and Lafferty 2011). Seasonal shifts may also influence the characteristics of interaction networks by changing the availability of food and host species density. Zarazúa-Carbajal et al. (2016) showed the importance of biotic and abiotic factors in the dynamics of host-bat fly interactions in temperate environments. It is necessary to assess the approach of seasonality in tropical parasite-host networks.

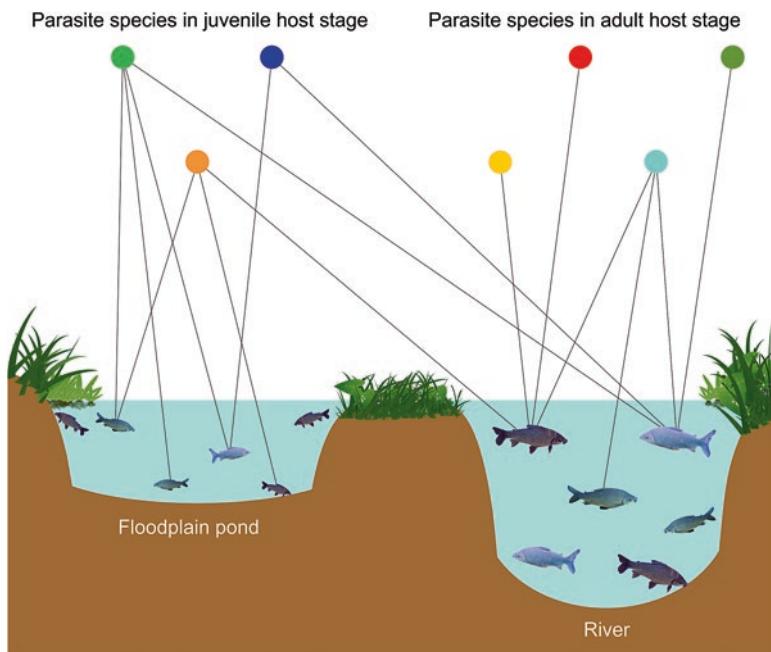


Fig. 9.2 Schematic representation of the variation in the parasite species composition in the Streaked prochilod, *Prochilodus lineatus* in a tropical floodplain. Ontogenetic shifts in the diet and habitat transition during the host developmental stages (i.e., from juvenile stage to adult stage) are factors driving the variation in the parasite species composition (circles). Colorful circles represent the parasite species. Photos credits: Celso Ikeda (fish)

9.3 Parasite Characteristics Influencing Network Topology

The patterns observed in the topology of host-parasite networks result from the match of several features of both interacting parts. Among these features, the amount of host species that a parasite is able to interact with is undoubtedly a crucial factor in network ecology. Host specificity is believed to be an intrinsic species attribute, with some extent of phylogenetic signal as it tends to be more similar among closely related taxa (Krasnov et al. 2011). It can be expressed as the amount or the diversity of hosts a parasite is able to colonize. Moreover, host specificity is not a fixed character; it can vary within a species according to the different localities of its geographic range or influences of the characteristics of host populations (e.g., body size and life stage) (Fig. 9.3a); in addition, it may be influenced especially by the composition of the host community (Fig. 9.3b), stressing the importance of the whole ecosystem in the organization of each network. This demonstrates the different scales of a study on host-parasite interactions.

Hosts represent both the habitat and food resource to parasites and are generally explored by parasite species from different lineages and with different life strategies, such as endoparasites or ectoparasites as well as parasites with simple or complex life

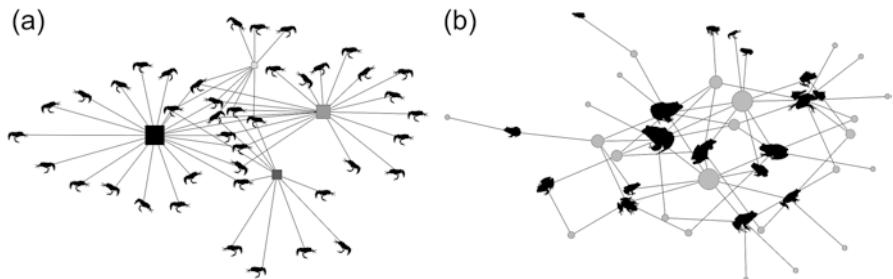


Fig. 9.3 Host-parasite networks. (a) Interaction network at the population level of hosts and their parasites where each node is an individual, which may interact with a differentiated number of parasites reflecting the influence of a particular host characteristics (e.g., sex or size) on the interaction pattern; (b) Host-parasite interaction network at the community level where each node is a species and the interactions reflect the total interactions observed in their populations. Squares and circles represent the parasite species and size of the symbols, the number of interactions. Hosts are illustrated in drawings of frogs. Data from parasite community available in da Graça et al. (2017)

cycles. This variety in the ways that parasites exploit a resource may increase the diversity of parasites associated with each host species (Bellay et al. 2013). Parasites of different species may exhibit different levels of host specificity, dependence, asymmetry, strength, and complementary specialization in such networks (Bellay et al. 2015b). In turn, high parasite specificity favors the formation of modules, while low parasite specificity contributes to an increased amount of links in ecological networks. Studies conducted in the Neotropics with amphibian hosts and their metazoan parasites demonstrated that the high prevalence of parasite species associated with a broad range of host species contributed to the high connectance and nestedness measures observed in this system (Campião et al. 2015a, b).

The variation in the degree of specificity among parasites with different life strategies and stages is also an important determinant of network structure. For instance, fish ectoparasites tend to show higher host specificity than the endoparasites associated with these hosts (Bellay et al. 2015a; Fig. 9.4). However, due to the strong phylogenetic signal in parasitism strategy, it is still not clear whether the influence is the mode of life itself or other intrinsic property of the parasite clade. Networks including only fish ectoparasites have proved significantly modular and weakly nested due to higher host specificity (Lima-Junior et al. 2012; Braga et al. 2014).

Parasites at larval stage are normally generalists in fish hosts (Bellay et al. 2013), which is probably a strategy to enhance the chance of completing the transmission cycle through different hosts. Moreover, parasites in larval stages are important connectors in modular networks due to their low host specificity (Bellay et al. 2013). In fact, the topology of fish-parasite networks is more closely related to the parasite developmental stage than to their lineages. Therefore, the presence of parasite larval stages may increase the strength of trophic links, contributing to the stability of ecological networks.

In brief, the amount of interactions of a parasite species in the network might reflect a trade-off between the benefit of having alternative resources (broader host availability) and the cost of developing adaptations that allow such associations

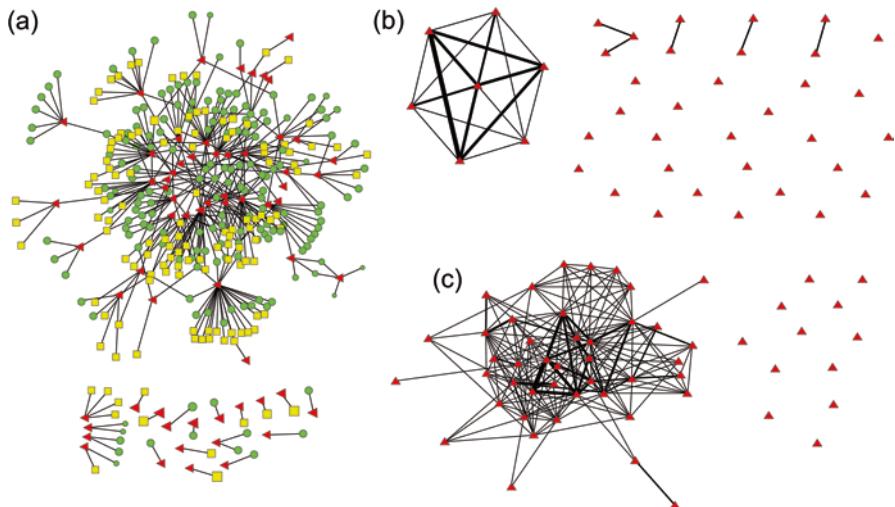


Fig. 9.4 Fish-parasite interaction network of the upper Paraná River floodplain, Brazil. (a) Bipartite network considering ectoparasites (yellow squares) and endoparasites (green circles); (b) unipartite host network, the links indicate that ectoparasite species sharing; (c) unipartite host network, the links indicate that endoparasite species sharing. In (b) and (c), red triangles correspond to the hosts and the thickness of the links indicates the intensity of parasite species are sharing by host species. Data available in Takemoto et al. (2009)

(Poulin 2007). To completely understand why some parasite species are associated with a broad spectrum of hosts, while some rely on a single host species, is still something to be inquired. Notwithstanding, it is a key factor underlying the topology of host-parasite networks. All of the varying patterns in host specificity above mentioned and discussed have profound influences on network topologies. So far, the evidence we have reached indicates that the presence of generalist parasites increases connectivity and nestedness measures, while the presence of specialists contributes to the formation of modules in host-parasite networks (Bellay et al. 2013; Campião et al. 2015b).

9.4 Robustness

Host extinctions or population decline may compromise the structure of parasite communities, as observed in a study on the fish-parasite network of the Upper Paraná River floodplain, Brazil (Dallas and Cornelius 2015). From a context of host-parasite interactions viewpoint, Pascual and Dunne (2006) defined robustness as an estimator of network structure maintenance when facing host species loss considering the secondary extinctions of parasite species.

Environmental changes, as well as epidemiological outbreaks, may culminate in the exclusion of host populations, destabilizing and significantly altering the structure of parasite communities (see Lafferty 1997). In this context, the intensity of the

removal effect of host species on a host-parasite network depends on the pattern of distribution of species interactions, whether they are generalists (i.e., interact with many species) or specialists (i.e., interact with few species), as well as their functional roles in the network (Guimerà and Amaral 2005; Pascual and Dunne 2006; Estrada 2007).

The influence of local extinctions of host species on the structure of host-parasite networks may be distinct for communities of ecto- and endoparasites, mainly due to different host specificities (Bellay et al. 2015a). Ecological networks have complex structures that may also vary according to the environmental conditions and their spatial and temporal variations, which govern the diversity of species and their interactions. In this sense, the introduction of new competitors and pathogens is a factor that may cause the decline of populations or even local extinctions (Davis 2003).

9.5 Parasites and Species Introduction

Species introductions into new environments may radically alter native communities, causing losses in local biodiversity (Michelan et al. 2010), especially in communities with very specific interactions such as those observed in the tropics. Invasions of potential hosts may alter the structural patterns of the networks, promoting interaction ruptures and cascades of parasite extinctions due to the competition between native and introduced hosts. Among the species of native parasites, those with a higher degree of specificity regarding the use of hosts would be the most sensitive to invasions due to a higher probability of extinction of their hosts. Table 9.1 describes some scenarios and possible changes in the structure of parasite-host networks as a function of species introduction.

Table 9.1 Possible scenarios of introduction in host-parasite networks

Event	Scenario	Structure
Introduced host species has parasites that can infect native hosts	1. Parasite with high specificity being restricted the host species phylogenetically close to the hosts in regions native to the parasite	Network structure will present few changes with increasing interactions only inside the module
	2. Parasite transmitted trophically but restricted to hosts phylogenetically close to hosts in native regions to the parasite but with similar eating habits	Network structure will show few changes with increased interactions between some modules
	3. Simple-cycle (i.e., monoxenous) generalist parasite (ectoparasite)	Network structure will present changes with increased connectivity and increased interactions between modules with possible small grouping of modules

Table 9.1 (continued)

Event	Scenario	Structure
	4. Generalist parasite transmitted trophically but restricted to hosts with similar eating habits (endoparasite)	Network structure will change with increasing interactions inside modules and between modules
	5. Complex cycle (i.e., heteroxenous) parasite transmitted trophically but generally to intermediate hosts, which infects by penetration into the skin	Network structure will present changes with increased connectivity and increased interactions between modules with possible small grouping of modules
	6. Strong competitor generalist parasite excluding native parasite species	Number of native parasite species may decrease; network with greater connectivity
	7. Strong competitor parasite with high specificity and restricted host species phylogenetically close to the host in native regions of the parasite	Number of native parasite species will decrease within the modules
	8. Generalist parasite and pathogenic to new hosts in the region introduced with possible elimination of populations of these hosts	Reduction in the number of host species and consequently of native and specialist parasites; high connectivity among species that remain in the network and low or absent modularity
The invasive host species acquires parasites from the native hosts	9. Invasive species of host acts as reservoir for the parasite acquired in the introduced region and is expected increase of the parasite abundance in the natural environment in other species of native hosts but restricted in phylogenetically close hosts	Increased connectivity and interactions between modules with possible clustering of small modules with related hosts
	10. Invasive species of hosts acts as a reservoir for the parasite of the introduced region and with the increase of the parasite abundance in the natural environment other species of native hosts are gradually infected	The increase of the connectivity and increase of the interactions between modules with possible grouping of small modules
Non-establishment	11. Parasite is not established unlike host introduced	Without obvious changes in the network; a decrease in connectivity may occur due to the greater number of host species in the habitat

Events involving several introduced parasite species with generalist interactions may contribute to increased network nestedness

The events and possible consequences of the scenarios described may occur simultaneously and the effect on the structure and organization of the networks is intensified according to the amount of species introduced in the environment. It is necessary to understand the consequences of invasions in order to make management decisions considering that even though at times the introduced host does not present high abundance, its parasites may be increasingly dispersed in the local host population. It is recommended to carry out further studies in this area in order to better understand the effects that a introduced parasite species may promote in different habitats.

9.6 Molecular Approach

The fast advance of molecular techniques has revolutionized the view of species diversity and evolution (Morand et al. 2015). This development has important implications to understand host-parasite network structure, since species identification is a key milestone when studying biological diversity, especially in the tropics, with so many species yet to be described. Taxonomic studies using molecular tools have revealed that many parasite taxa considered generalists actually encompass several cryptic species (Agosta et al. 2010; Braga et al. 2014). Molecular techniques have also allowed us to construct dated phylogenies with a satisfactory level of accuracy (da Graça et al. 2016). This expands even more the limits of understanding how host-parasite networks evolve and have been maintained throughout time. The advance of molecular tools with the completion of host and parasite phylogenies will certainly provide a better understanding on patterns and mechanisms underlying the structures of host-parasite networks.

9.7 Final Considerations

Over the past few years, an increasing number of network studies have greatly contributed to the understanding of host-parasite interactions in tropical aquatic ecosystems. However, it is still an incipient amount given the high species diversity of parasites and hosts, in addition to the little information available to establish comparisons between tropical and non-tropical networks, which may generate biased generalizations. The patterns of host-parasite networks may vary over time and the species development stages may contribute to this variation. Extinctions or new host-parasite interactions can be expected with the environmental changes caused by global changes and human activity in the tropical ecosystems, which might alter the patterns known to the networks. Finally, further ecological network studies with the use of molecular tools to taxonomic identification of parasites species should assess these important issues to improve the understanding on the host-parasite interactions in tropical ecosystems.

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Chapter 10

Interaction Networks in Tropical Reefs

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Abstract Tropical reefs are, figuratively, the underwater counterparts of tropical rainforests. Both complex, three-dimensional natural systems harbour an impressive diversity of species. The diversity of ecological interactions taking place among these species is no less striking: their intricate webs add another level of complexity to these natural systems. In this chapter, we dive into the ecological networks of tropical reefs to present an overview of some of the negative, positive, and neutral interactions among inhabitants of rocky and coral reef ecosystems. We discuss trophic interactions among species as food webs; territorialism and chasing behaviour as competitive networks of reef fish; cleaning behaviour illustrating mutualistic networks, and following associations exemplifying commensalistic networks among fish species. We close the chapter with a biogeographical perspective of interaction networks in tropical reefs across the globe to discuss how human activities have been threatening their plentiful life.

10.1 Introduction

Tropical reefs are one of the most productive and biologically diverse ecosystems (Odum and Odum 1955). Paired with tropical rainforests, reefs are the archetypes of natural ordered systems. These two three-dimensional systems host species with a

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large variety of life histories in regulated populations within complex ecological communities (Connell 1978).

Now imagine you could fly and see through these complex, diverse ecosystems. While this may be difficult in a rainforest, it is not so much when you dive in a colourful tropical reef. Reefs are oasis of life in the otherwise blue desert of open oceans. Biogenic reefs are built by corals, sponges, and coralline algae, and rocky reefs are geological formations that may result from rocks of different kinds and sizes; moreover, reefs can even be artificial structures such as shipwrecks. These habitats harbour an impressive collection of species: corals, gorgonians, crustaceans, worms, echinoderms, seaweeds, not to mention the most notable creatures, the abundant reef fish. None of these organisms are living isolated. A key component of this underwater kaleidoscope of colour and forms often escapes the eyes—ecological interactions. A more careful look into a tropical reef system reveals the many intricate webs of ecological interactions submerged in its plentiful live.

As in all ecological communities, dwellers and visitants of tropical reefs interact with one another (Odum and Odum 1955). These interactions are intra- and inter-specific, and can be negative, positive, or neutral for the interacting individuals. Interestingly, the effects of these ecological interactions can scale up from individuals to populations (i.e. affecting fitness), to communities (i.e. affecting structure), and even to ecosystems (i.e. affecting functioning). Several types of ecological interactions can be observed in a tropical reef, and fish are a conspicuous component of many of them. To name a few, reef fish interact trophically among themselves and with benthic organisms (e.g. invertebrates and seaweeds); some fish are territorial and aggressive towards other fish (and sometimes towards divers too); while others may be helpful by removing parasites from other animals. Such diversity of interaction types reflects the myriad of ecological processes taking place in the fascinating reef environment (e.g. Moberg and Folke 1999).

Assessing these interactions to understand the processes they mediate, however, is not an easy task. Apart from the obvious fact that they occur underwater—indifferent to our curiosity—recording the dynamic interactions among reef species is laborious, demanding many hours at sea and a combination of methods. Data on reef species interactions usually come from dedicated scuba or free dive underwater surveys (e.g. Grutter 2005), remote video recordings (e.g. Longo et al. 2014), and indirect evidence such as stomach contents and literature review (e.g. Arias-González et al. 2011). As data accumulate, one can employ the formalism of complex networks to unravel patterns of species interactions occurring underwater from the local (e.g. within 2 m² sampling quadrats) to the global scales (e.g. across biogeographical provinces).

When ecology meets network theory, species depicted as nodes are connected by links representing their biological interactions—be these negative, positive, or neutral (Fig. 10.1). The nature of the biological interaction describes if the network is directed or undirected (i.e., symmetric or asymmetric interactions between i and j), binary or weighted (i.e., qualitative or quantitative interactions), one- or two-mode (i.e., all species can interact, or there are two distinct sets of interacting species) (Boccaletti et al. 2006). Food webs, for instance, are traditionally represented by

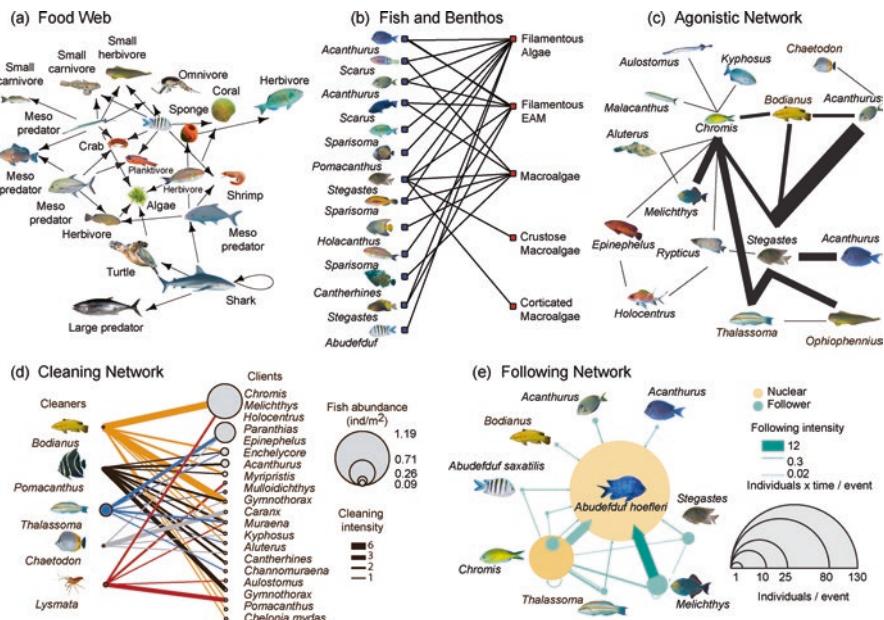


Fig. 10.1 Tropical reef interaction networks. (a) Direct binary one-mode network of a simplified food web. Nodes representing functional groups are linked to those they predate upon off the Virgin Islands (Opitz 1996). (b) Binary two-mode network of reef fish and benthos. Nodes representing fish genera are linked to the benthic functional groups they consume in Abrolhos, Brazil (Longo, unpub. data). (c) Indirect weighted one-mode network of agonistic behaviour among reef fish. Nodes representing genera are linked by the frequency they engage in territorial disputes at Ascension Island (Fontoura, Bonaldo, Floeter, unpub. data). (d) Weighted two-mode network of mutualism between cleaner and client reef species. Nodes representing genera (sizes proportional to abundance, individual/m²) are linked by number of cleaning events in Ascension Island (Morais et al. 2017). (e) Directed weighted one-mode network of following associations among reef fish. Nodes representing genera (sizes proportional to abundance) are linked by weighted directed links proportional to intensity of interactions from follower to nuclear species off Ascension Island (Morais et al. 2017)

directed one-mode networks (e.g. Yen et al. 2016). Species are connected by trophic interactions, either weighted arrows indicating the relative rate of energy transfer (e.g. grams of carbon/day) or interaction strength between taxa, or binary arrows indicating which resources a given species feeds on (Fig. 10.1a). If the focus is on a subset of trophic interactions—e.g. between reef fish and benthic community (Longo et al. 2014)—one can use two-mode networks to depict the interactions between two trophic levels (Fig. 10.1b). The same approach can be used to explore cleaning interactions (e.g. Guimarães et al. 2007). Although essentially trophic, cleaning interactions are by contrast mutualistic (e.g. Côté 2000) between two sets of species—cleaners and clients—which communally benefit from the interaction (Fig. 10.1d). Agonistic interactions among reef fish (Robertson 1996), on the other hand, can be represented by undirected one-mode networks in which species are

linked whenever they engage in disputes for resources, such as territory (Fig. 10.1c). Finally, commensalistic interactions such as following association among reef fish (e.g. Sazima et al. 2007) can be depicted by directed one-mode networks indicating which species follows and which is followed (Fig. 10.1e).

Networks give a panoramic snapshot of the liveliness of biological interactions. These static depictions are very useful to describe structure (e.g. Bascompte et al. 2003), infer function (e.g. Yen et al. 2016), and predict changes (Memmott et al. 2004) in ecological communities. By summarizing a wealth of empirical data into a network, we can immerse in its tangled structure in the search for emergent regularities. Some non-random network properties are common across biological systems. For instance, food webs can display similarities in connectance (i.e. proportion of realized links), degree distributions (i.e. number of trophic interactions across species; Dunne et al. 2002), and modularity (i.e. subsets of highly connected species; Stouffer and Bascompte 2011); whereas nestedness (i.e. hierarchical organization of interacting species into inclusive subsets) is a common pattern of two-mode mutualistic networks (e.g. Bascompte et al. 2003). Even though distinct processes may give rise to these structures, their implications for the ecological and evolutionary dynamics of the systems may be similar. Nested networks, for instance, may be robust against random species extinction regardless of the interaction type (Memmott et al. 2004), potentially reducing competition among sets of species and increasing the number of coexisting species (Bastolla et al. 2009). Therefore, the network approach offers us a privileged viewpoint to the biological processes operating on ecosystems, including tropical reefs.

Here, we explore interactions among tropical reef species to provide an underwater perspective to ecological networks and equalize the focus on terrestrial environments given so far in the previous chapters. Our goal is to offer an overview of some of the negative, positive, and neutral interactions among inhabitants of reef ecosystems. In the following sections, we briefly dive into marine food webs to examine trophic interactions among reef species; into networks of agonistic interactions (e.g. territorialism and chasing) to illustrate competitive behaviour between reef fish; and into cleaning behaviour to illustrate mutualism and following associations among fish to exemplify commensalism in rocky and coral reefs. We return from this dive to close the chapter with a biogeographical perspective of interaction networks in tropical reefs across the globe and ponder upon how human activities are threatening them.

10.2 Trophic Networks: Marine Food Webs

Predation is perhaps the most notable of the interactions among species—including marine ones. This notion and the interest on trophic interactions date back from Darwin's first descriptions of communities (Darwin 1859). The term food web, however, emerged in the early 1900s when Elton (1927) defined a set of “monophagous” consumers as a food chain, and a food web as a group of chains that

incorporated “polyphagous” consumers (Fig. 10.1a). The first representations of these trophic interactions consisted in descriptive diagrams with different trophic levels, indicating a link connecting predator and prey with notes on the natural history of these organisms. These diagrams provided a general scheme of “who eats whom” that were not necessarily taxonomically rigorous or comprised all the components within a community (Paine 1980). However, only when the consequences of the trophic interactions started to be revealed in the mid-1900s, Darwin’s interests on species coexistence started to benefit from our understanding of food webs.

The effects of trophic interactions in community dynamics were unravelled by Paine’s (1966) seminal experiment removing the ochre starfish (*Pisaster ochraceus*) from a rocky shore. This experiment demonstrated that predation by the ochre starfish could regulate the abundance, diversity, and distribution of benthic organisms in that rocky shore, enabling more species to coexist. This study also gave rise to the concept of keystone species (i.e. those whose interactions may have critical consequences for community dynamics) and had a remarkable impact on how food webs were studied and interpreted since then. It was no longer enough to describe who eats whom. Other metrics such as interaction strength (i.e. a quantitative approach of the link between predator and prey), connectance, and energy flow through trophic links (Lindeman 1942) were necessary to move forward in the understanding of food web dynamics.

Marine food webs are good examples of how dynamic interaction networks can be. Here, interaction strength, connectance, and the structure and length of food webs can be affected by multiple factors, for example, wave exposure, tides, currents, winds, upwelling regime, nutrient availability and, certainly, human interference (McClanahan and Branch 2008). Despite being highly dynamic, some general properties emerge from these webs. Most of the marine food webs characterized in the literature present a relatively large richness of trophic interactions, a high level of intermediate omnivore taxa, and an abundance of top predators comparable to terrestrial ecosystems (Dunne et al. 2004). Chain length may also vary among marine food webs depending on species richness, diversity, and complexity of the system (Link 2002; Dunne et al. 2004).

The association of high species diversity in highly connected webs could result in high structural robustness (Dunne et al. 2004). However, trophic interaction networks in reef ecosystems seem to be structured by “few strong and several weak” interactions with keystone species and groups (e.g. Longo et al. 2014). Central species can be identified in interaction networks by combining connectance and interaction strength. A simplified network of trophic interactions between fish and the benthos (Fig. 10.1b) of the Abrolhos Archipelago, north-eastern Brazil, shows that herbivorous fish are central species in this reef habitat. Interestingly, in tropical reef food webs, herbivores often play a central role or are keystone species, determining the structure and complexity of reef communities by controlling macroalgae abundance and diversity (e.g. Rasher et al. 2013). The loss of these strong interactions could have profound impacts in the structure of ecosystems, such as triggering phase shifts from a coral to an algae-dominated community, regardless of high species diversity and connectance.

The role of trophic interactions in structuring reef ecosystems goes beyond interaction strength. More than high abundance of herbivores, a proper assemblage of these consumers is necessary to establish trophic links with a larger array of primary producers (Rasher et al. 2013), generating redundancy (i.e. species that have common trophic links) and complementarity (i.e. species whose trophic links do not overlap but that contribute to high connectance when combined). Another emergent property in reef food webs is modularity, which may relate to redundancy and habitat partitioning. In the North Pacific Ocean, for instance, sea otters connect an oceanic and a coastal module of a food web (Estes et al. 2016). The emergence of these structures will also depend on reef characteristics—e.g. productivity, temperature, and habitat complexity—not to mention other kinds of interspecific interactions embedded in larger, multi-interaction ecological networks (e.g. Pocock et al. 2012; Dátilo et al. 2016). The ecological consequences of trophic interactions are, therefore, inherently linked to other ecological interactions.

10.3 Agonistic Networks: Territoriality and Chasing Among Reef Fish

Living in a tropical reef may be costly. Resources are not always abundant, thus tropical reef species often engage in agonistic interactions related to resource partitioning, parental care, and territoriality (Robertson 1996; Bonin et al. 2015). The outcomes of the agonistic behaviour are generally non-lethal, and subtler than trophic interactions. Similarly to predation, parasitism, and competition, agonistic interactions can be asymmetrical: while one individual benefits from protecting a resource, the others may not only be deprived of it but also suffer physical aggression. These interactions can also be detrimental for both species by reducing growth, reproduction, and survival rates (Robertson 1996). Therefore, agonistic behaviour imposes trade-offs to the participants. Partitioning and/or competing for limited resources is a daily task for the inhabitant of a tropical reef—but not an obvious one for the outsider observer.

Direct and indirect competition are often not easy to observe, despite their clear influence on the structure of ecological networks (e.g. Dátilo et al. 2014). This difficulty is particularly true in the heterogeneous, complex underwater reef ecosystems. Alternatively, agonistic disputes for resources are much more conspicuous and thus indicate resource-use overlap which essentially underpins direct or indirect competition among species (Peiman and Robinson 2010). In tropical reefs, fish species are constantly competing for shelter, food, and sexual mates (Bonin et al. 2015). Consequently, several species defend territories and are aggressive (e.g. Forrester 2015). Chasing events among individuals are common indicators of such disputes for resources; and serve as measurable, and reliable, proxies of interspecific competition (Robertson 1996).

The resultant network from these agonistic interactions can shed light into the prevalence of intra and interspecific disputes, and how these interactions can mediate

resource partitioning and competition. Moreover, they give insights on the consequences of agonistic behaviour and territoriality. For instance, engaging in these behaviours demands considerable energy (potentially influencing individual fitness) and can alter the density of fish populations in coral reefs, which in turn can influence community structure (see Robertson 1996; Bonin et al. 2015).

A network of agonistic chasing events depict species linked according to the frequency they chase each other (Fig. 10.1c). If these agonistic interactions are organized into a modular network, it could indicate either spatial segregation or association of taxonomically related species, or even reveal patterns of trait association (e.g. smaller species would not chase after potential predators). Modules could also emerge from neutral processes driven by species abundance (see Vázquez et al. 2007). Interaction strength can also be affected by those drivers. For example, in the agonistic network of fish in the reefs of Ascension Island, South Atlantic Ocean, the interaction strength among pairs of species were not driven by species abundance. Instead, species traits (e.g. the degree of diet overlap and/or aggressive territorial behaviour) influenced the intensity of agonism (Morais et al. 2017). Although agonistic behaviour is frequent in tropical reefs, there is another way to deal with limited resources: cooperation.

10.4 Mutualistic and Commensalistic Networks: Cleaning and Following Behaviour

Life in a tropical reef can be risky and competitive, especially if you are someone's resource or must compete for resources with someone else. Beyond escaping from and chasing after a competitor, risk and competition sometimes can be tempered by cooperative efforts. Interactions among reef species can also be positive. For instance, one species may benefit from other species' help on removing parasites or dead tissues (cleaning mutualism) while a smaller fish may benefit from following a larger one (following commensalism). In these interactions, the payoffs for the involved parties can be bilateral or neutral—but are rarely absent.

Cleaning mutualism is one of the most intriguing interactions among reef species both from an ecological (i.e. what are the consequences of cleaning?) and evolutionary (i.e. how these interactions were established or selected over time?) perspective (Floeter et al. 2007). During these associations, a “cleaner” species removes parasites, necrotic tissue, and mucus from the body surface of “clients”, contributing to its health (Grutter 2005). Cleaning behaviour has been reported in ca. 130 species of fish and crustaceans (Côté 2000), which can be facultative (i.e. species cleaning sporadically or only during juvenile stages) or obligate cleaners (i.e. species that clean throughout their lives; Grutter 2005). These interactions often occur at specific sites known as “cleaning stations”, characterized by prominent structures such as massive corals, sponges, and large rocks (Côté 2000), forming two-mode networks between cleaners and clients (Fig. 10.1d).

Following association is a neutral interaction observed among reef fish (Sazima et al. 2007) characterized as a temporary feeding association. Here, opportunistic species (“followers”) benefit from following bottom-foraging species (“nuclears”) by consuming the exposed food resources made available from the disturbed substrata (Sazima et al. 2007). The nuclear species does not receive any payoff, and also does not pay any costs or is harmed by this association. While the nuclear role is mostly played by fish (less often by octopuses, sea-stars, and turtles) several species may be followers (Sazima et al. 2007). Following interactions can be complex, involving large groups of individuals (up to several hundred) from different species: the “shoaling” associations (Lukoschek and McCormick 2000). On the other hand, when following involves only up to four individuals, they are called “attendant associations”. Attendant associations can be divided into four groups (Ormond 1980): when species aggregates to feed from exposed or leftover resources gained from the nuclear species (following and scavenging); when it aggregates to hunt cooperatively with other species with similar feeding habits; when it hunts by swimming alongside or above a nuclear species using it as a cover to get access to the prey (hunting by riding); and when the species has an easier access to the prey by mimicking harmless species (aggressive mimicry). Following associations can be described by one-mode networks indicating, for instance, the frequency of this commensalism in a given environment (Fig. 10.1e; Morais et al. 2017).

Both of these positive interactions are essentially trophic—directly trophic in the case of cleaning; indirectly in the following (through the exploration of a third food source). Thus, these interaction networks can give insights on underlying biological processes taking place in the community, such as niche partitioning. A nested cleaning interaction network, for instance, indicates that the distribution of mutualistic interactions is asymmetrical, with some species engaging in many interactions and others in fewer interactions that constitute subsets of the most connected species (Guimarães et al. 2007). Therefore, the community contains species with different resource-use strategies: a core of more generalist cleaner species (likely obligate mutualists) along with more specialist cleaners (likely facultative cleaners).

If these positive interactions are specific among some species, the network would be organized into modules. In this case, a given community would have cleaner species that interact only with a group of clients; or follower species that only associate with specific nuclear species. The modular structure suggests a high level of specialization among species within these interactions. For instance, fish species of the genus *Elacatinus* spp. are mainly obligate cleaners, and prefer clients associated to the bottom, such as parrotfishes, eels, and groupers. Alternatively, the network structure can be random, when only a few species interact, or when most species are generalists. This case is more common in reefs where the nuclear role is played by few species and the follower role is performed by several abundant species (e.g. feeding frenzy; Quimbayo et al. 2014). Such conditions seem to occur in some tropical reefs, particularly the more isolated ones such as oceanic islands. Therefore, comparing networks depicting different ecological interactions in tropical reefs around the globe can be profoundly revealing.

10.5 A Biogeographic Panorama of Tropical Reef Interaction Networks

The study of ecological networks at the community level provided several insights on the processes operating at local scales and on how the structure and resilience are related in ecosystems (Dunne et al. 2004; Bascompte et al. 2005). The relevance of this approach is unequivocal. However, a biogeographic perspective could shed light into the mechanisms operating at larger spatiotemporal scales and potentially on how communities are assembled.

The diversity and composition of biological communities are shaped by different processes across space and time. Large-scale processes (e.g. extinction, dispersal) and environmental filters determine which species will successfully colonize a site in a broader temporal scale (Mittelbach and Schemske 2015). Once established in a local community, species engage in biotic interactions (e.g. predation, competition, mutualism) that may affect the spatial distribution of species at local and regional scales. This balance between evolutionary and ecological processes, and the relative importance of biotic interactions on community structure across different spatial scales can be assessed through studies of species interactions in a macroecological context (Kissling and Schleuning 2015; Cantor et al. 2017).

Food webs, for instance, might conserve structural properties across a biogeographic scale (Fig. 10.2a). However, in a latitudinal comparison, food webs from temperate reefs would differ from tropical reefs by exhibiting lower species diversity, larger biomass, and for being more susceptible to changes in nutrient levels and seasonal dynamics. These webs also differ in their major consumers (McClanahan and Branch 2008). While fish are more central in tropical food webs, invertebrates are more important in temperate reefs (e.g. Estes et al. 2011, 2016).

Environmental and ecological gradients are also crucial to the understanding of large-scale patterns of interacting species (e.g. Trøjelsgaard et al. 2015). Temperature and isolation are examples of abiotic factors that affect the spatial distribution of species and, consequently, the diversity of species across spatial scales (Schemske et al. 2009). Regional diversity patterns have a clear influence over the topology of reef fish agonistic interactions networks, with a higher number of nodes and lower values of connectance and centralization according to the fish diversity gradient (Fig. 10.2b). Diversity may also promote stability and increase resilience (Dunne et al. 2004). On the other hand, while high regional diversity implies higher diversity of interacting species, we hypothesize that high modularity and lower connectance in agonistic networks can suggest and indicate spatial heterogeneity of species distribution or decreasing functional redundancy due to spatial segregation of species.

At larger scales, ecological and mutualistic networks may display general structural patterns such as nestedness and asymmetry of interaction distributions (Bascompte et al. 2003; Cantor et al. 2017). These resemblances among disparate networked systems motivated studies testing whether neutrality could explain the occurrence and strength of species interactions (e.g. Vázquez et al. 2009). In the

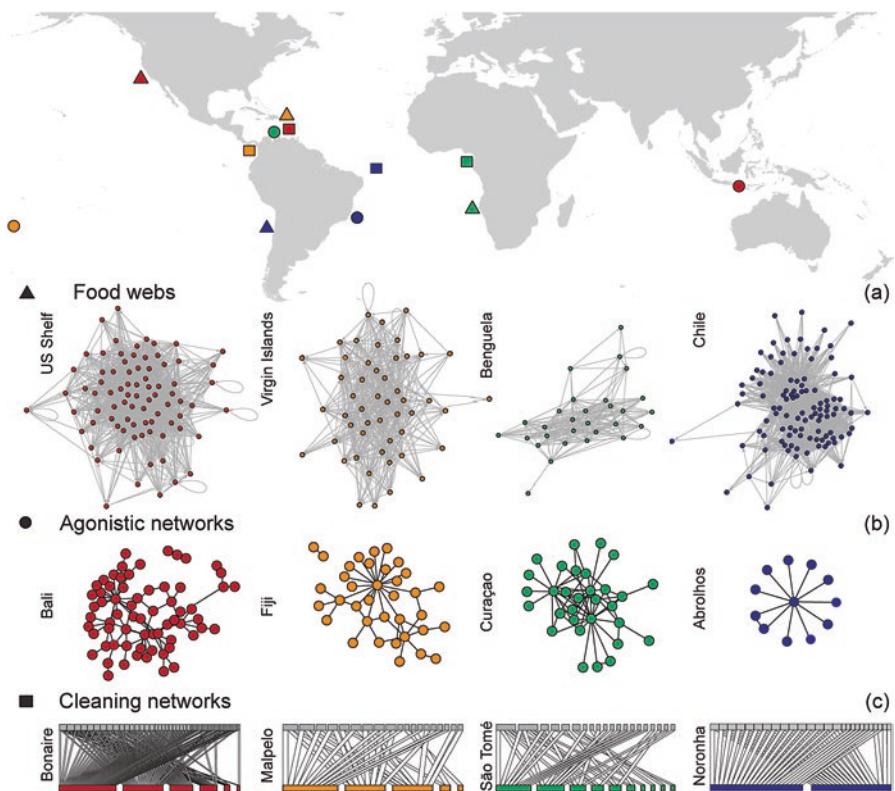


Fig. 10.2 Ecological networks from reefs across the globe. Positive (squares), negative (circles), and trophic (triangles) indicate networks from 12 representative tropical reef communities. In food webs (a), species (or functional groups when taxonomical level was unresolved) are connected by trophic interactions (see Yen et al. 2016). In agonistic networks (b), fish species are connected by territorial disputes (Fontoura, unpub. Data). In cleaning networks (c), cleaners (coloured) are connected to the client species (Quimbayo, unpub. Data)

case of cleaning mutualism among reef fishes, species abundance is the major driver of the frequency of species interactions, but it does not explain network structure alone. Evolutionary signals can influence cleaning interactions (since specialized cleaners from distinct biogeographic regions are taxonomically closer), and more mobile species are more likely to interact (Floeter et al. 2007). Binary cleaning networks from distinct reefs across the globe (Fig. 10.2c) vary in the number of cleaner and client species. However, the constant presence of some cleaners with a few links and others with many links suggests an evolutionary pressure over specialization and a wide array of opportunistic species.

The current theoretical challenges are to assess whether the structure of local ecological interactions scale up to larger spatial scales and whether these structures contribute to shape species distributions and diversity patterns at macroecological scales. A general overview of intrinsic properties of species associated with

abundance, phylogeny, and their functional role within networks can reveal evolutionary conservatism of functional roles and whether neutral processes (e.g. density-dependence) predict the structure of biotic interactions (e.g. Vázquez et al. 2007). Comparing the structure of ecological networks along geographic gradients can indicate how natural selection and evolutionary processes might vary according to environmental conditions. This is particularly important given the increasing human interference in the environment, especially large-scale disturbances such as climate change and habitat loss.

10.6 The Undesirable Link Between Humans and Reef Environments

It is no longer a mystery that ecological interactions are key components of life on Earth. Species are never isolated, but are inserted in multilevel interaction networks: from individuals to ecosystems, from local to biogeographic scales. The complex, combined effect of positive, negative, and neutral biotic interactions can shape the structure of biological communities (Paine 1980) and the dynamics of the populations within them (e.g. Pires et al. 2011). A current motivation for understanding the structure and dynamics of biological networks is to predict how this ecological complexity will respond to the growing anthropogenic impact on nature, and how one could alleviate its negative consequences (e.g. Pocock et al. 2012).

Tropical reefs suffer from a variety of anthropogenic impacts that operate at multiple spatial and temporal scales. These include overfishing, over harvesting of reef organisms, pollution, increasing sediment and nutrient output in the reefs, uncontrolled tourism, introduction of alien species and diseases, and climate change (e.g. Moberg and Folke 1999). These activities have dramatically changed interaction networks in reefs worldwide. Clear examples come from destabilization of marine food webs due to overexploitation of resources (e.g. Jackson et al. 2001; Estes et al. 2011, 2016). In theory, marine food webs should be relatively robust to overfishing of random species; however, fisheries industries are selective and often target key species, whose removal can subvert the food web structure. For instance, the loss of top predators and primary consumers caused dramatic changes in the biotic and abiotic conditions of ecosystems (i.e. phase shifts; Jackson et al. 2001; Estes et al. 2011, 2016). In tropical reefs, overfishing may cascade to decline herbivorous fish, contributing for a shift from healthy and coral-rich ecosystems to impoverished and algae-dominated systems (e.g. Bascompte et al. 2005).

Interaction networks can also be affected by the introduction of invasive species. When the lionfish (*Pterois volitans*, a Pacific species introduced in the Caribbean by the mid-1980s) was added to food web models of Caribbean reefs it figured above the native top predators which are sharks, rays, and groupers (Arias-González et al. 2011). These novel trophic interactions could lead to higher mortality but could also modulate competition. Climate change could have similar effects on food webs by facilitating tropical species to expand their ranges and enter subtropical food webs

(tropicalization; Vergés et al. 2014). The negative impact of humans on marine food webs (consequently, the functioning and structure of marine ecosystems) is clear; there is no reason to doubt that networks of other biotic interactions are disturbed too.

There are few clearer ways of capturing the urgency of understanding biotic interactions than the famous quote by Janzen (1974) on tropical rainforests: “*What escapes the eyes (...) is a much more insidious kind of extinction: the extinction of ecological interactions*”. It goes without saying that the warning also fits perfectly to tropical reefs. May we keep these underwater worlds complex, productive, and diverse in shapes, colours, and functions. Only then the coming generations can dive in their plentiful life to discover the importance of preserving their fragile interaction networks.

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Chapter 11

Ecological Networks in Changing Tropics

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Abstract Earth has an extremely dynamic surface which changes naturally across time. In the last century, however, vegetation cover underwent severe modifications due to human demands for natural resources and food production. These changes are deeply modifying the spatial distribution of native environments, which exist today mostly in small patches embedded in human dominated landscapes. This is even harsher in the tropics, where agricultural expansion is more intense. Ecologically, this means that native species have to cope with a heterogeneous set of new environments in which they did not evolve, bringing difficulties for the movement of foraging individuals. This can impair the encounters needed to establish biological interactions among individuals and different species. In this chapter, we explore how landscape changes can lead to variations in ecological networks structure and its consequences for biological and ecosystem services conservation. Although there is a general lack of complete and extensive studies regarding the effects of landscape changes on tropical ecological networks, there is growing evidence that, given a certain native vegetation cover, landscape heterogeneity may favor bigger and more complex networks across scales or ecological hierarchical levels. The relationship between landscape heterogeneity and the

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structure of ecological networks is however still an open field with many challenges and opportunities and a huge potential for application for conservation and environmental management.

11.1 Introduction

We live in an extremely dynamic world. The world surface changes naturally as a condition of the planet. However, in the last 70 years the planet's surface underwent large sweeping changes in a short period of time. The growing demand for food production, driven by the human population boom, agricultural techniques developed during the green revolution, as well as the cultural changes associated with the production of wealth and economy globalization, have led to the conversion of large areas of native vegetation into agricultural lands (Foley et al. 2005). This process is accompanied by a global biodiversity crisis which results in accelerated species extinction rates. In addition, there is no evidence of deceleration and the indicators of pressure over biodiversity increased in the last decade (Ceballos et al. 2015). For example, Hansen et al. (2013) showed intense transformations worldwide, with the loss of 2.3 million square kilometers of forest cover in only 12 year and the gain of only 0.8 million square kilometers of new forests at a global scale. This scenario becomes even more dramatic if we consider that in the tropical regions, where most terrestrial biodiversity is found, these transformations were even more intense. In the tropics, native vegetation has been heavily replaced by agricultural production areas dominated by extensive pastures or monocultures with intensive management (Ribeiro et al. 2009).

Changes in landscape structure such as the loss of native vegetation and reductions of environmental heterogeneity are among the main drivers of biodiversity loss (Stein et al. 2014) causing, for instance, along with exotic plants invasion, severe negative effects on flower visitors' functional diversity (Grass et al. 2013). Such changes in community structure may also be associated with changes at a more systemic level (Fort et al. 2016). Biodiversity is more than a collection of species. Biotic interactions involve many partners, are complex, dynamic and play an important role in the organization and persistence of biodiversity (Bascompte et al. 2003). These changes in community structure can have important consequences for interspecific interactions and thus for ecological processes depending on them (Valiente-Banuet et al. 2014). For example, Moreira et al. (2015) observed that pollinators' diversity was positively related to landscape heterogeneity and that oversimplifying the landscape had negative effects on the plant-pollinator networks structure, reducing its complexity (Fig. 11.1).

Much has been discussed about the principles behind the organization of ecological networks structure, where trait matching and the abundance distribution in the communities, are the major contributors to network formation (Blüthgen 2010). However, these two factors do not contribute in the same proportion since the majority of the variation in networks structure can be explained by the variation

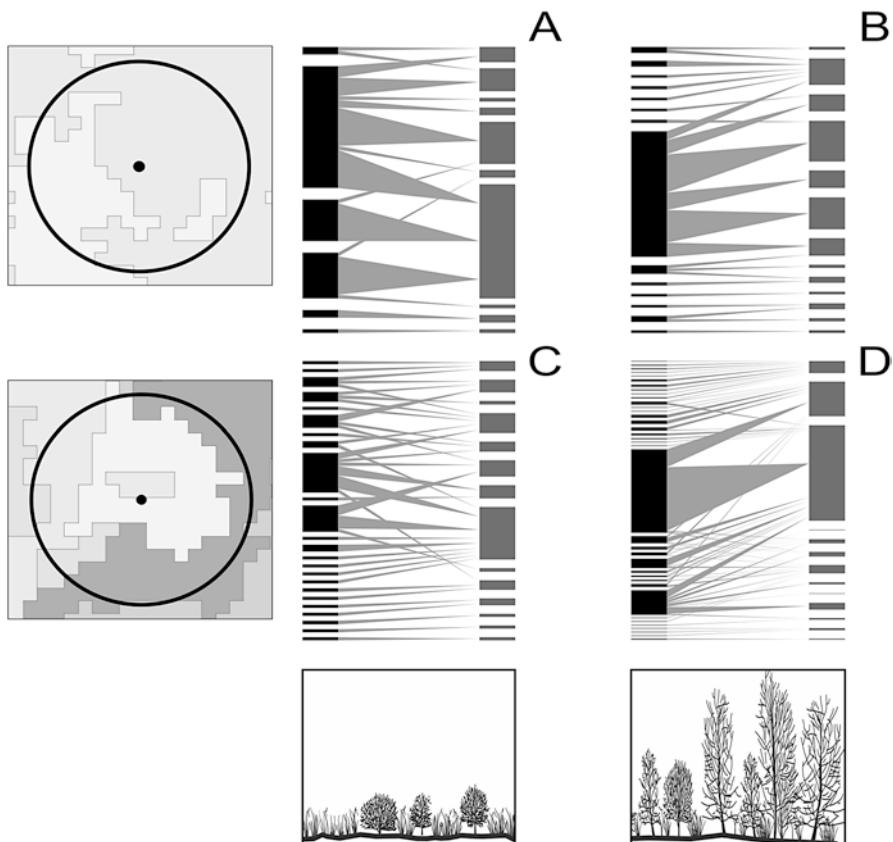


Fig. 11.1 Adaptation from the scheme summarizing the results from Moreira et al. (2015), with 4 of 27 studied landscapes representing the positive relationship between the plant-pollinator networks complexity (A to D), the vegetation heterogeneity (left to right) and landscape heterogeneity (top to bottom), including the number and proportion of the different land cover types (grey levels) as well as the complexity of its arrangement

in the community structure, such as species richness and relative abundance (Vázquez et al. 2009). The importance of those relationships is that network structure may be related with the ecological systems' emerging properties such as robustness and resilience, which are key factors to the maintenance of ecological processes and biodiversity conservation (Tylianakis et al. 2010). This can be well illustrated using pollination and predator-prey population dynamics, both good examples of fundamental processes for biodiversity maintenance in terrestrial ecosystems (Blüthgen 2010).

In this chapter, we will explore the most promising propositions for the relationship between landscape structure, biodiversity, and interaction networks, highlighting the latest evidences as well as the gaps and the implications of landscape management applied to biological conservation in the tropics.

11.2 Landscape Ecology

Landscape, viewed as “a heterogeneous mosaic composed by interactive landscape units, where heterogeneity exists for at least one parameter, one specific observer and at a particular scale” (Metzger 2001), allows for a wide and useful approach to understand environmental changes for many reasons. Most importantly, this approach turns the landscape into a system composed by elements that interact with each other. Those elements are classified into *landscape units* according to each type of landscape component, i.e., types of land cover, vegetation classes, or environments (Christian 1958). The criteria adopted in the definition of these units are fundamental since they have great influence on the meaning of landscape’s characterization. To be ecologically relevant, these criteria must be biologically based and explicitly explained according to the observer in question (Forman 1995).

Landscape ecology is, thus, not an organizational level or a scale of analysis. It is, instead, an approach to study how spatial heterogeneities are generated and can affect human society and biological processes across all organizational levels. The landscape heterogeneity can, then, be decomposed in two components: the configurational and compositional heterogeneities (Fig. 11.2). Composition includes the characteristics associated with the types of environments included in the landscape and their respective quantities (Forman 1995). Configuration deals with the spatial arrangement of landscape units.

Another consequence of that landscape definition is the impossibility of a functional characterization of its structure without a previous definition of the observer (Moreira et al. 2017). This observing agent can be interpreted in two ways, more literally as referring to organisms that directly observe, interpret, and react to the landscapes, or alternatively in a more metaphoric sense where the term observer may be best understood as the biological process of interest that may respond to the landscape heterogeneity. In the last sense, the observer can refer to a whole range of phenomena such as the reaction of individuals of a species, a certain behavior of these individuals, the populational dynamics, or the network of interspecific interactions between species (Boscolo et al. 2016).

For example, consider a frugivorous bird that has a seasonal migration. In each season, these birds are doing different things, such as mating, nesting, and migrating. The availability of the conditions and resources necessary for each of these activities varies in space/time at different scales. It is the same to say that a given individual experience the spatial variability in different ways during its lifetime depending on the specific activities that it does. Therefore, approaches considering multiple scales can be relevant, depending on the question being asked (Kotliar and Wiens 1990). If the question is relative to a specific behavior at an individual level, such as nest building, it is possible that only a single aspect of the landscape heterogeneity is relevant. However, if interest is on the reproductive success, multiple factors become relevant which may include the interaction among several individuals or species, such as the availability of nesting material, food resources, mates, predation and parasitism rate, and so on (Chittka and Thomson 2004; Turner

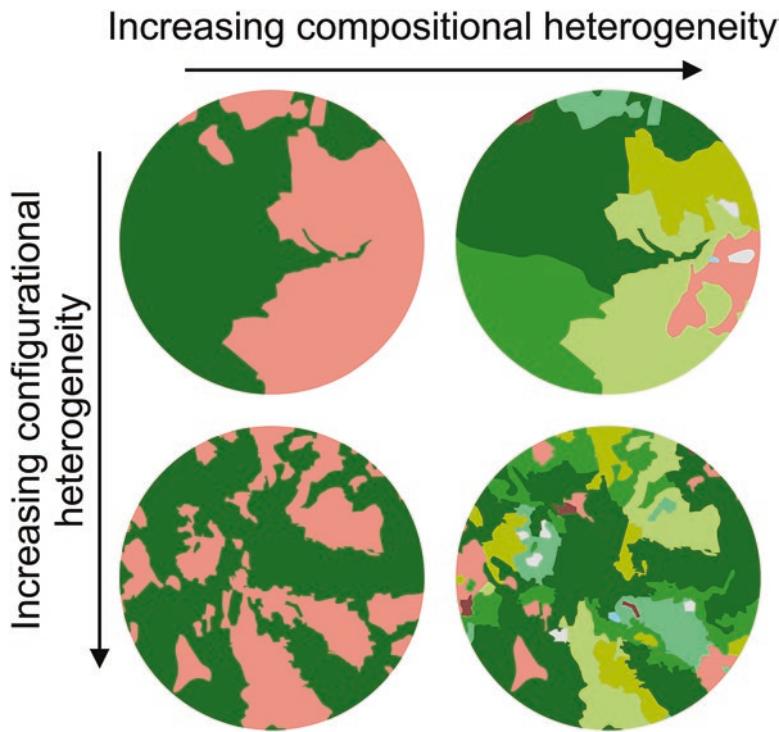


Fig. 11.2 Adapted from Fahrig et al. (2011), represents the two axes of landscape heterogeneity: compositional and configurational heterogeneity. The different color types represent different land cover types, the landscape units, reflecting the heterogeneity of some environmental characteristic relevant to the observer in question. The compositional heterogeneity increases with the number and evenness of landscape units, what must reflect levels of variation in the relevant characteristics. The configurational heterogeneity increases with the level of intricacy between landscape units and is proportional to the increase in the contact surface between them

and Gardner 2015). The meaning of spatial heterogeneity then changes completely from one question to another, while we may still be talking about the behavior of one individual.

Landscape perception will also be related to other levels of organization such as population dynamics, interspecific interactions, and ecological networks. The reproductive success of the individuals are determinant factors for the populational dynamics, which is determinant to the interspecific interactions that in turn produces the systems' networks. This framework imposes a challenge. In nature, all biological processes that respond to spatial variation are happening simultaneously and, in general, are interdependent from each other. Therefore, multiple levels of influence must be considered with regard to the relationship between landscape heterogeneity and interaction networks, attempting to the relevant spatial heterogeneity at each level as well as the scale of measurement and the hierarchical nature of the causal relationships involved (Turner and Gardner 2015).

11.3 Effects of Landscape Structure on Interaction Networks

In theory, any complex system can be represented and analyzed as interaction networks. In the last few decades, the developments of graph and system theories were incorporated in ecology to help understand what are the consequences of the community structure on the ecological interactions and emergent properties of these systems (Bascompte et al. 2003; Tylianakis et al. 2010). In this section, we will explore how landscape structure changes can lead to changes in ecological networks. We will also discuss what those changes in ecological networks may represent for ecosystem processes and biodiversity conservation. However, our intention here is not to exhaust all possible intersections between landscape ecology and network theory. We will focus mainly on mutualistic networks (e.g. plant-pollinator and plant-disperser interactions networks) given its relevance in the context presented before. In addition, interaction networks have many features, and there are multiple ways to mathematically describe them. You can find a full description of the network characteristics and their descriptors in Chaps. 3 and 13 of this book. Nonetheless, not all features are equally relevant regarding network function and stability, especially in relation to a landscape approach (Bascompte et al. 2003). Therefore, we will discuss mainly networks' characteristics whose relationship with landscape and systems' stability/productivity was previously proposed and tested (Tylianakis et al. 2010).

The study of mutualistic interaction networks provides an interesting assessment of landscape change impacts on biodiversity and the functioning of ecological processes, providing guidance to the conservation of both (Viana et al. 2012; Ferreira et al. 2013; Falcão et al. 2015; Moreira et al. 2015). However, there is still theoretical controversy and few empirical data regarding the effects of the loss of natural environments on network characteristics such as nestedness (how much of the interactions with specialists species are a subset of the interactions with generalists species) and complementary specialization— $H2'$ (the extent to which specialist species interact with other specialist species) (Soares et al. 2017). As suggested by Aizen et al. (2012), in the tropics, interactions between specialized species can be more sensitive to forest loss, whereas asymmetric interactions (specialist-generalist) or between generalized partners could be more resistant to landscape changes. This variation in response can promote shifts in interaction network characteristics, potentially affecting their robustness, leading to secondary extinctions, loss of interactions and, consequently, disruption of ecosystem functions (Soares et al. 2017).

To understand ecological systems as interactions networks and the effects of changes in landscape structure, it should be clear that we are dealing with a spatially/temporally oriented hierarchical complex system (Turner and Gardner 2015; Ferreira et al. 2015; Moreira et al. 2015). Independently of the scales of observations, landscape structure is one of the most important factors that will influence all levels. For example, at the lower levels landscape structure influences individuals' behavior (Cranmer et al. 2012), at intermediate levels it influences population dynamics (Pulliam et al. 1992), and at the higher levels it influences communities' biodiversity (Slancarova et al. 2014).

The characterization of the network structure includes aspects of the interacting partners and of the interactions themselves (Bascompte et al. 2003). First, to figure out the relationship between the landscape and network structure we should establish the mechanisms behind that relationship. Networks are representations of systems, and the landscape can affect the components of these systems, and consequently the system itself. The landscape spatial structure can directly affect the movement of organisms. To be possible for organisms to find each other and interact, individuals must move through space. For instance, regarding plant pollination by animals, because pollinators move through a landscape to reach flowering plants they have to face different environments and conditions, which can change their routes, directly interfering on pollen transfer probabilities. In this sense, landscape structural changes can modify the effectiveness of pollination process of native vegetation and agricultural fields merely by hindering pollinators' access and movement among flowers (Moreira et al. 2015).

Another aspect of the effects of landscape changes on interactions networks may be found in the effects of landscape heterogeneity over the organisms' foraging behavior (Cranmer et al. 2012). Animals, for example, tend to optimize foraging often preferring the nearest energy source because of its lower cost compared with farther ones. However, when the energy gain is significantly higher, individuals may assume higher costs, since the energy expended traveling a greater distance is well compensated (Lihoreau et al. 2011). In the more heterogeneous landscapes, the chances of having nearby alternative resources with high value to an organism is higher, and it may increase the chances of that organism to travel shorter distances from one landscape unit to another while increasing fitness and reducing survival costs. In these cases, the organisms' movement between landscape units with complementary resources is encouraged by the low traveling cost since the distances necessary to cross between units tend to be lower. Therefore, the interactions between species that depend upon organisms' movements across landscape units have higher probability to occur in more heterogeneous landscapes than in homogeneous ones, where resources may be spatially disaggregated (Cranmer et al. 2012). This can affect network size and number of interactions observed in a given site of the landscape as well as have effects on other important network characteristics since species will not meet their network counterparts (Vázquez et al. 2009).

Another example are the adaptations of many species to the variation in competitive pressure. Those mechanisms are activated depending on the context in which the species are embedded. They can be triggered by competitors' density or resource scarcity and include behavioral changes, such as the broadening or contraction of the diet breadth. Some animals tend to include more food items when under the influence of increased competitive pressure, expanding their diet. In more heterogeneous landscapes where the flux of organisms may be facilitated, more competitive pressure is expected in places with high value resources as more individuals of distinct species are drawn to it from further places (Moreira et al 2015). This can promote the diet expansion of the more plastic organisms that reside nearby (Fontaine et al. 2008). Such changes can affect network structure since the more plastic species will exhibit more interactions, increasing connectance, network nestedness, and changing

the interaction strength distribution, as well as the overall network specialization (Vázquez et al. 2009).

Invasive exotic species, for instance, are expected to present such behavioral plasticity, and are likely to compete with and/or facilitate the maintenance of native species and their interactions (Bartomeus et al. 2008). Taking pollination as an example, the most reported effect is the usurpation of interactions by the exotic species, which centralizes the interactions increasing the asymmetry of the network and decreasing the interactions strength between the native species. This is accompanied by the increase in abundance of species that benefits from the invasion (Soares et al. 2017). On the other hand, there are reports of no effects of invasive species on network metrics such as nestedness and connectance, what may indicate some network robustness, with a reorganization of the interactions, buffering the losses and behavioral changes caused by the introduction of super generalists exotic species (Padrón et al. 2009; Vilà et al. 2009; Falcão et al. 2017).

Theoretical models suggest that the structures of mutualistic networks are in general resilient to random extinctions, but the extinction of well-connected generalists can result in quick network collapse due to interactions and species loss (Kaiser-Bunbury et al. 2010). In tropical environments, where harsh landscape structural changes occur, the loss of key generalists is probable (Aizen et al. 2012). However, empirical data on the response of ecological network metrics to landscape changes is scarce (Soares et al. 2017). The available data indicates that after an environmental disturbance the network tends to reorganize towards a more stable form, allowing for the coexistence of species and maintenance of interactions (Nielsen and Totland 2014). However, in a recent review Soares et al. (2017) showed that environmental degradation influenced network metrics but degree, nestedness, and connectance (based on unweighted links) did not have a simple, linear, or unidirectional pattern of response to changes in environmental quality. Despite limited data, asymmetry and reciprocal specialization index (d' and $H2'$ respectively) showed the most consistent responses to environmental quality change.

In the tropics, landscape homogenization due to native vegetation loss can lead to the reduction in nestedness and specialization mostly because of specialist species loss (Moreira et al. 2015, Ferreira unpublished dataset). Another important highlight is that the role of the species changes, ranging between generalists and specialists under different conditions (Soares et al. 2017). There is a higher level of specialization in better preserved landscapes, and the composition of the network can vary even when its basic structure does not change (Nielsen and Totland 2014). This shows how interactions networks have a particular importance for ecological conservation. More resilient species may survive in a degraded landscape; however, its role in the networks may change in ways that compromise the ecological process underlined by those interactions (Aizen et al. 2012). For example, as a specialist pollinator changes its role in the network, becoming more generalist, may put pressure on other species, causing species loss and disruptions of ecological processes (Nielsen and Totland 2014).

In the end, landscape heterogeneity may favor bigger, more connected, and more nested networks across scales or hierarchy levels (Moreira et al. 2015). This happens because the number, strength, and distribution of interactions are closely related with the community structure (Vázquez et al. 2009). The landscape heterogeneity can also affect the density of individuals through two basic mechanisms. First, it can increase recruitment of species that can benefit from the supplementary or complementary resources available in different landscape units. For example, multivoltine species may have more reproductive cycles during the year in more heterogeneous landscapes when the different landscape units offer complementary or supplementary resources in different seasons, also reducing intraspecific competition (Burkle and Knight 2012). The second mechanism is associated with the presence of attractor sites in the landscapes, increasing beta diversity, for example (Veech and Crist 2007). More homogeneous landscapes may thus promote the concentration of individuals in few edges between the landscape units (Ferreira et al. 2015), whereas more heterogeneous landscapes tend to have populations more evenly distributed promoting the dilution of individuals (Moreira et al. 2015). The balance of these two mechanisms may determine the concentration of individuals in a given point in the landscape and in turn the probability of their interactions (Vázquez et al. 2009). On a broader level, landscape heterogeneity can promote higher beta and gamma diversity, which can function as source of diversity to the proximal level. The reduction of landscape heterogeneity generally involves the substitution of natural vegetation by agriculture or other land cover. In this context, species with more behavioral plasticity may be less affected or even favored, exhibiting increased abundance in landscapes with low levels of native vegetation cover, while species with less behavioral plasticity may be locally extinct (Ferreira et al. 2015). This process follows the regime-shift model that predicts a reduction in abundance and richness of specialized species and an increase of generalized ones at different landscape scales (Pardini et al. 2010). These changes tend to decrease the conservation state of networks in degraded landscapes (Soares et al. 2017).

At a proximal scale, more heterogeneous landscapes can promote the maintenance of higher species richness than the more homogeneous ones (Fahrig et al. 2011; Moreira et al. 2015). This happens because beyond the species that are associated with each environment and the common ones, heterogeneous landscapes also may sustain species that can survive only in regions where multiple environments are present (Fig. 11.3). Such situations are expected in cases where the species reproduce in one environment and forage in others or where vital resources are seasonally available in each landscape unit along the year. Regarding the configurational heterogeneity, landscapes with more heterogeneous configurations will also favor the maintenance of the species that depend or benefit from the presence of multiple environments, since it can lower the costs of movement between landscape units, as explained above. Richer communities will then tend to have networks that are larger more nested and with more specialist interactions (Bascompte et al. 2003; Moreira et al. 2015).

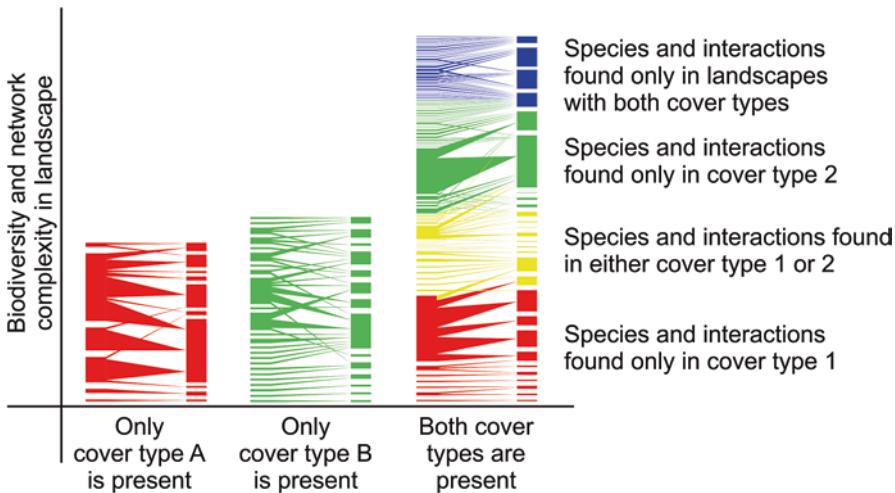


Fig. 11.3 Adapted from Fahrig et al. (2011), represents the effect of complementation between landscape units on biodiversity and network structure. Species diversity increases with the number of landscape units because they maintain the species associated with each landscape unit plus the species that require the multiple landscape units to survive. This process also affects the probability of interactions and the network complexity as observed by Moreira et al. (2015)

11.4 Interactions Networks Conservation, Management, and Future Perspectives

Populations' densities and interactions are highly variable in space and time (Petanidou et al. 2008). This natural intrinsic variation has to be considered in environmental management based on single species or single interaction. However, the structure of communities and interaction networks tend to be more stable over time than its constituents (Blüthgen et al. 2016). For that reason, the network structure could be the focus of management goals. However, not every stable state of a system represents a desirable state from the point of view of ecological process management. For example, reducing the diversity of plant species in a given environment may lead to a more stable state, which may not necessarily mean improvements in the ecological processes of that environment (Morales and Aizen 2002). Environmental degradation may lead the system to stable or resilient states, mainly by reducing the diversity of species and by changes in species' functions in these networks (Soares et al. 2017). Such stable states are undesirable from any biodiversity conservation perspective and may constitute a challenge to ecological restoration and management. Therefore, initiatives for conservation and management of ecological processes should aim not only on stability but also the complexity of ecological systems.

As interaction network structure reflects the general pattern and not the intrinsic spatial/temporal variation of the system, it is important to discuss which should be

the conservation target to networks in landscape management initiatives and how land use management can help us approaching the desirable state. Some of the mechanisms and tendencies involved in these relationships were discussed above. However, those need to be viewed with caution and carefully criticized. For instance, mutualistic networks tend to be nested. Additionally, network nestedness is expected to increase the resilience of plant-pollinator interactions (Bascompte et al. 2003). Should mutualistic network nestedness maintenance be a conservation goal? Should management targets be likely “to increase nestedness”? These questions have been raised and not answered yet, either theoretically or empirically (see Soares et al. 2017; Tylianakis et al. 2010).

Empirical evidence has shown that a higher nestedness in degraded landscapes can also indicate an increase in the resilience of a poorer undesirable state of the network (Soares et al. 2017). Even very simplified and degraded networks can maintain its nestedness and partially its functionality, without conserving the interactions richness and network complexity. Therefore, we should not set increases in nestedness as a management target. On the other hand, a management target such as the conservation of all interactions is difficult to pursue by several reasons, including the spatiotemporal dynamics of ecological systems.

Only the combined analysis of a set of metrics, including the network level and the underlying mechanisms observed at lower hierarchical levels will be able to indicate the conservation status of an interaction network and its relation to the landscape structure. Despite still incipient, there are some candidate metrics for that integrated analysis such as network size, interaction asymmetry, interaction specialization or selectivity ($H2'$), plus additional information about changes in species compositions and their roles in the interactions (Soares et al. 2017). Additionally, the comparative study of networks in different environments, associated with functional diversity and the measurement of ecological processes in order to investigate if there are network characteristics capable of reflecting the specificities of each ecosystem. Information of this nature may provide clues to the relevance of specific network structural patterns for the ecosystem functions in different environments and how they can be managed.

The network analysis also has great potential of application in monitoring of ecological restorations since it allows to evaluate the restoration process covering not only the development of the vegetal species but its interactions and increase of the complexity of the community. In this sense, the networks also contribute to the selection of the characteristics of the species that would be most important in the process of community formation, thus enhancing the restoration action. Finally, network analysis can serve as a parameter to evaluate the success of the restoration (Forup et al. 2008).

In fact, we still know too little about the consequences of landscape changes on the network structure to link diversity, stability, and function because of the lack of empirical studies. In addition, the magnitude of spatial-temporal variations in tropical landscapes is greater than in other regions because of the high diversity and species turnover (Nielsen and Totland 2014). Therefore, such studies are needed to separate the effects of natural variations from those resulting from anthropic impacts.

In general, the number of empirical studies on networks is scarce and in the tropics it is even smaller (Ferreira et al. 2013). Most of these studies do not relate the network structure to environmental gradients or provide empirical evidence of its impact on the ecological functions to which they are associated. Therefore, most of the conclusions about the impacts of networks' structure and dynamics over ecosystems functions are based on conceptual and mathematical models, and/or indirect relationships. Empirical studies could enable us to identify which network interactions are most affected by anthropic impacts, as well as to analyze the ecological significance of the behavior of these interactions at the community level. However, it is important to bear in mind that "absence of evidence is not evidence of absence." You can find a current perspective about the empirical gaps in this matter in the review by Soares et al. (2017).

Another interesting topic is the relationship between the dynamic aspects of both landscapes and ecological networks. There are some propositions about the consequences of the landscape dynamics for biological communities, biodiversity stability, and conservation such as the spatial insurance hypothesis, considering the interactions' turnover (Loreau et al. 2003). However, such relationships were not empirically evaluated yet. The same is true to the dynamics of interaction networks and its relation to function and stability that were usually studied through mathematical models (Vázquez et al. 2009). There is an interesting path emerging from the network field that can help coping with these problems, the multilayer approach to model ecological networks (Pilosof et al. 2017). This approach allows us to consider both temporal and spatial dynamics of interaction networks and can be associated with landscape hierarchical models. In sum, we can safely assert that the relationship between landscape heterogeneity and the structure of ecological networks is an open field with many challenges and opportunities and an enormous potential of application for conservation and environmental management in the tropics.

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Chapter 12

The Future of Ecological Networks in the Tropics

Luciano Cagnolo

Abstract Ecological networks are one of the best approaches to describe interactive communities of species. Accordingly, the development of network studies in the tropics is imperative given the high rates of habitat loss and transformation. To achieve this goal, we face the challenge of dealing with extreme complexity but lacking complete taxonomic and natural history information. In this chapter, I analyze the trajectory of network studies in the tropics over time and describe some promising avenues for the study of ecological networks in the next years. I built keyword co-occurrence networks of network studies in the tropics for four periods from 1970 to the present. The earliest network studies were concentrated on food webs; in the following decades, network studies rose dramatically and diversified, generating topic modules about different interaction types. The last period (2010–2016) reflects a mix of different research areas, with food web studies being less important and much more connected with other topics such as frugivory and myrmecophily. One of the major challenges of network research in the tropics is to increase the level of network complexity. Here, I propose two ways: merging different interaction types into single networks and disaggregating data into their spatial, temporal, and individual-level layers. The multilayer approach requires new conceptual and methodological frameworks that are starting to be formalized. One of these tools is barcode sequencing directly from DNA extracted from consumers, which provide strong physical evidence for the host association and facilitates phylogenetic analysis.

12.1 Introduction

The megadiversity of the humid tropics has always amazed naturalists, as could be noticed in the annotations and drawings of the nineteenth century (Bates 1864). The fascinating abundance and diversity of forms and colors of tropical species may

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have served as inspiration for the cornerstone work of Darwin and Wallace in 1858. Since those days to the present, important advances have been made in cataloging tropical biodiversity; however, most biologists agree that we still lack a nearly complete description of tropical diversity, particularly regarding small, non-conspicuous insects, fungi, and bacteria (Erwin 1991). Although this is problematic—but affordable—it is undoubtedly an urgent task considering the unprecedented rates of habitat loss and modification, with the consequent loss of associated species (Pimm and Raven 2000).

The study of ecological networks increased in the last decade since researchers have appreciated them as the most informative way to summarize and describe biological communities. From the earliest food web studies to the complex network approach in our days, ecological network science has evolved both in theory and tools as a consequence of merging ideas coming from physics, sociology, mathematics, and biology (Poisot et al. 2016). Network studies applied to biological communities succeed in understanding the robustness and fragility of ecosystems (Solé and Montoya 2006) and identifying key species and interaction paths (Aizen et al. 2012), which are the foundation of conservation management. In the tropics, the development of network studies is an urgent task given the high rates of habitat loss and transformation (Barlow et al. 2016). Nevertheless, developing network studies in the tropics requires facing the challenge of dealing with extreme complexity but still lacking complete taxonomic and natural history information.

In this chapter, I analyze the trajectory of tropical network studies over time, focusing on the comparison of the type of interactions studied and the concepts and tools applied. Finally, I describe some promising avenues for the study of ecological networks in the next years, both in their theoretical and methodological aspects.

12.2 The Evolution of Network Studies in the Tropics

The study of ecology through networks has a long history that can be traced back to the 1800s, as cited by Dunne (2006). In this section, I provide a revision of papers presenting network studies in the tropics by searching in Scopus and Google Scholar using the keywords “network + tropics OR tropical” and “food web + tropics OR tropical.” With this information, I built keyword networks for each of four periods (1970–1989, 1990–1999, 2000–2009, and 2010–2016), by establishing a link between words when they co-occurred in the title, abstract, or materials and methods section. The idea behind this analysis was to evaluate how concepts group together and to determine which ones are central nodes that connect different areas of study.

The keywords search focused on concepts associated with hypotheses (e.g., “equilibrium,” “bottom-up control”), countries where the studies were conducted, habitat type (e.g., “forest,” “freshwater”), statistics used to describe the networks (e.g., “connectance,” “nestedness”), interaction type (e.g., “competition,” “pollination”), sign of interactions (e.g., “mutualism,” “antagonism”), and organisms involved (e.g., “fishes,” “insects”). With this information, I constructed weighted one-mode networks, in which each tie in the edge list was valued by a positive num-

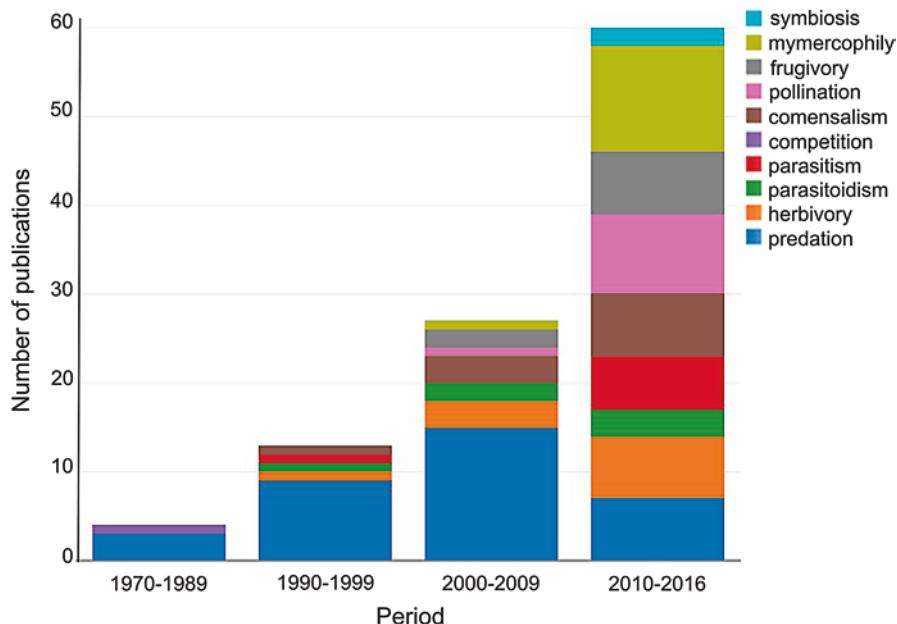


Fig. 12.1 Number of network studies of different interaction types in tropical ecosystems for four periods of time

ber that indicates its frequency of co-occurrence. These networks were examined to evaluate how words are grouped into highly connected groups (here referred to as “modules”) and therefore identify the concepts, tools, or organisms that serve as connectors between different areas of research (modules). By doing this, I expect to identify which concepts helped to integrate and generalize the science of ecology.

The number and diversity of interaction types in network studies conducted in the tropics has risen dramatically since the 1970s (Fig. 12.1). Accordingly, the concepts and tools applied in their study increased and diversified as well (Fig. 12.2). The 1970–1989 period presented only four studies in 20 years, with all of them being descriptions of antagonistic interactions, such as predation and competition, and three out of four being from aquatic habitats. The keyword network was sharply divided into two blocks, connected by the word “antagonism” (Fig. 12.2).

During the 1990s, the number of studies more than doubled those of the previous two decades. As in the previous period, antagonisms still prevailed but ecologists started to focus on interactions other than predation, such as herbivory and parasitoidism (Fig. 12.1). In the 1990s, ecological studies were influenced by research exploring regularities in food webs, which had been performed in previous years (Briand and Cohen 1984; Pimm and Kitching 1987). Although food web studies in aquatic systems were still important in the 1990s, there seemed to be more interest in what happens with insects and plants in tropical forests. Researchers incorporated new tools, such as the use of stable isotopes, to establish feeding links, statistics such as modularity to describe global aspects of network structure, and concepts of

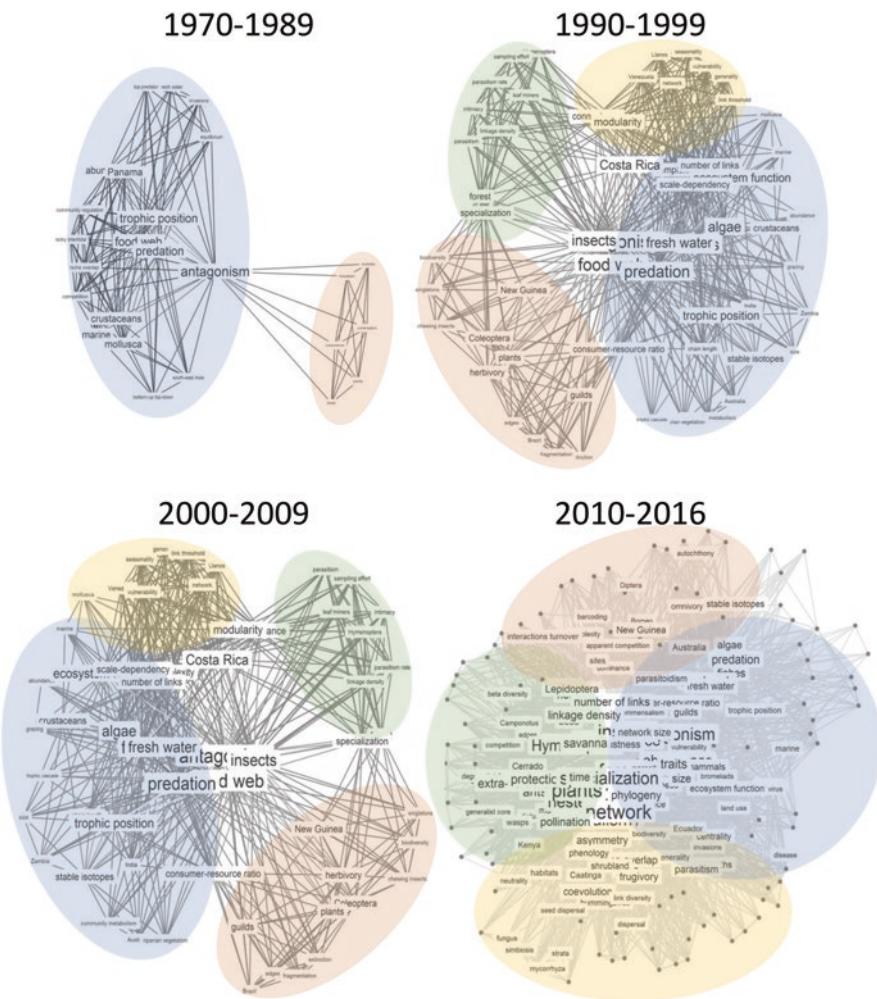


Fig. 12.2 Keyword networks of network studies in tropical ecosystems for four periods of time. Font size of keywords reflects their frequency of appearance, and colors reflect the approximate position of cohesive groups of keywords (modules)

scale-dependency of network properties; studies were also conducted in new (for network scientists) countries such as Costa Rica and New Guinea. The keyword network of this period was composed of four modules, with the largest ones being that of food web studies in aquatic systems. Consequently, the most frequent keywords were those related to food web studies, such as “predation,” “fishes,” and “antagonism” (Fig. 12.2).

In the following decade (2000–2009), the total number of studies rose, with the peculiarity of an increase in the relative importance of non-food web studies, which were less than half of the total (Fig. 12.1). Keystone papers evaluating regularities

in the patterns of mutualistic interactions (Jordano 1987) and the first analyses of pollination networks with food web tools and concepts (Memmott 1999) generated new enthusiasm. However, the keyword network still reflected the dominance of food web studies, showing a greater richness of concepts than in the previous period and the emergence of interest in new interaction types. Hence, the food web words formed a large module on the left side of the network graph, whereas the remaining keywords were placed in three modules, each one representing different lines of research associated with different interactions. The most frequent keywords were those related to food webs, such as “trophic position,” “fresh water,” and “stable isotopes” (Fig. 12.2).

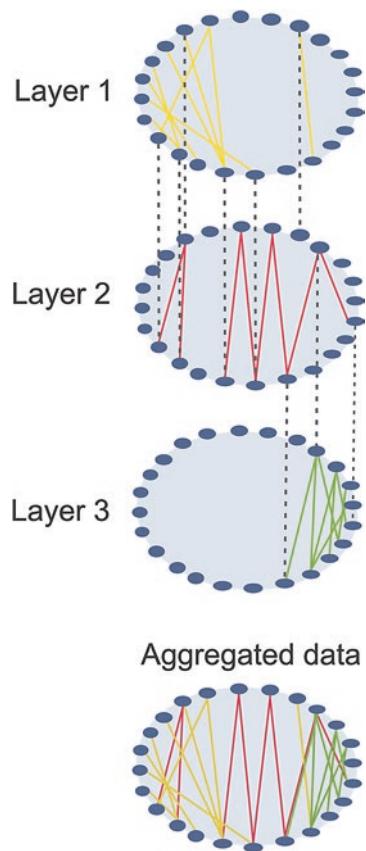
The last period analyzed comprises only seven years but is sufficient to demonstrate a dramatic increase in number and diversity of network studies in the tropics. The decrease in the interest in food webs is remarkably opposite to the increase of the remaining interaction types, particularly in myrmecophily (Fig. 12.1). The keyword network reflects these changes through a combination of different areas of research; although the food web module can still be recognized, it is relatively small and much more connected with other modules. Interestingly, there is a change in the research topics related to the most frequent keywords, with “specialization,” “plants,” and “pollination” being some of the most prominent ones (Fig. 12.2).

The evolution of the study of ecological networks in the tropics is not different from that in other latitudes (e.g., Dunne 2006), and the present of network studies in the tropics shows an amazing diversity of topics and, particularly, of interaction types. This diversity of studies requires the generalization—if possible—of the conceptual frame and methodological approaches to reach a unified theory of ecological networks. In the following sections, I outline what are considered the most promising avenues to achieve this goal.

12.3 The Future of Network Studies: Dealing with Complexity

Future studies in ecological networks have the main challenge of adding complexity. To achieve this goal, we must look at the several forms of oversimplification in the present status of network studies. For example, since biological communities are composed of individuals, populations, and species interacting in different ways, places, and times, incorporating complexity and realism requires studies to be multilayered. Multilayer networks are composed of different types of nodes and edges combined into a single representation (Pilosof et al. 2015). Accordingly, a multilayer network should have intralayer edges (i.e., those linking intralayer nodes) and interlayer edges (i.e., those linking nodes from different layers) (Fig. 12.3). Examples of multilayer networks in ecology are those that combine different interaction types (e.g., Pocock et al. 2012), habitats (e.g., Borthagaray et al. 2014), or points in times (e.g., Schoenly and Cohen 1991). The integration of the multilayer network theory

Fig. 12.3 Example of the composition of a multilayer network. Layers can be different points of time, sites, or interaction types; each layer has intralayer interactions (colored lines) and interlayer interactions (dotted lines) composed of shared nodes connecting different layers



into ecology requires coming out of the comfort zone of, for example, our organismal-taxonomic affinities, and provides an opportunity for multidisciplinary collaboration. Unfortunately, ecology science still lacks a proper conceptual frame and its appropriate tools (but see Pilosof et al. 2017 for a description of multilayer networks and tools for ecological studies). Below, I present a list of ideas and suggestions to incorporate complexity in research studies of ecological networks.

12.4 Combining Different Interaction Types

The study of ecological networks emerged as a consequence of understanding that species do not occur alone in ecosystems, and their fitness is a consequence of the interactions established with other species, among other factors. Most research has focused on the study of networks of particular interactions (e.g., herbivory, pollination) and involving particular guilds (e.g., leaf miner herbivores, hummingbird pollinators). Although network science was (and is) successful

in describing complex ecological systems, we still lack a comprehensive understanding of the biotic environment of species to draw more realistic conclusions.

Food web studies usually contain different types of interactions in a single web (e.g., herbivores, detritivores, and predators), but in the last few years, attempts have been made to explicitly merge different interaction types into network studies (Lewinsohn and Cagnolo 2012). For example, in a large network containing both mutualistic and antagonistic links from Spain, the ratio between mutualistic and antagonistic links per plant species was very heterogeneously distributed in the plant community, which resulted in a strong influence on total species richness (Melián et al. 2009). Pocock et al. (2012) assembled a “network of networks” from several studies conducted in an organic farm in southwest England. They found that networks did not covary in their robustness, suggesting that management actions that benefit one guild or functional group will not necessarily benefit others. Recently, a plant-centered mutualistic network including pollination, protection, and seed dispersal interactions did not show to be more robust than the sum of their parts, but more interestingly, some species that connected different sub-networks showed to have a disproportionate effect on community cohesion (Dátillo et al. 2016). These examples show diverse evaluations of how different layers are connected and influence each other in ecological communities. Unfortunately, ecology has a deficiency of structured protocols to evaluate the properties of these transition zones between networks that share species and are composed of different interaction types (Kéfi et al. 2016).

Merging different interaction types into a single network is a methodological challenge because it requires consistent sampling protocols and standardized statistics to make the effects of different interaction types comparable. Accordingly, Palla et al. (2005) proposed several statistics to describe multilayer networks where each node (species, individuals, etc.) i is a member of m_i networks (e.g., layers in Fig. 12.3). The overlap size $s_{a,b}^{\text{ov}}$ between networks a and b (e.g., layers 1 and 2 in Fig. 12.3) is the number of shared nodes, which represents a link between both networks (dotted lines in Fig. 12.3). The linkage level of a network a is d_a^{com} , called community degree. Finally, they propose s_a^{com} as the number of nodes in a network a . The distributions of these four parameters m_i , $s_{a,b}^{\text{ov}}$, d_a^{com} , and s_a^{com} are then used to describe multilayered networks (Palla et al. 2005). This approach is interesting because it focuses on the transition zones of interactive communities composed of species of different interaction types, and it allows us to evaluate the spread of disturbances across a large ecosystem (Olesen et al. 2010).

12.5 Adding Trophic Levels

There are few examples of merging different interaction types into a single network, but including several trophic levels into a single network is one of the straightforward ways. The earliest food web studies usually included species feeding in different

modes, mixing producers with secondary and tertiary consumers, and even scavengers (e.g., Polis 1991). Consequently, the concept of trophic levels became useful to understand the mechanisms of energy transfer from producers to the whole community (Cohen et al. 2009). However, the development of tools and concepts for the study of bipartite networks in the last 15 years has focused on the interaction between two contiguous trophic levels, usually plants and their associated animals. Although the advances in this topic are amazing, as is reflected by the fast growth of number and diversity of studies (Fig. 12.1), in the next decade the challenge will be to identify the interface of different trophic levels and understand how non-contiguous trophic levels influence each other.

The description of three-level networks is widespread in the ecological literature, particularly regarding plant-herbivore-parasitoid networks (e.g., Memmott et al. 1994; Lewis et al. 2002). These “tri-trophic” networks allow us to examine the reciprocal influence of extreme trophic levels mediated by the mid-level, but neither the classical food web approach nor the bipartite network analysis offers a proper conceptual and methodological framework to fully understand a tri-trophic structure. The bipartite approach ignores bottom-up and top-down effects of non-participant trophic levels. This is not irrelevant since, for example, herbivores in tropical forests have to deal with plant defenses and higher rates of predation and parasitism (Schemske et al. 2009), and it is likely that herbivore specialization has evolved and is maintained in response to one or both of these forces (Lewinsohn et al. 2005). Consequently, herbivores select host plants by searching for enemy-free space (Heard et al. 2006), and parasitoids are attracted differentially by plant volatiles (Boone et al. 2008), suggesting that non-participant trophic levels affect species interactions in other trophic levels.

Fontaine et al. (2011) proposed six different schemes resulting from merging two bipartite networks based on the combination of nested, modular, and random topologies. A particular topology, in which modules of the basal network (e.g., plant-herbivore) translate into modules in the upper network or vice versa, is interesting because it could be a clue of mutual influence. Accordingly, overlapped modules in consecutive bipartite networks may represent a co-evolutionary vortex of tri-trophic interactions; in addition, species and interactions that connect different tripartite modules may be keystones for community maintenance and species diversification (Leppänen et al. 2013). Moreover, it was argued that cascades, i.e., the influence of biotic interactions on species in contiguous upper or lower trophic levels (Polis et al. 2000) tend to be ameliorated in tropical systems as a consequence of reticulate networks and high species diversity (Dyer and Letourneau 1999); therefore, the extent of such cascades may also depend on the structure of the tripartite networks and the degree of overlap between successive modules.

The structural patterns of tripartite networks are unknown because there are scarce tools and concepts for their study. Murata (2010) proposed a method for detecting communities from tripartite networks composed of Internet users, URLs, and tags. Murata’s approach offers a solution to evaluate tripartite network modularity; this method employs spectral partitioning and can detect communities from

networks that are composed of thousands of nodes and tens of thousands of hyperedges. This is an example of the usefulness of paying attention to areas other than ecology and incorporate tools and concepts from other fields of study that could be applied to solve ecological questions.

12.6 Disaggregating Data: Adding Space, Time, and Individuals Information

Most network studies are the result of pooled interactions recorded at different places (sites, transects, points, etc.) and moments (Fig. 12.3). How much of the known network patterns is a consequence of the spatiotemporal accumulation of interactions? For example, most networks constructed with aggregated data overestimate the connectivity of species (Trøjelsgaard and Olesen 2016), affecting our predictions, for example, about the extent of secondary extinctions.

Aggregated data may mask the spatiotemporal roles of species. For example, Pimm and Lawton (1980) proposed that modularity in food webs may emerge as a consequence of habitat boundaries, as found in the Serengeti food web (Baskerville et al. 2011) and in a bumble bee-flower network (Dupont et al. 2014). Unfortunately, most studies actively select homogeneous plots for sampling and pooling data from different plots or sites; thus, the opportunity to evaluate the possibility that habitat generalists connect different modules composed of habitat specialists is missed.

Taking space and time into account is a fundamental task since before proposing any other explanation we should discard spatiotemporal overlap of interaction partners (Vázquez et al. 2009). Studies comparing networks across time and space found that macroscopic statistics (i.e., those that describe the global structure of a network, such as connectance and modularity) tend to be more stable than the microscopic structure (i.e., the identity and position of particular species and interactions) (Trøjelsgaard and Olesen 2016). Recording changes in the phenological intensity of biotic interactions through space would add another layer to the microscopic features of interaction networks and could contribute with a deeper understanding of fine-scale changes. Therefore, the inclusion of space and time to our network studies will allow us to identify species with important roles, which may be keystones for community persistence.

Another form of data aggregation is the accumulation of individual-level data into a single node, usually referring to species (Ings et al. 2009). Nevertheless, sometimes individuals display a variety of behaviors and morphological traits; for example, the invasive ant *Solenopsis invicta* showed a highly variable trophic level position between colonies in a 0.5-ha plot, with some colonies acting as primary consumers whereas others were top predators (Roeder and Kaspari 2017). How does this variability influence on the properties of ecological networks? As proposed for space and time, the aggregation of data overestimates connectivity and

underestimates specialization. For example, Tur et al. (2014) compared the modularity of a plant-pollinator network resolved at the level of plant species and pollinator individuals. Their main result reflects an increase in the modularity at the individual's level, mainly driven by phenology (Tur et al. 2014). These studies reveal large variability that individual partners show in their interactions; consequently, the individual-based networks do not seem to behave as the species-level network.

While depending on the question under study, the patterns of networks composed of aggregated data may lead to wrong conclusions (Poisot et al. 2014), which may result in a misunderstanding of ecosystem functioning and in reducing the prediction potential of ecology. Nevertheless, almost all the different kinds of data aggregation in network studies can be solved if we consciously plan our sampling design, incorporating the spatial and temporal scales that are relevant to the studied system.

12.7 Using Barcoding Techniques

There are remarkable examples of combinations of theory and natural history for the development of networks (e.g., Novotny and Basset 2005; Novotny et al. 2010), but the time necessary to acquire taxonomical and natural history knowledge is usually scarce. Ecologists have incorporated different approaches to solve the difficulty of cataloging interactions in complex environments. One of these tools is sequencing barcodes directly from DNA extracted from consumers, which provide strong physical evidence for the host association (Evans et al. 2016). As genes rather than morphology drive identifications, barcoding is less dependent upon taxonomic knowledge, making it particularly appreciated for studying poorly known taxa and ecosystems.

The use of barcoding in the construction of ecological networks is growing rapidly not only because it is an easy way of depicting interactions, but also because it facilitates the discovery of rare ones. Most network studies that used barcoding techniques coincide in showing a significant increase in the number of detected interactions, leading to higher complexity and more connected networks (e.g., Smith et al. 2008). The utility of barcoding in resolving plant-herbivore-parasitoid food webs is obvious, and recent studies have applied this approach creatively, providing responses to interesting questions. For example, González-Varo et al. (2014) extracted DNA from the surface of seeds in bird feces for the identification of bird-plant interactions. The difference with traditional frugivory studies lies in the possibility to evaluate not only “who eats who,” but the effectiveness of the dispersion process. This example reflects how barcoding techniques are improving network science and, hopefully, opening questions that may trigger a new wave of network studies in ecology.

12.8 Final Considerations

The study of networks in the tropics had blossomed in the last 16 years, dramatically increasing the diversity of studied interactions (Fig. 12.1). The evolution of network studies reveals interesting trends supported by increasing multidisciplinary. The studies conducted in the last 6 years have revealed that the increase in the diversity of interaction types catalyzed the mixing of concepts and tools from different areas of ecology and even from different areas of science (Fig. 12.2).

The possibility of incorporating new interactions into network science depends on the knowledge of natural history and the development of new tools that solve methodological difficulties. Although there are remarkable examples of combinations of theory and natural history in network studies, the possibilities of developing research in tropical forests for periods of time long enough to incorporate sufficient natural history knowledge is usually limited. Ecologists have incorporated different approaches to solve the difficulty of cataloging interactions in complex environments. One of these tools is barcode sequencing directly from DNA extracted from consumers, which provides strong physical evidence for associations while facilitating phylogenetic analysis (Evans et al. 2016). The future of networks in the tropics will necessarily rely on metabarcoding techniques to make diversity traceable, particularly regarding metamorphosing insects. Accordingly, there are promising examples showing differences in networks built using barcoding and classical techniques (Smith et al. 2008; Wirta et al. 2014; Evans et al. 2016).

One of the major challenges of network research in the tropics is to increase level of complexity. Here, I propose two ways: merging different interaction types into single networks and disaggregating data into their spatial, temporal, and individual layers. The multilayer approach requires new concepts and methods that are starting to be formalized (Pilosof et al. 2017). Particular attention should be paid to the transitions zones between layers because they could provide clues about keystone nodes and interactions that may be crucial for community stability and cohesion (Olesen et al. 2010; Pocock et al. 2012). Besides using the theory and tools developed by ecologists, we should pay attention to other areas of science such as sociology and engineering for inspiration.

Unlike any other field of science, ecology deals with the rush of habitat destruction. The need of ecological studies is particularly urgent in the tropics because the most diverse ecosystems are in developing economies, where nature conservation and the necessity of resources exploitation are in conflict. Accordingly, network science has the role of connecting species lists to ecosystem functions, a key priority in conservation ecology.

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Chapter 13

A Useful Guide of Main Indices and Software Used for Ecological Networks Studies

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Abstract Complex network analysis allows ecologists to implement interesting and diverse approaches to study interactions among the most diverse life forms. In the last decades, several tools and advances have been developed in software, randomizations, and computer graphics; increasing the quantity of ecologists that lead authorship when these analyses are used in their research. Thereby, some metrics and indices have been improved and others appeared as novel approaches, establishing a vast quantity of information in literature. In this chapter, you will be able to find a compendium of the main descriptors currently used in the literature, as well as the primary information to develop the statistical analysis and graph visualization. It is important to have enough criteria when using these metrics and indices, which must be complemented with both: knowledge concerning natural history and the logic and limitations of the indices and analysis, in order to avoid misleading conclusions.

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Table 13.1 Principal parameters, indices, functions, and metrics typically used in the analysis of ecological networks

Symbol	Network descriptors	Description	Software
n_x	Number of nodes	Species richness of any trophic level (e.g., plant n_1 , animal n_2) or number of individuals	Spreadsheet
S	Network order	Total number of nodes, which $S = n_1 + n_2 + \dots$ If n represents species richness the network is G (Delmas et al. 2017)	Spreadsheet
L	Network size	Number of edges present in the network, i.e., number of pairwise interactions (Delmas et al. 2017)	Spreadsheet
m	Number of interactions	Interaction frequency in a weighted web (Bascompte and Jordano 2013)	Spreadsheet
a_{ij}	Number of pairwise interactions between lower trophic level species i and higher trophic level species j	Pairwise interaction between partners i and j in a weighted web (Bascompte and Jordano 2013)	Spreadsheet
A_i, A_j	Total number of interaction records for lower trophic level (i) or higher trophic level (j)	Column or row sums in weighted networks (Bascompte and Jordano 2013) $A_i = \sum_{j=1}^{n_1} a_{ij}; A_j = \sum_{i=1}^{n_2} a_{ij}$	Spreadsheet, “ <i>bipartite</i> ” package in R (Dormann et al. 2008), Pajek (Batagelj and Mrvar 1998)
k_p, k_i	Degree of higher trophic level (j) or lower trophic level (i)	k_j is the number of interactions between higher trophic level j and lower trophic level i k_i is the number of interactions between lower trophic level i and higher trophic level j (Bascompte and Jordano 2013)	Spreadsheet, “ <i>bipartite</i> ” package in R (Dormann et al. 2008), Pajek (Batagelj and Mrvar 1998)
$\langle k_m \rangle, \langle k_n \rangle$	Average degree of any trophic level	$\langle k_m \rangle$ is average number of interactions for higher trophic level $\langle k_n \rangle$ is average number of interactions for lower trophic level (Bascompte and Jordano 2013)	Spreadsheet, “ <i>bipartite</i> ” package in R (Dormann et al. 2008), Pajek (Batagelj and Mrvar 1998)
$\langle k \rangle$	Average number of interactions per any two trophic levels	$\langle k \rangle = \frac{L}{n_1 + n_2}$	Spreadsheet, “ <i>bipartite</i> ” package in R (Dormann et al. 2008), Pajek (Batagelj and Mrvar 1998)

$P_{(k)}$	Degree distribution	Probability that a node has k edges within the network, $P_{(k)} = \frac{N_{(k)}}{S}$, in which $N_{(k)}$ is the number of nodes with k edges, and S is the number total of nodes in the network (Delmas et al. 2017)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008), Pajek (Battagelj and Mrvar 1998)
C_D	Degree centrality	Vertex: Simple count of the number of interactions established by a node $C_D(i) = k_i$, in Freeman (1977) or normalized by the maximum degree $C_D = \frac{C_D}{k_{\max}}$	“ <i>bipartite</i> ” package in R (Dormann et al. 2008), Pajek (Battagelj and Mrvar 1998)
		Whole graph: $C'_D(p_k) = \frac{\sum_{i=1}^n a(p_i, p_k)}{n-1}$, in Freeman (1978)	
C_C	Closeness centrality	Measures the proximity of a node to all other nodes in the network $C_C(i) = \sum_{j \neq i} \frac{d_{ij}}{n-1}$, in Freeman (1978) and Freeman et al. (1979)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
C_B	Betweenness centrality	Gives a measure of times a node is between two others nodes $C_B(i) = 2 \times \sum_{j < k: i \neq j} \frac{g_k(i) g_k(j)}{(n-1)(n-2)}$, in Freeman (1977)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
C_E	Eigenvector centrality	Provides a measure how influences all other nodes $C_E(i) = \frac{1}{\lambda} \sum_j A_{ij} C_E(j)$, where A_{ij} is 1 if i interacts with j and 0 otherwise, and λ is a constant, in Bonacich (1987)	“ <i>igraph</i> ” package in R (Csardi and Nepusz 2006)
C	Connectance	Proportion of established interactions relative to all possible interactions (Jordano 1987), $C = \frac{L}{n_1 \cdot n_2}$ for bipartite networks, see more information in Delmas et al. (2017)	Spreadsheet, “ <i>bipartite</i> ” package in R (Dormann et al. 2008)

(continued)

Table 13.1 (continued)

Symbol	Network descriptors	Description	Software
LD_q	Linkage density	The average number of interactions per node in the web, $\text{LD}_q = \frac{1}{2} \left(\sum_{k=1}^{n_1} \frac{a_{\bullet k}}{a_{\bullet \bullet}} m_{n_1, k} + \sum_{k=1}^{n_2} \frac{a_{k \bullet}}{a_{\bullet \bullet}} m_{n_2, k} \right)$ in Bersier et al. (2002), and the weighted connectance is calculated as $\frac{\text{LD}_q}{S}$, where S is the total number of all possible interactions in the web	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
CC	Clustering coefficient	For each node i : $\text{CC}_i = \frac{2N_i}{k_i(k_i - 1)}$ where k_i is i 's degree and N_i is the total number of interactions between i 's neighbors and the average local clustering coefficient: $\text{CC}_1 = \frac{\sum_i^c i}{S}$, in Watts and Strogatz (1998)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
M_B	Modularity	For the entire graph: $\text{CC}_2 = \frac{3N_c}{N_c}$, where N_c is the number of triangles in graph G and N_c is the number of 3-nodes subgraphs, in Soffer and Vázquez (2005) and Saramäki et al. (2007)	MODULAR (Marquitti et al. 2014)
c_i	Among-module connectivity	$M_B = \sum_{m=1}^{N_m} \left[\frac{l_m}{I} - \left(\frac{d_m^A d_m^B}{I^2} \right) \right]$ where N_m is the number of modules in the network, I is the total number of links, l_m is the number of links between nodes in module m , and d_m^A and d_m^B are the sum of the links of all nodes in module s which belong to A-set and B-set, respectively, in Barber (2007) A measure of how connected node i is to all modules: $c_i = 1 - \sum_{s=1}^{N_M} \left(\frac{k_{is}}{k_i} \right)^2, c \in [0,1]$	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
Z_i	Inside-module connectivity	$Z_i = \frac{K_{is} - K_s}{SD_{ks}}$, for more details see Guimerà and Nunes Amaral (2005)	

T	Matrix temperature	$T=kU$, where $U = \frac{1}{m,n} \sum u_{ij}$, where $u_{ij} = \left(\frac{d_{ij}}{D_g} \right)^2$. $T=0^\circ$ is defined for maximum nestedness in Atmar and Patterson (1993)	ANINHADO (Guimarães and Guimarães 2006), Nestedness Temperature Calculator (NTC) (Atmar and Patterson 1995)
N	Nestedness (matrix temperature based)	$N = \frac{100 - T}{100}$; which values range from 0 to 1 (maximum nestedness)—See above about T (Matrix temperature)	ANINHADO (Guimarães and Guimarães 2006)
NODF	Nestedness metric based on overlap and decreasing fill	$NODF = \left[\frac{n_2(n_2-1)}{2} + \left[\frac{\sum_{i < j}^n M_{ij} + \sum_{i < j}^{n_1} M_{ij}}{2} \right] \right]$ <p>lower trophic level, the second sum is across all pairs of higher trophic level, n_2 and n_1 are the total number of lower and higher trophic level, respectively. $M_{ij} = 0$ if $k_i = k_j$ and $M_{ij} = \frac{n_j}{\min(k_i, k_j)}$ otherwise (Almeida-Neto et al. 2007).</p>	ANINHADO (Guimarães and Guimarães 2006), “ <i>bipartite</i> ” package in R (Dormann et al. 2008)
η	Nestedness without the rule of decreasing fill	$\eta^{(n_2)} = \frac{\sum_{i < j}^{n_2} n_{ij}^{(n_2)}}{\sum_{i < j} \min(n_i^{(n_2)}, n_j^{(n_2)})},$ here defined for lower trophic level set n_2 , in Bastolla et al. (2009)	Nestedness Temperature Calculator (NTC) (Atmar and Patterson 1995)
on	Contribution to nestedness	This metric is a z-score relative to null models: $cn_i = \left(\frac{N - N_i}{\sigma N_i} \right)$, where N is the observed nestedness (NODF) of the network, N_i is the average of nestedness when randomizing just the interactions of the species i , and σN_i is the standard deviation of nestedness when randomizing just the interactions of the species i ($n = 100$ randomizations). Positive values of cn_i indicate a higher contribution of species (i) to the nested structure (Saavedra et al. 2011)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)

(continued)

Table 13.1 (continued)

Symbol	Network descriptors	Description	Software
W	Web asymmetry	Balance between species richness of any two trophic levels, $W = \frac{n_2 - n_1}{n_1 + n_2}$; positive numbers indicate more lower-trophic level nodes; negative, more higher-trophic level species; rescaled to $[-1, 1]$ (Blithgen et al. 2007)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
AS	Mutual dependence asymmetry	$n_i S_j = \frac{ (b_{ij} - b_{ji}) }{\max(b_{ij}, b_{ji})}$; where $b_{ij} = \frac{a_{ij}}{n_i}$ and $b_{ji} = \frac{a_{ij}}{n_j}$ and b values are the proportion of interactions between two partners, a_{ij} , relative to the totals of each partner $(n_i)_i$, $(n_j)_j$	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
H_i, H_j	Diversity of interactions (Shannon interactions) per higher trophic level (i) or lower trophic level (j)	$H_i = - \sum_{j=1}^{n_i} \left(\frac{a_{ij}}{n_i} \cdot \ln \frac{a_{ij}}{n_i} \right)$ (Bascompte and Jordano 2013)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
E_S	Evenness (Shannon entropy) of interactions across the matrix	$E_S = \frac{- \sum_i \sum_j p_{ij} \ln p_{ij}}{\ln(n_1 n_2)}$ (Bascompte and Jordano 2013)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
G_{qv}	Generality, or mean number of links per any higher trophic level mutualist	$G_{qv} = \sum_{j=1}^{n_i} \frac{n_{ij}}{m} 2^{H_j}$, adapted from Bersier et al. (2002) by Bascompte and Jordano (2013)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
	Vulnerability, or mean number of links per any lower trophic level	Replace j by i and n_i by n_2 in the equation for G_{qv} (Bascompte and Jordano 2013)	

L_q	Weighted interaction density	$L_q = 0.5 \left(\sum_{j=1}^{n_1} \frac{n_{1j}}{m} 2^{H_j} + \sum_{i=1}^{n_2} \frac{n_{ii}}{m} 2^{H_i} \right)$ (Bascompte and Jordano 2013)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
H_2	Interaction diversity	Network-level measure of diversity of interactions. $H_2 = - \sum_{i=1}^i \sum_{j=1}^j \left(\frac{a_{ij}}{m} \cdot \ln \frac{a_{ij}}{m} \right)$ (Blüthgen et al. 2006)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
H'_2	Measure of realized Eltonian specialization	A standardized H_2 to account for the total number of records each node has (A_i, A_j), (Blüthgen et al. 2006; Devictor et al. 2010)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008) or in: http://rxc.sys-bio.net/ by Blüthgen and Blüthgen
d'	Species-level measure of specificity	$d' = \frac{(d_i - d_{\min})}{d_{\max} - d_{\min}}$, where $d_i = \sum_{j=1}^c \left(p_{ij}' \ln \frac{p_{ij}'}{q_j} \right)$ with c the number of resources, p_{ij}' the proportion of interactions divided by the sum of performances of node i , and q_j the sum of interactions of resource j divided by the total number of interactions in the matrix (Blüthgen et al. 2006, 2007)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
AS'	Scaled mutual dependence asymmetry	Provides the average difference in the interaction strengths of partners: $nS'_{ij} = \frac{\sum(b_{ij}' - b_{ji}')}{k_i}$, where k_i is the number of interactions for species i , and b_{ij}' and b_{ji}' are scaled interaction-strength values (Bascompte and Jordano 2013)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)
C_{score}	C-score	Represents the average number of checkerboard units for each unique species pair. For M species, there are $P = \frac{M(M-1)}{2}$ species-pairs, and hence $C_{score} = \sum \sum_{i < j} \frac{C_{scoreij}}{P}$ (Stone and Roberts 1990)	“ <i>bipartite</i> ” package in R (Dormann et al. 2008)

(continued)

Table 13.1 (continued)

Symbol	Network descriptors	Description	Software
B_w	Network dissimilarity	$B_w = T - C_s^T (T-1) - 1$, when $C_s^T = \frac{T}{T-1} \left(1 - \frac{S_f}{\sum_i n_i} \right)$, in which T is sites and S_f is the number of interactions and n is local richness, for more details see Poisot et al. (2012)	“betalink” package in R (Poisot 2016)
B_{ww}	Additive partition of the beta diversity of interactions	$\beta_{ww} = \beta_{sr} + \beta_{os}$, i.e., the additive partition of the beta diversity of interactions, since β_{sr} (species turnover) and β_{os} (interaction rewiring) are a subset of β_{ww} (whittaker beta diversity of networks). Then $\beta_w = \frac{a+b+c}{(2a+b+c)/2} - 1$, where b is the number of unique species of the first network, c is the number of unique species of the second network, and a is the number of shared species between networks.	
G_c	Network core-peripheral	$G_c = \frac{(K_i - K_{mean})}{\sigma K_i} k_i$ = mean number of links for higher or lower trophic level in a network, k_{mean} = mean number of links for all higher or lower trophic level in a network, and σ_k = standard deviation of the number of links for all higher or lower trophic level in a network. Species with $G_c > 1$ are the node with more interactions in relation to others in the same trophic level, namely the central core of highly node of the network (Dátillo et al. 2013)	“Network Descriptors” to name, a brief description appears in “Description” and when applicable “Software” refers to the most common to use although others can do the same analysis. See below Table 13.2 for more details about “Software.” Higher trophic level, e.g., refers to animals and lower trophic levels to plants, but it can be <i>parasitoid</i> , <i>inquiline</i> , <i>predator</i> , <i>prey</i> , etc. Hereafter, we chose to use n_1 to the higher trophic level (e.g., A) and n_2 to lower trophic level (e.g., P) because then, we are not being restricted. For more details about network analysis, see Bersier et al. (2002), Bascompte and Jordano (2007), Dornmann et al. (2008), Ulrich et al. (2009), Vázquez et al. (2009), Rayfield et al. (2011), Bascompte and Jordano (2013), Dátillo et al. (2016) and Delmas et al. (2017)

Table 13.2 Some useful software for network analysis and draw graphs

Software		Brief description	Source
ANINHADO		Provides calculation of NODF and Temperature, commonly used measures of nestedness (Guimarães and Guimarães 2006)	https://www.guimaraes.bio.br/soft.html
Cytoscape		Useful for visualizing networks and allows to implement these with attribute data. This is an open source software (Shannon et al. 2003)	http://www.cytoscape.org/
Gephi		Affords to visualizing and nice exploration for networks. This is an open-source and free software (Bastian et al. 2009)	https://gephi.org/
MODULAR		Calculates the modularity in networks using two different modularity metrics and also includes two null models (Marquitti et al. 2014)	http://sourceforge.net/projects/programmodular/
Pajek		It is a profitable program for analyzing network using various metrics, as well as offering good drawing tools (Batagelj and Mrvar 1998)	http://mrvar.fdv.uni-lj.si/pajek/
R software	“ <i>betalink</i> ” package	Calculates the beta-diversity of interactions, besides providing visualization of the networks (Poisot 2016)	https://CRAN.R-project.org/package=betalink
	“ <i>bipartite</i> ” package	Provides helpful tools for visualizing webs and to calculates the most used indices in network ecology (Dormann et al. 2008)	https://CRAN.R-project.org/package=bipartite
	“ <i>foodweb</i> ” package	Measures of food web network structure besides tools for visualizing graphs (Perdomo et al. 2012)	https://CRAN.R-project.org/package=foodweb

(continued)

Software		Brief description	Source
	“igraph” package	Provides a good networks analysis and graphs visualization, besides calculates commonly used indices (Csardi and Nepusz 2006)	https://CRAN.R-project.org/package=igraph , http://igraph.org/
	“mangal” package	Offers tools to manage data on ecological interactions (Poisot et al. 2016)	http://mangal.io/
	“network” package	Allows to edit network objects (Butts et al. 2008)	https://CRAN.R-project.org/package=network
	“statnet” package	Allows to perform network data, be the representation, visualization, analysis and simulation, (Handcock et al. 2008)	https://CRAN.R-project.org/package=statnet
	“econullnetr” package	Useful to detects resource preferences by ecological networks analysis using null models (Vaughan et al. 2017)	https://CRAN.R-project.org/package=econullnetr

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