

## 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 (Dáttilo 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 Wedekin 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 (Thébault 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 (Thébault and Fontaine 2010) and inter-specific 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 (Dáttilo 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).

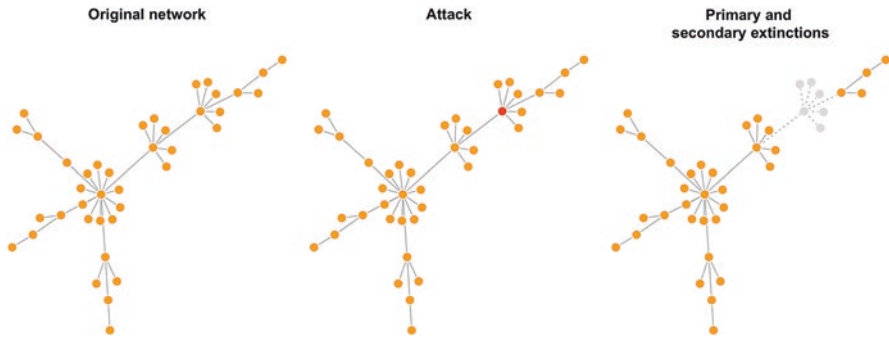
#### Box 4.1 Stability Analysis

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>	$M = \begin{bmatrix} f_1(x_1, \dots, x_n) \\ \vdots \\ f_m(x_1, \dots, x_n) \end{bmatrix}$
<i>Jacobian matrix</i>	$J_M = \begin{bmatrix} \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_n} \end{bmatrix}$
<i>Community matrix</i>	$J_M _{\bar{x}^*} = \begin{bmatrix} \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_1(x_1, \dots, x_n)}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_1} & \dots & \frac{\partial f_m(x_1, \dots, x_n)}{\partial x_n} \end{bmatrix}_{\bar{x}^*}$

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.

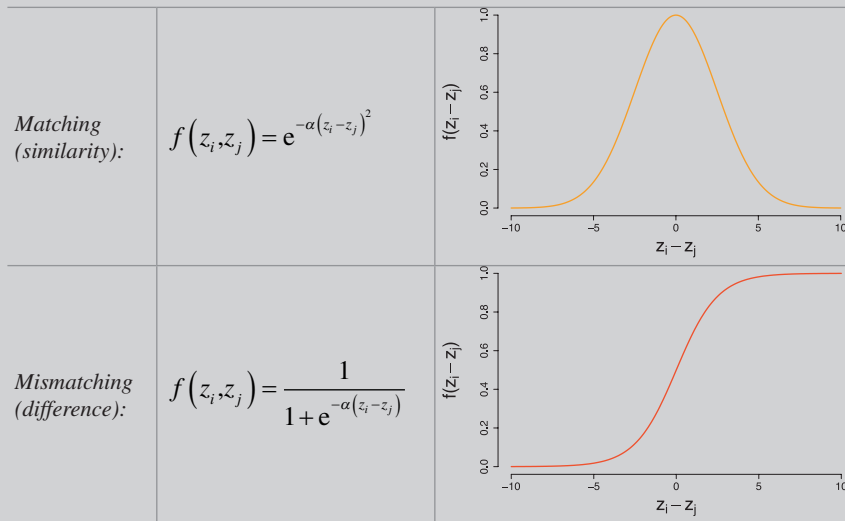
### 4.3 Evolutionary Dynamics

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,  $\alpha$  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  $\theta_i$  is the optimum trait favored by the abiotic environment and  $\gamma_i$  modulates the sensitivity of such abiotic optimum (Nuismer et al. 2010). Using quantitative genetic approaches, we may express how the trait changes ( $\Delta z_i$ ) 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).

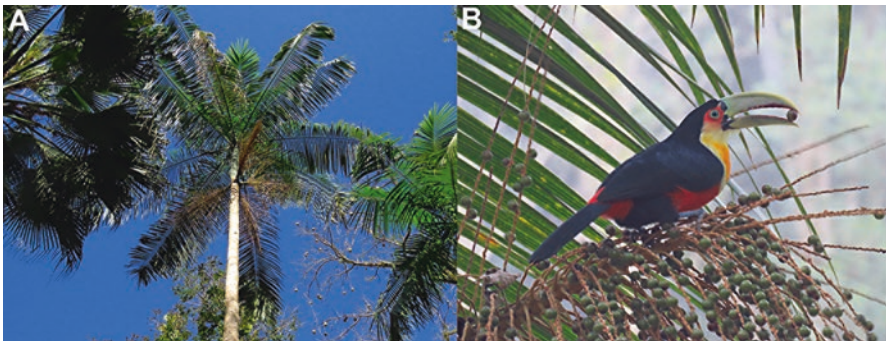
Eco-evolutionary feedbacks that lead to the stability of traits and population densities are known as cryptic eco-evolutionary dynamics (Kinnison et al. 2015). Such cryptic dynamics may explain why species-rich communities are more resilient to perturbations (Strauss 2014). The dynamical outcomes of 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; Dáttilo 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; Dáttilo 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 (Barracough 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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