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Different tolerances of symbiotic and nonsymbiotic ant-plant networks to species extinctions

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Abstract

The knowledge of the mechanisms that shape biodiversity–stability relationships is essential to understand ecological and evolutionary dynamics of interacting species. However, most studies focus only on species loss and ignore the loss of interactions. In this study, I evaluated the topological structure of two different ant-plant networks: symbiotic (ants and myrmecophytes) and nonsymbiotic (ants and plants with extrafloral nectaries). Moreover, I also evaluated in both networks the tolerance to plant and ant species extinction using a new approach. For this, I used models based on simulations of cumulative removals of species from the network at random. Both networks were fundamentally different in the interaction and extinction patterns. The symbiotic network was more specialized and less robust to species extinction. On the other hand, the nonsymbiotic network tends to be functionally redundant and more robust to species extinction. The difference for food resource utilization and ant nesting in both ant-plant interactions can explain the observed pattern. In short, I contributed in this manner to our understanding of the biodiversity maintenance and coevolutionary processes in facultative and obligate mutualisms.

Keywords mutualistic interactions; ecological networks; robustness; loss species; modularity.

1 Introduction

One of the central goals in biological conservation is to understand how different ecological mechanisms shape biodiversity (Van Jaarsveld et al., 1998; Loreau et al., 2001; Groom et al., 2006). The recent increases in species extinction rates have increased the researcher's interest as to how these losses may affect ecosystems functioning and help us in management actions towards species and ecosystem conservation (Casey and Myers, 1998; Berglind, 2000; Stuart et al., 2004; Jones et al., 2007). However, most studies have focused only on species loss and ignore loss of species interactions (Janzen, 1974; Memmott et al., 2007; Dyer, 2010; Blüthgen, 2012). Ecological interactions have an important role in the structure and stability of populations and communities over space-time (Janzen, 1974; Burslem et al., 2005; Del-Claro and Torezan-Silingardi, 2009; Dyer et al., 2010; Dormann, 2011; Nedorezov, 2011; Zhang, 2011; Elsadany, 2012; Zhang, 2012a, 2012b). Thus, understanding how and why these loss of species interactions occur is important for our current knowledge about the ecological dynamics of interacting species (Wilmers, 2007; Kaiser-Bunbury et al., 2010; Pocock et al., 2012).

Ecological interactions are increasingly at risk from local and global extinction as a consequence of disturbances caused by human activities, including habitat loss, altered land use, introduction of alien species

and climate change (Kearns et al., 1998; Biesmeijer et al., 2006; Zhang et al., 2006; Sayadi and Sayyed, 2011; Zhang and Chen, 2011; Zhang and Liu, 2012; Zhang and Wu, 2012; Zhang and Zhang, 2012). Recently, studies about ecological networks have provided important insights into mechanisms that contribute to the stability and structural organization of species interactions at community level (Medan et al., 2007; Morales and Vázquez, 2008; Nielsen and Bascompte, 2007; Rezende et al., 2007; Stang et al., 2007; Vázquez et al., 2007, 2009; Zhang, 2011; Zhang, 2012a). In mutualistic networks, the extinction of one of the interaction partners can lead to coextinction of the other partner, and it has important consequences for ecological system dynamics (Wilson, 1992; Solé and Montoya, 2001; Dunne et al., 2002; Memmott et al., 2004; Dorman, 2011; Blüthgen, 2012). The extinction risk of an organism depends on the number of interactive partners, as organisms with higher number of partners are more robust to extinction (Ashworth et al., 2004; Memmott et al., 2004). Moreover, the specialization level of the organism also influences the whole ecological and evolutionary dynamics of the system (Ashworth et al., 2004; Memmott et al., 2004; Vázquez and Simberloff, 2002; Stang, 2007). A specialist interacting with a generalist is less prone to extinction (Melian and Bascompte, 2002; Memmott et al., 2004), and the loss of specialized interactions can destabilize the system (Bascompte et al., 2005; Bascompte et al., 2006; May, 1973; McCann et al., 1998; Kokkoris et al., 1999; Neutel et al., 2002).

A good system in which to study questions about coextinction in mutualistic networks is the ant-plant mutualism. Ants and plants can interact positively in different ways, from facultative to highly specialized relationships (Rico-Gray and Oliveira, 2007; Dáttilo et al., 2009a). In this paper, I used as a model the symbiotic and nonsymbiotic ant-plant interactions to study the loss of interactions on mutualistic networks. In both kinds of interactions ants defend the plants against potential herbivores (Vasconcelos, 1991; Del-Claro et al., 1996; Oliveira et al., 1999; Rico-Gray and Oliveira, 2007). In symbiotic ant-plant interactions, plants known as myrmecophytes provide nesting sites in cavities called domatia, and, often food to their resident ant colonies (Benson, 1985; Mckey and Davidson, 1993; Leroy et al., 2008). On the other hand, in nonsymbiotic ant-plant interactions, plants produce nutritious liquid in their extrafloral nectaries for ants (Baker et al., 1978; Rico-Gray and Oliveira, 2007). In this case, as the resource offered by plants is seasonal over space-time, the ants do not have "fidelity" of foraging on the same plant, and therefore the interactions tend to be less specialized (Rico-Gray et al., 1998; Díaz-Castelazo et al., 2004; Schoereder et al., 2010). In contrast to nonsymbiotic ant-plant interactions that have a variety of interchangeable partners, both myrmecophyte and ants are highly specialized, involving only one or a few partners (Benson, 1985; Blüthgen et al., 2007; Guimarães et al., 2007). In some cases, the specialization degree between ants and myrmecophytes is so high, that ant queens use volatile cues to discriminate their host-plants from nonmyrmecophytic species at the time of colonization (Edwards et al., 2006; Dáttilo et al., 2009b).

Here, I hypothesize that although the interaction between ants and myrmecophytes is extremely specialized and compartmentalized (Benson, 1985; Fonseca and Ganade, 1996; Guimarães et al., 2007), the symbiotic ant-plant networks are more vulnerable to species extinction compared to nonsymbiotic ant-plant networks. Moreover, I expected that the difference in natural history of symbiotic and nonsymbiotic ant-plant interactions could generate differences in the topological structure of both networks. In order to test my hypothesis, I used databases from literature about the frequency of interactions of symbiotic and nonsymbiotic ant-plant networks in two tropical rainforests.

2 Material and Methods

2.1 Datasets

In literature, there are few ecological datasets about ant-plant interactions based on the frequency of partner interactions (quantitative data). Because of this, I only used two datasets in this study from literature of

symbiotic and nonsymbiotic ant-plant networks. The symbiotic study of ant-plant interactions was carried out by Davidson et al. (1989) from September through November in 1985 and 1986 in the Amazon tropical rainforest at the Parque Nacional Manu, Madre de Dios, Peru (11°52' S, 71°22' W). The authors walked 4.800 m of trails and recorded the occurrence of different ant species in all myrmecophyte individuals found. The nonsymbiotic study was carried out by Blüthgen et al. (2004) between September 1999 and May 2002 in the rainforest at the Australian Canopy Crane in Cape Tribulation, Far North Queensland, Australia (16°07' S, 145°27' E), including patches of open secondary forest. The authors collected ants consuming nectar in extrafloral nectaries during the day and night. Observed plants were haphazardly selected and irregularly distributed throughout the forest.

2.2 Network topology

In order to describe the network topology of both nonsymbiotic and symbiotic ant-plant networks, I calculated the following metrics: links per species, network specialization, modularity and nestedness. I calculated the level of specialization networks using the specialization index (H_2') [ranges from zero (extreme generalization) to one (extreme specialization)]. This index is mathematically derived from the Shannon entropy, and it is based on the deviation from the expected probability distribution of the interactions (Blüthgen et al., 2006). The index is robust to changes in sampling intensity and the number of interacting species (see more details about this index in Blüthgen et al., 2006, 2007). The bipartite graphs and all metrics were made in bipartite package (Dormann et al., 2009) using the R-Project software version 2.15.0 (R Development Core Team, 2005).

I calculated the modularity of both networks using the modularity index M (range 0-1). This index estimates the degree at which groups of species (ants and plants) interact more among each other than with species in other groups in the network (Newman and Girvan, 2004). High values of M indicate that the ants and plants form modules that are semi-independent of other interactions within the network (Olesen et al., 2007). I tested the significance of index M for each network through 1000 simulated networks generated by Null Model II (Bascompte et al., 2003), in order to assess whether the value of M observed in the empirical network is higher than expected for networks of equal size and with similar heterogeneity in interactions among species. In this null model, the probability of an interaction occurring is proportional to the level of generalization (degree) of plant and ant species (Bascompte et al., 2003). I made the null model network through a routine in MATLAB, and I calculated the M using the software Netcarto (Guimerà and Amaral, 2005). Although this index is used for bipartite network, my null models control any potential effects of bipartite structure on modularity (Pires et al., 2011).

I also used the *NODF* index (Nestedness metric based on Overlap and Decreasing Fill) to estimate the nestedness value of networks, using ANINHADO software (Guimarães and Guimarães, 2006). This metric is a much better nestedness metric than others and less prone to type-I statistical error, since it is based on the nestedness of all pairs of columns and rows in the matrix (Almeida-Neto et al., 2008). To assess if the nestedness value observed was higher than expected by random interaction patterns, I tested the nestedness of each network with 1000 networks generated by Null Model II.

2.3 Robustness to extinctions

I calculated the robustness of symbiotic and nonsymbiotic ant-plant networks to species extinction in both trophic levels (plants and ants) based on cumulative removals of species from the network at random (Burgos et al., 2007). Initially, I removed one species from one trophic level (e.g. ants), and when species from the other trophic level (e.g. plants) were connected only to the initial removed species, they were also removed from the network, indicating secondary losses. Afterwards, I was removing randomly all remaining species until all species from the trophic level chosen were removed (Mello et al., 2011). For more information about

this procedure, please see Dormann et al. (2009). Moreover, I calculated the area under the extinction curve (R) proposed by Burgos et al. (2007) to measure the robustness of networks, where $R= 1$ corresponds to a very slow decrease in the curve until the point at which almost all species of one trophic level are eliminated (more robust network), and $R= 0$ corresponds to a very fast decrease in the curve as soon as any species is lost (less robust network). I ran 100 randomizations for each network to simulate the species removals. I chose the R index because it is more robust and it is not sensitive to the shape of the curve when compared to the index proposed by Memmott et al. (2004), called Attack Tolerance Curve (ATC).

3 Results

Both networks studied here had different numbers of interacting species. The symbiotic network had 8 plant species and 18 ant species, while the nonsymbiotic network had 51 plant species and 41 ant species (see Fig. 1A-B). The nonsymbiotic network also had approximately four times more links per species (3.097) than the symbiotic network (0.807). Additionally, nestedness was higher in the nonsymbiotic network ($NODF= 22.11$) than in the symbiotic network ($NODF= 15.96$). Nonsymbiotic networks exhibited a significantly nested topology ($P= 0.01$). However, the nestedness value observed in symbiotic network was more equal than expected by random patterns of interaction ($P= 0.999$).

Symbiotic ant-plant network was more specialized ($H_2'= 0.926$) than the nonsymbiotic network ($H_2'= 0.193$). In both networks, I did not observe significantly higher modularity than expected by the heterogeneity of interactions (Nonsymbiotic: $P= 0.999$; Symbiotic: $P= 0.151$). However, there was lower modularity in the nonsymbiotic network ($M= 0.302$) than in the symbiotic network ($M= 0.763$).

The robustness to cumulative extinctions had different patterns in nonsymbiotic and symbiotic ant-plant networks (see Fig. 2). The simulations of cumulative removals of species showed that the nonsymbiotic network is very robust for both removals of plant and ants than the symbiotic network, since their extinction curves declined more slowly. The robustness of the nonsymbiotic network was relatively high, both for plants ($R= 0.680$) and ants ($R= 0.773$) (see Fig. 2A-B). However, in the symbiotic network, the robustness was low both for plants ($R= 0.449$) and ants ($R= 0.446$) (see Fig. 2C-D).

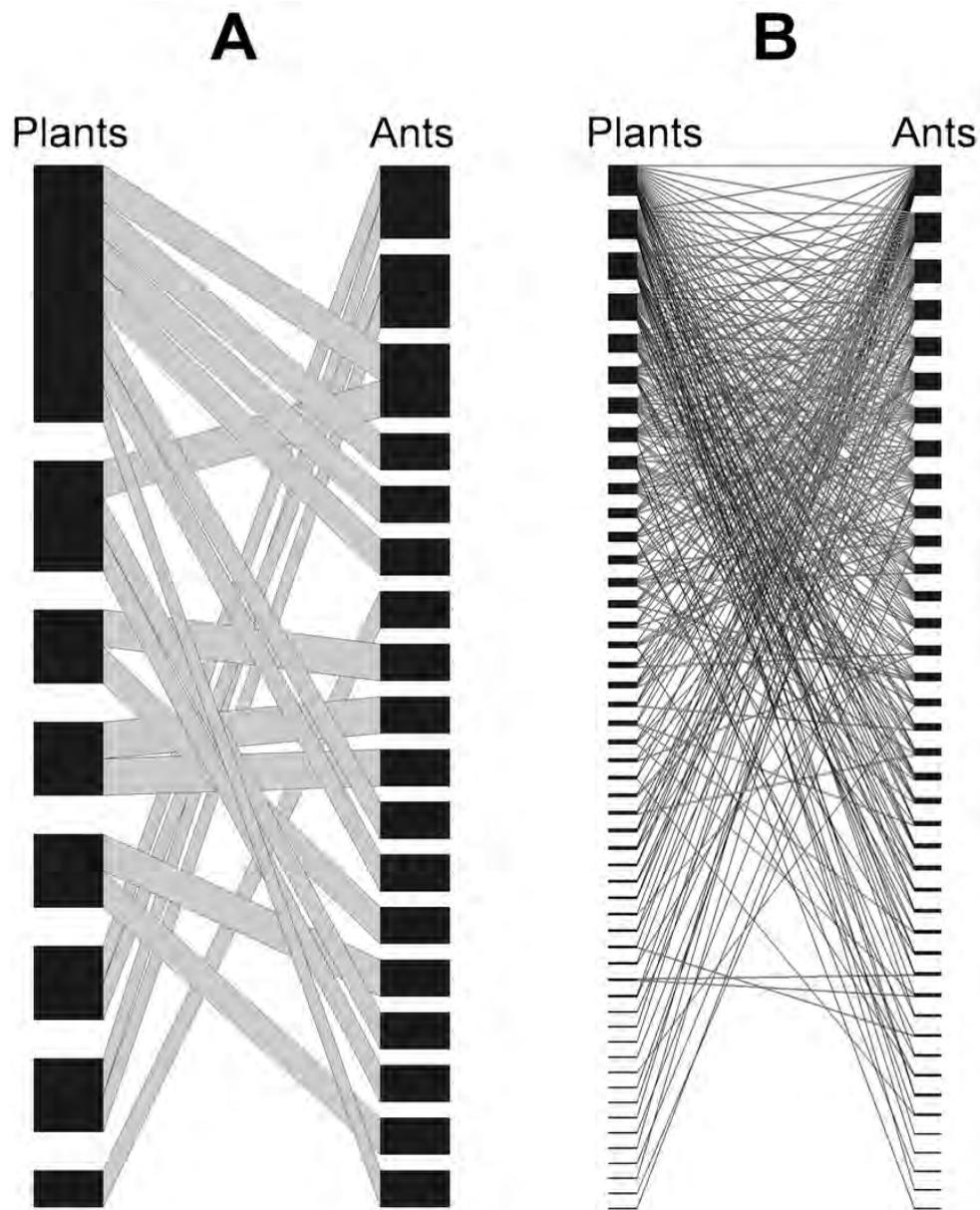


Fig. 1 Bipartite graphs of (A) symbiotic and (B) nonsymbiotic ant-plant networks. Symbiotic network represents mutualistic interaction between ants and myrmecophytes plants (database: Davidson et al., 1989). Nonsymbiotic network represents the mutualistic interactions between ants and plants with floral and extrafloral nectaries (database: Blüthgen et al., 2004). The nodes on the left represent different plant species, and the nodes on the right correspond to ant species that interact positively with the plants. Lines, also called "links", connect positively interacting species.

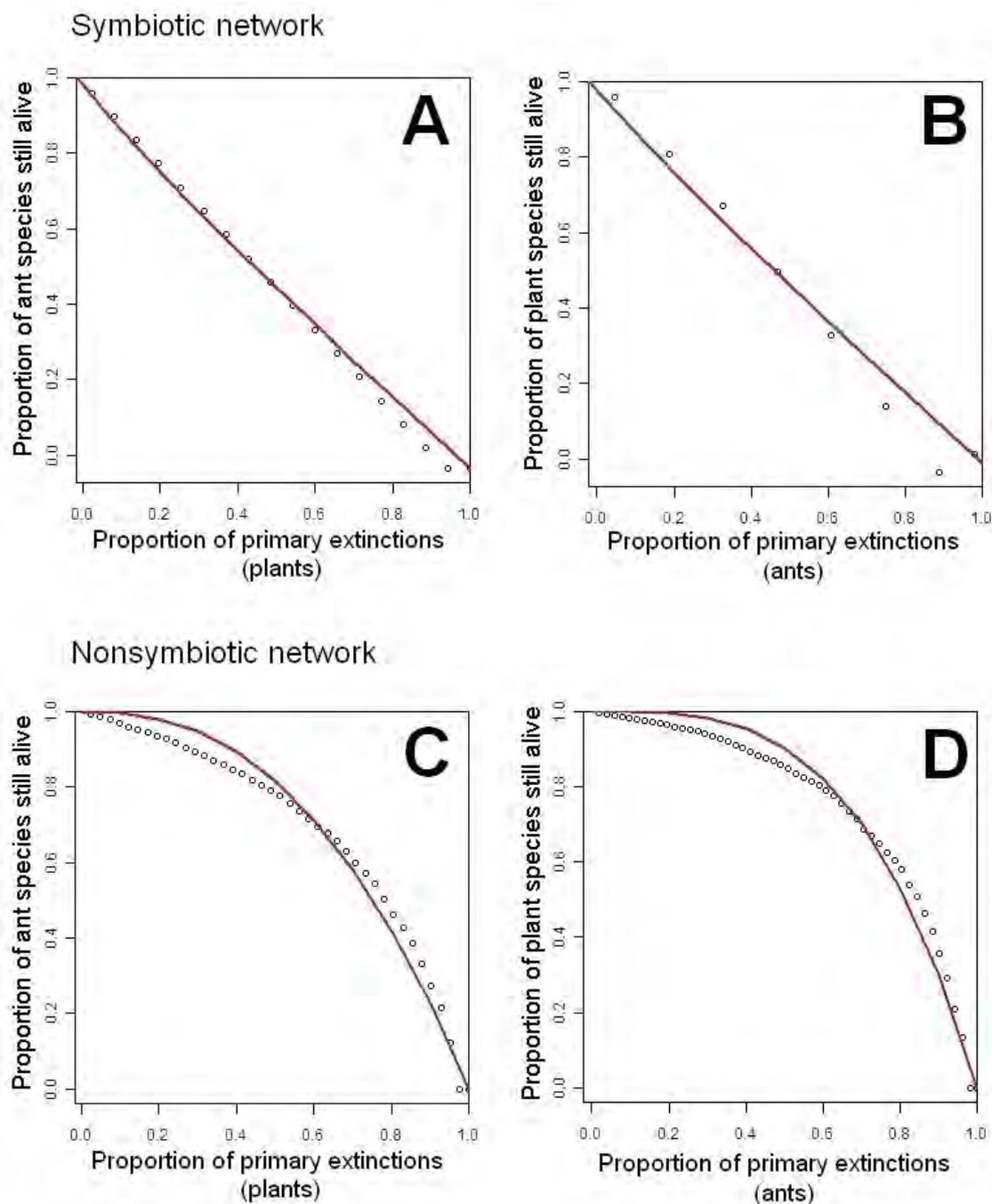


Fig. 2 Robustness to cumulative species removal of (A) plants and (B) ants in symbiotic network (database: Davidson et al., 1989), and (C) plants and (D) ants in nonsymbiotic network (database: Blüthgen et al., 2004).

4 Discussion

Currently, thousands of species become extinct each year and the role of most of these species in their ecosystems will hardly ever be understood (Röckstrom et al., 2009; Lee and Jetz, 2011; Wilson et al., 2011). In megadiversity regions (i.e., tropical forests) many species depend on one another during their ontogeny and the loss of one partner can lead to coextinctions, which represents the irreplaceable loss of evolutionary history of species interacting (Boucher et al., 1982; Stachowicz, 2001; Tillberg and Breed, 2004). Here, I showed that symbiotic networks are less robust for both ants and plants species extinction compared to nonsymbiotic networks. They can generate different influences on the ecological and evolutionary dynamics of ant-plant

interaction. Moreover, I also showed the topology structure of symbiotic and nonsymbiotic ant-plant networks differ fundamentally in the interactions pattern in tropical forests.

Symbiotic network showed a high level of specialization and modularity. These results corroborate with previous studies where the authors showed that symbiotic ant-plant networks are formed by isolated groups of species (Fonseca and Ganade, 1996; Blüthgen et al., 2007; Guimarães et al., 2007). However, the results demonstrated that there was low specialization and modularity in nonsymbiotic networks. The difference in specialization and modularity of these networks is possibly due to difference in the intimacy degree of ant-plant interactions. In symbiotic ant-plant interactions, the ants obligatory inhabit myrmecophytes, and during their ontogeny the number of overlapping partners is practically non-existent (Benson, 1985; Fonseca and Ganade, 1996; Heil and McKey, 2003). In nonsymbiotic interactions nectar is a seasonal resource (Rico-Gray et al., 1998; Díaz-Castelazo et al., 2004; Blüthgen et al., 2007; Schoereder et al., 2010). Thus, when a plant does not secrete nectar, the ants can use other resources available on foliage. Therefore, this kind of ant-plant interaction is less specialized and facultative (Schoereder et al., 2010). The ant's ability to change of a nectar possibly occurs because the physiological and nutritional requirements of ants that feed on EFNs are very similar (Blüthgen et al., 2007).

In my results, even where the nestedness was not significant in symbiotic network, the nonsymbiotic network was more nested. It is known that nonsymbiotic ant-plant networks are a lot more nested than symbiotic network, and only 15.38 % of the symbiotic network was significantly nested. (Guimarães et al., 2007). Moreover, according to Bastolla et al. (2009) the nested pattern in mutualistic networks reduces interspecific competition enhancing the number of coexisting species. Thus, as the nonsymbiotic network is more nested than the symbiotic network it is expected that the nested pattern of nonsymbiotic networks could also be generated by the low level of specialization of ant-plant interaction.

Several studies have showed the role of functional redundancy on the stability of ecological communities (Walker, 1992; Rosenfeld, 2002; Petchey et al., 2007; Joner et al., 2011). Based on the insurance hypothesis (Yachi and Loreau, 1999), systems with high functional redundancy are more resilient to disturbances (Walker, 1995; Naeem, 1998; Fonseca and Ganade, 2001). This is because different species perform similar roles in ecosystem function, and when a species is extinct other species "dampens" the system (Lawton and Brown, 1993; Rosenfeld, 2002; Mouchet et al., 2010). Here, due to high generalization of the nonsymbiotic network, it is expected that these networks are functionally redundant, because there is low specificity in this interaction. So, when I remove species from nonsymbiotic networks, the extinction curves declined more slowly compared with symbiotic networks, because the deletion of one species does not necessarily cause the deletion of other partner species. Biologically, arboreal ants do not depend exclusively on the food offered by a particular plant species and also supplement their diet with insect exudates (honeydew) (Davidson et al., 2004). Moreover, in tropical regions many honeydew tend to be more productive and spatially more concentrated when compared with extrafloral nectaries (Blüthgen et al., 2004b). Thus, when a plant species with extrafloral nectaries is extinct, the ants can substituted this resource by other liquid resources commonly found in tropical environments. On the other hand, due to the high specialization of partners in ant-plant symbiotic interactions, the change of traits or exclusion of one partner directly affects the ecological maintenance of the other partner (Guimarães et al., 2007). In addition, even using only one network for each ant-plant interaction, I believe that, the pattern found in this study will be repeated in other networks with the same differences in natural history, with more specialized ecological networks being more susceptible to species losses.

Here, I showed that specialized ant-plant interactions are highly susceptible to loss of species and this pattern should occur in other plant-animal networks with a high degree of specialization. Thus, the loss of very specialized interactions can lead to a cascade effect of loss of other species and all ecological services provided

by them. In addition, the resilience of biological communities is not based only on high functional redundancy but also on how functionally similar species respond to environmental disturbance (Elmqvist et al., 2003; Folke, 2006; Nyström, 2006; Laliberte et al., 2010). Thus, I suggest as a topic for future studies that one evaluates response diversity in different ant-plant mutualistic networks after disturbances in order to assess whether different tolerance also occurs for these networks as regards species extinction in natural environments.

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D'Áttilo W (2012) Different tolerances of symbiotic and nonsymbiotic ant-plant networks to species extinctions. *Netw Biol* 2:127â€“138CrossRefGoogle Scholar. D'Áttilo W, Dyer L (2014) Canopy openness enhances diversity of antâ€“plant interactions in the Brazilian Amazon rain forest. *Biotropica* 46:712â€“719CrossRefGoogle Scholar. D'Áttilo W, Rico-Gray V, Rodrigues DJ, Izzo TJ (2013a) Soil and vegetation features determine the nested pattern of ant-plant networks in a tropical rainforest. *Ecol Entomol* 38:374â€“380CrossRefGoogle Scholar. D'Áttilo W, Izzo TJ, Vasconcelos HL, Rico-Gray V (2013b) Strength of the modular In this study, I evaluated the topological structure of two different ant-plant networks: symbiotic (ants and myrmecophytes) and nonsymbiotic (ants and plants with extrafloral nectaries). Moreover, I also evaluated in both networks the tolerance to plant and ant species extinction using a new approach. For this, I used models based on simulations of cumulative removals of species from the network at random. Both networks were fundamentally different in the interaction and extinction patterns. The symbiotic network was more specialized and less robust to species extinction. On the other hand, Mutualism is a symbiotic relationship in which both species benefit. An example of mutualism involves goby fish and shrimp (see Figure below). The nearly blind shrimp and the fish spend most of their time together. The shrimp maintains a burrow in the sand in which both the fish and shrimp live. When a predator comes near, the fish touches the shrimp with its tail as a warning. Then, both fish and shrimp retreat to the burrow until the predator is gone. From their relationship, the shrimp gets a warning of approaching danger. The fish gets a safe retreat and a place to lay its eggs. [Figure 2 Microbial endophytes are present in all known plant species. The ability to enter and thrive in the plant tissues makes endophytes unique, showing multidimensional interactions within the host plant. Several vital activities of the host plant are known to be influenced by the presence of endophytes. They can promote plant growth, elicit defense response against pathogen attack, and can act as remediators of abiotic stresses. To date, most of the research has been done assuming that the interaction of endophytes with the host plant is similar to the plant growth-promoting (PGP) microbes present