Article

Robustness of plant-plant networks with different levels of habitat modification and interaction intimacy

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Abstract

Anthropogenic modification of natural environments is the main causes of species extinction in the globe, which directly leads to loss of interspecific links and modifies the structure of ecological networks. The objective of present study is to evaluate the effect of human-induced habitat modification on the connectivity and robustness of ecological interaction networks composed by plant-epiphyte and plant-parasite interactions. In total were analyzed eight distinct binary networks of plant-plant interactions in Brazil, being three epiphyte networks and five parasite networks occurring both in conserved and anthropized habitats. The results show that the human-induced habitat modification influences the connectance of plant-plant networks, since networks of anthropized habitats had greater connectance than the networks of conserved habitats. In addition, the results showed higher values of robustness in the plant-parasite networks when compared to plant-epiphyte networks, and these differences were mainly observed in anthropized habitats. This study presented a new approach for studies of plant-plant ecological interactions, because is the first to compare the effect of human-induced habitat modification on the plant-plant network robustness.

Keywords Brazil; coextinctions; ecological networks; habitat loss; Neotropical interactions.

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1 Introduction

Anthropogenic habitat modification is the main causes of species extinction in the globe (Smart et al., 2006), which directly affects the loss of interspecific links, disrupting ecological networks and compromising the functioning of ecosystems (Tylianakis et al., 2010). Plants are the organisms more frequently studied concerning to ecological interaction networks in terrestrial ecosystems. There are a very large bibliography about the effects of habitat disturbance on networks involving plant-animal interactions (review in Hagen et al., 2012), but there are still relatively few studies focused on plant-plant interactions. In this sense, an issue unexplored is how plant-plant networks are affected by human-induced habitat modification.

There is a relative consensus that human-induced habitat modification has negative consequences on native plant species richness (Ellis et al., 2012). These negative effects are directly linked to deforestation of natural vegetation cover and to colonization with exotic plant species (Didham et al., 2007). Thereby, habitat-specialized native plant species tend to be more vulnerable to habitat degradation and exotic competition than generalist native plants. In this sense, while natural habitats are composed exclusively by native plant species (including a great proportion of specialized species), anthropized habitats tend to be dominated by generalist native plant species and exotic plant species. Because the generalist and exotic plants tend to have many connections in the network, it is expected that networks of anthropogenic habitats be more connected and robust than networks of natural habitats.

Ecological interactions between plant species can vary from antagonistic (e.g., interactions between host-plants and parasite plants) to comensalistic interactions (e.g., interactions between host-plants and epiphyte plants) (Montesinos, 2015). The level of intimacy of interaction and degree of biological association between partners can influence the structure and dynamic of interactions within a network (Pires and Guimarães Jr, 2013). For example, the parasite life-form lead the plants to have some level of specialization in the use of host-plants, because they are intimate linked to their host-plants. Parasite plants can be hemiparasites (partially parasitic), presenting leaves for photosynthesis and also absorbing nutrients from the host-plant through its haustoria, or holoparasites (totally parasitic) use exclusively the host resources (Thompson, 1994; Norton and Lange, 1999). All these two types of parasites depend on their hosts and therefore, extinction of host species can lead to loss from parasitic species (i.e., secondary extinctions). On the other hand, epiphyte plant species live on host-plants as inquilines in a commensalistic way, without parasitism (Silva et al., 2010). Therefore, plant-epiphyte communities tend to have more occasional links between the plants, resulting in networks with high connectivity and nestedness (Burns, 2007). Since specialized plant species are more prone to local extinction due to the habitat modification (Didham et al., 2007), plant-parasite networks are expected to have lower levels of connectivity and robustness to secondary extinctions than plant-epiphyte networks.

The objective of present study is to evaluate the effect of habitat modification on the structure and robustness of plant-plant networks with distinct levels of ecological association (plant-epiphyte versus plant-parasite interactions). To describe the plant-plant networks were used the connectance and the network robustness to secondary extinctions. Given the biological homogenization and dominance of generalist plants in human-modified habitats, it is tested the hypothesis that plant-plant interaction networks in anthropic habitats have higher connectance and robustness than networks of conserved habitats. Moreover, since plant-parasite links lead to more intimate interactions between host- and hosted-plants than commensalistic links, it is expected to find a lower level of connectance and robustness in plant-parasite networks.

2 Material and Methods

2.1 Network compilation

Plant-plant interaction networks were compiled from data available in the Google Scholar data base (<https://scholar.google.com.br/>). The search was focused on studies investigating the association between epiphytes (e.g., orchids, bromeliads, etc.) or parasites (e.g., mistletoes) and their host-plants at local level. In order to allow network structure analysis, were used only studies that listed the plant species involving in the interactions and were composed by at least three host-plant species and three hosted plant species (epiphytes or parasites). In total were compiled eight distinct binary networks of plant-plant interactions, being three epiphyte networks and five parasite networks (Table 1; Fig. 1).Networks were characterized concerning the habitat conservation status in “conserved habitats” (i.e., habitats characterized by natural vegetation with little or no anthropic effect, such as primary forest) and “anthropized habitats”(i.e., habitat with secondary or planted vegetation under strong anthropic influence, such as urban gardens) according the original description of authors.

Table 1 Networks of parasite and epiphyte interactions compiled from literature data for Brazil. Legend: S_{host} = richness of host-plant species; S_{hosted} = richness of hosted plant species (epiphytes or parasites); S_{total} = total species richness; C = connectance (pure value).

Network	Habitat conservation status	Network type	S_{host}	S_{hosted}	S_{total}	C	Latitude
Azevedo (2010)	Anthropized	Epiphyte	3	14	17	0.548	-23.067
Fontoura et al. (2009)	Conserved	Epiphyte	35	20	55	0.141	-22.783
Leal et al. (2006)	Anthropized	Parasite	6	3	9	0.722	-25.430
Moura et al. (2009)	Anthropized	Parasite	26	4	30	0.413	-8.054
Pereira (2014) – net 1	Conserved	Parasite	11	13	24	0.154	-2.751
Pereira (2014) – net 2	Conserved	Parasite	15	10	25	0.200	-2.751
Rotta (2001)	Anthropized	Parasite	27	3	30	0.457	-25.418
Sousa & Colpo (2017)	Conserved	Epiphyte	3	7	10	0.571	-23.819

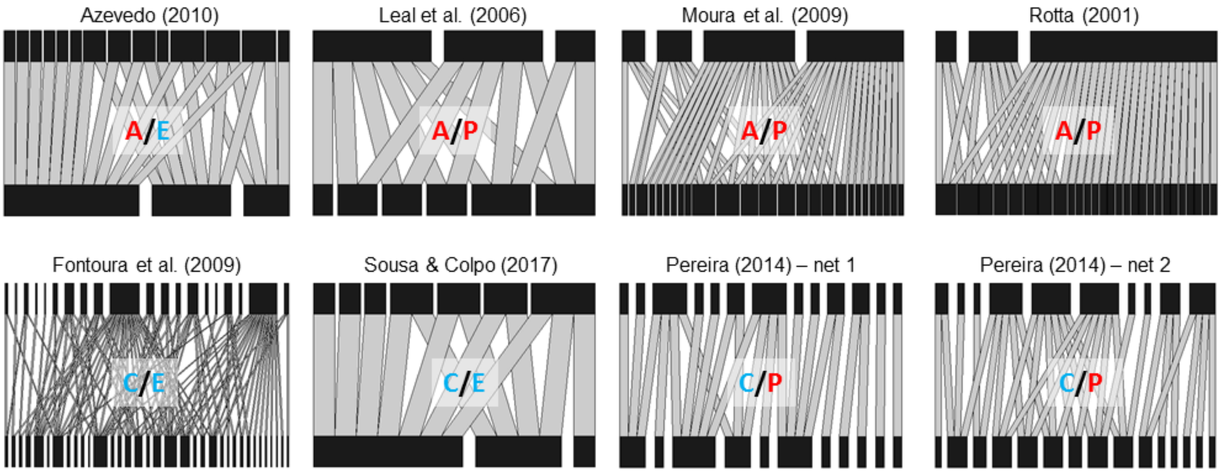

Fig. 1 Structure of the plant-plant networks analyzed in this study. For each network, lower bars represent host plant species and upper bars represent hosted plant species (parasites or epiphytes). Bar thickness is proportional to the number of interactions of each species (drawn at different scales). Networks were ordered by habitat conservation status (A = Anthropized habitats; C = conserved habitats) and network type (E = epiphyte network; P = parasite network).

2.2 Evaluating the network structure

In order to describe the structure of plant-plant networks were used the network connectance, and two measures of robustness to secondary extinctions (random and realistic). Connectance was evaluated because is the most commonly used descriptor of topological structure of bipartite binary networks (review in Dormann et al., 2009), and can influence the fragility of ecological networks to coextinctions (Dunne et al., 2002). The connectance is a measure of proportion of potential interactions that are realized in the network (Zhang, 2011, 2012).The connectance is negatively influenced by network size (i.e., total number of species) (Dunne et al., 2002, Araújo et al., 2015), and to control this effect, the connectance was calculated as the residuals from a linear regression between the number of realized interactions and the number of potential interactions (both log-transformed) (hereafter “residual connectance”). Residual connectance therefore allows the comparison of different-sized networks in terms of higher or lower connectance than expected based on their size (positive and negative residuals, respectively) (Araújo et al., 2015). In the present study, connectance (pure value) was used only to describe the networks, while residual connectance was used in the analyses.

Robustness is a measure of the resistance degree of the network to coextinctions (Dormann et al., 2009; Zhang, 2016, 2018; Araújo et al., 2017). To characterize the network robustness was used the exponent of the curve generated by the proportion of remaining hosted plant species in function of the proportion of primary extinctions of host-plant species (Fig. 2). In this sense, was calculates the robustness considering two different scenarios. In the scenario 1 the primary extinctions are random (i.e., all host-plant species have the same probability of extinction), which was called “random robustness”. In the scenario 2, the chance of extinction is inversely proportional to the number of host-plant links (i.e., the host species with the less links are extinct first). Because this is a more realistic scenario this measure was called “realistic robustness”. We performed all network analyses using Bipartite package (Dormann et al., 2008) from R program (R Development Core Team, 2015).

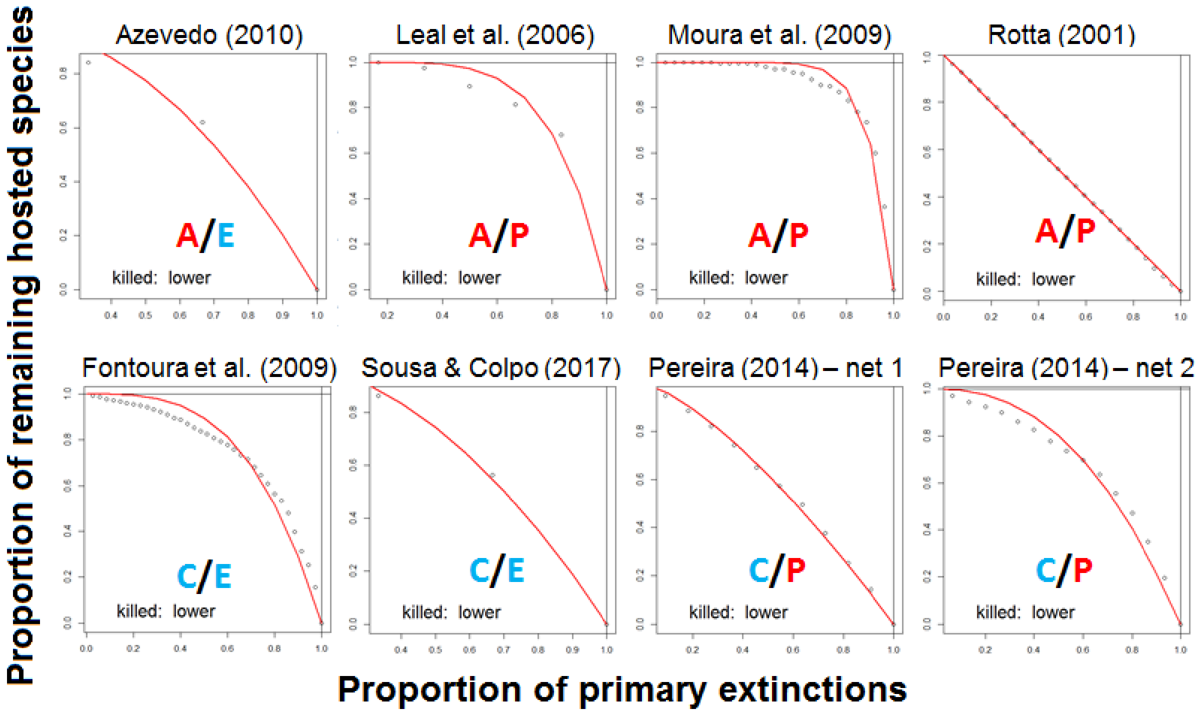

Fig. 2 Robustness to secondary extinctions of hosted species (epiphytes or parasites) resulting from random primary species loss (host-plants) in different plant-plant networks in Brazil. Networks were ordered by habitat conservation status (A = Anthropized habitats; C = conserved habitats) and network type (E = epiphyte network; P = parasite network). A less inclined curve pattern, indicating greater robustness, is found for parasite networks in anthropized habitats, such as the networks of Leal et al. (2006) and Moura et al. (2009).

2.3 Data analyses

Because the plant-plant networks compiled ranged in the location and sampling effort, the sampled taxonomic range was used as additional explanatory variables, in order to control for the confounding effects. Taxonomic range is a measure of level of taxonomic inclusion in the study because different studies ranged in the number of sampled plant families. For example, some authors often choose to limit the sampling procedure within a taxon, including only plants from a given family (e.g., Rotta, 2001, Sousa and Colpo, 2017), while some other studies sampled several families of plants (e.g., Fontoura et al., 2009). The sampled taxonomic range was calculated as the number of host-plant families (log-transformed) summed to number of hosted plant families (log-transformed) sampled in each study. Although latitude is an important geographic variable related to possible general climatic differences among areas, it was not included in the final analyses because it did not influence any of the variables of interest (all p values > 0.05). To test the effects of habitat type (conserved versus anthropized habitats), network type (parasite versus epiphyte networks) and sampled taxonomic range on the connectance, random robustness and realistic robustness of plant-plant networks were used generalized linear models (glm's).

3 Results

Connectance of plant-plant networks was moderately high, with a mean value of $C = 0.40 \pm 0.21$ (mean ± SD), reaching a maximum value of $C = 0.72$ in the Leal et al. (2006) network (Table 1). Connectance values were higher for networks of anthropized habitats ($C = 0.53 \pm 0.13$) than for networks of preserved habitats ($C = 0.26 \pm 0.20$). Comparing the connectance values between the different network types, was found $C = 0.42 \pm 0.24$ for epiphyte networks and $C = 0.38 \pm 0.22$ for parasite networks.

The statistical analyses showed that the residual connectance differs significantly between plant-plant networks of conserved and anthropized habitats ($F_{(1,3)} = 24.48$, $p = 0.01$, Table 2). In general, networks of anthropized habitats were more connected than expected by network size, while networks of conserved habitats were less connected than expected by size (Fig. 3).

Table 2 Generalized linear models of the effects of habitat type (anthropized versus conserved), network type (epiphytes versus parasites) and sampled taxonomic range on the residual connectance, random robustness and realistic robustness of plant-plant interaction networks in Brazil.

Network variable	Explanatory variable	*F*	*p*
Residual connectance	Intercept	0.239	0.659
	Habitat type	24.48	0.016
	Network type	3.792	0.147
	Network type*Habitat type	4.929	0.113
	Sampled taxonomic range	0.050	0.837
Random robustness	Intercept	261.37	0.001
	Habitat type	6.914	0.078
	Network type	17.92	0.024
	Network type*Habitat type	29.70	0.012
	Sampled taxonomic range	3.684	0.151
Realistic robustness	Intercept	781.99	<0.001
	Habitat type	2.376	0.221
	Network type	47.35	0.006
	Network type*Habitat type	87.37	0.003
	Sampled taxonomic range	23.58	0.017

The network robustness based on random robustness (Table 2) was significantly influenced by network type ($F_{(1,3)} = 17.92$, $p = 0.02$), and interaction between network type and habitat type ($F_{(1,3)} = 29.70$, $p = 0.01$). Plant-plant networks composed by parasitic interactions were more robustness to random primary extinctions than epiphyte networks, which was mainly observed in anthropized habitats (Fig. 4). A similar pattern was observed to realistic robustness (Table 2), where also were found significant effects of network type ($F_{(1,3)} = 47.35$, $p< 0.01$) and interaction between network type and habitat type ($F_{(1,3)} = 87.37$, $p< 0.01$)on the network robustness. In this sense, parasite networks were more robust to primary extinction of more rare species than the epiphyte networks, mainly in the anthropized habitats (Fig. 5). Additionally, the realistic robustness also was influenced by sampled taxonomic range ($F_{(1,3)} = 23.58$, $p = 0.01$), being that networks with larger sample range were more robust than networks that sampled few taxa.

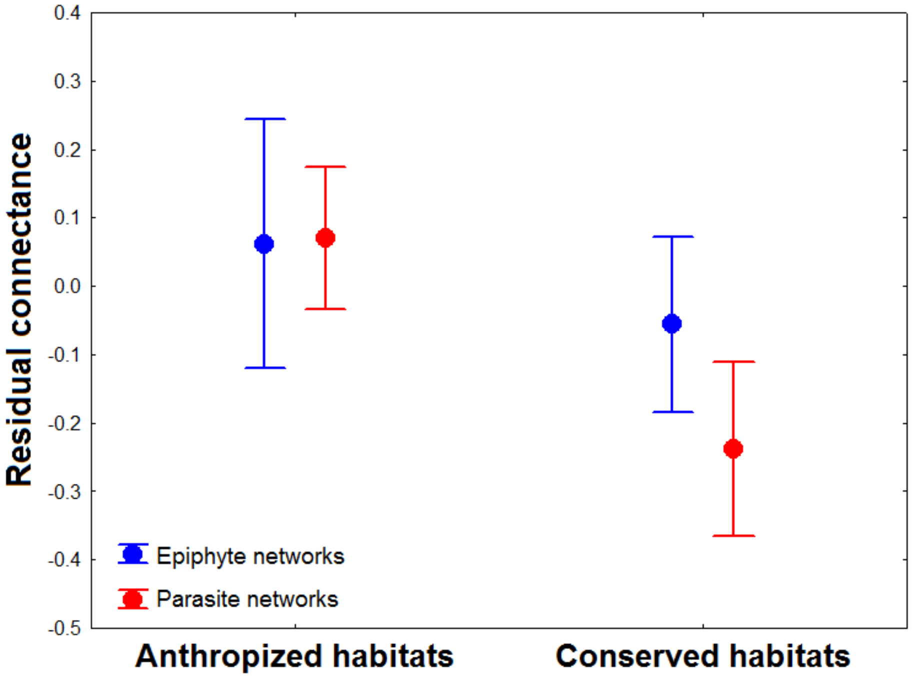

Fig. 3 Comparison between residual connectance between the different habitat type (anthropized versus conserved) and network type (epiphytes versus parasites).

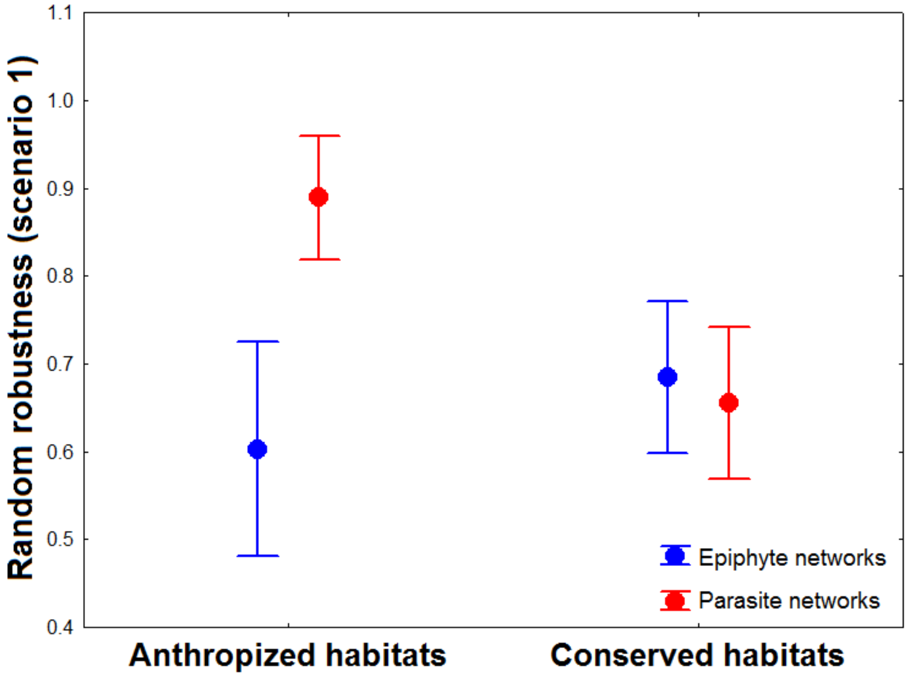

Fig. 4 Comparison between random robustness (scenario 1) between the different habitat type (anthropized versus conserved) and network type (epiphytes versus parasites).

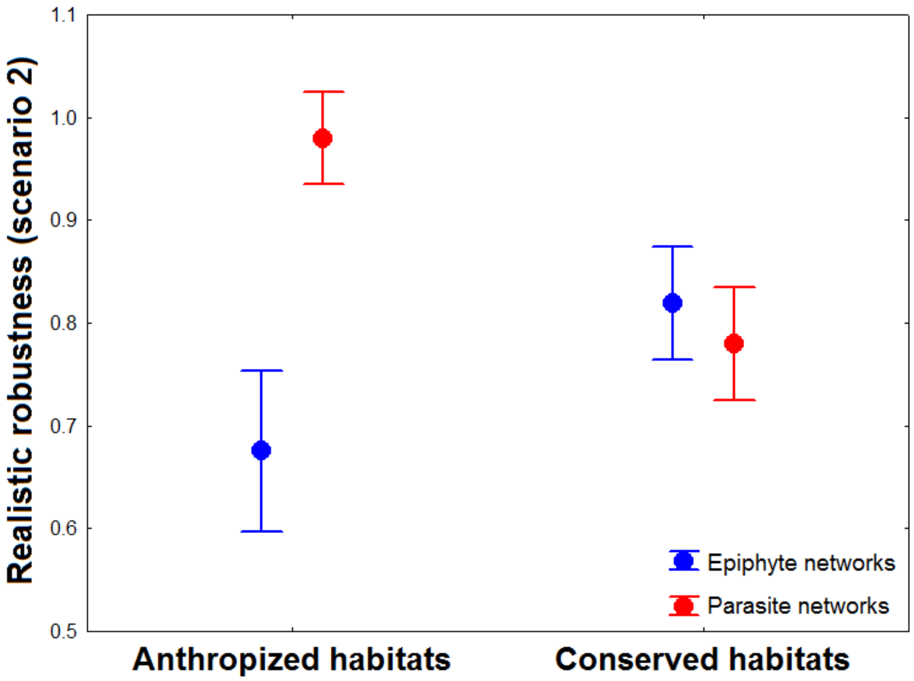

Fig. 5 Comparison between realistic robustness (scenario 2) between the different habitat type (anthropized versus conserved) and network type (epiphytes versus parasites).

4 Discussion

The results show that the human-induced habitat modification influences the connectance of plant-plant networks. As expected, the networks of anthropized habitats had greater residual connectance than the networks of conserved habitats. This result corroborates previous studies that point out that habitat modification can influence the connectivity of ecological networks (Hagen et al., 2012; Araújo et al., 2015). Contrary to residual connectance, the robustness of plant-plant networks was significantly influenced by network type (epiphytes versus parasites) and by interaction between network type and habitat type. To contrary of expectative, the results show that parasite interaction networks were more robust (considering both scenarios of primary extinctions) than epiphyte networks, mainly in anthropized habitats.

In addition to the anthropogenic habitats have less plant species richness (Ellis et al., 2012) they present microclimatic characteristics and species composition different of natural environments. The opening up and the homogenization of natural vegetation, for instance, have been shown to cause a series of changes in environmental conditions, such as increasing microclimatic oscillations and reducing the natural buffer against pollution (Smart et al., 2006). Besides that, exotic plant species are usually more common in human-disturbed habitats due both to direct introduction and to habitat invasion (Didham et al., 2007; Parker et al., 2010). In this context, the anthropic habitats are characterized by species that are few selective in their ecological links, which results in a great connectivity inside the networks in these environments. On the other hand, no effect of the type of interaction on the residual connectance was found, contrary to what was expected. This result may be due to the strength exerted by the habitat type, especially in anthropic habitats, limiting the species more specialized, generating a high degree of connectance in the network (independently of the type of interaction).

The results showed higher values of robustness in the plant-parasite networks when compared to plant-epiphyte networks, and these differences were mainly observed in anthropized habitats. This result contrary the initial expectation that plant-parasite networks would have lower robustness because are characterized by more intimate links, as compared to plant-epiphytes networks that have more occasional links.

The main explanation for this unexpected result can be related to degree of host specificity of parasite plants (Norton and Carpenter, 1998). In a thematic review, Arruda et al. (2012) point out that much of the Neotropical parasitic plants are host-generalists, and that extreme host specialization is rare. Despite this, there is evidence that the specificity of parasitic plants may be dependent on the scale of observation, since they may have a local preference for a particular host (Arruda et al., 2006; Grenfell and Burns, 2009). In this sense, the level generalization or local specialization of the parasite plants can be dependent on multiple factors related to the dispersant animals of their seeds, as well as the characteristics of the host-plants (Arruda et al., 2012). At network level, a large variation in the specialization range of species, from many specialists to generalists, can generate a nested pattern of interactions, which is usually very robust (Piazzon et al., 2011).

This study presented a new approach for studies of plant ecological interactions, because is the first to compare the effect of habitat modification on the plant-plant network robustness. Combining data available from the literature to build networks with different types of plant interactions, the results shown that habitat modification influences the network connectance, which was higher in networks of anthropized habitats than in conserved habitat networks. In addition, the results indicate that the level of ecological association (interaction intimacy) influences in the network structure and dynamic, since networks composed of parasite links were more robust than networks of epiphytic links. It is findings can be interpreted as general patterns that emerged, despite the high heterogeneity among the plant-plant networks analyzed.

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