Article

Evaluating the network structure of different Neotropical plant-plant interactions

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Abstract
Plant species can be used as hosts by other plant species, both in antagonistic interactions (e.g., parasitism), and in commensal interactions (e.g., epiphytism). In this study, plant-plant interaction networks were constructed using the literature available from Brazil in order to contrast networks composed by parasitic versus epiphytic plants. Eight plant-plant networks were analysed: five plant-parasite networks and three plant-epiphyte networks. The network structure was characterised using the following network metrics: network size, number of interactions, connectance, modularity and nestedness. In total, plant-plant networks comprised 110 host-plant species and 60 hosted-plant species (parasites or epiphytes) with 269 distinct interactions. Network size, number of interactions, modularity and nestedness did not differ between different types of networks. On the other hand, network connectance in plant-plant networks was significantly different between habitat types (conserved versus anthropised habitats). The present study represents a pioneer systematic investigation showing that structure of plant-plant networks is influenced by habitat conservation status, regardless of the type and the intimacy of interactions between species.

Keywords commensalism; ecological networks; epiphytes; mistletoes; parasitism.

1 Introduction

Plant species can interact in a variety of ways, from mutually negative associations, such as competition, to mutually positive interactions, such as facilitation (Montesinos, 2015; Zhang, 2014, 2017). At the community level, plant-plant interactions can influence the diversity (Saiz et al., 2017), structure and dynamics of the plant community (Aschehoug, 2011). In several cases, plant species can be used as hosts by other plant species, both in antagonistic interactions such as parasitism, and in commensal interactions, such as epiphytes. In this sense, the links between host plant species and hosted plant species (i.e., parasites or epiphytes) can be used to build networks of ecological interactions (Poisot et al., 2016). In ecological interaction networks, the degree of

biological association and the intimacy of interaction between partners can influence the specialisation and structure of interactions within the community (Guimarães et al., 2007; Pires and Guimarães, 2013; Benítez-Malvido and Dáttilo, 2015). Because of the different types of ecological interactions involving parasites, epiphytes and their host plants, it is expected that plant-parasite networks have different structures in comparison to plant-epiphyte networks, although this is still an unexplored issue.

In parasitism, parasite plant species have their life associated with a host plant and are positively benefitted by the interaction, in contrast with the host (Thompson, 1994). In the Neotropics, the main group of parasite plants is the family Loranthaceae, popularly called mistletoes (Arruda et al., 2012). The parasitism of mistletoes is considered an ecological interaction with a high degree of biological association between parasite and host, because parasites are physically linked to their hosts and affect and are affected by host-plant physiology due to similar hormonal pathways (Pennings and Callaway, 2012). Consequently, parasitism leads to plants having some level of specialisation in the use of host plants, because they require morphological and ecological adaptations to be able to access the host food resources (Norton and Carpenter, 1998). An important adaptation of parasite plants is the haustorium, a modified root that penetrates the host plants and connects them to the conductive system (Norton and Lange, 1999). Haustoria are present both in hemiparasites, which are partially parasitic for undertaking photosynthesis, and in holoparasites, which are devoid of chlorophyll and exclusively use the host's resources (Thompson, 1994; Norton and Lange, 1999).

Epiphytes are plants that germinate and live on other plants, but in a commensal way without parasitic-roots and negative effects on the hosts, contrary to parasite plant species (Zotz, 2016). The majority of vascular epiphytes are ferns and monocots, especially aroids, bromeliads and orchids (Zotz, 2016), the latter being the most important group in the Neotropical region (Silva et al., 2010). As epiphytic plants live as commensals on their hosts, they generally are not selective about the species of *phorophytes* used (Kersten et al., 2009). Thus, epiphyte species tend to use several host plant species and hosts tend to harbour several epiphyte species (Silva et al., 2010). In this context, plant-epiphyte networks are dominated by stochastic interactions which result in a high level of connection and nestedness in this network type (Burns, 2007; Silva et al., 2010).

In this study, plant-plant interaction networks were constructed using the literature available from Brazil in order to contrast networks comprised by parasite plants versus epiphyte plants. Network structure was described using different measures related to the diversity (network size and number of interactions) and specialisation (connectance, modularity and nestedness) of ecological interactions. Since plant-parasite links lead to more intimate interactions between host and hosted plant species than commensal links, I tested the hypothesis that plant-parasite networks have a higher degree of specialisation compared to plant-epiphyte networks.

2 Material and Methods

2.1 Data compilation

Networks were built from data available in the literature about plant-plant interactions from Brazil. The search for these studies was performed in Google Scholar (<https://scholar.google.com.br/>), the most inclusive database presenting studies in English and Portuguese. Only were used studies that investigated the association between vascular epiphytes (e.g., orchids, bromeliads, etc.) or parasites (e.g., mistletoes) and their host-plants at the local level and listed the plant species involved in the interactions. In order to allow network structure analysis, only networks with at least three host plant species and three hosted plant species (epiphytes or parasites) were used. The compilation resulted in the survey of seven studies that allowed the construction of eight distinct binary networks (presence-absence interaction lists) of plant-plant interactions (Table 1).

Table 1 Characteristics of plant-plant networks built based on literature data for different parasite and epiphyte interactions in Brazil.

Network code	Network reference	Network type	Habitat type	Host richness	Hosted richness
1	Azevedo (2010)	Epiphyte	Anthropized	3	14
2	Fontoura et al. (2009)	Epiphyte	Conserved	35	20
3	Leal et al. (2006)	Parasite	Anthropized	6	3
4	Moura et al. (2009)	Parasite	Anthropized	26	4
5	Pereira (2014) – area 1	Parasite	Conserved	11	13
6	Pereira (2014) – area 2	Parasite	Conserved	15	10
7	Rotta (2001)	Parasite	Anthropized	27	3
8	Sousa and Colpo (2017)	Epiphyte	Conserved	3	7

2.2 Network structure

Each plant-plant interaction list was used to build an adjacency matrix A, where a_{ij} = number of interactions between the host-plant species j and the hosted plant species i. In order to describe the structure of networks composed by epiphytes and parasites, I used the following network descriptors for each plant-plant network: network size, number of interactions, connectance, modularity and nestedness. These network descriptors were adopted because they are commonly used to describe the topological structure of bipartite networks composed of binary interactions (review in Dormann et al., 2009), as can be observed in several recent studies investigating ecological networks (Kuang and Zhang, 2011; Zhang, et al., 2014; Jiang and Zhang, 2015a-b; Jiang et al., 2015; Pinho et al., 2017; Almeida and Mikich, 2018; Traveset et al., 2018; Zhang, 2011, 2012, 2018).

To calculate the network size, I counted the total number of host and hosted plant species in each network (i.e., the species richness), while the number of interactions is the total number of realised links between them. Connectance is the proportion of possible interactions that are realized in a network (Dunne et al., 2002; Dorman, 2011; Dormann et al., 2008; Zhang, 2011, 2012, 2018), and therefore greater connectance results in lower network specialization (Araújo et al., 2015). Due to the negative relationship between network size and connectance (Dunne et al., 2002), connectance values were calculated as the residuals from a linear regression between the number of realised interactions and the number of potential interactions (both log-transformed). This approach controls for the effects of network size and allows comparisons of connectance among different types of ecological networks (Olesen and Jordano, 2002; Araújo et al., 2015; Araújo and Daud, 2018). Modularity was computed using the bipartite modularity index Q (Barber, 2007) through the DIRTLPAwb+ algorithm in order to detect network modules (Beckett, 2016). The nestedness was calculated using the Nestedness metric based on Overlap and Decreasing Fill (NODF) (Almeida-Neto et al., 2008). The NODF accounts for the paired overlap and the decreasing fill of the matrix representing an interaction network, and takes values between 0 (perfectly non-nested) and 100 (perfectly nested). Networks were built and analysed using the 'bipartite' package (Dormann et al., 2008) in the R environment version 3.4.1 (R Development Core Team, 2015).

2.3 Data analyses

The network type (epiphyte versus parasite networks) was used as the main explanatory variable from the plant-plant network structure. However, as the plant-plant interaction lists used in this study ranged in the habitat conservation status, location and sampling effort, I used as additional explanatory variables the habitat

type, latitude and the sampled taxonomic range, in order to control for the confounding effects. Habitat type was adopted considering the habitats where the plants were sampled as "conserved habitats" (i.e., habitats characterised by natural vegetation with little or no anthropic effect, such as primary forest) or "anthropised habitats" (i.e., habitat with secondary or planted vegetation under strong anthropic influence, such as urban gardens) according to the original description of authors. Latitude was used as a geographic variable related to possible general climatic differences among areas. Besides that, different compiled studies ranged in the number of sampled plant families. For example, some authors often chose 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 number of plant families included in the study can influence the taxonomic and phylogenetic diversity in the network, and consequently the interaction network structure. In order to control this effect, I used the variable "sampled taxonomic range", which was calculated as the number of host-plant families summed to the number of hosted plant families sampled in each study (both log-transformed).
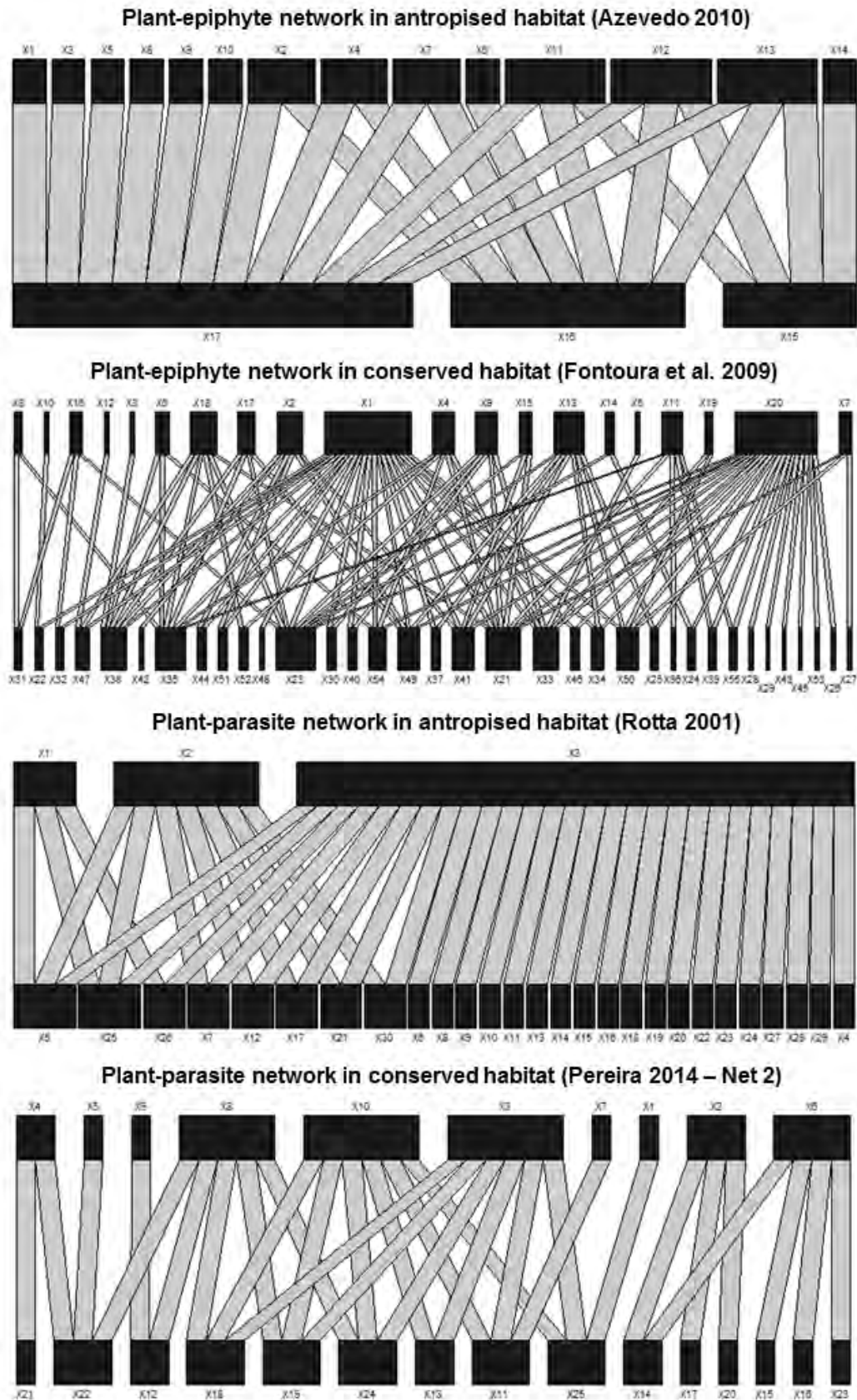
Generalized linear models (GLMs) were used to test the effects of network type, habitat type and other control variables on the descriptors of network structure. To avoid inflating the models with several explanatory variables, the effects of potentially confounding variables were examined through Pearson correlations of these variables with network size and number of interactions (Table 2). Since latitude had no significant effects, this variable was not included in the GLMs. Explanatory variables used in the models were network type (epiphytes vs. parasites), network size (anthropised vs. conserved) and sampled taxonomic range. The complete models were simplified by omitting non-significant terms in a backward stepwise regression and later subjected to residual analysis to test the adequacy of the error distribution. To meet normality requirements, I applied logarithmic transformations to the network size, number of interactions and sampled taxonomic range. Statistical analyses were performed in R version 3.4.1 (R Development Team, 2015).

Table 2 Pearson correlation matrix between the number of interactions (log), network size (log) and the control variables latitude and sampled taxonomic range (log) of plant-plant networks in Brazil. Asterisk indicates significant linear correlation ($P< 0.05$).

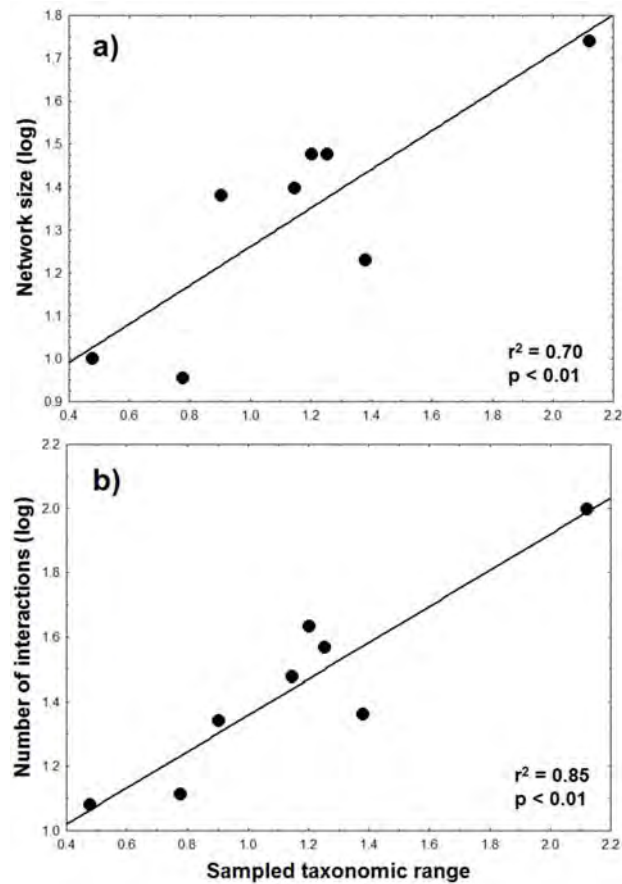|	Number of interactions (log)	Network size (log)	Latitude	Sampled taxonomic range (log)
Number of interactions (log)	1.00			
Network size (log)	0.96*	1.00		
Latitude	-0.11	-0.29	1.00	
Sampled taxonomic range (log)	0.92*	0.84*	0.09	1.00

3 Results

In total, the eight plant-plant networks analysed were composed of 110 host-plant species and 60 hosted-plant species, comprising 269 distinct interactions (Supplementary Material 1 and 2; Fig. 1). Of these, epiphyte networks represented 134 interactions occurring between 41 host-plant species and 37 epiphyte plant species, while parasite networks were composed of 70 host-plant species, 24 parasite plant species, and 137 distinct interactions. Host-plant communities were mainly dominated by Fabaceae with 18 species (25.7%) in the parasite networks and Sapotaceae with six species (14.6%) in the epiphyte networks. The main family of epiphytes was Bromeliaceae with 17 species (45.9%), while Loranthaceae was the main parasite plant family with 18 species recorded (75%).

Plant-epiphyte network in antropised habitat (Azevedo 2010)

Plant-epiphyte network in conserved habitat (Fontoura et al. 2009)

Plant-parasite network in antropised habitat (Rotta 2001)

**Plant-parasite network in conserved habitat (Pereira 2014 – Net 2)**

Fig. 1 Examples of 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). Species codes are presented in the Supplementary Material 2.

No effect was observed of network type and habitat type on the network size and number of interactions (Table 3), but these variables were positively influenced by sampled taxonomic range (Fig. 2a and Fig. 2b, respectively). On the other hand, connectance was higher in the networks of anthropised habitats than in the networks of preserved habitats (Table 3; Fig. 3). In turn, modularity and nestedness did not were influenced by network type, habitat type or sampled taxonomic range (Table 3).

Fig. 2 Relationship between sampled taxonomic range (log) and a) network size (log) and b) number of interactions (log) in plant-plant networks.
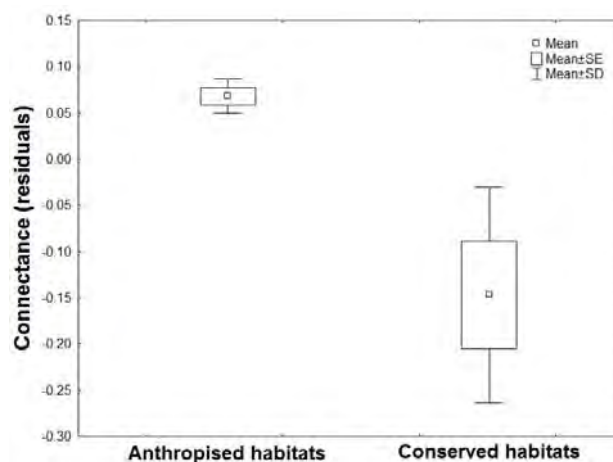
Fig. 3 Comparison between network connectance of plant-plant networks located in different habitat type (anthropised versus conserved).

Table 3 Analysis of variance of the complete generalized linear models (GLMs) evaluating the multiple effects of explanatory variables (network type, habitat type and sampled taxonomic range) on the network metrics (network size, number of interactions, connectance, modularity and nestedness) of plant-plant networks in Brazil. Values of *F* and *P* are those of the regression coefficients in the general model.

Network metrics	Explanatory variables	*F*-value	*p*-value
Network size (log)	Sampled taxonomic range	22.878	0.003
	Habitat type (anthropised vs. conserved)	4.317	0.129
	Network type (epiphytes vs. parasites)	2.815	0.192
	Network type*Habitat type	4.355	0.128
Number of interactions (log)	Sampled taxonomic range	34.251	0.001
	Habitat type (anthropised vs. conserved)	0.396	0.574
	Network type (epiphytes vs. parasites)	2.180	0.236
	Network type*Habitat type	1.639	0.291
Connectance	Sampled taxonomic range	0.152	0.723
	Habitat type (anthropised vs. conserved)	13.179	0.011
	Network type (epiphytes vs. parasites)	5.210	0.107
	Network type*Habitat type	4.929	0.113
Modularity	Sampled taxonomic range	2.339	0.224
	Habitat type (anthropised vs. conserved)	6.354	0.065
	Network type (epiphytes vs. parasites)	6.934	0.078
	Network type*Habitat type	5.174	0.108
Nestedness	Sampled taxonomic range	3.683	0.127
	Habitat type (anthropised vs. conserved)	2.949	0.147
	Network type (epiphytes vs. parasites)	2.069	0.210
	Network type*Habitat type	9.503	0.054

4 Discussion

Despite an extensive search in the literature, only seven studies and eight networks were obtained in the present compilation. This low number of networks is due to the majority of studies conducted with epiphytes and/or parasites not to identify host plant species, which limits information on plant-plant interactions. However, despite the low number of studies found, a high number of species and interactions were listed in each of the networks in particular. This indicates that the networks were well sampled in their interactions and, therefore, to analyze the structural patterns of these networks can give a good idea of the structure of plant-plant networks with different types of interactions.In the present study, habitat type and sampled taxonomic range showed effects on the structure of plant-plant interaction networks. These results corroborate previous studies pointing out anthropic and sampling effects on the structure of ecological networks (Piazzon et al., 2011; Araújo et al., 2015, Staniczenko et al., 2017).

The results indicate that after controlling for possible confounding effects (e.g., sampling taxonomic range, latitude and habitat type), no differences were found in the size, number of interactions and structure of networks of epiphytic versus parasitic plants. This means that the intimacy of the interaction does not seem to be important for the structure of interactions between host and hosted plants. A possible explanation for these results is that parasitic plants are slightly generalist as their hosts (Norton and Carpenter, 1998). Confirming this, there are evidences that some loranthaceous mistletoes can parasitize a wide range of host species (Norton and Lange, 1999), so that the connectivity in plant-parasite networks can be so high than in networks with less

intimate interactions, such as plant-epiphyte networks.

Additionally, the results indicate that habitat conservation status and sampling taxonomic range influenced plant-plant network structure, regardless of the type of ecological interaction. The levels of connectance of the plant-plant networks were not influenced by network type, but were significantly affected by habitat type. Networks of anthropised habitats were more connected than networks of conserved habitats. This result is in agreement with Villa-Galaviz et al. (2012) who found higher connectance of ecological networks in highly anthropised habitats (pasture) when compared to more natural habitats (mature and secondary forests). The main explanation for this result is the higher effect of habitat modification on more specialist species (i.e., rare species), which contribute with rare links to the network (Tylianakis et al., 2010, Dorado et al., 2011). Thus, generalist species that have many links are more frequent in anthropised habitats, consequently increasing the connectivity of the networks in these conditions. The sampled taxonomic range positively influenced network size and number of interactions. This indicates that the larger the number of taxa (i.e., plant families) sampled in the networks, the higher the realized in interactions in the network.

The present study represents a pioneer systematic investigation contrasting the structures of plant-plant interactions between plant-epiphyte and plant-parasite networks. The results show that the structure did not differs between networks of parasites vs. epiphytes, but anthropic habitats have plant-plant networks more connected than conserved habitats, corroborating previous studies (Villa-Galaviz et al., 2012). Future studies can move forward the understanding of plant-plant interaction networks with species-level analyses, for example, looking at how specific species behave in different interactions and environments.

Acknowledgment

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