

Mistletoes Play Different Roles in a Modular Host–Parasite Network

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ABSTRACT

Antagonistic interactions between host plants and mistletoes often form complex networks of interacting species. Adequate characterization of network organization requires a combination of qualitative and quantitative data. Therefore, we assessed the distribution of interactions between mistletoes and hosts in the Brazilian Pantanal and characterized the network structure in relation to nestedness and modularity. Interactions were highly asymmetric, with mistletoes presenting low host specificity (*i.e.*, weak dependence) and with hosts being highly susceptible to mistletoe-specific infections. We found a non-nested and modular pattern of interactions, wherein each mistletoe species interacted with a particular set of host species. *Psittacanthus* spp. infected more species and individuals and also caused a high number of infections per individual, whereas the other mistletoe species showed a more specialized pattern of infection. For this reason, *Psittacanthus* spp. were regarded as module hubs while the other mistletoe species showed a peripheral role. We hypothesize that this pattern is primarily the result of different seed dispersal systems. Although all mistletoe species in our study are bird dispersed, the frugivorous assemblage of *Psittacanthus* spp. is composed of a larger suite of birds, whereas *Phoradendron* are mainly dispersed by *Euphonia* species. The larger assemblage of bird species dispersing *Psittacanthus* seeds may also increase the number of hosts colonized and, consequently, its dominance in the study area. Nevertheless, other restrictions on the interactions among species, such as the differential capacity of mistletoe infections, defense strategies of hosts and habitat types, can also generate or enhance the observed pattern.

Abstract in Portuguese is available in the online version of this article.

Key words: Brazilian Pantanal; coevolution; dispersal; host–mistletoe interaction network; interaction asymmetry; nestedness.

SPECIES INTERACTIONS ARE SHAPED BY COEVOLUTIONARY PROCESSES OCCURRING among interacting species along the continuum of mutualism–antagonism and in a species' geographical range (Thompson & Fernandez 2006). Among antagonistic species, mistletoes are obligate hemiparasitic species that establish a life-long vascular connection with single plant individuals for acquiring water and minerals (Norton & Carpenter 1998, Watson 2001). This interaction results in a retarded growth rate and, ultimately, increased mortality of the infected host (Maloney & Rizzo 2002, but see MacRaid *et al.* 2009).

At the community level, assemblages of mistletoes and hosts species form complex networks of species. The structure of inter-specific networks has been described for different types of interactions (Memmott *et al.* 1994, Memmott 1999, Bascompte *et al.* 2003, Guimarães *et al.* 2006, Lewinsohn *et al.* 2006, Burns 2007, Blick & Burns 2009). A network structure reveals how ecological interactions are organized and is useful for understanding the underlying processes that operate in these interactions

(Bascompte *et al.* 2003, Jordano *et al.* 2003, Guimarães *et al.* 2006). Nestedness and modularity are the most frequent patterns reported for ecological networks, and these can occur exclusively or simultaneously (Lewinsohn *et al.* 2006). A nested pattern implies that a few generalists interact with one another and with specialized species, providing pathways for the persistence of specialists (Bascompte *et al.* 2003, Bascompte & Jordano 2007, Ollerton *et al.* 2007). On the other hand, a set of interacting species exhibit modules or compartments if there are recognizable subsets of interacting organisms, such that the species are more linked within subsets than across (Fonseca & Ganade 1996, Lewinsohn *et al.* 2006).

Nested patterns of interactions are commonly observed in pollination, seed dispersal (Bascompte *et al.* 2003), cleaning and ant–plant symbioses (Guimarães *et al.* 2006, Guimarães *et al.* 2007a), parasite–host interactions (Rohde *et al.* 1998), and fish and anemone host interactions (Ollerton *et al.* 2007). Burns (2007) reported nestedness in commensalism relationships between epiphytes and host trees, and he attributed the observed nested pattern to an epiphyte succession process in which earlier epiphytes facilitate the colonization of later recruiting species. On

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the other hand, a study by Blick and Burns (2009) showed no support for nestedness in mistletoe- and liana-host species networks (Burns, 2007; Sfair *et al.* 2010).

A derived property of nestedness is the asymmetry in species interactions (*i.e.*, rich-link species vs. poor-link species), which generates functional redundancy and allows mutualistic communities to endure disturbances such as the disappearance of species and interactions (Bascompte & Jordano 2007). Likewise, the combination of strong-weak dependences (*i.e.*, asymmetry) among mutualistic organisms is hypothesized to allow species to coexist (Bascompte & Jordano 2006). Asymmetry is generally related to species abundance and frequency of interactions, with abundant species exhibiting more links and stronger effects on the interacting species (Vázquez *et al.* 2007, Burns 2007). Nevertheless, deterministic processes, such as forbidden links (*e.g.*, phenological mismatching and size and structural constraints), may also influence a network structure (Jordano *et al.* 2003). Thus, the diversity, abundance and deterministic processes of species should be considered in order to understand their interaction patterns (Burns 2007). In this sense, quantitative information (*e.g.*, frequency of interactions) may provide a more comprehensive understanding of network organization and species coexistence (Bascompte & Jordano 2006).

Interacting organisms may alternatively exhibit modular patterns, which are mostly expected in antagonistic interactions (Raffaelli & Hall 1992, Prado & Lewinsohn 2004, but see Memmott *et al.* 1994), although modularity has also been found in mutualistic interactions (Dicks *et al.* 2002; Guimarães *et al.* 2007b, Olesen *et al.* 2007, Kratochwil *et al.* 2009). Recently, it has been recognized that modularity and nestedness do not preclude each other and may, in fact, occur simultaneously (Olesen *et al.* 2007, Carstensen & Olesen 2009, Fortuna *et al.* 2009). Modularity may reflect phylogenetic splits and a high stability that result from constraints on species interactions (Lewinsohn *et al.* 2006). In Fortuna *et al.* (2009), modules are formed by bat colonies using different groups of trees, which help to slow down the spread of diseases or parasites within the population and limit the information to closely related individuals among bat colonies. Within modules, species or nodes might exhibit different roles according to the amount of links they exhibit inside and outside the modules (Olesen *et al.* 2007). For instance, species that interact with a large number of other species might be regarded as network or module hubs, while species that link to few species but 'glue' the modules together are classified as connectors. Alternatively, species that are connected to few other species are classified as peripherals (Olesen *et al.* 2007).

Few studies have described the network structure and pattern of asymmetry of parasitism (but see Memmott *et al.* 1994, Lewinsohn *et al.* 2006, Vacher *et al.* 2008), and likewise, little is known about networks of interacting plants (Burns 2007, Sfair *et al.* 2010). In this context, our study focused on the mistletoe-host system of the Brazilian Pantanal to analyze the patterns of parasitism interactions under the network framework. Specifically, we addressed the following questions: (1) do antagonistic interactions among mistletoes and host plants display nestedness, modu-

larity or both patterns? (2) How asymmetric are the interactions between mistletoes and hosts species? (3) Which species are the keystone hubs? Nestedness will reveal whether plant-plant networks exhibit the same asymmetrical pattern (poor- vs. rich-link species interactions) found in other ecological antagonistic and mutualistic systems (Rohde *et al.* 1998, Bascompte *et al.* 2003; Guimarães *et al.* 2006; Guimarães *et al.* 2007a). In contrast, modularity analysis will reveal the link affinity between sets of hosts and mistletoe species, as observed in some antagonisms (Thébault & Fontaine 2010) and intimate mutualisms (Guimaraes *et al.* 2007b).

METHODS

STUDY SITE.—The Pantanal, located in central Brazil and part of Bolivia and Paraguay, is the world's largest freshwater wetland, encompassing 140,000 km² of lowland floodplain of the upper Rio Paraguai basin (Swartz 2000). Natural seasonal flooding and human activities (land conversion to agriculture) create a diverse mosaic of habitats such as grasslands, human-created pastures, cerrados (savanna-like), cerrado woodlands, marshes, semi-deciduous forests, gallery forests and floating mats (Harris *et al.* 2005). We conducted this study from September to November of 2006 at the Fazenda Rio Negro, which is a private area of 7500 ha in the Nhecolândia region of Brazil. The average annual rainfall is 1192.5 mm, and the mean monthly temperature is 26°C, ranging from 19°C to 33°C (N=4 yr; D. Eaton, unpubl. data).

STUDIED SPECIES AND DATASET.—We carried out an extensive survey of trees infected by mistletoes for 5–7 d per month for a total of 19 d. Within an area of 254 ha, we used pre-existing trails of 15 km that covered the distinct vegetation types of the Pantanal. Habitats included in the survey were gallery forests, cerrados, semi-deciduous forests (interior and edges) and pastures. Gallery forests occur along both of the margins of the Rio Negro River and are subject to seasonal flooding. The most abundant plant species are *Guarea kunthiana* (Meliaceae), *Inga vera* (Fabaceae) and *Attalea phalerata* (Arecaceae) (C. Donatti, pers. comm.). The cerrado is a savanna type of vegetation, and its physiognomy varies from open field (campo limpo) to cerrado (cerrado woodland) (Prance & Schaller 1982). This biome is dominated by species such as *Syngonanthus* spp. (Eriocaulaceae), *Rhynchospora cf. trispicata* (Cyperaceae), *Miconia elegans* (Melastomataceae), *Anacardium humile* (Anacardiaceae), *Vochysia bankeana* (Familia), *Curatella americana* (Dilleniaceae) and *Caryocar brasiliense* (Caryocaraceae) (C. Donatti, pers. comm.). Semi-deciduous forests occur on higher non-flooded ground, especially on slopes, and also in elevated non-flooded forest islands within the savanna or cerrado areas. It is also interspersed with the cerrado, but differs in its taller trees with larger trunks and in its species composition (Prance & Schaller 1982). This forest type contains species such as *Albizia niopoides* (Fabaceae), *Albizia saman* (Fabaceae) and *Ficus* spp. (Moraceae) (C. Donatti, pers. comm.). Finally, pastures are human-made habitats dominated by grasses and subject to cattle activity (trampling and selective foraging) (Prance & Schaller 1982).

Infected hosts were identified and georeferenced with the aid of a GPS device, and then the species and number of mistletoe individuals were recorded for each infected host. We attempted to sample only established mistletoes, and therefore, we excluded parasites smaller than 30 mm (*i.e.*, recent infections). We registered and identified 243 individuals of 41 host species (Appendix) and four mistletoe species, namely *Psittacanthus cordata* G. Don (Loranthaceae), *Psittacanthus calyculatus* (Hoffmans) G. Don (Loranthaceae), *Phthirusa abdita* S. Moore (Loranthaceae) and *Phoradendron* spp. Nutt. (Viscaceae). *Psittacanthus cordata* is frequently found in the 'capões' (woodlots), which are natural patches of forests surrounded by flood-prone, grass-dominated fields (Prance & Schaller 1982). Fruiting occurs from September to November (M. Côrtes & J. Genini, pers. obs.), and the berries are 8.7 ± 1.7 mm in diameter and 17.0 ± 3.2 mm in length ($N=25$). *Psittacanthus calyculatus* is frequently found in isolated areas, in the margins of open forests and on shrubs. Fruiting occurs from July to October (Pott & Pott 1994), and fruits range from 9.7 ± 1.6 mm in diameter to 14.1 ± 0.9 mm in length ($N=26$). *Phthirusa abdita* is mainly found in the cerrado, especially in cerradão or in open forests (Pott & Pott 1994), and there is no information about their fruiting period. *Phoradendron* spp. have inconspicuous, greenish-yellow flowers and are either anemophilous or entomophilous. Its fruits are berries that range from 1.7 ± 0.2 mm in diameter to 2.8 ± 0.3 mm in length ($N=20$). Fruiting in Fazenda Rio Negro occurs from September to November.

MISTLETOE-HOST NETWORK.—We used qualitative and quantitative matrices to characterize the pattern of interaction between mistletoes and host species. The binary qualitative matrix was composed of the occurrence of interaction between a mistletoe species and a particular host species, whereas the quantitative matrix presented the average number of mistletoe infections per host species. The qualitative network of our mistletoe-hosts was defined by an adjacency matrix R describing trophic interactions between H (*i.e.*, host plant species) and M (*i.e.*, mistletoe species) within the Pantanal region, where $r_{ij}=1$ if the host plant i is infected by the mistletoe j and zero otherwise (Jordano 1987, Bascompte *et al.* 2003). A lack of interaction between a given mistletoe species and a host plant species does not necessarily mean that the interaction does not occur, only that we did not observe the interaction in the field.

QUANTITATIVE MATRIX.—We used the average number of infections of each mistletoe species per individual to investigate the intensity of parasitism in each host species. In the quantitative matrix, we calculated a measure of dependence (Jordano 1987, Bascompte & Jordano 2006) for each mistletoe-host pair that represents either the susceptibility of the host species to a particular mistletoe species or the level of parasitism specificity between the mistletoe and a particular host. We followed Bascompte and Jordano (2006) for the quantitative metrics, which were originally applied to mutualisms. As the host species do not depend on mistletoes, however, we will refer to these measures as susceptibility and dependence for hosts and mistletoe species,

respectively. The susceptibility d_{ij}^H of host species i on mistletoe species j was calculated as the ratio between the number of infections produced by mistletoe j on host species i and the total number of infections on plant host i . In a similar way, we calculated d_{ji}^M for the dependence of mistletoe species j on host species i as the ratio between the number of infections produced by mistletoe j on host species i and the total number of infections produced by mistletoe species j (Bascompte & Jordano 2006). We used these dependence values to calculate asymmetry between pairs of interacting species as follows:

$$AS(i,j) = \frac{|d_{ij}^H - d_{ji}^M|}{\max(d_{ij}^H, d_{ji}^M)}$$

where d_{ij}^H is the dependence values of host species i on mistletoe j , d_{ji}^M is the dependence values of mistletoe species j on host species i and $\max(d_{ij}^H, d_{ji}^M)$ is the maximum value between d_{ij}^H and d_{ji}^M (Bascompte & Jordano 2006). Distributions of dependences and asymmetry values were represented in histograms. We then checked if the observed values were much different from what one would expect under random numbers given the observed row and column totals. We drew the networks in Pajek (<http://vlado.fmf.uni-lj.si/pub/networks/pajek/>).

NESTEDNESS.—We used *NODF* to estimate nestedness using a qualitative matrix (Guimarães & Guimarães 2006, Almeida-Neto *et al.* 2008). We compared the observed degree of nestedness of the network with 1000 replicates using null model 2, in which the probability of a given cell to be occupied is the average of the probabilities of occupancy of its row and column (Bascompte *et al.* 2003). Null model 2 controls for important differences in species abundances and potential sampling bias (Bascompte *et al.* 2003). It is calculated as follows:

$$\left(\frac{P_i}{M} + \frac{P_j}{H} \right) / 2$$

where P_i is the number of interactions of host species i , P_j is the number of interactions of mistletoe j (Bascompte *et al.* 2003) and M and H are the number of mistletoe and host species. The P -value was defined as the probability of a null model replicate being equally or more nested than the observed networks.

MODULARITY.—We used *NETCARTO* software (Guimerà & Amaral 2005a,b, Guimerà *et al.* 2005) to estimate the level of modularity, number of modules and species behavior within the mistletoe-host network. The program used Guimerà's algorithm, which is based on simulated annealing and identifies modules by maximizing the networks modularity M (see Guimerà & Amaral 2005a for further details).

$$M = \sum_{s=1}^{NM} \left(\frac{I_s}{I} - \left(\frac{k_s}{2I} \right)^2 \right)$$

where N_M is the number of modules, I is the total number of links in the network, I_s is the number of links between species in module s and k_s is the sum of the degrees of all species in module s (Guimerà & Amaral 2005a, Olesen *et al.* 2007). The number of links each species exhibits is the degree. M values range from 0 to $1 - 1/N_M$, when $M=0$ species are placed at random into modules or else all species are in the same module (Guimerà & Amaral 2005a, Olesen *et al.* 2007). We ran 100 randomizations of the empirical network and calculated the significance level of the observed M by comparing it with the average randomized M (Guimerà *et al.* 2005).

To identify the role that each species plays in the network, we calculated two parameters: the within-module degree, \bar{z} , and the among module connectivity, c . The within-module degree \bar{z} measures how well connected a species (i) is to the other species in the module and is defined as

$$\bar{z} = \frac{k_{is} - \bar{k}_s}{SD_{k_s}}$$

where k_{is} is the number of links of i to other species in its own module s , and \bar{k}_s and SD_{k_s} are the average and standard deviation within the module k of all species in s , respectively (Guimerà & Amaral 2005a, Olesen *et al.* 2007). High values of \bar{z} indicate a high within-module degree, and low values indicate that the species interacts with few species within its module. Species are classified according to the \bar{z} score in module hubs ($\bar{z} \geq 2.5$) and non-hubs ($\bar{z} < 2.5$) (Guimerà & Amaral 2005a).

On the other hand, the among-module connectivity c measures how well distributed the links of species i are among different modules and is defined as

$$c = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i} \right)^2$$

where k_i is degree of species i and k_{it} is the number of links from i to species in module t . Values of c are close to 1 when links are randomly distributed among all the modules and 0 if all of links are within a single module (Guimerà & Amaral 2005a, Olesen *et al.* 2007).

In this study, we used the \bar{z} and c scores to classify species with respect to their roles in the system as follows: peripheral ($\bar{z} \leq 2.5$ and $c \leq 0.62$), connectors ($\bar{z} \leq 2.5$ and $c > 0.62$), module hubs ($\bar{z} > 2.5$ and $c \leq 0.62$) and network hubs ($\bar{z} > 2.5$ and $c > 0.62$) (see Olesen *et al.* 2007 for definitions). We used qualitative data to evaluate nestedness and modularity, as we are not aware of a quantitative method to evaluate modularity and also because we wanted to use the same kind of data and randomization procedure to analyze both patterns.

RESULTS

We recorded 724 mistletoe parasite individuals (*i.e.*, number of infections) on 243 individuals from 50 host species. Among

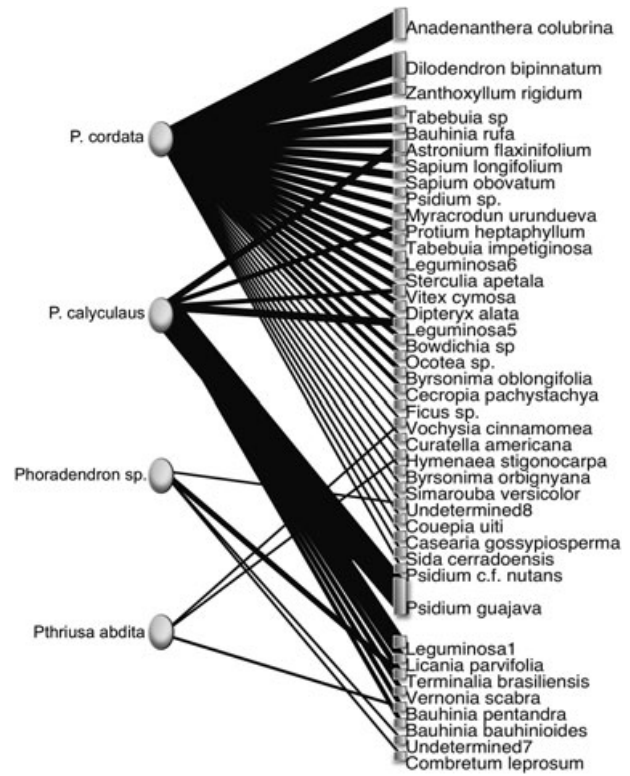


FIGURE 1. Pattern of interactions between mistletoes (circles) and hosts species (rectangles). Lines represent the interactions between mistletoes and host species, line thickness indicates the strength of the interaction, and the sizes of the rectangles correspond to the line thickness. Species are sorted according to the average number of mistletoe infections.

mistletoe species, *P. cordata* infected the highest number of host species (Fig. 1; Table 1). The percentages of infected host species, individuals and infections are detailed in Table 1. The most infected host species were *Astronium flaxinifolium* (Anacardiaceae) ($N=33$; 13.6%) by the two *Psittacanthus* species; *Bauhinia pentandra* (Fabaceae) ($N=24$; 9.9%) by *P. calyculus* and *P. abdita*; and *Sapium longifolium* (Euphorbiaceae) ($N=23$; 9.5%), *Vitex cymosa* (Lamiaceae) ($N=17$; 7%), and *Cecropia pachystachya* (Urticaceae) ($N=16$; 6.6%) by *P. cordata*. We recorded a total of 724 mistletoe individuals (*i.e.*, infections). The host species with more infections per

TABLE 1. Intensity of mistletoe infection given as the percentages of infected host species, individuals and infections at Fazenda Rio Negro, Pantanal, Brazil.

Mistletoes	Host species (%)	Host individuals (%)	Infections (%)
<i>Psittacanthus cordata</i>	78 (N=32)	60 (N=145)	60 (N=435)
<i>Psittacanthus calyculus</i>	27 (N=11)	34 (N=83)	37 (N=266)
<i>Pthirusa abdita</i>	17 (N=4)	6 (N=9)	2 (N=16)
<i>Phoradendron</i> spp.	17 (N=3)	6 (N=6)	1 (N=7)

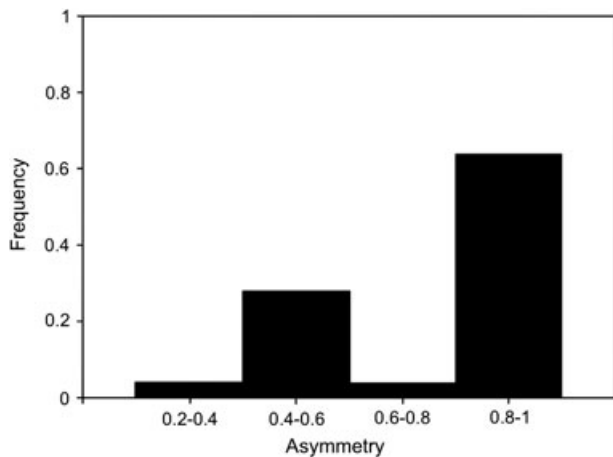


FIGURE 2. Frequency distribution of asymmetry values for pair wise interactions between mistletoes and hosts species (mean number of infections).

individual were *Psidium guajava* (Myrtaceae) (12.8 ± 9.8 ; Fig. 1) (mean \pm SD) by *P. calyculatus*; and *Anadenanthera colubrina* (Fabaceae) (10.3 ± 14.4 , Fig. 1) and *Dilodendron bipinnatum* (Sapindaceae) (9 ± 0 ; Fig. 1) by *P. cordata*. The observed patterns of interaction strength differed significantly from random patterns ($t=3.01$; $P<0.001$).

Most of the pairwise interactions between mistletoes and hosts were highly asymmetric (Fig. 2), with mistletoes interacting more weakly with hosts. In general, mistletoes depended very weakly on specific host species, which indicates low infection specificity (Fig. S1A), whereas host species were highly susceptible to a particular mistletoe species (Fig. S1B).

We did not find a significant nested pattern ($NODF=0.22$; $P=0.924$). We did find a significant modular pattern of interactions between mistletoes and hosts ($M=0.42$; $P=0.041$) with the presence of four modules corresponding to the four mistletoe species and a set of infected host species. The low α (within-module connectivity) and ϵ (among-module connectivity) values of host species indicated that most host plants exhibited a peripheral role, interacting poorly within and among the modules (*i.e.*, few interactions inside and outside the modules). The two *Psittacanthus* species were classified as module hubs because they interacted with a large number of species in its module and with few species outside their module (high α , low ϵ). *Phthirusa* and *Phoradendron* were classified as peripherals, and their modules were much smaller than *Psittacanthus* modules (Fig. S2). The lack of connector species indicates that species in each module are quite independent from the species in other modules and that there is not much overlap in the interactions between hosts and mistletoe species from different modules.

DISCUSSION

Our mistletoe–host network was highly asymmetric and showed a non-nested, modular structure. Highly asymmetric distributions of dependences in mutualisms are thought to be generated by coevolutionary complementarity (*e.g.*, matching phenotypic traits

favoring interactions between plants and pollinator) and coevolutionary convergence (*e.g.*, convergence of traits among plants dispersed by birds rather than mammals) (Bascompte & Jordano 2006). Asymmetry in antagonisms, on the other hand, is shaped by coevolutionary alternation (Nuismer & Thompson, 2006) (*e.g.*, selection favoring mistletoes attacking less-defended hosts), which operates in highly specific systems (Bascompte & Jordano 2006). *Psittacanthus* mistletoes established highly generalist associations with the plant species, while the host species were mostly susceptible to infection by a single mistletoe species. Therefore, asymmetry in the mistletoe–host network is the combination of interactions between generalist mistletoes and infection-specific hosts.

Studies of plant–plant antagonistic networks have focused on nestedness and negative cooccurrence patterns of interactions among species (Blick & Burns 2009). Negative cooccurrence patterns might reflect community assembly rules in species distributions, which state that local communities are assembled from regional species pools by local-scale processes (Blick & Burns 2009). In Blick and Burns (2009), negative cooccurrence patterns indicate that the local process partly shaping host specificity is competition among species. These patterns can also indicate processes leading to a reduction in overlap between species. Vázquez *et al.* (2005) and Vacher *et al.* (2008) found evidence for nestedness in animal parasite–host networks and tree–fungus networks, respectively, and argued that the observed patterns partly result from the abundance of species.

A nested pattern suggests that biological processes such as passive sampling (species abundance and/or ubiquity), asymmetric interaction strength (species ecological specialization) and phenotypic complementarity (species morphological specialization) structure the system (Ulrich *et al.* 2009). Hypothetically, among the conditions that could have favored a nested distribution in the mistletoe–host network are homogeneous habitats or hosts; species with constant niche requirements regardless of the host; and equal chances for mistletoes to colonize or parasitize all host species in the study area. The mistletoe–host network showed a modular, non-nested pattern; thus, the system was not structured by random events (Blake 1991). The lack of nestedness might be caused by a differential capacity for infection by mistletoe species and/or defense strategies of hosts, by the dispersal capacity of mistletoes (*i.e.*, seed dispersers) or by the mosaic of habitat types, resulting in a heterogeneous composition of host species throughout the study site.

Modular analysis may indicate whether there are restrictions on the interactions among species, such as some degree of host specificity. Modules in the mistletoe–plant network indicate that associations are not established at random and that generalization occurs within only a subset of plant species. We found that each mistletoe species corresponded to a single module associated with a set of host species that were linked to each other by a few interactions. Dupont and Olesen (2009) found a similar topology in pollination networks with a few module hub species and many species identified as peripherals. In our system, most of the interactions occurred in *Psittacanthus* modules, particularly *P. cordata*,

which played a keystone role by interacting with a large number of host species within its module. Likewise, *Psittacanthus* spp. also interacted with more individuals per host species and infected hosts more intensively, as opposed to *P. abdita* and *Phoradendron* sp., which showed a more restricted pattern of parasitism. Phylogeny may be an important factor defining the composition of host species within modules. For instance, host plants from the *Psittacanthus* spp. modules included higher taxonomic diversity (at the family level) than did modules of *Phoradendron* and *Phthirusa*.

Ecological processes such as feeding behavior and movement patterns of avian seed dispersers might explain the distribution and differential levels of mistletoe infections on hosts (Reid 1989, Monteiro *et al.* 1992, Martínez del Río *et al.* 1995, Martínez del Río *et al.* 1996, Lopez de Buen & Ornelas 1999, Aukema & Martínez del Río 2002). Recently, Rist *et al.* (2011) attributed the small-scale distribution patterns of the mistletoe *Taxillus tomentosus* solely to dispersal processes. Thus, differences in the interactions exhibited by mistletoes in Pantanal may be, primarily, due to the composition, abundance and behavior of seed dispersers (Norton & de Lange 1999). Indeed, *Psittacanthus* spp. seeds are dispersed by several species of birds, especially fly-catchers, thrushes and tanagers (C. Donatti & M. Galetti, unpubl. data), whereas *Phoradendron* seeds are dispersed by few specialized seed dispersers, such as *Euphonia* (Restrepo *et al.* 2002, Cazetta & Galetti 2007). In Pantanal, *Euphonia chlorotica* (Fringilidae) was responsible for 85 percent of the visits to *Phoradendron* fruits (C. Donatti, unpubl. data). Unfortunately, little is known about *Phthirusa* seed dispersal. In a more specialized interaction, as between *Phoradendron* and *Euphonia* (Carlo & Aukema 2005, Ward & Paton 2007), frugivore behavior may cause a restricted pattern of mistletoe–host interactions.

Blick and Burns (2009) found that most mistletoe species infected only one or a small number of host species and suggested that specialized host preferences resulted from coevolutionary processes acting upon interacting species. However, mistletoes exhibit different interaction patterns with host species throughout their geographical range, and while specialized interaction patterns are favored by the advantages of interacting with relatively abundant hosts, generalized interaction patterns may be advantageous in heterogeneous communities (Norton & Carpenter 1998, Norton & De Lange 1999), which may be true for *Psittacanthus* in Pantanal. *Phoradendron* and *Phthirusa* are more restricted to gallery forests and cerrados, respectively. Yet, the host species infected by these two mistletoes are not exclusive to these habitats; thus, specificity is expected to be more related to micro-habitat suitability or habitat preferences by its seed dispersers, than to the physiological compatibility between mistletoes and hosts.

The modular pattern of the mistletoe–host network and the role of each mistletoe species appear to be closely related to their dispersal agents. Mistletoe species that exhibited a module hub role were associated with a wider array of dispersal agents, suggesting that this mechanism contributes to a wider host use by these species. The asymmetry in interaction strength is the result of the host species linking to just one of the mistletoe species, which resulted in the peripheral role presented by all host species.

The small overlap among host species infected by each mistletoe species may, to some degree, also result from a balance between mistletoe specialization and host resistance (Medel *et al.* 2004).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. List of hosts'n species at Fazenda RioNegro, Pantanal.

FIGURE S1. Frequency distributions of interaction strength-values within a parasitic mistletoe–host plant community.

FIGURE S2. The roles of the species in the Pantanalmistletoe–host network.

APPENDIX S1. List of hosts'n species.

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LITERATURE CITED

- AMEIDA-NETO, M., P. GUIMARÃES, P. R. JR. GUIMARÃES, R. D. LOYOLA, AND W. ULRICH. 2008. A consistent metric for nestedness analysis in ecological systems: Reconciling concept and quantification. *Oikos* 117: 1227–1239.
- AUKEMA, J. E., AND C. MARTÍNEZ DEL RÍO. 2002. Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology* 83: 3489–3496.
- BASCOMPTE, J., AND P. JORDANO. 2006. The structure of plant-animal mutualistic networks. In M. Pascual and J. A. Dunne (Eds.) *Ecological networks: linking structure to dynamics in food webs*, pp. 143–159. Oxford University Press, New York.
- BASCOMPTE, J., AND P. JORDANO. 2007. Plant-animal mutualistic networks: The architecture of biodiversity. *Annu. Rev. Ecol. Syst.* 38: 567–593.
- BASCOMPTE, J., P. JORDANO, C. J. MELIÁN, AND J. M. OLESEN. 2003. The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* 100: 9383–9387.
- BLAKE, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. *Conserv. Biol.* 5: 58–66.
- BLICK, R., AND K. BURNS. 2009. Network properties of arboreal plants: Are epiphytes, mistletoes and lianas structured similarly? *Perspect. Plant Ecol. Evol. Syst.* 11: 41–52.
- BURNS, K. 2007. Network properties of an epiphyte metacommunity. *J. Ecol.* 95: 1142–1151.
- CARLO, T. A., AND J. E. AUKEMA. 2005. Female-directed dispersal and facilitation between a tropical mistletoe and a dioecious host. *Ecology* 86: 3245–3251.

- CARSTENSEN, D. W., AND J. M. OLESEN. 2009. Wallacea and its nectarivorous birds: Nestedness and modules. *J. Biogeogr.* 36: 1540–1550.
- CAZETTA, E., AND M. GALETTI. 2007. Frugivoria e especificidade por hospedeiros na erva-de-passarinho *Phoradendron rubrum* (L.) Griseb (Viscaceae). *Rev. Bras. Bot.* 30: 351–357.
- DICKS, L. V., S. A. CORBET, AND R. F. PYWELL. 2002. Compartmentalization in plant-insect flower visitor webs. *J. Anim. Ecol.* 71: 32–43.
- DUPONT, Y. L., AND J. M. OLESEN. 2009. Ecological modules and roles of species in heathland plant-insect flower visitor networks. *J. Anim. Ecol.* 78: 346–353.
- FONSECA, C. R., AND G. GANADE. 1996. Asymmetries, compartments and null interactions in an Amazonian ant-plant community. *J. Anim. Ecol.* 65: 339–347.
- FORTUNA, M. A., A. G. POPA-LISSENAU, C. IBÁÑEZ, AND J. BASCOMPTE. 2009. The roosting spatial network of a BIRD-predator bat. *Ecology* 90: 934–944.
- GUIMARAES, P. R., V. RICO-GRAY, P. S. OLIVEIRA, T. J. IZZO, S. F. DOS REIS, AND J. N. THOMPSON. 2007b. Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Curr. Biol.* 17: 1797–1803.
- GUIMARÃES, P. R., AND P. GUIMARÃES. 2006. Improving the analyses of nestedness for large sets of matrices. *Environ. Model. Softw.* 21: 1512–1513.
- GUIMARÃES, P. R., V. RICO-GRAY, S. F. DOS REIS, AND J. N. THOMPSON. 2006. Asymmetries in specialization in ant-plant mutualistic networks. *Proc. R. Soc. Lond. B* 273: 2041–2047.
- GUIMARÃES, P. R., C. SAZIMA, S. F. DOS REIS, AND I. SAZIMA. 2007a. The nested structure of marine cleaning symbiosis: Is it like flowers and bees? *Biol. Lett.* 3: 51–54.
- GUIMERÀ, R., AND L. A. N. AMARAL. 2005a. Functional cartography of complex metabolic networks. *Nature* 433: 895–900.
- GUIMERÀ, R., AND L. A. N. AMARAL. 2005b. Cartography of complex networks: Modules and universal roles. *J. Stat. Mech. Theory Exp.*, art no P02001.
- GUIMERÀ, R., S. MOSSA, A. TURTSCHI, AND L. A. N. AMARAL. 2005. The worldwide air transportation network: Anomalous centrality, community structure and cities' global roles. *Proc. Nat. Acad. Sci. USA* 102: 7794–7799.
- HARRIS, M. B., W. TOMAS, G. MOURÃO, C. J. DA SILVA, E. GUIMARÃES, F. SONODA, AND E. FACHIM. 2005. Safeguarding the Pantanal Wetlands: Threats and Conservation Initiatives. *Conserv. Biol.* 19: 714–720.
- JORDANO, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *Am. Nat.* 129: 657–677.
- JORDANO, P., J. BASCOMPTE, AND J. M. OLESEN. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.* 6: 69–81.
- KRATOCHWIL, A., M. BEIL, AND A. SCHWABE. 2009. Complex structure of pollinator-plant interaction-webs: Random, nested, with gradients or modules? *Apidologie* 40: 634–650.
- LEWINSOHN, T. M., P. I. PRADO, P. JORDANO, J. BASCOMPTE, AND J. M. OLESEN. 2006. Structure in plant-animal interaction assemblages. *Oikos* 113: 174–184.
- LOPEZ DE BUEN, L., AND J. F. ORNELAS. 1999. Frugivorous birds, host selection and the mistletoe *Psittacanthus schiedeianus*, in central Veracruz, Mexico. *J. Trop. Ecol.* 15: 329–340.
- MACRAIL, L. M., J. Q. RADFORD, AND A. F. BENNETT. 2009. Other communities: Box mistletoe (*Amyema miquelii*) parasitism is not detrimental to the health of grey box (*Eucalyptus microcarpa*) trees at a regional scale. *Ecol. Manage. Restor.* 10: 148–150.
- MALONEY, P. E., AND D. M. RIZZO. 2002. Dwarf mistletoe – host interactions in mixed-conifer forests in the Sierra Nevada. *Phytopathology* 92: 507–602.
- MARTÍNEZ DEL RIO, C., M. HOURDEQUIN, A. SILVA, AND R. MEDEL. 1995. The influence of cactus size and previous infection on bird deposition of mistletoe seeds. *Aust. J. Ecol.* 20: 571–576.
- MARTÍNEZ DEL RIO, C., A. SILVA, R. MEDEL, AND M. HOURDEQUIN. 1996. Seed dispersers as disease vectors: Bird transmission of mistletoe seeds to plant hosts. *Ecology* 77: 912–921.
- MEDEL, R., E. VERGARA, A. SILVA, AND M. KALIN-ARROYO. 2004. Effects of vector behavior and host resistance on mistletoe aggregation. *Ecology* 85: 120–126.
- MEMMOTT, J. 1999. The structure of a plant pollinator food web. *Ecol. Lett.* 2: 276–280.
- MEMMOTT, J., H. C. J. GODFRAY, AND I. D. GAULD. 1994. The structure of a tropical host-parasitoid community. *J. Anim. Ecol.* 63: 521–540.
- MONTEIRO, R. F., R. P. MARTINS, AND K. YAMAMOTO. 1992. Host specificity and seed dispersal of *Psittacanthus robustus* (Loranthaceae) in South-East Brazil. *J. Trop. Ecol.* 8: 307–314.
- NORTON, D. A., AND M. A. CARPENTER. 1998. Mistletoes as parasites: Host specificity and speciation. *Trends Ecol. Evol.* 13: 101–105.
- NORTON, D. A., AND P. J. DE LANGE. 1999. Host specificity in parasitic mistletoes (Loranthaceae) in New Zealand. *Funct. Ecol.* 13: 552–559.
- NUISMER, S. L., AND J. N. THOMPSON. 2006. Coevolutionary alternation in antagonistic interactions. *Evolution* 60: 2207–2217.
- OLESEN, J. M., J. BASCOMPTE, Y. L. DUPONT, AND P. JORDANO. 2007. The modularity of pollination networks. *Proc. Nat. Acad. Sci. USA* 104: 19891–19896.
- OILLERTON, J., D. MCCOLLIN, D. G. FAUTIN, AND G. R. ALLEN. 2007. Finding NEMO: Nestedness engendered by mutualistic organization in anemone-fish and their hosts. *Proc. R. Soc. Lond. B Biol. Sci.* 274: 591–598.
- POTT, A., AND V. J. POTT. 1994. Plantas do Pantanal. EMBRAPA, CPAP, Corumbá, MS, Brazil, 320 pp.
- PRADO, P. I., AND T. M. LEWINSOHN. 2004. Compartments in insect-plant associations and their consequences for community structure. *J. Anim. Ecol.* 73: 1168–1178.
- PRANCE, G. T., AND G. B. SCHALLER. 1982. Preliminary study of some vegetation types of the Pantanal Mato Grosso, Brazil. *Brittonia* 34: 228–251.
- RAFFAELLI, D., AND S. J. HALL. 1992. Compartments and predation in an estuarine food web. *J. Anim. Ecol.* 61: 551–560.
- REID, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: Components of seed dispersal quality. *Ecology* 70: 137–145.
- RESTREPO, C., S. SARGENT, D. J. LEVEY, AND D. M. WATSON. 2002. The role of vertebrates in the diversification of New World Mistletoes. In D. J. Levey, W. R. Silva, and M. Galetti (Eds.) *Seed dispersal and frugivory: ecology, evolution and conservation*, pp. 83–98. CABI, Wallingford, UK.
- RHODE, K., W. B. WORTHEN, M. HEAR, B. HUEGUENY, AND J. F. GUÉGHAN. 1998. Nestedness in assemblages of metazoan ecto- and endoparasites of marine fish. *Int. J. Parasitol.* 28: 543–549.
- RIST, L., R. UMA SHAANKER, AND J. GHAZOUL. 2011. The spatial distribution of mistletoe in a Southern Indian Tropical Forest at multiple scales. *Biotropica* 43: 50–57.
- ROHDE, K., W. B. WORTHEN, M. HEAR, B. HUGUENY, AND J. F. GUÉGAN. 1998. Nestedness in assemblages of metazoan ecto- and endoparasites of marine fish. *Int. J. Parasitol.* 28: 543–549.
- SFAIR, J. C., A. L. C. ROCHELLE, A. A. REZENDE, J. VAN MELISB, V. L. WEISER, AND F. R. MARTINS. 2010. Nested liana-tree network in three distinct neotropical vegetation formations perspective. *Plant Ecol. Evol.* 12: 277–281.
- SWARTZ, F. A. 2000. The Pantanal in the 21st century for the planet's largest wetland, an uncertain future. In F. A. Swartz (Ed.) *The Pantanal of Brazil, Bolivia and Paraguay*, pp. 1–24. Hudson MacArthur Publishers, Gouldsboro.
- THOMPSON, J. N., AND C. FERNANDEZ. 2006. Temporal dynamics of antagonism and mutualism in a geographically variable plant-insect interaction. *Ecology* 87: 103–112.
- THÉBAULT, E., AND C. FONTAINE. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329: 853–856.

- ULRICH, W., M. ALMEIDA-NETO, AND N. GOTELLI. 2009. A consumer's guide to nestedness analysis. *Oikos* 118: 3–17.
- VACHER, C., D. PLOU, AND M. L. DESPREZ-LOUSTAU. 2008. Architecture of an antagonistic tree/fungus network: The asymmetric influence of past evolutionary history. *Plos ONE* 3: e1740.
- VÁZQUEZ, D. P., C. J. MELLÁN, N. M. WILLIAMS, N. BLÜTHGEN, B. R. KRASNOV, AND R. POULIN. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116: 1120–1127.
- VÁZQUEZ, D. P., R. POULIN, B. R. KRASNOV, AND G. I. SHENBROT. 2005. Species abundance and the distribution of specialization in host–parasite interactions. *J. Anim. Ecol.* 74: 946–955.
- WARD, M. J., AND D. C. PATON. 2007. Predicting mistletoe seed shadow and patterns of seed rain from movements of the mistletoebird, *Dicaeum birundinaeum*. *Aus. Ecol.* 32: 113–121.
- WATSON, D. M. 2001. Mistletoe – a keystone resource in forests and woodlands worldwide. *Annu. Rev. Ecol. Syst.* 32: 219–249.