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## Research article

# Nested liana-tree network in three distinct neotropical vegetation formations

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## ABSTRACT

Despite the increasing number of studies on lianas, few of them have focused on liana and host-tree (phorophyte) interactions from a network perspective. Most studies found some network structure in other systems, such as plant facilitation and host-epiphyte. However, a recent study found no structure in a small network of liana–phorophyte interactions. Our aim was to investigate the hypothesis that rich, highly diverse systems yield large interaction networks with some structure. If so, networks of liana–phorophyte interactions in highly diverse systems will have one or more of the following structures: compartmentalized, nested or compound. We sampled three highly diverse vegetation formations: a tropical rainforest, a tropical seasonally dry forest, and a woodland savanna, all in southeastern Brazil. We used simulated annealing to test compartmentalization and found no compartment in any of the three networks analyzed. By means of a modified classical temperature index, we found a nested structure in all three sites sampled. We inferred that these nested structures might result from phorophyte characteristics and sequential colonization by different liana species and might promote increased diversity in tropical tree formations. We propose that, according to the system complexity and the different variables associated with site and liana–phorophyte characteristics, a network may have a structure, which arises in more complex systems. Since we have investigated highly diverse systems with large networks, nestedness could be clearly detected in our study.

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## Introduction

Woody climbing plants (lianas) and their host-plants (phorophytes) are considered to engage in antagonistic interactions. Lianas compete with trees above ground for light and below ground for nutrients, both in the stages of seedling (Toledo-Aceves and Swaine, 2008) and sapling (Dillenburg et al., 1993a,b, 1995; Schnitzer et al., 2005). Consequently, lianas decrease phorophyte fecundity (Kainer et al., 2006) and growth rate (Campanello et al., 2007).

The studies cited above focused on pairs of particular species, but recently Blick and Burns (2009) analyzed the interaction between all species of lianas and phorophytes in a community and found no structure in the liana–phorophyte network. The absence of structure may be due to their small network, since

larger mutualistic networks are more prone to have some structure (Bascompte et al., 2003; Guimarães et al., 2006; Rodríguez-Gironés and Santamaría, 2006; Olesen et al., 2007; Almeida-Neto et al., 2008; Bastolla et al., 2009). However, networks of different interaction types, such as parasitism and mutualism, have some structure, which may assume three basic forms: compartmentalized (or modular), nested, and compound (Lewinsohn et al., 2006). A compartmentalized structure is characterized by recognizable subsets of interacting species that are more linked within subsets than across them (Lewinsohn et al., 2006). Ant-plant mutualism (Fonseca and Ganade, 1996) and pollination (Dicks et al., 2002; Olesen et al., 2007) display a compartmentalized network structure. In a nested structure, species with fewer interactions are subsets of species with more interactions (Bascompte et al., 2003). In our investigation, if a network were nested, liana species with fewer interactions would link to phorophyte species with more interactions, and phorophytes would display the same pattern. In addition, liana and phorophyte species with more interactions tend to link to each other, establishing a dense core of interactions.

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Although most nested bipartite graphs had been found for mutualistic interactions (Bascompte et al., 2003; Guimarães et al., 2006, 2007), nestedness was also reported in parasitism networks (Rohde et al., 1998; Timi and Poulin, 2007; Graham et al., 2009). Hence, we assume that the implications of nestedness can be generalized to antagonistic interactions (Graham et al., 2009), such as those between lianas and phorophytes. We must highlight that both compartmentalization and nestedness may be detected in the same network, and one structure may be complementary to the other (Olesen et al., 2007). According to Fortuna et al. (2010), the presence of both structures in the same network may be due to connectance (matrix fill): if connectance is low, nested networks tend to be also modular, but if connectance is high the relationship between these two structures is negative, implying in the existence of trade-offs in the community organization. A bipartite graph can also have a compound structure, i.e., each compartment has its own nested structure, as found for a community of herbivores and Asteraceae inflorescences in Brazil (Lewinsohn et al., 2006) and for bats and their roosting sites (Fortuna et al., 2009). The analysis of a compound network structure is only applicable when compartments are detected.

The same kind of ecological interaction can be represented by networks with different structures, e.g., mutualistic networks may be either nested (Bascompte et al., 2003) or compartmentalized (Dicks et al., 2002), depending on the importance of the characters, the seasonality, and the behavior of the species and site sampled (Dicks et al., 2002). However, the size of a network may also influence the detection of a structure. On the one hand, pollination networks with more than 50 species are significantly nested and some are modular, whereas networks with more than 150 species are always modular (Olesen et al., 2007). On the other hand, smaller networks can have a haphazardly arisen structure. For example, significant nestedness can be detected in small networks (Rodríguez-Gironés and Santamaría, 2006), because they may be nested by chance, irrespective of the metric used (Almeida-Neto et al., 2008). Guimarães et al. (2006) suggested that only rich systems show nestedness, since the nestedness value increases as the network size increases (Bascompte et al., 2003; Guimarães et al., 2006; Rodríguez-Gironés and Santamaría, 2006; Almeida-Neto et al., 2008; Bastolla et al., 2009). Therefore, structures such as compartmentalization and nestedness tend to arise as a system becomes more complex.

Our aim is to investigate the hypothesis that rich, highly diverse systems yield large interaction networks with some structure. If this hypothesis holds, the network of interactions between lianas and phorophytes will show some structure in the most important types of tropical vegetation, namely, rainforest, seasonal forest, and savanna.

## Methods

### Site characteristics and sampling

We sampled lianas and trees rooted within plots in three different sites, all in the state of São Paulo, southeastern Brazil (Fig. 1). These sites have different plant formations, to which different sampling designs were applied, considering the peculiarities of each community, such as average height, diameter, and density of lianas and trees. For example, the savanna woodland has thinner and smaller trees than those in the tropical rainforest, so the minimum 15 cm of trunk perimeter at breast height (PBH) used to sample the tropical rainforest would include few individuals if adopted in the savanna plots. In all three sites, the sampled area corresponded to 1 ha divided into 100 plots of 10 m × 10 m each (contiguous in

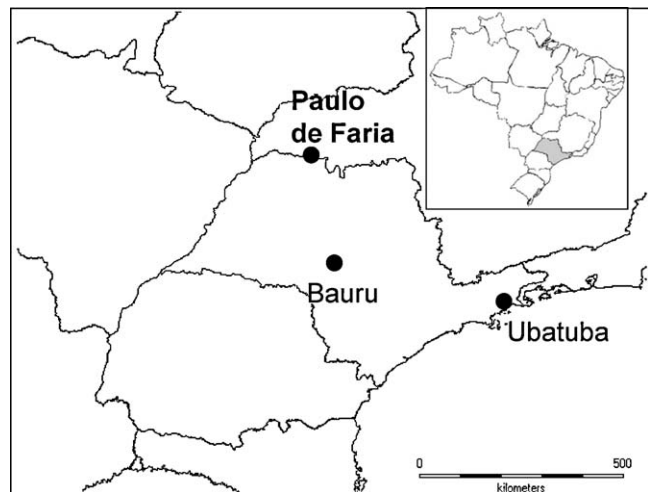


Fig. 1. The three areas sampled in the state of São Paulo, Brazil, have distinct vegetation types: tropical rainforest (Ubatuba), tropical seasonally dry forest (Paulo de Faria), and savanna woodland (Bauru).

the rain and seasonal forests, and random in the savanna woodland).

The first site (23°21'54"–59"S and 45°05'02"–04"W, 348–394 m above sea level) is a tropical rainforest in the municipality of Ubatuba, in the Parque Estadual da Serra do Mar, a conservation unit of 47,500 ha. The climate is Af (after Koeppen, 1948), i.e., humid tropical with no dry season. The mean annual temperature is 20.6 °C, and mean annual rainfall is 2320 mm (van Melis and Martins, unpublished). We surveyed all dead and living plants with PBH ≥ 15 cm (Rochelle et al., unpublished) and all lianas with DBH (stem diameter at breast height) ≥ 1 cm (van Melis and Martins, unpublished).

The second site (19°55'–58"S and 49°31'–32"W, 400–495 m above sea level) is a fragment of 435.73 ha of tropical seasonally dry forest (Rezende et al., 2007) in the municipality of Paulo de Faria. The climate is Koeppen's Aw, i.e., hot humid tropical with summer rain and dry season in winter, with mean annual temperature of 24 °C and mean annual rainfall of 1245 mm. We excluded plots with densely tangled lianas, and sampled living trees with DBH ≥ 3 cm and lianas with DBH ≥ 1 cm.

The third site (22°19'41"–21'06"S and 48°59'49"–49°01'12"W, 519–603 m above sea level) is a fragment of 321.71 ha of savanna woodland in the municipality of Bauru. The climate is Koeppen's Cwa, i.e., hot temperate with a wet season from September to June and a short dry season in July and August (Weiser, 2007). Mean annual rainfall is 1331 mm, and mean annual temperature is 22.6 °C. We sampled all living trees with DBH ≥ 0.1 cm and all lianas with DSH (stem diameter at soil height) ≥ 0.1 cm (Weiser, 2007).

### Compartmentalization

To estimate the number of modules, we used the algorithm developed by Guimerà and Amaral (2005), based on simulated annealing. First, the method identifies modules in the network and, then, maximizes the modularity. The index of modularity  $M$  is:

$$M \equiv \sum_{s=1}^{N_M} \left[ \frac{l_s}{L} - \left( \frac{d_s}{2L} \right)^2 \right]$$

where  $N_M$  is the number of modules,  $l_s$  is the number of links between nodes in modules,  $L$  is the number of links in the network, and  $d_s$  is the sum of degrees (number of links) of the nodes in module  $s$  (Guimerà and Amaral, 2005).  $M=0$  indicates that all nodes are placed at random into modules or all nodes are in the same cluster (Guimerà and Amaral, 2005). We generated 100 random networks with the same matrix fill as the original matrix and examined whether the original network was more or less modular than the random networks.

Although an algorithm for bipartite network was available (Guimerà et al., 2007), we used the algorithm for one-mode network (Guimerà and Amaral, 2005). We considered this was the best approach in our case, because: (1) the one-mode network algorithm looks for modules in the entire network; (2) in the two-mode network algorithm, the group of lianas does not necessarily correspond to the group of trees; (3) null models are not available for the two-mode network algorithm. This approach was the same adopted by Olesen et al. (2007).

### Nestedness

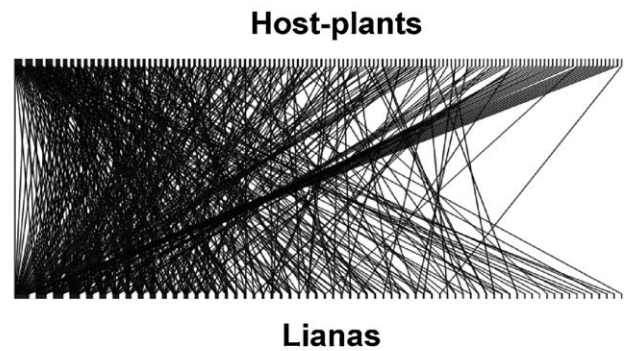
We adopted the same modified nestedness ( $N_{Tm}$ ) index that Blick and Burns (2009) used to analyze their matrix of interactions between lianas and phorophytes. The classical temperature index (for calculation details, see Atmar and Patterson, 1993) has received some criticism, especially due to issues related to the algorithm used in the software, the isocline of perfect order employed to calculate nestedness temperature, the underestimation of type I error in the null model (Fischer and Lindenmayer, 2002; Rodríguez-Gironés and Santamaría, 2006), and to the fact that this method is more sensitive to matrix fill, shape and size than similar metrics (Almeida-Neto et al., 2008). Moreover, according to Rodríguez-Gironés and Santamaría (2006) and Almeida-Neto et al. (2007, 2008), classical temperature ( $T$ ) should not be considered a disorder measure, since a random distribution of presences in the matrix would not return  $T=100$ . The nestedness index we used alleviates some of the problems mentioned above and furnishes a more conservative value (Ulrich, 2006). Following Blick and Burns's (2009) procedure, we calculated  $N_{Tm}$  and compared the observed values with those obtained from 1000 random matrices generated by default in the *NESTEDNESS* software, using fixed row and column totals with sequential swap method of matrix fill (Ulrich, 2006). The nestedness value ( $N_{Tm}$ ) is obtained from the formula  $N_{Tm} = (100 - T)/100$ . Values range from 0 to 1, where 1 represents maximum nestedness (Bascompte et al., 2003). We used the nestedness value ( $N_{Tm}$ ) in relation to the temperature value itself ( $T$ ), since we intended to emphasize nestedness and not matrix disorder (Bascompte et al., 2003).

## Results

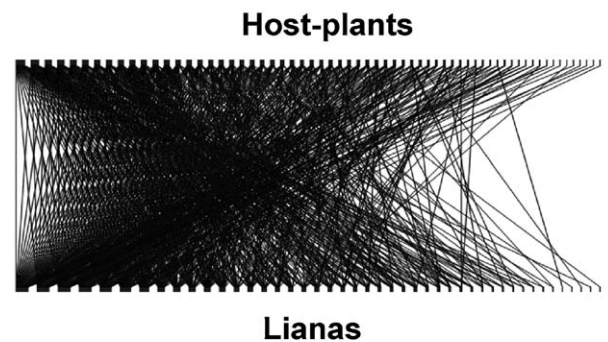
### Sampling

Ubatuba was the richest site in lianas and trees (66 liana and 210 tree species), followed by Bauru (39 liana and 140 tree species) and Paulo de Faria (45 liana and 87 tree species). However, only 125, 119, and 64 tree species, respectively, had associated lianas in those sites (Fig. 2). These species were the ones we considered in our network analyses. The proportion of tree species that were free from lianas varied in each community: 40.47% in Ubatuba, 26.43% in Paulo de Faria, and 15% in Bauru. The number of links between lianas and phorophytes also varied among sites: 459 in Ubatuba, 1704 in Paulo de Faria, and 955 in Bauru (Fig. 2). Matrix fill was affected by species number and link density: the highest matrix fill

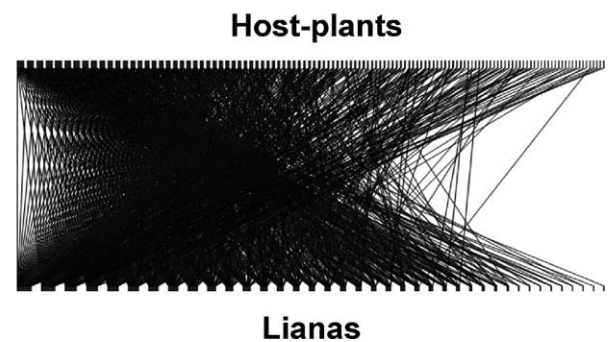
### (a) Ubatuba



### (b) Paulo de Faria



### (c) Bauru



**Fig. 2.** Network representation of liana–phorophyte (host-plants) associations in the three sites under study. Species of lianas and phorophytes are represented by squares and the associations between them are represented by lines. The figures were rearranged to maximize nested structures.

occurred in Paulo de Faria (0.2291), followed by Bauru (0.2057) and Ubatuba (0.0556).

### Compartmentalization

We did not detect compartments in any liana–phorophyte interaction matrix. In Ubatuba, the modularity index ( $M=0.396467$ ) was lower than the null models, with a mean of 0.403178 ( $SD=\pm 0.005851$ ). The modularity in Paulo de Faria was lower ( $M=0.177980$ ) than the null models (mean=0.204906;  $SD=\pm 0.005294$ ). In Bauru, the modularity index was also lower ( $M=0.188853$ ) than the null models, with a mean of 0.196114 ( $SD=\pm 0.003995$ ).

### Nestedness

Interaction matrices showed high nestedness values when we used the temperature value modified by Ulrich (2006) in Ubatuba ( $N_{Tm}=0.95$ ), Paulo de Faria ( $N_{Tm}=0.87$ ), and Bauru ( $N_{Tm}=0.93$ ). All these values indicate significantly nested networks ( $p < 0.05$ ).

### Discussion

We found a nested pattern in the liana–phorophyte networks for all three samples. Our result is different from Blick and Burns's (2009), in which a network of 9 liana and 16 phorophyte species had no pattern. Our result confirmed the hypothesis that some structure arises in large networks, whereas small networks have haphazardly arisen structures. Blick and Burns's (2009) results may be related to their matrix fill (or connectance) which was of 47%. For a small network with a matrix fill close to 40%, the chance of a random matrix to be significantly nested is small (Nielsen and Bascompte, 2007). The matrix fill must be very high to yield a significant nestedness value for a small matrix (Nielsen and Bascompte, 2007). Our networks were large and had a low matrix fill (less than 25%). According to Nielsen and Bascompte (2007), increased sampling efforts yield large networks, which also have a low matrix fill, as is the case of our matrices. Therefore, because our networks were large with a low matrix fill, we could easily detect significant nestedness.

Given that we found a nested structure in the liana–phorophyte network of each of these formations, which are very different from one another, though highly diverse, we confirmed our hypothesis that interaction structures are more easily recognizable in richer systems. However, our matrices were not large enough to split into compartments. This result corroborated the statement by Olesen et al. (2007) that compartments arise only in very large networks. A compartmentalized structure can derive from restrictions to species ranges (Lewinsohn et al., 2006), pollination syndrome and phenology (Dicks et al., 2002), stronger link specificity, and larger networks (Olesen et al., 2007). A compartmentalized structure also arises in networks of systems in which parasite or pathogen spread is slowing down (Guimerà et al., 2007). We speculate that we would probably detect compartments in our networks if our samples were larger.

However, we also believe that the interaction structure may be influenced by the characteristics of the sites sampled. For example, pollination networks can be either nested (Bascompte et al., 2003) or compartmentalized (Dicks et al., 2002). In this case, compartmentalization may be explained by pollination syndromes, animal and plant seasonality, and pollinator behavior (Dicks et al., 2002), as well as by network size (Olesen et al., 2007). Similarly, we suppose that a liana–phorophyte network might have no structure (as in Blick and Burns, 2009) or might be nested (as in our results), depending on the characteristics of the sampled sites, trees, and lianas. For example, all sites we sampled are in tropical climates with high yearly average temperatures, whereas Blick and Burns (2009) analyzed samples collected in the colder climate of New Zealand.

The process of nestedness build-up is related to species abundance and to temporal and spatial distribution processes (Vázquez et al., 2009). The nested structure is less sensitive to species loss, keeping a strong cohesion in the network (Memmott et al., 2004). The significant nestedness values we found for the three areas sampled are similar to the ones observed in most studies using the bipartite graph approach (Bascompte et al., 2003; Guimarães et al., 2006, 2007; Selva and Fortuna, 2007; Graham

et al., 2009), including those emphasizing plant–plant interaction (Burns, 2007; Verdú and Valiente-Banuet, 2008; Blick and Burns, 2009; Silva et al., 2010). Nestedness has considerable implications for plant–plant interactions. In epiphyte–phorophyte interactions, nestedness would derive from sequential colonization by epiphytes. Once an epiphyte establishes on a tree, it creates favorable conditions for the establishment of other epiphytes in a facilitation process (Burns, 2007; Blick and Burns, 2009). According to Pinard and Putz (1994), lianas that have already reached tree canopy would facilitate climbing for other lianas. Nestedness was also found in networks of facilitation among desert plants (Verdú and Valiente-Banuet, 2008). The facilitation process preserves plant diversity, because generalist nurse-species promote the growth of several specialist facilitated-species (Verdú and Valiente-Banuet, 2008). Likewise, several studies suggested that some phorophytes, generally the largest (Nesheim and Økland, 2007; Carrasco-Urra and Gianoli, 2009; Ding and Zang, 2009; Jiménez-Castillo and Lusk, 2009; Homeier et al., 2010), have more lianas. Smaller or juvenile trees, which do not reach the forest canopy, would be used as a shortcut by lianas, especially those with tendrils, when trying to reach taller trees (Carsten et al., 2002). Therefore, liana richness increases as phorophyte diameter increases (Burns and Dawson, 2005).

In general, nestedness denotes the presence of specialist and generalist species, i.e., species displaying numerous links and species with fewer links. Besides, 40.47% of tree species in Ubatuba, 26.43% in Paulo de Faria, and 15% in Bauru did not have associated lianas. Therefore, in all communities we analyzed, there was a gradient in the liana–phorophyte association, which ranged from species without interaction, through species with few interactions, to those with many links. Other studies using different statistical and mathematical tools obtained similar results. Carsten et al. (2002), Muñoz et al. (2003), and Nesheim and Økland (2007) also found specificity between lianas and phorophytes, i.e., certain trees never had lianas, whereas others had many of them. According to Nesheim and Økland (2007), some phorophyte species would have more lianas than others, whereas some trees would have fewer lianas than expected. Some factors, such as size, stem roughness, flexibility of trees (Carsten et al., 2002; Chittibabu and Parthasarathy, 2001; Nesheim and Økland, 2007), and the climbing mode of lianas (Carsten et al., 2002) would contribute to the specificity of liana–phorophyte associations. Yet Padaki and Parthasarathy (2000) and Pérez-Salicrup et al. (2001) found that the relationship between liana and phorophyte species is not species-specific. Other variables for trees, such as canopy illumination (Malizia and Grau, 2006), size (Nesheim and Økland, 2007; Carrasco-Urra and Gianoli, 2009; Ding and Zang, 2009; Jiménez-Castillo and Lusk, 2009; Homeier et al., 2010), fruit type (Carsten et al., 2002), compound leaves (Carse et al., 2000), spiny trunk (Maier, 1982), and palms (Carse et al., 2000; Pérez-Salicrup et al., 2001; Campanello et al., 2007) would be more important than phorophyte identity. Therefore, phorophytes with few lianas or without them would probably have some characteristics that would decrease or hinder their occupation by lianas. Additionally, generalist phorophyte and liana species would have other features that would promote their association. These particular differences among species would result in the nested structure of liana–phorophyte associations we found.

Our study showed that lianas and phorophytes have a nested interaction structure in the three sites analyzed. We did not find compartmentalized or compound structures nor, as Blick and Burns (2009) described, networks with no structure. We assume that phorophyte characteristics and their sequential colonization by lianas are plausible explanations for nestedness, which is also related to increased tree and liana diversity in tropical

forests. Future works may determine the causes of nestedness in liana–phorophyte associations.

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