Weak phylogenetic signal for specialisation in antagonistic liana–tree networks

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**Background:** Antagonistic interactions, such as parasitism and herbivory, are generally specialised and have a strong phylogenetic signal for specialisation. As lianas and trees interact antagonistically, we expect to find phylogenetic signal for specialisation.

**Aims:** We aimed to answer the following questions: (1) Is the liana–tree network specialised? (2) Is the specialisation of a liana–tree network related to the abundance of both the life forms? (3) Is liana and tree specialisation related to species phylogeny? (4) Do phylogenetically related liana species occupy phylogenetically related tree species, and vice versa?

**Methods:** For three areas in southern Brazil, we calculated the specialisation value of each liana and tree species (d) and of the entire network (H^d_2). Binomial regression and null models were used to test the role of abundance on d and H^d_2, respectively. We searched for the presence of phylogenetic signal with phylogenetic independent contrasts for d'. We also compared the similarity of species sets and their interaction with phylogenetic distance between them using Mantel test.

**Results:** All three networks had significant values of H^d_2, but the values of d' did not have significant phylogenetic signals. Closely related lianas did not share similar host-tree assemblages and vice versa. Rare species were more specialised than abundant species, and abundance did not influence H^d_2.

**Conclusions:** Our study indicates that the significant H^d_2 may be due to co-evolution in some lineages of lianas and trees. Nevertheless, the abundance of species may also play an important role in species interaction, mainly rare species.

**Keywords:** antagonist interaction; climber; ecological network; generalism; phorophyte; vine

**Introduction**

Species affinity with interacting species varies greatly, ranging from extreme specialisation to none. One way to assess how specialised interacting species are by analysing interaction networks. A network is a representation of the interactions that species establish among them, in such a way that species are represented by dots, and the interactions are represented by lines linking the dots (Bascompte and Jordano 2007). In a network, specialisation can be regarded as the limitation of the number of species with which a particular species interacts; conversely, generalist species (low specialisation value), can interact with a large number of other species. The degree of specialisation depends on different kinds of factors linked to, for example, species phenodynamics, geographic distribution (Thompson 1994, 2005), environment (Schleuning et al. 2011) and type of interaction. For instance, herbivore–plant networks have more narrow specialists, whereas pollination networks have more generalists (Fontaine et al. 2009). Extreme specialisation is predicted for parasites that complete all their developmental stages in a single host and for prey–predator systems when the prey species is abundant throughout the year, moves slowly and is geographically predictable (Thompson 1994).

Although these examples consider plant–animal and animal–animal relationships, different kinds of plant–plant interactions also occur, such as parasitism, competition, facilitation and allelopathy (Thorpe et al. 2011). For instance, the relationship between lianas and their host trees has been regarded as competition, since lianas reduce host-tree fecundity, growth and survival (Putz and Institute 1980; Schnitzer et al. 2005). In disturbed tropical forest fragments, lianas can become super-abundant (Laurance et al. 2001) and hinder tree growth (Schnitzer and Bongers 2002; Schnitzer et al. 2005), thus jeopardising the forest natural regeneration and leading to a paraclimax state (Schnitzer and Bongers 2002; Schnitzer et al. 2005; Campanello et al. 2007).

However, in spite of the great importance of liana–tree interaction for the fate of tropical forests, very little attention has been paid to the analysis of their networks. Blick and Burns (2009) found a random network for a very simple liana–tree system in New Zealand, but Sfair et al. (2010) found a nested network in three highly diverse Brazilian formations and concluded that the
nestedness gave stability to the system. To complement this debate, here we propose an alternative way to analyse liana–tree networks by asking whether lianas or trees would be specialised, as seen in animal–plant antagonistic networks. Since liana–tree interaction is always antagonistic, be it parasitic or competitive, we expected that their networks would resemble those of host–parasite (Thompson 1994) and herbivore–plant interactions (Fontaine et al. 2009), showing a high degree of specialisation.

Liana–tree interaction is strongly influenced by species abundance. For instance, at least 60% of interactions between lianas and trees are explained by species abundance (Sfair 2011). Abundance may also be related to some network structures of mutualistic (e.g. nestedness; Vázquez et al. 2009) and herbivore networks (e.g. compartmentalisation; Cagnolo et al. 2011). In mutualistic interactions, rare pollinators are more prone to be specialised (Dorado et al. 2011), which may influence the entire network specialisation. Because the relationship between specialisation and species abundance is unknown for antagonistic networks, we expect that rare species also influence specialisation in liana–tree networks.

The interactions amongst species may be shaped in part by the phylogenetic relationship among related species (Thompson 1994). Actually, 69% of antagonistic systems have phylogenetic signal (Gómez et al. 2010), that is phylogenetically related species tend to resemble each other in most phenotypic traits (Blomberg et al. 2003). If this holds for plant–plant interactions, specialisation may be phylogenetically conserved, that is more closely related species would be more specialised or more generalised than distantly related species. In animal–plant mutualistic interaction (Rezende et al. 2007) and plant–plant facilitation interaction (Verdú and Valiente-Banuet 2011), phylogeny has a strong influence shaping their networks. Similarly, for our investigation we proposed that phylogenetically related liana species have theoretically the potential to be associated with similar sets of trees, and phylogenetically related tree species may potentially be supporting similar sets of liana species. In other words, we expected that the interaction between liana and tree species would be phylogenetically determined. To guide our investigation we put forward the following questions: (1) Is the liana–tree network specialised in comparison with a random assembly of species? (2) Is the specialisation of liana–tree network related to the abundance of species? (3) Is liana and tree specialisation related to species phylogeny? (4) Do phylogenetically related liana species occupy phylogenetically related tree species, and are phylogenetically related tree species climbed by phylogenetically related liana species?

**Materials and methods**

We sampled lianas and trees rooted within plots in three different sites (a tropical rainforest, a tropical semi-deciduous seasonal forest and a savanna woodland) in the state of São Paulo, south-eastern Brazil. Different sampling designs were applied in view of the characteristics of each community, such as the average height, diameter, density of lianas and trees and our previous knowledge of the flora. In all three sites, the sampled area consisted of one 1-ha plot.

The first site (23°21’57” S and 45°05’03” W, 348–394 m above sea level) is a tropical rainforest in the municipality of Ubatuba (hereafter rainforest), in the Parque Estadual da Serra do Mar, a conservation unit of 47,500 ha. The climate is humid tropical with no dry season (Af after Köppen 1948). The mean annual temperature is 20.6°C, and the mean annual rainfall is 2320 mm (Sfair 2011). We surveyed all living plants with DBH (stem diameter at breast height) ≥ 4.8 cm and all lianas with DBH ≥ 1 cm.

The second site (19°56’39” S and 49°31’49” W, 400–495 m above sea level) is a fragment of 435.73 ha of the tropical semi-deciduous seasonal forest in the municipality of Paulo de Faria (hereafter seasonal forest). The climate is hot humid tropical with summer rain and dry season in winter (Köppen’s Aw), with mean annual temperature of 24°C and mean annual rainfall of 1245 mm. Since trees of the seasonal forest are shorter and have more slender trunks than those in the rainforest, we sampled living trees with DBH ≥ 3 cm and lianas with DBH ≥ 1 cm.

The third site (22°20’23” S and 49°00’30” W, 519–603 m above sea level) is a 296-ha fragment of savanna woodland in the municipality of Bauru. The climate is hot subtropical with a wet season from September to June and a short dry season in July and August (Köppen’s Cwa). The mean annual rainfall is 1331 mm, and the mean annual temperature is 22.6°C. In the savanna woodland, trees occur in much greater density, but are much shorter and have much more slender trunks than in the rain forest and semi-deciduous forest. Hence, we sampled all living trees with DBH ≥ 0.1 cm. Like the trees, lianas are much more slender in the savanna woodland, and we sampled all lianas with DSH (stem diameter at soil height) ≥ 0.1 cm.

To assess how specialised or generalised a liana (or tree) species and a network were, we used the specialisation indexes (d′ and H′ 0.5, respectively) implemented by Blüthgen et al. (2006) for quantitative networks. This index is defined as “the deviation from a conformity expected by the overall utilisation of potential partners” (Blüthgen et al. 2007, 341). It emphasises the proportional availability of the species niche and is based on the Shannon entropy-like diversity index (Blüthgen et al. 2006). We calculated for each species the value of d′, which ranges from 0 to 1, from the most generalised to the most specialised case, respectively. This index is preferable to other indices of specialisation (e.g. Bascompte et al. 2006; Vázquez et al. 2007) because d′ is more robust against variation in matrix size, shape and sampling effort (Blüthgen et al. 2006, 2008). We carried out binomial regressions between d′ and species abundance for each of three sites.
If specialised or generalised species prevailed in the network, we expected it to be more specialised or more generalised, respectively. To assess how specialised or generalised were our networks, we calculated the specialisation index $H'_s$ (Blüthgen et al. 2006) for the entire network. Like $d'$, $H'_s$ ranges between 0 and 1, for extreme generalisation and specialisation, respectively. To test the departure of the network specialisation index from random, we compared the observed $H'_s$ value with that obtained after 1000 randomisations, in which the marginal totals and the number of interactions in each random network were the same as in the original network (Vázquez et al. 2007). After carrying out the randomisations, we calculated a $H'_s$ value and the correspondent confidence interval (at 95% of probability) that would be expected if all interactions were established at random in the network.

Then, we assessed whether the $H'_s$ observed value was within, below or above the confidence interval of the expected value of $H'_s$. Proceeding this way, we could have the probability that the observed $H'_s$ was less or more specialised than that of the null model: if it fell within the confidence interval, it was not significantly different from random; but if it was below or above the confidence interval, the network would be generalised or specialised, respectively (Blüthgen 2010). We also carried out null models based on the relative abundance of species and compared the distribution of $H'_s$ generated by the null models with observed value. For each site separately, the relative abundance of each liana species was multiplied by the relative abundance of each tree species resulting in a probability of interaction between species of both life-forms. The total number of interactions found in the original matrix was distributed in the matrix according to the probability of interactions. Therefore, abundant species were more prone to interact. This procedure was repeated 100 times, and for each time, the $H'_s$ was calculated. Therefore, we generated 100 values of specialisation that was compared with the original value of $H'_s$ by confidence interval. If abundance was important to the specialisation of liana–tree network, observed $H'_s$ would lie within the confidence interval of specialisation values generated by the null model. Nevertheless, if rare or abundant species do not influence network specialisation, observed $H'_s$ should be outside the confidence interval of specialisation values from the null model. We carried out specialisation analyses for species and network with the package Bipartite for the R environment (Dormann et al. 2008).

To assess whether phylogenetic relatedness was related to the specialisation of lianas and trees and the whole network specialisation degree, we first built the respective phylogenetic trees for lianas and trees in each site with the tool Phylomatic, implemented in Phylcom (Webb et al. 2008). Phylomatic matches the family names of the sampled species with those contained in a megatree built by the Angiosperm Phylogeny Group (APG) (Stevens 2001 onwards). We excluded ferns and unidentified angiosperms from our analysis because the APG system does not match them with the phylogenetic tree.

We calibrated our phylogenetic trees with the dated angiosperm megatree of Davies et al. (2004), which uses the maximum ages for family clades, and used the command Phydist on Phylcom (Webb et al. 2008), which returns a matrix of pair-wise phylogenetic distances for all tree and liana species found in each 1-ha plot.

Once the phylogenetic trees were built, we could look for the presence of phylogenetic signal in the specialisation index $d'$ of liana and tree species in each site. We did this with the descriptive statistic $K$, which is the ratio between the observed and the expected phylogenetic signal calculated by the Brownian evolution model. $K < 1$ indicates that the species resemble each other less than expected by Brownian model. $K > 1$ indicates that the close species are more similar than expected by Brownian model (Blomberg et al. 2003). To test for significant phylogenetical signal, we carried out Phylogenetic Independent Contrasts (PIC), in which the variance of the contrasts of the original phylogeny is calculated. If species in a community tend to have phylogenetical signal, the variance of the contrasts tend to be low. This variance was compared against 1000 randomisations of the specialisation values across the tips of the phylogenetic tree of lianas and trees in each area (Blomberg et al. 2003). Here we used one-tailed test, in which if the original variance of PIC was lower than the variances of the randomisations, we rejected the null hypothesis of no phylogenetical signal (Blomberg et al. 2003). We used the Picante package in the R environment (Kembel et al. 2010) for this analysis.

We also tested whether closely related lianas shared similar sets of host trees and vice versa, that is whether closely related host trees were climbed by similar sets of lianas. To carry out this test for the lianas, we analysed the correlation between the phylogenetic distances among liana species and the similarity of the respective host-tree species sets. We used the Horn–Morisita index to express the similarity among different sets of host trees, because we had count data. This matrix of similarity was compared to the phylogenetic distance matrix of liana species using the Mantel test. The value of the correlation coefficient was compared to a null model, in which the phylogenetic distances within all pairs of lianas species were randomised 10,000 times (Legendre and Legendre 1998). We used the same procedure to test whether closely related host-tree species interacted with similar sets of lianas species.

Results

The rainforest had 117 species of trees, 58 species of lianas and 615 interactions between the two life forms. The seasonal forest had 62 species of trees, 45 species of lianas and 1702 interactions. The savanna woodland had 119 species of trees, 39 species of lianas and 4229 interactions between them.

The median of specialisation value $d'$ was lower than 0.5 for lianas and trees in the rainforest, seasonal forest and savanna woodland (Figure 1). In the rainforest the...
most specialised tree was *Malouetia arborea* (Vell.) Miers (Apocynaceae; $d' = 0.83$), whereas the most specialised liana was *Paullinia seminuda* Radlk. (Sapindaceae; $d' = 0.91$). In the seasonal forest, the most specialised tree was *Ficus citrifolia* Mill. (Moraceae; $d' = 0.42$), and the most specialised liana was *Heteropterys argyrophaea* A.Juss. (Malpighiaceae; $d' = 0.68$). In the savanna woodland, the most specialised tree was *Psidium guineense* Sw. (Myrtaceae; $d' = 0.4305$), whereas the most specialised liana was *Dolichandra unguis-cati* (L.) L.G.Lohmann (Bignoniaceae; $d' = 0.34$; Table S1).

We found a negative relationship between $d'$ and abundance for trees and lianas in the seasonal forest ($t = -0.86$; $P = 0.39$ for trees and $t = -1.80$; $P = 0.07$ for lianas) and savanna woodland ($t = -4.94$; $P < 0.05$ for trees and $t = -4.08$; $P < 0.05$ for lianas), but not for the rainforest ($t = -0.86$; $P = 0.39$ for trees and $t = -1.80$; $P = 0.07$ for lianas; Figure 2).

In spite of these results, the entire network was more specialised than expected by the null model at all three sites ($P < 0.05$; Figure 3). The generalisation was low in the rainforest ($H_2' = 0.216$; Figure 3), the seasonal forest ($H_2' = 0.122$, Figure 3) and the savanna woodland ($H_2' = 0.085$, Figure 3). The entire network was also more specialised than expected by the null model based on species abundance for the three sites ($P < 0.05$; Figure 4).

The phylogenetic signals for specialisation were non-significant in the rainforest ($K = 0.35$; $P = 0.15$ for trees and $K = 0.32$; $P = 0.57$ for lianas), the seasonal forest ($K = 0.49$; $P = 0.07$ for trees and $K = 0.36$; $P = 0.33$ for lianas) and the savanna woodland ($K = 0.32$; $P = 0.62$ for trees and $K = 0.41$; $P = 0.18$ for lianas). Although the entire network tended to specialisation, phylogenetically related lianas did not share similar host-trees sets. The comparison between pairwise phylogenetic distances of...
lianas and similarity of host tree was not significant in the rainforest ($r = -0.01; P = 0.60$), the seasonal forest ($r = 0.10; P = 0.051$) and the savanna woodland ($r = -0.01; P = 0.52$). Likewise, we did not observe phylogenetically related host trees being climbed by similar liana sets, that is we did not observe significant correlation between the pairwise phylogenetic distances of trees and the similarity of liana sets in the rainforest ($r = 0.01; P = 0.29$), the seasonal forest ($r = 0.03; P = 0.28$) and the savanna woodland ($r = -0.01; P = 0.78$).

**Discussion**

The relative abundance of the species may strongly influence network structure, such as nestedness (Vázquez et al. 2009). Nevertheless, abundance alone does not explain the network specialisation of lianas and trees found in the three sites in Brazil. In fact, if abundance were important to network structure, the network would be less specialised than observed. Part of this result may be due to rare species: our results indicate that rare species may play an important role in specialisation as they appear to be more specialised than abundant species. Thus, rare species should be related to the high specialisation value of network.

In pollination networks, high specialisation may result from sampling bias owing to insufficient sampling of rare interactions (Dorado et al. 2011). This is not our case. Nevertheless, one mechanism that could explain the high specialisation of rare species is the constant co-evolution of defences and counter-defences, such as those between animals and plants (Thompson 2005), as observed in other antagonistic networks (Thompson 1994; Fontaine et al. 2009). In the case of plants, the putative defences

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**Figure 2.** Binomial regression analyses between species specialisation ($d'$) and the abundance of species for trees and lianas. Rf, rain forest; SF, seasonal forest; WS, savanna woodland.
of trees against lianas could be analogous to traits that are frequent in animal–plant antagonistic interaction. For instance, some tree species with spiny (Maier 1982) and exfoliating barks (Campanello et al. 2007) are less prone to be occupied by lianas. Moreover, the architecture of palms enables new leaves to emerge from the terminal bud, grow vertically and then spread out and lean downwards, which hinders liana occupation on palms (Putz and Institute 1980). Lianas, on the other hand, have various climbing systems, such as tendrils and twining. Twiners tend to climb taller trees, whereas tendril lianas tend to climb smaller ones (Carsten et al. 2002). As some tree species reside mainly in the understorey, such as Psychotria capitata Ruiz & Pav (Rubiaceae), probably tendril lianas would specialise on them. The variation of specialisation values of tree and liana species found in this study indicate that some specialised species may follow the co-evolution of defences and counter-defences between lianas and trees.

In spite of higher specialisation found in rainforest in relation to the null model based on abundance, rare species are not more specialised than abundant ones. In this area, rare species have great variation of specialisation values.

For instance, two rare species with only one individual had very different specialisation value: Guaea macrophylla subsp. tuberculata (Vell.) T. D. Penn (Meliaceae) had a specialisation value of 0.78, whereas Siparuna guianensis Aubl. (Siparunaceae), 0.06. This value may indicate that coevolution is stronger in some species, but not in others. For example, G. macrophylla subsp. tuberculata is a small tree of the Atlantic forest, reaching no more than 10 m, indicating that few lianas use this species as host plants. In the rainforest, only Phanera microstachya (Raddi) L. P. Queiroz (Fabaceae) and P. seminuda Radlkl. (Sapindaceae) were found on this tree species.

The weak phylogenetical signal found in tree–liana interaction resembles herbivore–plant systems. In this case, animal specialists consume mainly abundant plant species, favouring rare species. If related plants have similar defence strategies, the abundant species are limited by the herbivores, and distant related species are promoted in the community (Cavender-Bares et al. 2009). In fact, abundant liana species climb mainly abundant tree species, indicating that abundance may play an important role in liana–tree network structure (Sfair 2011). If lianas can
eventually diminish tree abundance due to liana negative effects (Stevens 1987; Schnitzer et al. 2005), distantly related species may be promoted in the community. Therefore, our study indicates that there is co-evolution in some lineages of lianas and trees, resulting in specialisation of the interaction.

Lianas are very opportunistic, climbing mainly on trees in the neighbourhood (Garrido-Pérez and Burnham 2010), in spite of their long distance clonal colonisation (Yorke et al. 2013). The trees that are available in the neighbourhood are not necessarily phylogenetically similar, which may influence the interaction between species, since we found that phylogenetically similar liana species did not interact with phylogenetically similar tree species, and vice versa. This pattern was also found in orchid and host-tree networks, indicating that interaction between the two growth forms was not mutually advantageous, and other functional traits that are not phylogenetically conserved may influence epiphyte establishment, such as bark thickness (Silva et al. 2010).

In the case of liana–tree interaction, probably the proximity of trees to lianas may be an important factor influencing liana attachments.

Conclusions

Regardless the vegetation type, the unrelated specialisation of lianas and trees species and their phylogeny confirm that specialisation and generalisation may follow different pathways (Thompson 1994). Our results highlight the importance of rare species in network structure due the fact that they appear more specialised. These rare species may also influence specialisation of the entire community, indicating their interaction may not be due to chance, but to the coevolution between species.

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Supplemental data

Supplemental data for this article can be accessed here.

Notes on contributors

Julia Caram Sfair is interested in liana–tree interactions from a community perspective. André Rochelle’s research interests include liana dispersal and its phylogeny.

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