Species traits and abundance influence the organization of liana–tree antagonistic interaction

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Abstract The interaction among species can be influenced by neutral processes, in which more abundant species have high effect on the structure of interaction, or can be influenced by trait matching. Despite both variables (abundance and species traits) influencing the interaction of species in mutualistic networks, few studies showed their importance in antagonistic networks. Here, we posed the question: what are the main predictors of the liana–tree interactions: species abundance, biological traits or both? In a savanna woodland fragment in south-eastern Brazil, we sampled lianas and trees in 1 ha, where we recorded the abundance, maximum height and bark roughness of tree species, as well as abundance, maximum diameter and climbing system of liana species. For each species, we calculated their contribution to nestedness (n_i), which is a measure of network structure, and performed simple linear regressions between n_i and abundance and species traits. Abundant species contribute more to n_i than rare species, indicating that neutral processes affect interactions between lianas and trees, probably because lianas are opportunistic and climb trees in their neighbourhood. The only trait related to n_i was tree height, which can indicate that light availability can have a considerable role on network structure between both growth forms. Therefore, the importance of species abundance and tree height can be related to opportunism of lianas on climbing the most suitable tree in their neighbourhood.

Key words: cerrado, climber, ecological network, nestedness, savanna woodland.

INTRODUCTION

Different factors can drive the interaction among species in a community. For mutualistic plant–animal interactions, species can interact randomly, in which most abundant species have a high probability of interaction (Vázquez *et al.* 2005; Burns 2006; Dáttilo *et al.* 2014), or the trait matching among species can be the major determinant to species interaction and, thus, the ecological network structure (Chamberlain & Holland 2009; Olesen *et al.* 2011; Eklöf *et al.* 2013; Vizentin-Bugoni *et al.* 2014). Alternatively, both trait and abundance can together influence the interaction among mutualistic plant and animal species (Stang *et al.* 2006, 2009; Vázquez *et al.* 2009a,b; Chamberlain *et al.* 2010; González-Castro *et al.* 2015; Olito & Fox 2015). For antagonistic plant–animal interactions, such as parasitism and herbivory, the three scenarios are also possible: only abundance (Vázquez *et al.* 2005; Calatayud *et al.* 2017), only trait (Eklöf *et al.* 2013) or both (Canard *et al.* 2014).

Interactions between lianas and trees can be considered an antagonistic interaction (Stewart & Schnitzer 2017), as they compete mainly for nutrients and light (Dillenburg *et al.* 1993; Schnitzer *et al.* 2005; Cai *et al.* 2009; Álvarez-Cansino *et al.* 2015). Previous studies showed that some traits of lianas and trees may affect their probability of interaction (Putz 1984a). For example, trees with spiny (Maier 1982) or exfoliating bark (Campanello *et al.* 2007), pioneers and smaller trees (Clark & Clark 1990; Homeier *et al.* 2010) are less prone to carry lianas. On the other hand, lianas dispersed by wind, with latex and twining–climbing strategies, are more prone to climb a particular species of shrub (Garbin *et al.* 2014). In spite of the importance of these traits, recent studies showed that light can be the main factor influencing liana occupancy (Sfair *et al.* 2013, 2016). Therefore, tree features related to light competition, such as maximum height (Poorter *et al.* 2006) and crown illumination (Clark & Clark 1992), are better predictors of liana occupancy than other traits (Sfair *et al.* 2013).

Liana and tree species do not interact randomly: regardless of their species composition and environmental features, the interactions between lianas and

trees are structured in a nested pattern in tropical (Sfair *et al.* 2010) and temperate (Calatayud *et al.* 2017) forests. In nested networks of interactions, generalist species interact with each other in a dense core of interactions. In addition, specialist species tend to interact with generalist species, but less frequently with specialist species (see Bascompte *et al.* 2003 for detailed description of nested pattern of ecological networks). Among the set of species that compose the nested structure, some may contribute more, while other contribute less to nestedness (Vidal *et al.* 2014). This variation may be related to species-specific phenotypic traits (Selva & Fortuna 2007); as some traits may affect the occupation by particular liana species, this may interfere with the contribution of each species to nestedness (Vidal *et al.* 2014). For instance, if there is variation in the ability of liana species to occupy trees with distinct species traits, each tree species can only have a very particular set of lianas and both will show low contributions to the degree of nestedness of the entire community. In this sense, the variation of phenotypic traits is an important factor affecting the contribution of each species to nestedness (Selva & Fortuna 2007; Vidal *et al.* 2014).

In addition to the phenotypic traits of interacting species, species abundance may also affect their contribution to nestedness. For instance, if interactions are random at the individual level (*i.e.* neutral interactions; Krishna *et al.* 2008), abundant species has more interactions than rare ones (Vázquez *et al.* 2009a,b; Calatayud *et al.* 2017), possibly affecting each species' contribution to nestedness. As both neutral and trait matching processes can explain nestedness at the network level for mutualistic (Krishna *et al.* 2008; Vázquez *et al.* 2009a,b; Chamberlain *et al.* 2010) and host–parasite networks (Canard *et al.* 2014), one next step will be to investigate whether the same processes are affecting variation in network structure at the species level (Vidal *et al.* 2014) for competition networks of lianas and trees.

Despite the importance of both abundance and traits on structuring mutualistic networks (Stang *et al.* 2006, 2009; Vázquez *et al.* 2009a,b; Chamberlain *et al.* 2010; González-Castro *et al.* 2015; Olito & Fox 2015), the relative importance of these drivers affecting antagonistic networks is still poorly known (Canard *et al.* 2014 for host–parasitic networks). Here, we investigated the variation in biological traits (maximum height and bark roughness for trees, and maximum diameter and climbing mode for lianas) and abundance of lianas and trees in a savanna woodland, and explored how this variation can contribute to network structure of antagonistic interactions. Specifically, we aimed to determine whether the main predictors of the organization of liana–tree interactions are abundance, biological traits or both.

METHODS

Data sampling

The studied area was a fragment of savanna woodland (321.71 ha) in the municipality of Bauru, São Paulo, Brazil (22°19′41″–21′06″S and 48°59′49″–49°01′12″W, 519–603 m asl). This area has a short dry season from July to August and an average annual precipitation of 1306 mm (Weiser 2007). Despite many studies assessing the dynamics and conservation of the Brazilian savannas (also known as 'cerrado') (e.g. Coutinho 1978; Durigan & Ratter 2016; Strassburg *et al.* 2017), few of them investigated lianas and their interaction with trees (but see Weiser 2007; Sfair *et al.* 2010, 2016). We recorded all living trees and shrubs (hereafter identified as 'tree') with a diameter at breast height ≥0.1 cm and all lianas with a stem diameter at soil height ≥0.1 cm rooted in 1-ha area. For detailed information about the studied area and the vegetation characterization, see Weiser (2007) and Sfair *et al.* (2010).

For each individual tree, we recorded its height and the bark roughness, whereas for each individual liana, we recorded its diameter and climbing system. Taller trees are more prone to have lianas (Pinard & Putz 1994; Pérez-Salicrup *et al.* 2001; Malizia & Grau 2006; Campanello *et al.* 2007; Sfair *et al.* 2013, 2016), and we considered the maximum height of tree species (H_{max}) in the studied area as a trait that can influence liana climbing. Alternatively, we also considered the maximum diameter of liana species (D_{max}) in the studied area as a trait influencing liana–tree interaction; lianas tend to invest more on shoot growth than diameter (Schnitzer & Bongers 2002), and larger lianas tend to be older and occupy more trees (Dias & Sfair 2014).

For the categorical variables, tree bark roughness and liana climbing system, we accounted the most frequent category recorded in the studied site for the species (Weiser 2007). The bark of savanna woodland species ranges from totally smooth to deeply cracked (Weiser 2007), and in this study, we considered a categorical classification of bark roughness modified from Campbell and Newbery (1993), Torres *et al.* (1994) and Carse *et al.* (2000): smooth, intermediate and rough bark. Rough barks are more prone to have lianas than smooth barks because lianas have more area to attach to (Talley *et al.* 1996; Carse *et al.* 2000; Carsten *et al.* 2002; Reddy & Parthasarathy 2006; Campanello *et al.* 2007). We accounted the climbing systems twiner or tendrillar: in general, twiner lianas tend to occupy larger trees (Putz 1984b; Carsten *et al.* 2002), whereas tendrillar lianas tend to occupy more trees (Pérez-Salicrup & de Meijere 2005). Other traits also related to the probability of liana occupancy on a tree, such as spiny (Maier 1982) or exfoliating bark (Campanello *et al.* 2007), and pioneers (Clark & Clark 1990), were not considered as they are under-represented by the species in the studied area.

Data analysis

The contribution of a species to nestedness (n_i) refers to the degree to which the interactions of a given species overlap, on average, with those of the other species in the network

(Astegiano *et al.* 2015) and is based on the qualitative NODF (nestedness metric based on overlap and decreasing fill (Almeida-Neto *et al.* 2008; Vidal *et al.* 2014). For tree species, we computed n_i as the average proportion of lianas species shared between each tree and the other tree species in the network. Similarly, for liana species, n_i corresponds to the average proportion of tree species shared between each liana and the other liana species (Vidal *et al.* 2014). If the number of interactions of liana species i is equal to the number of interactions of a tree species, the pairwise nestedness is $n_i = 0$. Thus, $n_i = 0$ represents the lack of contribution of the pair of species i in generating nestedness, as there is no difference in number of interactions between them (no 'decreasing fill', Almeida-Neto *et al.* 2008). If the number of interactions of liana species differs, for example the species i interacts with fewer tree species, their n_i is the proportion of interactions of liana species with fewer interactions that are nested in the interactions of species with more interactions (Vidal *et al.* 2014). For details of n_i calculation, see Appendix B in Vidal *et al.* (2014).

We used simple linear regression to verify whether abundance and the species traits H_{max} and D_{max} influenced the organization of liana–tree interactions. The response variable was n_i, whereas the independent variables were abundance, H_{max} and D_{max}. Abundance and D_{max} were natural log (ln)-transformed to achieve the homogeneity of variance. For the categorical traits, bark roughness and climbing system, we performed an analysis of variance and *t*-test, respectively, in which these traits were the independent and n_i was the dependent variables. The significance of the statistical models was adjusted by Bonferroni correction separately for lianas and trees. All analyses were performed in R programming language version 3.1 (R Core Team, 2015, R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/).

RESULTS

We found 39 species of lianas and 140 species of trees, in which 119 tree species (85%) had associated lianas. The most abundant tree species was *Xylopia aromatica* (Lam.) Mart (Annonaceae) with 1126 individuals (≈10% of 11173 tree individuals), and the most abundant liana was *Serjania lethalis* A. St.-Hil. (Sapindaceae) with 420 individuals (≈15% of 2793 liana individuals).

The mean ± standard deviation of H_{max} of trees and D_{max} of lianas was 7.14 ± 3.75 m and 3.89 ± 3.84 cm, respectively. In relation to bark roughness, 44.3% of the trees had intermediate, whereas 38.6% had smooth and 17.1% had rough bark. The percentage of liana species with tendrillar and twiner climbing system was 57.9% and 42.1%, respectively.

The savanna woodland liana–tree network was significantly nested (NODF = 54.71, $P < 0.05$ based on null model 2 in Bascompte *et al.* 2003). The n_i ranged from 98.94 [*Ocotea pulchella* (Nees & Mart.) Mez] to 15.25 (*Psidium guineense* Sw) with a mean of 45.14 ± 26.84 for trees, and from 91.28 (*Serjania*
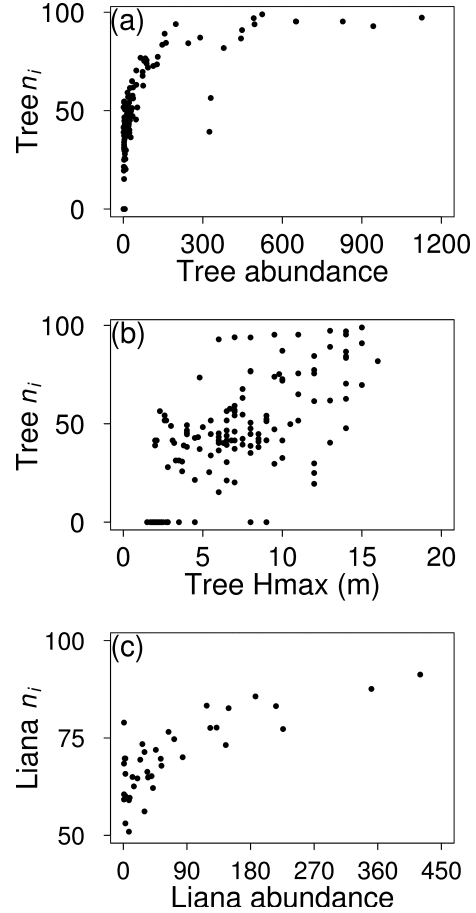

Fig. 1. Significant relations between the contribution of a species to nestedness (n_i) and abundance and traits of lianas and trees. Simple linear regression between (a) tree species abundance and n_i ($r^2 = 0.72$, $F_{1,138} = 367.9$, $P_{adj} < 0.05$); (b) between tree height (H_{max}) and n_i ($r^2 = 0.44$, $F_{1,138} = 110.8$, $P_{adj} < 0.05$); and (c) between liana abundance and n_i ($r^2 = 0.61$, $F_{1,37} = 57.67$, $P_{adj} < 0.05$). Liana and tree abundances were ln-transformed prior to statistical analyses.

lethalis A. St.-Hil) to 50.94 (*Heteropterys syringifolia* Griseb) with a mean of 69.91 ± 9.59 for lianas.

Species contribution to nestedness increased with more abundant ($r^2 = 0.72$, $F_{1,138} = 367.9$, $P_{adj} < 0.05$; Fig. 1a) and taller species ($r^2 = 0.44$, $F_{1,138} = 110.8$, $P_{adj} < 0.05$; Fig. 1b), but did not vary according to bark roughness ($F_{2,137} = 0.1$, $P_{adj} = 1$). Similarly, n_i of lianas increased with abundant species ($r^2 = 0.61$, $F_{1,37} = 57.67$, $P_{adj} < 0.05$; Fig. 1c), but not with their maximum diameter ($r^2 = 0.11$, $F_{1,37} = 4.6$, $P_{adj} = 0.11$) and climbing system ($t = -1.07$, d.f. = 34.01, $P_{adj} = 0.87$).

DISCUSSION

In accordance with previous studies about mutualistic (e.g. Stang *et al.* 2006, 2009; Krishna *et al.* 2008;

Vázquez *et al.* 2009b; Chamberlain *et al.* 2010; Olito & Fox 2015; González-Castro *et al.* 2015) and antagonistic networks between host–parasite animals (Canard *et al.* 2014), we also found a significant influence of biological traits and abundance on organizing liana–tree antagonistic interaction. In general, abundance plays a major role on species contribution to nestedness, as more abundant tree and liana species contribute more to network structure than rarer species, indicating that most of the network structure is the outcome of neutral processes. Only taller trees contributed positively to nestedness, indicating the importance of light in comparison with other traits previously related as determinant for liana–tree interaction. Nevertheless, tree bark, and diameter and climbing mode of lianas did not influence species contribution to nestedness, showing the relative low importance of traits to network structure. Overall, our results give support to liana opportunism on climbing closer, taller and more illuminated trees.

Lianas can grow and eventually occupy trees far away from initial rooting point as they can sprout after falling from tree canopies (Yorke *et al.* 2013). Nevertheless, most lianas climb on the most suitable trees in the neighbourhood of their initial rooting point (Vleut & Pérez-Salicrup 2005; Garrido-Perez & Burnham 2010; Roeder *et al.* 2015). Thus, the probability of interaction with a tree depends on the trees available around the initial rooting point of a liana; that is, it can be considered as by chance. If interactions are neutral, that is are random at the individual level (Krishna *et al.* 2008), abundant species have more probability of interaction than rare ones (Vázquez *et al.* 2009a,b; Calatayud *et al.* 2017). Therefore, when taking into account the probability of interaction among liana and tree species, the most abundant liana species are more prone to interact with more abundant tree species in a community, contributing more to network structure (Vidal *et al.* 2014). Consequently, this feature confers robustness to ecological networks, as the most abundant species are less prone to local extinction (Sfair *et al.* 2015), and the removal of a species that contributes more to nestedness tends to decrease overall network persistence more than the removal of a weak contributor (Vidal *et al.* 2014). Mathematical simulations showed that these strong contributors to network structure are the nodes that are less vulnerable to extinction (Saavedra *et al.* 2011).

Tree height proved to be an important predictor of liana climbing at the individual level (Sfair *et al.* 2013) and at the species level (this study). The association of tree height and liana occupancy may be a consequence of three not mutually exclusive processes. First, as one liana reaches the forest canopy, other liana can climb it. Therefore, taller trees are more prone to have lianas due to the facility of lianas

to climb each other (Pinard & Putz 1994). Second, it is reasonable to consider that taller trees are generally older and have had more time to accumulate lianas (Pérez-Salicrup *et al.* 2001; Malizia & Grau 2006; Campanello *et al.* 2007). Third, larger trees intercept more light than shorter trees, providing an ideal environment for lianas. As the local features of rooting point of lianas can be important for their probability of interaction with trees in the neighbourhood (Nesheim & Økland 2007; Nogueira *et al.* 2011), trees with more exposed canopies generally have more lianas (Sfair *et al.* 2013, 2016) and taller trees can contribute more to nestedness probably because lianas climb preferentially on them.

Despite the importance of tree height, liana and other tree traits were not related to network structure. Lianas and trees interact antagonistically (Stewart & Schnitzer 2017) and compete mainly for nutrients and light (Dillenburg *et al.* 1993; Schnitzer *et al.* 2005; Cai *et al.* 2009; Álvarez-Cansino *et al.* 2015). The negative effects of competition between both growth forms are related mainly to trees; it is proved that lianas decrease tree growth rate (Campanello *et al.* 2007) and fruit production (Fonseca *et al.* 2009), resulting on high mortality risk of highly infected trees (Phillips *et al.* 2009). In spite of these negative effects, our results showed that the lianas traits are less important in predicting their occupation on a tree species than their abundance and, consequently, their contribution to nestedness. In fact, lianas are very opportunistic and tend to climb closer (Roeder *et al.* 2015) and taller trees (Sfair *et al.* 2013, 2016), and consequently, liana traits can play a minor role on tree species preference. For example, lianas with tendrils tend to occupy mid-sized and small trees because these trees offer thinner branches that tendrils may easily encircle (Carsten *et al.* 2002). On the other hand, twiner lianas are found more frequently on larger trees (Carsten *et al.* 2002) and tend to be more specialized than tendril ones (Garbin *et al.* 2014). Despite the fact that structural features of lianas may influence their climbing on particular tree individuals, these features seem not to be associated with particular tree species; some tree species reside mainly in the understory, such as *Psychotria capitata* Ruiz & Pav (Rubiaceae), but generally the height of a tree varies with ontogeny. Therefore, twiner and tendril lianas may climb the same tree species depending on its ontogeny.

It is known that species traits and abundance can both influence the mutualistic (Stang *et al.* 2006, 2009; Vázquez *et al.* 2009a,b; Chamberlain *et al.* 2010; González-Castro *et al.* 2015; Olito & Fox 2015) and antagonistic interactions (Canard *et al.* 2014). Despite that some tree species are more prone to carry lianas with some particular traits (Garbin *et al.* 2014), our results do not give evidence of liana

traits influencing liana–tree interaction. In fact, our results give support to the fact that lianas are opportunistic and tend to climb taller trees in their neighbourhood (Carrasco-Urra & Gianoli 2009; Sfair *et al.* 2013, 2016; Roeder *et al.* 2015), which can be determinant on the structure of networks between both growth forms. The fact that most abundant species contribute more to network structure confers robustness to the interaction at community level and, thus, can potentially prevent the collapse of network structure.

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