South African Journal of Botany 103 (2016) 108–125

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Phylogenetic interactions among lianas in a southeastern Brazilian semideciduous tropical forest

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ARTICLE INFO

Article history:
Received 11 May 2015
Received in revised form 14 July 2015
Accepted 1 September 2015
Available online 2 December 2015

Edited by JD Flores Rivas

Keywords:
Seasonal forest
Climbing traits
Phylogenetic signal
Facilitation
Quantile regression

ABSTRACT

Biotic interactions play an important role in structuring community spatial pattern, which is also influenced by species resource use and reproductive success. Since plants are sessile organisms, biotic interactions may be reflected in the pattern of species co-occurrence. The pattern of species co-occurrence may change with the predominance of positive or negative interactions among the species along evolutionary history and environmental gradients. Considering the relative influence of phylogeny and environmental gradients, we expected lianas co-occurring on the same host tree (phorophyte) to (1) be phylogenetically more related than expected by chance; and (2) respond to abiotic variation along a gradient. We sampled 1 ha with 100 plots of 10 × 10 m each in a tropical semideciduous forest in SE Brazil. We investigated the presence of phylogenetic signal in climbing traits of lianas co-occurring on the same phorophyte and tested for the co-occurrence of liana-phorophyte pairs across the space and environmental gradients. Closely related liana species co-occurred more frequently than expected by chance on the same phorophyte species. Climbing traits of liana species showed a significant phylogenetic signal. Canopy openness had a high influence on the co-occurrence of lianas. We assume that stochastic processes, such as dispersal limitation, fragment history in relation with canopy openness, are the main drivers of the number of lianas co-occurrence on microscale.

1. Introduction

Woody climbers or lianas represent generally 15–45% of all species of a tropical forest, summing up 40% of the tropical forest leaf area and leaf productivity (Schnitzer, 2005). They compete with trees above ground for light and below ground for nutrients, decreasing trees fecundity (Kainer et al., 2006) and growth rate (Campanello et al., 2007). Lianas use well developed specialized morphological adaptations to find a means of support, i.e., shoots with twining stems, tendrils, hooks, or adventitious roots, to reach the forest canopy and get suitable light conditions to grow (Putz, 1984a; DeWalt et al., 2000). Therefore, host tree (phorophyte) species may be assumed as a stable, important set of resources for liana species (Sfair and Martins, 2011).

Tropical forests have been attracting much attention of the ecologists for their heterogeneous habitat (Wright, 2002; Leigh et al., 2004; Feeley et al., 2007). Heterogeneous habitat, such as those found in topographic gradients, affect local biological processes and support diverse communities (Collins and Klahr, 1991; Enoki, 2003). Some species compete for resources and tend to predominate and grow better than other species (Sammul et al., 2000), while some species may facilitate the establishment of other ones (Callaway, 1995; Bruno et al., 2003). Facilitation is frequently found between seedlings of one species and adults of other species and may lead to species aggregation in space (Callaway and Walker, 1997). Competition and facilitation are more apparent in small neighborhoods because plant species interact directly with nearest individuals (Stoll and Weiner, 2000). Such ecological interactions may leave a signature on the community spatial pattern (Russo et al., 2005; Silva et al., 2010), because the species spatial pattern is the result of their use of resources and reproductive success (Condit et al., 2000; Götzenberger et al., 2011). As competitively inferior species are unable to persist in the neighborhood of competitively superior ones, a lower number of co-occurring species than expected at random may arise from competition. On the contrary, a higher number of co-occurring species may arise from facilitation (Lieberman and Lieberman, 2007; Perry et al., 2009). Therefore, species spatial pattern may offer important clues of the predominant forces structuring community assembly (Hubbell, 2001; Silva et al., 2010).

Positive interactions have been repeatedly reported to be more important than interspecific competition for community assembly in systems subjected to environmental constraints (Callaway, 1995; Bruno et al., 2003). Therefore, the predominance of facilitation or

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[1] In memoriam.

http://dx.doi.org/10.1016/j.sajb.2015.09.011
0254-6299/

competition and the resulting pattern of species co-occurrence should change along an environmental gradient (Silva et al., 2010). If so, we expect that liana co-occurrence is predicted to be more frequent in stressful environments, such as sites with great slope and shallow, poor soils. Additionally, species co-occurrence patterns may be also influenced by species evolutionary history. Phylogenetically related plant species commonly present a high degree of evolutionary stasis (Qian and Ricklefs, 2004) and trait conservatism related to environmental tolerances (i.e. light, soil moisture and pH; Prinzing et al., 2001). If so, closely related plant species are expected to have similar habitat uses (i.e. phylogenetic niche conservatism: Wiens and Graham, 2005; Losos, 2008). As a result, we expect that closely related liana species may co-occur more frequently than expected at random on the same phorophyte i.e. many individuals of lianas co-occurring on the same individual tree. However, competitive exclusion tends to be stronger among closely related species sharing a large number of traits (Webb et al., 2002) because facilitation has been predominantly found among phylogenetically distant plant species (Valiente-Banuet et al., 2006). Therefore, the pattern of co-occurrence of related lianas on the same phorophyte may also offer clues of the role of evolutionary history in the interaction of species.

In this study, we assessed the relative influence of phylogeny and environmental filters on the co-occurrence pattern of lianas on the same phorophyte. We tested (1) whether the co-occurring lianas on the same phorophyte species are more phylogenetically related than expected by chance and (2) whether the lianas are associated with abiotic factors (i.e. soil chemical variables like organic matter, Al, P, Ca, Mg, K, pH, cation exchange capacity of soil, soil depth, slope and canopy openness). In summary, we tried to answer the following questions: (1) Do all liana species have the same chance to co-occur with other on a phorophyte? (2) How is the phylogenetic co-occurrence of lianas expected by chance on the phorophyte? (3) What is the role of abiotic variables in structuring the co-occurrence of lianas species? (4) How much variation in the frequency of lianas co-occurrence is explained by the abiotic variables?

2. Materials and Methods

2.1. Study site and sampling

We surveyed a fragment of the Tropical Semideciduous Seasonal Forest of about 245 ha in Campinas municipality (22°50′S, 46°55′W), São Paulo state, southeastern Brazil. Climate of the region is rainy tropical with long dry winter (Cwa; Koeppen, 1948; Cielo-Filho et al., 2007). The mean annual temperature is between 22 °C and 24 °C, and the mean annual rainfall is 1,372 mm. The rainy season usually lasts from October to March, in which the average precipitation reaches 1,141.5 mm and the average temperature is 24 °C; the dry season usually occurs from April to September, when the average precipitation is 283 mm and the average temperature is 20 °C (CEPAGRI, 2011, data for the period of June 1988 to October 2008). The altitude of the site varies between 630 to 760 m a.s.l., and the predominant soil is Acrisol (FAO nomenclature).

In the southern portion of the fragment, 100 plots of 10 m × 10 m each were randomly placed using the irrestricted randomization procedure (Cielo-Filho et al., 2007). In each plot we recorded phorophytes with DBH ≥ 5 cm and lianas with DSH (stem diameter at soil height) ≥ 1 cm following Gerwing et al. (2006) and Schnitzer et al. (2008) protocols. In the center of each plot we extracted 500 g from the superficial soil, which was sent to Campinas Agronomic Institute to determine organic matter, Al, P, Ca, Mg, K, pH, and cation exchange capacity, potential acidity (H + Al), extractable bases (SB), base saturation (V) and soil texture (silt, sand and clay). We also estimated the percentage of canopy openness with a spherical convex densiometer at the breast height (Lemmon, 1956). Using two plot sides as a coordinate system, we drew three random points at which we used a meter-scaled metal rod to measure soil depth and a clinometer to measure slope angle in degrees and used their average for data analysis.

2.2. Phylogenetic data

We constructed a phylogenetic tree for all sampled lianas with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic tree (Webb and Donoghue, 2005) (Fig. 1). The phylogenetic tree was based on the information from the current Phylomatic tree (R20080417), which is based on information from several published phylogenies (Webb and Donoghue, 2005). We assigned the branch length of the phylogenetic tree using BLADJ (branch length adjustment) averaging algorithm of the Phylocom software package (Webb et al., 2011). This algorithm took the phylogeny generated by Phylomatic, fixed the root node at 137 million years before present (i.e., the age of the eudicots clade) and fixed other nodes we had age estimative from Wikström et al. (2001). It then sets all other branch lengths by placing the nodes evenly between dated nodes, and between dated nodes and terminals of age "0". This has the effect of minimizing variance in branch length, within the constraints of dated nodes. It thus produces a pseudo-chronogram that can be useful for estimating phylogenetic distance (in units of time) between taxa for, for instance, the analysis of community phylogenetic structure. (Webb, 2000; Webb et al., 2008). Polytomies in family nodes were resolved using *multi2di* command of "ape" package in R environment.

2.3. Data analyses

To answer our question whether the liana species have equal chance of co-occurrence on the same phorophyte, we generated a distribution of expected frequencies for each liana–liana potential pair of species. This approach was adopted because the occurrence of two liana species on the same phorophyte was observed in the field with the highest frequency. We followed Lieberman and Lieberman (2007) to generate a null model, in which combinations of pairs of species reflect a random sampling of the community: (1) we computed the observed number of liana–liana pairs; (2) we randomized the occurrence of each liana species in the pair and recorded the number of random pairs; (3) we repeated these steps 999 times and estimated a random mean and standard deviation (SD) for the null species assemblages; and (4) we compared the observed number of pairs to those expected by chance and computed P values. We ran the analysis in the R environment (R Development Core Team, 2011) with the function available at http://www.cerradoecology.com/codes.html.

To answer our second question about the role of facilitation or niche conservatism in the co-occurrence of liana on the same phorphyte, we searched for a relationship between liana phylogenetic distances and the frequency with which pairs of lianas co-occurred on the same phorophyte. A negative relationship (i.e. increasing co-occurrence associated with decreasing phylogenetic distances) would indicate that closely related lianas occurred on the same phorophytes, whereas a positive relationship would indicate competition among lianas for the phorophyte through excluding closely related specie. We did quantile regressions (Cade et al., 1999) with those species pairs which co-occurred more often than expected by chance because it would give strong imprints of the interactions. If competition among lianas is greater between closely related species than between distantly related ones, a broad range of phylogenetic distances is expected to emerge between those liana species that co-occur on the same phorophytes more often than expected by chance. Therefore, the phylogenetic distance between lianas in each pair may have decreased variance with increasing number of co-occurrences; in such a way that a triangular relationship with a negatively sloping hypotenuse may arise. In these cases, quantile regressions are recommended (Cade et al., 1999). We used 'quantreg' package (Koenker, 2008) for R environment (R Development Core Team, 2011) to examine the nature of this upper bound with quantile