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ORIGINAL ARTICLES

The role of heterogeneity on climber diversity: is liana diversity related to tree diversity?

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ABSTRACT

The richness and abundance of climbers vary among communities and may depend on soil properties, climate, perturbation history and variables of community structure. Our aim was to test the hypothesis that, in spite of the influence of these variables, climber diversity may also be related to tree diversity. We gathered data from a rainforest site, three sites of seasonal semideciduous forest, and two sites of savanna with different physiognomies in SE Brazil. Diversity descriptors were represented by species abundance distribution (SAD), richness, and Shannon index (H'). We compared trees for richness using rarefaction analysis, for SAD using Kolmogorov-Smirnov test, and for H' using t-test with Bonferroni sequential correction. The same analyses were performed for climbers. Also, we compared floristic similarity of climbers and trees among the sites using modified Sørensen index for abundance. The relationship among the diversity descriptors between climbers and trees was tested with linear regression. The diversity descriptors varied similarly among the sites, indicating that trees and climbers respond in similar way to variation of factors. We suppose that the major variable that influences the similar variation of diversity of trees and climbers is fragmentation process. For example, continuous forests would have more richness than fragmented ones. Tree H' showed a significant positive relationship with climber richness; the other descriptors did not show any significant relationship. Shannon H' is a heterogeneity index that considers both richness and SAD, attaining maximum values when the species number is great and all the species have similar abundances. We propose that a) the greater the tree H', the greater the heterogeneity of the tree community; b) this heterogeneity would be expressed by many different combinations of traits favorable or unfavorable to climbers; c) each combination would appear with some abundance; and d) this heterogeneity would enhance the number of potential niches for climbers, thus promoting climber richness.

Key words: *Abundance, Heterogeneity, Liana, Shannon Index, Richness*

Introduction

Although the distribution patterns of organisms both at community and population levels have been addressed by many authors (Brown, 1984), they are still hard to explain because of many variables influencing them (Schnitzer, 2005; Ricklefs, 2006). One way to overcome the great complexity of this issue is to focus on a particular group, such as trees, herbs or climbers (Schnitzer, 2005). Climbers are more abundant (number of individuals, Schnitzer, 2005) and richer (number of species, van der Heidjen and Phillips, 2009) in tropical than in temperate systems. In tropical systems, climbers are favored by stronger dry season, because they can access deep soil water and do not suffer xylem embolism (Meinzer *et al.*, 1999; Schnitzer, 2005), keeping their leaves during the unfavorable season (Putz and Windsor, 1987). In consequence, climbers invest in growth, while trees shed their leaves and decrease growth rate during dry season (Meinzer *et al.*, 1999; Schnitzer, 2005).

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Climber abundance and richness may also be related to perturbation (Senbeta *et al*., 2005; DeWalt *et al.*, 2006; Muthuramkumar *et al*., 2006), which can be caused by humans, such as deforestation (Laurance *et al*., 2001), or by natural events, such as hurricanes (Allen *et al*., 1997) and gap formation (Schnitzer *et al*., 2000). Gaps, for example, have high temperatures and low humidity, creating conditions similar to seasonally dry tropical forests, which are favorable to climber growth (Schnitzer, 2005). In gaps, climbers decrease growth of non-pioneer and promote growth of pioneer trees (Schnitzer *et al*., 2000; Campanello *et al*., 2007). Schnitzer *et al*. (2000) proposed that climber diversity in tropical forests is kept by gap formation, because in shaded sites germination rates of climber species is low (Sanches and Válio, 2002). However, climber abundance is greater in intermediate successional phases, because canopy is low and light is plentiful, promoting climber growth (Madeira *et al*. 2009). For this reason, liana density would be more related to forest structure than soil and climate factors (Van der Heidjen and Phillips, 2008). On the other hand, Nesheim and Økland (2007) stated that nutrient and light availability would be important during the initial stages of climber development, but tree traits would become more important when climbers start to ascend.

Papers addressing abundance and richness of climbers generally emphasize the role of factors such as those of climate, soil and perturbation related to forest structure. In this work, we propose a relation between diversity of climbers and trees. Few works have focused on tree diversity as a variable that can influence climber diversity: Watanabe and Suzuki (2008) found a positive relationship between rattans and trees diversity, and Caballé and Martin (2001) observed that low abundance and high richness of trees were related with low richness and abundance of climbers through time. Therefore, tree diversity can influence climber diversity, since, for example, greater abundance of trees can provide more support availability and, therefore, increase climber abundance.

Our aim was to test the hypothesis that diversity of climbers is related to diversity of trees. To address this issue, we considered species abundance distribution (SAD), richness, and Shannon's H' index of heterogeneity as descriptors of diversity, and investigated whether the descriptors of climbers and trees are different among six sites in southeastern Brazil and related to each other in each site.

Materials and Methods

Data collection

We considered six sites in southeastern Brazil (Fig. 1), consisting of rainforest, seasonal forest and savanna, which are the most important tropical vegetation formations covering the greatest area in the Neotropics. In each of these sites the sample design was adapted to the vegetation peculiarities. Ubatuba (23º21'59''S and 45º05'03''W) is a tropical wet forest in Köppen's (1948) Af climate. This site is a relatively continuous forest, with 47500 ha. The altitude is between 348 and 395 m, the annual mean temperature is 20.25 ºC and the annual mean precipitation is 2624 mm. In 1 ha Rochelle (2008) sampled all trees with PBH (perimeter at breast height) > 15 cm and van Melis (2008), all lianas (woody climbers) with DBH (diameter at breast height) > 1 cm.

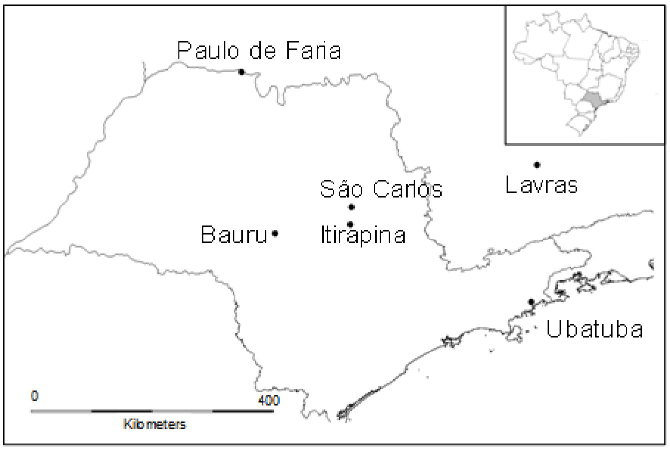

Fig. 1: The six sites sampled in southeastern Brazil.

Paulo de Faria (19º57’S e 49º31’W, 400 to 495 m above sea level) is a seasonally dry tropical forest, with Köppen’s (1948) Aw climate. The annual mean temperature is 27 ºC and the annual mean precipitation, 1405 mm. In the fragment with total area of 435.73 ha, all trees with DBH ≥ 3cm and lianas with DBH ≥ 1cm were sampled (Rezende, 2005) in a grid of 100 contiguous plots of 10 x 10 m each, thus making up 1 ha.

Itirapina (22º13`S e 47º51`W, 762 m above sea level) is a fragment of dense savanna with an area around 60 ha. The climate is Köppen’s (1948) Cwa, with annual mean temperature of 21.4 ºC and annual mean precipitation of 1394.3 mm. Polo (*in prep.*) considered all trees and lianas with DSH (diameter at soil height) > 3 cm and > 1cm, respectively, in two separated grids of 100 contiguous plots of 5 x 5 m, each one making up 0.5 ha.

São Carlos (21º57’S e 47º50’W, 850 m above sea level) is a seasonal dry tropical forest fragment of 112 ha (Hora and Soares, 2002, Silva and Soares, 2002). The climate is a transition between Köppen’s (1948) Cwa and Awa, with mean annual temperature of 25.4 ºC and mean annual precipitation of 1440 mm. Silva and Soares (2002) sampled all trees with DBH ≥ 5 cm in 1 ha of non-contiguous plots with 0.02 ha each, and Hora and Soares (2002) sampled all lianas with DBH ≥ 2.5 cm in 0.75 ha of non-contiguous plots of 0.01 ha.

Bauru (22º20’30’’S e 49º00’30’’W, 510 to 540 m above sea level) is a woodland savanna covering a 321.71 ha of fragment. The climate is Köppen’s 1948) Cwag’, with mean annual temperature of 22.4 º C and mean annual precipitation of 1306 mm (Weiser 2007). This author sampled all trees with DBH ≥ 0.1 cm and all lianas with DSH ≥ 0.1 cm in 1 ha of sampling plot.

Lavras (21º19’25.2” S e 44º59’53.1” W, 920 to 1180 m above sea level) is a seasonal dry tropical forest in a Köppen’s (1948) Cwa climate with mean annual temperature of 19.4 and mean annual precipitation of 1529.5 mm (Castro, 2004; Appolinário, 2008). The sampling included three forest fragments with total area of 48.9 ha. All trees with DSH > 5 cm were sampled in 54 plots of 200 m² (total of 1.08 ha) by Castro (2004), whereas Appolinário (2008) sampled all climbers with DBH > 1 cm in 52 out of these 54 plots.

Data analysis

We considered richness, species abundance distribution (SAD) and Shannon’s H’ heterogeneity index as diversity descriptors. By using these three descriptors we were able to take into account all aspects included in the concept of diversity, which considers not only the number of individuals (abundance) and the number of species (richness), but also the relationship between these two variables (H’). According to McGill *et al.* (2007), in spite of information loss, these descriptors complement each other: richness and H’ are univariate and easily understandable variables, and SAD, although more complicated, provides more information, such as the discrimination of rare, intermediate and abundant species.

We tested for difference of richness of climbers and trees among the sites with rarefaction analysis using the accumulated number of individuals as sampling effort (Gotelli and Colwell, 2001; Magurran, 2004). The rarefaction curve was constructed by random sampling of N individuals repeated 1000 times (Hurlbert 1971; Krebs 1999) with confidence interval of 95% (Hurlbert, 1971; Krebs, 1999; Gotelli and Colwell, 2001) using Analytic Rarefaction 1.3 software (Holland, 2003). We plotted the rarefaction curve until 606 individuals for trees, since the smallest sample had 604 individuals in São Carlos (Fig. 2). The rarefaction curve for climbers was plotted until 550 individuals, since the smallest sample had 528 individuals in São Carlos (Fig. 3).

SAD is the distribution of the observed number of individuals of each species in a community (McGill *et al.*, 2007). According to Tokeshi (1999), SAD is a detailed representation of the community, whereas the species richness is a basic information. We compared the SADs among all sites with Kolmogorov-Smirnov test, following Magurran (2004).

We considered the logarithm on base *e* for Shannon heterogeneity index (Magurran 2004) and compared the values with adapted t-test (Hutcheson, 1970; Zar, 1999), applying Bonferroni sequential correction (Rice, 1989; Sokal and Rohlf, 2003). This correction decreases the Type I error among all comparisons (Sokal and Rohlf, 2003; Gotelli and Ellison, 2004).

We compared tree and climber species similarities among all sites with Sørensen index modified by Chao *et al.* (2005). The modified Sørensen index takes into account the species abundance in each sample and is based on the probability of two random individuals, each from one sample, to belong to the same species (Chao *et al.*, 2005). This index is also less sensitive to sample size and considers the species estimate for each site (Chao *et al.*, 2005). For this reason, for each comparison we made 1000 replications. We used Spade software for calculations of modified Sørensen index (Chao and Shen, 2003), which reduces the bias when a substantial number of species is missing (Chao *et al.*, 2006).

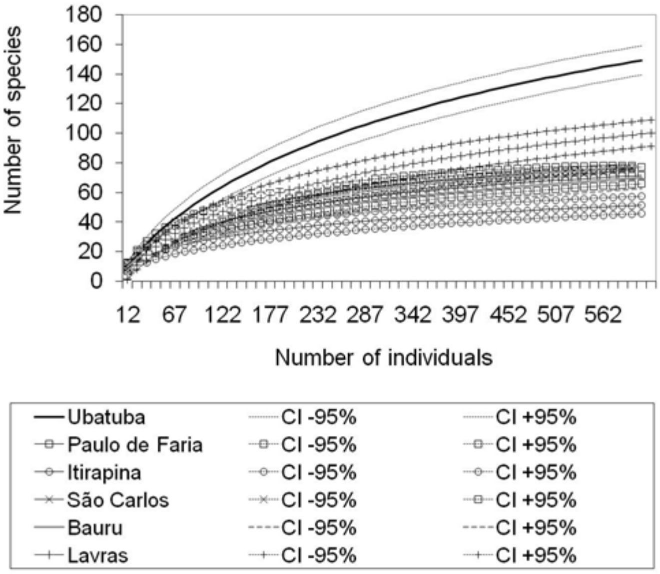

Fig. 2: Rarefaction curves for trees until 606 individuals. Continuous lines represent averages and dotted lines, 95% confidence intervals.

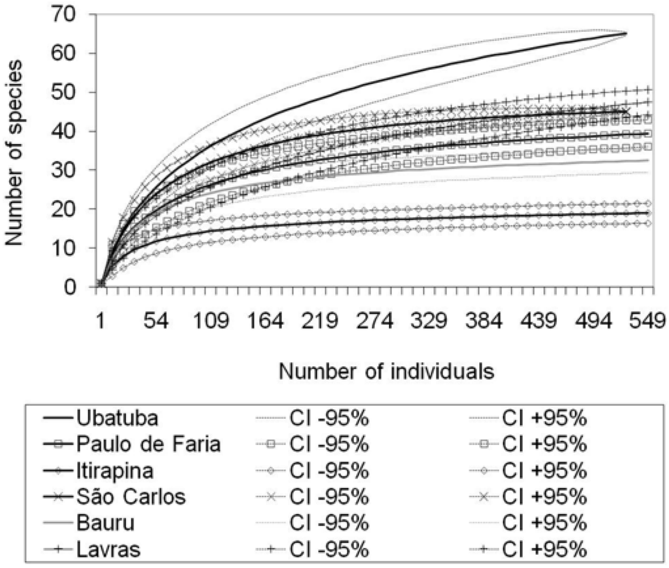

Fig. 3: Rarefaction curves for climbers until 550 individuals. Continuous lines are the mean resample and dotted lines, 95% confidence intervals.

We tested for the relation of the descriptors between climbers and trees with simple linear regression analysis. The explanatory variables were the descriptors of tree diversity and the response variables were the descriptors of climber diversity. We also used Bonferroni sequential correction to decrease Type I error of multiple tests with the same set of values (Sokal and Rohlf, 2003; Gotelli and Ellison, 2004).

Results

Trees

Tree richness was not significantly different among Bauru, São Carlos and Paulo de Faria, but was significantly smaller in Itirapina and greater in Ubatuba and Lavras (Fig. 2). SAD for trees in Ubatuba differed from all other samples (Table 1). The values of H’ differed among all sites, except between Paulo de Faria and Bauru (Table 1). Ubatuba had the greatest and Itirapina had the smallest H’ (Table 2). Generally, tree species were different among all sites, which showed a general floristic similarity smaller than 10%. However, São Carlos and Paulo de Faria had 61.17% of common species, Bauru and Itirapina had 63.32%, Lavras and Itirapina had 28 %, and Lavras and Bauru had 48.80% of common species (Table 3). These results were expected, since São Carlos and Paulo de Faria are seasonally dry tropical forests, whereas Bauru and Itirapina are savannas. The standard error was relatively small, indicating high precision of the data (Chao *et al*. 2006).

Climbers

The rarefaction results for climbers (Fig. 3) were similar to those for trees (Fig. 2): richness did not differ among Bauru, São Carlos, Paulo de Faria and Lavras, but Itirapina had fewer and Ubatuba more species than the other sites (Fig. 3). As for trees, SAD for climbers was different in Ubatuba against all other sites (Table 4). We also found differences between Paulo de Faria and Itirapina and between Itirapina and São Carlos (Table 4). Shannon index was different among all sites, except between Paulo de Faria and Bauru, between Paulo de Faria and Lavras and between Bauru and Lavras (Table 5). The floristic similarity of climbers among all sites was similar to that of trees: the greatest values were between the savannas Itirapina and Bauru (65.41%) and between the seasonally dry forests Paulo de Faria and São Carlos (40.66%; Table 3). Generally, the Sørensen index was smaller than 20% among all other comparisons, implying a low similarity among sites (Table 3). The standard error was also small (less than 0.04), indicating high precision of the data (Chao *et al*. 2006).

Relationship among diversity descriptors

There was no significant correlation between tree abundance and climber abundance, tree richness and climber richness, climber richness and tree abundance, climber abundance and tree richness, climber abundance and tree H’, climber H’ and tree abundance, climber H’ and tree richness, and between tree H’ and climber H’ (Table 6). However, we found a significant positive correlation between tree H’ and climber richness (Table 6).

Discussion

The variations of richness, abundance and Shannon index among the sites were similar for trees and climbers, indicating that the same factors affect similarly the diversity descriptors of climbers and trees. One of these factors might be the anthropogenic fragmentation, since forest fragments generally have smaller plant richness than continuous areas (Laurance, 2008). With exception of Ubatuba, all the other sites were fragments with different areas and shapes. Being a relatively continuous forest, Ubatuba had the greatest species richness. Also, Ubatuba had the smallest values of floristic similarity with other sites. Most tree species in the Brazilian Atlantic rainforest, such as Ubatuba, have restricted distribution (Scudeller *et al*., 2001, Caiafa and Martins, 2010), implying in great floristic differences in relation to other forest types. The inclusion of environmental heterogeneity in the sample can also yield a great species richness, as was the case of Lavras, once different fragments and ecological corridors (Castro, 2004) were sampled. The species richness in a fragment is also dependent on matrix characteristics, edge influence, and perturbation history (Laurance, 2008), which are factors that could explain the much smaller richness of climbers and trees in Itirapina. This cerrado small fragment is surrounded by a 30-m wide firebreaker separating it from plantations of *Pinus elliottii* and *Eucalyptus saligna* (personal observation).

Our hypothesis that abundance, richness and H’ of climbers would be related to tree diversity descriptors was only partially confirmed, because the only significant relationship among diversity descriptors we found was that between tree H’ and climber richness. We propose that H’ can be considered an indicative of internal heterogeneity of the community and that the more heterogeneous the community is, the greater the number of climber species. Environmental heterogeneity may be created by both abiotic variables -- such as topography, temperature, precipitation and substrate – and biotic variables, such as evapotranspiration (Wilson, 2000). Therefore, it is possible to regard the forest as a mosaic of resource availability (Grace, 1991) shared among species, thus contributing to their coexistence (Ricklefs, 1977). More heterogeneous environments can support more diversity than less heterogeneous ones (Rosenzweig, 1995; Lundholm and Larson, 2003; Pausas *et al.,* 2003; Leigh *et al.,* 2004; Dufour *et al*., 2006). For example, in South Africa Thuiller *et al*. (2006) showed that topographic heterogeneity could improve plant richness both by increasing the number of niches in space and by keeping the number of niches relatively stable in time. Environments with microtopographic heterogeneity also have more abundance of some species, greater biomass and more rare species (Vivian-Smith, 1997).

Table 1: Kolmogorov-Smirnov test for SAD (in bold) and t-Test for Shannon H' indices for trees among the six sites (*p < 0,05).

	Ubatuba	Paulo de Faria	Itirapina	São Carlos	Bauru	Lavras
Ubatuba		4741.23 *	6430.88 *	3659.24*	8425.55 *	5690.26 *
Paulo de Faria	-19.71 *		979.18	795.35	536.12	1622.78
Itirapina	-35.55 *	11.41 *		1517.09 *	1339.97	3073.66 *
São Carlos	13.74 *	-3.53 *	-13.56 *		1512.93	861.08
Bauru	-25.93 *	-0.095	19.32 *	-4.24 *		3070.20
Lavras	-10.64*	14.19 *	37.92 *	7.48 *	24.89 *	

Table 2: Abundance (individuals.ha^{-1}), richness (species.ha^{-1}) and Shannon H' diversity index (nats.individual^{-1}) with their respective variance for trees in the six sites.

	Ubatuba	Paulo de Faria	Itirapina	São Carlos	Bauru	Lavras
Richness	207	87	82	77	140	157
Abundance	1876	1419	4662	604	11173	5179.42
H'	4.48	3.58	3.15	3.79	3.56	4.012
Variance H'	9.83 x 10^{-4}	9.74 x 10^{-4}	3.18 x 10^{-4}	1.56 x 10^{-3}	1.4 x 10^{-4}	2.54 x 10^{-4}

Table 3: Floristic similarity indicated by Sørensen index (± standard error) among all sites, considering trees (results in bold) and climbers.

	Ubatuba	Paulo de Faria	Itirapina	São Carlos	Bauru	Lavras
Ubatuba		0.031 (± 0.006)	0.028(± 0.003)	0.064(± 0.010)	0.077(± 0.008)	0.083(± 0.015)
Paulo de Faria	0		0.009(± 0.003)	0.611(± 0.058)	0.079(± 0.009)	0.075(± 0.012)
Itirapina	0	0.076(± 0.012)		0.021(± 0.005)	0.633(± 0.019)	0.280(± 0.018)
São Carlos	0.036(± 0.009)	0.406(± 0.016)	0.022(± 0.010)		0.016(± 0.003)	0.058(± 0.015)
Bauru	0	0.147(± 0.007)	0.654(± 0.036)	0.0878(± 0.013)		0.498(± 0.013)
Lavras	0	0.093(± 0.008)	0.101(± 0.008)	0.1041(± 0.013)	0.187(± 0.009)	

Table 4: Kolmogorov-Smirnov test values for SAD (in bold) and t-Test for Shannon indices of climbers among the six sites (*p < 0,05).

	Ubatuba	Paulo de Faria	Itirapina	São Carlos	Bauru	Lavras
Ubatuba		1864.11 *	1276.47 *	1604.30 *	1662.00 *	2166.50 *
Paulo de Faria	6.91 *		417.97 *	283.98	123.70	259.33
Itirapina	25.90 *	-27.13 *		383.14 *	338.42	395.34
São Carlos	2.88 *	3.56 *	-23.06 *		214.83	432.91
Bauru	7.75 *	-0.35	33.08 *	-4.13 *		231.17
Lavras	7.60 *	-2.24	17.11 *	4.79 *	-2.22	

Table 5: Abundance, richness and Shannon diversity index (nats.individual^{-1}) of climbers with their respective variance value for the six sampled areas.

	Ubatuba	Paulo de Faria	Itirapina	São Carlos	Bauru	Lavras
Richness/ha	65	45	25	45	39	51
Abundance/ha	526	1427	2778	528	2793	711.43
Shannon H'	3.42	2.98	1.91	3.20	2.96	2.877
Variance H'	2.46 x 10^{-3}	8.33 x 10^{-4}	6.74 x 10^{-4}	2.27 x 10^{-3}	3.16 x 10^{-4}	2.3 x 10^{-3}

Table 6: Regression analysis results among diversity descriptors of climbers and trees (*p< 0,05) after sequential Bonferroni correction. (*p < 0.05)

Tree		Climber	Intercept	Regression Coefficient	Adjusted R²	F	P
Abundance	x	Abundance	455.066	2.534	0.367	3.899	0.1195
Richness	x	Richness	-9.278	2.984	0.4652	5.349	0.0818
Abundance	x	Richness	8883.5	-105.1	-0.09114	0.5824	0.4879
Richness	x	Abundance	147.90429	-0.01570	-0.1176	0.4737	0.5291
Shannon Index	x	Abundance	4.2515375	-0.0003355	0.5486	7.075	0.0564
Shannon Index	x	Richness	2.249313	0.033616	0.9489	93.88	0.0006 *
Abundance	x	Shannon Index	9665	-1906	-0.1689	0.2774	0.6262
Richness	x	Shannon Index	-20.64	50.36	0.06631	1.355	0.3091
Shannon Index	x	Shannon Index	1.7171	0.7072	0.5738	7.73	0.0498*

Spatial heterogeneity can influence diversity both by increasing the number of habitats types and by affecting ecological processes – such as dispersal and competition (Dufour *et al*., 2006) – through the spatial configuration of habitats. The environmental heterogeneity was shown also to be positively related to diversity in theoretical (Palmer, 1992) as well as in practical studies with animal diversity (Tews *et al*., 2004).

Similarly, the increased heterogeneity of the tree community would yield an increased heterogeneity of traits of the potential supports for climbers, since tree species have characters that promote or avoid climber occupation. Among the tree characters inhibiting climbers Putz (1984) recognized palm architecture, spiny trunk, fast growing, ant mutualism, dead leaves retention and exfoliating bark. For example, in a semideciduous forest in Argentina, Campanello *et al*. (2007) found that palms were 69.5% less infested by climbers. Besides, some palms, such as *Bactris* spp., have spiny trunk that hinder occupation by climbers, probably due to the fall of the spines with liana weight (Maier, 1982). Tree species with large leaves, flexible trunk (Putz, 1984) or with exfoliating bark (Talley *et al*., 1996; Campanello *et al*., 2007) also have fewer climbers. Putz (1984) suggested that climbers hinder shade-tolerant and slow-growing trees, and promote indirectly the pioneer species. Pioneer species, such as *Cecropia* spp., do not have lianas (Putz, 1984; Campanello *et al*., 2004), and in species of this genus, symbiotic ants remove climbers by cutting their apical meristems (Janzen, 1969). On the other hand, other tree characters, such as slow growth (Putz 1984), rough bark (Carsten *et al*., 2002), and multiple stems (Reddy and Parthasarathy, 2006) promote climber occupation.

A complementary explanation about the relation of tree H' to climber richness is the biotic interaction hypothesis (Currie *et al*., 2004). This hypothesis states that speciation rate is due to biotic interactions, which increase opportunities for evolutionary diversification in some sites (Currie *et al*., 2004). For example, many plant species of temperate climates are pollinated and dispersed by wind, whereas most tropical species are pollinated and dispersed by animals. The evolution of tropical flowers and diaspores is related to the evolution of animal pollinators and dispersers, thus leading to an increase of richness of animals and plants in the tropics (Schemske, 2002). In an analogue way, a great Shannon index represents similar relative abundance of the species combined with a great number of species. If trees have a great H', then the tree community present many different combinations of traits that promote or inhibit their occupation by climbers, and the different combinations of traits occur with great, similar relative abundances. Therefore, from the viewpoint of the climbers, the tree community would represent a gradient ranging from totally favorable trait combinations to totally unfavorable trait combinations. This gradient of favorableness would occur not only along space but also through time, since communities have spatial structure and also temporal dynamics. The combination of spatial and temporal variation of favorableness/unfavorableness would imply in great heterogeneity, thus allowing the speciation towards a great number of climber species, according to the biotic interaction hypothesis. Additionally, Sfair *et al*. (2010) showed that the interaction structure between lianas (woody climbers) and host-trees is nested. In spite of negative interaction between lianas and trees, nestedness also characterizes mutualistic and facilitation networks. In these cases, nestedness decreases competition and increases diversity (Bastolla *et al*., 2009, Verdú and Valiente-Banuet, 2008). We suppose that nestedness also increases diversity in liana-tree network. According to the biotic interaction hypothesis, we propose that the heterogeneity of tree traits and the great number of their different combinations influence positively not only the speciation rate of climbers, thus increasing climber richness, but also their coexistence, thus maintaining climber richness.

Conclusion

Climber abundance is dependent on climate (Schnitzer, 2005) and forest structure (van der Heijden and Phillips, 2008). Sites with short or absent dry season have more climber richness (van der Heijden and Phillips, 2009). We propose that a great heterogeneity of the tree community represents a great number of potential sites for climbers, thus also increasing their richness. It is possible that sites with different dry season durations (van der Heijden and Phillips, 2009) combined with tree heterogeneity can enhance the rates of climber speciation.

References

Allen, B.P., E.F. Pauley and R.R. Sharitz, 1997. Hurricane impacts on liana populations in and old-growth Southeastern Bottomland Forest. Journal of Torrey Botanical Society, 124(1): 34-42.

Appolinário, V., 2008. Taxocenose de trepadeiras em fragmentos e corredores florestais de Lavras (MG): aspectos estruturais e ecológicos. M. S. thesis, Universidade Federal de Lavras, Lavras, M.G.

Bastolla, U, M.A. Fortuna, A. Pascual-García, A. Ferrera, B. Luque and J. Bascompte, 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458(7241): 1018-1021.

Brown, J.H., 1984. On the relationship between abundance and distribution of species. American Naturalist 124(2): 255-279.

Burns, K.C. and J. Dawson, 2005. Patterns in the diversity and distribution of epiphytes and vines in a New Zealand forest. Austral Ecolology 30(8): 883-891

Caballé, G. and A. Martin, 2001. Thirteen years of change in trees and lianas in a Gabonese rainforest. Plant Ecology 152(2): 167-173.

Caiafa, A..N. and F.R. Martins, 2010. Forms of rarity of tree species in the southern Brazilian Atlantic rainforest. Biodiversity and Conservation 19(9): 2597-2618.

Campanello, P.I., J.F. Garibaldi, M.G. Gatti and G. Goldstein, 2007. Lianas in a subtropical Atlantic Forest: host preference and tree growth. Forest Ecology and Management 242(2-3): 250-259.

Carsten, L.D., F.A. Juola, T.D. Male and S. Cherry, 2002. Host associations of lianas in a south-east Queensland rain forest. Journal of Tropical Ecology, 18(1): 107-120.

Castro, G.C., 2004. Análise da estrutura, diversidade florística e variações espaciais do componente arbóreo de corredores de vegetação na região do Alto Rio Grande, MG. M. S. thesis, Universidade Federal de Lavras, Lavras, M.G.

Chao, A., R.L. Chazdon, R.K. Colwell and T.J. Shen, 2005. A new statistical approach for assessing compositional similarity based on incidence and abundance data. Ecology Letters 8(2): 148-159.

Chao, A., R.L. Chazdon, R.K. Colwell and T-S Shen, 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. Biometrics, 62(2): 361-371.

Chao, A and T-J Shen, 2003. Program SPADE (Species Prediction And Diversity Estimation). Available via http://chao.stat.nthu.edu.tw. Accessed 02 March 2009.

Currie, D.J., G.G. Mittelbach, H.V. Cornell, R. Field, J.F. Guégan, B.A. Hawkins, D.M. Kaufman, J.T. Kerr, T. Oberdorff, E. O'Brien and J.R.G. Turner, 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters, 7(12): 1121-1134.

DeWalt, S.J., K. Ickes, R. Nilus, K.E. Harms and D.F.R.P. Burslem, 2006. Liana habitat associations and community structure in a Bornean lowland tropical forest. Plant Ecology, 186(2): 203-216.

den Dubbelden, K.C. and B. Oosterbeek, 1995. The availability of external support affects allocation patterns and morphology of herbaceous climbing plants. Functional Ecology, 9(4): 628-634.

Dufour, A., F. Gadallah, H.H. Wagner, A. Guisan and A. Buttler, 2006. Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. Ecography, 29(4): 573-584.

Gotelli, N.J. and R.K. Colwell, 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4(4): 379-391.

Gotelli, N.J. and A.M. Ellison, 2004. A Primer of Ecological Statistics. Sinauer Associates, Inc..

Grace J., 1991. Physical and ecological evaluation of heterogeneity. Functional Ecology 5(2): 192-201.

Holland, S.M., 2003. Analytic Rarefaction 1.3. Available via http://www.uga.edu/strata/software/anRareReadme.html. Accessed 30 May 2008.

Hora, R.C. and J.J. Soares, 2002. Estrutura fitossociológica da comunidade de lianas em uma floresta estacional semidecidual na Fazenda Canchim, São Carlos, SP. Revista Brasileira de Botânica 25(3): 323-329.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52(4): 577–585.

Hutcheson, K., 1970. A test for comparing diversities based on the Shannon formula. Journal of Theoretical Biology 29(1): 151-154.

Janzen, D.H., 1969. Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. Ecology 50(1): 147-153.

Köppen, W., 1948. Climatologia. Fondo de Cult. Economica.

Krebs, C.J., 1999. Ecological Methodology, 2nd edn. Addison-Welsey Educational Publishers, Inc.

Laurance, W.F., 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biological Conservation 141(7): 1731-1744.

Laurance, W.F., D. Pérez-Salicrup, P. Delamônica, P.M. Fernside, S. D'Angelo, A. Jerozolinski, L. Pohl and T.E. Lovejoy, 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82(1): 105-116.

Leigh JR, E.G., R.P. Davidar, C.W. Dick, J.P. Puyravaud, J.Terborgh, H. ter Steege and S.J. Wright, 2004. Why do some tropical forests have so many species of trees? Biotropica 36(4): 447-473.

Lundholm, J.T. and D.W. Larson, 2003. Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. Ecography, 26(6): 715-722.

Macía, M.J., K. Roukolainen, H. Tuomisto, J. Quisbert and V. Cala, 2007. Congruence between floristic patterns of trees and lianas in a southwest Amazonian rain forest. Ecography, 30(4): 561-577.

Madeira, B.G., M.M. Espírito-Santo,S.D. Neto, Y.R.F. Nunes, G.A.S. Azofeifa, G.W. Fernandes and M. Quesada, 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. Plant Ecology, 201(1): 291-304.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing.

Maier, F.E., 1982. Effects of physical defenses on vine and epiphyte growth in palms. Tropical Ecology 23: 212-217.

McGill, B.J., R.S. Etienne, J.S. Gray, D. Alonso, M.J. Anderson, H.K., Benecha, M. Dornelas, B.J. Enquist, J.L. Green, F. He, A.H. Hurlbert, A.E. Magurran, P.A. Marquet, B.A. Maurer, A. Ostling, C.U. Soykan, K.I. Ugland and E.P. White, 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters., 10(10): 995-1015.

Meinzer, F.C., J.L. Andrade, G. Godstein, M. Holbrook, J. Cavelier and S.J. Wright, 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. Oecologia. 121(3): 293-301.

Muthuramkumar, S., S.N. Ayyappan, N. Parthasarathy, D. Mudappa, T.R.S. Raman, M.A. Selwyn MA and L.A. Pragasan, 2006. Plant community structure in Tropical Rain Forest fragments of the Western Ghats, India. Biotropica 38(2): 143-160.

Nabe-Nielsen, J. and P. Hall, 2002. Environmentally induced clonal reproduction and life history traits of liana *Machaerium cuspidatum* in an Amazonian rain forest, Ecuador. Plant Ecology 162(2): 215-226.

Nesheim, I. and R.H. Økland, 2007. Do vine species in neotropical forests see the forest or the trees? Journal of Vegetation Science 18(3): 395-404.

Palmer, M. W., 1992. The coexistence of species in fractal landscapes. American Naturalist 139(2): 375-397.

Pausas, J.G., J. Carreras, A. Ferré and X. Font, 2003. Coarse-scale plant species richness in relation to environmental heterogeneity. Journal of Vegetation Science 14(5): 661-668.

Price, E.A. and C. Marshall, 1999. Clonal plants and environmental heterogeneity – an introduction to the proceedings. Plant Ecology 141(1/2): 3-7.

Putz, F.E., 1984. How trees avoid and shed lianas. Biotropica 16(1): 19-23.

Putz, F.E. and D.M Windsor, 1987. Liana phenology in Barro Colorado Island, Panama. Biotropica 19(4): 334-341.

Reddy, M.S. and N. Parthasarathy, 2006. Liana diversity and distribution on host trees in four inland tropical dry evergreen forests of peninsular India. Tropical Ecology 47(1): 109-123.

Rezende, A.A., 2005. Comunidade de lianas e sua associação com árvores em uma floresta estacional semidecidual, M.S. thesis. Universidade Estadual de Campinas, Campinas, S.P.

Rice, W.R., 1989. Analyzing tables of statistical tests. Evolution 43(1): 223-225.

Ricklefs, R.E., 1977. Environmental heterogeneity and plant species diversity: a hypothesis. American Naturalist 111(978): 376-381.

Ricklefs, R.E., 2006. Evolutionary diversification and the origin of diversity-environment relationship. Ecology 87(7): S3-S13.

Rochelle, A.L., 2008. Heterogeneidade ambiental, diversidade e estrutura da comunidade arbórea de um trecho da Floresta Ombrofila Densa Atlantica. M. S. thesis, Universidade Estadual de Campinas, Campinas, S.P.

Rosenzweig, M.L., 1995. Species diversity in space and time. Cambridge University Press.

Sanches, M.C. and I.F.M. Válio, 2002. Seed and seedling survival of some climber species in a Southeast Brazilian Tropical Forest. Biotropica 34(2): 323-327.

Schemske, D.W., 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. In Foundations of tropical biology: key papers and commentaries, Eds., Chazdon, R. and T. Whitmore. Chicago: University of Chicago Press, pp: 163-173.

Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166(2): 262-276.

Schnitzer, S.A., J.W. Dalling and W.P. Carson, 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. Journal of Ecology 88(4): 655-666.

Scudeller, V.V., F.R. Martins and G.J. Shepherd, 2001. Distribution and abundance of arboreal species in the atlantic ombrophilous dense forest in Southeastern Brazil. Plant Ecology 152(2): 185-199.

Senbeta, F., C. Schmitt, M. Denich, S. Demissew, P.L.G. Vlek, H. Presinger, T. Woldemariam and D. Teketay, 2005. The diversity and distribution of lianas in the Afromontane rain forests of Ethiopia. Diversity and Distributions 11(5): 443-452.

Sfair, J.C., A.L.C. Rochelle, A.A. Rezende, J. van Melis, V.L. Weiser and F.R. Martins, 2009. Non-randomness in liana-tree network: evidence of nestedness in three distinct vegetation formations. Submitted

Silva, L.A. and J.J. Soares, 2002. Levantamento fitossociológico em um fragmento de floresta estacional semidecídua, no município de São Carlos, SP. Acta Botanica Brasilica 16(2): 205-216.

Sokal, R.R. and J.F. Rohlf, 2003. Biometry – The Principles and Practice of Statistics in Biological Research, 3rd edn. W.H. Freeman and Company.

Stueffer, J.F., H.D. Kroon and H.J. During, 1996. Exploitation of environmental heterogeneity by spatial division of labor in a clonal plant. Functional Ecology 10(3): 328-334.

Talley, S.M., W.N. Setzer and B.R. Jackes, 1996. Host associations of two adventitious-root-climbing vines in a North Queensland Tropical Rain Forest. Biotropica 28(3): 356-366.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M.C. Wuchmann, M. Schwager and F. Jeltsch, 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31(1): 76-92.

Thuiller, W., G.F. Midgley, M. Rouget and R.M. Cowling, 2006. Predicting patterns of plant species richness in megadiverse South Africa. Ecography 29(5): 733-744.

Tokeshi, M., 1999 Species coexistence: ecological and evolutionary perspectives. Blackwell Publishing.

van der Heijden, G.M.F. and O.L. Phillips, 2008. What controls liana success in Neotropical forests? Global Ecology and Biogeography 17(3): 372-383.

van der Heijden, G.M.F. and O.L. Phillips, 2009. Environmental effects on Neotropical lianas species richness. Journal of Biogeography 36(8): 1561-1572.

van Melis, J., 2008 Lianas: biomassa em floresta neotropicais e relação riqueza e biomassa em um trecho de Floresta Ombrofila Densa Atlântica. M.S. thesis, Universidade Estadual de Campinas, Campinas, S.P.

Verdú, M and A. Valiente-Banuet, 2008. The nested assembly of plant facilitation networks prevents species extinctions. American Naturalist 172(6): 751-760.

Vivian-Smith, G., (1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. Journal of Ecology 85(1): 71-82.

Watanabe, N.M. and E. Suzuki, 2008. Species diversity, abundance, and vertical size structure of rattans in Borneo and Java. Biodiv Conserv 17(3): 523-538.

Weiser, V.L., 2007. Árvores, arbustos e trepadeiras do cerradão do Jardim Botânico Municipal de Bauru, SP. PhD thesis, Universidade Estadual de Campinas, Campinas.

Wilson, S.D., 2000. Heterogeneity, diversity and scale in plant communities. In The ecological consequences of environmental heterogeneity, Eds., Hutchings, M.J., E.A. John and A.J.A. Stewart. Oxford: Blackwell Science, pp: 53-70.

Zar, J.H., 1999. Biostatistical analysis. Upper Saddle River: Prentice Hall.