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Shift in Abundance From Seedling to Juvenile Gives Lianas Advantage Over Trees: A Case Study in the Atlantic Forest Hotspot

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Abstract

The Atlantic Forest has been threatened by frequent human disturbances that affect its ecological processes. Lianas are an important component of tropical forest dynamics and, under chronic disturbance, may proliferate vigorously, potentially arresting secondary succession and hindering forest recovery. Our study aims to analyze abundance and diversity of liana and trees in different life stages in a disturbed semidecidual seasonal tropical forest fragment in southeast Brazil. We sampled the species richness and relative abundance in the following life stages of lianas and trees: I—seed (as seed arrival and seed bank processes), II—seedling, III—juvenile, and IV—adult. Lianas are more abundant than trees after the seedling stage, while trees showed more rarefied species richness only at the seed rain stage. Our results show that dispersal does not seem to be a bottleneck for either liana or tree community in disturbed fragments, but competition at the seedling stage may give lianas advantage over trees. Lianas may proliferate abundantly in forest fragments, even decades after disturbance. We recommend interventions for the management and restoration of disturbed forest fragments dominated by lianas to target this life form in life stages where they suppress the forest community, such as after the seedling stage.

Keywords

climbing plants, tree, competition, disturbed forest, Atlantic Forest, life stages

Introduction

The Atlantic Forest is the third largest biome of Brazil, originally occupying more than 1.4 million square kilometers, with wide latitudinal and altitudinal ranges (from 3° to 30°S and from sea level to 2,700 m asl) that foment its vast biodiversity (Joly, Metzger, & Tabarelli, 2014). However, due to intensive human occupation, it is today considered one of the most threatened hotspots in the world (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Currently, the native vegetation cover of the Atlantic Forest is reduced to less than 16% of its original area, composed mostly by small and isolated disturbed forest remnants embedded in human-modified landscapes (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Such process of fragmentation increases forest area under edge effect and increases the encroachment of human-mediated disturbances, generating impacts such as the loss of biodiversity and ecosystem services in both local and regional scales (Barlow et al., 2016; Haddad et al., 2015).

According to Murcia (1995), forest fragmentation generates changes in three effect categories: (a)

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abiotic—change in environmental conditions due to proximity with a distinct matrix; (b) direct biotic—changes in the abundance and distribution of species due to the environmental conditions near the edge and according to the physiological tolerance of each species to the edge conditions; and (c) indirect biotic—changes in the degree and frequency of species interactions, such as predation, competition, seed dispersal, and pollination. Despite all the potential changes in the forest ecological processes due to fragmentation, species and ecological groups adapted to forest interior are usually hindered in small forest fragments (Tabarelli, Peres, & Melo, 2012), making them key biodiversity refuges in human-modified landscapes (Matos et al., 2016).

The biotic and abiotic changes in forest fragments lead to the proliferation of disturbance-adapted species, such as lianas (Addo-Fordjour & Owusu-Boadi, 2016; Campbell et al., 2018). Lianas are woody climbing plants that require support to reach the forest canopy, although, in some species, the need for support is facultative (Gerwing et al., 2006). Most of the liana ecology studies in the tropics were carried out in large, continuous forests, considering aspects such as diversity, abundance, species richness, and liana–tree interactions (Álvarez-Cansino, Schnitzer, Reid, & Powers, 2015; García León, Martínez-Izquierdo, Mello, Powers, & Schnitzer, 2017; Kainer, Wadt, & Staudhammer, 2014; Pérez-Salicrup, Schnitzer, & Putz, 2004; Schnitzer & Bongers, 2002). In old-growth forests, lianas are more abundant in early stages of succession, in forest gaps, and on fertile soils (Barry, Schnitzer, Breugel, & Hall, 2015; Dalling et al., 2012; Gentry, 1984; Hegarty & Caballé, 1984; Schnitzer, Dalling, & Carson, 2000).

Studies that approached the process that favor liana dominance over trees in disturbed semidecidual tropical forest fragments point out liana resilience (Barry et al., 2015; Pinard, Putz, & Licona, 1999) and efficient water use and carbon absorption (Álvarez-Cansino et al., 2015; Cai, Schnitzer, & Bongers, 2009; Chen, Bongers, Cao, & Cai, 2008; Chen et al., 2015) as processes favoring this life form. In this context, high liana abundance may hinder successional development of the forest community by changing tree phenology (García León et al., 2017) reducing tree growth and sap flow (Álvarez-Cansino et al., 2015; Martínez-Izquierdo, García León, Powers, & Schnitzer, 2016) and affecting natural regeneration (Martínez-Izquierdo et al., 2016; Schnitzer et al., 2000).

Forest fragments in human-modified landscapes are important for the connection of habitat areas, for biodiversity maintenance, and to supply seeds for natural regeneration and nearby restoration actions (Augusto, Tabanez, & Viana, 2000; C. L. Rezende, Uezu, Scarano, & Araujo, 2015). Nevertheless, many of these forest fragments are threatened by chronic human disturbances that can compromise their potential ecological benefits on the long term (Arroyo-Rodríguez et al., 2015; Farah et al., 2014; García León et al., 2017; Martínez-Izquierdo et al., 2016). Despite their ecological role, forest fragments are often neglected in forest restoration projects, which commonly focus in totally deforested areas (Rodrigues et al., 2011; Viani, Mello, Chi, & Brancalion, 2015). Restoring disturbed forest fragments through low-cost techniques, such as liana cutting, may be a cost-efficient approach for biodiversity conservation in human-modified landscapes (César et al., 2016; Marshall et al., 2016; Paul & Yavitt, 2011; Viani et al., 2015).

In this context, this work contributes to the knowledge of the life cycles of tree and liana communities in disturbed forest fragments in human-modified landscapes. We sampled plant community in a semideciduous seasonal tropical forest fragment of the Atlantic Forest to (a) quantify tree and liana abundance in different stages of their life cycle—seed (divided on seed rain and seed arrival processes), seedling, juvenile, and adult—and (b) indicate in which life stage lianas become more abundant than trees in a forest fragment. Considering that lianas dominate adult forest community in many disturbed forest fragments and that greater sorting pressure happens in early stages of life cycles, we expect lianas to be more abundant than trees after the seedling stage.

Methods

Study Site

We used a 14-ha forest fragment located in Piracicaba county, São Paulo State, southeast Brazil, on coordinates 22° 42′ 40″S and 47° 37′ 30″W. The climate of the region is classified as Cwa, according to Köppen–Geiger climate classification, with hot and wet summers and dry winters (Alvares, Stape, Sentelhas, De Moraes Gonçalves, & Sparovek, 2013). The average annual precipitation in the study site is 1,275 mm with monthly averages of 209.5 mm during the rainy season (October to March) and 34.5 mm during the dry season (April to September). The average monthly temperature is 21.6°C, with monthly minimum temperature of 17.5°C and maximum of 24.7°C. Vegetation of the study site is characterized as semidecidual seasonal tropical forest belonging to the *interior* subregion of the Atlantic Forest, the most threatened vegetation type of this hotspot (Laurance, 2009; Ribeiro et al., 2009). Semidecidual forests of the Atlantic Forest Biome are characterized by a period of physiological latency of the trees caused by either drought or low temperatures, when around 20% to 50% of trees lose their leaves (Instituto Brasileiro de Geografia e Estatística, 2012).

Fragmentation occurred in our study region more than 200 years ago, and as commonly found in forest fragments in human-modified landscapes, our study site has historically suffered chronic disturbances, such as selective logging, cattle grazing, and hunting. The most recent severe impact was a fire that burned most of the remnants 35 years before data gathering. Since then, tree community composition has changed little and ruderal plants proliferated vigorously (Catharino, 1989). High abundance of lianas and emergent trees in a discontinuous canopy for long time (>20 years) has led us to infer that successional processes may be hindered in our study site due to liana competition advantage over trees (Pinard et al., 1999; Schnitzer et al., 2000).

Experimental Design and Data Gathering

We allocated 30 circular plots of 10-m radius ($\sim$314 m^2) in forest sectors dominated by lianas. Plots were allocated in a stratified random design to sample the heterogeneity of liana-dominated sectors. In these plots, we sampled the abundance and richness of lianas and self-supporting woody plants (hereafter *trees*) in different life stages. The life stages of lianas and trees and their related ecological processes considered in this study were as follows: I—seed (seed rain and seed bank processes), II—seedling, III—juvenile, and IV—adult. We divided the life stage seed in two ecological processes: seed rain and seed bank. This division aims to highlight the difference in reproductive strategies of trees and lianas, where the first invest on seeds that can stay in the seed bank for long periods and the former invests more on clonal reproduction (Ledo & Schnitzer, 2014; Penalosa, 1984). Inclusion criteria differ among life forms adapted from the literature on tropical trees and lianas (Connell & Green, 2000; Kurzel, Schnitzer, & Carson, 2006). The following are the inclusion criteria and sampling methods for each life stages

Seed rain. In seven randomly selected circular plots, we installed three square seed traps of 0.6 m side (0.36 m^2) at 20 cm above the soil. The material gathered in each seed trap was collected every 15 days for 1 year. We used magnifying lens and sieves to locate tree and liana seeds in the material gathered from the seed traps.

Seed bank. In eight randomly selected circular plots, we collected four soil subsamples of $20 \times 20 \times 5$ cm each (the last dimension refers to depth). We removed the surface layer of litter and fine roots for collecting the seed bank. After collection, each subsample was moved to a plant nursery and spread in an area 2 times the surface area of the soil seed bank sampled. Seed bank samples were kept under direct sunlight and irrigated 3 times a day. Emerging seedlings were counted, identified, and removed weekly until no more seedlings arose. The nursery where seed bank was spread had few wind-dispersed trees located dozens of meters from the seed bank and that did not occur in the forest studied. These tree species could be easily identified—and removed—in the event of germinating in the exposed seed bank.

Seedlings. We considered in this class all trees <40 cm in height and diameter at breast height (DBH) <1.58 cm (DBH referring to circumference at breast height of 5 cm, which most of the trees are sampled in the study region), and liana individuals with diameter 0.5 to 1.5 cm. The inclusion criteria for tree seedlings were adapted from Connell and Green (2000). The inclusion criteria for liana seedlings were based on the minimal size of lianas for forest dynamics studies suggested by the protocol of Gerwing et al. (2006). Both life forms were sampled once in four 3×3 m subplots allocated in the outer limits of the 30 randomly selected circular plots. Liana's diameter was measured according to the protocols proposed by Gerwing et al. (2006) and Schnitzer, Rutishauser, and Aguilar (2008), and we excavated superficial roots and followed liana stems to guarantee that we would not sample the same apparent gene more than once. We considered only the largest stem of each liana to define its diameter class.

Juveniles. In this class, we included all trees DBH 1.58–10.0 cm and lianas 1.5–2.5 cm in diameter. Both life forms were sampled only once in this life stage. Trees were sampled in the 10-m circular plot, while lianas were sampled in four 3×3 m subplots allocated in the outer limits of the 30 randomly selected circular plots.

Adult. We considered in this class all trees DBH > 10 cm and lianas diameter >2.5 cm (Kurzel et al., 2006). Both life forms were sampled only once in this life stage. Trees were sampled in the 10-m circular plot, while lianas were sampled in four 3×3 m subplots allocated in the outer limits of the 30 randomly selected circular plots.

We understand that the life stage classifications of plants as seedlings, juveniles, and adults based on diameter alone may be a rough estimate for most species, especially for lianas, and should be considered more as a criterion for size grouping than for other physiological and phenological characteristics (e.g., flowering, fruiting, and senescence). Kurzel et al. (2006) show that approximately 100% of lianas with diameter > 2.5 cm reach the forest canopy, which can be used as a proxy for adult lianas. Despite its intrinsic inaccuracies, the classification of life stages was considered the best way to compare the dynamic of trees and lianas in this study and was in accordance of field observations.

To estimate species richness, sampled individuals were identified to the lowest taxonomic level possible with the

Table 1. Number of Individuals and Species of Trees and Lianas Sampled in Four Life Stages.

	Seed rain	Seed bank	Seedling	Juvenile	Adult
Total					
Abundance	8,889	777	3,392	661	378
Species richness	59	43	161	114	96
Trees					
Abundance	4,940 (56%)	689 (88%)	1,908	334	278
Species richness	36 (61%)	25 (58%)	78	54	57
Most abundant species	*Aloysia virgata* (76%)	*Trema micranta* (40%); *A. virgata* (19%)	*Hybanthus* (46%); *Trichilia clausseni* (12%); *Trichilia casaretti* (10%)	*Piper amalago* (27%); *Trichilia elegans* (9%)	*Urera baccifera* (17%); *Bauhinia forficata* (11%)
Lianas					
Abundance	3,949 (44%)	88 (12%)	1,484	327	100
Species richness	23 (39%)	18 (42%)	83	60	39
Most abundant species	*Calopogonium mucunoides* (61%)	*Pereskia aculeata* (38%); *Cardiospermum grandiflorum* (18%)	*Mansoa difficilis* (13%); *Dicella bracteosa* (9%); *Lundia obliqua* (9%)	*Fridericia triplinervia* (10%); *Serjania fuscifolia* (8%); *L. obliqua* (8%)	*F. triplinervia* (14%)

Note. Seed (Seed Rain and Seed Bank Processes), Seedling, Juvenile, and Adult in a Disturbed Seasonal Tropical Forest Fragment of the Atlantic Forest in Southeast Brazil. Percentages in parentheses show the relative abundance and species richness of trees and lianas for a given life stage; or the relative abundance of the most common species for each life form at a given life stage. Sampling methods differed for lianas and trees in postgermination stages, and thus, we do not show relative abundance and species richness in these life stages since they would not represent relative abundance in these communities.

help of specialists, literature, and materials stored in the Escola Superior de Agricultura (ESA) herbarium in the Luiz de Queiroz College of Agriculture of the University of São Paulo (ESALQ/USP), Brazil. Morphospecies that could not be identified to the species level were considered as different species in each life stage, since the aim of this research is to compare abundance and richness in the same life stage. One should not extrapolate richness obtained in each life stage to the whole community, as it is likely that the same species could be considered as different morphospecies among life stages.

Data Analyses

We compared the densities of trees and lianas on each life stage using the Welch's (1938) t test considering a $\alpha = .05$ when the data respected the assumption of normality, what happened for seed arrival, seed bank, juveniles, and adults. We carried out logarithmic transformation for juveniles and adults and square root transformation for seed bank in order to normalize the data. For seedlings, we used the nonparametric Wilcoxon-Mann–Whitney test for paired samples. We used different sampling protocols for each life stage of trees and lianas, and we consider the life stages independent from one another. To compare densities of trees and lianas with different sampling sizes, we extrapolated abundance of each sample to a hectare before data analyses. Outliers were removed for statistical analysis but kept for graphical figures and mean calculations. Abundance results are shown as average ±1 standard deviation (SD).

To compare rarefied species richness between trees and lianas in each life stage, we developed rarefaction curves using the software PAST 3.15. Rarefaction curves represent the average number of species for 10,000 repetitions of sampling and their upper and lower 95% confidence interval.

Results

For the seed life stage processes, we sampled a total of 8,889 seeds in the seed rain and 777 individuals germinated in the seed bank. In the postgermination life stages, we sampled 3,392 seedlings, 661 juveniles, and 378 adult plants. The details of the number of individuals and species of trees and lianas sampled and the most common species are given in Table 1. The complete list of the species found for each life form in each life stage is in the Supplementary File 1.

At the seed rain, trees ($M = 6.473$, $SD = 0.531$) and lianas ($M = 6.550$, 0.433) do not differ in their abundances, $t(11.53) = -0.3$, $p = .77$, although at the seed bank trees ($M = 5{,}312{,}500$, $SD = 2{,}024{,}129$) are substantially more abundant than lianas ($M = 687{,}500$, $SD = 502{,}227.2$), $t(11.55) = -7.9$, $p < .0001$. At the seedling stage, tree ($M = 18{,}145$, $SD = 9{,}309.448$) and liana ($M = 14{,}117$, $SD = 5{,}998.33$) abundances do not differ statistically ($Z = 1.34$, $p = .19$). However, after the seedling stage, lianas ($M = 3{,}244$, $SD = 1{,}444.5$) have higher abundance than trees ($M = 1{,}551$, $SD = 529.73$) at juvenile stage, $t(45.26) = 5.3$, $p < .0001$, and at adult stage (lianas: $M = 1{,}021.8$, $SD = 545.45$, trees: $M = 401.3$, $SD = 139.24$), $t(44.56) = 6.53$, $p < .0001$ (see Figure 1).

Compared with trees, lianas have a greater proportion of individuals that move on to the next life stages. Lianas show more absolute abundance after the seedling stage, dominating the forest community until the adult stage (Figure 1). For rarefied species richness, trees also have more species only in the seed rain, and, after germination, both life forms have similar rarefied species richness (Figure 2; Table 2).

Discussion

In the context of the small and chronically disturbed tropical forest fragment considered in this study, we observed that, at the seed rain stage, trees and lianas have similar abundance, indicating that dispersal is not a limitation on the settlement of both life forms. At the seed bank level, trees are more abundant than lianas, which could be explained by the investment on short-lived seeds and clonal reproduction strategy in lianas (Ledo & Schnitzer, 2014; Yorke, Schnitzer, Mascaro, Letcher, & Carson, 2013). However, liana abundance greatly surpasses trees after the seedling stage. This result supports the long-standing paradigm in tropical forest ecology that the structure of mature tree communities reflects processes that operated at earlier life stages (Green, Harms, & Connell, 2014).

Lianas may play a role in the greater sorting pressures during early life stages of tropical trees (Baldeck et al., 2013). A study in dam-induced forest fragments in the Amazonian Forest showed increased dominance of lianas on the seedling layer in more degraded forest fragments (Jones, Peres, Benchimol, Bunnefeld, & Dent, 2017). Moreover, a liana removal experiment in the same area of this study showed lower mortality for experimentally planted pioneer tree seedlings on areas with lianas compared with liana free plots (César et al., 2016).

The shift on liana and tree abundances at the seedling stage could be explained by a stronger habitat filtering over trees at earlier life stages (Baldeck et al., 2013; Jones et al., 2017). However, many studies have shown evidence for strong competition of lianas over trees and the greater likelihood of lianas to advance in the life stages when compared with trees (Gerwing & Vidal, 2002; Ledo & Schnitzer, 2014; Martínez-Izquierdo et al., 2016; Muscarella et al., 2013). A synergic effect of disturbance filtering and competition may be acting on the liana advantage over trees after the seedling stages.

The high abundance of liana seedlings in the forest fragment, despite the low abundance of liana on the seed bank, may be related to the clonal vegetative reproduction strategy of this life form (Gerwing & Vidal, 2002; Ledo & Schnitzer, 2014). Higher abundance of trees in the seed bank was caused primarily by orthodox pioneer species, which composed 81% of tree seed bank; on the other hand, pioneer species composed only 2% of tree seedling bank (Supplementary File 1). Lianas seeds may be more recalcitrant (i.e., prone to germination soon after reaching the soil) and reaching greater abundances than trees in the seedling stage, as the result shows. Lianas, although able to propagate vegetatively, depend mostly on seed germination for establishment (Tres et al., 2007). In the disturbed forest fragment studied, seed dispersal may not be a limitation for establishment or propagation of both life forms, although the seed bank is an important source for tree recolonization.

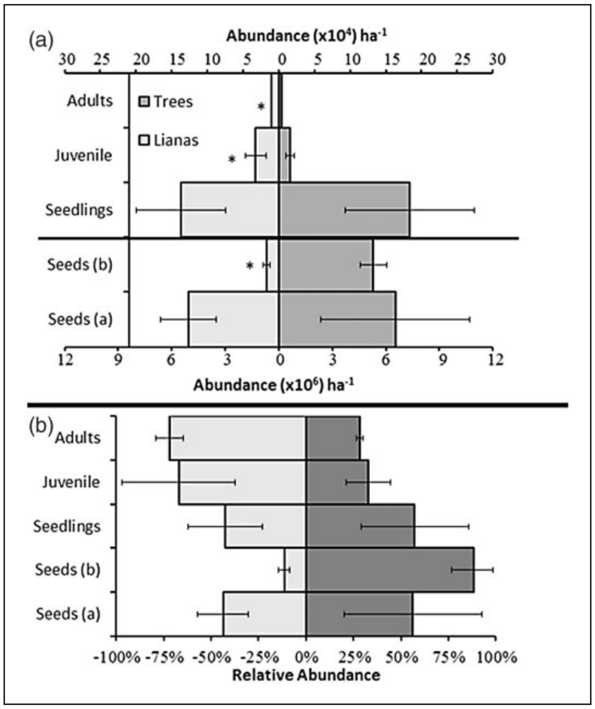

Figure 1. (a) Abundance of trees and lianas in each life stage. Seed abundances are dimensioned to the lower horizontal axis, while the other life stages are dimensioned in the upper axis of the graph. (b) Relative abundance of trees and lianas in each stage: Seeds (a) seeds from the seed rain, seeds (b) seeds from the soil seed bank. Asterisks indicate difference between tree and liana abundance for a given life stage ($\alpha = .05$).

Implications for Conservation

Liana abundance in our study site is considerably higher than in other sites of the Atlantic Forest. The estimated abundance of lianas with diameter $\geq$1 cm in our study site is approximately 3 times the abundance of lianas with similar diameter sampled in a 650-ha semidecidual forest fragment by A. A. Rezende, Ranga, & Pereira (2007). When compared with studies that used higher diameter inclusion criteria, such as in Campanello, Garibaldi, Gatti, and Goldstein (2007), that sampled lianas $\geq$2.5 cm, the area of this study still showing an

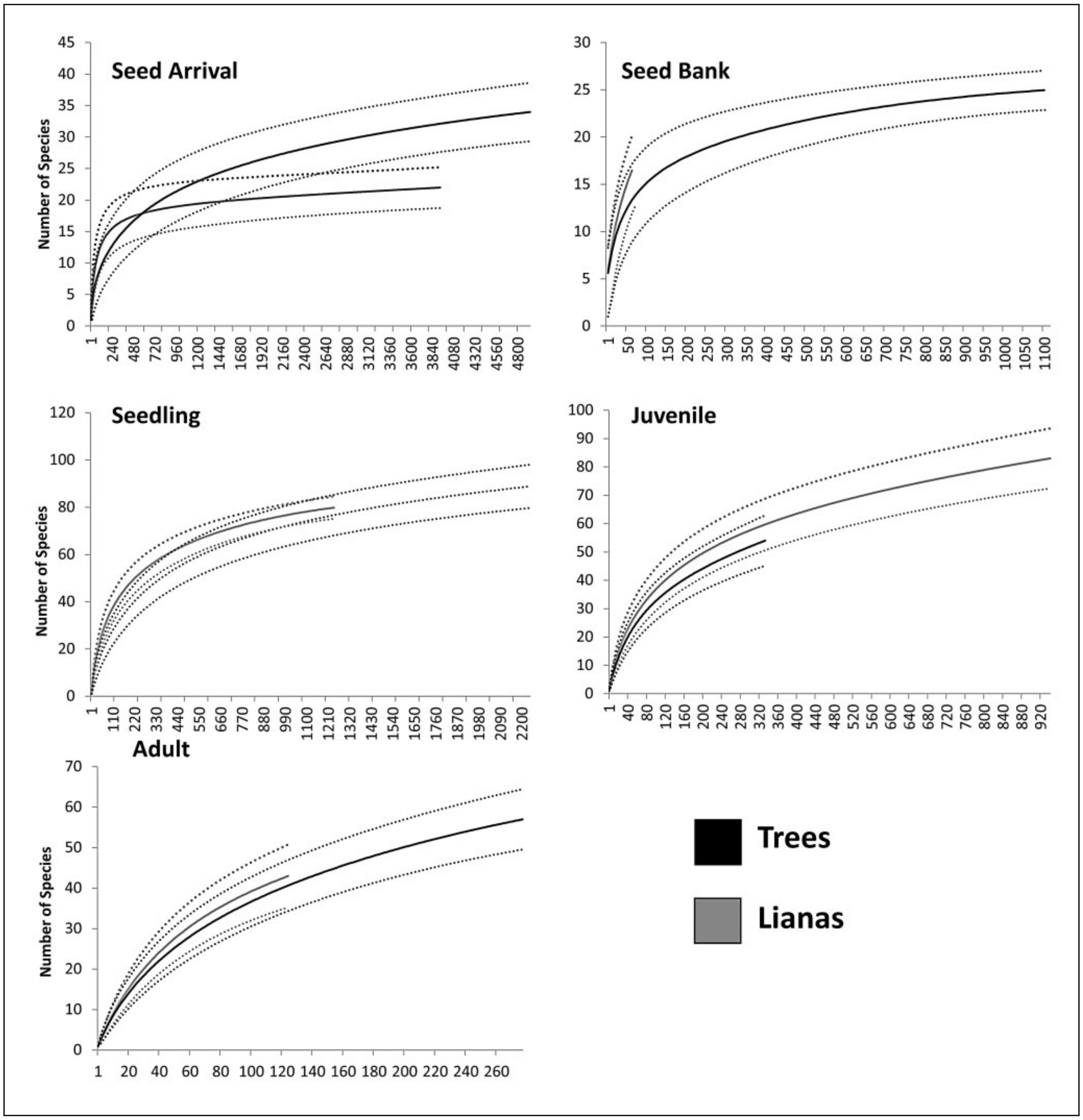

Figure 2. Rarefied species richness curves in different seed processes (seed rain and seed bank) and life stages (seedling, juvenile, and adult) for trees and lianas. Dotted lines indicate lower and upper 95% confidence intervals. Note that graphs have different scales.

abundance 2 times higher than in Campanelloet al. (2007) study site for lianas ≥2.5 cm. The higher liana abundance in our study site indicates that some species of this life form may benefit from the disturbance condition to displace tree species and potentially arrest succession in the area (César et al., 2016; Schnitzer et al., 2000). In this context, human interventions could accelerate the recuperation of successional processes and forest structure (César et al., 2016; Marshall et al., 2016; Viani et al., 2015).

Although conservation of old-growth forests is crucial for biodiversity conservation and maintenance of ecosystem services (Gibson et al., 2011; Stephenson et al., 2014), second-growth and disturbed forest fragments have a great potential to recover ecosystem services and provide habitat for native species (Chazdon et al., 2009; Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013; Poorter et al., 2016; Vidal, Mangueira, Farah, Rother, & Rodrigues, 2016). Although these forest fragments may provide suboptimal habitat for some species, in many cases, they are the only refuge available for native species in human-modified landscapes and the only source of seeds for regenerating disturbed areas or areas under ecological restoration.

The restoration of forest fragments should focus in controlling liana abundance after the seedling life

Table 2. Relative Abundance of Trees and Lianas in Different Life Stages in a Disturbed Seasonal Semideciduous Tropical Forest Remnant in Southeast Brazil.

Life stage	Seed (%)	Seedling	Juvenile	Adult
Relative number of individuals based on the previous life stage				
Trees	100.00	0.16	8.64	25.42
Lianas	100.00	0.24	23.68	31.50
Relative number of individuals based on the initial number of seeds				
Trees	100.00	0.16	0.01	0.004
Lianas	100.00	0.24	0.06	0.018

stage, when lianas begin to dominate the forest community. Cutting lianas may be a cost-efficient strategy to release the tree community from liana competition in order to increase the recovery of trees and the canopy structure (César et al., 2016; Marshall et al., 2016; Viani et al., 2015). The high abundance and rarefied species richness of the tree seed rain indicates that dispersal may not be a limitation to recover disturbed forest fragments, while tree competition with lianas in more advanced life stages may be a crucial factor. Given the high abundance of native trees in our study site, seedling plantings to recover forest structure may be considered only in forest sectors with lower tree abundance or in gaps, in order to reintroduce late-successional native tree species, given the high abundance of pioneer species in disturbed forest fragments (Tabarelli, Aguiar, Ribeiro, Metzger, & Peres, 2010).

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