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Short Communication

Early Response of Tree Seed Arrival After Liana Cutting in a Disturbed Tropical Forest

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Abstract

Most remaining tropical forests are under some level of chronic human disturbance, which may favor the proliferation of disturbance-adapted native plants, like some species of tropical lianas. These plants may alter forest structure and composition, but little is known about their effect on ecological processes, such as seed rain. We analyzed the early effects of overabundant lianas on the seed rain of animal-dispersed tree species for 1 year. We analyzed the effect of overabundant lianas on seed rain by cutting all lianas in experimental plots of 314.1 m^2, establishing 12 paired plots with and without liana cutting in a disturbed Atlantic Forest remnant in Southeastern Brazil. Rarefied tree seed species richness was higher in plots dominated by lianas (10.9 ± 0.2 and 8.3 ± 1.2 for 500 seeds sampled in liana-dominated and liana-cut plots, respectively), but seed abundance was lower (209 ± 138 and 984 ± 421 seeds m^{-2} in liana-dominated and liana-cut plots, respectively). Pioneer seed abundance (316.0 ± 116.3 seeds m^{-2}) and species density (3.2 ± 0.3 species $trap^{-1}$) did not differ among treatments. Lianas may eventually increase local seed rain diversity, while suppressing local tree seed rain abundance. Understanding the impact of the dominance of ruderal species in ecological processes that maintain tropical forests communities, such as seed rain, is crucial to guide the directions for conservation and management of degraded remnants.

Keywords

Atlantic forest, disturbance, liana, plant dominance, seed rain, seed dispersal

Most of tropical forest regions are under some level of chronic human-mediated disturbance, such as fire, hunting, and logging (Pimm et al., 2014). These frequent disturbances may exceed the resilience thresholds of forest ecosystems and may change their structure and successional development (Tabarelli, Peres, & Melo, 2012). Alterations in the forest structure and dynamics of the predisturbance habitat may favor native ruderal species such as some species of lianas (Schnitzer, Dalling, & Carson, 2000).

Lianas are plant life forms that require support from trees to reach the forest canopy (although in some species, this support may be facultative) and may proliferate vigorously after disturbance. Lianas compete very effectively against trees for resources, especially in seasonally dry forests, given their overall very efficient water use and resource allocation (Chen et al., 2015). If liana infestation and chronic disturbance are maintained for long periods, tree growth and mortality can be altered in tropical forests, leading to loss of canopy height and stratification (Farah et al., 2014; Schnitzer et al., 2000). Except for tree biomass accumulation and growth (César et al., 2016; Schnitzer, Van Der Heijden, Mascaro, & Carson, 2014; Wright, Tobin, Mangan, & Schnitzer, 2015), few studies analyzed the effect of lianas in key ecological processes for recovery of the tree community such as seed rain. The literature is also scarce for tree fruiting and flowering under liana competition (García León, Martínez Izquierdo, Mello, Powers, & Schnitzer, 2017;

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Kainer, Wadt, & Staudhammer, 2014; Michel, Robinson, & Sherrry, 2015).

Tropical forests are dynamic systems that depend on the presence of a temporary or permanent seed bank accumulated through seed rain, which determines the recruitment of new individuals into the community (Ghazoul & Sheil, 2010). Seed dispersal is a complex ecological process with several knowledge gaps, including the effects of nontree plant dominance in the abundance and composition of tree seed rain (Kainer et al., 2014; Muler et al., 2014). Seed rain constitutes as a fundamental step of the dispersal process and an important mechanism contributing to the remarkable diversity of tropical tree communities (Harms, Wright, Calderón, Hernández, & Herre, 2000). In human-modified landscapes with chronic forest disturbance, defaunation and simplification of forest structure by degradation may alter dispersal, production, and morphological attributes of seeds (Galetti & Dirzo, 2013).These same conditions favor ruderal liana proliferation as detailed earlier.

Few studies evaluated the effect of lianas on tree seed arrival, focusing more on a commercial seed production context (see example for the Brazil nut, *Bertholletia excelsa*, in Kainer et al.'s, 2014, study) or fruiting and flowering by plants (García León et al., 2017). Nevertheless, the relationship of lianas with seed-disperser fauna has been more investigated (Michel et al., 2015), being suggested that lianas are major structural elements for the movement of arboreal mammals across the forest canopy (Emmons & Gentry, 1983). Lianas play an important role in seasonal tropical forests by providing food for fauna in the dry season, when most trees are not fruiting (Morellato & Leitão-Filho, 1996). They also interact in diverse ways with birds by providing food (through flowers and fruits) and nesting sites (for a review, see Michel et al., 2015). In the context of disturbed tropical forest remnants dominated by lianas, their potential impacts on tree seed rain and dispersion at the community scale, or the potential impacts on seed-disperser fauna, are unknown (but see García León et al., 2017).

We evaluated the effect of native lianas proliferating vigorously in a disturbed tropical forest on the abundance, species density, and rarefied species richness (RSR) of the seed rain of animal-dispersed trees. From our best knowledge, our study is pioneer in assessing the effect of liana infestation in the seed rain at the community level. We chose to analyze tree seed rain of animal-dispersed tree species because (a) this dispersal syndrome is more influenced by habitat quality than other syndromes, (b) the majority of tree species in tropical forests are animal dispersed (Howe & Smallwood, 1982), (c) animal-dispersed trees represent 60% and 70% of all trees and pioneer trees in our study site, respectively. Because density of lianas is inversely related to tree abundance (Schnitzer et al., 2000) and seed production (García León et al., 2017; Kainer et al., 2014), we expect lower abundance, species density, and RSR of the seed rain of animal-dispersed trees in plots dominated by lianas. We also evaluated pioneer tree seed abundance and pioneer tree species density. Considering that lianas commonly proliferate in more open, disturbed areas (Schnitzer et al., 2000), we expect greater abundance and species density of pioneer tree seeds in areas dominated by lianas.

Method

Study Site

We investigated the effect of liana overabundance on seed rain of animal-dispersed trees in a 14-ha semideciduous seasonal tropical forest remnant in the municipality of Piracicaba, São Paulo State, Brazil. This forest type is part of the interior biogeographical region of the Atlantic Forest, one of the most threatened with <8% forest cover remaining (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Similarly to all forest remnants in human-modified landscapes in our study region, our study site has historically suffered several human-mediated disturbances of varying magnitudes, including selective logging, cattle grazing, and hunting, and chronic disturbances of small magnitude related to cattle grazing that occurred until 2 years before data gathering. The most recent severe impact was a fire that burned most of the remnant 35 years before our study. Since then, tree community composition has changed very little and lianas proliferated vigorously. This forest remnant is embedded near the urban perimeter of the study region and, although there are similar-sized forest remnants near (<300 m) our study site, they are in similar, or worse, structural condition, and the total native forest cover 1 km around the remnant studied is <10%. Nevertheless, as much as 100 bird species have been observed in the region surrounding the remnant (<1 km around the remnant; Alexandrino et al., 2013).

Our study was carried out in sectors of the forest remnant dominated by ruderal lianas and with reduced tree basal area (hereafter "disturbed sectors"). These sectors were at first identified visually, then we proceeded to place 10-m circular plots (314.15 m^2) randomly to sample tree community structure and richness and quantify how much tree community in degraded sectors differ from that in plots in less degraded sectors (with more tree basal area; for more details in plot allocation, see César et al., 2016). Tree basal area in degraded sectors was approximately one third of basal area in less degraded sectors of the same forest remnant, and community was dominated by trees of Fabaceae, Meliaceae (mainly *Trichilia* spp. P.Browne) and scratchbush (*Urera baccifera* (L.) Gaudich. ex Wedd., Urticaceae). In disturbed sectors,

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previous studies estimated ~7,000 lianas ha^{-1} (César et al., 2016) in our study site, demonstrating its context of high liana abundance. Additionally, in spite of the high species richness of native lianas (86 species), three species dominate forest community in degraded sectors (representing ~30% of all individuals): bell vine (*Mansoa difficilis* (Cham.) Bureau & K.Schum., Bignoniaceae), "pente-de-macaco" (*Lundia obliqua* Sond., Bignoniaceae), and chestnut vine (*Dicella bracteosa* (A.Juss.) Griseb, Malpighiaceae) (Mello, F. N. A., 2015). For more information of forest composition and structure in degraded and less degraded sectors, see César et al. (2016). We selected disturbed, liana-dominated sectors of the remnant to assess seed rain based on low tree basal area and high liana cover by few liana species.

Experimental Design

We installed six pairs of circular plots of 12-m radius (452.4 m^2) in patches with less developed forest structure and dominated by lianas, as mentioned earlier. The average distance between plots of the same pair was 36.5 ± 9.7 m (min: 21 m, max: 46 m), and the average distance between pairs was 59.6 ± 16.6 m (min: 48 m, max 88 m; Figure 1). We randomly selected one plot of each pair to have all lianas cut at 1-m height using machetes. Given the risk of accidents and damage to tree crow, cut lianas were left to decompose in the canopy. Two weeks after liana cutting, we installed three 0.6×0.6 (0.36 m^2) seed traps at 0.2 m above ground in each of the 12 plots, and seed rain was collected every 2 weeks for a year. In order to avoid plot edge effect and minimize the influence of lianas that could be on the forest canopy originating from outside the plot, we installed seed traps in the inner 5-m circumference in the 12-m radius plot.

To assess if forest structure was similar among paired plots, we sampled all trees with diameter at breast height (DBH)>1.6 cm in the inner 10-m circumference of the plots before liana cutting, and 6 months after liana cutting, we installed four 3×3 m subplots next to all plots, outside the influence of liana cutting, and counted all lianas DBH $\geq$ 1.0 cm diameter at 1.3 m from the rooting point in each plot. We summed liana abundance and basal area of the four subplots in each plot to compare liana community structure between plots.

Data Analysis

We combined seeds collected in the three seed traps in each plot to obtain mean values of seed rain of a given plot. Sampled seeds were counted, separated into morphospecies and identified to the lowest possible taxonomic level by comparison with a reference collection assembled during the study and also by consulting specialists and the literature. Animal-dispersed species were classified as pioneer or nonpioneer according to Swaine and Whitmore (1988). We compared seed rain abundance, species density, and pioneer seed abundance of

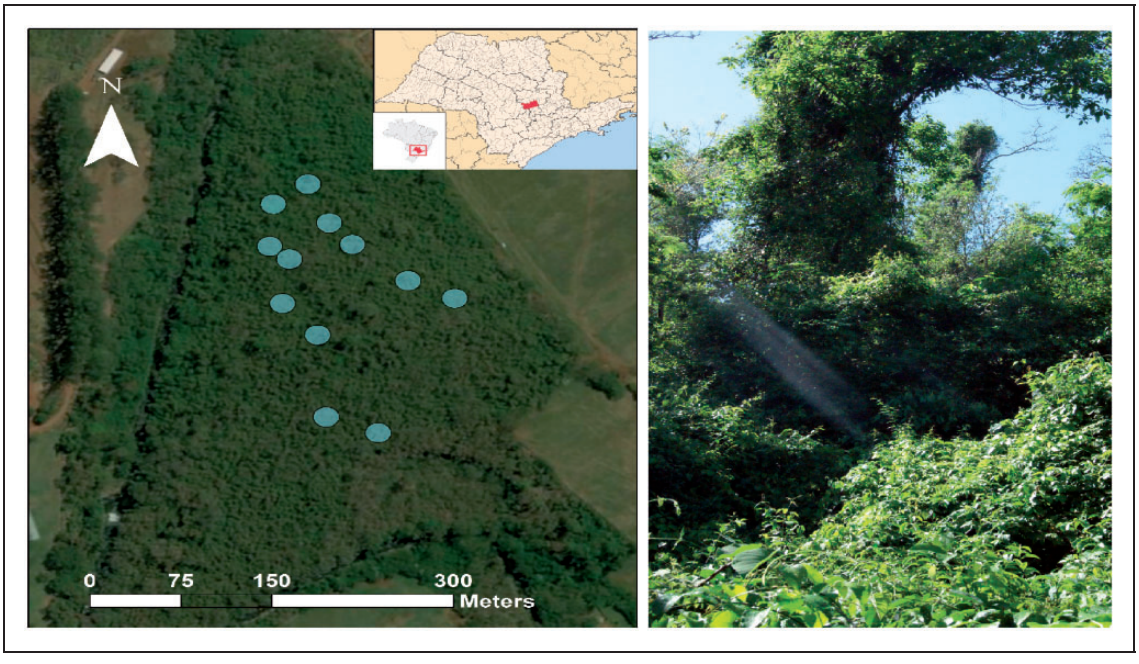


Figure 1. Left: Location of the circular plots for seed rain gathering in a 14-ha semideciduous seasonal tropical forest remnant of the Atlantic Forest in the county of Piracicaba São Paulo, Southeast Brazil (location in the detail figure). Right: overall aspect of disturbed sectors of the forest remnant, where we conducted this experiment.

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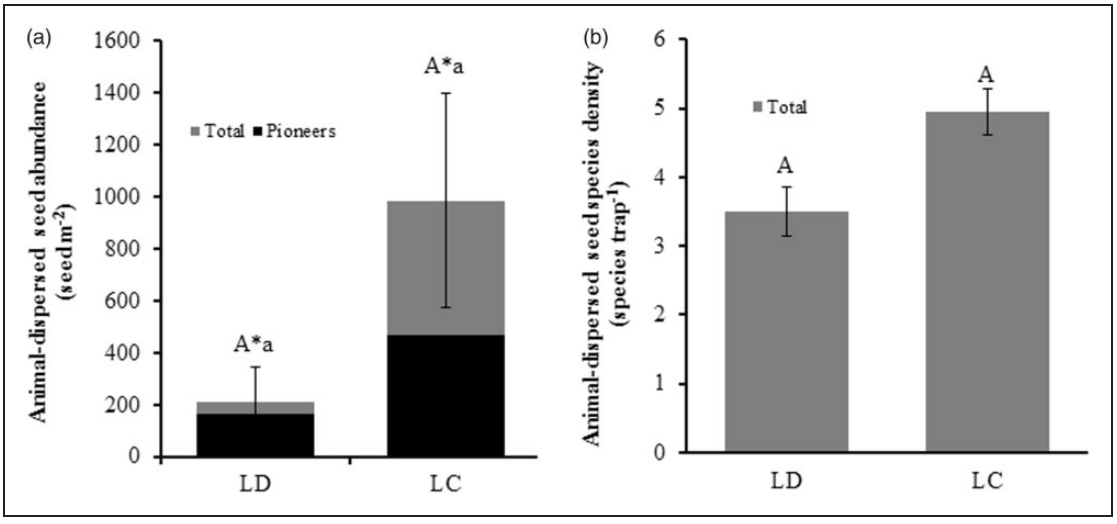


Figure 2. Animal-dispersed tree seed rain abundance (a) and species density (b) in a chronically disturbed seasonal tropical forest remnant dominated by lianas. LD = liana-dominated plots; LC = plots were all lianas were cut. Bars under the same letters do not differ for $\alpha = .05$. Capital letters refer to total seed rain and lowercase to pioneer seed rain. Bars refer to 1 standard error. Low pioneer species richness prevented this type of analysis. *Marginal significance ($p < .08$).

animal dispersed trees between liana-dominated and liana-cut plots using paired t tests ($\alpha = .05$). RSR was compared between liana-dominated and liana-cut plots by creating species rarefaction curves with 95% confidence interval derived from 1,000 permutations using the software PAST, Version 3.12 (Hammer, Harper, & Ryan, 2001). To discuss if differences in RSR were due to seed abundance, we calculated Pielou's equitability index for the seed rain collected in liana-cut and liana-dominated plots, and seed rain similarity between plots in each pair was calculated using the Chao-Jaccard dissimilarity index between paired plots. These analyses were carried out using the package "vegan" in R 3.0 (Chao, Chazdon, Colwell, & Shen, 2004; Oksanen et al., 2016; R Development Core Team, 2013). Tree (DBH $\geq$ 1.6 cm) and liana (diameter $\geq$ 1 cm) communities between liana-dominated and liana-cut plots were compared using the paired t test ($\alpha = .05$).

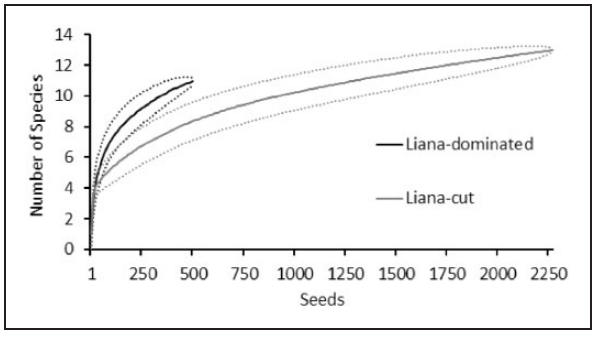


Figure 3. Rarefied species richness curves based on 95% confidence intervals for seed rain of animal-dispersed tree seeds in plots dominated by lianas (black line) and plots where liana cutting was carried out (gray line) in a semideciduous seasonal tropical forest.

Results

Tree basal area (12.8 ± 5.1 m^2 ha^{-1}, $t_{(1,\ 5)} = -1.07$, $p = .33$), pioneer tree basal area (6.6 ± 2.7 m^2 ha^{-1}, $t_{(1,5)} = -.01$, $p = .99$), liana abundance ($2{,}432 \pm 739$ lianas ha^{-1}, $t_{(1,5)} = -0.44$, $p = .68$), and liana basal area (3.1 ± 0.7 m^2 ha^{-1}, $t_{(1,5)} = -0.32$, $p = .76$) did not differ between both groups of plots before liana cutting.

We collected a total of 2,788 seeds (215 ± 297 seeds m^{-2}) belonging to 15 species of animal-dispersed trees (3.2 ± 0.9 species trap^{-1}). Given the high variance in the seed rain data, we did not detect statistical differences for overall, $t_{(1,\ 5)} = -2.20$, $p = .08$, and pioneer, $t_{(1,5)} = -1.11$, $p = .32$, seed abundance of animal-dispersed species between liana-dominated and liana-cut plots. However, mean seed abundance was approximately 5 and 3 times higher in liana-cut plots for all animal-dispersed seeds and pioneer animal-dispersed seeds, respectively (Figure 2). Tree species density, $t_{(1,\ 5)} = -0.81$, $p = .46$, did not differ between liana dominated and liana cut. Because only three pioneer species were sampled in the seed rain, we could not compare statistically pioneer species density between treatments (Figure 2).

Liana-dominated plots had higher RSR of animal-dispersed seeds than liana-cut plots (Figure 3). Pielou's equitability index was similar between liana-cut (0.42 ± 0.20) and liana-dominated plots (0.47 ± 0.12), $t_{(1,5)} = -0.43$, $p = .68$. Species composition was similar among paired plots: Of the six pairs of plots, five had a

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Chao-Jaccard dissimilarity index < 0.3 and in one pair dissimilarity was 0.92 (average: 0.36, median: 0.23, min: 0.11, max: 0.92). The complete list of species sampled can be found in Supplementary File 1, while all diversity indexes are detailed in Supplementary File 2.

Discussion

We found a tendency for higher seed abundance in liana-cut areas due to a quick response by fast-growing heliophyte trees that produce many seeds after release from liana competition. However, higher RSR of animal-dispersed seeds in liana-dominated plots suggests that, in spite of the suppression of seed production by pioneer trees, lianas create favorable conditions for a diverse seed rain, which we hypothesize that may be a consequence of lianas ubiquitous contribution to supply food and shelter to animals (Michel et al., 2015), which could be addressed by future studies. Although higher abundance of individuals for a small group of species can lower the values found in species rarefaction curves when compared to communities with lower abundance, this is not the case in our study, since equitability index was similar for the seed rain community in liana-cut plots and in liana-dominated plots.

High abundance of nontree native plants may affect animal-dispersed seed rain in distinct ways, but few studies discussed the changes in seed rain caused by those species. Muler et al. (2014) observed a higher seed density in bamboo-dominated sites, fostered by greater pioneer and animal-dispersed seeds recorded after palm heart harvesting. In tropical forests, lianas commonly proliferate in sites with more open canopy such as gaps (Schnitzer et al., 2000). Ruderal lianas may also hinder on the long term, the structural development of disturbed forest remnants (Farah et al., 2014), by increasing tree mortality and reducing tree growth and recruitment (Martínez-Izquierdo, García, Powers, & Schnitzer, 2016). The disturbed forest sectors where we carried out our study had fewer trees than less disturbed sectors, therefore the effect of lianas on seed rain, merged with forest structure changes, may have benefited their proliferation (Farah et al., 2014; Schnitzer et al., 2000).

In more conserved tropical forests, lianas contribute to the maintenance of ecological processes are an important food source for fauna and increase environmental heterogeneity by creating different microhabitats for species regeneration in the community. Our study highlights the role of liana dominance in shaping a key ecological process for the recovery of chronically disturbed forests, while also showing that the impacts of dominance by ruderal native species are challenging to predict. In a global context in which remaining native forests are being exposed to unprecedented levels of human-mediated disturbance, understanding the ecological role of ruderal lianas in the ecological processes of disturbed tropical forests may play a key role for their management and conservation.

Implications for Conservation

Human-mediated disturbances of tropical forests alter their structure and ecological processes. These alterations benefit proliferation of some nontree life forms species, such as lianas, while compromising others, like epiphytes. As liana populations increase, they may effectively affect tree canopy productivity. We ask here how this increase in lianas might influence the seed rain, a fundamental ecological process to forest dynamic. We found that liana overabundance affect diversity of the seed rain of animal-dispersed trees, and we found indications that they may alter seed abundance in the short term. In a short term, we conclude that lianas may increase seed rain RSR by supplying shelter and food for disperser fauna, while suppressing overall tree seed production by competition with pioneer trees.

Liana cutting should be carried out parsimoniously in liana-dominated forest sectors, in relatively small areas and in a mosaic design, in order to mitigate possible impacts to the disturbance-adapted seed disperser fauna that may benefit from liana infestation (Michel et al., 2015; Morellato & Leitao-Filho, 1996) and the many other native species persisting in degraded and second-growth tropical forests (Alexandrino et al., 2013; Chazdon et al., 2009). Additionally, liana cutting should aim sectors predominantly dominated by abundant ruderal and resilient liana species, such as the dominant species in our study site, to minimize impact on rare or late successional liana species, which also occur in degraded forest remnants in the study region.

Our results highlight the need for long-term monitoring to understand the consequences of changes in the seed rain on the subsequent stages of regeneration in disturbed forests. We hope our results foment the discussion on the role of disturbance adapted nontree life forms in ecological process that maintain forests and point the directions for conservation and management.

Declaration of Conflicting Interests

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