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LARGE TREES DRIVING NEIGHBOURHOOD ASSEMBLY THROUGH SIMULTANEOUS FACILITATIVE AND COMPETITIVE EFFECTS IN A WOODLAND SAVANNA

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Large trees are key components of forest communities and can influence several ecosystem processes. Moreover, in the savannas where mainly light is not a limiting factor in plant growth, the effects of large trees in plant community as facilitators or promoting local competition are still unclear. For the purpose of the study, 9 plots of 100 m^2 were demarcated in a savanna woodland situated in a conservation unit and without fire register in Brazil. Plots were delimited surrounding large trees with different size diameter and all the structural and functional traits were measured in the surrounding community. A total of 395 plants were sampled and recorded in 73 species and 32 botanical families. The study found that large trees were associated with higher litter deposition and the dominance of forest species with shallow crowns, higher wood density and leaf nitrogen content and lower specific leaf area. These results indicated that large trees could facilitate shade-tolerant species in increasing competition for light with shade-intolerant species. Therefore, large trees could contribute to forest tree species conservation in savanna environments, allowing the coexistence of forest and savanna species at local scale.

Keywords: Function traits, functional diversity, functional composition, community-weighted mean, competition process.

INTRODUCTION

Large trees are not merely enlarged versions of smaller trees. Both the size and the age of a tree affect characteristics such as the crucial role in hydrological and carbon cycles, releasing more water to the atmosphere and stocking more carbon than hundreds of small and young trees (Lindenmayer & Laurance 2017). In fragmented landscapes, large trees promote the connectivity among natural areas that help seed dispersers and pollinators which increase the gene flow among vegetation patches and provide shelter as well as nesting sites for many vertebrate species (Laurance et al. 2000, Remm & Lõhmus 2011).

The issue on how a large tree can affect its neighboring community, either by facilitating the performance of smaller plants (Fichtner et al. 2017) or by increasing local competition (Punchi-Manage et al. 2015) remain unexplored. Past research indicated that a large tree could change the local microhabitat by reducing temperature variation, wind exposure and atmospheric water stress (Niinemets & Valladares 2004). Their wide crowns reduced the surface runoff through rainfall interception as well as increased surface water infiltration (Lida et al. 2018). Moreover, large trees potentially modified the soil beneath their crown due to the accumulation of litter, animal feces and mycorrhiza-fungi agents present in their extensive root system, increasing soil pH and nutrient availability (Holdo et al. 2012). Thus, a large focal tree may promote higher species diversity, seedlings density and biomass in its neighbourhood vegetation.

Despite the potential facilitative effects, large trees can also cause some competitive effects due to draining of water for carbon assimilation and nutrient transport from their well-developed root system which increase neighbouring tree mortality (Ludwig et al. 2004). Moreover, large trees can strongly reduce light availability beneath their crowns of which can reduce the establishment and survival of smaller trees and change species composition toward shade-tolerant species (Rozendaal & Chazdon 2015).

These patterns can increase local competition resulting in lower species richness, density and biomass in the neighborhood vegetation (Fichtner et al. 2017).

Most studies evaluating the facilitative and competitive effects of large trees were conducted in tropical forest communities (Punchi-Manage et al. 2015, Zhang et al. 2016). However, these relationships pertaining to some savannas species are still unexplored especially once they are adapted to high luminosity and well-drained soils (Haridasan 2000, Silva et al. 2013). The interactions between neighboring trees can be explored through the interspecific functional trait variation; an approach that aids researchers to comprehend the drivers of community functional composition and dynamics (Lasky et al. 2014). Therefore, if large trees play a role in savanna neighbourhood assembly, their effects are likely to facilitate the establishment of forest species possessing a suite of traits typically from shade-tolerant species that are otherwise poor colonizers of savanna (Geiger et al. 2011).

In the current study, the diameter size of large trees in relation to their neighbouring tree community in a savanna woodland was evaluated. Considering that large trees can mediate neighborhood assembly through greater shade and potential soil fertility; the study hypothesised that focal tree size would be positively related to litter biomass deposition, neighboring community density, basal area and species and functional diversity. Moreover, the study expected that the neighbouring tree community would be dominated by species typically from forest formations rather than savannas and with traits typically from shade-tolerant species with higher wood density and lower specific leaf area, leaf nitrogen content and crown length ratio.

MATERIALS AND METHODS

Study site

The study site was at the Estação Ecológica de Pirapitinga (18°21'21" S and 45°19'49" W) at an altitude ranging from 570 to 630 m (Figure 1). Estação Ecológica de Pirapitinga is a conservation unit, covering 1,090 ha and considered one of the largest savanna reserves in Southeastern Brazil. Due to the construction of an artificial reservoir (Três Marias Hydroelectric Power Plant) in 1962, the station became a peninsula (Figure 1) and since then, no fire events were registered. The mean annual rainfall is 1,138 mm, of which 88% is concentrated in the wet season (October to April). During the driest quarter (May to September), rainfall is less than 30 mm per month. The meantemperature is 22.7 °C, whereas the minimum and maximum temperatures are 13.3 °C and 31.0 °C, respectively (Alvares et al. 2013). The soil type is primarily clayey with 20% of sand content, pH around 4.9 and soil cation exchange capacity around 8 cmol kg^{-1} (FAO & ISRIC 2012).

The dominant vegetation at the station is the cerrado stricto sensu which covers more than 70% of the area. It is a typical savanna vegetation with trees 3–7 m in height and a high density of shrubs and grasses. The woodland savanna is characterised by a short but almost closed canopy with 50–90% tree cover and trees reaching a height of 8–12 with typical savanna and forest species and few grass species (Ribeiro & Walter 2008). The fire suppression increased woodland savanna cover in the park over the last decades through wood encroachment process. However, the study area has large canopy gaps due to the fall of large trees, which favors the establishment of savanna species.

Focal tree selection and sampling plots

The focal trees which consisted of nine trees with diameter at breast height ranging from 11 to 76 cm and height ranging from 9 to 22 m were selected for the study. Each selected focal tree was the largest tree with a radius of 25 meters to avoiding potential effects of others large trees. Sample plots were established extending in perpendicular lines of five meters from the stem of each focal tree to cardinal points (North, South, East and West directions), delimiting four quadrants of 5 × 5 m and each sampling plot area of 10 × 10 m (Figure 1). In each sampling plot, all the vascular plants with height > 1 m and stem diameter at ground level ≥ 1 cm were identified and had their stem and height measured. Litter samples were collected using a 1 m^2 steel template and oven-dried at 70 °C for 48 hours up to obtain a constant weight of litter biomass (Caldeira et al. 2008).

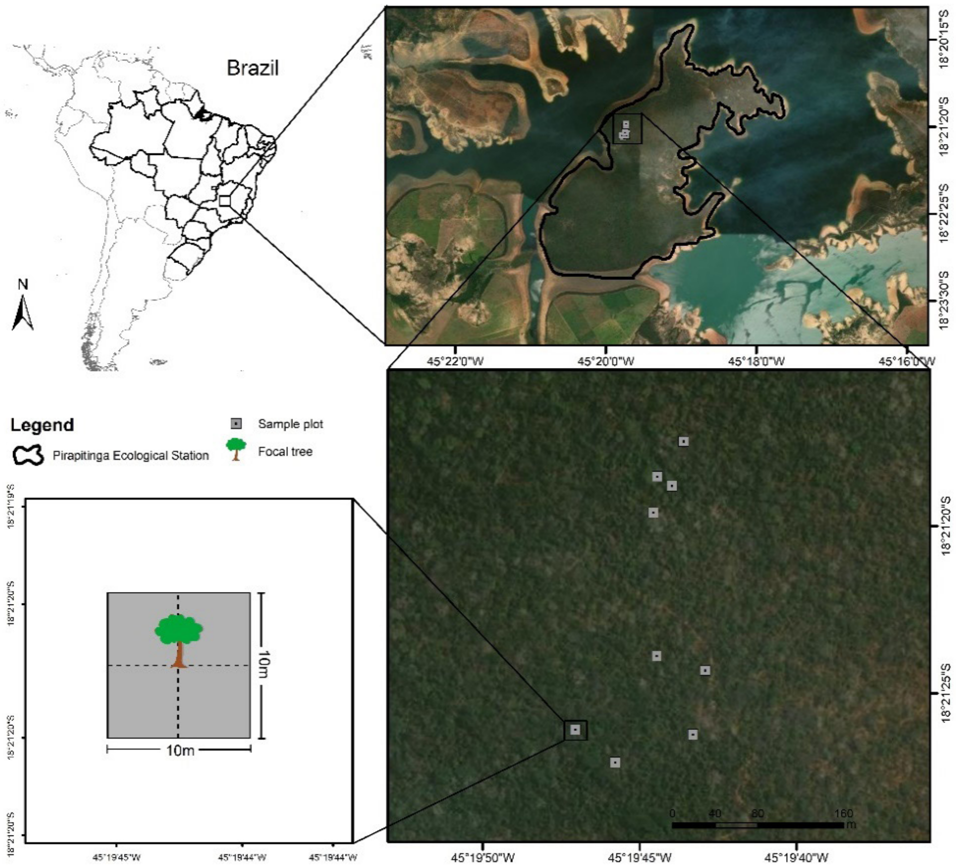

Figure 1 Location of the study area (Estação Ecológica de Pirapitinga), sampling plots distribution and experimental design for sampling plots delimitation

Neighborhood structure and species and functional diversity

Five functional traits usually related to species competitive potential and their strategies along a successional gradient were evaluated; wood density, specific leaf area, leaf nitrogen content, crown length ratio and species dominant habitat for savanna or forest species. All functional data were obtained from data compilation for each species (Martins & Batalha 2006, Cianciaruso et al. 2012, Prado-Junior et al. 2016), except for crown length ratio that was measured during our sampling. Crown length ratio was measured as the ratio between the height of lower foliage and the height of each individual sapling surrounding the large tree (Borges et al. 2018).

Calculations for the nine plots consisted of plant density (individuals ha^{-1}), basal area of the stem (m ha^{-1}), species richness, Fisher diversity index, functional richness, functional dispersion, and community-weighted mean for each functional trait values. High functional richness values were associated with a high number of functions in the community and functional dispersion indicated the basal area of species was more distributed over the niche space. Community-weighted mean values were calculated separately for each trait (wood density, specific leaf area, leaf nitrogen and crown length ratio and weighted by species relative basal area. The community-weighted mean trait values were also calculated according to the type of habitat that the species commonly occurs in savanna or forest. The species diversity, functional diversity indices and community-weighted mean trait values were calculated using the Vegan (Oksanen et al. 2013) and FD (Laliberté et al. 2014) packages in R version 3.6.3 (R Core Team 2020).

Data analysis

Bivariate linear models were used to evaluate the focal large tree size related to the litter biomass, the structural metrics and the species and functional diversity of the neighbouring community. The focal tree stem diameter was highly correlated with focal tree height (Pearson's $r = 0.88$, $p < 0.01$) and focal tree crown length (Pearson's $r = 0.76$, $p < 0.05$). Subsequently, focal tree stem diameter was used as a more accurate variable as a fixed factor and each of the community metrics described above as response variable in each model. In order to evaluate the relationship between species composition and focal tree stem diameter, a partial Mantel test was performed (considering the effect of spatial distance among focal trees) between the species similarity matrix among plots (based on species abundance and Morisita-Horn index) and the matrix composed by the absolute difference in focal tree stem diameter between pairs of sampling plots. In order to access the significance of the partial Mantel test (Spearman index) we used the Monte Carlo method with 1,000 permutations. With the aim to account for potential spatial dependence among our plots, simultaneous autoregressive (SAR) models were performed based on the geographical coordinates of each plots sampled (Kissling & Carl 2007). While to verify the removal of the spatial autocorrelation effect on the models, Moran's I tests on the simultaneous autoregressive model residuals was performed (i.e., Moran's I test p-values > 0.05 indicated no spatial correlation). All statistical analysis was performed using R version 3.6.3 (R Core Team 2020) and the following packages; 'lme4' (Bivand & Wong 2018) and 'spdep'.

RESULTS

A total of 395 plants distributed into 73 species and 32 botanical families were sampled in the study. The mean litter biomass was 173 g m^{-2} (ranged from 110 to 230 g m^{-2}). The study found that litter biomass was positively related to the stem diameter of the focal large tree. With regard to the functional composition metrics, the study also found that stem diameter of the focal large tree was positively related to community-weighted mean of wood density and community-weighted mean of leaf nitrogen content, and negatively related to community-weighted mean of specific leaf area, community-weighted mean of crown length ratio and percentage of savanna species (Table 1). These results indicated that the surrounding plant community of larger trees in savanna woodlands was dominated by forest species that invested in shallow crowns with denser wood and leaves with lower specific

Table 1 Results of the simultaneous autoregressive (SAR) models of the relationships between focal tree diameter and the neighboring community structure, species and functional diversity

Variables	SAR				Moran's I Test
	Intercept	β	p-value	R^2	p-value
Litter biomass	135.73	0.927	<0.01*	0.56	0.22
NI	3741.40	12.286	0.65	-	0.40
BA	7.09	0.022	0.71	-	0.33
S	17.35	0.001	0.86	-	0.37
Fisher	11.11	0.026	0.26	-	0.63
CWM SLA	12.68	-0.019	<0.01*	0.55	0.55
CWM WD	0.58	0.002	<0.05*	0.49	0.24
CWM Nit	19.53	0.060	<0.05*	0.28	0.55
CWM CLR	0.59	-0.002	<0.01*	0.44	0.45
CWM Sav	0.67	-0.007	<0.05*	0.17	0.35
FRic	0.12	-0.001	0.47	-	0.62
FDis	0.25	-0.001	0.62	-	0.42

Litter biomass = litter biomass, NI = number of individuals, BA = mean basal area, S = species richness, Fisher = Fisher diversity index, CWM SLA = community-weighted mean of specific leaf area, CWM WD = community-weighted mean of wood density, CWM Nit = community-weighted mean of foliar nitrogen, CWM CLR = community-weighted mean of crown length ratio CWM Sav = community-weighted mean of Savanna species, FRic = functional richness index, FDis = functional dispersion index, * = indicate significant differences (p<0.05) leaf area but higher nitrogen content. The study also found no significant relationships between stem diameter of the focal large tree and the structural (plant density and basal area), species diversity (species richness and Fisher diversity) and functional diversity metrics (functional richness and dispersion) of the neighborhood community (Table 1). The partial Mantel test showed that stem diameter of the focal large tree was not related to the species composition in the neighborhood ($r = 0.293$, $p = 0.137$).

DISCUSSION

Potential facilitative effects of large trees in soil nutrient availability

Based on the results, the tree size was positively related to litter biomass and community-weighted mean leaf nitrogen content. Litter biomass beneath the larger focal tree was over two times compared to the smaller trees. Large trees had a high leaf mass fraction and produced more litter biomass which composed by leaves and small branches as compared to small trees (Ludwig et al. 2004). Higher soil fertility under larger trees was reported for a wide range of savannas, where available nitrate (NO_3^-) and ammonium cations (NH_4^+) were four times higher under large trees than in open savannas (Osborne et al. 2020). Litter deposition increased soil organic carbon and nutrient availability for trees, which facilitated the establishment of species with high leaf nitrogen content (Prado-Junior et al. 2016). Leaf nitrogen content was positively related to net primary productivity (Pérez-Harguindeguy et al. 2013), which indicated that these species had higher photosynthetic rates and net carbon gain, thus increasing their fitness in the shaded understory (Pyles et al. 2018).

Large trees driving functional composition in the neighborhood community

The study hypothesised that focal tree size should be positively related to community structural (plant density and basal area), taxonomic (species composition, richness and diversity) and functional diversity metrics (functional richness and dispersion). Surprisingly, no significant relationships were found for any of these metrics. However, functional composition was significantly related to focal tree size, with higher dominance of forest species with denser wood, shallow crowns and lower specific leaf area.

As savanna species were adapted to high light availability and well-drained and poor soils; forest species could take advantage of these environmental conditions created by large trees to establish and grow faster compared to savanna species (Reich et al. 2003). The higher wood density and lower specific leaf area of community beneath the larger trees could be related to higher dominance of shade-tolerant species compared to light-demanding pioneer species because of their lower relative growth, respiration rates and higher leaf longevity (Poorter & Bongers 2006). The lower crown length ratio of species surrounding larger trees was also an indicator of limiting light. These result indicated that species were postponing the crown expansion by investing more biomass in height expansion, which helped them getting access to better light conditions (Poorter & Bongers 2006). Moreover, lower crown length species were less vulnerable to self-shading, thus improving fitness in shaded conditions (Bueno et al. 2018).

Large trees can contribute to savannas resilience

The woodland savannas contained both savanna and forest species, and could act as a species relic for both environments (Hoffmann et al. 2009). Frequent fires in savanna ecosystems generally limited the succession of forest species due to their thinner bark and higher rates of top kill than savanna species (Geiger et al. 2011, Rochimi et al. 2021). In the absence of fire events, fire sensitive species might experience an increase in density and tree size, thus maintaining the forest conditions (Sathya & Jayakumar 2017). These ecological filters promoted by large trees could drive the shifts in their neighbourhood species composition by going towards a higher dominance of shade-tolerant forest species and reflected in a higher niche differentiation and more efficient uptake and use of limiting resources (Durigan et al. 2020).

CONCLUSIONS

Our study concluded that large trees could drive functional changes of their neighbourhood towards a forest environment by increasing soil nutrients and reducing light availability and consequently contributing to the establishment of shade-tolerant forest species. Although the forest species had positive feedback in the surrounding large trees, these process could limit growth of grasses and juveniles of savanna species. Thus, studies that associate large trees with other growth forms were needed to understand large trees effects on the whole ecosystem.

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