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Population structure of understory, canopy/emergent tree species in Brazilian Atlantic Forest remnants with different Conservation status

Estrutura populacional de espécies arbóreas de sub-bosque e dossel/emergentes em remanescentes de Mata Atlântica Brasileira com diferentes estados de conservação

Estructura de la población de especies arbóreas del sotobosque y del dosel/emergentes en los remanentes de la Mata Atlántica brasileña con diferentes estados de conservación

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Yves Rafael Bovolenta
ORCID: https://orcid.org/0000-0001-9684-1848
Faculdade Pitágoras, Brazil
E-mail: yvesrbovolenta@gmail.com
Diego Resende Rodrigues
ORCID: https://orcid.org/0000-0002-9495-8943
Universidade Estadual do Norte do Paraná, Brazil
E-mail: diegopardal@uenp.edu.br
Edmilson Bianchini
ORCID: https://orcid.org/0000-0002-4764-3324
Universidade Estadual de Londrina, Brazil
E-mail: bianchi@uel.br
José Antonio Pimenta
ORCID: https://orcid.org/0000-0001-7486-8855
Universidade Estadual de Londrina, Brazil
E-mail: josepimenta58@gmail.com

Abstract

The size and spatial structures of populations are a synthesis of demographic attributes and indicators of competitive ability, colonization, and survival. In this study, the objective was to analyze the height and spatial pattern of an understory and canopy/emergent tree populations group in two protected fragments of seasonal semideciduous forest, one with a history of selective logging and another without selective logging evidences. Six species with high importance values (IV) from different guilds were selected and height and spatial pattern analysis was realized in both areas. Then, comparison of results was realized in an area with history of selective logging and another without selective logging evidences. Differences in height and spatial pattern were found between the two areas, including species not directly exploited. In Logged Forest the size structure for all species presented a higher coefficient of skewness, showing a greater proportion of young trees. Random distribution was observed for the majority of species in both areas. Some emergent/canopy species had a deficit of individuals in the largest size classes and the majority of understory species showed more individuals in Logged Forest. Selective Logging changed the pattern of populations. Selecting species based on IV together with spatial patterns data contribute to demonstrating the impacts of exploitation. The Logged Forest is surrounded by an agricultural matrix, limiting arrival and dispersion of propagules of shade-tolerant species. Efforts to connect surroundings fragments to Logged Forest will be necessary.

Keywords: Forest fragmentation; Forest regeneration; Population ecology; Selective logging; Tropical forest.

Resumo

O tamanho e a estrutura espacial das populações são uma síntese de atributos demográficos e indicadores de capacidade competitiva, colonização e sobrevivência. Neste estudo, o objetivo foi analisar o tamanho e a estrutura espacial de um grupo de populações arbóreas de sub-bosque e dossel/emergentes em dois fragmentos de Floresta Estacional Semidecidual, um com histórico de corte seletivo de madeira e outro sem evidências de corte seletivo. Seis espécies com altos valores de importância e de guildas diferentes foram selecionadas e a análise de tamanho e estrutura espacial foi realizada em ambas as áreas. Em seguida, comparamos os resultados das espécies na área com histórico de corte seletivo com a área que não sofreu corte seletivo. Diferenças de tamanho e estruturas espaciais foram encontradas entre as duas áreas, incluindo espécies que não exploradas diretamente. Na floresta em que ocorreu o corte seletivo, a estrutura de tamanho para todas as espécies apresentou um maior coeficiente de assimetria, mostrando uma maior proporção de

juvenis. O padrão de distribuição aleatória foi observado para a maioria das espécies em ambas as áreas. Algumas espécies do dossel/ emergentes tiveram menor abundância nas maiores classes de altura. O corte seletivo alterou o padrão das populações. Selecionar espécies baseado no VI juntamente com padrões de distribuição espacial contribuem em demonstrar os impactos da exploração. A área com histórico de corte seletivo é circundada por matriz agrícola, limitando a chegada e dispersão de propágulos de espécies tolerantes à sombra. Esforços para conectividade com fragmentos do entorno serão necessários.
Palavras-chave: Fragmentação florestal; Regeneração florestal; Ecologia populacional; Corte seletivo de madeira; Floresta tropical.

Resumen
El tamaño y estructura espacial de las poblaciones son una síntesis de atributos demográficos e indicadores de capacidad competitiva, colonización y supervivencia. En este estudio, el objetivo fue analizar el tamaño y la estructura espacial de un grupo de poblaciones de árboles de sotobosque y dosel/emergentes en dos fragmentos de bosque semideciduo, uno con historia de tala selectiva y el otro sin evidencia de tala selectiva. Se seleccionaron seis especies con valores altos de importancia (VI) y de diferentes gremios y se realizó el análisis de tamaño y estructura espacial en ambas áreas. comparamos los resultados por área. Se encontraron diferencias de tamaño y estructuras espaciales entre las dos áreas, incluidas las especies no explotadas directamente. En el bosque donde se realizó la tala selectiva, la estructura de tamaño para todas las especies mostró un coeficiente de asimetría más alto, mostrando una mayor proporción de juveniles. El patrón de distribución aleatoria se observó para la mayoría de las especies en ambos fragmentos. Algunas especies de dosel/emergentes tuvieron menor abundancia en las clases de mayor altura. La tala selectiva cambió el patrón de poblaciones. La selección de especies basada en VI junto con los patrones de distribución espacial contribuye a demostrar los impactos de la exploración. El área con antecedentes de tala selectiva lo es rodeada por una matriz agrícola, lo que limita la llegada y propagación de propágulos de especies tolerantes a la sombra. Se hacen necesarios los esfuerzos para la conectividad con otros fragmentos de bosque en los alrededores.
Palabras clave: Fragmentación forestal; Regeneración forestal; Ecología de poblaciones; Tala selectiva; Bosque tropical.

1. Introduction

The Brazilian Atlantic Forest has one of the highest levels of biological diversity and number of endemic species in the World (Lima et al., 2020; Ribeiro et al., 2009; Santo-Silva et al., 2016; Santos et al., 2018; Zucchi et al., 2018). However, this Biome has a widespread devastation scenario in which most remaining forests are small isolated fragments and under intense anthropic pressure (Callaghan et al., 2019; Liebsch et al., 2016). Considering the anthropic pressures, selective logging has a major impact on these forests (Brocardo et al., 2018; Cunha et al., 2021; Eisenlohr et al., 2015; Lammertink et al., 2020; Lima et al., 2020; Rutishauser et al., 2016; Silva & Vibrans, 2019).

Selective logging may change the local microclimate, survival and species regeneration, resulting in a completely altered habitat (Guariguata & Ostertag, 2001). The direct effects of extracted individuals in association with the microclimatic changes cause variations in survival, growth, and reproduction rates of tree populations, which directly affect size and spatial structure (Solís et al., 2009; Tsingalia, 2010). The recovery success of the populations will determine the forest's regeneration, defining forest regeneration as a process by which the disturbed forest reaches Mature Forest characteristics (Saldarriaga & Uhl, 1991; Tabarelli et al., 1999).

The size structure may be considered a synthesis of demographic attributes of recruitment, mortality, and individual growth rates (Kelly et al., 2001). The spatial structure (or spatial distribution) is an outcome of the competitive ability, colonization, and survival of populations (Maestre et al., 2008). Thus, these aspects of population structure play role as an important indicator of forest regeneration, despite not replacing the study of demography and the spatial distribution processes (Berry et al., 2008; Rodrigues et al., 2016).

Studies have used the population structure as a way to understand effects of natural (Batista & Platt, 2003; Coomes & Allen, 2007) and anthropic disturbances on species (Liebsch et al., 2021; Sapkota et al., 2009; Silva & Vibrans, 2019; Souza, 2007; Tsingalia, 2010). A higher proportion of juveniles than adult trees has been found in exploited forests (Souza, 2007) and the spatial pattern may change between exploited and unexploited forests (Sapkota et al., 2009) considering that gap recruitment has been shown to be important for individual tree placement (Plotkin et al., 2000).

Light plays a major role in plant dynamics (Tang & Dubayah, 2017; Valladares & Niinemets, 2008), particularly in areas with high heterogeneity like in selectively Logged Forests (Rodrigues et al., 2016, 2019). However, species may respond differently according to their characteristics, such as shade tolerance degree or forest stratum (Bianchini et al., 2010; Laurans et al., 2014; Swaine & Whitmore, 1988).

Size and spatial structure of understory and canopy/emergent tree populations in two forest fragments with different histories of human action were analyzed. Differences in tree populations structure between areas are expected based on selective logging occurred in one of studied fragments in comparison to an area without anthropogenic action signals. We tested the hypothesis that canopy species have a higher proportion of individuals in the first size classes and a higher aggregate distribution correlated with canopy openness in exploited areas. Understory species probably have lowest abundance in the exploited forest due to their dependence on shade throughout all their life cycle.

2. Material and Methods

Two Atlantic Forest fragments, classified as seasonal semideciduous forest (SOS Mata Atlântica & INPE, 2020; Veloso et al., 1991), were selected for study (Figure 1). The São Francisco Forest State Park (23º09'55" S, 50º33'51" W) has 832.58-ha localized in north of Paraná state, Brazil. This area suffered disorderly selective logging until 1994 when it became a protected area. Therefore, it has some environmental imbalances, such as wide gaps and excessive lianas and bamboos. It will be referred to as the "Logged Forest" in this paper. The Godoy Forest State Park (23º27'10" S, 51º15'11" W) has 680-ha currently connected to other fragments, totaling almost 2800-ha (Vicente, 2006). The Godoy Forest State Park is also localized in north of Paraná, Brazil, and it has no selectively logging history (Torezan, 2006). It is referred to as the "Mature Forest" in this paper.

According Köppen classification, the region's climate is characterized as Cfa - humid subtropical mesothermal (Alvares et al., 2013), with average rainfalls between 1200–1400 mm in Logged Forest and 1400–1600 mm in Mature Forest. Rainfalls is distributed unevenly throughout the year, in both cases (Nitsche et al., 2019). Both areas have high fertility soil. In Logged Forest the predominant soils are Eutroferric Red Latosols and Nitosols, with inclusions of Chernosols and Gleysols. Eutroferric Red Latosols and Nitosols in association with Entisols in Mature Forest (Santos et al., 2013).

The species were selected based on their importance values (IV) obtained from a phytosociological inventory performed in the study areas (Silva & Soares-Silva, 2000; Tomé et al., 1999; Zama et al., 2012) and field observations. They were divided into two groups regarding forest stratum: understory species - *Actinostemon concolor* (Spreng.) Müll. Arg. (Family: Euphobiaceae, popular name: Laranjeira do mato; IV: 9.79 (Soares-Silva & Barroso, 1992)), *Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & Wess. Boer (Family: Moraceae, popular name: Falsa espinheira; IV: 8.77 (Tomé et al., 1999)), and *Inga marginata* Willd. (Family: Fabaceae, popular name: Ingá-feijão; IV: 5.71 (Tomé et al., 1999)); canopy species - *Campomanesia xanthocarpa* O. Berg. (Family Myrtaceae, popular name: Guabiroba; IV: 3.77 (Tomé et al., 1999)) and *Cabralea canjerana* (Vell.) Mart. (Family Meliaceae, popular name: Canjarana; IV: 8.50 (Tomé et al., 1999)); and emergent species - *Aspidosperma polyneuron* Müll. Arg (Family Apocynaceae, popular name: Peroba-rosa; IV: 12.46 (Tomé et al., 1999). All selected are shade tolerant species (Silva; Soares-Silva, 2000; Zama et al., 2012). *A. polyneuron* and *C. canjerana* have high commercial value and were mainly exploited in Logged Forest (Carvalho, 1994; Tomé et al., 1999; Zama et al., 2012).

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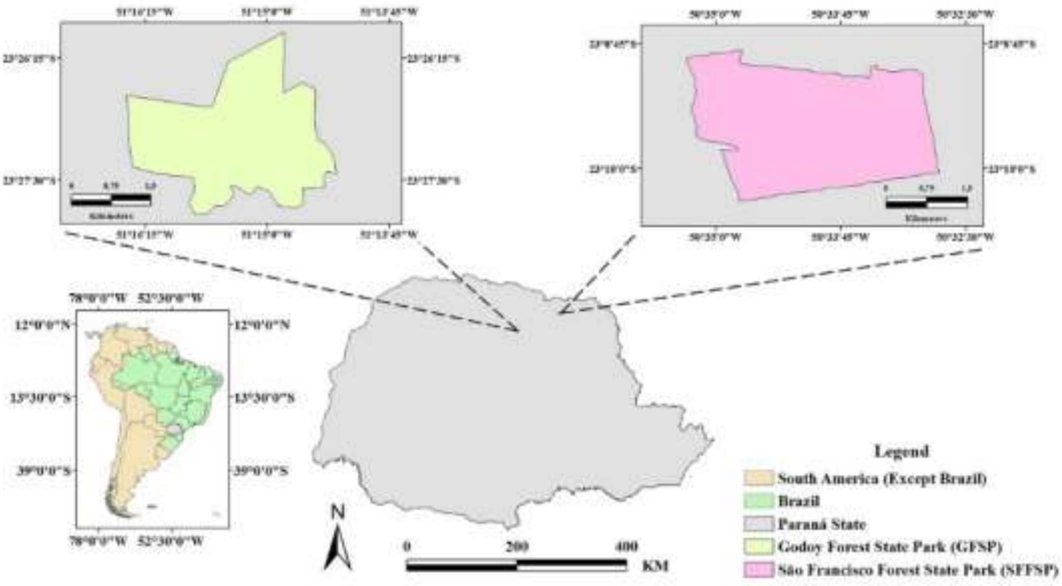
Figure 1. Map of South America, with a zoom on the two study areas in the northern region of the Paraná state, southern Brazil. Source: Google Earth Pro, IBGE maps and ArcGIS software (version 10.5).



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In each area, 30 plots of 100 m^2 (10 m × 10 m) were established and subdivided into 120 subplots of 25 m^2 (5 m × 5 m). The plots were allocated contiguously, totaling 3000 m^2 of sampled area per forest (50 m × 60 m). Nested sampling designs are preferred for identifying the spatial pattern without knowing the spatial scale of the process (Dale & Fortin, 2014).

The sampling area in Mature Forest is in the north portion of fragment that has been considered reference for Mature Forests (Haddad et al., 2016). In Logged Forest an area with similar characteristics to the Mature Forest sampling area were searched, with similar topography, away from edge effects and without excessive lianas or bamboos but with selective logging evidence (presence of sawn trunks of *A. polyneuron* nearby).

The total height (forest floor to top of crown, in meters) of all individuals of the six species within plots using a tape measure or Vernier caliper and a laser distance measurer. *Actinostemon concolor* and *Inga marginata* are abundant in small size classes. Therefore, for these species' subplots of 4 m^2 were established in a corner of each 100 m^2 plot to sample individuals ≤50 cm (*A. concolor*) and ≤30 cm (*I. marginata*) in height and the relative density was used.

Frequency distributions of individuals in size classes were made to compare the size structure (height structure) of populations among areas. The size classes used are different for the species of understory and canopy due to the size characteristics of each group of species. The Kolmogorov-Smirnov test was used to compare the height structure of each species between areas (Brower & Zar, 1984; Siegel & Castellan Jr, 1975). The moment skewness coefficient was used to evaluate the symmetry of tree size distributions (Cramér, 1999). The moment skewness coefficient is positive for size distributions with many individuals in the first size classes and few individuals in the larger classes, and it is negative for size distributions with many individuals in the larger size classes and few individuals in the first size classes (Bendel et al., 1989; Wright et al., 2003). All tests were performed with BioEstat 5.0 statistic software (Ayres et al., 2007).

The number of individuals for subplot and subplot center coordinates was used to determine the spatial pattern of each species. The spatial pattern was analyzed using Moran's I spatial autocorrelation coefficient (Legendre & Fortin, 1989), testing the null hypothesis that the Moran's I coefficient, at each distance class, is not significantly different from zero, indicating randomness (Legendre; Fortin, 1989). Therefore, Moran's coefficient varies generally from -1 to 1; positive values of Moran's I correspond to positive autocorrelation and negative values of Moran's I correspond to negative autocorrelation. A spatial correlogram was built based on I values as a function of the distance classes, and its significance was tested using the Bonferroni criterion (Oden, 1984).

The canopy cover index was evaluated in each plot using a spherical densitometer (Lemmon, 1956). Four measurements at breast level (1.30 m) taken from the center of the plot towards each corner were obtained for each plot for the average estimate. The relation between the spatial patterns of the individuals of each species and canopy cover was estimated with partial Mantel tests (Legendre; Fortin, 1989). The p-level for these tests was determined by a permutation procedure (999 interactions). The autocorrelation analyses and partial Mantel tests were performed with Passage Software (Rosenberg & Anderson, 2011). The average canopy cover index (CCI) for each area was calculated and compared by t-test using R-studio version 1.3.959 (RStudio, 2020). Maps of individuals distribution in plots and 3D scatter plots of species were made in Rstudio version 1.3.959 using ggplot2 and scatterplot3d packages (RStudio 2020).

3. Results and Discussion

The Analysis of height structure showed differences of each population of the selected species between the study areas (Kolmogorov-Smirnov test, $p<0.05$, Table 1), except for height distribution of *C. xanthocarpa*. The most of species had a greater proportion of individuals in the first size classes (seedlings and small saplings) in Logged Forest than in Mature Forest (moment skewness coefficient, Figure 2), except for the height structure of *A. concolor* and *I. marginata*.

Table 1. Results of the comparison of Height structure by Kolmogorov- Smirnov test (D) of understory (*A. concolor*, *S. bonplandii*, and *I. marginata*) and canopy/emergent tree populations (*C. xanthocarpa*, *A. polyneuron*, and *C. canjerana*) between two study areas: Godoy Forest State Park (Mature Forest) and São Francisco Forest State Park (Logged Forest), Paraná state, Brazil.

Species/Stratum		
Understory species	**D**	**p**
A. concolor	0.166	<0.01
S. bonplandii	0.086	<0.01
I. marginata	0.334	<0.01
Emergent/canopy species	**D**	**p**
C. xanthocarpa	0.143	>0.05
A. polyneuron	0.210	<0.01
C. canjerana	0.243	<0.01

Source: Authors.

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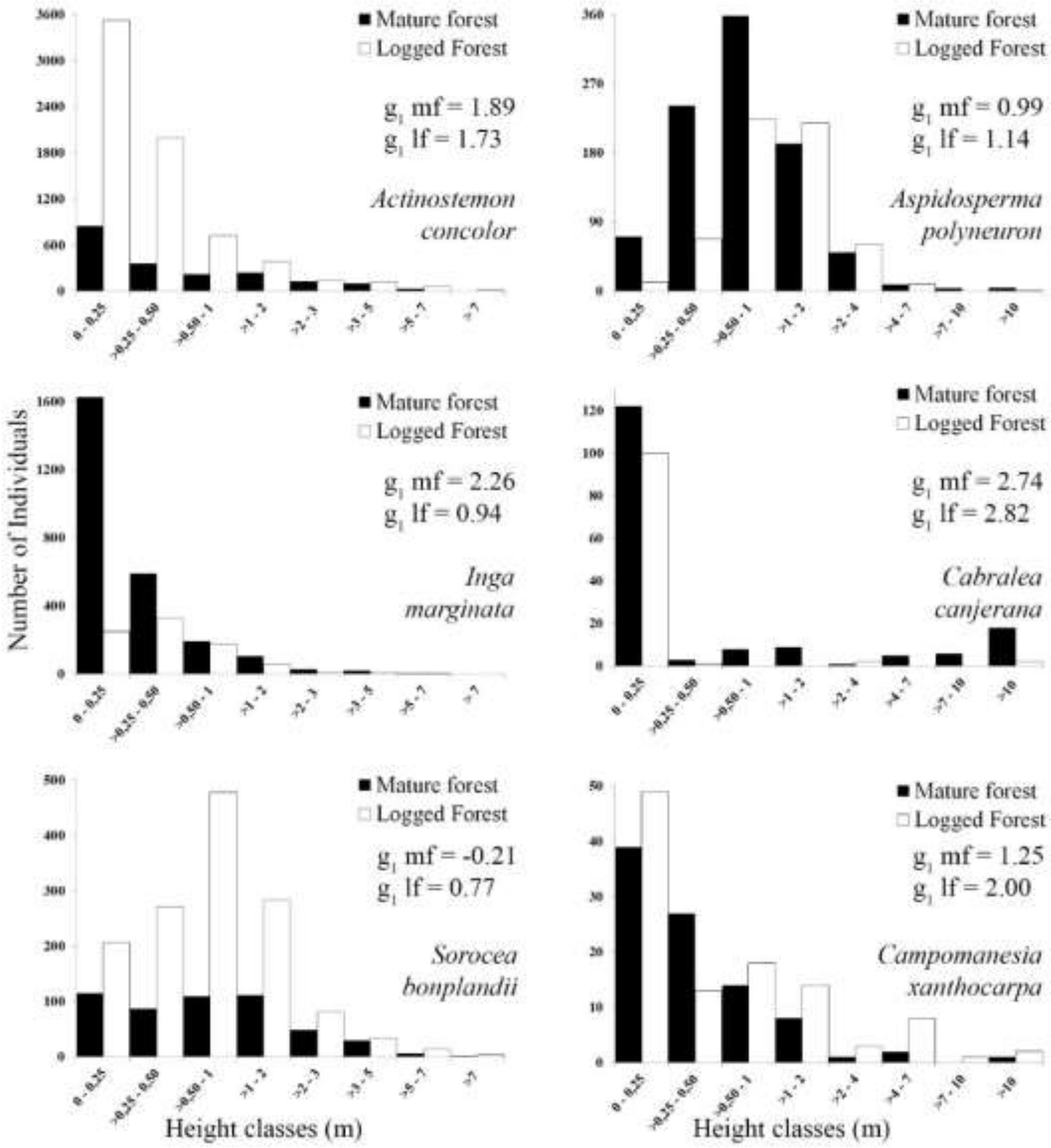
Figure 2. Height classes of understory (*A. concolor*, *S. bonplandii*, and *I. marginata*) and canopy/emergent tree populations (*C. xanthocarpa*, *A. polyneuron*, and *C. canjerana*) in two study areas: Godoy Forest State Park (Mature Forest) and São Francisco Forest State Park (Logged Forest), Paraná state, Brazil. g_1 mf = The moment skewness coefficient in Mature Forest. g_1 lf = The moment skewness coefficient in Logged Forest.



Source: Authors.

All populations were represented in most of the size classes, except species with high commercial value, like *A. polyneuron*. The highest classes of *A. polyneuron* (> 7.0 meters of height) and the intermediate and highest classes of *C. canjerana* (> 0.50 meters of height) were underrepresented in Logged Forest, with one individual compared to nine in Mature Forest for *A. polyneuron* and four individuals compared to 47 in Mature Forest for *C. canjerana* (Figure 2). The commercially valuable emergent/canopy species (*A. polyneuron* and *C. canjerana*) have a deficit of individuals in the largest size classes in the exploited area, while *C. xanthocarpa* have a good development in both fragments.

Differences were observed when compared height and spatial structure between Logged and Mature Forests. Changes in size structure of species were found in other similar studies as a consequence of selective logging of tree species (Liebsch et al., 2021; Rodrigues et al., 2016, 2019). The understory species *A. concolor* and *S. bonplandii* showed more individuals in

Logged Forest while there were fewer of most of the other species. There were more individuals of *A. concolor* and *S. bonplandii* in Logged Forest, with a higher number of individuals in all size classes, mainly in the smaller ones. Primack and Lee (1991) observed that an understory shade-tolerant population had some tendency to increase in size 11 years after logging, suggesting that the growth may be associated with the building phase of that forest. Higher seedling growth was found by Montgomery and Chazdon (2002) for shade-tolerant species and by Pearcy (1983) for understory species in areas with moderate light increase.

The understory species *I. marginata* did not perform like other species of understory species group and there were fewer individuals in all size classes, mainly in the smaller classes in Logged Forest when compared to the Mature Forest. *S. bonplandii* and *A. concolor* have, respectively, 3.6 and 2.7 times more individuals in the exploited forest than in Mature Forest. On the other hand, *I. marginata* has 3.0 times fewer individuals in Logged Forest.

The canopy/emergent species *C. canjerana* (canopy) and *A. polyneuron* (emergent) also had fewer individuals in Logged Forest, both species being 1.6 times fewer individuals in Logged Forest. Although emergent/canopy species reach the canopy layer of the forest, they can compete with the understory species while they are occupying the lower strata of the forest (Laurans et al., 2014; Onoda et al., 2014). These results suggest competition between understory species with advantages for *S. bonplandii* and *A. concolor* in Logged Forest.

The plant size structure is different between areas in multiple stratums (understory, and emergent/canopy species), showing a smaller proportion of larger individuals and a greater number of individuals smaller than 1 m tall and 1 cm in height in Logged Forest, an indication of regeneration process. These results can be interpreted by less competition in the canopy (Bertolini et al., 2020) due to the removal of adults and the consequent increased availability of light in the understory that can positively influence the rates of flower and fruit production, germination, seedling establishment, and sapling growth (Smith, 2000), stimulating the forest regeneration (Rodrigues et al., 2019).

Evident differences mainly were found when observing the lower number of individuals in the larger and intermediate size classes of *C. canjerana* and larger classes of *A. polyneuron* (canopy/emergent species) in Logged Forest, which are study species that have wood of high economic value (Carvalho, 1994; Tomé et al., 1999).

Nevertheless, changes were found in size structure of almost all species, including those that were not directly exploited. Disturbances lead to changes in environmental conditions, creating a new habitat with important variations in light, moisture, and temperature (Burton et al., 2009; Guariguata & Ostertag, 2001), which directly influence the birth and mortality rates of populations (Getzin et al., 2008; Poorter et al., 2008).

Campomanesia xanthocarpa was the only species that had the same height structure in both areas. The allometric relationship between trunk diameter and total height for individuals of this species in the same period also was also similar (Bovolenta, 2011). These observations suggest that *C. xanthocarpa* developed similarly in both areas. *Campomanesia xanthocarpa* seems to have a good development and plasticity in areas with different environmental resources and conditions, since it occurs in areas of rainforest and also in areas with higher luminosity, like in the Cerrado biome (Sobral et al., 2015).

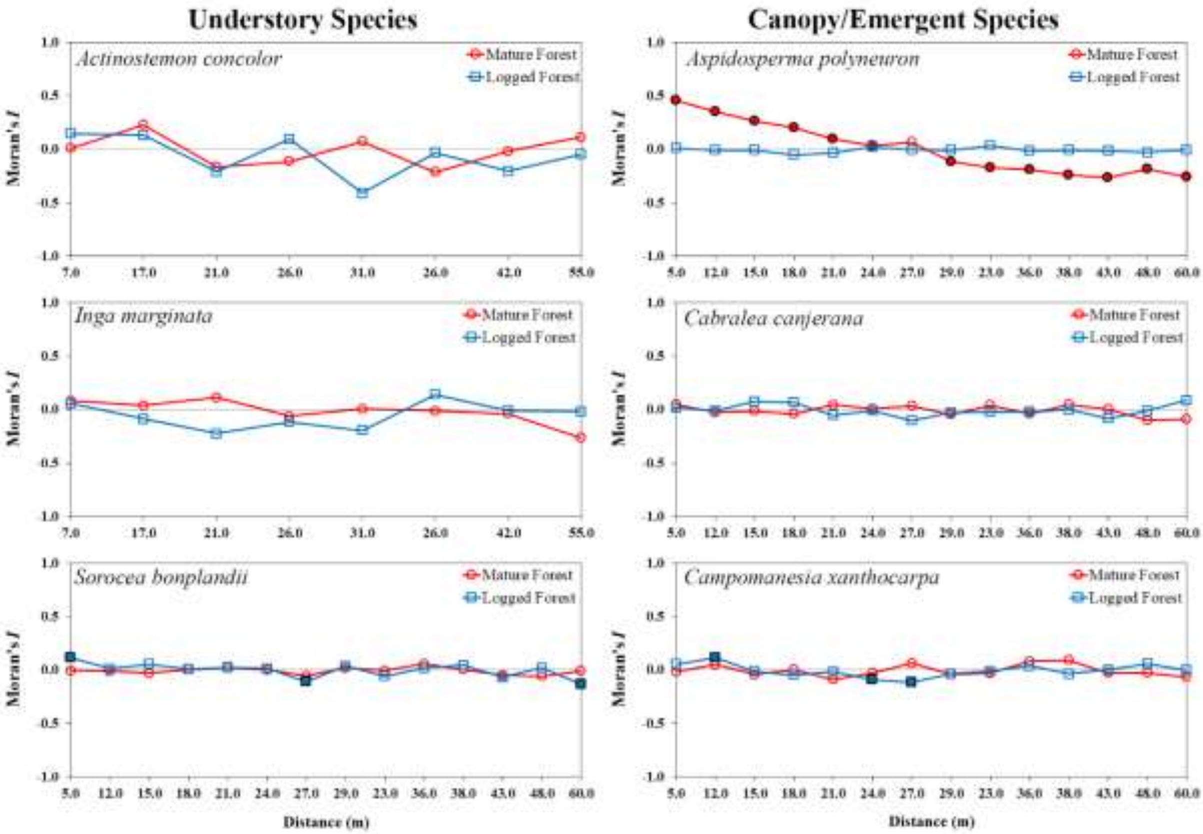
The understory species in Mature Forest not showed spatial autocorrelation among individuals, suggesting a random spatial distribution (Table 2, Figures 3, 5-8). The same result was observed for the understory species in Logged Forest, except *S. bonplandii*, which had an aggregate spatial distribution in small clumps (5 m) and a negative autocorrelation at larger distances (27 and 60 m) (Figure 3, 5-8).

Table 2. Significance of autocorrelation by Bonferroni's test (α <0.05) for understory species and canopy/emergent species in both study areas, Godoy Forest State Park (Mature Forest) and São Francisco Forest State Park (Logged Forest), Paraná state, Brazil. Values represents corrected significance of Bonferroni's test (α) of *Moran's I*. *** = (α <0.05); ns = not significant values.

Species/Stratum	Mature Forest	Logged Forest
Understory species		
Actinostemon concolor	0.5449^{ns}	0.3094^{ns}
Inga marginata	0.1911^{ns}	0.6779^{ns}
Sorocea bonplandii	1.0000^{ns}	0.0076^{***}
Emergent/canopy species		
Aspidosperma polyneuron	0.0000^{***}	1.0000^{ns}
Cabralea canjerana	0.3389^{ns}	0.1176^{ns}
Campomanesia xanthocarpa	0.3321^{ns}	0.0266^{***}

Source: Authors.

Figure 3. Spatial correlogram of understory species and canopy/emergent species in both study areas, Godoy Forest State Park (Mature Forest, red) and São Francisco Forest State Park (Logged Forest, blue), Paraná state, Brazil, respectively. Solid points represent significant correlations of Moran's I ($p < 0.05$, Bonferroni corrected for number of distance classes). Unfilled points are non-significant values for correlograms. Dashed line represents zero autocorrelation.



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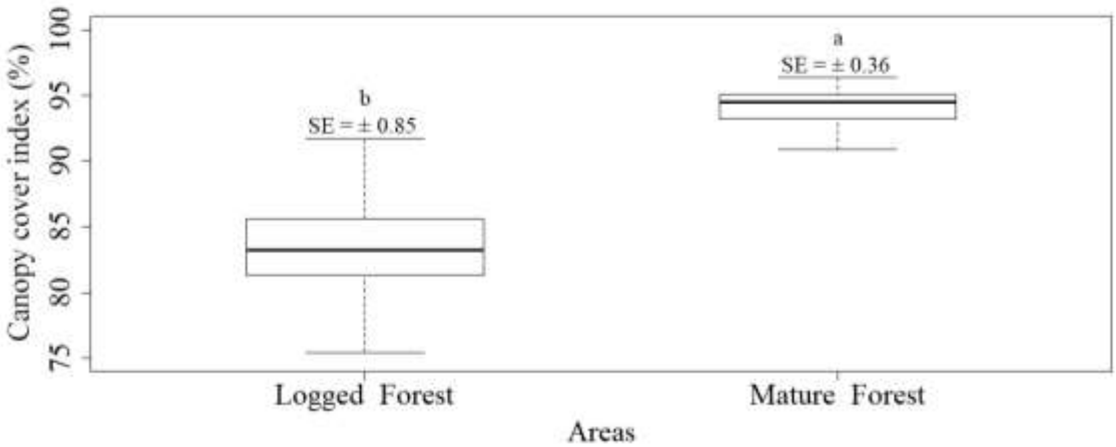
In Mature Forest two species of the canopy/emergent group species, *C. xanthocarpa* and *C. canjerana*, presented a random spatial distribution (Figure 3, 5-8), while *A. polyneuron* had a spatial pattern with distribution in a gradient, where the species was positively autocorrelated at short distances and negatively autocorrelated at long distances (Figure 3, 5-8). In Logged

Forest *A. polyneuron* and *C. canjerana* had a random spatial distribution while *C. xanthocarpa* had an aggregate spatial distribution in clumps of ca. 12 m (Figure 3, 5-8).

The canopy cover index (Figure 4) as higher in Mature Forest, (93.96% ± SE = 0.36) compared to the Logged Forest (83.51% ± SE 0.85). The partial Mantel test did not indicate a correlation between the spatial structure of individuals and the canopy cover in each of the plots for all species in both areas (for all species p>0.05).

Figure 4. Canopy cover index of Mata São Francisco State Park (Logged Forest) and Mata dos Godoy State Park (Mature Forest). Boxes show median, the 95% confidence interval, 25th and 75th percentiles, the standard error (SE). Bars indicate range distribution. Letters indicate a statistically significant difference in canopy cover index (CCI) between areas.



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The occupation of forest area by populations in both study areas was widespread, i.e., all populations had individuals in most of the plots and there were no correlations between canopy cover of each forest with the spatial distribution of any species. A random distribution was observed for three *A. concolor*, *I. marginata*, and *C. canjerana* of the six studied species between areas (Figure 3, 5-8).

I. marginata and *C. canjerana* had a wide distribution, represented mainly by seedlings and individuals of the first size classes, in both sampled areas. This result suggests that seed dispersal is effective, because the seedlings are also germinating far away from adult individuals. The results possibly indicate presence of a seed dispersing fauna even in Logged Forest, because *I. marginata* and *C. canjerana* are zoochoric species (note that *C. canjerana* has few adults in Logged Forest).

A. concolor occupied large continuous zones in both studied areas with many individuals in all size classes, indicating that this species occupies the forest understory in abundance. *A. concolor* may occur in larger agglomerations that the limits of our sample area. Thus, we suggest tests in other ranges for spatial distribution of that species.

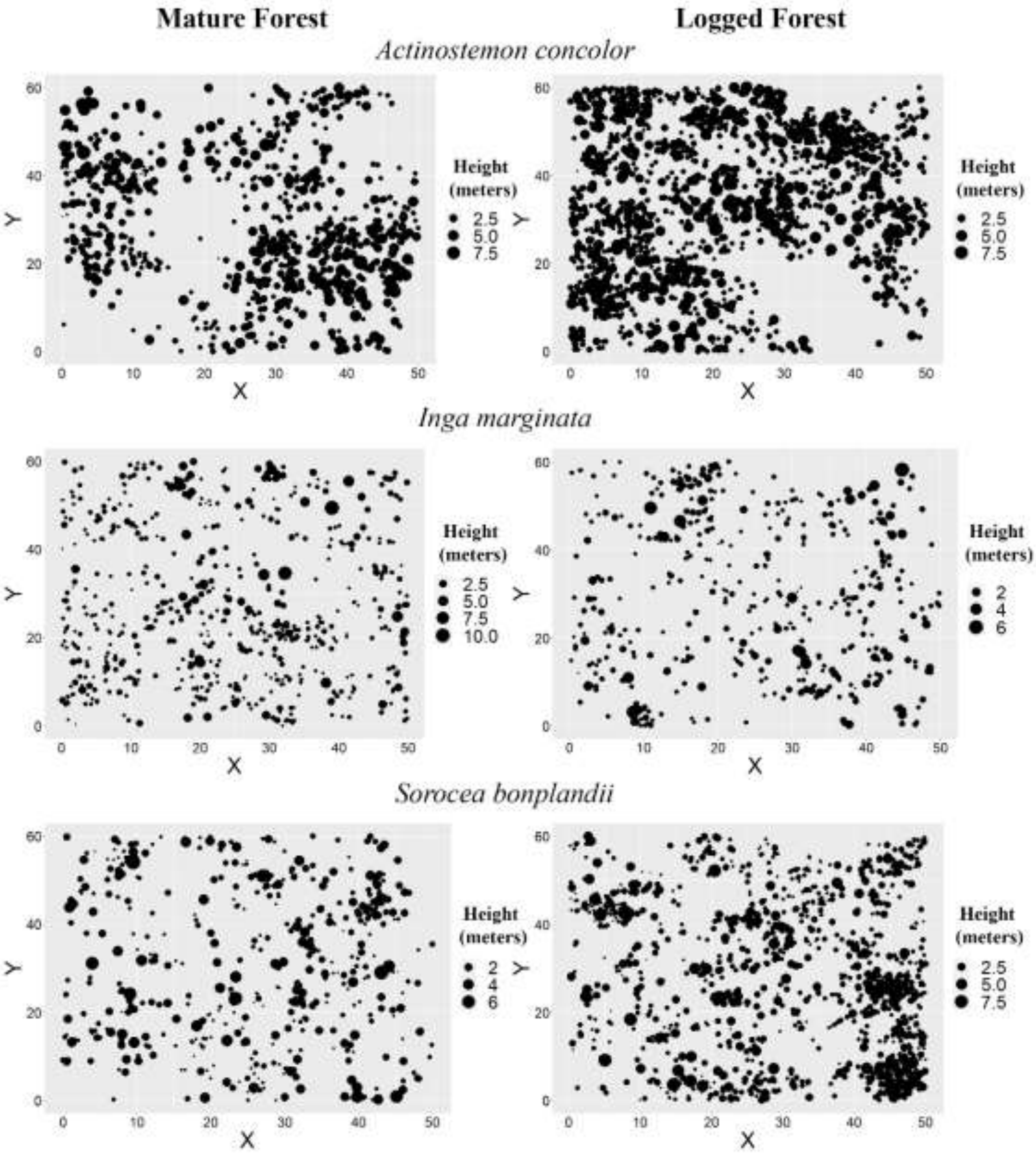
S. bonplandii and *C. xanthocarpa* had random distribution in Mature Forest, but aggregate spatial distribution in small clumps in Logged Forest. *Sorocea bonplandii* was abundant in both areas, occupying the majority of plots with many individuals, but in Logged Forest there was a higher density of saplings in some sites. For example, in one subplot of 5 m × 5 m, 76 individuals from this species were found. *Campomanesia xanthocarpa* was less abundant in both areas, but the aggregate distribution in Logged Forest was also due to the higher density of individuals in the smaller size classes. A higher degree of aggregation in smaller individuals is common for tropical tree species (Condit et al., 2000; Fonseca et al., 2004; Morel et al., 2018). Condit et al., (2000) found that the aggregation of juveniles suggests habitat-related patchiness or dispersal limitation.

The spatial distribution of *A. polyneuron* in Mature Forest was typically a gradient distribution (see distribution in gradient in Legendre; Fortin, 1989). There was a high density of individuals in one of the ends of the sampled area that progressively decreased toward the other end, where the largest specimens are (potential dispersers). *Aspidosperma polyneuron* is an anemochory species and the larger individuals of that species that exceed the canopy forest have their seed dispersal facilitated by greater exposure to wind, which takes their seeds farther away from the parent plant. Fonseca et al., (2004), studying *A. polyneuron* populations in the southeast of Brazil, found a negative correlation between the abundance of seedlings and adults.

This spatial pattern in Mature Forest can suggest the success of the seed dispersal process and the influence of natural enemies on the distance from parental plant (Brachtvogel et al., 2020; Chisholm & Fung, 2020; Jia et al., 2020).

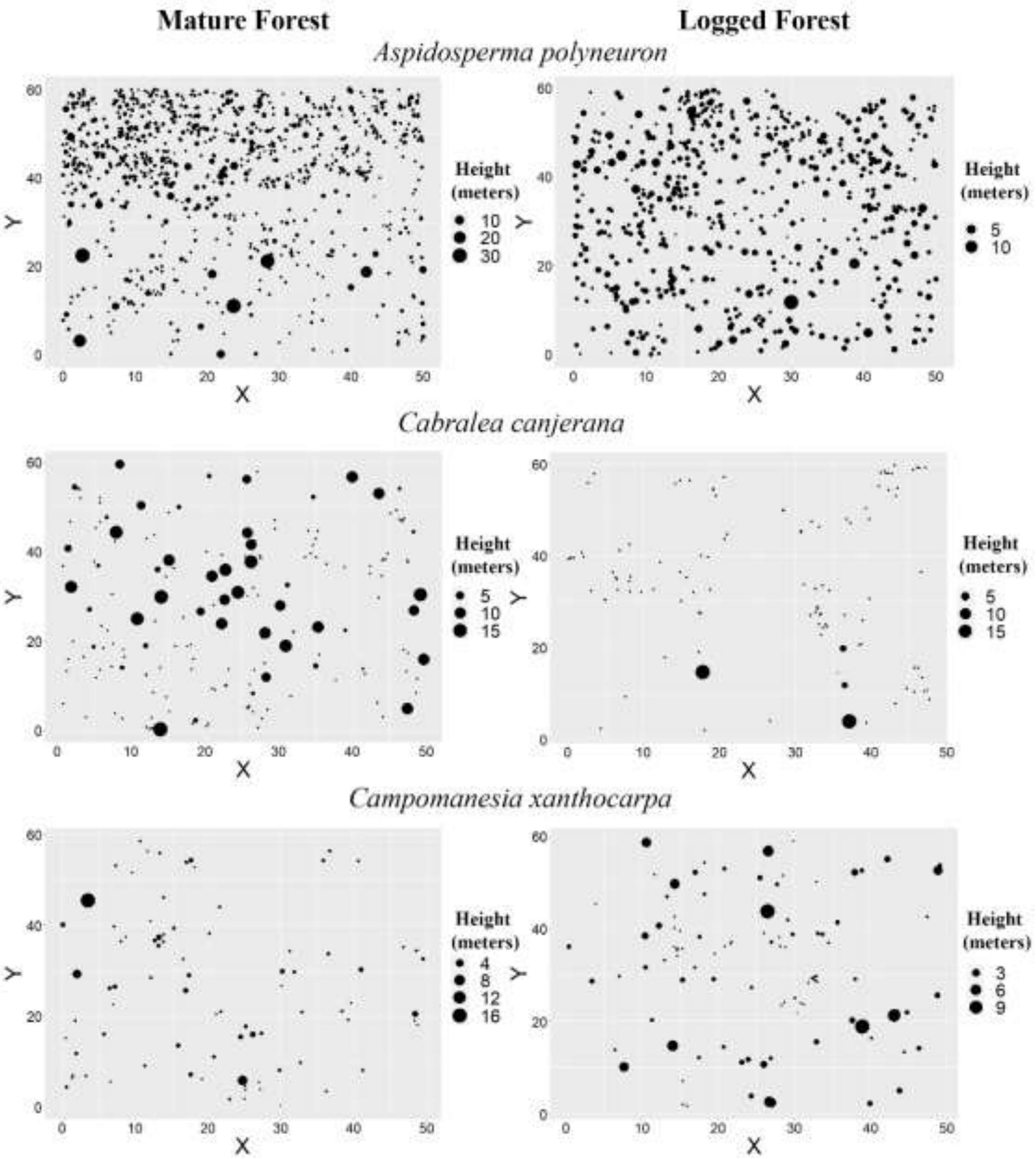
On the other hand, *Aspidosperma polyneuron* had many individuals randomly distributed throughout the Logged Forest without the presence of large adult specimens inside or next to the sampled area and with few individuals in first height class (11 individuals lower than 0.25 meter). Probably the majority of individuals in the area were established before the logging. Seedlings and saplings of this species grow slowly and remain a long time in the shaded understory of the forest (Silva Ribeiro et al., 2020). The removal of adults and consequent low (or no) seedling recruitment is aggravated by such species characteristics as slow growth rate and anemochory syndrome (smaller range), which may make the recovery of *A. polyneuron* very slow and difficult.

Figure 5. Understorey species maps of individuals distribution (*A.concolor*, *I. marginata* and *S. bonplandii*) along the sample areas (50 m × 60 m) in both study areas, Godoy Forest State Park (Mature Forest) and São Francisco Forest State Park (Logged Forest), Paraná state, Brazil, respectively. Column on the left represents populations of Mature Forest and columns on the right represents Logged Forest.



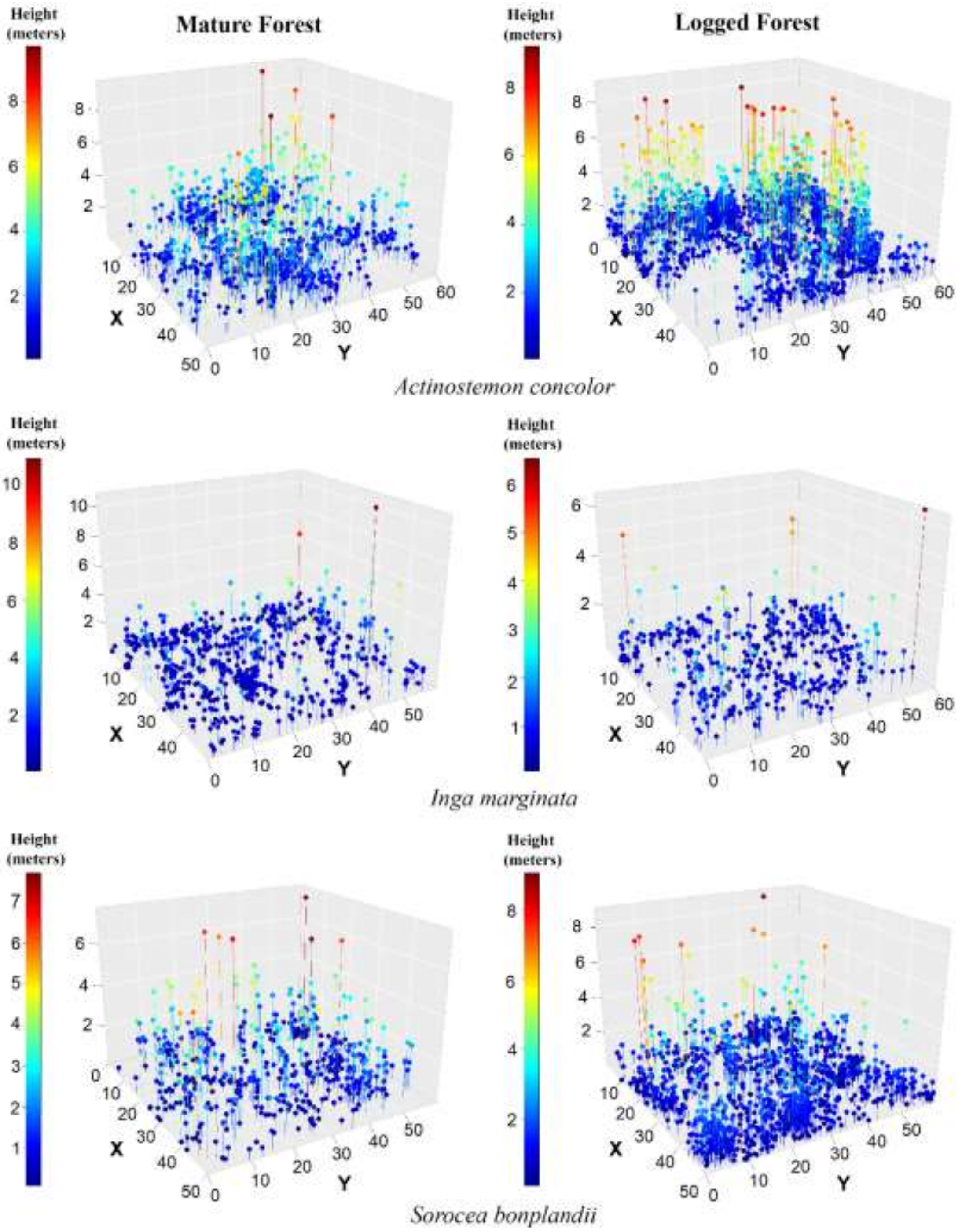
Source: Authors.

Figure 6. Emergent/canopy species maps of individuals distribution (*A. polyneuron*, *C. canjerana* and *C. xanthocarpa*) along the sample areas (50 m × 60 m) in both study areas, Godoy Forest State Park (Mature Forest) and São Francisco Forest State Park (Logged Forest), Paraná state, Brazil, respectively. Column on the left represents populations of Mature Forest and columns on the right represents Logged Forest.



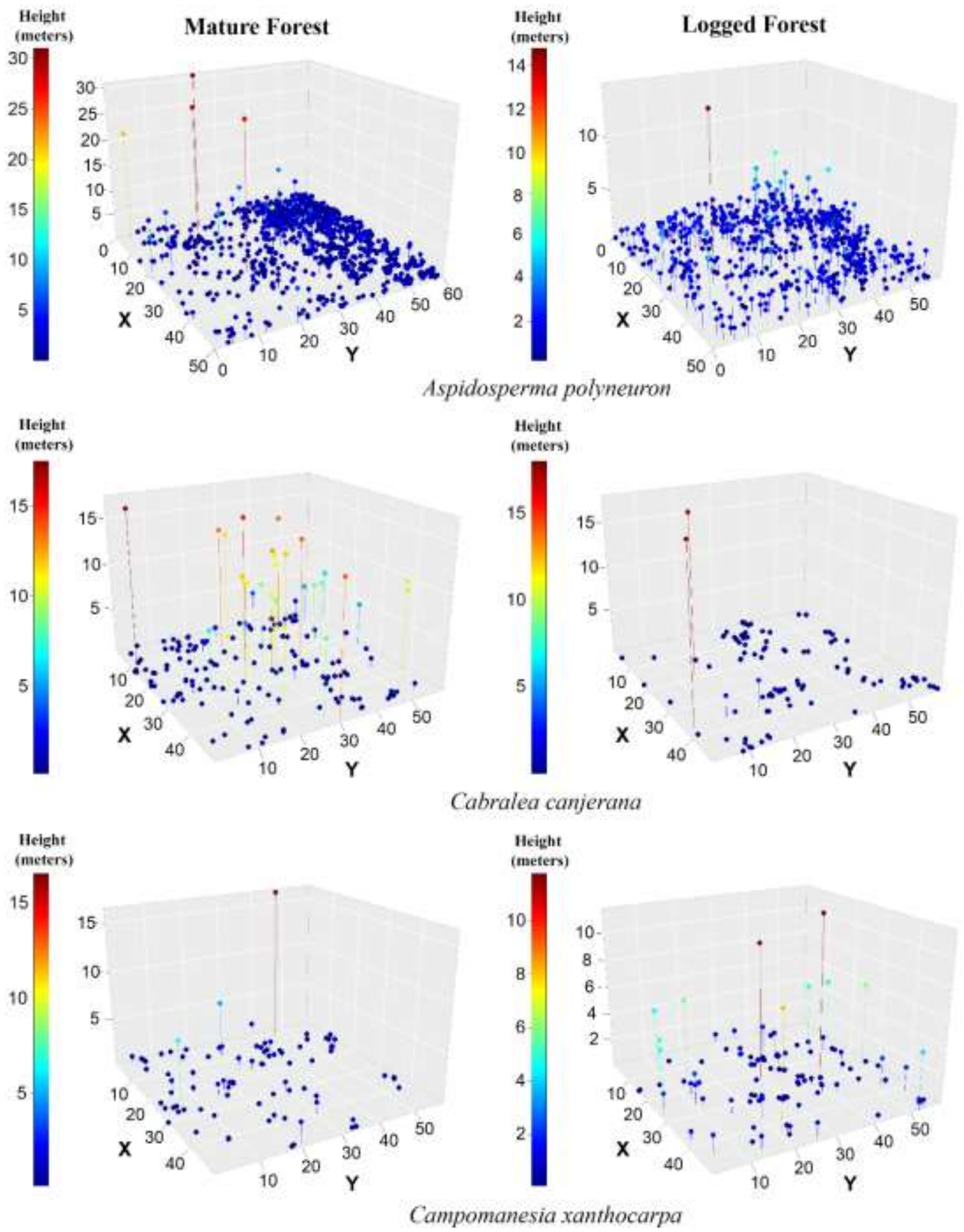
Source: Authors.

Figure 7. Understorey species 3D scatter plot distribution individual maps (*A. concolor*, *I. marginata* and *S. bonplandii*) along the sample areas (50 m × 60 m) in both study areas, Godoy Forest State Park (Mature Forest) and São Francisco Forest State Park (Logged Forest), Paraná state, Brazil, respectively. Column on the left represents populations of Mature Forest and columns on the right represents Logged Forest.



Source: Authors.

Figure 8. Emergent/canopy species 3D scatter plot distribution individual maps (*A. polyneuron*, *C. canjerana* and *C. xanthocarpa*) along the sample areas (50 m × 60 m) in both study areas, Godoy Forest State Park (Mature Forest) and São Francisco Forest State Park (Logged Forest), Paraná state, Brazil, respectively. Column on the left represents populations of Mature Forest and columns on the right represents Logged Forest.



Source: Authors.

4. Conclusion

Selectively logged areas have features different than the expected structure when compared to Mature Forest even after becoming a protected area. An abundance of understory species in the logged area was not expected and deserves greater attention in future studies, since it is poorly documented in the literature. The low occurrence of adults and saplings of *A. polyneuron* is a concern mainly because of the slow growth and limited dispersal of this species, which may have implications for the viability of this population. The importance value (IV) is an index that highlights the horizontal importance of each species in Tree Community. The index considers aspects population of Abundance, frequency and relative dominance in relation to the Tree Community, demonstrating which species are most successful in exploiting the resources. Therefore, selection of species with higher IV together with specie spatial distribution patterns can help to demonstrate the impacts of selective logging more clearly in space and time. In addition, shade-tolerant species are more affected by selective logging since the main effect of logged species causes an increase in luminosity in the lower strata forest, favoring shade-intolerant species in comparison to shade-tolerant species. The Selectively logged area of study (SFFSP) is surrounded by agricultural matrix, which may impose more barriers to arrival and dispersion of shade-tolerant species propagules (group of species characteristic of forest interior), showing the importance of efforts to achieve connectivity with surrounding fragments.

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References

Alvares, C. A., Stape, J. L., Sentelhas, P. C., Moraes, G., Gonçalves, J. L. M., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, *22*(6), 711–728. doi.org/10.1127/0941-2948/2013/0507

Ayres, M., Ayres J, M., Ayres, D. L., & Santos, A. D. A. (2007). *Aplicações estatísticas nas áreas das ciências bio-médicas*. Instituto Mamirauá.

Batista, W. B., & Platt, W. J. (2003). Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. *Journal of Ecology*, 197–212.

Bendel, R. B., Higgins, S. S., Teberg, J. E., & Pyke, D. A. (1989). Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. *Oecologia*, *78*(3), 394–400. doi.org/10.1007/BF00379115

Berry, N. J., Phillips, O. L., Ong, R. C., & Hamer, K. C. (2008). Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. *Landscape Ecology*, *23*(8), 915–929. doi.org/10.1007/s10980-008-9248-1

Bertolini, I. C., Watzlawick, L. F., Sens, T. M. Z. G., Vantroba, A. P., Schran, J. A., & Pott, C. A. (2020). Influência das variáveis climáticas no incremento diamétrico de *Bauhinia forficata* Link, *Mimosa scabrella* Benth. e *Schinus terebinthifolius* Raddi. *Research, Society and Development*, *9*(4), e185942859–e185942859.

Bianchini, E., Garcia, C. C., Pimenta, J. A., & Torezan, J. (2010). Slope variation and population structure of tree species from different ecological groups in South Brazil. *Anais Da Academia Brasileira de Ciências*, *82*(3), 643–652. doi.org/10.1590/S0001-37652010000300012

Bovolenta, Y. R. (2011). *Influência do estado de conservação de fragmentos florestais na estrutura de populações de espécies arbóreas de diferentes estratos verticais*. Dissertação de Mestrado, Universidade Estadual de Londrina, Londrina, PR, Brasil.

Brachtvogel, C., Pereira, Z. V., & Silva, S. M. (2020). Spatial variation of seed rain in deciduous tropical forest. *Research, Society and Development*, *9*(9), e879997956–e879997956

Brocardo, C. R., Pedrosa, F., & Galetti, M. (2018). Forest fragmentation and selective logging affect the seed survival and recruitment of a relictual conifer. *Forest Ecology and Management*, *408*, 87–93.

Brower, J. E., & Zar, J. H. (1984). *Field and laboratory methods for general ecology*. Brown Publishers.

Burton, J. I., Zenner, E. K., Frelich, L. E., & Cornett, M. W. (2009). Patterns of plant community structure within and among primary and second-growth northern hardwood forest stands. *Forest Ecology and Management*, *258*(11), 2556–2568. doi.org/10.1016/j.foreco.2009.09.012

Callaghan, C. T., Bino, G., Major, R. E., Martin, J. M., Lyons, M. B., & Kingsford, R. T. (2019). Heterogeneous urban green areas are bird diversity hotspots: insights using continental-scale citizen science data. *Landscape Ecology*, *34*(6), 1231–1246. doi.org/10.1007/s10980-019-00851-6

Carvalho, P. E. R. (1994). *Espécies florestais brasileiras: recomendações silviculturais, potencialidades e uso da madeira*. Colombo: EMBRAPA-CNPF.

Chisholm, R. A., & Fung, T. (2020). Janzen-Connell effects are a weak impediment to competitive exclusion. *The American Naturalist*, *196*(5), 649–661. doi.org/10.1086/711042

Condit, R., Ashton, P. S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S. P., Foster, R. B., Itoh, A., & LaFrankie, J. V. (2000). Spatial patterns in the distribution of tropical tree species. *Science*, *288*(5470), 1414–1418. doi.org/10.1126/science.288.5470.1414

Coomes, D. A., & Allen, R. B. (2007). Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology*, *95*(1), 27–40. doi.org/10.1111/j.1365-2745.2006.01179.x

Cramér, H. (1999). *Mathematical methods of statistics*. Princeton: Princeton University Press. doi.org/10.2307/2226151

Cunha, J. A. S., Fonsêca, N. C., Cunha, J. S. A., dos Santos Rodrigues, L., de Gusmão, R. A. F., & Lins-e-Silva, A. C. B. (2021). Selective logging in a chronosequence of Atlantic Forest: drivers and impacts on biodiversity and ecosystem services. *Perspectives in Ecology and Conservation*, *19*(3), 286–292.

Dale, M. R. T., & Fortin, M. J. (2014). *Spatial analysis: a guide for ecologists*. Cambridge: Cambridge University Press.

Eisenlohr, P. V, Oliveira-Filho, A. T., & Prado, J. (2015). The Brazilian Atlantic Forest: new findings, challenges and prospects in a shrinking hotspot. *Biodiversity and Conservation*, *24*, 2129–2133. doi.org/10.1007/s10531-015-0995-4

Fonseca, M. G., Martini, A. M. Z., & dos Santos, F. A. M. (2004). Spatial structure of *Aspidosperma polyneuron* in two semi-deciduous forests in Southeast Brazil. *Journal of Vegetation Science*, *15*(1), 41–48. doi.org/10.1111/j.1365-2745.2008.01377.x

Getzin, S., Wiegand, T., Wiegand, K., & He, F. (2008). Heterogeneity influences spatial patterns and demographics in forest stands. *Journal of Ecology*, *96*(4), 807–820.

Guariguata, M. R., & Ostertag, R. (2001). Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, *148*(1), 185–206.

Haddad, T. M., Hertel, M. F., Bianchini, E., & Pimenta, J. A. (2016). Architecture of four tree species from different strata of a semideciduous forest in southern Brazil. *Australian Journal of Botany*, *64*(2), 89–99. doi.org/10.1071/BT15199

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Lin, G., Hao, Z., & Bagchi, R. (2020). Tree species traits affect which natural enemies drive the Janzen-Connell effect in a temperate forest. *Nature Communications*, *11*(1), 1–9. doi.org/10.1038/s41467-019-14140-y

Kelly, C. K., Smith, H. B., Buckley, Y. M., Carter, R., Franco, M., Johnson, W., Jones, T., May, B., Ishiwara, R. P., & Pèrez-Jimènez, A. (2001). Investigations in commonness and rarity: a comparative analysis of co-occurring, congeneric Mexican trees. *Ecology Letters*, *4*(6), 618–627.

Lammertink, M., Fernández, J. M., & Cockle, K. L. (2020). Comparison of nesting ecology of three co-existing Atlantic Forest woodpeckers reveals narrow specialization in the Helmeted Woodpecker *Celeus galeatus*. *Acta Ornithologica*, *55*(1), 101–110.

Laurans, M., Hérault, B., Vieilledent, G., & Vincent, G. (2014). Vertical stratification reduces competition for light in dense tropical forests. *Forest Ecology and Management*, *329*, 79–88.

Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological analysis. *Vegetatio*, *80*(2), 107–138.

Lemmon, P. E. (1956). A spherical densiometer for estimating forest overstory density. *Forest Science*, *2*(4), 314–320.

Liebsch, D., Maçaneiro, J. P., Marcon, A. K., & Galvão, F. (2016). Influência de impactos antrópicos em fragmentos de Floresta Ombrófila Mista em Santa Catarina. *Pesquisa Florestal Brasileira*, *36*(87), 277–287.

Liebsch, D., Velazco, S. J. E., Mikich, S. B., Marques, M. C. M., & Galvão, F. (2021). Effects of selective logging, fragmentation, and dominance of bamboos on the structure and diversity of Araucaria Forest fragments. *Forest Ecology and Management*, *487*, 1-9 (118961).

Lima, R. A. F., Oliveira, A. A., Pitta, G. R., de Gasper, A. L., Vibrans, A. C., Chave, J., Ter Steege, H., & Prado, P. I. (2020). The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. *Nature Communications*, *11*(1), 1–16.

Lima, T. A., Beuchle, R., Griess, V. C., Verhegghen, A., & Vogt, P. (2020). Spatial patterns of logging-related disturbance events: a multi-scale analysis on forest management units located in the Brazilian Amazon. *Landscape Ecology*, *35*(9), 2083–2100.

Maestre, F. T., Escudero, A., & Bonet, A. (2008). *Introducción al análisis espacial de datos en ecología y ciencias ambientales: métodos y aplicaciones*. Dykinson: Universidad Rey Juan Carlos.

Montgomery, R., & Chazdon, R. J. (2002). Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, *131*(2), 165–174.

Morel, J. D., Pereira, J. A. A., dos Santos, R. M., de Aguiar-Campos, N., & Machado, E. L. M. (2018). Functional Characterization of an Anthropized Atlantic Forest Fragment. *Journal of Tropical Forest Science*, *30*(4), 537–545.

Nitsche, P. R., Caramori, P. H., Ricce, W. da S., & Pinto, L. F. D. (2019). *Atlas Climático do Estado do Paraná*. IAPAR.

Oden, N. L. (1984). Assessing the significance of a spatial correlogram. *Geographical Analysis*, *16*(1), 1-16.

Onoda, Y., Saluñga, J. B., Akutsu, K., Aiba, S., Yahara, T., & Anten, N. P. R. (2014). Trade-off between light interception efficiency and light use efficiency: implications for species coexistence in one-sided light competition. *Journal of Ecology*, *102*(1), 167–175.

Pearcy, R. W. (1983). The light environment and growth of C3 and C4 tree species in the understory of a Hawaiian forest. *Oecologia*, *58*(1), 19–25.

Plotkin, J. B., Potts, M. D., Leslie, N., Manokaran, N., LaFrankie, J., & Ashton, P. S. (2000). Species-area curves, spatial aggregation, and habitat specialization in tropical forests. *Journal of Theoretical Biology*, *207*(1), 81–99.

Poorter, L., Hawthorne, W., Bongers, F., & Sheil, D. (2008). Maximum size distributions in tropical forest communities: relationships with rainfall and disturbance. *Journal of Ecology*, *96*(3), 495–504.

Primack, R. B., & Lee, H. S. (1991). Population dynamics of pioneer (*Macaranga*) trees and understorey (*Mallotus*) trees (Euphorbiaceae) in primary and selectively logged Bornean rain forests. *Journal of Tropical Ecology*, 439–457.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, *142*(6), 1141–1153.

Rodrigues, D. R., Bovolenta, Y. R., Pimenta, J. A., & Bianchini, E. (2016). Height structure and spatial pattern of five tropical tree species in two seasonal semideciduous forest fragments with different conservation histories. *Revista Árvore*, *40*(3), 395–405. doi.org/10.1590/0100-67622016000300003

Rodrigues, D. R., Bovolenta, Y. R., Pimenta, J. A., & Bianchini, E. (2019). Selective logging alters allometric relationships of five tropical tree species in seasonal semi-deciduous forests. *Journal of Forestry Research*, *30*(5), 1633–1639. doi.org/10.1007/s11676-018-0705-7

Rosenberg, M. S., & Anderson, C. D. (2011). PASSaGE: pattern analysis, spatial statistics and geographic exegesis. Version 2. *Methods in Ecology and Evolution*, *2*(3), 229–232.

RStudio. (2020). *R Studio: integrated development environment for R.* Version 1.3.1056, 1048.

Rutishauser, E., Hérault, B., Petronelli, P., & Sist, P. (2016). Tree height reduction after selective logging in a Tropical Forest. *Biotropica*, *48*(3), 285–289.

Saldarriaga, J. G., & Uhl, C. (1991). Recovery of forest vegetation following slash-and-burn agriculture in the upper Rio Negro. In A. Gómez-Pompa, T. C. Whitmore, & M. Hadley (Eds.), *Tropical rain forest: regeneration and management* (pp. 303–312). London: Blackwell Science.

Santo-Silva, E. E., Almeida, W. R., Tabarelli, M., & Peres, C. A. (2016). Habitat fragmentation and the future structure of tree assemblages in a fragmented Atlantic forest landscape. *Plant Ecology*, *217*(9), 1129–1140.

Santos, H. G., Jacomine, P. K. T., Anjos, L. H. C., Oliveira, V. Á., Lumbreras, J. F., Coelho, M. R., Almeida, J. A., Cunha, T. J. F., & Oliveira, J. B. (2013). *Sistema brasileiro de classificação de solos*. doi.org/ISBN 978-85-7035-198-2

Santos, J. S., Leite, C. C. C., Viana, J. C. C., dos Santos, A. R., Fernandes, M. M., de Souza Abreu, V., do Nascimento, T. P., dos Santos, L. S., de Moura Fernandes, M. R., & da Silva, G. F. (2018). Delimitation of ecological corridors in the Brazilian Atlantic Forest. *Ecological Indicators*, *88*, 414–424.

Sapkota, I. P., Tigabu, M., & Odén, P. C. (2009). Spatial distribution, advanced regeneration and stand structure of Nepalese Sal (*Shorea robusta*) forests subject to disturbances of different intensities. *Forest Ecology and Management*, *257*(9), 1966–1975.

Siegel, S., & Castellan Jr, N. J. (1975). *Estatística não-paramétrica para ciências do comportamento*. Artmed Editora.

Silva, D. A. da, & Vibrans, A. C. (2019). Canopy Architecture After Selective Logging in a Secondary Atlantic Rainforest in Brazil. *Floresta e Ambiente*, *26*(4).

Silva, F. C., & Soares-Silva, L. H. (2000). Arboreal flora of the Godoy Forest State Park, Londrina, PR. Brazil. *Edinburgh Journal of Botany*, *57*(1), 107–120.

Silva Ribeiro, J. E., Figueiredo, F. R. A., dos Santos Coêlho, E., & Leite, A. P. (2020). Aspectos morfofisiológicos de Ceiba glaziovii sob níveis de sombreamento. *Research, Society and Development*, *9*(8), e257985736–e257985736

Smith, H. (2000). Phytochromes and light signal perception by plants: an emerging synthesis. *Nature*, *407*(6804), 585–591.

Soares-Silva, L. H., & Barroso, G. M. (1992). Fitossociologia do estrato arbóreo da floresta na porção norte do Parque Estadual Mata dos Godoy, Londrina-PR, Brasil. *In "Anais Do VIII Congresso Da Sociedade Botânica de São Paulo".*

Sobral, M., Proença, C., Souza, M., Mazine, F., & Lucas, E. (2015). *Myrtaceae in lista de espécies da flora do Brasil*. Rio de Janeiro: Jardim Botânico Do Rio de Janeiro.

Solís, S., Lobo, J., & Grimaldo, M. (2009). Phenology and recruitment of *Caryocar costaricense* (Caryocaceae), an endemic tree species of Southern Central America. *Revista de Biología Tropical*, *57*(3), 771–780.

SOS Mata Atlântica & INPE. (2020). *Atlas dos Remanescentes Florestais da Mata Atlântica*. https://mapas.sosma.org.br/

Souza, A. F. (2007). Ecological interpretation of multiple population size structures in trees: the case of *Araucaria angustifolia* in South America. *Austral Ecology*, *32*(5), 524–533.

Swaine, M. D., & Whitmore, T. C. (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio*, *75*(1–2), 81–86. doi.org/10.1007/BF00044629

Tabarelli, M., Mantovani, W., & Peres, C. A. (1999). Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation*, *91*(2), 119–127. doi.org/10.1016/S0006-3207(99)00085-3

Tang, H., & Dubayah, R. (2017). Light-driven growth in Amazon evergreen forests explained by seasonal variations of vertical canopy structure. *Proceedings of the National Academy of Sciences*, *114*(10), 2640–2644.

Tomé, M., Miglioranza, E., Vilhena, A. H. T., & Fonseca, E. P. (1999). Composição florística e fitossociológica do Parque Estadual Mata São Francisco. *Revista Do Instituto Florestal*, *11*(1), 13–23.

Torezan, J. M. D. (Ed.). (2006). *Ecologia do Parque Estadual Mata dos Godoy*. Editora ITEDES.

Tsingalia, M. (2010). Impacts of selective logging on population structure and dynamics of a canopy tree (*Olea capensis*) in Kakamega forest. *African Journal of Ecology*, *48*(3), 569–575.

Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, *39*.

Veloso, H. P., Rangel Filho, A. L. R., & Lima, J. C. A. (1991). *Classificação da vegetação brasileira, adaptada a um sistema universal*. Brasília: Instituto Brasileiro de Geografia e Estatística (IBGE).

Vicente, R. F. (2006). O Parque Estadual Mata dos Godoy. In J. M. D. Torezan (Ed.), *Ecologia do Parque Estadual Mata dos Godoy*. (pp. 13–18).

Wright, S. J., Muller-Landau, H. C., Condit, R., & Hubbell, S. P. (2003). Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology*, *84*(12), 3174–3185.

Zama, M. Y., Bovolenta, Y. R., Carvalho, E. S., Rodrigues, D. R., Araujo, C. G., Sorace, M. A. F., & Luz, D. G. (2012). Florística e síndromes de dispersão de espécies arbustivo-arbóreas no Parque Estadual Mata São Francisco, PR, Brasil. *Hoehnea*, *39*, 369–378. dx.doi.org/10.1590/S2236-89062012000300002

Zucchi, M. I., Sujii, P. S., Mori, G. M., Viana, J. P. G., Grando, C., Silvestre, E. de A., Schwarcz, K. D., Macrini, C. M., Bajay, M. M., & Araújo, F. L. (2018). Genetic diversity of reintroduced tree populations in restoration plantations of the Brazilian Atlantic Forest. *Restoration Ecology*, *26*(4), 694–701.