

Drivers of Restoration Trajectory of a Community of Regenerant Plants: Natural Regeneration or Tree Seedling?

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Abstract

Tree plantation is the most used technique for ecological restoration, although passive restoration requires a lower investment of resources. This research aimed to compare the composition and structure of the community of regenerant plants in areas under restoration through Assisted Natural Regeneration and mixed native Tree Planting, in the same area. We randomly placed 12 plots of 100 m² each and sampled all the regenerating individuals found within them. We compared both restoration methods regarding growth pattern, dispersal syndromes, and successional groups. In both methodologies, trees and shrubs were the most abundant growth forms. The pioneer successional class was the most abundant in number of individuals for both treatments. We concluded that the two restoration methods allowed the regeneration of native species. We propose that Assisted Natural Regeneration is a viable restoration strategy, capable of boosting the initial processes of the community, especially in a matrix surrounded by remaining forests.

Keywords: Seasonal forest, biodiversity, growth form, successional group, dispersal syndrome.

1. INTRODUCTION

Tree planting is the most used technique for ecological restoration (Schorn et al., 2010), although passive restoration requires a lower investment, especially in areas of difficult access (Leal-Filho et al., 2013), relying only on successional processes to recover spontaneously, like the arrival of propagules and seed banks (Chazdon, 2012). In this method, natural regeneration occurs in tropical forests through seeds and seedling soil banks, seed rain, and resprouters (Calegari et al., 2013; Piña-Rodrigues & Aoki, 2014; Almeida, 2016).

The techniques of forest restoration aim to potentially maximize the environmental resilience, favoring the natural mechanisms that result in the natural recovery of the environment (Campello, 1998). In general, they must recreate ecologically viable communities by protecting and fostering the natural ability of ecosystems to change along the process of ecological succession (Oliveira & Engel, 2018). However, the success of restoration through Assisted Natural Regeneration

is linked to the characteristics of the surrounding landscape (Pereira et al., 2013), the conditions of the site, the control and management of invasive grasses (Souza et al., 2012; Freitas et al., 2019; Rodrigues et al., 2019), and species functional traits (Passareti et al., 2020). In the tropics, natural regeneration creates mosaics of fragments of different ages and history of disturbances (Schilling et al., 2016), making secondary forests a common forest type on the landscape. Forest remnants vary in composition and biotic and abiotic characteristics, which affect the supply of seeds to its surroundings (Santos, 2018).

Following the actual global climate change scenario, Brazil will reach the highest expected losses in forest vegetation cover by 2050 (Bastin et al., 2019). In Brazil, there is currently a liability of approximately 21 million hectares of protected areas that must be restored (Sae, 2013; Soares Filho et al., 2014; Planaveg, 2017). International commitments undertaken by Brazil involve the restoration of 12.5 million hectares by 2030, of which 2.2 million hectares represent passive restoration through natural regeneration (Brasil, 2017).

The development of low-cost restoration models contributes to the rapid expansion of forest regeneration. Given the potential of restoration through natural recovery, it is critical to analyze the development of ecological processes that enable forests under restoration to reach the desired scenario which, in this case, is the reestablishment of the original forest cover.

Our hypothesis is that the ecological restoration by natural regeneration is as efficient as restoration by conventional planting of seedlings, as long as there is adequate management on the area, such as control of leaf-cutting ants and exotic grasses. Furthermore, we believe that nearby forest remnants contribute to the arrival of propagules for the succession of the areas. For this purpose, we have compared, on the same landscape, the composition and structure of regenerating communities in areas restored by Assisted Natural Regeneration and mixed native Tree Planting.

2. MATERIAL AND METHODS

2.1. Study site

This study was carried out in 4.73 hectares under restoration in the municipality of Borborema, São Paulo State, Brazil (21°43'38.94"S latitude, 49°3'1.18" W longitude) (Figure 1). The altitude varies from 384 to 387 m asl, and the vegetation is represented by remnants of the tropical seasonal semideciduous forest. The climate is tropical, with dry winters, classified as *Aw* by Köppen (1948). The annual mean temperature and rainfall are 22.2 °C and 1,231 mm, respectively. The driest month is August, with a historical average rainfall of 19 mm. The warmest and wettest month is January, with a mean precipitation of 234 mm and a temperature of 24.8 °C. The average temperature in June, the coldest month, is 18.5 °C (Climate-Data, 2019). The area is located in a zone seized by the "Promissão" hydroelectric dam, in which the fodder grass *Paspalum notatum* Flügge is used as pasture. In order to run the experiment, the expropriation elevation level of the reservoir (i.e., the area buffering the water reservoir where agricultural and construction activities are prohibited for safety reasons), as well as the normal maximum elevation level were identified through georeferencing equipment.

Adjacent to the study area, a fragment of approximately 4 hectares of tropical seasonal semideciduous forest with secondary vegetation, in an intermediary stage of regeneration, presents tree and shrub plants covering the herbaceous vegetation. The trees have approximately 10 meters high, with some higher individuals. The canopy is discontinuous and has openings with a predominance of shrub and herbaceous species. We have observed epiphytes and the presence of mainly woody vines, and litter distributed throughout the entire area. We observed

some species such as *Trema micrantha* (L.) Blume, *Croton floribundus* Spreng., *Albizia niopoides* (Benth.) Burkart, *Schinus terebinthifolia* Raddi, *Aloysia virgata* (Ruiz & Pav.) Juss., *Rhamnidium elaeocarpum* Reissek, *Vitex megapotamica* (Spreng.) Moldenke, *Mabea fistulifera* Mart., *Solanum paniculatum* L., *Ananas* sp., and *Psychotria carthagenensis* Jacq.

2.1.1. Restoration methods

In October 2014, the study area was fenced to reduce external degradation factors such as cattle grazing and others. After that, we have implemented two restoration methods: (a) Assisted Natural Regeneration (ANR) and (b) mixed native seedlings Tree Planting (TP). The ANR occupied 2.47 ha and the TP 2.26 ha. In November 2014, we carried out the suppression of leaf-cutter ants and the application of 2.5 liters.ha⁻¹ of glyphosate (N-phosphonomethyl glycine) in both areas for the control of the non-native invasive grass *P. notatum*. Another round of the herbicide was applied again every semester for two years in the ANR.

Fifteen days after the first suppression of invasive grasses in TP, in November 2014, 1 ton.ha⁻¹ of dolomitic limestone was applied, followed by harrowing. We subsoiled the harrowed area to 60 cm depth, with a 3-meter spacing between the subsoiling lines and applied a chemical N:P:K (20:5:20; 660 kg.ha⁻¹) superphosphate fertilizer. In December 2014, seedlings from 97 native species were planted using manual planters, with a spacing of 3 x 2 m (Additional file 1). Later, we carried out the maintenance activities every four months during three years, controlling the invasive grasses with herbicides (2.5 liters.ha⁻¹ of glyphosate), seedling fertilization with N:P:K (20:5:20; 400 kg.ha⁻¹), seedlings crowning, and leaf-cutting ants control.

In both experimental areas the soil type was the same, being characterized as deep friable soils, with high drainage. The main types of soil found in the area are red latosols and argisols, with basalt rocks being found in the region.



Figure 1. Location of the study areas around the hydroelectric reservoir in Borborema, São Paulo, Brazil. ANR = Assisted Natural Regeneration, TP = mixed native Tree Planting.

2.2. Data sample

2.2.1. Inventory and functional classification

We have randomly placed six 4 x 25 m permanent plots after four and three years for TP and ANR, respectively, totaling 12 permanent plots of 100 m² each. All individuals higher than 50 cm high and with a circumference at breast height (CBH) lower than 15 cm were classified as regenerants, and were measured and identified to the lowest possible taxonomic level. In the TP, we have considered regenerants as the non-planted individuals mainly found between planting rows.

The species were identified in the field, or later, in the herbarium, when necessary. The spelling of the scientific names, the valid names, and the synonyms were checked according to The Plant List (2013). In order to determine different functional groups, all species were classified according to their growth form, successional group, and dispersal syndrome according to the São Paulo database of species for restoration (Barbosa et al., 2017).

2.3. Data Analyses

We have calculated the phytosociological parameters for shrubs and trees according to Moro & Martins (2011). The species diversity was calculated using the Shannon-Weaver Index (H') and the Equitability was calculated based

on Pielou (J'). The species distribution in the community was evaluated by the Sorensen similarity coefficient (Martins & Santos, 1999), in order to compare the floristic similarity between the restoration methods and the list of species planted in TP.

The abundance and richness of regenerants were calculated and the restoration methods were compared using the Student's t-test. We compared the percentage of growth forms, dispersal syndromes, and successional groups between the restoration methods through the Kruskal-Wallis non-parametric test (both at 5% probability level). When significant differences were detected, Dunn's tests were performed. All statistical analyses were carried out using the R software (R Core Team, 2020).

3. RESULTS

We sampled a total of 981 individuals (estimated 8,175 individuals.ha⁻¹), distributed in 66 species and 24 botanical families (Table 1). Only six species totaled 67.8% of the individuals, namely *Senegalia polyphylla* (184 individuals), *Vernonanthura polyanthes* (142), *Sida santaremensis* (133), *Solanum paniculatum* (106), *Solanum mauritianum* (58), and *Desmodium incanum* (42). The botanical families that accounted for 55.5% of species richness and that represented 85.1% of the density were the following: Asteraceae (10 species), Malvaceae (nine), Fabaceae (six), Solanaceae (five), Myrtaceae (four), and Verbenaceae (four). Four herbaceous species in the ANR were not identified.

Table 1. List of regenerant species ordered by family and sampled in restoration sites at the region of Borborema, São Paulo State, Brazil, containing the abundance (number of individuals), growth form, dispersal syndrome, and successional group, for different restoration methods. ANR: Assisted Natural Regeneration, TP: Tree Planting; Anemo: wind dispersal; Zoo: animal dispersal; Auto: another dispersal strategy; P: pioneer; NP: non-pioneer.

Species	Family	Abundance		Growth Form	Dispersal Syndrome	Successional Group
		ANR	TP			
<i>Astronium graveolens</i> Jacq.	Anacardiaceae	0	2	Tree	Anemo	NP
<i>Schinus terebinthifolia</i> Raddi	Anacardiaceae	3	3	Tree	Zoo	P
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	0	2	Tree	Zoo	NP
<i>Oxypetalum appendiculatum</i> Mart.	Apocynaceae	0	5	Vine	Anemo	P
<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	Arecaceae	5	3	Tree	Zoo	NP
Asteraceae 1	Asteraceae	0	1	Herb	Anemo	P
<i>Chromolaena maximiliani</i> (Schrad. ex DC.) R.M. King & H. Rob.	Asteraceae	17	0	Shrub	Anemo	P
<i>Emilia sonchifolia</i> (L.) DC. ex Wight	Asteraceae	1	0	Herb	Anemo	P
<i>Erechtites hieracifolius</i> (L.) Raf. ex DC.	Asteraceae	7	0	Herb	Anemo	P
<i>Galinsoga parviflora</i> Cav.	Asteraceae	1	0	Herb	Anemo	P

Continues...

Table 1. Continued...

Species	Family	Abundance		Growth Form	Dispersal Syndrome	Successional Group
		ANR	TP			
<i>Mikania campanulata</i> Gardner	Asteraceae	0	2	Vine	Anemo	P
<i>Porophyllum ruderale</i> (Jacq.) Cass.	Asteraceae	5	0	Herb	Anemo	P
<i>Pterocaulon lanatum</i> Kuntze	Asteraceae	8	1	Shrub	Anemo	P
<i>Solidago chilensis</i> Meyen	Asteraceae	1	0	Shrub	Anemo	P
<i>Vernonanthura polyanthes</i> (Sprengel) Vega & Dematteis	Asteraceae	134	8	Shrub	Anemo	P
<i>Handroanthus ochraceus</i> (Cham.) Mattos	Bignoniaceae	0	3	Tree	Anemo	NP
<i>Trema micrantha</i> (L.) Blume	Cannabaceae	1	2	Tree	Zoo	P
<i>Ipomoea nil</i> (L.) Roth	Convolvulaceae	0	1	Vine	Auto	P
<i>Erythroxylum pelleterianum</i> A.St.-Hil.	Erythroxylaceae	0	6	Shrub	Zoo	NP
<i>Croton floribundus</i> Spreng.	Euphorbiaceae	0	3	Tree	Auto	P
<i>Mabea fistulifera</i> Mart.	Euphorbiaceae	14	7	Tree	Auto	P
<i>Albizia niopoides</i> (Benth.) Burkart	Fabaceae	1	0	Tree	Auto	P
<i>Desmodium incanum</i> DC.	Fabaceae	36	6	Shrub	Zoo	P
<i>Enterolobium contortisiliquum</i> (Vell.) Morong	Fabaceae	1	0	Tree	Auto	P
<i>Parapiptadenia rigida</i> (Benth.) Brenan	Fabaceae	1	0	Tree	Auto	NP
<i>Peltophorum dubium</i> (Spreng.) Taub.	Fabaceae	0	1	Tree	Auto	P
<i>Senegalia polyphylla</i> (DC.) Britton & Rose	Fabaceae	8	176	Tree	Auto	P
<i>Aegiphila sellowiana</i> Cham.	Lamiaceae	0	1	Tree	Zoo	P
<i>Hyptis suaveolens</i> (L.) Poit.	Lamiaceae	0	1	Herb	Auto	P
<i>Ocimum campechianum</i> Mill.	Lamiaceae	1	0	Herb	Auto	P
<i>Nectandra lanceolata</i> Nees & Mart.	Lauraceae	2	2	Tree	Zoo	NP
<i>Guazuma ulmifolia</i> Lam.	Malvaceae	1	1	Tree	Zoo	P
Malvaceae 1	Malvaceae	0	4	Shrub	-	-
<i>Sida cordifolia</i> L.	Malvaceae	2	0	Shrub	Auto	P
<i>Sida rhombifolia</i> L.	Malvaceae	7	3	Shrub	Auto	P
<i>Sida santaremensis</i> Monteiro	Malvaceae	97	36	Shrub	Auto	P
<i>Sidastrum paniculatum</i> (L.) Fryxell	Malvaceae	15	0	Shrub	Auto	P
<i>Urena lobata</i> L.	Malvaceae	5	3	Shrub	Zoo	P
<i>Waltheria communis</i> A.St.-Hil.	Malvaceae	1	0	Shrub	Auto	P

Continues...

Table 1. Continued...

Species	Family	Abundance		Growth Form	Dispersal Syndrome	Successional Group
		ANR	TP			
<i>Wissadula subpeltata</i> (Kuntze) R.E.Fr.	Malvaceae	1	11	Shrub	Auto	NP
<i>Guarea guidonia</i> (L.) Sleumer	Meliaceae	5	0	Tree	Zoo	NP
<i>Trichilia pallida</i> Sw.	Meliaceae	1	2	Tree	Zoo	NP
Myrtaceae 1	Myrtaceae	0	7	Tree	Zoo	NP
<i>Psidium cattleianum</i> Sabine	Myrtaceae	1	0	Tree	Zoo	NP
<i>Psidium guajava</i> L.	Myrtaceae	22	0	Tree	Zoo	P
<i>Syzygium cumini</i> (L.) Skeels	Myrtaceae	5	0	Tree	Zoo	P
<i>Passiflora edulis</i> Sims	Passifloraceae	0	1	Vine	Zoo	P
<i>Myrsine umbellata</i> Mart.	Primulaceae	0	1	Tree	Zoo	NP
<i>Rhamnidium elaeocarpum</i> Reissek	Rhamnaceae	2	4	Tree	Zoo	NP
<i>Psychotria carthagenensis</i> Jacq.	Rubiaceae	8	1	Shrub	Zoo	NP
<i>Serjania</i> sp.	Sapindaceae	1	0	Vine	Anemo	NP
<i>Smilax campestris</i> Griseb.	Smilacaceae	21	10	Vine	Zoo	P
<i>Solanum americanum</i> Mill.	Solanaceae	6	0	Shrub	Zoo	P
<i>Solanum capsicoides</i> All.	Solanaceae	8	0	Shrub	Zoo	P
<i>Solanum mauritianum</i> Scop.	Solanaceae	58	0	Tree	Zoo	NP
<i>Solanum palinacanthum</i> Dunal	Solanaceae	3	0	Shrub	Zoo	P
<i>Solanum paniculatum</i> L.	Solanaceae	73	33	Shrub	Zoo	P
Unknown 1	Unknown 1	1	0	Herb	-	-
Unknown 2	Unknown 2	1	0	Herb	-	-
Unknown 3	Unknown 3	6	0	Herb	-	-
Unknown 4	Unknown 4	11	0	Herb	-	-
<i>Cecropia pachystachya</i> Trécul	Urticaceae	2	1	Tree	Zoo	P
<i>Aloysia virgata</i> (Ruiz & Pav.) Juss.	Verbenaceae	0	10	Tree	Auto	P
<i>Citharexylum myrianthum</i> Cham.	Verbenaceae	1	0	Tree	Zoo	P
<i>Lantana camara</i> L.	Verbenaceae	0	4	Shrub	Zoo	P
<i>Stachytarpheta cayennensis</i> (Rich.) Vahl	Verbenaceae	1	0	Shrub	Auto	P
TOTAL		613	368			

The species with the highest IVI in the ANR treatment were *S. mauritianum* (IVI= 67.54; 22.5%), *S. paniculatum* (56.96; 18.9%), *Psidium guajava* (51.26; 17%), *Mabea fistulifera* (20.12; 6.7%), and *Acrocomia aculeata* (12.56; 4.2%), which together represented 78.9% of the sampled individuals and 69.5% of the IVI (Table 2), with dominance of the Solanaceae family (58.1% of the individuals).

The species with highest IVI in the TP treatment were *S. polyphylla* (IVI = 94.08; 31.4%); *S. paniculatum* (39.79; 13.3%); *Handroanthus ochraceus* (18.94; 6.3%); *Aloysia virgata* (18.70; 6.2%); and *Schinus terebinthifolia* (IVI = 17.30; 5.8%), which represented 83% of the individuals and 63% of the IVI for this restoration method. Fabaceae and Solanaceae showed the highest dominance (Table 3).

Table 2. Phytosociology of regenerant species (trees and shrubs) sampled in the Assisted Natural Regeneration (ANR) area, at the region of Borborema, São Paulo State, Brazil. N = number of individuals sampled; AD = absolute density; RD = relative density; AF = absolute frequency; RF = relative frequency; ADo = absolute dominance; RDo = relative dominance; CVI = Crown Value Index; IVI = Importance Value Index.

Species	N	AD	RD	AF	RF	ADo	RDo	CVI	IVI
<i>Solanum mauritianum</i>	58	966.7	26.61	100	12.5	1.65	28.43	55.04	67.54
<i>Solanum paniculatum</i>	73	1216.7	33.49	100	12.5	0.64	10.97	44.46	56.96
<i>Psidium guajava</i>	22	366.7	10.09	100	12.5	1.67	28.67	38.76	51.26
<i>Mabea fistulifera</i>	14	233.3	6.42	33	4.17	0.55	9.54	15.96	20.12
<i>Acrocomia aculeata</i>	5	83.3	2.29	67	8.33	0.11	1.93	4.23	12.56
<i>Senegalia polyphylla</i>	8	133.3	3.67	50	6.25	0.12	02.01	5.68	11.93
<i>Cecropia pachystachya</i>	2	33.3	0.92	33	4.17	0.28	4.81	5.72	9.89
<i>Schinus terebinthifolia</i>	3	50.0	1.38	50	6.25	0.02	0.34	1.71	7.96
<i>Syzygium cumini</i>	5	83.3	2.29	33	4.17	0.07	1.14	3.43	7.60
<i>Enterolobium contortisiliquum</i>	1	16.7	0.46	17	02.08	0.26	4.42	4.88	6.96
Unknown	3	50.0	1.38	33	4.17	0.04	0.63	02.01	6.17
<i>Psychotria carthagenensis</i>	8	133.3	3.67	17	02.08	0.02	0.36	04.03	6.11
<i>Citharexylum myrianthum</i>	1	16.7	0.46	17	02.08	0.20	3.47	3.93	6.01
<i>Guarea guidonia</i>	5	83.3	2.29	17	02.08	0.06	1.11	3.40	5.48
<i>Guazuma ulmifolia</i>	1	16.7	0.46	17	02.08	0.05	0.91	1.37	3.45
<i>Nectandra lanceolata</i>	2	33.3	0.92	17	02.08	0.02	0.36	1.28	3.36
<i>Rhamnidium elaeocarpum</i>	2	33.3	0.92	17	02.08	0.01	0.15	01.07	3.15
<i>Parapiptadenia rigida</i>	1	16.7	0.46	17	02.08	0.02	0.39	0.84	2.93
<i>Psidium cattleianum</i>	1	16.7	0.46	17	02.08	0.01	0.18	0.64	2.73
<i>Trichilia pallida</i>	1	16.7	0.46	17	02.08	0.00	0.08	0.54	2.62
<i>Trema micrantha</i>	1	16.7	0.46	17	02.08	0.00	0.06	0.52	2.60
<i>Albizia niopoides</i>	1	16.7	0.46	17	02.08	0.00	0.04	0.50	2.58

Table 3. Species (trees and shrubs) regenerating in the mixed native Tree Planting (TP), at the region of Borborema, São Paulo State, Brazil. Legend: N = number of individuals sampled; AD = absolute density; RD = relative density; AF = absolute frequency; RF = relative frequency; ADo = absolute dominance; RDo = relative dominance; IVI = Importance Value Index; and CVI = Crown Value Index.

Species	N	AD	RD	AF	RF	ADo	RDo	CVI	IVI
<i>Senegalia polyphylla</i>	176	2933.3	64.9	83	10.87	0.07	18.26	83.21	94.08
<i>Solanum paniculatum</i>	33	550	12.2	50	6.52	0.08	21.09	33.27	39.79
<i>Handroanthus ochraceus</i>	3	50	1.1	33	4.35	0.05	13.48	14.59	18.94
<i>Aloysia virgata</i>	10	166.7	3.7	83	10.87	0.02	4.14	7.83	18.7
<i>Schinus terebinthifolia</i>	3	50	1.1	33	4.35	0.04	11.85	12.95	17.3

Continues...

Table 3. Continued...

Species	N	AD	RD	AF	RF	AD _o	RD _o	CVI	IVI
<i>Mabea fistulifera</i>	7	116.7	2.6	50	6.52	0.02	4.15	6.73	13.26
<i>Croton floribundus</i>	3	50	1.1	50	6.52	0.01	4.01	5.11	11.64
<i>Acrocomia aculeata</i>	3	50	1.1	50	6.52	0.01	2.07	3.18	9.7
<i>Myrtaceae 1</i>	7	116.7	2.6	33	4.35	0.01	1.85	4.44	8.78
<i>Trema micrantha</i>	2	33.3	0.7	33	4.35	0.01	3.23	3.97	8.32
<i>Rhamnidium elaeocarpum</i>	4	66.7	1.5	33	4.35	0.01	1.82	3.29	7.64
<i>Tapirira guianensis</i>	2	33.3	0.7	33	4.35	0.01	1.89	2.63	6.98
<i>Guazuma ulmifolia</i>	1	16.7	0.4	17	2.17	0.02	4.4	4.77	6.94
<i>Erythroxylum pelleterianum</i>	6	100	2.2	17	2.17	0.01	1.93	4.14	6.31
<i>Trichilia pallida</i>	2	33.3	0.7	33	4.35	0	0.91	1.65	5.99
<i>Nectandra lanceolata</i>	2	33.3	0.7	33	4.35	0	0.26	1	5.35
<i>Myrsine umbellata</i>	1	16.7	0.4	17	2.17	0	1.31	1.68	3.85
<i>Astronium graveolens</i>	2	33.3	0.7	17	2.17	0	0.91	1.65	3.82
<i>Cecropia pachystachya</i>	1	16.7	0.4	17	2.17	0	0.91	1.28	3.45
<i>Aegiphila sellowiana</i>	1	16.7	0.4	17	2.17	0	0.91	1.28	3.45
<i>Peltophorum dubium</i>	1	16.7	0.4	17	2.17	0	0.58	0.95	3.12
<i>Psychotria carthagenensis</i>	1	16.7	0.4	17	2.17	0	0.04	0.41	2.58

In both methods of restoration, *A. aculeata*, *Cecropia pachystachya*, *Guazuma ulmifolia*, *M. fistulifera*, *Nectandra lanceolata*, *Psychotria carthagenensis*, *Rhamnidium elaeocarpum*, *S. terebinthifolia*, *S. polyphylla*, and *S. paniculatum* were part of the community of regenerants, representing 37.5% of all

the sampled species (32 species). Among the total number of regenerant species found in each method (ANR = 218; TP = 271), the common species represented 55% (ANR) and 83.3% (TP) of individuals, but they differed in abundance ($T = 2.38$, p -value = 0.03).

Table 4. Parameters of structure, density, and richness of the community of regenerants in areas under restoration using the Assisted Natural Regeneration (ANR) and mixed native species Tree Planting (TP) methodologies, at the age of four years, at the Borborema region, state of São Paulo, Brazil. Implementation and planting were carried out in 2014.

Parameters	Total	(ANR)	(TP)
Abundance (n)	981	613	368
Density (individuals.ha-1)	8,175	10,216	6,133
Shannon-Weaver Index (H')		2.61	2.26
Pielou Equability (J')		0.682	0.622
Sorensen similarity index		0.48	
Sorensen similarity index for species planted in TP		0.08	0.09
Families	24	18	23
Genera	52	37	35
Species	66	44	35
Growth form (richness)			
Tree		19 (45%)	19 (57%)
Shrub		18 (40%)	12 (34%)
Herb		9 (20%)	2 (0.5%)
Vine		2 (5%)	5 (14%)

Continues...

Table 3. Continued...

Parameters	Total	(ANR)	(TP)
Successional group (richness)			
Pioneers		33 (75%)	25 (71%)
Non-pioneers		11 (25%)	12 (34%)
Dispersal syndrome (richness)			
Zoochoric		22 (50%)	20 (57%)
Autochoric		13 (29%)	10 (28%)
Anemochoric		9 (20%)	7 (20%)
Growth form (abundance)			
Tree		134 (33%)	231(71%)
Shrub		423 (69%)	116 (31%)
Herb		34 (5%)	2 (0.5%)
Vine		22 (3%)	19 (5%)
Dispersal syndrome (abundance)			
Zoochoric		269 (43%)	93 (25%)
Autochoric		150 (24%)	249 (67%)
Anemochoric		175 (28%)	22 (5%)
Successional group (abundance)			
Pioneers		509 (83%)	320 (86%)
Non-pioneers		85 (13%)	44 (11%)

Although the ANR treatment had a significantly higher abundance of regenerants than the TP treatment (Table 4, Figure 2), the diversity and the equitability were similar, with a 48% similarity in the floristic composition between the two methodologies. In both restoration methods, trees were the dominant growth form (41%) compared

to shrubs (33%) and other life forms (herbs 17% and vines 9 %), with the abundance of tree growth forms not being different from that of shrubs ($t = 2.3816$, $p\text{-value} = 0.038$), although both were significantly different from the other growth forms (vines and herbs), in both treatments (Figure 3).

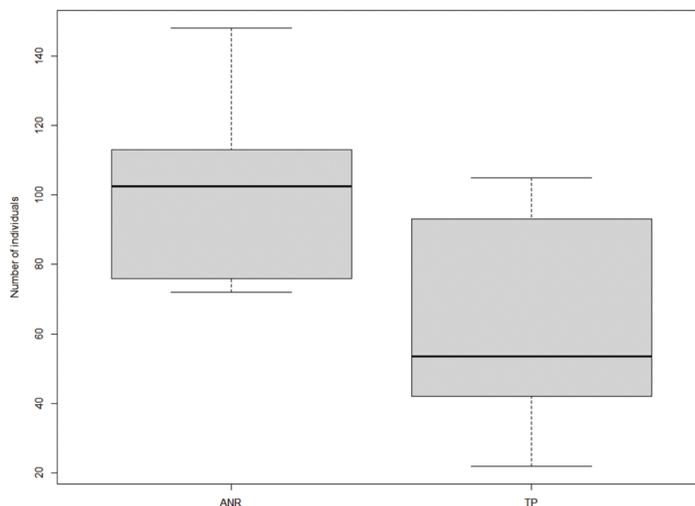


Figure 2. Boxplot of the abundance of regenerants in the two sampled areas, at the Borborema region, state of São Paulo, Brazil. Legend: ANR = number of regenerants in the Assisted Natural Regeneration area and TP = number of regenerants in the mixed native species Tree Planting (TP) area.

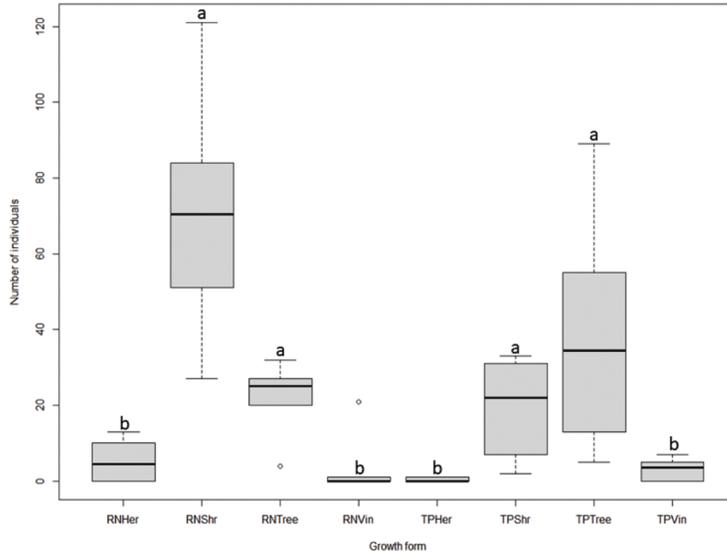


Figure 3. Boxplot of the abundance of regenerants per growth form in the Assisted Natural Regeneration (ANR) and mixed native Tree Planting (TP) methods, at the Borborema region, state of São Paulo, Brazil. Legend: RNTree = number of tree regenerants in the Natural Regeneration Area, RNshr = number of shrub regenerants in the Natural Regeneration Area, RNvin = number of vine regenerants in the Natural Regeneration Area, RNher = number of herbaceous regenerant in the Natural Regeneration Area, TPtree = number of tree regenerants in the mixed native species Tree Planting Area, TPshr = number of shrub regenerants in the mixed native species Tree Planting Area, TPvin = number of vine regenerants in the mixed native species Tree Planting Area, TPher = number of herbaceous regenerant in the mixed native species Tree Planting Area. Letters above boxes indicates statistically significant differences.

The number of individuals with anemochoric and zoochoric dispersion syndromes was significantly different between the two regeneration methods ($H = 17.05$, $p\text{-value} < 0.01$), being more abundant in the RN (Figure 4). Whereas autochory dominated in the TP treatment, the

syndromes did not differ in the ANR treatment. Within each method, the successional groups differed from each other ($H = 18.20$, $p\text{-value} < 0.01$), with pioneers being more abundant in the ANR treatment than in the TP treatment (Figure 5).

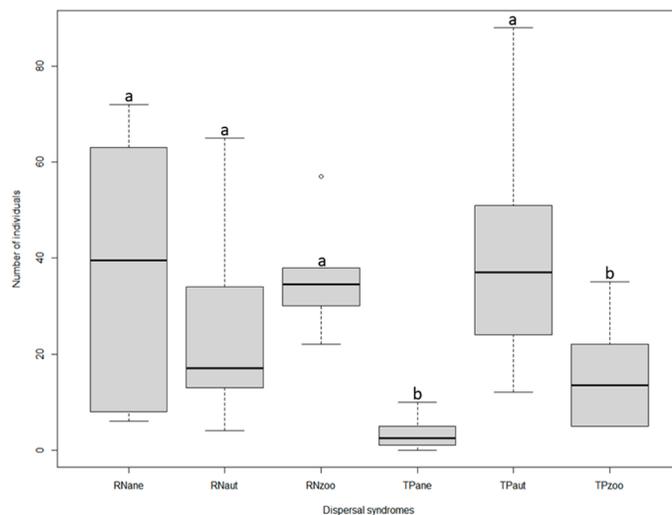


Figure 4. Boxplot of the abundance of regenerants according to their dispersal syndrome in the sampled areas (3A), at the Borborema region, state of São Paulo, Brazil. Legend: RNane = number of regenerants of anemochoric dispersal syndrome in the Natural Regeneration Area, RNzoo = number of regenerants with zoochoric dispersal syndrome in the Natural Regeneration Area, RNaut = number of regenerants with autochorous dispersal syndrome in the Natural Regeneration Area, TPzoo = number of regenerants with zoochoric dispersal syndrome in the mixed native species Tree Planting Area, TPaut = number of regenerants with autochorous dispersal syndrome in the mixed native species Tree Planting Area. Letters above boxes indicates statistically significant differences.

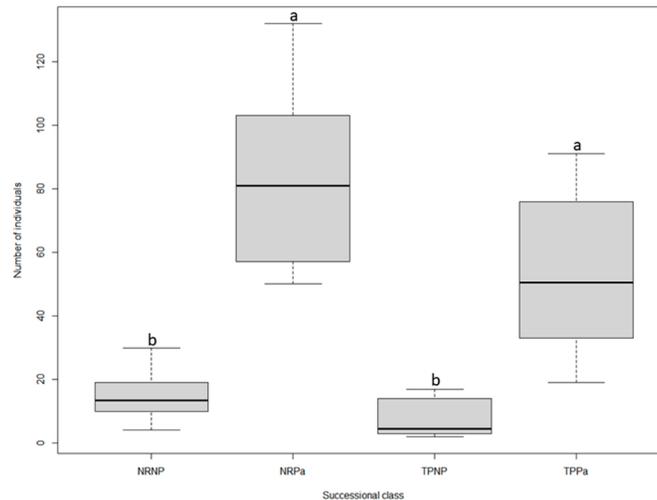


Figure 5. Boxplot of the abundance of regenerants in each successional class at the Borborema region, state of São Paulo, Brazil. Legend: NRPa = abundance of pioneer regenerants in the Natural Regeneration Area, NRNP = abundance of non-pioneer regenerants in the Natural Regeneration Area, TPPa = abundance of pioneer regenerants in the mixed native species Tree Planting Area and TPNP = abundance of non-pioneer regenerants in the mixed native species Tree Planting Area. Letters above boxes indicates statistically significant differences.

4. DISCUSSION

In both restoration methods, the composition, richness, and abundance of families were similar to those found in other areas of natural regeneration and native forests. The families Asteraceae, Malvaceae, Fabaceae, and Solanaceae are frequently found in areas undergoing natural regeneration (Engel & Parrota, 2001; Alvarenga et al., 2006; Bertocine & Rodrigues, 2008; Schorn et al., 2009) and in seasonal forests (Garcia et al., 2011; Sciopini et al., 2013; Fernandes et al., 2018). Previous studies have shown that Asteraceae, Malvaceae, and Solanaceae occur in more open areas and forest gaps associated with environments with high luminosity and under natural regeneration (Bertocine & Rodrigues, 2008; Seubert et al., 2017; Ubert et al., 2018). In the ANR treatment we observed these families among shrubs and pioneer herbaceous species. We observed the same for Fabaceae, which is one of the most abundant families in seasonal forests (Garcia et al., 2011; Sciopini et al., 2013; Fernandes et al., 2018).

Most species were trees, shrubs, and herbs in the two restoration methods and most species richness comes from zoochoric and pioneer species, a typical pattern in areas at an early stage of regeneration (Engel & Parrota, 2001; Bertocine & Rodrigues, 2008). However, the studied areas showed differences in composition, structure, density, growth forms, and dispersal syndromes. The ANR treatment presented a higher density of individuals than the TP treatment, with almost twice as many regenerant species. However, these regenerants were mostly shrubs. Many authors argue that this group of plants arrive at the early stages of succession, when a high amount of pioneer shrub and tree species is found, which are later replaced by other species of more advanced successional

stages (Yarranton & Morrison, 1974; Baylão Junior et al., 2013; Coutinho et al., 2019). We observed that even with a high number of pioneer species in the area, non-pioneer plants are present in the ANR treatment. We believe that this area continues to follow a trajectory of succession, since the landscape scenario revealed the presence of fragments that favor the input of seed rain, contributing to the succession process (Vieira & Scariot, 2006; Prach & Walker, 2019).

In areas restored using the Assisted Natural Regeneration treatment, many species arrive at the place when propagules are brought by biotic or abiotic dispersers (Gorchov et al., 1993; Vieira & Scariot, 2006; Pinã-Rodrigues & Aoki, 2014; Dallabrida et al., 2017). We believe that these dispersers were significant both for the density and richness of the ANR regenerants, because there was a similar input of autochoric, anemochoric, and zoochoric species (Figure 3), despite the predominance of anemochoric herbaceous species of the Asteraceae family.

The similarity of the areas was almost 50% and, probably, one of the factors that affected the composition of species may be the biotic and abiotic dispersal in the ANR treatment, since the surroundings of the area were characterized by pastures and seasonal forest remnants, which may contribute to the flow of propagules (Arenas et al., 2017). In the mixed native species Tree Planting Area, abiotic dispersal may have played a critical role since *S. polyphylla* was very abundant in this area.

The similarity of regenerant species between the restoration sites considering the seedlings planted in the TP area was lower than 10%. This must be related to the fact that the most planted species have not yet started to reproduce. The trees planted in the TP treatment (Additional file 1) were already well established, presenting a canopy, and were contributing to

the ecological processes of the area. However, they were not yet mature, nor were producing seeds. This may explain the fact that the sampled regenerating species must be related to the arrival of propagules from the surrounding areas, as other authors have already shown in their studies (Wurdele jr, 1997; Pinã-Rodrigues & Aoki, 2014; Arenas et al., 2017).

4.1. Phytosociology

The majority of the tree species with the highest Importance Value Index (IVI) in the ANR treatment came from external communities since they are species different from those planted in the TP treatment. The two species that presented the highest Importance Value Index (IVI), *S. mauritianum* and *S. paniculatum*, belong to the Solanaceae family. These species have already been pointed out as pioneer species in forest restoration areas (Ferreira & Vieira, 2017; Seubert et al., 2017). *S. mauritianum* occurred in all sampled plots, which contributed to the observed high IVI, the high relative dominance, and the high frequency of the species. On the other hand, regarding *S. paniculatum*, the high IVI was related to the high density of individuals, with the highest value found in the study area and also due to its relative high frequency. The third most important species in the study area, *P. guajava*, showed large stems and a high relative dominance, being found in all plots with a high frequency. This species is considered to be a pioneer, presenting a zoochoric dispersal syndrome, and being highly appreciated by birds (Coutinho et al., 2019). Also, *M. fistulifera* and *A. aculeata* are among the species with the highest IVI and intermediate values of density, frequency, and relative dominance. However, *M. fistulifera*, which is autochoric, and one of the species found in areas adjacent to the study, is probably introduced in the area by dispersion.

In the TP treatment, the tree species with the highest Importance Value Index were already planted in 2014, except for *S. paniculatum*, which was found in the fragment adjacent to the experiment. The high density, frequency, and relative dominance of *S. polyphylla* contributed to the high IVI of this species, since it had many individuals and regenerants in almost all the plots. *S. polyphylla* is an autochoric pioneer species, widely used in restoration areas due to its high density populations (Durigan et al., 2016). *S. paniculatum* was second in the IVI ranking, since it had a high relative dominance in the area, followed by *H. ochraceus*, *A. virgata*, and *S. terebinthifolia*, which presented intermediate values of density, frequency, and dominance.

The restoration areas already have defined regenerating communities. However, they showed differences in floristic composition, life forms, and similarity, and the planted tree species contributed little to the community of regenerant plants, up to four years after planting.

4.2. Feasibility of restoration methods

The Tree Planting method is more common than the Assisted Natural Regeneration in restoration, despite the economic and environmental potential of the assisted regeneration (Chazdon & Gariguata, 2016), since it is widely known that the success of ecological restoration is higher for natural regeneration (Crouzeilles et al. 2017). Nevertheless, it is still important to design case studies to investigate the role of natural regeneration for tropical restoration (Uriarte & Chazdon, 2016). In our study, the Assisted Natural Regeneration was similar to the assisted Tree Plantation (TP) regarding the floristic composition of regenerants, with a higher number of zoochoric species and individuals, despite the lower abundance of tree species. The restoration trajectory appears to be occurring faster in the ANR treatment. ANR areas presented species that are not commonly produced in forest nurseries, a fact that may increase the richness of restoration projects, providing opportunities for the fauna and for the plant species themselves. Considering the costs of seedling production, transportation, and the maintenance practices carried out in both areas, it is possible to observe that, so far, the ANR technique has been more efficient than the TP treatment in promoting the return of the diversity, structure, and potential attractiveness for the fauna, as well as providing soil cover.

The remnants of natural vegetation surrounding the restoration areas tend to foster the input of seeds and the increase of density of natural regeneration closer to the border of these remnants (Viana et al., 2010). A recent review demonstrated that the landscape configuration drives the recovery of the density and richness of species, depending more on the soil conditions, and especially on the distance and size of the nearest forest remnants than on the richness and density of the planted seedlings (Suganuma et al., 2018). However, the evolution of restoration in seasonal forests depends on the age of the restoration, which is the strongest factor driving most community attributes (Suganuma & Durigan, 2015). Therefore, based on these studies and on our results, we can propose that, for both areas, the succession process still depend on the landscape matrix and on the time elapsed after the beginning of the restoration.

5. CONCLUSION

We concluded that the two restoration methods allowed the regeneration of native plants, forming communities with high numbers of pioneer species. The natural regeneration was a more efficient strategy for the abundance of regenerating individuals and for the variety of dispersion syndromes. The two techniques were able to boost the initial processes of community regeneration in a matrix surrounded by forest remnants.

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SUPPLEMENTARY MATERIAL

The following online material is available for this article:

Additional file 1. List of species planted in 2014 in mixed native tree planting (TP) in the region of Borborema, São Paulo State, Brazil.

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