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Forest regeneration and seed rain in the conversion of a stand of *Pinus* sp. into native forest

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Resumo

Regeneração florestal e chuva de sementes na conversão de um talhão de *Pinus* sp. em floresta nativa. No sul do Brasil, as Florestas Nacionais (NF) são Unidades de Conservação de uso sustentável. Porém, a grande maioria apresenta cobertura significativa de plantações de *Pinus* spp., estabelecidas para promover a silvicultura comercial. Atualmente, seus planos de manejo propõem a conversão de povoamentos de *Pinus* em florestas nativas. *Pinus* spp. são invasoras preocupantes, cujo recrutamento espontâneo é um desafio para a restauração florestal. Este trabalho objetivou analisar a chuva de sementes e a composição da comunidade lenhosa em um estande em que os indivíduos de *Pinus* foram eliminados para conduzir a regeneração natural (REG), em uma NF na Mata Atlântica Meridional. A chuva de sementes foi quantificada na área em restauração (REG) e dentro de um estande adjacente de *Pinus* (PIN). A estrutura da comunidade arbórea foi analisada em REG, PIN e em uma Floresta de Araucária Nativa (NAT). Um ano após o corte do *Pinus*, a chuva de sementes de espécies lenhosas foi de 1.802 e 1.502 sementes m^{-2}.ano^{-1} em REG e PIN, respectivamente. REG apresentou maior diversidade que PIN e não apresentou *Pinus* na chuva de sementes. REG e NAT apresentaram maior diversidade de espécies arbóreas que a PIN, embora a REG tenha apresentado as menores densidade e área basal. No entanto, 188 plantas jovens de *Pinus* sp.ha^{-1} foram observadas na REG, indicando a necessidade de ações complementares de restauração.

Palavras-chave: Floresta Ombrófila Mista; Invasão biológica; Mata Atlântica; Restauração ecológica; Restauração passiva

Abstract

In Southern Brazil, the National Forests (NF) are protected areas of sustainable use; however, most of them present a significant cover with old plantations of *Pinus* spp. established to foster commercial forestry. Nowadays, the NF management plans propose the conversion of *Pinus* stands into native forests. *Pinus* spp. are worrisome

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invasive plants whose spontaneous recruitment is a challenge to forest restoration. This paper aims to analyze seed rain and woody community composition in a stand where *Pinus* trees were eliminated to drive spontaneous regeneration (REG) in an NF in the Southern Atlantic Forest. The seed rain was measured in the restoring area and inside an adjacent *Pinus* stand (PIN). The tree community structure was analyzed comparatively in REG, PIN, and in a Native Araucaria Forest (NAT). One year after *Pinus* cutting, the seed rain of woody species was 1,802 and 1,502 seeds $m^{-2}.year^{-1}$ in REG and PIN, respectively. REG's seed rain had higher diversity than PIN and absence of *Pinus* seeds. REG and NAT presented higher diversity of tree species than PIN, although REG had the lowest basal area and tree density. Nevertheless, 188 *Pinus* $seedlings.ha^{-1}$ were observed in REG, which indicates that complementary restoration actions are needed.

Key words: Atlantic Forest; Biological Invasion; Ecological Restoration; Mixed Ombrophilous Forest; Passive restoration

Introduction

Invasive plants promote the reduction in the abundance and diversity of native plant and animal communities and can critically modify the hydrology and the physical-chemical environment (SIMBERLOFF et al., 2010 and references therein). The magnitude and the direction of these impacts are widely variable, depending on the biological species attributes (VILÀ et al., 2011; RICCIARDI et al., 2013; MOYANO et al., 2020) and community traits (RICHARDSON; PYŠEK, 2006).

In Brazil, *Pinus* species are considered worrisome invasive plants of wide ecological adaptability (BECHARA et al., 2013), occurring spontaneously even in protected areas, generating many impacts on flora, fauna, and biogeochemical processes (BURGUEÑO et al., 2013; ZILLER; DECHOUM, 2013). Pinaceae is one of the ten most invasive plant families globally, and *Pinus* is the genera of wood species with the greatest invasiveness (PYŠEK, 1998; RICHARDSON; REJMÁNEK, 2004). In the Araucaria Forest (officially named Mixed Ombrophilous Forest) of Southern Brazil, *Pinus elliottii* Engelm., *P. glabra* Walter, and *P. taeda* L. are the most invasive plants of the *Pinus* genera (ZENNI; SIMBERLOFF, 2013). The *Pinus* cultivation surpasses 1.5 million hectares in Brazil, with more than 87% in the three southern states: Rio Grande do Sul, Santa Catarina, and Paraná (ASSOCIAÇÃO BRASILEIRA DE PRODUTORES DE FLORESTAS PLANTADAS, 2013).

The National Forest Conservation Units (NF) in Southern Brazil are nowadays classified as Conservation Units of Sustainable Use by Brazilian Law (Federal law 9,985, 2000). Most of them started as experimental areas with non-native (introduced) and native species to stimulate commercial forestry. However, the contribution of the NF to commercial forestry became negligible, and the scope of the NF changed in the last decades contemplating conservation goals and promoting ecosystem services. The four NFs in the state of Santa Catarina encompass 7,216 ha, including the Chapecó National Forest (CNF), which covers 1,591 ha. According to the change in objectives, the Management Plan of the CNF contemplates managing actions such as "… to restore areas back to their natural condition with native forests, in a spontaneous or induced way" (ICMBIO, 2013). Based on that assumption, the conversion of *Pinus* stands to native forests was started with clear-felling and extraction of *Pinus* wood in the last decade.

The CNF is located in the Atlantic Forest in the transition of the Araucaria Forest and Seasonal Forest domains. The Atlantic Forest is a highly reduced and fragmented biodiversity hotspot (RIBEIRO et al., 2009). Due to the considerable reduction and conversion of the forests, ecological restoration has been considered among the most critical initiatives for the conservation and recovery of the native biodiversity in the Atlantic Forest (SCARANO; CEOTTO, 2015).

Ecological restoration methods applied in the Atlantic Forest include seedling planting, nucleation, direct seeding, assisted natural regeneration, as well as mixed methods. Active methods, including direct seeding and seedling planting, are the most popular (BRANCALION et al., 2016; GUERRA et al., 2020). However, the methods that take advantage of spontaneous forest regeneration, where there is a potential for it, are considered more effective for tropical forests (CROUZEILLES et al., 2017; SHIMAMOTO et al., 2018) and can be highly cost-effective for forest restoration in the Atlantic Forest (DE REZENDE et al., 2015).

On the other hand, the presence of non-native invasive species may require eradication or suppression measures (MCGEOCH et al., 2010; PRIOR et al., 2018). Considering the invasiveness of the *Pinus* spp., simply abandoning a fallow after *Pinus* spp production would not achieve satisfactory restoration standards. In sandy coastal ecosystems, clear-felled *Pinus* plantations presented a strong tendency towards the regeneration of *Pinus* species, both in the Southern and Northern hemispheres (STURGESS; ATKINSON, 1993; BECHARA et al., 2013). Based on studies focused on the coastal Atlantic Forest over sandy soils where *Pinus* invasiveness is massive, Bechara et al. (2013; 2014) recommended monitoring *Pinus* recruitment during forest restoration. However, in other ecoregions within the Atlantic Forest, such as the Araucaria Forest and Seasonal Forest, information about *Pinus* recurrence is scarce. The study of Guidini et al. (2014) in the Santa Catarina Araucaria Forest indicates that the invasiveness of *Pinus taeda* L. in the mature forest is low due to its pioneer features, which was confirmed by a long-term survey at the same site; however, the established trees in pioneer communities tend to remain alive (SPIAZZI et al., 2017). Scipioni et al. (2018) also confirmed that the presence of *P. taeda* in an Araucaria Forest remnant is associated with a pioneer community and the neighborhood of a *Pinus* stand. Besides, specimens planted inside the Araucaria forest tend to die under the closed canopy of a mature forest (EMER; FONSECA, 2011).

Our goal was to quantify and compare the seed rain in a stand where *Pinus* was eliminated to drive passive regeneration (REG) and in a remaining *Pinus* plantation stand (PIN). The seed rain in REG can indicate if dispersion is a limitation to spontaneous regeneration and if the *Pinus* seeds originated in the neighboring *Pinus* stands still reached the area. Besides, we aimed to describe the spontaneous regeneration of native-woody species, and to compare the woody community in the early restoration phase (one year after *Pinus* harvesting) in the REG with PIN woody composition, and also with a native mature Araucaria forest (NAT) in the vicinities. Another goal was to quantify *Pinus* species recruitment in the REG site. This information is relevant since there is a possibility that *Pinus* regeneration can threaten native forest regeneration.

This information could support forest management decisions in other *Pinus* plantations to be converted into forests with native species in the Araucaria Forest and Subtropical Seasonal Forest geographic coverage.

Material and Methods

Study area

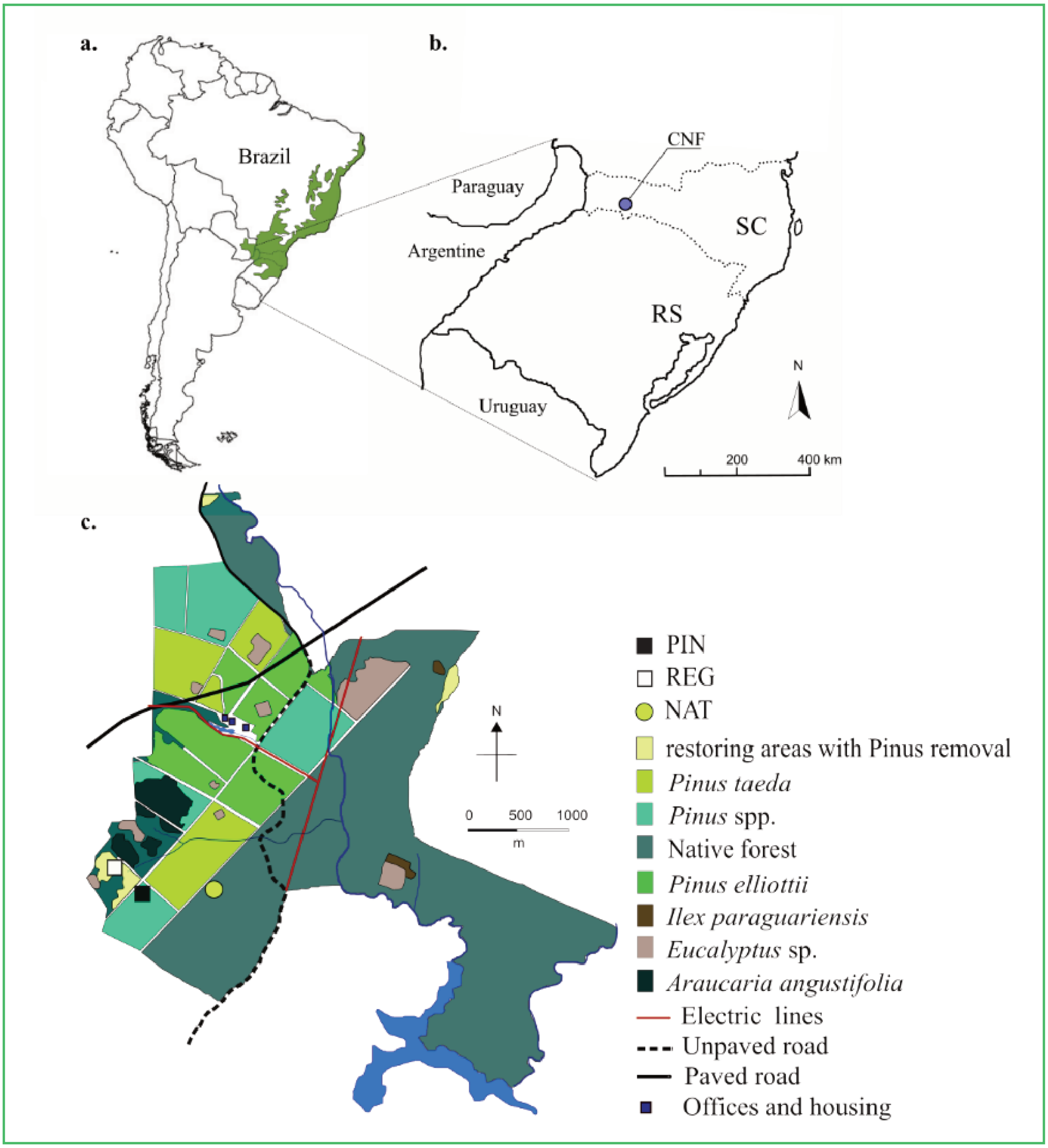
The study site is located in the Chapecó National Forest (CNF), whose headquarters are under the coordinates 27°5’18.54”S and 52°46’49.62”W. The CNF has 1,591 ha. The climate is subtropical, with well-distributed rains during the year and an average temperature of 22°C in the warmest month. The predominant soils are Oxisoils (ICMBIO, 2013).

The native vegetation is Araucaria Forest (Mixed Ombrophilous Forest) in transition to the Seasonal Deciduous Forest (BORDIN et al., 2019), and it reaches 60.7% of the protected area. The *Pinus* stands (*P. taeda* and *P. elliottii*) occupy 26.3% of the area reaching nearly 400 ha and date back to 1962. The thinning of *Pinus* stands started in 1978 and was suspended in 2002 (ICMBIO, 2013).

Our study counted on three sample locations as treatments. First, the area undergoing restoration (REG) with 10.82 ha in the southwest end of the CNF 27°6’4.00”S and 52°47’31.10”W (Figure 1), where the *Pinus* trees were removed. *Pinus* harvesting was carried out starting in 2013 and ending in 2015. Second, an adjacent *Pinus* spp. (mixed *P. taeda* and *P. elliottii*) stand (PIN) without recent (i. e., in the last two decades) managing interventions (27°6’11.66”S and 52°47’21.11”W, Figure 1).

Finally, an area of old-growth native forest (NAT) covered by vegetation in transition from Mixed Ombrophilous Forest (Araucaria Forest) to Seasonal Deciduous Forest without anthropogenic perturbation during the last 55 years was used as a reference for analysis of the woody species community (27°6’18”S and 52°47’05”W, Figure 1).

FIGURE 1: Map of South America displaying the Atlantic Forest in green (a), the Chapecó National Forest (CNF) in the state of Santa Catarina (b), and the CNF vegetation (c). REG = area where the *Pinus* trees were harvested to enhance spontaneous regeneration; PIN = sample location in the *Pinus* spp. (mixed *P. taeda* and *P elliottii*) stand nearest to the REG area; NAT= sample location in the Araucaria Native Forest. Adapted from ICMBIO (2013).



Seed rain

In August 2016 (one year after the end of the *Pinus* harvesting), 12 circular seed traps with 0.48 m of diameter and height of 10 cm above the ground were installed at the REG, and the other 10 seed traps inside the adjacent *Pinus* stand (PIN), with a spacing of 20 m between them. The seed traps corresponded to a total horizontal area of 2.17 and 1.81 m², respectively.

The seeds were gathered at intervals of 29 to 35 days, between September 2016 and August 2017, performing a total of eleven collections in one year. The dates of seed collection during 2016 were September 21, October 26, November 24, December 23; during 2017, they were January 24, February 24, March 31, May 05, June 09, July 14, and August 17. Results are presented as seeds m^{-2} day^{-1} for comparisons.

The seeds were counted and the species were identified according to the literature (LORENZI, 2008; 2009-2016) and by the authors, compared with individuals in the surroundings. The dispersal syndromes were classified according to Van der Pijl (1982). The similarity regarding the composition of the seed rain was calculated with the Morisita index.

Woody community structure

Despite the importance of all plant growth forms for the restoration, the analyses of vegetation were restricted to the woody species, considering the more precise taxonomic knowledge available for this synusia and the possibility of comparison with other studies. The woody synusia was described through 12 contiguous 20 x 25 m plots arranged in two parallel lines of six plots in each vegetation type. Only trees and palms with a diameter at breast height (dbh) ≥ 5 cm were included. The sampled area was 0.6 ha in each stand (REG, PIN, and NAT). The species richness of the woody communities of REG, PIN, and NAT were compared using species accumulation curves performed through the software EstimateS 9.1.0 (COLWELL, 2013). All the data were obtained between September 2016 and May 2017. The scientific names were checked for synonyms and accepted names in the electronic databases "Lista de Espécies da Flora do Brasil" (FLORA DO BRASIL, S. d.) and The Plant List v. 1.1 (THE PLANT LIST, 2020). Family classification followed APG IV (ANGIOSPERM PHYLOGENY GROUP, 2016).

The relative density (RD) of each species was determined according to RD = n_i/AD where n_i is the number of individuals of the species *i* per unit area and AD is the absolute density (number of individuals of all species per unit area). The AD corresponds to the total number of sampled individuals in each vegetation category. The basal area was obtained from each individual's circumference, measured at 20 cm above ground level with a measuring tape.

The diversity in the woody communities was evaluated using the indexes of Shannon (H'), evenness (J), Simpson (D), and the Rényi index profile (RÉNYI, 1961) with the software PAST 3.25 (HAMMER et al. 2001). The Rényi index curve is a method used to compare the different indexes of diversity in a synthetic approach (MELO, 2008). Woody communities were compared using the Morisita index. Unless otherwise stated, *Pinus* spp. was included in the synecological analysis and data presentation.

The communities were compared statistically regarding Basal Area ($m^2.ha^{-1}$) and Density (ind. ha^{-1}), considering each plot as a replication (n=12). Data of basal area were not normally distributed for the three vegetation categories and for the density of individuals from the *Pinus* area (Shapiro-Wilk test [SHAPIRO; WILK, 1965], $P > 0.05$), therefore the vegetation categories were compared with a Kruskal-Wallis test followed by a Mann-Whitney pairwise test.

The successional classification of each species was determined based on the criteria of Coelho et al. (2016), and also consulting Ruschel et al. (2007) and Carvalho (2003-2014). The dispersal syndromes were classified according to Van der Pijl (1982). The proportions of individuals presenting different dispersal syndromes and different successional categories were compared considering the treatments altogether, using the Chi-square model, followed by a Monte Carlo permutation with 9,999 replications. The statistical procedures were executed in the software PAST 3.25 (HAMMER et al. 2001).

In addition, to the data of the woody community structure in the three vegetation categories (REG, PIN, and NAT), the recruits of *Pinus* spp. (seedlings at least 5 cm high) were quantified in REG to verify the regeneration of these non-native species in the restoring area.

Results

Seed rain

In the regeneration area (REG), 3,130 seeds.m^{-2} of 19 species and ten botanic families were found during the entire collection period (one year). No seeds of *Pinus* or other introduced species were observed. In the *Pinus* stand (PIN) 1,608 m^{-2}.year^{-1} seeds from six species (including *Pinus* spp.) and five families were observed. A complete list of species in the seed rain is presented in the supplementary material (Appendix – Table S1). Hereafter, only the data of the woody species will be presented in detail and discussed. In REG and PIN, 57.5% and 93.4 % of the seeds were from woody species, respectively (Table 1). REG presented eight woody species in the seed rain while the PIN presented only two. *Pinus* seeds were 95.6% of the PIN seed rain.

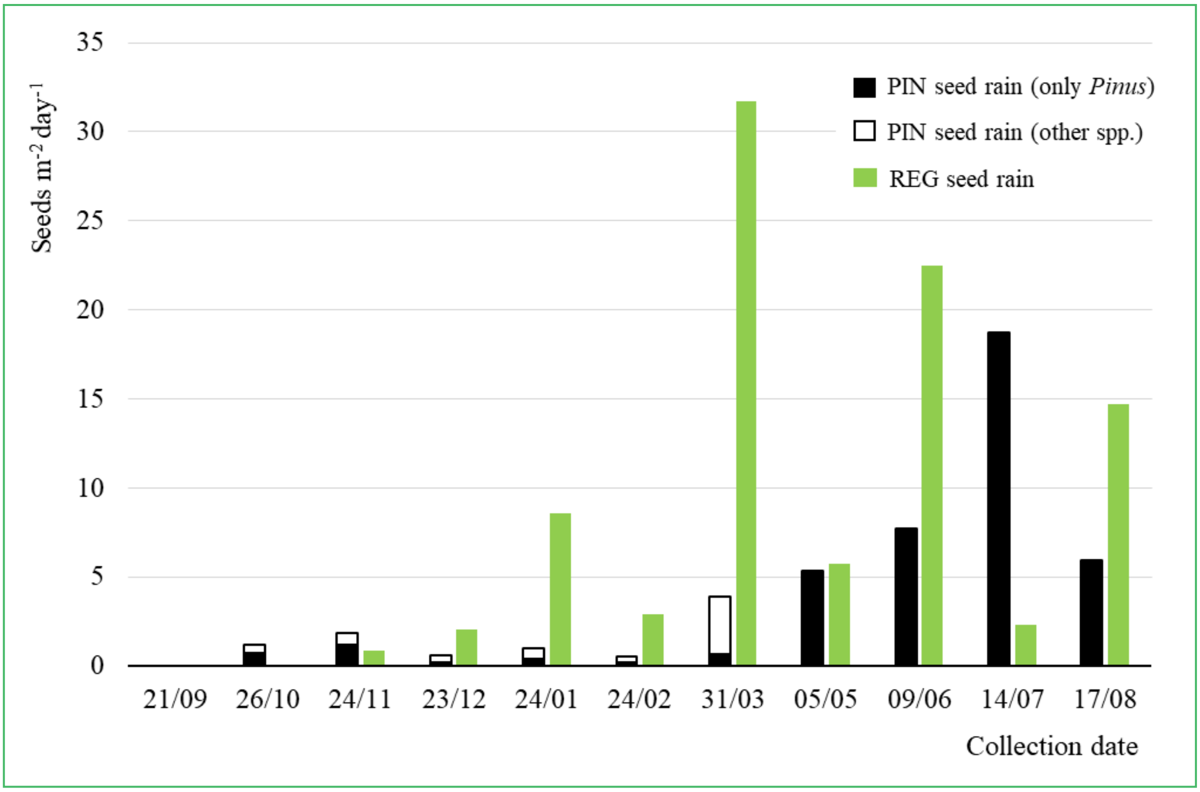
Seeds of the anemochoric *Baccharis dracunculifolia* DC. were 87.0%, and the zoochoric species accounted for 12.3% of the total REG seed rain. Anemochory also dominated seed rain in the PIN area, however it corresponded only to the *Pinus* seeds (Table 1). The amount of the seed rain corresponding to zoochoric species was 221.3 and 66.4 seeds m^{-2}.yr^{-1} in REG and PIN, belonging to six and one species, respectively. The group of zoochoric species was widely dominated by the seeds of *Solanum mauritianum* Scop., which reached 93.7% of the zoochoric seeds in the REG seed rain (Table 1). The Morisita index between the seed rain composition of the two areas was 0.0031.

Seed rain in the REG was heavier between March and August 2017 reaching its maximum in March of that year. In PIN, the peak was in July 2017, widely dominated by the *Pinus* seed rain (Figure 2).

TABLE 1: Seed rain of woody species in the regeneration area (REG) and adjacent *Pinus* stand (PIN), FLONA Chapecó, 2016-2017. * indicates introduced species.

Families and species	**Seeds m^{-2} yr $^{-1}$**		**Dispersion**
	REG	**PIN**	
Asteraceae			
Baccharis dracunculifolia DC.	1,566.8		ANE
Euphorbiaceae			
Manihot grahamii Hook.	13.4		AUT
Lauraceae			
Nectandra megapotamica (Spreng)Mez	0.5		ZOO
Ocotea puberula (Reich.) Ness	0.5		ZOO
Pinaceae			
Pinus spp.*		1,435.3	ANE
Primulaceae			
Myrsine umbellata Mart.	8.8	66.4	ZOO
Salicaceae			
Casearia sylvestris Sw.	3.2		ZOO
Sapindaceae			
Cupania vernalis Camb.	0.9		ZOO
Solanaceae			
Solanum mauritianum Scop.	207.4		ZOO
Total	**1,801.5**	**1,501.7**	

FIGURE 2: Seed rain (seeds m^{-2} day^{-1}) in the area undergoing restoration (assisted natural regeneration) by *Pinus* removal (REG) and within an adjacent *Pinus* stand (PIN), between September 2016 and August 2017 in the Chapecó National Forest (CNF), Brazil.



Tree community

Taken as a whole, the 3 areas presented 74 different tree species, including one not identified. The composition of the communities (REG, PIN, and NAT) are presented in Tables 2-4. Except for *Citrus reticulata*, *Hovenia dulcis*, and *Pinus* sp., all the other species are native of the Araucaria Forest in transition with the Seasonal Deciduous Forest, typical of the region.

TABLE 2: Composition of woody community in the regeneration forest (REG), in abundance order; species, number of individuals (n), relative density (RD), basal area (BA, cm^2), dispersion mechanism (DS) and successional guild (SG). ZOO = zoochoric species, ANEMO = Anemochoric species, P = Pioneer, M = mid-successional, and L = late-successional. * indicates introduced species. The other species are native of the Araucaria Forest in transition with the Seasonal Deciduous Forest.

Species	n	RD	BA	DS	SG
Trema micrantha (L.) Blüme	65	0.298	2,447	ZOO	P
Myrsine umbellata Mart.	18	0.083	8,385	ZOO	M
Tabernaemontana catharinensis DC.	13	0.060	1,537	ZOO	M
Albizia niopoides (Spruce ex Benth.) Burkart	11	0.050	1,100	ANEMO	M
Aegiphila brachiata Vell.	9	0.041	341	ZOO	P
Nectandra lanceolata Nees	9	0.041	450	ZOO	M
Jacaranda micrantha Cham.	9	0.041	636	ANEMO	M
Syagrus romanzoffiana (Cham.) Glasmann	7	0.032	2,168	ZOO	M
Araucaria angustifolia (Bertol.) Kuntze	7	0.032	654	ZOO	P
Solanum mauritianum Scop.	6	0.028	167	ZOO	P
Ilex paraguariensis A. St. Hil.	5	0.023	591	ZOO	L
Casearia decandra Jacquin	5	0.023	504	ZOO	L
Ocotea puberula (Rich.) Nees	5	0.023	135	ZOO	M
Ocotea diospyrifolia (Meisn.) Mez	4	0.018	648	ZOO	L
Strychnos brasiliensis (Spreng.) Mart.	4	0.018	233	ZOO	L
Baccharis dracunculifolia DC.	4	0.018	183	ANEMO	P
Nectandra megapotamica (Spreng) Mez	3	0.014	835	ZOO	M
Casearia sylvestris Sw.	3	0.014	313	ZOO	P
Cupania vernalis Cambess.	3	0.014	228	ZOO	M
Matayba eleagnoides Radlk.	3	0.014	121	ZOO	M
Luehea divaricata Mart.	2	0.009	698	ANEMO	M
Cabralea canjerana (Vell.) Mart.	2	0.009	166	ZOO	L
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	2	0.009	70	ZOO	L
Myrsine coriacea (Sw.) Roem. & Schult.	2	0.009	43	ZOO	P
Allophylus edulis (A. St. Hil. et al.) Niederl.	1	0.005	482	ZOO	M
Balfourodendron riedelianum (Engler) Engler	1	0.005	127	ANEMO	L
Parapiptadenia rigida (Benth.) Brenan	1	0.005	115	ANEMO	M
Diatenopterix sorbifolia Radlk.	1	0.005	87	ANEMO	M
Celtis iguanae (Jacq.) Sarg.	1	0.005	81	ZOO	M
Machaerium stipitatum Vogel	1	0.005	76	ANEMO	M
Erythroxyllum deciduum A. St.-Hil.	1	0.005	72	ZOO	M
Sapium glandulosum (L.) Morong	1	0.005	62	AUTO	P
Cedrela fissilis Vell.	1	0.005	54	ANEMO	M
Muellera campestris (Mart. ex Benth.) Silva & Azevedo	1	0.005	52	ANEMO	M
Machaerium paraguariense Hassler	1	0.005	42	ANEMO	M
Pinus sp. *	1	0.005	41	ANEMO	P
Cordyline spectabilis Kunth & Bouché	1	0.005	32	ZOO	P
Peltophorum dubium (Spreng.) Taubert	1	0.005	32	ANEMO	M
Zanthoxylum rhoifolium Lamarck	1	0.005	26	ZOO	M
Prunus myrtifolia (L.) Urban	1	0.005	20	ZOO	M
Annona neosalicifolia H. Rainer	1	0.005	18	ZOO	M

TABLE 3: Composition of woody community in the *Pinus* stand (PIN), in abundance order; species, number of individuals (n), relative density (RD), basal area (BA, cm^2), dispersion mechanism (DS) and successional guild (SG). ZOO = zoochoric species, ANEMO = Anemochoric species, P = Pioneer, M = mid-successional, and L = late-successional. * indicates introduced species. The other species are native of the Araucaria Forest in transition with the Seasonal Deciduous Forest.

Species	n	RD	BA	DS	SG
Pinus spp. *	150	0.444	156,668	ANEMO	P
Myrsine umbellata Mart.	68	0.201	7,946	ZOO	P
Araucaria angustifolia (Bertol.) Kuntze	27	0.080	1,210	ZOO	P
Ilex paraguariensis A. St.-Hil.	22	0.065	1,102	ZOO	L
Coussarea contracta (Walp.) Müll.Arg.	16	0.047	682	ZOO	L
Nectandra megapotamica (Spreng) Mez	9	0.027	544	ZOO	M
Nectandra lanceolata Nees	7	0.021	13,300	ZOO	M
Prunus myrtifolia (L.) Urban	7	0.021	311	ZOO	M
Jacaranda micrantha Cham.	5	0.015	156	ANEMO	M
Allophylus edulis (A. St. Hil. et al.) Niederl.	4	0.012	114	ZOO	M
Albizia niopoides (Spruce ex Benth.) Burkart	2	0.006	3,183	AUTO	M
Ateleia glazioveana Baill.	2	0.006	88	ANEMO	P
Casearia sylvestris Sw.	2	0.006	3,887	ZOO	P
Cordia americana (L.) Gottschling & J.S.Mill.	2	0.006	133	ANEMO	M
Styrax leprosus Hook. & Arn.	2	0.006	81	ZOO	M
Syagrus romanzoffiana (Cham.) Glasmann	2	0.006	71	ZOO	M
Cedrela fissilis Vell.	1	0.003	804	ANEMO	M
Chrysophyllum gonocarpum (Mart. & Eichler) Engler	1	0.003	731	ZOO	L
Citrus reticulata Blanco *	1	0.003	380	ZOO	M
Hovenia dulcis Thunb. *	1	0.003	380	ZOO	P
Matayba eleagnoides Radlk.	1	0.003	314	ZOO	M
Muellera campestris (Mart. Ex Benth.) Silva & Azevedo	1	0.003	201	AUTO	M
Ocotea diospyrifolia (Meisn.) Mez	1	0.003	177	ZOO	M
Picrasma crenata (Vell.) Engl.	1	0.003	29	ZOO	M
Sapium glandulosum (L.) Morong	1	0.003	16	ZOO	P
Tabernaemontana catharinensis DC.	1	0.003	32	ZOO	P
Urera bacifera (L.) Gaudich. ex Wedd.	1	0.003	63	ZOO	L

TABLE 4: Composition of woody community in old-growth native forest (NAT), in abundance order; species, number of individuals (n), relative density (RD), basal area (BA, cm^2), dispersion mechanism (DS) and successional guild (SG). ZOO = zoochoric species, ANEMO = Anemochoric species, P = Pioneer, M = mid-successional, and L = late-successional. All species are native of the Araucaria Forest in transition with the Seasonal Deciduous Forest.

Species	**n**	**RD**	**BA**	**DS**	**SG**
Coussarea contracta (Walp.) Müll. Arg.	72	0.268	14,284	ZOO	L
Actinostemon concolor Müll. Arg.	45	0.167	2,681	ZOO	L
Araucaria angustifolia (Bertol.) Kuntze	18	0.067	26,678	ZOO	P
Ocotea diospyrifolia (Meisn.) Mez	18	0.067	19,878	ZOO	M
Sorocea bonplandii (Baill.) Burger, Lanj. & Boer	16	0.059	1,106	ZOO	L
Helietta apiculata Benth.	8	0.030	3,049	ANEMO	P
Diatenopterix sorbifolia Radlk.	7	0.026	1,840	ANEMO	M
Psychotria suterella Müll. Arg.	7	0.026	294	ZOO	L
Ruprechtia laxiflora Meisner	6	0.022	2,017	ANEMO	M
Apuleia leiocarpa (Vogel) J. F. Macbr.	5	0.019	4,216	AUTO	M
Cedrela fissilis Vell.	5	0.019	5,669	ANEMO	M
Banara tomentosa Clos.	4	0.015	572	ZOO	M
Chrysophyllum marginatum (Hook. & Arn.) Radlkofer	4	0.015	550	ZOO	L
Cabralea canjerana (Vell.) Mart.	3	0.011	373	ZOO	L
Campomanesia xanthocarpa Berg	3	0.011	160	ZOO	M
Casearia decandra Jacquin	3	0.011	363	ZOO	L
Casearia sylvestris Sw.	3	0.011	792	ZOO	P
Cordia ecalyculata (Vell.) Arrab. & Steud.	3	0.011	144	ZOO	M
Luehea divaricata Mart.	3	0.011	3,759	ANEMO	M
Monteverdia ilicifolia (Mart. ex Reissek) Biral	3	0.011	776	ZOO	L
Nectandra megapotamica (Spreng.) Mez	3	0.011	593	ZOO	M
Parapiptadenia rigida (Benth.) Brenan	3	0.011	2,470	ANEMO	M
Balfourodendron riedelianum (Engler) Engler	2	0.007	443	ANEMO	L
Cordia americana (L.) Gottschling & J. S.Mill.	2	0.007	2,400	ANEMO	M
Myrsine umbellata Mart.	2	0.007	488	ZOO	P
Peltophorum dubium (Spreng.) Taubert	2	0.007	3,892	ANEMO	M
Alchornea triplinervia (Spreng.) Müll.Arg.	1	0.004	14,103	ZOO	M
Annona neosalicifolia H. Rainer	1	0.004	1,134	ZOO	M
Ateleia glazioveana Baill.	1	0.004	1,696	ANEMO	P
Chrysophyllum gonocarpum (Mart. & Eichler) Engler	1	0.004	26	ZOO	L
Cupania vernalis Camb.	1	0,004	3,526	ZOO	M
Sp. 01 (not identified)	1	0.004	7,390		
Eugenia rostrifolia Legrand	1	0.004	284	ZOO	L
Ilex brevicuspis Reissek	1	0.004	201	ZOO	M
Ilex integerrima (Vell.) Loes.	1	0.004	346	ZOO	M
Machaerium paraguariense Hassler	1	0.004	1,320	ANEMO	M
Miconia pusilliflora (DC.) Naudin	1	0.004	698	ZOO	L
Myrcia multiflora (Lam.) DC.	1	0.004	452	ZOO	M
Myrocarpus frondosus Freire Allemão	1	0.004	8,825	ANEMO	M
Myrsine loefgrenii (Mez) Imkhan.	1	0.004	314	ZOO	M
Prunus myrtifolia (L.) Urban	1	0.004	2,734	ZOO	M
Schefflera morototoni (Aubl.) Maguire et al.	1	0.004	491	ZOO	P
Trichilia elegans A. Jussieu	1	0.004	280	ZOO	L
Vernonanthura discolor (Spreng.) H. Rob.	1	0.004	3,117	ANEMO	P
Zanthoxylum petiolare A. St.-Hil. & Tul.	1	0.004	284	ZOO	M

The restoring area (REG) and the old-growth forest (NAT) presented very similar diversity profiles in terms of richness, Shannon and Simpson indexes, and evenness (Table 5). On the other hand, PIN present lower values of diversity considering the same indexes. REG and NAT are also similar regarding the species accumulation curve (Figure 3) and the Rényi diversity profile (Figure 4). In turn, the species accumulation curve and the Rényi profile of PIN indicate a lower diversity. Despite the similar diversity between REG and NAT, REG exhibit the lowest density of individuals (363 ind ha^{-1}), which corresponds to 41% in relation to the density of the individuals in the NAT (Table 5).

Although REG and NAT were similar regarding diversity, the communities were very distinct in composition. Whereas pioneer and mid-successional species dominated REG, late-successional species dominated NAT. Pioneer individuals predominated in PIN (excluding *Pinus* spp.) with 54%, and also in the REG, with 45%. The individuals of mid-successional species reached almost the same value of the pioneer individuals in the REG site (45% and 44% respectively, Table 5). The pioneer individuals were only 13% in NAT, where the late-successional individuals predominated with 59% (Table 5). The proportion of individuals of different successional categories differed significantly between REG, PIN and NAT (considering the treatments altogether), according to the Chi-square test (Monte Carlo *P* = 0.0001),

A higher basal area was observed in PIN (41.2 m^2.ha^{-1}) with a lower value in REG (2,8 m^2.ha^{-1}) and an intermediate value for NAT (24,5 m^2.ha^{-1}) (Table 5).

FIGURE 3: Species accumulation curves in restoring area (REG), Pinus stand (PIN), and native forest (NAT). The vertical bars indicate the standard error.

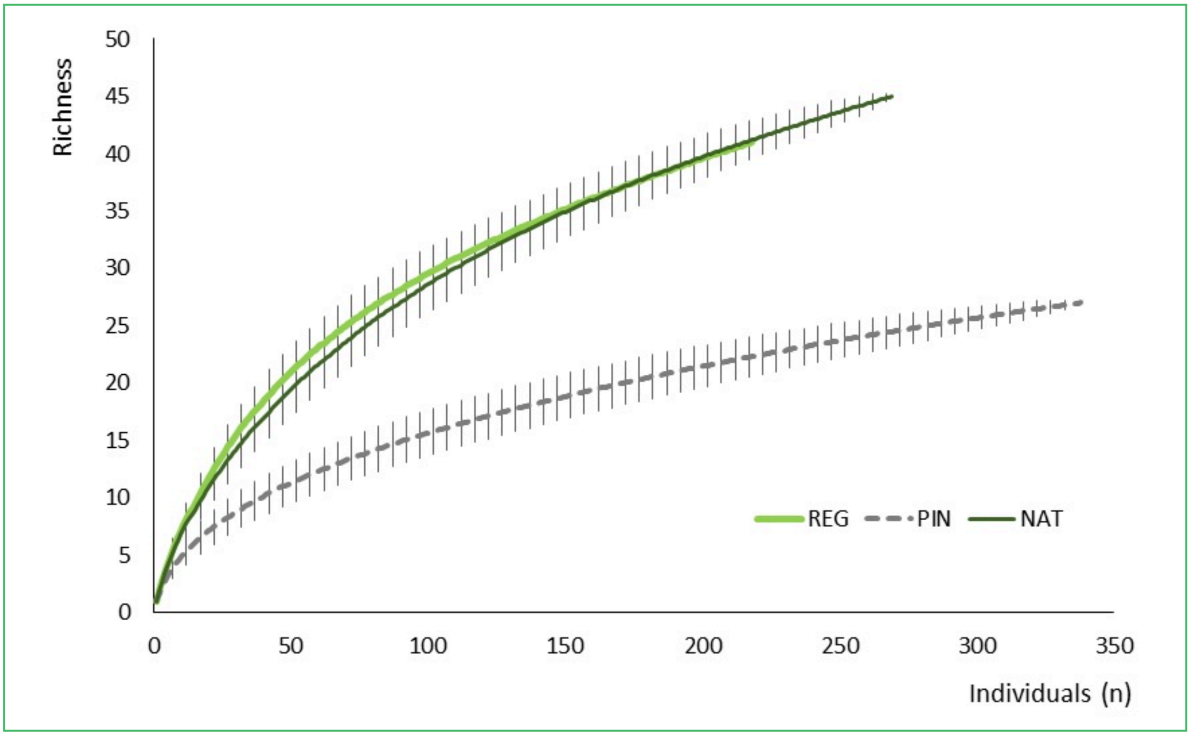


FIGURE 4: Rényi profile of diversity for the three vegetation categories: regenerating area (REG), native forest (NAT), and the stand of *Pinus* spp. (PIN).

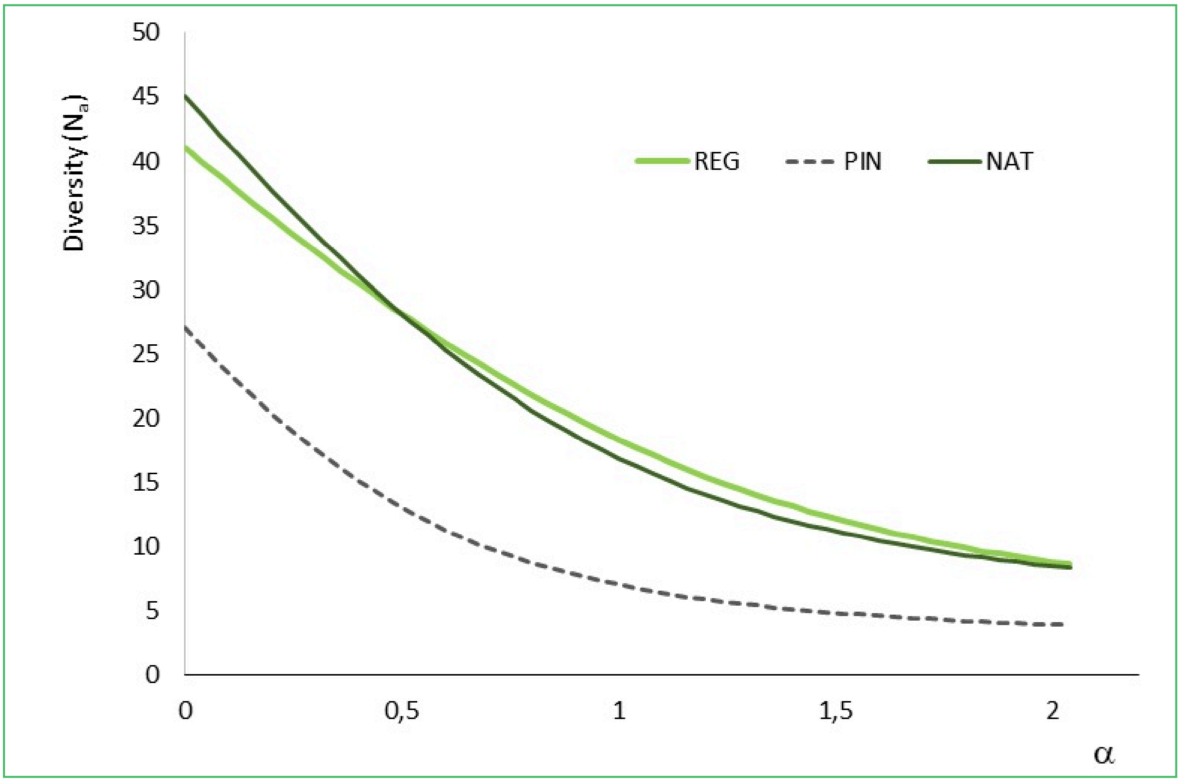


TABLE 5: Tree community in the restoring area (REG), in the *Pinus* spp. stand (PIN), and in the old-growth native Araucaria forest (NAT). All data were recorded in samples of 0.6 ha and including trees with dbh ≥ 5.0 cm. Values inside parentheses in the PIN column were calculated excluding *Pinus* spp. individuals. The communities were compared regarding Basal Area ($m^2.ha^{-1}$) and Density (ind./ha) with the Kruskal-Wallis test and different letters indicate significant differences in the Mann-Whitney pairwise test ($P < 0.01$).

	REG	PIN	NAT
Richness	41	27	45
Shannon index	2.91	1.95	2.83
Simpson index (1/D)	0,89	0,75	0,88
Evenness	0.78	0.59	0.74
Density (ind./ha)	363 ± 357 a	883 ± 209 b	870 ± 204 b
Pinus spp. Individuals	1	250	0
Basal area ($m^2.ha^{-1}$)	2.75 ± 2.65 a	41.23 ± 10.72 c	24.45 ± 7.63 b
Pinus spp. basal area ($m^2.ha^{-1}$)	0.007	18.46	0
Zoochoric individuals (%)	88.5	51.8 (93.1)	82.4
Anemochoric individuals (%)	11.0	47.3 (5.3)	15.7
Autochoric individuals (%)	0.5	0.9 (1.6)	1.9
Pioneer individuals (%)	45.4	74.6 (54.2)	12.7
Secondary individuals (%)	44.0	13.6 (24.5)	28.0
Late-successional individuals (%)	10.6	11.8 (21.3)	59.3
Dominant species*	*Trema micranta* *Myrsine umbellata* *Tabernaemontana catharinensis* *Albizia niopoides*	*Myrsine umbellata* *Araucaria angustifolia* *Ilex paraguariensis* *Coussarea contracta*	*Coussarea contracta* *Actinostemon concolor* *Araucaria angustifolia* *Ocotea diospyrifolia*

* Dominant species did not include the *Pinus* individuals.

The zoochory predominates in all vegetations, with 93% of the individuals in PIN (excluding *Pinus* spp.), 89% for the REG, and 82% for the NAT. Anemochoric individuals were 5%, 11% and 16%, respectively (Table 5). The proportion of the different dispersal syndromes in the areas differed significantly in the Chi-square test (Monte Carlo $P = 0.0051$).

Besides the individual of *Pinus* sp. detected in REG in the upper strata (Table 2), 112 recruits (dbh < 5.0 cm) of *Pinus* sp. were recorded, representing 187 recruits ha^{-1} (Table 3).

The REG community assemblage presented a higher similarity with the PIN assemblage (Morisita index of 0.140) than with NAT (Morisita index of 0.046). The former areas also have the presence of *M. umbellata* among the four dominant species (Table 5) in common. The Morisita index between PIN and NAT was 0.110.

Discussion

The seed rain recorded in REG (8.58 seeds m^{-2}.day^{-1}) is among the highest records for the Araucaria Forest, where seed rain intensity ranges between 0.2-12.16 seeds m^{-2}.day^{-1} (MIKICH; POSSETTE, 2007; TRES; REIS, 2009a; DOS SANTOS et al., 2011). The value could also be considered high compared with the value of 1.72 seeds m^{-2}.day^{-1} observed by Barbosa and Pizo (2006) in a galley forest within the Seasonal Semideciduous Forest domain, eight years after restoration began. Notwithstanding, REG is a regenerating area at a very early stage, making it difficult to compare with other studies. Besides, all the zoochoric species in the seed rain of REG are small-seeded, according to the criteria of Costa et al. (2012), that is, measuring less than 15 mm. In addition, all of them are already present in the woody sinusya. Therefore, evidence that the seed rain can aggregate diversity in this regeneration stage is lacking, suggesting seed rain limitation. Such seed limitation could be a widespread phenomenon in tropical forests, especially regarding the large-seeds species, even when a higher forest cover in the vicinities as source propagules is available (DALLING et al., 2002; COSTA et al., 2012).

The anemochoric dispersion predominated in the seed rain of REG. However, it was represented by only one species (*B. dracunculifolia*). As a general rule, zoochoric dispersion dominates the seed rain of woody species in the Atlantic Forest (TOMAZI et al., 2010; DOS SANTOS et al., 2011; COSTA et al., 2012). Nevertheless, in a restoration context, the anemochory can predominate (BARBOSA; PIZO, 2006).

The absence of seeds of other anemochoric species also suggests seed limitation; however, the influence of this limitation in the future of the restored forest remains an open question. It should be stressed that the individuals of anemochoric species in the woody strata of REG were only 11%, which could be considered low values for the non-riparian forests in the Southern Atlantic Forest. NAT presented almost 16% of anemochoric individuals. In mature forests of the region, Ruschel et al. (2007) and Benvenuti-Ferreira and Coelho (2009) recorded respectively 19 and 41% of anemochoric individuals. In turn, Maçaneiro et al. (2018) recorded 27% of anemochoric trees in the upper layer and 24% in the lower layer in an Araucaria Forest in the state of Santa Catarina. The anemochoric species tend to be the tallest trees in dense forests, facilitating seed dispersion (HORN et al., 2001; GIEHL et al., 2007). Besides, they represent the predominant fraction of basal area in the hinterland forests of Southern Brazil (e. g., RUSCHEL et al., 2007; BENVENUTI-FERREIRA; COELHO, 2009), and therefore have a crucial contribution to the structure of the forest.

The absence of *Pinus* in the seed rain of REG suggests that the *Pinus* recruits (and the one individual with dbh ≥ 5.0 cm) were more probably originated from the seed bank or remnant juvenile individuals that survived *Pinus* cutting and harvesting. Although the seeds of *P. taeda* can surpass 11 km when dispersed, most released seeds are susceptible to local neighborhood dispersion in distances ranging from 5 to 140 m (WILLIAMS et al., 2006). However, Jankovski (1985), in a test to check dispersion capacity, had obtained only 3.7% of the total amount of *Pinus* seeds from a *P. taeda* stand in seed traps 55-60 m apart. Cooper (1957) reported that more than 90% of the *P. elliottii* seeds fall within 45 m from the seed source. Therefore, the distance between REG and the source of *Pinus* seeds (at least 250 m) could explain why *Pinus* seeds were not detected in the seed rain of the REG.

The seed rain of *Pinus* spp. exhibited a peak between May and August. The viability of the seeds of *P. elliottii* in the seed bank fall under 2% after 180 days (BECHARA et al., 2013). Seeds of *Pinus taeda* L. retain viability for a few months, and few seeds remain viable (not more than 0.1 percent) in the second year after seed fall (LITTLE; SOMES, 1959; BAKER; LANGDON, 1990). The retention of the viability of *Pinus* seeds in Brazilian sites requires additional studies. Nevertheless, *Pinus* clearing and extraction could be executed outside the *Pinus* seed crop peak, opening an alternative for the management to forest conversion. Further studies considering the seed bank of *Pinus* stands can contribute to the improvement of these methods.

The zoochoric dispersion group was predominant in the woody communities studied here, with proportion above 82%. Zoochory is typically dominant in the woody communities of forests in the austral Atlantic Forest, with proportions ranging between 55 and 90% of the tree individuals (RUSCHEL et al., 2007; BENVENUTI-FERREIRA; COELHO, 2009; DUARTE et al., 2009). The result corroborates the importance assigned to the zoochory in the forest succession and ecological restoration in the Southern Atlantic Forest (TRES; REIS, 2009b; DOS SANTOS et al., 2011).

As expected, the predominance of pioneer species in REG is coherent with an early phase of secondary succession. However, the presence of the late-successional species in the tree synusia in REG (10.6% of relative density) is noteworthy, which probably includes native individuals that survived *Pinus* cutting and harvesting, since that proportion is very similar to that of the community in the *Pinus* stand (11.8%). The presence of late-successional species only one year after *Pinus* harvesting can contribute to the effective recovery of the tree community in the long term. The tree community in the mature forest or advanced successional stages in the South Atlantic Forest usually present dominance of late-successional species, at least concerning relative density (RUSCHEL et al., 2007; BENVENUTI-FERREIRA; COELHO, 2009), which was confirmed by our data from the old-growth forest (NAT). Moreover, the individuals of mid-successional species also exhibit an expressive value (44%) in REG, which can contribute to secondary succession. As pioneer individuals die, mid-successional species can replace them in the canopy, while the forest grows and slowly acquires late-successional species.

One year after the conclusion of *Pinus* harvesting, the spontaneous regeneration could be considered satisfactory, presenting a higher diversity compared to the PIN stand. Species diversity of natural regeneration in REG reached values close to the undisturbed native forest, besides the community composition differences, which presented more similarity with the *Pinus* stand community. However, this may be a consequence of the initial stage of succession in REG and the predominance of typical species from the early stages of ecological succession. Continued monitoring can be a relevant contribution to know the successional potential in this context.

The high density of recruiting *Pinus* sp. plants in the restoration site is equivalent to 75% of the *Pinus* adult trees in the stand plantation. Although the survival potential of these individuals is unknown, the finding indicates the necessity of complementary actions of control to avoid its reestablishment. Bechara et al. (2013) observed massive recruitment in the *P. elliottii* after harvesting an adult pine stand in a coastal sandy plain in Southern Brazil, attaining 27 plants m^{-2} after 2.5 years. However, the mortality rate was also high, reaching 70% after 2.5 years. On the other hand, Spiazza et al. (2017) observed 100% survival for *P. taeda* (dbh $\geq$ 5 cm) after four years in a Mixed Ombrophilous Forest in an advanced successional stage. This suggests a higher survival potential of the *P. taeda* individuals, once established. Besides, future natural gap openings in the secondary forest (as the pioneer species die) can offer opportunities for *Pinus* recruitment (SPIAZZA et al., 2017). Therefore, the recruiting *Pinus* sp. plants in REG deserves attention.

The analyses carried out suggest that spontaneous regeneration can potentially replace the Araucaria Forest from *Pinus* plantations without neglecting actions to control *Pinus* recruiting individuals.

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APPENDIX

TABLE S1: Species in the seed rain (seed m^{-2}); with respective Dispersion Syndrome (DS); between September 2016 and August 2017 (365 days); in the restoration site (REG) and in the *Pinus* stand (PIN); Chapecó National Forest; Brazil. * non-native species; ANE = anemochoric; AUT = autochoric e ZOO = zoochoric species.

Families and species	**REG**	**PIN**	**DS**
Asteraceae			
Baccharis dracunculifolia DC.	1,566.8		ANE
Mikania cordifolia (L.f.) Willd.	88.5		ANE
Senecio brasiliensis (Spreng.) Less.	22.6		ANE
Asteraceae 1	9.2		ANE
Asteraceae 2	131.8		ANE
Euphorbiaceae			
Manihot grahamii Hook.	13.4		AUT
Fabaceae			
Senegalia recurva (Benth.) Seigler & Ebinger	1.4		ANE
Lauraceae			
Nectandra megapotamica (Spreng) Mez	0.5		ZOO
Ocotea puberula (Reich.) Ness	0.5		ZOO
Melastomataceae			
Leandra australis (Cham.) Cogn.		92.9	ZOO
Pinaceae			
Pinus spp.*		1,435.3	ANE
Poaceae			
Poaceae 1	626.7	12.7	AUT
Primulaceae			
Myrsine umbellata Mart.	8.8	66.4	ZOO
Rosaceae			
Rubus brasiliensis Mart.	43.8		ZOO
Rubus erythrocladus Mart. ex Hook. F.	250.2		ZOO
Salicaceae			
Casearia sylvestris Sw.	3.2		ZOO
Sapindaceae			
Cupania vernalis Camb.	0.9		ZOO
Solanaceae			
Solanum sp.		0.6	ZOO
Solanum mauritianum Scop.	207.4		ZOO
Solanum variabile Mart.	152.1	0.6	ZOO
Undetermined families			
Morphospecies 1	0.5		
Morphospecies 2	1.8		
Total seeds.m^{-2}	**3,130.0**	**1,608.4**	
Number of botanical families	**10**	**5**	
Total species	**19**	**6**	