

Species diversity in the soil seed bank is higher for young forests than for mature forests in the Subtropical Atlantic Forest

La diversidad de especies en el banco de semillas del suelo es mayor para los bosques jóvenes que para los bosques maduros en el Bosque Atlántico Subtropical

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SUMMARY

Species diversity can contribute to the resilience of the ecosystem and can be assessed through the soil seed bank (SSB). SSB is an indicator of forest development after the occurrence of disturbances. Thus, this study aimed at evaluating the relation of the soil fertility with the soil seed bank and the variation of seed bank species diversity at distinct successional stages after abandonment of pasture (25, 35, 45 and > 50 years). Ten samples of soil were collected per site, being distributed in trays and arranged in a greenhouse for a germination analysis. Results indicate that species diversity in SSB is higher in young forests than in mature forests. In addition, soil characteristics are different among successional stages, in which the young forests are associated with higher availability of nutrients. Finally, forests in early stages have higher potential for recovery of degraded areas in relation to the forest seed bank in advanced stages.

Key words: successional stage, fertility, species richness, disturbance.

RESUMEN

La diversidad de especies puede contribuir a la resiliencia del ecosistema y puede evaluarse a través del banco de semillas del suelo (SSB). El SSB es un indicador del desarrollo forestal después de la ocurrencia de disturbios. Por lo tanto, este estudio tuvo como objetivo evaluar la relación de la fertilidad del suelo con el banco de semillas del suelo y la variación de la diversidad de especies en distintas etapas sucesionales después del abandono del pasto (25, 35, 45 y > 50 años). Se recogieron diez muestras de suelo por sitio, se distribuyeron en bandejas y se dispusieron en invernadero para el análisis de germinación. Los resultados indican que la diversidad de especies en el SSB es mayor en los bosques jóvenes que en los bosques maduros. Además, las características del suelo son diferentes entre las etapas sucesionales, los bosques jóvenes están asociados con una mayor disponibilidad de nutrientes. Finalmente, los bosques en etapas tempranas tienen un mayor potencial para la recuperación de áreas degradadas en relación con el banco de semillas forestales en etapas avanzadas.

Palabras clave: etapa sucesional, fertilidad, riqueza de especies, perturbación.

INTRODUCTION

Biodiversity is generally related to species diversity, which can be characterized by species richness (Melo 2008) associated with their density. It is a simple and effective method for determination of disturbance patterns in tropical forests (Melo 2008, Gibson *et al.* 2011). Thus, the quality of species diversity in a community can interfere with the ecosystem resilience (Chami *et al.* 2011) and have a fundamental role to define the conservation stage of forest remnants (Maçaneiro *et al.* 2016).

Tropical forests account for more than 50 % of global biodiversity, and ecological changes, such as deforestation,

fragmentation or environmental disturbances (as harvesting, pasture and fire), can affect the regeneration potential of these forests (Wilson *et al.* 2016) and, consequently, biological diversity. In secondary forests, with occurrence of constant disturbances, there is a decrease in diversity and, consequently, the richness of species is affected (Gibson *et al.* 2011). According to Chazdon (2014), secondary forests have gradually expanded around the world, representing the largest proportion in tropical forests, although little is known about the effects of disturbances on these remnants and at different successional stages (Goosem *et al.* 2016). Therefore, secondary forests should be prioritized for conservation, as they are the ones that complement

primary forests in the provision of ecosystem services, in addition to being beneficial to tropical forest biota (Gibson *et al.* 2011). In this sense, studies indicate that the BBS in young forests has less species richness when compared to intermediate stages and mature forests, that is, diversity generally increases with the age of the forests (Dullius *et al.* 2016, Goosem *et al.* 2016). In contrast, studies developed by Liebsch *et al.* (2008) and Zanini *et al.* (2014) indicate that mature forests have higher floristic richness.

One way to quantify the diversity of tropical forest species is through the soil seed bank (Chami *et al.* 2011), in which it is possible to understand the dynamics of vegetation and define strategies to accelerate the process of ecological succession (Scott *et al.* 2010). The seed bank often leads vegetation from early stages to advanced stages, after the occurrence of disturbances (Cho *et al.* 2018). Some studies have associated the soil seed bank as an indicator of vegetation development after disturbances (Cho *et al.* 2018). According to Yassir *et al.* (2010), disturbances affect the successional trajectory of forests, and consequently the floristic composition, increasing the number of shrubs, grasses and ferns, and became benefic for the colonization of exotic plants (Tng *et al.* 2015). For example, Bossuyt and Honnay (2008) point out that the occurrence of grasses in early stages is natural. Likewise, in mature forests, the absence of this group of plants occurs mainly due to the decrease in luminosity within the forest (Koncz *et al.* 2011).

In this same sense, the capability of the regeneration in the area is associated through soil fertility (Silva *et al.* 2012). Studies indicate that the level of disturbance and soil fertility will have an influence in the diversity of the environment (Carmona 1995, Silva *et al.* 2012). When soil fertility is low, the seed bank is mostly colonized by exotic plants and species richness decreases (Carmona 1995).

To contribute to the knowledge about the variation in the species diversity in SSB, this research aimed at answering the following questions: a) is species diversity in the soil seed bank higher in mature forests than in young forests? b) are soil fertility and soil seed bank in forests associated in distinct successional stages? For this, we expect to find higher diversity of species in mature forests, since recent studies have pointed out that the soil seed bank varies depending on the successional stage and the time of abandonment of the areas. We also hope to find higher density and species richness in the seed bank with higher levels of fertility.

METHODS

Study area. This project was carried out in the city of Blumenau, Santa Catarina, Southern Brazil. According to the Köppen classification, the climate is humid subtropical mesothermal with warm summers and no dry season. Annual mean temperature fluctuates between 18 °C and 22 °C, annual mean precipitation from 1,400 to 1,800 mm well distributed during the year and relative humidity between 75 and 80 % (Alvares *et al.* 2013).

The region has irregular terrain, characterized by hills in the south and valleys in the north. Average altitude is 21 m a.s.l. The city is located in the watershed of the Itajaí river, within the sub-basin of the Itajaí-açu river. The soil is characterized as Red-Yellow Argisols (Brazilian soil classification).

The vegetation in the study site correspond to the phytoecological region of the Tropical Rain Forest. The study area was previously occupied by pastures, which were abandoned in different periods, and currently has native vegetation in different successional stages: S1 = 25 years (initial stage), S2 = 35 years (intermediate stage), S3 = 45 years (late-successional stage) and S4 > 50 years (old-growth forest), respectively. The study area is located in a remnant in urban environment, with low connectivity with other areas covered with forests. In the south area of these sites, there is a native forest, and in the other locations there is urbanization.

Data collection. The soil samples with potential seeds were collected in four sites, within different regeneration ages after abandonment. In each site, ten samples of soil within a 1.40 m² area were randomly collected (n = 40, total area = 56.00 m²). Plant litter and soil were collected at 15 cm depth with a shovel. The soil samples were collected in August 2017 (winter) and stored in plastic bags, tagged and transported to the tree nursery at the Regional University of Blumenau (FURB). For the germination experiment, the samples were located into forty plastic trays (60 cm x 40 cm x 10 cm), organized in seedbeds and in a greenhouse. As control measure, we organized three plastic trays containing substrate only.

The evaluation of germination capacity was conducted weekly per 6 months to obtain the number of germinated seeds (total and per species). The germinating species were identified and then grouped into families, life forms and origin (native or exotic). After identification, they were removed from the trays. The unidentified germinated seeds were replanted in polyethylene bags with substrate.

To obtain the chemical properties of the soil, in each site ten soil samples were collected at 0-20 cm depth. Afterwards, we stored the samples in plastic bags and sent them to the Laboratory of Soil Analysis of EPAGRI (*Empresa de Pesquisa Agropecuária e Extensão Rural de Santa Catarina*) to obtain the following chemical variables: clay content (m/v - %), pH, phosphorus (P - mg/dm³), potassium (K - mg/dm³), organic matter (%), aluminum (Al - cmolc/dm³), calcium (Ca - cmolc/dm³), magnesium (Mg - cmolc/dm³), SMP index and potential acidity (H+Al - cmolc/dm³) and cation exchange (CTC - cmolc/dm³), aluminum saturation (CEC Al - %), base saturation (CEC V - %) and base sum (S) were calculated.

Data analyses. The density of seeds germinated in SSB was calculated for all sampled plots. The differences in seed density according successional stages were tested

using ANOVA, with Tukey - Kramer *post-hoc* tests at the significance level $\alpha = 5\%$. The assumptions of normality were met according to Zar (2010).

To compare the species richness of SSB among sites, rarefaction curves using the Mao Tau method were constructed, using the number of seeds germinated per species. After, we generalized the comparisons among species richness, Shannon index (H' , napierian logarithm) and Simpson index ($1/D$), using diversity profiles from the Rényi Series. In this analysis, we converted the H' and $1/D$ index into the effective number of species following the recommendations of Jost (2006), since this conversion gives them a set of common and easily interpretable behaviors and properties. After this conversion, diversity is always measured in units of number of species, regardless of the index used.

The relationship among the species composition from the SSB with chemical characteristics of the soil were analyzed through principal coordinate analysis - PCoA (Legendre and Legendre 2012). Matrices of abundance of germinated individuals and the Bray-Curtis distance were

used. The significance of the PCoA was tested using Monte Carlo tests, with 999 permutations. Finally, the floristic similarity among groups and the statistical significance of the groups ordered by PCoA were tested through ANOSIM, using the abundance matrices and the Bray-Curtis distance (Legendre and Legendre 2012).

RESULTS

In total, 2,916 individuals were collected, within 51 species and 27 botanical families (table 1). The most representative life forms were herbs (43.1 %) and trees (33.3 %), and the least representative were shrubs (17.6 %), climbers (3.9 %) and bamboo (2 %).

The origin of the species present in BSS is predominantly native to the region. Three species (5.9 %) were found to be exotic in the region, one herbaceous, one shrub and one tree. The three exotic species represented 0.7 % of the germinated individuals and were mostly present in S1 (table 2).

Table 1. Species and number of seeds in the soil seed bank in four successional stages of the Atlantic Forest in southern Brazil. S1 = 25-yr-old recovery site (initial stage), S2 = 35-yr-old (intermediate stage), S3 = 45-yr-old (late-successional stage), and S4 = 50-yr-old (old-growth forest); Ex = exotic species, Na = native species, Te = Tree, Sh = Shrub, He = Herb, Cl = Climber, Ba = Bamboo. Values per 56.00 m².

Parámetros del suelo de las cuatro etapas sucesionales de la Selva Atlántica en el sur de Brasil. S1 = sitio de recuperación de 25 años (etapa inicial), S2 = 35 años (etapa intermedia), S3 = 45 años (etapa de sucesión tardía) y S4 = 50 años (bosque maduro).

Family	Species	Study site				Life Form
		S1	S2	S3	S4	
Apiaceae	<i>Centella asiatica</i> (L.) Urb.	18				He
Asteraceae	<i>Erechtites valerianifolius</i> (Wolf) DC.	3	4	1	4	He
	<i>Piptocarpha axillaris</i> (Less.) Baker			13	3	Te
	<i>Pterocaulon</i> sp.			1	1	He
Bignoniaceae	<i>Jacaranda micrantha</i> Cham				3	Te
Cannabaceae	<i>Trema micrantha</i> (L.) Blume	7	15	11	46	Te
Commelinaceae	Not identified		4	16		He
Cyperaceae	<i>Conyza bonariensis</i> (L.) Cronquist		1		2	Sh
	<i>Cyperus hermaphroditus</i> (Jacq.) Standl.	15	1	1		He
	<i>Fimbristylis complanata</i> (Retz.) Link	151			4	He
	<i>Fimbristylis dichotoma</i> (L.) Vahl	12			4	He
	<i>Rhynchospora nervosa</i> (Vahl) Boeckler	185	16		3	He
	<i>Scleria distans</i> Poir.	47			4	He
	<i>Scleria gaertneri</i> Raddi	17	23			He
	<i>Scleria panicoides</i> Kunth.		1			He
Dilleniaceae	<i>Davilla rugosa</i> Poir.		2	3		Sh

Table 1. Continue

Table 1. Continued

Erythroxylaceae	<i>Erythroxylum umbu</i> Costa-Lima	4				Te
Euphorbiaceae	<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	1		3	4	Te
	<i>Tetrorchidium rubrivenium</i> Poepp.				1	Te
Fabaceae	<i>Mimosa bimucronata</i> (DC.) Kuntze	4	1			Te
Hypoxidaceae	<i>Hypoxis decumbens</i> (L.)	22	27	2		He
Liderniaceae	<i>Lindernia diffusa</i> (L.) Wettst	159				He
Lygodiaceae	<i>Lygodium volubile</i> Sw.	1				He
Malvaceae	<i>Sida planicaulis</i> Cav.	25				Sh
Melastomataceae	<i>Chaetogastra clinopodifolia</i> DC.	73	22		1	He
	<i>Leandra australis</i> (Cham.) Cogn.	162	772	212	272	Sh
	<i>Miconia formosa</i> Cogn.			1		Te
	<i>Miconia cinnamomifolia</i> (DC.) Naudin		11	18	31	Te
	<i>Ossaea amygdaloides</i> (DC.) Triana.	1	17	10	21	Sh
	<i>Pleroma granulorum</i> (Desr.) D. Don	8		1		Sh
	<i>Pleroma urvilleanum</i> (DC.) P.J.F.Guim. & Michelang.	71	25			Sh
Menispermaceae	<i>Cissampelos andromorpha</i> DC.	1		3		Te
Moraceae	<i>Ficus gomelleira</i> Kunth				2	Te
	<i>Ficus luschnathiana</i> (Miq.) Miq.			1		Te
Peraceae	<i>Pera glabrata</i> (Schott) Baill.	4	13	26		Te
Phyllantaceae	<i>Hyeronima alchorneoides</i> Allemão			1		Te
Phytolaccaceae	<i>Phytolacca thyrsoiflora</i> Fenzl. ex J.A.Schmidt	1			2	Sh
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	14	14	15	4	Te
Poaceae	<i>Hiladaea pallens</i> (Sw.) C.Silva & R.P.Oliveira	17	6	6		He
	<i>Ichnanthus</i> sp.		4			He
	<i>Merostachys</i> sp.			13		Ba
	<i>Paspalum nutans</i> Lam.	10				He
	<i>Rugoloa pilosa</i> (Sw.) Zuloaga			11		He
	<i>Steinchisma laxum</i> (Sw.) Zuloaga	7			1	He
Rosaceae	<i>Rubus rosifolius</i> Sm.				1	Sh
Rubiaceae	<i>Coccocypselum lanceolatum</i> (Ruiz & Pav.) Pers.			3	3	He
	<i>Sabicea villosa</i> Willd. ex Schult.		2			Te
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.	1				Te
Solanaceae	<i>Solanum americanum</i> Mill.		1			He
	<i>Solanum mauritianum</i> Scop.		1			Te
Urticaceae	<i>Cecropia glaziovii</i> Sneathl.	4	10	49	40	Te
Total	-	1,045	993	421	457	-

When comparing the successional stage sites, there was a higher occurrence of non-tree species, with a predominance of the herbs group in S1 (table 2). Likewise, significant differences were detected among sites, showing significant differences in density and similarity between

the initial stages (S1 and S2) when compared to advanced stages (S3 and S4) (table 2, table 3). The S1 showed higher values of diversity (Shannon and Simpson) indicating more abundant richness and uniformity of the species represented in this successional stage.

Table 2. Comparison of seed bank characteristics of the four successional stages of the Atlantic Rainforest in Southern Brazil. S1 = 25-yr-old recovery site (initial stage), S2 = 35-yr-old (intermediate stage), S3 = 45-yr-old (late-successional stage), and S4 = 50-yr-old (old-growth forest).

Lista de especies en las cuatro etapas sucesionales de la selva atlántica en el sur de Brasil. S1 = sitio de recuperación de 25 años (etapa inicial), S2 = 35 años (etapa intermedia), S3 = 45 años (etapa de sucesión tardía) y S4 = 50 años (bosque maduro); Te = Árbol, Sh = Arbusto, Él = Hierba, Cl = Trepadora, Ba = Bambú.

Parameters	Study site			
	S1	S2	S3	S4
Total Species Richness (S)	30	24	24	23
Tree Species	8	7	10	9
Non-Tree Species	22	17	14	14
Shannon's Diversity (<i>H'</i>): Tree and Non-Tree	12.24	3.08	6.93	4.93
Simpson's Diversity (<i>1/D</i>): Tree and Non-Tree	8.80	1.64	3.45	2.64
Density (seeds ha ⁻¹): Tree	2,796 ± 970 ^a	4,659 ± 1,612 ^{ab}	9,892 ± 4,397 ^b	9,606 ± 3,072 ^b
Density (seeds ha ⁻¹): Non-Trees	72,115 ± 26,999 ^a	66,380 ± 21,648 ^a	19,713 ± 9,377 ^b	23,154 ± 8,063 ^b
Density (seeds ha ⁻¹): Tree and Non-Trees	74,910 ± 27,230 ^a	71,039 ± 21,678 ^a	29,606 ± 9,831 ^b	32,760 ± 9,089 ^b

Values followed by the same letter do not differ from each other by the ANOVA test.

Table 3. Results of abundance-based Bray-Curtis index of similarity for trees and non-trees among soil seed banks of four recovery sites of the Atlantic Rainforest in Southern Brazil. S1 = 25-yr-old recovery site (initial stage), S2 = 35-yr-old (intermediate stage), S3 = 45-yr-old (late-successional stage), and S4 = 50-yr-old (old-growth forest).

Comparación de las características del banco de semillas de las cuatro etapas sucesionales de la Selva Atlántica en el sur de Brasil. S1 = sitio de recuperación de 25 años (etapa inicial), S2 = 35 años (etapa intermedia), S3 = 45 años (etapa de sucesión tardía) y S4 = 50 años (bosque maduro).

Life Form / Site	Bray-Curtis Similarity			
	S1	S2	S3	S4
Tree				
S1	-	0.27	0.004	0.001
S2	0.58	-	0.51	0.01
S3	0.34	0.58	-	0.22
S4	0.18	0.40	0.58	-
Non-Tree				
S1	-	0.001	0.001	0.001
S2	0.28	-	0.001	0.004
S3	0.27	0.39	-	1.00
S4	0.28	0.48	0.76	-

In the initial stage (S1), a richness of 26 species was recorded, considering the standardization of 413 germinated seeds, while the other sites indicated a decrease in species richness (advanced stage (S3) = 24 species, old-growth forest (S4) = 22 species and intermediate stage (S2) = 19 species. Although the individuals did not approach the stabilization of rarefaction curves within each analyzed site,

we found a considerable increase in the number of species according to the youngest stages of succession (figure 1).

The diversity profiles indicated that species diversity in SSB varied according to the successional stages analyzed (figure 2). In initial stage forests (S1), species diversity was higher when compared to intermediate (S2), advanced (S3) and mature (S4) stages.

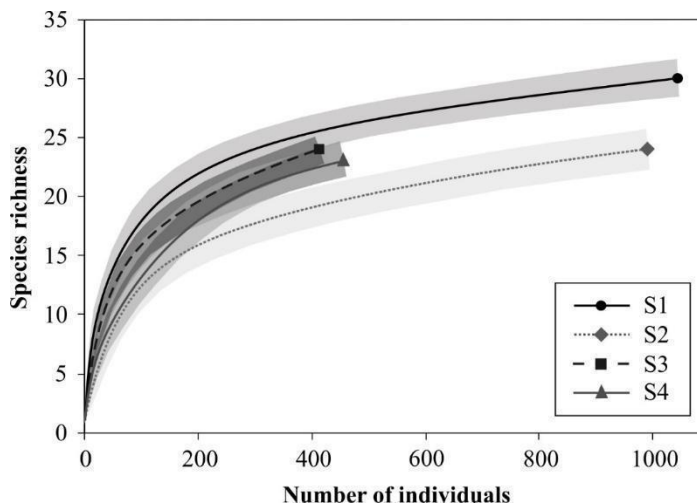


Figure 1. Rarefaction curves and 95 % confidence intervals by the number of individuals sampled in soil seed bank within successional stages S1 = 25-yr-old, S2 = 35-yr-old, S3 = 45-yr-old and S4 = old-growth forest.

Análisis de coordenadas principales (PCoA) con diferencias de Bray-Curtis para la riqueza total de especies de la comunidad para cuatro sitios de recuperación de la Selva Atlántica en el sur de Brasil. S1 = sitio de recuperación de 25 años (etapa inicial), S2 = 35 años (etapa intermedia), S3 = 45 años (etapa de sucesión tardía) y S4 = 50 años (bosque maduro).

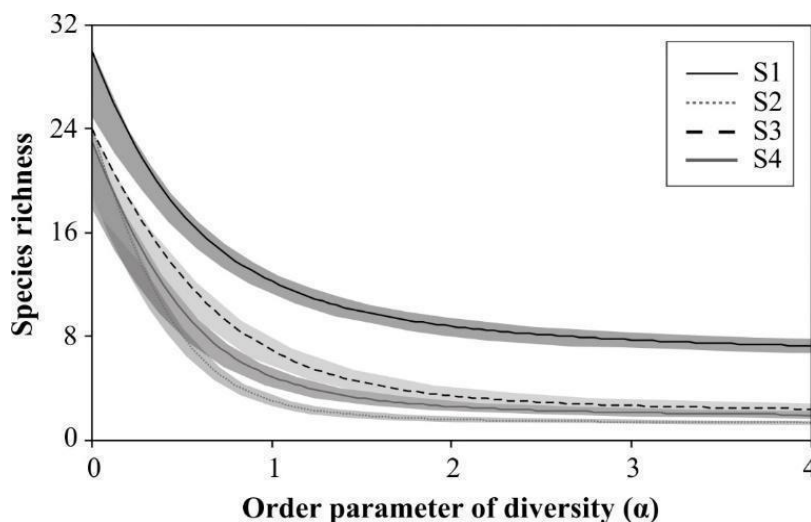


Figure 2. Diversity profiles build using Rényi's Series for soil seed bank in different successional stages of the Atlantic Rainforest in Southern Brazil. S1 = 25-yr-old recovery site (initial stage), S2 = 35-yr-old (intermediate stage), S3 = 45-yr-old (late-successional stage), and S4 = 50-yr-old (old-growth forest).

Curvas de rarefacción e intervalos de confianza del 95 % según el número de individuos muestreados en etapas sucesionales S1 de 25 años de edad, S2 = 35 años de edad, S3 = 45 años de edad y S4 = bosque maduro.

The first two axes of PCoA explained 92.6 % (axis 1 = 60 %, axis 2 = 32.6 %) of the variance data and were significant (Monte Carlo, $P < 0.05$). The chemical soil properties that significantly correlated with axis 1 were SMP, pH, CECV, Ca, S, Clay, CECAl, Al, Organic matter (OM), H + Al and CEC. Meanwhile significant variables for axis 2 were P and K (figure 3, table 4). The first two axes of PCoA revealed that early stage sites have high levels of SMP, pH, CECV, Ca and S in the soil, while in advanced stage and mature forests the highest levels are clay, CECAl, Al, OM, H + Al and CEC, respectively. Additionally, the intermediate successional stage showed high K and low P levels. The first two ordering axes discriminated a strong gradient between soil chemical properties and SSB (figure 3). These axes segregated into three floristic groups: the first, located in sites with an initial succession stage (S1); the second, in sites with an intermediate succession stage (S2); and the third, in sites with advanced stage and mature forests (S3 and S4) (figure 3).

DISCUSSION

This study revealed that the floristic diversity of the seed bank is directly associated with the successional stage, since young forests presented larger floristic richness when compared to mature forests. Differently, the studies by Liebsch *et al.* (2008) and Zanini *et al.* (2014) showed that mature forests showed higher floristic richness. This variation in floristic richness at different successional stages is directly associated with the environmental and struc-

Table 4. Soil parameters of the four successional stages of the Atlantic Rainforest in Southern Brazil. S1 = 25-yr-old recovery site (initial stage), S2 = 35-yr-old (intermediate stage), S3 = 45-yr-old (late-successional stage) and S4 = 50-yr-old (old-growth forest).

Soil characteristics	Study site			
	S1	S2	S3	S4
Clay (%)	27.0	29.0	30.0	34.0
pH-H ₂ O 1:1	4.6	3.9	4.1	3.7
SMP index	5.1	4.5	4.6	4.5
P (mg/dm ³)	5.5	5.2	6.1	5.0
K (mg/dm ³)	39.8	54.2	44.2	29.4
Organic matter (%)	2.2	3.4	3.2	3.2
Al (cmolc/dm ³)	1.4	2.7	2.4	2.9
Ca (cmolc/dm ³)	0.7	0	0	0
Mg (cmolc/dm ³)	0.7	0.5	0.7	0.3
H+Al (cmolc/dm ³)	12.8	25.6	21.5	24.1
CEC pH 7.0 (cmolc/dm ³)	14.3	26.2	22.3	24.4
CEC Al (%)	48.2	80.7	75.0	91.5
CEC V (%)	10.5	2.4	3.6	1.1
Sum bases	1.5	0.6	0.8	0.3

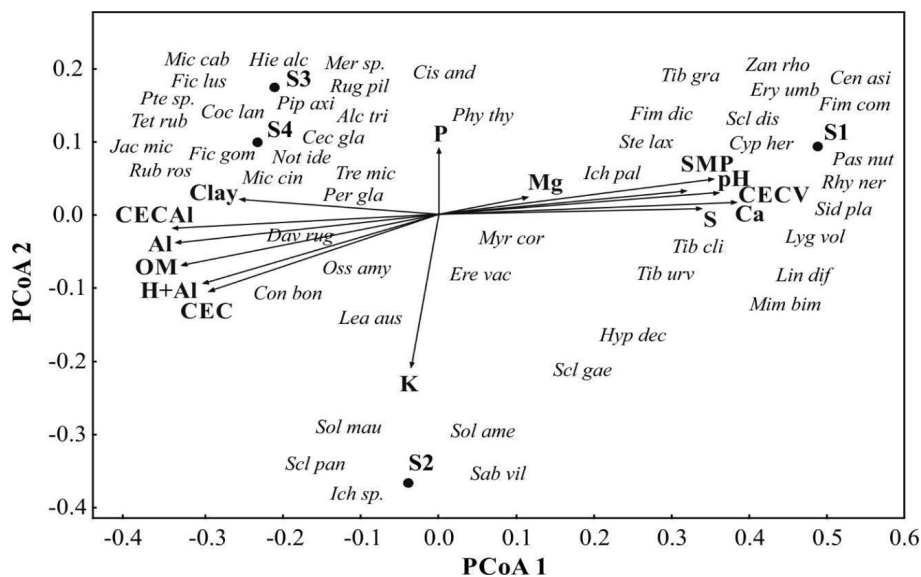


Figure 3. Principal Coordinates Analysis (PCoA) with Bray-Curtis dissimilarities for total community species richness for four recovery sites of the Atlantic Rainforest in Southern Brazil. S1 = 25-yr-old recovery site (initial stage), S2 = 35-yr-old (intermediate stage), S3 = 45-yr-old (late-successional stage) and S4 = 50-yr-old (old-growth forest).

Creación de perfiles de diversidad utilizando la serie Rényi para diferentes etapas sucesionales de la Selva Atlántica en el sur de Brasil. S1 = sitio de recuperación de 25 años (etapa inicial), S2 = 35 años (etapa intermedia), S3 = 45 años (etapa de sucesión tardía) y S4 = 50 años (bosque maduro).

tural variations of the forest, where these factors increase the complexity of the processes and interactions during the forest succession. For example, some species characteristic of the region has suffered anthropic pressure, which can limit the distribution of species and modify the structure and complexity of the forest (Zanini *et al.* 2014).

Therefore, we believe that in the study area, the history of land use may be affecting succession continuity, limiting the floristic richness of the most advanced environments (old-growth forests). In addition, the study area is located in a remnant in the urban environment, with low connectivity with other areas covered with forests, a fact that limits the entry of species, especially in the more advanced stages of succession where dispersion is more strongly reliant on fauna.

Not only environmental variations and land use influence the differences observed in the succession process, but also stochastic and niche processes. According to Chazdon (2014, 2016), initial successional stages are highly influenced by stochastic processes, while in advanced stages the ecological niche prevails. Among the stochastic processes, we can mention the soil seed bank, derivative from dispersion. Therefore, considering that the environment has suffered disturbances in the past, as sites S1 and S2 were previously occupied by pastures, the propagules from the soil seed bank become essential for degraded vegetation recovery. According to Cho *et al.* (2018), the recovery of abandoned areas, after the implantation of agriculture or pasture, is mainly determined by the composition of the seed bank and vegetation adjacent to these environments. Although areas S1 and S2 have a history of use with pastures, we have not observed significant density and diversity of exotic species in these environments.

In this study, the largest number of seeds was observed in area S1, followed by areas S2, S3 and S4, respectively, corroborating with Bourgeois *et al.* (2017) and Derroire *et al.* (2016). According to these authors, as the complexity of the forest increases, the floristic diversity decreases, although the seed bank maintains the regeneration and recovery capacity of the forests, especially when formed by species whose propagules present dormancy and form the persistent seed bank. Although S1 has the highest richness, studies suggest that the seed bank recovery potential is low, because the area in general is dominated by generalist species, such as herbs and grasses (Gunaratne *et al.* 2014). In the same way, the floristic richness can be associated with the age of the site, and 50-year-old forests have, in general, the totality in floristic richness, that is, the forest will not undergo many changes over the years, being in dynamic equilibrium (Martin *et al.* 2013).

In this regard, we observe that the same pattern occurs in density and floristic similarity. Since sites S1 and S2 have higher densities and are floristically similar, while in sites S3 and S4 there is a gradual decrease in density, though remaining similar. According to Helsen *et al.* (2015), variations in density and similarity among com-

munities are associated with the types of the local species, and as the succession increases there is loss of generalist species and increase in specialist species. In this study, the change in the composition of the seed bank suggests this transition of species types, mainly related to life forms. Another factor that can influence density is the increase in competition. In this study, we observed a higher density of herbs in the early stages, such as *Rhynchospora nervosa*, *Fimbristylis complanata*, *Lindernia diffusa*. As the successional stage increases there is a reduction in these species and replacement with new ones such as *Alchornea triplinervia*, *Tetrorchidium rubrivenium*, *Miconia cinnamomifolia*, among others. According to Yamada *et al.* (2013), herbs have persistent seeds; nevertheless, a gradual decline occurs as the succession increases.

Shrubs and trees are generally characteristic of advanced stages, having a minimum presence in the seed bank, as they present non-dormant seeds with fast germination (Cho *et al.* 2018), forming a seedling bank. In this sense, only *Leandra australis* was observed in all sites and in high density. This species has high germination potential and the seeds do not present dormancy (Cáceres and Monteiro-Filho 2007), causing high resilience in the studied sites.

In addition to changes in floristic composition, we expect changes in the successional stage to be associated with the chemical properties of the soil. According to Chazdon (2014), environmental conditions in tropical forests are favorable for the establishment and growth of plants in different successional stages, and the relationship between soil properties and succession stage generally occurs in tropical forests (Derroire *et al.* 2016).

Not only the presence of herbs, but also the type of soil and its characteristics, directly influence the seed bank and the natural regeneration of forests. In the present study, the chemical properties of soils varied in relation to the successional stage, with S1 showing the highest fertility when compared to S4. Other authors considered that young forests, having generalist species (grasses), may present denser and less fertile soils, as they undergo changes both in structure and in physical-chemical properties and in the cycling of nutrients (Sobanski and Marques 2014).

Silva *et al.* (2019) affirm that generalist species tend to improve soil conditions, which can increase water retention, prevent erosion and increase fertility. This statement corroborates with our study and may be a decisive factor for the establishment of species in the environment. In this sense, in young forests, there is less stock of nutrients retained in the biomass, as they are under development. In advanced stage forests, there is a larger proportion of the nutrient stock of the site retained in the vegetation, thus decreasing this quantity in the soil. This fact, in addition to others such as the history of previous use, contributes to the understanding of the differences between the levels of soil fertility under forests in different successional stages and their effects on the seed bank.

CONCLUSIONS

Our results show that species diversity in the soil seed bank is larger in young forests than in mature forests, and therefore the original hypothesis has not been confirmed. Results also showed that the species richness in the seed bank in young forests is predominated by herbs species, while in mature forests there is a distribution between herbs and shrub/tree species.

Soil characteristics, especially those related to fertility, are different among successional stages. Higher levels were found, for most of the analyzed nutrients, in soils under forest in early stages. Finally, considering the results obtained, it can be said that forests in early stages have a seed bank with partial potential for recovering areas compared to forests in more advanced stages.

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