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THE SOIL SEED BANK AS AN INDICATOR OF ALTITUDINAL GRADIENT IN A MONTANE TROPICAL FOREST

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The study was conducted in a portion of tropical montane forest in the Caparaó National Park, Brazil. The aim of this work was to assess the changes in seed bank composition, density and richness along an altitudinal gradient and across seasons, and to analyse the floristic links between the forest soil seed bank, seed rain, regeneration layer and adult tree layer. The seed bank data were collected in the dry and rainy seasons at seven different elevations, ranging from 1112 – 1550 m above sea level. The floristic relationships were analysed through the species lists derived from previous studies at these same locations. The results showed seed density and species richness varied among different elevations, but did not vary with gradient. Seed bank density and richness varied significantly across seasons, with the highest averages found in the rainy season. In the floristic composition, the higher elevations showed more similar composition than to the lower elevations. Seed bank composition was floristically different from the seed rain, the regeneration layer and the adult tree layer of the forest. Our results showed that the soil seed bank was influenced by both altitude and environmental seasonality. The findings highlighted the importance soil seed bank as a mechanism of post-disturbance forest regeneration.

Keywords: seed stock, ecological succession, elevation, seasonality, tropical forest.

INTRODUCTION

Forest regeneration depends on mechanisms involved in the deposition of propagules in the plant community and also on disturbances that shaped patterns and processes of a given forest across time (Cirne-Silva et al. 2020). In this context, the usually species-rich seed bank on the forest floor stored large quantities of dormant propagules, mainly belonging to pioneer species (Johnstone et al. 2016). Seed banks were thus involved in several natural processes in the forest, such as initial population establishment and maintenance of species diversity (Souza et al. 2017).

Coupled with seed rain, the seed bank was the main source of regeneration in forest ecosystems (Piotto et al. 2019). However, its composition tends to differ locally in the regeneration and adult tree layers (Luo et al. 2017). These features made seed bank composition crucial to understand forest responses to disturbance, and a valuable tool to understand ecological succession. The availability of viable seeds indicated the self-sustaining capacity of plant communities and their principal potential to recover from eventual disturbances (Calegari et al. 2013).

The distribution of species in forest communities was linked to many factors including the variations in altitude (McCain & Grytnes 2010). Small shifts in altitude entailed changes in the local microclimate and influenced species germination and regeneration strategies (Oda et al. 2016). However, patterns of species richness and density in seed banks along altitudinal gradients were still unclear.

Multiple studies in forests around the world found conflicting results about species richness and density in seed banks along altitudinal gradients. In previous studies, no significant variation of seed density was found following altitude change (Cummins & Miller 2002) and some other reported increasing richness and density with increasing altitude (Espinosa et al. 2013). Conversely, other studies identified a decreasing trend in seed bank richness and density from lower towards higher elevations (Ma et al. 2010, An et al. 2020). Tropical montane forests provided an opportunity to advance the understanding of soil seed banks along altitudinal gradients.

Other than spatial variation with the altitude, seed banks changed in response to seasonality (Grombone-Guaratini & Rodrigues 2002). Such changes provided information on the persistence or transience of the soil seed bank along the year (Venn & Morgan 2010). Seasonality was known to play a major role in species distribution in different vegetation formations (Schimitt et al. 2013, Amissah et al. 2018, Nunes et al. 2020). However, knowledge on the influence of seasonality on seed bank characteristics was still incipient, especially in ombrophilous forests with mild seasonal fluctuations.

The study aimed to assess seed bank differences across an altitudinal gradient, seasonal climate conditions effect on the seed bank and to determine the relationship between the forest seed bank, seed rain and established vegetation.

MATERIALS AND METHODS

Study area

This study was carried out in the Santa Marta valley. It was located in the southern portion of the Caparaó National Park (Parque Nacional do Caparaó, PNC) in the municipality of Ibitirama, Espírito Santo state, Brazil. The national park is a protected area with 31,853 hectares located on the limits between the states of Espírito Santo and Minas Gerais, Brazil (20° 37′ – 20° 19′ S and 41° 43′ – 41° 45′ W) (Figures 1a and 1b). The sample plots used in this study were distributed along two valley slopes, following the upstream direction and located at seven different elevations (Figure 1c). In each study zone, four plots of 2 m × 20 m were set up with a total of 28 plots. The plots were prepared at steep terrain with various directions of exposure (Table 1).

Based on the Köppen's climate classification for Brazil, the study area has a predominant climate of subtropical highland (Alvares et al. 2013). Temperatures are mild throughout the year with averages varying between 19 – 22 °C. The relative air humidity is usually above 70% and the mean annual precipitation is around 1400 mm (MMA 2015). The elevation in the Santa Marta valley varies between 800 – 2300 m above sea level.

The microbasin of Santa Marta valley is composed of ombrophilous forests with two distinct physiognomies. They are the dense ombrophilous montane forest (between 500 – 1500 m) and upper montane forest (above 1500 m) (IBGE 2012). The soils in the Santa Marta valley are classified as dystrophic yellow latosol, dystrophic red-yellow latosol, dystrophic humic cambisol and folic organosol (Castro 2018).

Data collection

The seed bank data were collected on two occasions in the year 2016. One at the end of the rainy season in April and another one at the end of the dry season in September. Surface soil samples excluding litter (25 cm × 25 cm × 8 cm) were collected in three randomly selected points within each plot.

The three seed bank subsamples were homogenised into one composite sample by plot to a total of 28 samples. The collected materials were taken to a nursery and distributed on plastic trays (30 cm × 22 cm × 6 cm). The trays were kept in a greenhouse and covered with shade cloth (65% shade) under automatic daily irrigation. After six months of each collection, monthly evaluations for germinated seeds were done based on the seedling emergence method. Seedlings were allowed to grow for later identification (Brown 1992).

Seedling identification was carried out by comparing seedlings with specimens stored in herbaria from the study region and in virtual herbaria with aid from literatures and taxonomists. Taxonomic classification was based on APG IV (The Angiosperm Phylogeny Group 2016) and species nomenclature on *Flora do Brasil 2020* lists.

The floristic relationships were analysed using the species lists derived from seed rain (Perini et al. 2019), regeneration layer (Abreu 2017) and adult tree layer inventories (Araújo 2016). These data were previously recorded at the same altitudinal zones and locations Santa Marta valley. Only morphotypes identified at the species level were considered for the

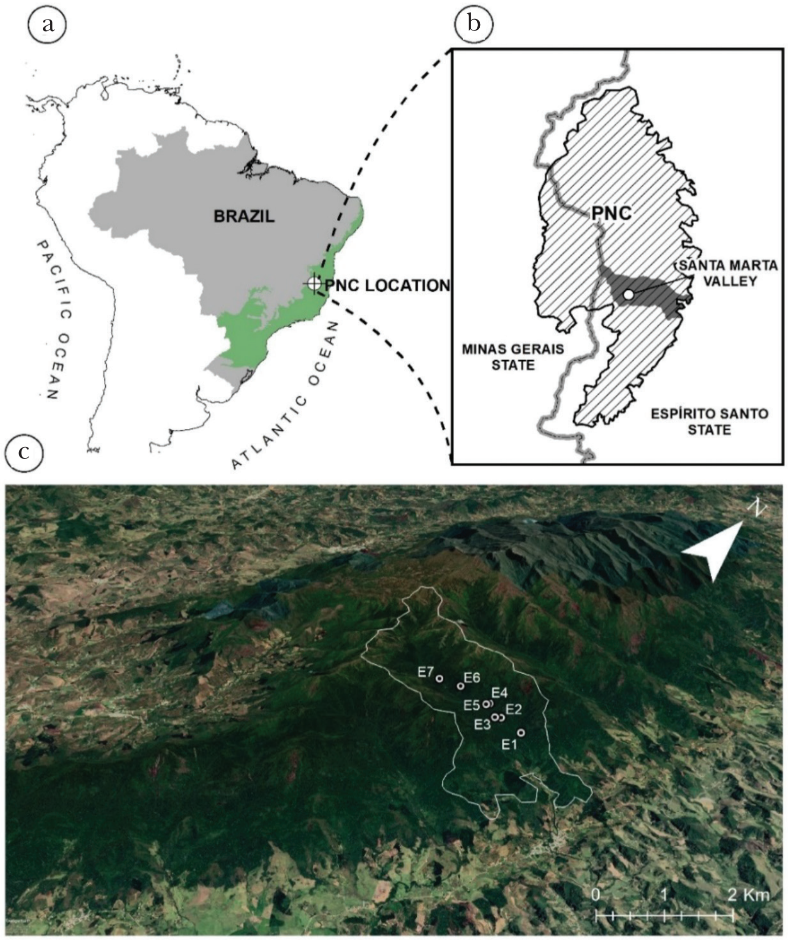

Figure 1 Location of the study area (a) and (b) and depiction of the elevations (c) with 28 plots established in the Santa Marta valley, Caparaó National Park, Brazil

Table 1 Altitudinal distribution, average declivity and direction of terrain exposure for seven study plots along the Santa Marta valley, Caparaó National Park, Brazil

Study plots	Elevation (m)	Average declivity (%)	Direction of terrain exposure
E1	1112	69.55	East/Northeast
E2	1219	58.29	East/Southeast
E3	1302	75.00	Northeast
E4	1319	75.00	East
E5	1391	48.24	North
E6	1420	73.39	South/Southeast
E7	1550	58.00	Northeast

analysis. The seed rain study counted 235,296 propagules among 40 morphotypes identified at the species level (Perini et al. 2019). In the regeneration layer, 2,055 trees were recorded among 136 morphotypes identified at the species level (Abreu 2017). In the adult tree layer, 3,603 living trees were documented, belonging to 343 morphotypes identified at the species level (Araújo 2016).

Data analysis

Phytosociological parameters such as density and frequency of germinated seeds, Margalef richness index, Shannon diversity index and Pielou evenness were calculated in the study. The seed bank contained absolute density and species richness which did not meet the parametric assumptions, they were submitted to the non-parametric Kruskal–Wallis test ($p < 0.05$) to evaluate their significant differences among elevations. The effect of seasonality on the seed bank was assessed by the Mann–Whitney test with the same level of significance ($p < 0.05$) using the altitude data as a whole.

Floristic similarities among elevations for both seasons were assessed by the Bray–Curtis index (Magurran 2013). Based on the Bray–Curtis index and on species abundances, clustering analysis was performed through the unweighted pair group method with arithmetic mean (UPGMA). The consistency of the groups, were performed by bootstrap resampling with 1000 repetitions (Efron & Tibishirani 1993). The fit between the graphic representation of similarity and the original abundance matrix were assessed by calculating their cophenetic correlation coefficient.

The floristic links between the seed bank, seed rain, regeneration layer and adult tree layer were analysed with non-metric multidimensional scaling with Sorensen similarity index for species presence or absence data. The significance of non-metric multidimensional scaling axes were assessed with Monte Carlo permutational test. All scientific names drawn from the previously cited studies (Araújo 2016, Abreu 2017, Perini et al. 2019) were checked and updated as necessary by referring to the *Flora do Brasil 2020* list.

RESULTS

The study found that the density of germinated seeds and richness index differed significantly ($p < 0.05$) among different elevations in both dry and rainy seasons. The differences, however did not follow the altitudinal gradient. In the rainy season, the seed bank recorded at elevations points E2, E3, E4 and E7 stored the highest density of seeds in the gradient. However, with regards to species richness by Margalef index, the highest values were observed at the elevations points E2, E3, E5 and E7, which did not differ statistically from each other. In the dry season, elevations points E1, E2, E3, E4 and E5 displayed the highest density values, while E1, E2, E3 and E4 also displayed the highest richness values (Table 2).

The Mann–Whitney test showed the number of propagules stored in the soil differed significantly between seasons ($U = 5.165$; $p < 0.05$). In all altitudinal zones, the seed bank stored more propagules during the rainy season than during the dry season. We also found that seed bank species richness differed significantly between seasons ($U = 4.992$; $p < 0.05$), with higher Margalef index values in the rainy season than in the dry season (Table 3).

The clustering analysis for the soil seed bank along the altitudinal gradient revealed two groups (Figure 2). Group 1 represented the higher elevations (1420–1550 m) and group 2 represented the lower elevations (1112–1391 m). Within the second group, the analysis suggested the formation of two other subgroups. The

Table 2 Seed density and Margalef richness index of the soil seed banks collected in the rainy and dry seasons for seven study plots

Plot and altitude (m)	Rainy season		Dry season	
	Density (seeds m^{-2})	Margalef richness index	Density (seeds m^{-2})	Margalef richness index
E1 - 1,112	11.14 c*	1.30 b	5.71 ab	0.86 ab
E2 - 1,219	32.71 a	2.28 a	10.43 a	1.54 a
E3 - 1,302	17.57 abc	2.21 a	12.14 a	0.90 a
E4 - 1,319	28.57 ab	1.41 b	7.29 ab	0.82 ab
E5 - 1,391	15.86 bc	1.63 ab	8.00 a	0.47 bc
E6 - 1,420	12.14 c	1.37 b	2.14 b	0.39 bc
E7 - 1,550	25.71 ab	1.99 a	2.71 b	0.21 c

*Average values followed by the same letter within the same column do not differ statistically from each other, according to a Kruskal–Wallis test ($p < 0.05$)

Table 3 General parameters of the soil seed bank collected in the rainy and dry seasons

Parameters	Rainy season	Dry season
Diversity (H')	3.83	3.07
Evenness (J')	0.76	0.77
Number of individuals	1006	303
Number of species (and morphotypes)	151	54
Number of families	19	14
Density (seeds m^{-2})	574.86	173.14
Margalef richness	21.69	9.27

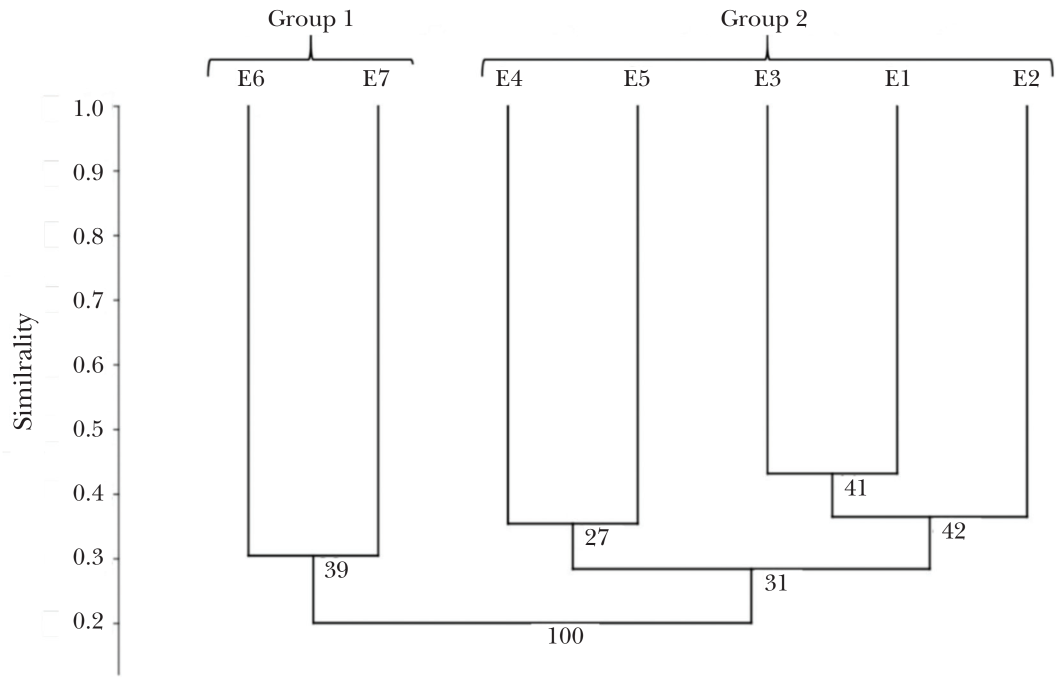

Figure 2 Unweighted pair group method with arithmetic mean dendrogram with Bray–Curtis distances for the floristic similarity among the soil seed bank recorded at different elevations

Node consistency was obtained from 1000 bootstrap resamplings.
E1 = 1112 m a.s.l, E2 = 1219 m a.s.l, E3 = 1302 m a.s.l, E4 = 1319 m a.s.l., E5 = 1391 m a.s.l., E6 = 1420 m a.s.l., E7 = 1550 m a.s.l.

subgroups showed the seed banks of the lower elevations at E1, E2 and E3 were more similar to each other than the seed banks of the elevations E4 and E5. The dendrogram coefficient of cophenetic correlation was 0.7439, suggesting that the data were not severely distorted by the unweighted pair group method with arithmetic mean analysis.

The non-metric multidimensional scaling analysis suggested the formation of three groups. The first group was formed by the regeneration and adult tree layers, the second group was formed by the seed bank and a third group was formed by the seed rain. This pattern was consistent in all altitudinal zones along the gradient. The non-metric multidimensional scaling analysis had a stress value of 9.82%, indicating that it reliably represented the data (Figure 3).

Sorensen similarity values corroborated the non-metric multidimensional scaling analysis results. The highest Sorensen value was observed between the regeneration layer and the adult tree layer (Table 4). According to the analysis, the seed bank was more floristically distant from the seed rain than from the regeneration and adult

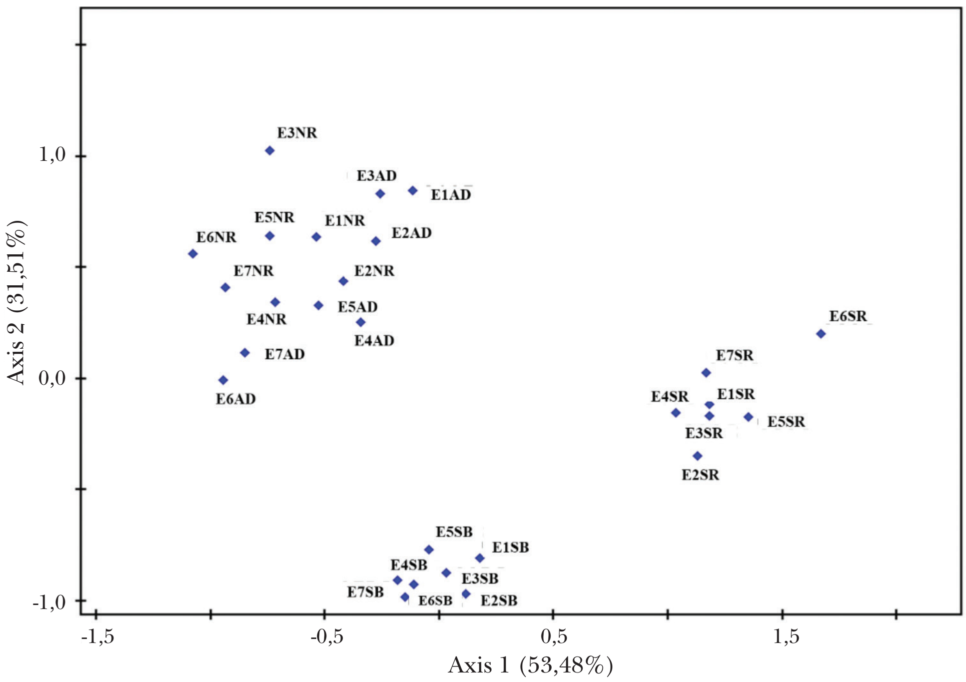

Figure 3 Non-metric multidimensional scaling of the floristic links between soil seed bank, seed rain, regeneration layer and adult tree layer along seven elevations

E1 = 1112 m a.s.l., E2 = 1219 m a.s.l., E3 = 1302 m a.s.l., E4 = 1319 m a.s.l., E5 = 1391 m a.s.l., E6 = 1420 m a.s.l., E7 = 1550 m a.s.l.; AD = adult tree layer, SB = soil seed bank, SR = seed rain, NR = natural regeneration layer

Table 4 Sorensen similarity index between the adult tree layer, soil seed bank, seed rain and natural regeneration layer

	AD	SB	SR	NR
AD	1	-	-	-
SB	0.1005	1	-	-
SR	0.0343	0.0294	1	-
NR	0.5103	0.1023	0.0211	1

AD = adult tree later, SB = soil seed bank, SR = seed rain, NR = natural regeneration layer

tree layers of the forest, although the index was not specifically high between the regeneration and adult tree layers.

DISCUSSION

Data for both density and species richness differed significantly among different elevations. However, these differences did not follow the altitudinal gradient. Other authors investigating seed bank variation in an altitudinal gradient concluded that species richness and density were not generally influenced by altitude shifts (Lu et al. 2010). Other factors, such as soil fertility (Luz et al. 2018), declivity (Muvengwi & Ndagurwa 2015) and seed predation (Bakker et al. 2018) may effect seed bank richness and density more than altitude variation. Another fact that may influence the result was that seed rain density also lacked an altitudinal pattern along the same gradient (Perini et al. 2019).

Although not a noticeable feature of dense ombrophilous forests, seasonality may also promote shifts in soil seed bank density (Grombone-Guaratini & Rodrigues 2002, Santos et al. 2020). The results from this work showed that seed bank density varied significantly between the rainy and dry seasons, with highest abundance recorded during the rainy season in all altitudinal zones. It was well recorded that seasonal variation in fruiting and seed dispersal largely influenced seed abundance in tropical forest communities (Saulei & Swaine 1988). Perini et al. (2019) found that the highest deposition of propagules through seed rain in this portion of the forest happened between November and March which coincided with the rainy season. The previous observations could explain the differences in seed density found in the soil from this study.

The results highlighted the differences in richness and density between the rainy and dry seasons in the highest elevation of the gradient (E7). The study found high averages in the rainy season, and low averages in the dry season for both parameters for richness and density. The seeds from species inhabiting the highest altitude likely lacked mechanisms that would help them to endure unfavourable abiotic conditions, causing them to lose viability during the dry season (Kim & Donohue 2013).

The groups which emerged from the clustering analysis corroborated the floristic similarity among spatially closer altitudinal zones, in relation to more distant zones. The observations suggested that species were associated with certain environmental characteristics along the gradient (Luz et al. 2018). In tropical forests, altitude factor caused environmental changes especially in temperature and humidity, that shifted species composition along the gradient (Song et al. 2013, Oda et al. 2016, Luz et al. 2018). Previous studies in the same area showed that litter accumulation, organic matter content and soil acidity explained these compositional shifts along the gradient (Araújo 2016, Abreu 2017).

In the study of floristic links between seed bank, seed rain, regeneration layer and adult tree layer, the floristic distance between the seed bank and the other categories was evident. This differentiation was related to the species ecological groups. Seeds stored in the soil predominantly belong to early succession species (Wang et al. 2013, Correia & Martins, 2015), whereas the regeneration layer was predominantly composed by late secondary species. The reports explained the low similarity between the soil seed bank and the regeneration layer, and the high similarity between the regeneration layer and the adult tree layer.

The small number of late succession species found in the seed bank could be explained by two factors. First factor was related to appropriate conditions, the recalcitrant seeds from late succession species germinated shortly after their dispersal. While the second factor related to some species which were likely to produce large seeds in small numbers and rendered them susceptible to predation (Baider et al. 1999).

The floristic dissimilarity between the seed bank and the established adult community reflected the state of advanced succession and high conservation status of the forest. In undisturbed or little disturbed mature forests, it was presumed that adult individuals belonging to early succession species had already been replaced by individuals from later succession species. Nevertheless, the natural dynamics of the forest ecosystem such as the treefall gaps, which allowed the germination of soil-stored seeds and ensured pioneer individuals remained in the community, regardless of disturbance level or the forest successional stage (Franco et al. 2012). Although the seed bank was constantly enrichened by seed rain, the research found no direct floristic link between them, since both groups remained isolated in the non-metric multidimensional scaling analysis results and distanced in the cluster analysis. These results suggested that most seeds from the seed rain were exposed to predation. Another possible explanation was that the seeds immediately germinated and contributed the seedling bank, although the study found low similarity between the seed rain and the regeneration layer (Piotto et al. 2019).

CONCLUSIONS

The study recorded that the altitudinal gradient had a strong influence on the seed bank composition but not in the richness or density of seeds. Across the altitudinal gradient, altitudinal zones were closer to each other had more similar composition than the more distant ones. However, the variation of species richness and seed density did not follow the altitudinal gradient.

The study found that even for the ombrophylous forest, seed bank density and diversity differed strongly between seasons with contrasting precipitation. The findings linked the differences to the timing of species fruiting and seed dispersal. Study results showed the highest averages of density and richness in the seed bank during the rainy season. The finding was supported by a previous study at this site, where most propagule deposition happens in the rainy season.

The soil seed bank which mostly consisted of pioneer species, played an important role in forest resilience. In face of potential disturbances, the germination of soil-stored seeds favoured forest community recomposition which was an important regeneration path for forest succession.

The floristic distance found between the soil seed bank and the regeneration and adult tree layers reflected the successional stage of the forest. Late secondary species predominated in both established regeneration and adult layers, whereas the seed bank stored dormant seeds from pioneer species. The low similarity found between the soil seed bank and the seed rain seemed to be influenced by other processes, such as seed predation and absence of seed dormancy.

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