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Original Article

Conservation of Nature

Soil Seed Banks in a Forest Under Restoration and in a Reference Ecosystem in Southeastern Brazil

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ABSTRACT

The current study aims to characterize the soil seed banks in a forest under restoration and in a seasonal semideciduous forest remnant, as well as to quantitatively and qualitatively compare them in order to evaluate the seed bank potential to influence the restoration process. In total, 60 samples of soil seed banks were collected in two adjacent forests (30 in a 2.18-ha forest undergoing restoration process based on the planting of seedlings belonging to different tree species, after the forest was subjected to bauxite mining activity; and 30 in a 5.30-ha preserved forest fragment). The soil seed bank of the forest undergoing restoration recorded higher density of emerged seedlings than that of the reference ecosystem. Although the shrub-tree species in the investigated forests lacked floristic similarity, the highly similar dispersal syndrome distribution and the successional category of shrub-tree species in them have indicated that both forests underwent ecological processes. Therefore, the restoration process implemented in the mined area has successfully recovered the soil seed bank after a few years.

Keywords: Atlantic Forest; bioindicators; floristic similarity; forest restoration; mining.

1. INTRODUCTION

Forest restoration processes create sustainable plant communities that represent the original composition and diversity of degraded areas (Jefferson, 2004; Courtney et al., 2009). The ecosystem restoration goal lies on promoting and expanding the possibility of implementing ecological restoration and natural succession processes, as well as on enhancing biodiversity and stability in a given region (Tres et al., 2007; Martins, 2016).

Soil seed banks play a key role in recovering different ecosystems and in preserving their resilience (Mackenzie & Naeth, 2010). The assessment of the density and richness of seed banks from different plant species is essential to support the decision making about the most appropriate restoration techniques to be adopted in restoration projects (Martins, 2016). Soil seed bank features are determined based on viable seeds found in the soil (Caldato et al., 1996; Schorn et al., 2013). The seed banks are dynamic systems presenting certain inputs (such as seed rains resulting from active seed dispersal mechanisms) and outputs (such as seed germination, seed viability loss, predation or seed death) (Caldato et al., 1996; Gasparino et al., 2006). Although herbs and grasses prevailed in the soil seed bank of degraded hillslopes in Southern Wello (Ethiopia), these plant species should not be ignored, since they can help covering degraded soils and reducing soil erosion (Kebrom & Bekele, 2000).

The composition and resilience of soil seed banks found in environments undergoing restoration process change due to degrading activities performed before restoration techniques and to the way restoration is conducted (Navarra & Quintana-Ascencio, 2012; Stroh et al., 2012). The high seed density and species richness found in seed banks help improving plant development in degraded environments (Ma et al., 2010).

It is important to evaluate areas undergoing restoration processes to help improving restoration techniques and to investigate the effectiveness of objectives outlined in restoration projects (Stanturf et al., 2014). In addition, it is essential to evaluate the remaining forest areas near the one undergoing restoration in order to compare data collected from both areas (Keddy & Drummond, 1996; Jaunatre et al., 2013).

Studies focused on investigating soil seed banks in restoring and fragmented forests in the Atlantic Forest domain have revealed different results regarding the density of emerging seedlings. In total, 554 seedlings m^{-2} were found in a given area after six restoration years, whereas 1,056 seedlings m^{-2} were recorded after nine restoration years (Sorreano, 2002). Previous studies had also found 857.6 seedlings m^{-2} in a secondary forest in a kaolin mining area located in Minas Gerais State, Brazil (Martins et al., 2008): 771 seedlings m^{-2} in an area were subjected to 40 restoration years (Miranda Neto et al., 2014), 357 seedlings m^{-2} in an area were subjected to 23 restoration years (Correia & Martins, 2015) and, finally, 2,489 seedlings m^{-2} in an area restored for 10 years after being subjected to bauxite mining activity (Miranda Neto et al., 2017). The variation in soil seed density in different areas is associated with several factors such as the history of the area, propagule source and dispersing fauna (Franco et al., 2012).

Thus, environmental mitigation measures to what extent the restoration of areas degraded by mining activities is necessary. The mining sector plays a key role in the Brazilian economy; however, its current social and environmental effects, as well as findings from previous studies about mining operations, should be taken into consideration at the time to assess viable alternatives to minimize possible damages caused by this sector (Barros et al., 2012).

Brazil is one of the largest ore producers and it holds the largest mineral reserves in the world (Magno, 2015). Bauxite mining has several negative and positive effects on the environment. For example, mining activities can present the following negative environmental effects: vegetation suppression, water quality degradation, ecosystem function loss, different effects on fauna, as well as noise, dust, and particulate emissions (Bebbington & Bury, 2009; Koch, 2015). However, other activities can decrease the negative impact of mining, mainly the ones resulting from topographical conditioning and revegetation processes (Guimarães et al., 2012).

Therefore, studies focused on using soil seed banks as indicators to evaluate and monitor forests undergoing restoration aim to help understanding the natural regeneration potential of areas facing different disturbances. (Calegari et al., 2013; Martins et al., 2015). Furthermore, it is essential to understand seed bank resources to substantiate the decision-making about future interventions focused on improving ecological processes taking place in restored ecosystems (Martins et al., 2015).

The current study aimed to characterize the soil seed bank found in a forest undergoing restoration after being subjected to bauxite mining and in a seasonal semideciduous forest remnant (reference ecosystem), as well as to quantitatively and qualitatively compare them in order to evaluate the seed bank potential to influence restoration processes.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in two adjacent forests herein named as Forest 1 (a 2.18-ha forest undergoing restoration process based on the planting of seedlings belonging to different tree species, after it was subjected to bauxite mining activity) and Forest 2 (reference ecosystem - a 5.30-ha of preserved forest fragment at mid-successional stage).

The investigated forests are located in São Sebastião da Vargem Alegre County (21°04′20″S and 42°38′11″W), Minas Gerais State, Southeastern Brazil, whose local altitude ranges from 792 to 832 m above sea level. Grasslands, preserved secondary forest fragments, eucalyptus plantations and mining areas can be seen in the study site.

The region presents humid temperate climate with dry winters and hot summers, which is classified as Cwa, according to Köppen's climate classification (Sá Júnior et al., 2012).

Seasonal semideciduous mountain forest is the typical vegetation in the region and it belongs to the Atlantic Forest domain. Forest 1 was subjected to bauxite extraction by Votorantim Metais in 2008; subsequently, the company implemented recomposition and restoration processes based on these stages: topographic recomposition, deposition of soil fertile layer (0.30 m of topsoil was collected and stored before mining, near the area where the mining activity took place), soil acidity correction, phosphate fertilization, basic fertilization and planting of tree species (Table 1), at 3.0 m x 2.0 m spacing and side dressing. The restoration process was concluded in 2010 and the study about the soil seed bank in Forest 1 was conducted in 2015.

Forest 2, which is a preserved remnant stretch of a secondary seasonal semideciduous forest at mid-successional stage, was used as reference ecosystem to help the Forest 1 assessment process. Forest 2 presents the following structural characteristics: average canopy opening of 19.07%; 2.62 tree individuals m^{-2} in the natural regeneration layer; and 6,339 kg ha^{-1} of mean accumulated litter on the forest floor (Silva et al., 2018).

2.2. Data collection and analysis

Thirty 2.0 m × 2.0 m plots were allocated for study in each forest (Forest 1 and Forest 2) in 2015; they were distributed in six rows with five plants, which were spaced 5 m between plots and 40 m between rows. Since these are adjacent areas without physical separation, they were distributed based on the delimitation of the investigated forests, wherein 30 plots in Forest 1 mirrored 30 plots in Forest 2. A 0.25 m × 0.30 m wooden frame was cast in the center of each plot, where surface soil samples were collected 5.0 cm down in the ground, by disregarding the non-decomposed plant litter. In total, 60 samples (30 samples in Forest 1 and 30 samples in Forest 2) were collected and subjected to soil seed bank analysis.

The 60 soil samples were placed in properly labeled transparent plastic bags and sent to the shade house of the Research Plant Nursery at Federal University of Viçosa, Viçosa County, Minas Gerais State, where they were transferred to 0.25 m × 0.30 m × 0.05 m plastic trays with drainage holes at the bottom and arranged on 1-m-high bench tops. The trays were covered with 50% shading cloth to avoid external contamination. Two trays filled with sterilized sand were also arranged on the bench tops and used as controls. Soil samples were subjected to scheduled sprinkler irrigation (four 3-min-long irrigations on a daily basis) for six months. The soil seed bank was evaluated throughout this period based on the indirect seedling emergence method (Brown, 1992). Emerging seedlings were counted and identified once every two weeks; next, they were promptly removed from the trays.

Species were classified into families, and all their scientific names and respective authors were updated, according to the Angiosperm Phylogeny Group IV (2016).

Table 1. List of tree species used in the planting of Forest 1 (forest under restoration process).

Botanical family	Species	SC	DS
Anacardiaceae	*Schinus terebinthifolius* Raddi	P	Zoo
	Tapirira guianensis Aubl.	ES	Zoo
Apocynaceae	*Tabernaemontana laeta* Mart.	P	Zoo
Bignoniaceae	*Jacaranda puberula* Cham.	ES	Ane
	Sparattosperma leucanthum (Vell.) K.Schum.	ES	Ane
Bixaceae	*Bixa orellana* L.	P	Zoo
Boraginaceae	*Cordia trichotoma* (Vell.) Arráb. ex. Steud.	ES	Ane
Cannabaceae	*Trema micrantha* (L.) Blume	P	Zoo
Caricaceae	*Jacaratia spinosia* (Aubl.) A.DC.	P	Zoo
Euphorbiaceae	*Croton floribundus* Spreng.	P	Zoo
	Joannesia princeps Vell.	ES	Auto
Fabaceae	*Anadenanthera macrocarpa* (Benth.) Brenan	ES	Ane
	Andira anthelmia (Vell.) Benth.	ES	Zoo
	Apuleia leiocarpa (Vogel) J.F.Macbr.	LS	Ane
	Enterolobium contortisiliquum (Vell.) Morong	P	Zoo
	Erythrina falcata Benth.	P	Auto
	Hymenaea courbaril L.	LS	Zoo
	Inga edulis Mart.	ES	Zoo
	Leucaena leucocephala (Lam.) de Wit *	P	NC
	Machaerium nyctitans (Vell.) Benth.	ES	Ane
	Peltophorum dubium (Spreng.) Taub.	ES	Ane
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	ES	Auto
	Schizolobium parahyba (Vell.) Blake	P	Ane
	Senna multijuga (Rich.) H.S.Irwin & Barneby	ES	Auto
Lamiaceae	*Aegiphila integrifolia* (Jacq.) Moldenke	ES	Zoo
Lauraceae	*Aniba firmula* (Nees & Mart.) Mez	LS	Zoo
Malvaceae	*Ceiba speciosa* (A.St.-Hil.) Ravenna	LS	Ane
	Luehea divaricata Mart. & Zucc.	ES	Ane
Melastomataceae	*Tibouchina granulosa* (Desr.) Cogn.	P	Zoo
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	LS	Zoo
	Cedrela fissilis Vell.	LS	Ane
	Guarea guidonia (L.) Sleumer	LS	Zoo
	Melia azedarach L. *	P	Zoo
Moraceae	*Artocarpus heterophyllus* Lam. *	NC	Zoo
	Morus nigra L. *	NC	Zoo
Myrtaceae	*Syzygium cumini* (L.) Skeels *	P	Zoo
	Eucalyptus sp. *	P	NC
Rosaceae	*Cydonia oblonga* Mill. *	NC	NC
	Eriobotrya japonica (Thunb.) Lindl. *	LS	Zoo
Rubiaceae	*Genipa americana L.*	LS	Zoo
Sapindaceae	*Sapindus saponaria* L.	LS	Auto
Solanaceae	*Solanum bullatum* Vell.	P	Zoo
	Solanum mauritianum Scop.	P	Zoo
	Solanum paniculatum L.	P	Zoo
Vochysiaceae	*Callisthene fasciculata* Mart.	LS	Ane

SC: Successional category (P: Pioneer, ES: Early secondary, LS: Late secondary); DS: Dispersal syndrome (Ane: anemochory, Zoo: zoochory, Auto: autochory); *Exotic species in Brazil.

The Wilcoxon test for paired samples ($p < 0.05$) was used to compare mean values recorded for density of individuals and species richness in the forest undergoing restoration (Forest 1) to those recorded for the reference ecosystem (Forest 2).

Based on Gandolfi et al. (1995), samples were classified into successional categories for Brazilian seasonal semideciduous forests, as follows: pioneer, early secondary and late secondary species. They were also classified as zoochorous, anemochorous and autochorous species, based on propagule dispersal syndromes, according to van der Pijl (1982).

Floristic, dispersal syndrome and successional category similarities in bush-tree species between seed banks in Forest 1 and Forest 2, as well as species planted in Forest 1 and the ones found in Forest 2, were assessed. A floristic survey comprising Forest 2 species was conducted based on walking visits to forest sections, once a month for six months (Table 2).

Jaccard similarity coefficient was used to assess floristic similarity based on a qualitative matrix composed of data about the presence and absence of plant species. Morisita coefficient was used to assess the dispersal syndrome and successional category

Table 2. Floristics of the shrub-tree species from the Forest 2 (reference ecosystem).

Botanical family	Species	SC	DS	Hb
Annonaceae	*Annona cacans* Warm.	LS	Zoo	T
	Xylopia brasiliensis Spreng.	LS	Zoo	T
	Xylopia sericea A.St.-Hil.	ES	Zoo	T
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire et al.	P	Zoo	T
Arecaceae	*Euterpe edulis* Mart.	LS	Zoo	P
	Syagrus romanzoffiana (Cham.) Glassman	ES	Zoo	P
Asteraceae	*Piptocarpha macropoda* (DC.) Baker	P	Ane	T
	Vernonanthura divaricata (Spreng.) H.Rob.	P	Ane	T
Bignoniaceae	*Jacaranda micrantha* Cham.	ES	Ane	T
Boraginaceae	*Cordia sellowiana* Cham.	ES	Zoo	T
Clusiaceae	*Garcinia gardneriana* (Planch. & Triana) Zappi	LS	Zoo	T
Cyatheaceae	*Cyathea phalerata* Mart.	ES	Ane	P
Erythroxylaceae	*Erythroxylum deciduum* A.St.-Hil	LS	Zoo	T
	Erythroxylum pelleterianum A.St.-Hil	LS	Zoo	T
Euphorbiaceae	*Alchornea glandulosa* Poepp. & Endl.	P	Zoo	T
	Alchornea triplinervia (Spreng.) Müll.Arg.	P	Zoo	T
	Aparisthmium cordatum (A. Juss.) Baill.	ES	Auto	T
	Croton urucurana Baill.	P	Auto	T
	Maprounea guianensis Aubl.	ES	Auto	T
Fabaceae	*Apuleia leiocarpa* (Vogel) J.F. Macbr.	LS	Ane	T
	Bauhinia forficata Link	P	Auto	T
	Dalbergia nigra (Vell.) Allemão ex Benth.	ES	Ane	T
	Machaerium nyctitans (Vell.) Benth.	ES	Ane	T
	Peltophorum dubium (Spreng.) Taub.	ES	Ane	T
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	ES	Auto	T
	Pterogyne nitens Tul.	ES	Ane	T
	Tachigali rugosa (Mart. ex. Benth.) Zarucchi & Pipoly	LS	Ane	T
Hypericaceae	*Vismia guianensis* (Aubl.) Choisy	P	Zoo	T
Lacistemataceae	*Lacistema pubescens* Mart.	ES	Zoo	T
Lamiaceae	*Aegiphila integrifolia* (Jacq.) Moldenke	P	Zoo	T
Lauraceae	*Nectandra oppositifolia* Nees	LS	Zoo	T
	Ocotea corymbosa (Meisn.) Mez	ES	Zoo	T
Malvaceae	*Pseudobombax grandiflorum* (Cav.) A.Robyns	ES	Ane	T
Melastomataceae	*Miconia cinnamomifolia* (DC.) Naudin	P	Zoo	T
	Miconia pusilliflora (DC.) Naudin	ES	Zoo	T

SC: Successional category (P: Pioneer, ES: Early secondary, LS: Late secondary); DS: Dispersal syndrome (Ane: anemochory, Zoo: zoochory, Auto: autochory); Hb: Habit (T: Tree, S: Shrub, P: Palm tree); U: Uncharacterized.

Table 2. Continued...

Botanical family	Species	SC	DS	Hb
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	LS	Zoo	T
	Cedrela fissilis Vell.	LS	Ane	T
	Guarea guidonia (L.) Sleumer	LS	Zoo	T
	Trichilia catigua A.Juss.	LS	Ane	T
	Trichilia elegans A.Juss.	LS	Zoo	T
Moraceae	*Sorocea bonplandii* (Baill.) W.C.Burger et al.	LS	Zoo	T
Myristicaceae	*Virola bicuhyba* (Schott ex Spreng.) Warb.	LS	Zoo	T
Myrtaceae	*Myrcia splendens* (Sw.) DC.	ES	Zoo	T
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	ES	Zoo	T
Primulaceae	*Myrsine coriacea* (Sw.) R.Br. ex Roem. & Schult	ES	Zoo	T
	Myrsine umbellata Mart.	ES	Zoo	T
Rosaceae	*Prunus myrtifolia* (L.) Urb.	LS	Zoo	T
Rubiaceae	*Amaioua guianensis* Aubl.	LS	Zoo	T
	Bathysa nicholsonii K.Schum	ES	U	T
	Coffea arabica L.	U	U	S
	Guettarda viburnoides Cham. & Schltdl.	LS	Zoo	T
	Psychotria vellosiana Benth.	LS	Zoo	T
Rutaceae	*Hortia brasiliana* Vand. ex. DC.	LS	Zoo	T
	Zanthoxylum rhoifolium Lam.	P	Zoo	T
Salicaceae	*Casearia decandra* Jacq.	ES	Zoo	T
	Casearia sylvestris Sw.	P	Zoo	T
Sapindaceae	*Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl.	P	Zoo	T
	Matayba elaeagnoides Radlk.	ES	Zoo	T
Siparunaceae	*Siparuna guianensis* Aubl.	LS	Zoo	T
Urticaceae	*Cecropia glaziovii* Snethl.	P	Zoo	T
	Urera baccifera (L.) Gaudich. ex Wedd.	P	Zoo	T
Vochysiaceae	*Vochysia* sp.	U	Ane	T

SC: Successional category (P: Pioneer, ES: Early secondary, LS: Late secondary); DS: Dispersal syndrome (Ane: anemochory, Zoo: zoochory, Auto: autochory); Hb: Habit (T: Tree, S: Shrub, P: Palm tree); U: Uncharacterized.

similarities based on a quantitative matrix composed of data about species density.

Unweighted Pair Group Method with Arithmetic Mean (UPGMA) was used to interpret floristic, dispersal syndrome and successional category similarities; similar samples were clustered, depending on the selected variables, in order to generate a dendrogram.

3. RESULTS

3.1. Seed bank in the forest undergoing restoration (Forest 1)

In total, 4,872 seedlings from 61 plant species and 25 botanical families were identified in Forest 1 seed bank. Seven of the species were only identified at genus level, whereas one remained undetermined, although it was identified at family level (Table 3). Forest 1 seed bank had 2,165 propagules m^{-2}, which were distributed as follows: 1,497 grasses m^{-2}, 607 bushes m^{-2}, 59 trees m^{-2}, and two uncharacterized species m^{-2}. No seedling emerged in the control trays; this outcome showed lack of contamination with seeds from external sources in the experiment.

Botanical families Asteraceae, Phyllanthaceae, Plantaginaceae, Poaceae, Cyperaceae and Lamiaceae were significantly abundant and accounted for 91.79% of emerging seedlings. Family Asteraceae accounted for 37.64% of emerging seedlings; it was followed by family Phyllanthaceae (18.53%), which was only represented by species *Phyllanthus tenellus* Roxb.

Table 4 shows the distribution of species and individuals based on successional category and on dispersal syndrome.

Table 3. Floristics and phytosociology of the species from the F1 soil seed bank (restoration forest).

Botanical family/species	NI	RD(%)	RF(%)	SC	DS	Hb
Amaranthaceae						
Amaranthus blitum L.	17	0.35	0.87	U	U	H
Asteraceae						
Adenostemma verbesiana (L.) Kuntze	3	0.06	0.65	U	Ane	H
Ageratum conyzoides L.	671	13.78	4.77	P	Ane	H
Baccharis dentata (Vell.) G.M.Barroso	3	0.06	0.43	P	Ane	S
Baccharis dracunculifolia DC.	38	0.78	3.04	P	Ane	S
Baccharis trinervis Pers.	3	0.06	0.43	P	Ane	S
Bidens pilosa L.	8	0.16	0.43	P	Ane	H
Chromolaena odorata (L.) R.M.King & H.Rob	2	0.04	0.43	U	Ane	S
Conyza bonariensis (L.) Cronquist	48	0.99	4.77	P	Ane	H
Conyza canadensis (L.) Cronquist	21	0.43	3.04	P	Ane	H
Emilia fosbergii Nicolson	19	0.39	2.17	P	Ane	H
Erechtites hieracifolius (L.) Raf. ex DC.	29	0.60	3.04	P	Ane	H
Eupatorium sp.	1	0.02	0.22	U	Ane	S
Gnaphalium purpureum L.	40	0.82	3.47	ES	Ane	H
Gnaphalium sp.	2	0.04	0.43	U	Ane	H
Lessingianthus glabratus (Less.) H.Rob.	2	0.04	0.22	P	Ane	S
Porophyllum ruderale (Jacq.) Cass.	9	0.18	1.52	P	Ane	H
Sonchus oleraceus L.	9	0.18	1.95	U	Auto	H
Vernonanthura phosphorica (Vell.) H.Rob.	877	18.00	6.51	P	Ane	S
Vernonanthura westiniana (Less.) H.Rob.	14	0.29	2.60	P	Ane	S
Vernonia sp.	3	0.06	0.65	P	U	S
Youngia japonica (L.) DC.	32	0.66	1.30	ES	Ane	H
Boraginaceae						
Varronia curassavica Jacq.	2	0.04	0.43	P	Zoo	S
Brassicaceae						
Raphanus raphanistrum L.	3	0.06	0.43	P	Auto	H
Cannabaceae						
Trema micrantha (L.) Blume	96	1.97	3.04	P	Zoo	T
Cyperaceae						
Cyperus esculentus L.	317	6.52	1.95	P	Ane	H
Cyperus haspan L.	35	0.72	1.30	P	Ane	H
Cyperus meyenianus Kunth	31	0.64	1.52	P	Ane	H
Kyllinga brevifolia Rottb.	33	0.68	1.74	P	U	H
Euphorbiaceae						
Euphorbia heterophylla L.	6	0.12	0.43	U	Zoo	H
Fabaceae						
Leucaena leucocephala (Lam.) de Wit	5	0.10	0.43	P	U	T
Indeterminate						
Ideterminate 1	4	0.08	0.87	U	U	U
Lamiaceae						
Marsypianthes chamaedrys (Vahl) Kuntze	1	0.02	0.22	P	Auto	H
Mesosphaerum suaveolens (L.) Kuntze	386	7.93	4.56	P	Zoo	S
Lauraceae						
Nectandra lanceolata Nees	8	0.16	0.87	LS	Zoo	T
Lythraceae						
Cuphea carthagenensis (Jacq.) J.Macbr.	28	0.57	1.95	U	Ane	H

NI: Number of individuals; RD: Relative density; RF: Relative frequency; SC: Successional category (P: Pioneer, ES: Early secondary, LS: Late secondary); DS: Dispersal syndrome (Ane: anemochory; Zoo: zoochory; Auto: autochory); Hb: Habit (T: Tree, S: Shrub, H: Herb); U: Uncharacterized.

Table 3. Continued...

Botanical family/species	NI	RD(%)	RF(%)	SC	DS	Hb
Malvaceae						
Sida rhombifolia L.	26	0.53	1.74	P	Ane	H
Triumfetta rhomboidea Jacq.	8	0.16	1.08	P	Zoo	S
Melastomataceae						
Clidemia hirta (L.) D.Don	5	0.10	0.43	P	Zoo	S
Tibouchina sp.	1	0.02	0.22	U	Zoo	T
Onagraceae						
Ludwigia tomentosa (Cambess.) H.Hara	6	0.12	0.43	P	Ane	S
Oxalidaceae						
Oxalis corniculata L.	83	1.70	4.12	U	Auto	H
Phyllanthaceae						
Phyllanthus tenellus Roxb.	903	18.54	5.42	ES	Auto	H
Plantaginaceae						
Scoparia dulcis L.	469	9.64	3.04	P	Ane	H
Poaceae						
Andropogon bicornis L.	13	0.27	1.52	P	Ane	H
Eleusine indica (L.) Gaertn.	1	0.02	0.22	P	Ane	H
Melinis minutiflora P.Beauv.	9	0.18	1.08	P	Ane	H
Melinis repens (Willd.) Zizka	1	0.02	0.22	P	Ane	H
Paspalum notatum Flüggé	1	0.02	0.22	P	Ane	H
Paspalum sp.	281	5.77	4.12	P	Ane	H
Setaria parviflora (Poir.) Kerguélen	16	0.33	0.87	P	Ane	H
Urochloa decumbens (Stapf) R.D.Webster	137	2.81	4.56	P	Ane	H
Urochloa sp.	4	0.08	0.43	P	Ane	H
Rosaceae						
Rubus sp.	2	0.04	0.22	U	Zoo	H
Rubiaceae						
Borreria latifolia (Aubl.) K.Schum.	4	0.08	0.43	ES	Auto	H
Scrophulariaceae						
Buddleja stachyoides Cham. & Schltdl.	14	0.29	0.22	P	U	S
Solanaceae						
Physalis angulata L.	1	0.02	0.22	P	Ane	H
Solanum americanum Mill.	56	1.15	3.90	P	Zoo	H
Solanum mauritianum Scop.	23	0.47	2.17	P	Zoo	T
Urticacaceae						
Cecropia hololeuca Miq.	1	0.02	0.22	P	Zoo	T
Verbenaceae						
Lantana camara L.	1	0.02	0.22	P	Zoo	S
Total	4,872	100.00	100.00			

NI: Number of individuals; RD: Relative density; RF: Relative frequency; SC: Successional category (P: Pioneer, ES: Early secondary, LS: Late secondary); DS: Dispersal syndrome (Ane: anemochory; Zoo: zoochory; Auto: autochory); Hb: Habit (T: Tree, S: Shrub, H: Herb); U: Uncharacterized.

Table 4. Distribution of species and individuals in relation to the successional category and to the dispersal syndrome from the F1 soil seed bank (restoration forest).

	Dispersal syndrome (%)				Sucessional category (%)			
	Zoo	Ane	Auto	U	P	ES	LS	U
Specie	21.31	59.01	9.84	9.84	72.13	6.56	1.64	19.67
Individual	12.21	65.64	20.59	1.56	76.50	20.10	0.16	3.24

P: Pioneer, ES: Early secondary, LS: Late secondary, Ane: anemochory, Zoo: zoochory, Auto: autochory, U: Uncharacterized.

3.2. Reference ecosystem seed bank (Forest 2)

In total, 764 seedlings from 58 plant species and 25 botanical families emerged in Forest 2 seed bank. Eight of these species were only identified at genus level, whereas three remained unidentified and were also not classified at family level (Table 5). Density measurements showed 340 propagules m^{-2}, which were distributed as follows: 157 trees m^{-2}, 104 grasses m^{-2}, 78 bushes m^{-2} and two creepers m^{-2}. There was not seedling emergence in the control trays; this outcome showed lack of contamination with seeds from external sources in the experiment.

Botanical families Solanaceae, Poaceae, Melastomataceae and Asteraceae stood out for their abundance; they accounted for 79.19% of emerging seedlings. Family Solanaceae accounted for 25.92%

Table 5. Floristics and phytosociology of the species from the F2 soil seed bank (reference ecosystem).

Botanical family/species	NI	RD	RF	SC	DS	Hb
Asteraceae						
Ageratum conyzoides L.	1	0.13	0.41	P	Ane	H
Baccharis dentata (Vell.) G.M.Barroso	1	0.13	0.41	P	Ane	S
Conyza bonariensis (L.) Cronquist	4	0.52	1.63	P	Ane	H
Eclipta prostata (L.) L.	1	0.13	0.41	P	Ane	H
Erechtites hieracifolius (L.) Raf. ex DC.	29	3.80	4.08	P	Ane	H
Eupatorium sp.	8	1.05	2.86	U	Ane	S
Gnaphalium purpureum L.	8	1.05	2.04	ES	Ane	H
Helichrysum elatum A.Cunn. ex DC.	1	0.13	0.41	ES	Ane	H
Vernonanthura divaricata (Spreng.) H.Rob.	1	0.13	0.41	P	Ane	T
Vernonanthura phosphorica (Vell.) H.Rob.	28	3.67	5.71	P	Ane	S
Vernonanthura westiniana (Less.) H.Rob.	26	3.40	6.93	P	Ane	S
Cannabaceae						
Trema micrantha (L.) Blume	34	4.46	4.90	P	Zoo	T
Cyperaceae						
Kyllinga brevifolia Rottb.	2	0.26	0.41	P	U	H
Scleria gaertneri Raddi	5	0.65	0.41	U	Zoo	H
Euphorbiaceae						
Alchornea glandulosa Poepp. & Endl.	1	0.13	0.41	P	Zoo	T
Alchornea triplinervia (Spreng.) Müll.Arg.	15	1.96	3.67	P	Zoo	T
Maprounea guianensis Aubl.	12	1.57	2.86	ES	Auto	T
Fabaceae						
Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima	2	0.26	0.82	ES	Ane	T
Hypericaceae						
Vismia guianensis (Aubl.) Choisy	7	0.92	2.86	P	Zoo	T
Indeterminate						
Indeterminate 1	1	0.13	0.41	U	U	T
Indeterminate 2	1	0.13	0.41	U	U	C
Indeterminate 3	1	0.13	0.41	U	U	C
Lamiaceae						
Aegiphila integrifolia (Jacq.) Moldenke	3	0.39	1.22	ES	Zoo	T
Mesosphaerum suaveolens (L.) Kuntze	1	0.13	0.41	P	Zoo	H
Malvaceae						
Ceiba speciosa (A.St.-Hil.) Ravenna	1	0.13	0.41	LS	Ane	T
Sida sp.	1	0.13	0.41	P	Ane	H

NI: Number of individuals; RD: Relative density; RF: Relative frequency; SC: Successional category (P: Pioneer, ES: Early secondary, LS: Late secondary); DS: Dispersal syndrome (Ane: anemochory; Zoo: zoochory; Auto: autochory); Hb: Habit (T: Tree, S: Shrub, H: Herb, C: Climber); U: Uncharacterized.

Table 5. Continued...

Botanical family/species	NI	RD	RF	SC	DS	Hb
Melastomataceae						
Clidemia hirta (L.) D.Don.	96	12.58	6.11	P	Zoo	S
Leandra niangaeformis Cogn.	4	0.52	1.63	P	Zoo	S
Miconia cinnamomifolia DC. Naudin	4	0.52	1.22	P	Zoo	T
Miconia latecrenata DC. Naudin	2	0.26	0.82	P	Zoo	T
Miconia sellowiana Naudin	10	1.31	1.63	P	Zoo	T
Tibouchina granulosa (Desr.) Cogn.	20	2.62	4.49	P	Zoo	T
Meliaceae						
Trichilia elegans A.Juss.	1	0.13	0.41	LS	Zoo	T
Myrtaceae						
Myrcia splendens (Sw.) DC.	1	0.13	0.41	ES	Zoo	T
Oxalidadaceae						
Oxalis corniculata L.	1	0.13	0.41	U	Auto	H
Phyllanthaceae						
Phyllanthus tenellus Roxb.	3	0.39	1.22	ES	Auto	H
Phytolaccaceae						
Phytolacca americana L.	3	0.39	1.22	P	Zoo	H
Piperaceae						
Piper sp.	2	0.26	0.82	P	Zoo	S
Poaceae						
Andropogon bicornis L.	6	0.79	1.63	P	Ane	H
Panicum sellowii Ness	15	1.96	2.04	P	Ane	H
Paspalum sp.	3	0.39	0.41	P	Ane	H
Urochloa sp.	139	18.20	2.86	P	Ane	H
Primulaceae						
Myrsine parvula (Mez) Otegui	3	0.39	0.82	ES	Zoo	T
Rubiaceae						
Coccocypselum aureum (Spreng.) Cham. & Schltdl.	1	0.13	0.41	U	Zoo	H
Coccocypselum sp.	2	0.26	0.82	U	Zoo	H
Genipa americana L.	4	0.52	1.22	LS	Zoo	T
Guettarda uruguensis Cham. & Schltdl.	1	0.13	0.41	ES	Zoo	S
Psychotria sp.	4	0.52	1.22	LS	Zoo	S
Rutaceae						
Zanthoxylum rhoifolium Lam.	2	0.26	0.82	P	Zoo	T
Salicaceae						
Casearia decandra Jacq.	4	0.52	1.63	ES	Zoo	T
Sapindaceae						
Serjania laruotteana Cambess.	1	0.13	0.41	U	Auto	C
Solanaceae						
Solanum americanum Mill.	8	1.05	1.63	P	Zoo	H
Solanum cernuum Vell.	18	2.36	3.27	P	Zoo	T
Solanum mauritianum Scop.	167	21.87	6.12	P	Zoo	T
Solanum paniculatum L.	5	0.65	1.22	P	Zoo	S
Styracaceae						
Styrax sp.	1	0.13	0.41	U	Zoo	T
Urticaceae						
Cecropia glaziovii Snethl.	7	0.92	2.04	P	Zoo	T
Cecropia hololeuca Miq.	31	4.06	4.90	P	Zoo	T
Total	764	100.00	100.00			

NI: Number of individuals; RD: Relative density; RF: Relative frequency; SC: Successional category (P: Pioneer, ES: Early secondary, LS: Late secondary); DS: Dispersal syndrome (Ane: anemochory; Zoo: zoochory; Auto: autochory); Hb: Habit (T: Tree, S: Shrub, H: Herb, C: Climber); U: Uncharacterized.

of emerging seedlings (species *Solanum mauritianum* Scop. was well represented in this family) and it was followed by family Poaceae (21.34%).

Table 6 presents the distribution of species and individuals based on successional category and on dispersal syndrome.

3.3. Comparison between forest undergoing restoration (Forest 1) and reference ecosystem (Forest 2)

The mean density of emerging seedlings (number of individuals m^{-2}) deriving from the seed bank was different (Z=4.638; p<0.001) between the two investigated forests; the forest undergoing restoration recorded higher seedling emergence (2,165 ± 1,788 seedlings m^{-2}) than the reference ecosystem (340 ± 324 seedlings m^{-2}) (Figure 1).

The mean species richness per m^2 did not show significant difference (Z=0.462; p=0.643) between forests, the forest under restoration recorded 27.0 ± 5.6 species m^{-2}, whereas the reference ecosystem recorded 25.7 ± 11.1 species m^{-2} (Figure 1).

There was not floristic similarity among Forest 1 and Forest 2 seed banks, species planted in in Forest 1, and adult shrubby-tree species found in Forest 2 (Figure 2). Forest 1 seed bank recorded the emergence of 22 shrub-tree seedling species, whereas 35 species were identified in Forest 2 seed bank. The following shrub-tree species were often found in the seed bank of both forests: *Baccharis dentata* (Vell.) G.M.Barroso, *Cecropia hololeuca* Miq., *Clidemia hirta* (L.) D.Don., *Eupatorium* sp., *Solanum mauritianum*, *Trema micrantha* (L.) Blume, *Vernonanthura phosphorica* (Vell.) H.Rob. and *Vernonanthura westiniana* (Less.) H.Rob.

Both forests showed high similarity in dispersal syndrome; Morisita index values ranged from 0.84 to 0.99. The highest similarity was recorded between Forest 2 seed bank and Forest 2 flora (Figure 3).

Both forests also presented highly similar successional category; Morisita index values ranged from 0.65 to 0.95, except between Forest 2 flora and Forest 1 seed bank (0.43). The highest similarity was observed between species in successional categories of Forest 1 plantings and Forest 2 flora (Figure 4).

Table 6. Distribution of species and individuals in relation to the successional category and to the dispersal syndrome from the F2 soil seed bank (reference ecosystem).

	Dispersal syndrome (%)				Sucessional category (%)			
	Zoo	Ane	Auto	U	P	ES	LS	U
Specie	55.17	31.03	6.90	6.90	58.62	17.24	6.90	17.24
Individual	61.12	36.00	2.23	0.65	90.84	4.97	1.31	2.88

P: Pioneer, ES: Early secondary, LS: Late secondary, Ane: anemochory, Zoo: zoochory, Auto: autochory, U: Uncharacterized.

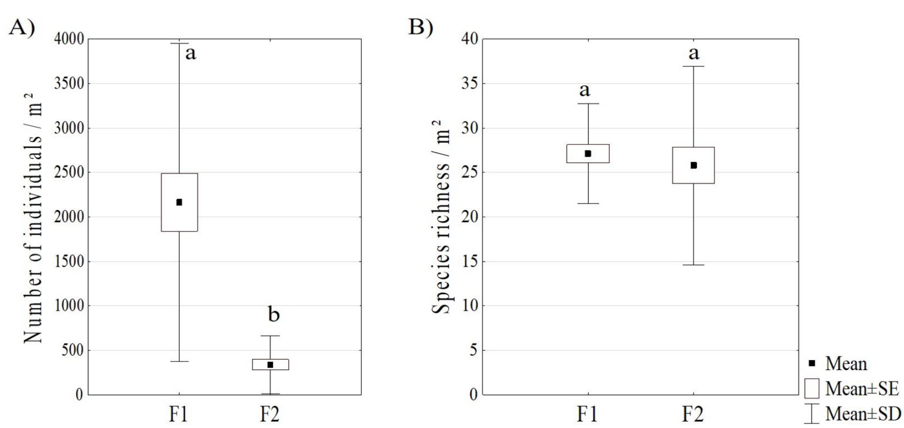

Figure 1. Number of individuals m^{-2} (A) and species richness m^{-2} (B) in soil seed banks from the forest undergoing restoration (F1) and from the reference ecosystem (F2). SE = Standard error; SD = Standard deviation. Means followed by the same letter did not differ from each other in the Wilcoxon test (p>0.05).

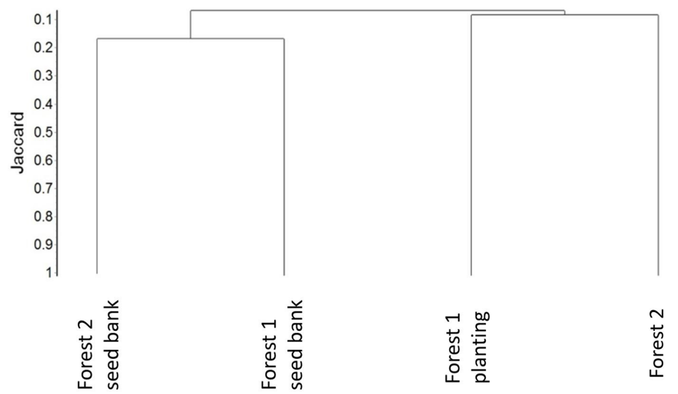

Figure 2. Floristic similarity dendrogram generated through the unweighted pair group method with arithmetic mean (UPGMA), based on the Jaccard similarity coefficient for data about the absence and presence of shrub-tree species in Forest 1 and Forest 2 seed banks, species planted in Forest 1 (Forest 1 planting), and species found in Forest 2, São Sebastião da Vargem Alegre County, MG, Brazil.

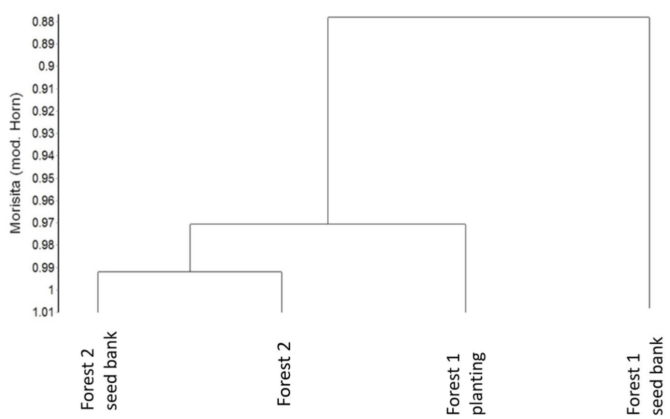

Figure 3. Dispersal syndrome similarity dendrogram generated through the unweighted pair group method with arithmetic mean (UPGMA), based on Morisita coefficient from a matrix composed of quantitative density data about shrubby-tree species in Forest 1 and Forest 2 seed banks, species planted in Forest 1 (Forest 1 planting) and species found in Forest 2, São Sebastião da Vargem Alegre County, MG, Brazil.

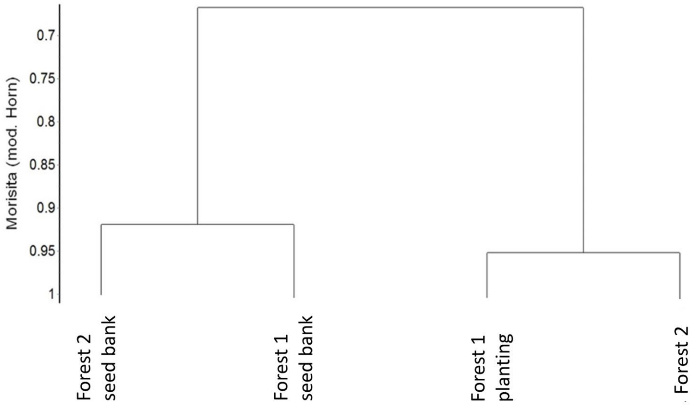

Figure 4. Successional category similarity dendrogram generated through the unweighted pair group method with arithmetic mean (UPGMA) method, based on Morisita coefficient from a matrix composed of quantitative density data about shrubby-tree species in Forest 1 and Forest 2 seed banks, species planted in Forest 1 (Forest 1 Planting), and species found in Forest 2, São Sebastião da Vargem Alegre County, MG, Brazil.

4. DISCUSSION

Soil seed banks in areas undergoing early succession process tended to have larger number of seeds, whereas the number of viable seeds decreased as the successional process advanced, as shown in several studies (Araújo et al., 2001; Baider et al., 2001; Sorreano, 2002; Franco et al., 2012).

The seed bank in the forest undergoing restoration presented the highest density of herbaceous individuals and herbaceous species richness; this outcome was similar to the ones found in other studies conducted in tropical forest areas undergoing secondary succession process (Martins et al., 2008; Calegari et al., 2013; Figueiredo et al., 2014; Oliveira et al., 2018). These species are essential to enable the succession process in altered areas during their first colonization stage (Araujo et al., 2004). Herbaceous species can adapt better to disturbed areas and improve soil conditions (Silva-Weber et al., 2012) by enhancing water retention; therefore, they help preventing soil erosion and increase the amount of organic matter in the soil. This improvement in soil conditions favors the development of pioneer bush-tree species.

The reference ecosystem seed bank recorded higher density of tree individuals and tree species richness because it was a well-preserved forest remnant at mid-successional stage. Herbaceous species density tends to decrease, and tree species density tends to increase in soil seed banks as the succession process advances (Baider et al., 2001; Calegari et al., 2013).

Family Asteraceae represented a particularly large number of species and individuals identified in Forest 1 seed bank; most of them presented herbaceous habit and anemochorous dispersal syndrome, a fact that significantly increased their dissemination and, therefore, their abundance in the seed bank. Franco et al. (2012) also found larger number of herbaceous species in their study site, mainly of species belonging to family Asteraceae, which stood out for the highest number of species in the analysis of the seed bank of a seasonal semideciduous forest stretch in Minas Gerais State. Similar findings were also reported in other surveys conducted in tropical forests of the Atlantic Forest domain (Baider et al., 2001; Sccoti et al., 2011; Figueiredo et al., 2014). Species belonging to family Asteraceae present efficient adaptive ability and can be found in different phytophysiognomies (Beretta et al., 2008). Family Asteraceae stands out among angiosperms for its great diversity, which results from the colonization of different habitats and from efficient pollination and seed dispersion methods (Beretta et al., 2008).

Notably, *Melinis minutiflora* P.Beauv., *Urochloa decumbens* (Stapf) R.D.Webster and *Leucaena leucocephala* (Lam.) de Wit, which are invasive exotic species that can negatively affect the forest succession process, were found in Forest 1. The high growth, reproduction and dissemination ability of these invasive species can hinder, or even prevent, the establishment of native species that play a key role in forest healing and succession processes; therefore it is important taking into consideration the risk of having these invasive species becoming established species in disturbed areas (Franco et al., 2012). Thus, controlling these species, which often find favorable resources available to their perpetuation in areas undergoing restoration, is crucial to avoid compromising the forest restoration process (DeMeester & Richter, 2009; Kettenring & Adams, 2011).

4.1. Successional categories and dispersal syndromes

Soil seed banks mostly comprise pioneer species, which form the persistent seed bank and maintaining viable seeds in the soil for a long period of time, until the environmental conditions are appropriate for germination (Araújo et al., 2001; Erfanzadeh et al., 2010). These pioneer species found in the seed bank are responsible for healing clearings in tropical forests (Pereira et al., 2010; Correia & Martins, 2015). Thus, the composition and density of the seed banks evaluated in the current study suggest that they can be resilient to forest disturbances. However, it is essential highlighting the importance of monitoring and, if necessary, controlling the incidence of invasive exotic species in these areas.

Species presenting anemochorous dispersal syndrome prevailed in Forest 1 seed bank due to high herbaceous species density and richness, a fact that facilitated their dissemination in the area. Conversely, Forest 2 seed bank showed predominance of species with zoochorous dispersal syndrome, since Forest 2 is a well-preserved forest remnant at mid-successional stage. Zoochorous dispersal is the dispersal mode most often found in tropical forests (Sansevero et al., 2011), mainly in larger areas and fragment aggregations (Jesus et al., 2012).

Guimarães et al. (2014) have investigated the seed bank of four areas undergoing restoration process in the seasonal semideciduous forest phytophysiognomy belonging to the Atlantic Forest domain; each area was subjected to different restoration method types. Based on their results, anemochorous dispersal syndrome was the most dominant dispersion type (43.5% species); families Asteraceae and Poaceae recorded the highest number of anemochorous species. Similarly, Miranda Neto et al. (2017) conducted a study in a forest undergoing restoration after being subjected to bauxite mining activity and found predominance of anemochorous dispersion species, which mainly comprised herbaceous species; Poaceae was the most abundant family in the investigated site.

According to the present study, most bush-tree species presenting zoochorous dispersal syndrome were found along the strata of Forest 2. Thus, forests undergoing restoration process should naturally experience seed and seedling bank enrichment over time, since this forest type is attractive to seed dispersing fauna. The large number of zoochorous species assessed in Forest 2 flora helps conserving the fauna associated with the phytophysiognomy (Coelho et al., 2016) investigated in the present study. Moreover, Forest 2 houses key species for the restoration of degraded areas, such as *Euterpe edulis* Mart. This species has great reproductive ability, since its fruits are very attractive to the wild fauna (Matos & Bovi, 2002), a fact that facilitates its regeneration in the understory of forests, as well as its secondary growth, in addition to accelerating ecological succession processes through natural enrichment (Ribeiro et al., 2011).

4.2. Similarities

Floristic dissimilarity among Forest 1 and Forest 2 seed banks, Forest 1 planting and Forest 2 flora may be explained by the fact that a large percentage of adult tree species found in Forest 2 belong to the successional groups of late and early secondary species. Most of these species do not often form seed banks because they have large seeds that cannot easily move in plant litter and, consequently, they are hardly incorporated in the soil (Martins et al., 2015) and get more exposed to predators such as small rodents and ants. The density of viable seeds in Forest 2 seed bank tended to decrease because Forest 2 is a forest remnant at mid-successional stage. Despite the dissimilarity between Forest 1 seed bank and Forest 1 planted species, the natural enrichment of the forest undergoing restoration based on mid-successional stage forest species should take place within a few years and, consequently, the floristic similarity between them should increase due to the proximity of the two forests.

Although there is no floristic similarity between shrub-tree species in the investigated forests, the high similarity in the distribution of dispersal syndrome and successional category of shrub-tree species indicates that similar ecological processes have taken place in Forests 1 and 2. Moreover, the forest undergoing restoration is comparable to the reference forest in terms of configuration and distribution of propagule dispersal modes and ecological groups. Ecological processes provide important information about whether a given area undergoing restoration process can be resilient and reverse biodiversity losses (Brancalion et al., 2010; Bullock et al., 2011), as well as about the necessary conditions for forest succession implementation (Scheller et al., 2007).

5. CONCLUSION

The soil seed bank in the forest undergoing restoration process after being subjected to bauxite mining activity recorded higher density of emerging seedlings than that of the reference ecosystem. The higher seedling density found in the soil seed bank of the forest undergoing restoration is mostly attributed to pioneer herbaceous and shrub species. This outcome suggests their resilience potential in case of natural or anthropic disturbances.

The highly similar dispersal syndrome distribution and successional category of shrub-tree species indicated that ecological processes have taken place in both forests.

Therefore, we conclude that the restoration performed in the mined area has successfully recovered the soil seed bank density after a few years, as well as that the enrichment of tree species in this seed bank will naturally happen due to its proximity to the reference ecosystem (mid-successional stage forest).

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