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Ecology of the Seed Bank in the Amazon Rainforest

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Abstract

The seed bank is directly related to forest resilience because it contributes to the greatest number of regenerants after the occurrence of disturbances. Changes in seed density, floristic composition, and life forms completely alter the successional trajectory of forest environments. These changes are directly related to land use. For example, suppression of the seed bank can occur in pastures, that experience frequent fires with increase of density of seeds and predominance of herbs are typical of highly degraded areas, such as Poaceae, Rubiaceae, Asteraceae, and Cyperaceae. Melastomataceae seedlings are an important component of the seed bank in the Amazon rainforest. On the other hand, Urticaceae has greater representation in forests that exhibit low-impact land use. Any change in seed bank functionality is bound to compromise the diversity, regeneration potential and overall maintenance of tropical forests. Therefore, it is necessary to expand studies that investigate seed banks in the Amazon rainforest. It is as important to prioritize sampling methods and pursue standardization of data presentation, as well as improve the identification of species that occur in the seed bank.

Keywords: floristic composition, forest disturbance, anthropic changes, forest regeneration, land use

1. Introduction

The seed bank, or stock of viable seeds in the soil, can be defined as a set of latent, or dormant, seeds capable of originating adult plants [1, 2]. Studying the composition of the seed bank and understanding its role in regeneration are important to the conservation and management of tropical forests, as well as the control and eradication of invasive species in agrosilvopastoral systems [3–8]. The seed bank is influenced by the local plant community, history of land use, and forest matrix in general, it also has spatial and temporal variations [5, 9–12]. Spatial variations occur both horizontally and vertically; however, the greatest amounts of seed are observed in the upper layers [13–16]. Temporal variation occurs as a result of both loss and incorporation of seeds in the soil [13, 17]. The incorporation of seeds is the result of seed rain, which also presents seasonality owing to the different fruiting patterns of the species [9, 18, 19]. The rate of seed loss in the soil depends intrinsic loss of viability resulting from dispersal, environmental conditions, predation, and attack of pathogens [17, 20, 21].

Seeds of pioneer species are found in high density in the soils of tropical forests and constitute the main reserve of propagules for the regeneration of areas subject to disturbances [10, 22–24]. Most pioneer species have quiescent diaspores, owing to

canopy light conditions or temperature variations [25–27], and compound the persistent seed bank [10, 22–24]. Species that compound the transitional seed bank have a lower density and are composed of late species of the forest succession [10, 14, 22], commonly forming a seedling bank [28, 29]. Consequently, floristic composition of the tropical rainforest seed bank does not reflect the composition of species in the arboreal, or regenerating, strata of old-growth forests [8, 14, 29]. Thus, seed bank serve to allow the establishment of a set of species that do not occur in vegetation or that present in low density in old-growth forests, but persist in the seed bank [18, 30–32].

After formation of a clearing by natural or anthropic disturbance, the quantity of seeds in the soil decreases as a consequence of recruitment rates or loss of seed viability [14, 29, 33]. After the establishment of pioneer species and subsequent fruiting, seed density in the soil increases in the initial stages [9, 21, 24, 29, 33, 34]. The, with the advance of forest succession, the number of seeds in the seed bank tends to decrease and return to pre-disturbance equilibrium [9, 21, 24, 29, 33, 34]. The seed bank plays a major role in the re-establishment of plant communities subjected to medium and high-intensity disturbances and can have a wide impact on the dynamics of plant communities during the process of ecological succession [35–38]. For example, in forest areas of the Amazon burned and converted to pasture, almost no vestiges of the seed bank, remain [39]. Nonetheless, pioneer species of *Vismia* were reported to dominate regeneration [40, 41]. In contrast, areas with some seed bank left intact were initially reported to already be occupied by pioneer species of *Cecropia*, allowing a larger set of plant species to regenerate under its canopy [36, 39, 42–44]. In terms of forest management, the role of the seed bank in the regeneration of forests increases in importance, when compared to the seed rain, both in clearings and trails generated by skidders [45].

The seed bank is known for its low contribution to the establishment of late species in the forest succession in which these groups derived from dispersion and stock seedlings [1, 14]. However, the seed bank can be considered highly diverse in life forms thus contributing to the restructuring of forest strata [33, 46]. The abundance of herbs and shrubs in the seed bank of forest environments can be a consequence of the surrounding matrix, as well as the history of land use [5, 14, 22]. It is a reflection of vegetation that has already undergone some type of anthropic or natural change [5, 29, 33, 47]. In general, herbaceous and shrub species are more commonly found in altered areas and secondary vegetation [14]. However, disturbances that occur around the forest also contribute to the entry of ruderal, or invasive, species in the seed bank [5]. Notwithstanding this phenomenon, forest areas surrounding pastures or agricultural areas change the density and floristic composition of the seed bank in these areas [5]. This gives rise to the entry of common trees and shrubs into the seed bank of forest areas [5]. The seed bank in tropical forests is, therefore, highly variable. At the same time, studies reporting on this natural component of the Brazilian rainforest are scarce. Therefore, this chapter aims to analyze variations in density, family abundance, and life forms of the seed bank in *terra firme* forest of the Amazon rainforest, as well as assess the impact of the main changes in land use in this region on seed bank characteristics.

2. Materials and methods

Data were obtained from published and unpublished scientific reports and monographs written by undergraduate students under the supervision of Dr. Niwton Leal Filho of the National Institute for Amazon Research (INPA). One dataset contains complete data on density and floristic composition. We used 17 datasets from a seed bank in *terra firme* forest of the Amazon rainforest, which dataset [48–50] was not included in the floristic composition. **Table 1** list all datasets

Study area location	Latitude and longitude	Type of disturbance	EA	N	A	D	DS	Reference
(1) Old-growth forest (with no evidence of anthropogenic changes in the last 60 years or more)								
Biological Dynamics of Forest Fragments Project (BDFFP), Amazonas, Brazil	2°25' S; 59°50' W	—	—	90	0.70	2	913 ± 1112	unpublished data
Experimental Station of Tropical Forestry (EEST), Amazonas, Brazil	2°37'38" S; 60°09'11" W	—	—	30	0.71	3	722	unpublished data
Biological Dynamics of Forest Fragments Project (BDFFP), Manaus, Amazonas, Brazil	2°25' S; 59°50' W	—	—	45	1.01	3	662 ± 741	[7]
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°36'50" S; 60°12'13" W	—	—	160	5.03	5	498 ± 437	[46]
Adolfo Ducke Forest Reserve, Amazonas, Brazil	02°53' S; 59°58' W	—	—	1440	11.31	2	460	[19]
River Capim Farm, Paragominas, Pará, Brazil	03°37'59.9" S; 48°32'46.8" W	—	—	60	3.75	5	423	[57]
Adolfo Ducke Forest Reserve (riparian or bottomlands forest, with periodic flooding), Amazonas, Brazil	02°53' S; 59°58' W	—	—	72	4.32	10	367	[58]
Adolfo Ducke Forest Reserve, Amazonas, Brazil	02°53' S; 59°58' W	—	—	30	0.24	5	299	unpublished data
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°37' S; 60°09' W	—	—	30	0.24	5	246	unpublished data
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°37' S; 60°09' W	—	—	40	0.31	3	194 ± 263	unpublished data
Ferreira Penna Scientific Station (ECFPn), Melgaço, Pará, Brazil	1°42'30" S; 51°31'45" W	—	—	100	6.25	5	94 ± 61	[50]
(2) Forest fragments								
Biological Dynamics of Forest Fragments Project (BDFFP), Amazonas, Brazil	2°25' S; 59°50' W	Remaining isolated forest fragments of 1 ha	25	90	0.70	2	4073 ± 3578	unpublished data
Biological Dynamics of Forest Fragments Project (BDFFP), Amazonas, Brazil	2°25' S; 59°50' W	Remaining isolated forest fragments of 10 ha	25	90	0.70	2	3829 ± 2565	unpublished data

Study area location	Latitude and longitude	Type of disturbance	EA	N	A	D	DS	Reference
Biological Dynamics of Forest Fragments Project (BDFFP), Amazonas, Brazil	2°25' S; 59°50' W	Remaining isolated forest fragments of 1 ha	30	45	1.01	3	1690 ± 2530	[7]
Biological Dynamics of Forest Fragments Project (BDFFP), Amazonas, Brazil	2°25' S; 59°50' W	Remaining isolated forest fragments of 10 ha	30	45	1.01	3	1309 ± 787	[7]
Science Grove of the National Institute for Amazon Research (INPA), Manaus, Amazonas, Brazil	03°08' S; 60°10' W	Urban fragment of 13 ha, with a history of selective logging before the creation of the preservation area	47	30	2.40	5	1264 ± 969	unpublished data
Science Grove of the National Institute for Amazon Research (INPA), Manaus, Amazonas, Brazil	3°05'50"S; 59°59'10" W	Urban fragment of 13 ha, with a history of selective logging before the creation of the preservation area	47	30	0.24	5	747	unpublished data
Mindú Park, Manaus, Amazonas, Brazil	03°07' S; 59° 05' W	Urban fragment of 31 ha, with a history of selective logging before the creation of the preservation area	30	30	0.24	5	633	unpublished data
Biological Dynamics of Forest Fragments Project (BDFFP), Amazonas, Brazil	2°25' S; 59°50' W	Remaining isolated forest fragments of 100 ha	30	45	1.01	3	576 ± 450	[7]
Petro Set, preservation area, Manaus, Amazonas, Brazil	03°04' S; 59°58'W	Urban fragment of 2 ha intensely altered, with a history of selective logging before the creation of the preservation area	40	30	0.24	5	410	unpublished data
Federal University of Amazonas (UFAM), Manaus, Amazonas, Brazil	03°4.34' S; 59°57.30' W	Urban fragment of 800 ha, with a history of selective logging before the creation of the preservation area	55	30	0.24	5	395 ± 68	unpublished data

Study area location	Latitude and longitude	Type of disturbance	EA	N	A	D	DS	Reference
(3) Forests with logging of wood species								
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°36'50" S; 60°12'13" W	The area explored in forest management, clearing of exploration	14	30	0.71	3	2219	unpublished data
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°36'50" S; 60°12'13" W	Explored area of forest management, tractor trail	14	30	0.71	3	1561	unpublished data
Experimental Genetic Resource Station "José Haroldo", Benevides, Pará, Brazil	01°10' S; 48°20' W	Old-growth forest with logging of wood species	17	25	6.25	8	1427 ± 729	[59]
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°36'50" S; 60°12'13" W	Explored area of forest management, tractor trail	21	30	0.71	3	1274	unpublished data
Experimental Genetic Resource Station "José Haroldo", Benevides, Pará, Brazil	01°10' S; 48°20' W	Old-growth forest with logging of wood species	30	25	6.25	8	756 ± 250	[59]
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°36'50" S; 60°12'13" W	The area explored in forest management, clearing of exploration	21	30	0.71	3	711	unpublished data
River Capim Farm, Paragominas, Pará, Brazil	03°37'59.9" S; 48°32'46.8" W	Logging and woody waste	1	120	7.50	5	317 ± 413	[57]
(4) Secondary forests (with evidence of natural and anthropogenic changes)								
Biological Dynamics of Forest Fragments Project (BDFFP), farm Esteio, Manaus, Amazonas, Brazil	2°24'48" S; 59° 52'21" W	With a history of abandoned pasture	7	32	1.28	3	8085	[39]
Experimental Genetic Resource Station "José Haroldo", Benevides, Pará, Brazil	01°10' S; 48°20' W	Abandoned pasture with burning history	6	25	6.25	8	2848 ± 537	[59]
Biological Dynamics of Forest Fragments Project (BDFFP), Manaus, Amazonas, Brazil (three topographic positions: plateaus, slopes, and bottomlands)	2°30' S; 60°10' W	Abandoned pasture with history of fires	20	21	2.65	5	2187 ± 1137	[60]

Study area location	Latitude and longitude	Type of disturbance	EA	N	A	D	DS	Reference
Experimental Station of Tropical Forestry (EEST), Manaus, Amazonas, Brazil	2°36'50" S; 60°12'13" W	Blowdown	6	160	5.03	5	704 ± 770	[46]
(5) Agriculture areas								
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Agroforestry systems	> 5	20	0.45	5	9540	[48]
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Agroforestry systems	> 5	20	0.45	5	8909	[48]
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Cassava cultivation	< 5	20	0.45	5	8329 ± 122	[49]
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Cassava cultivation	< 5	20	0.45	5	7471 ± 203	[49]
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Agroforestry systems	> 5	20	0.45	5	7173	[48]
Kilometer 2 of the road to Balbina Village (PAS3), near the clover on BR-174, Amazonas, Brazil	2°03'57" S; 60°01'20" W	Pasture	20	20	0.45	5	6153 ± 75	[61]
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Agroforestry systems	> 5	20	0.45	5	3320	[48]
km 50 of the BR-174 (PAS2), Manaus to Presidente Figueiredo, Amazonas, Brazil	2°03'57" S; 60°01'20" W	Pasture	14	20	0.45	5	3209 ± 48	[61]
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Cassava cultivation	< 5	20	0.45	5	2691 ± 116	[49]
Esteio Farm (PAS1), Manaus to Presidente Figueiredo, Amazonas, Brazil	2°03'57" S; 60°01'20" W	Pasture	9	20	0.45	5	2593 ± 59	[61]
Manacapuru, Amazonas, Brazil	3°16'20" S; 60°33'07" W	Cassava cultivation	< 5	20	0.45	5	1962 ± 27	[49]
Kilometer 2 of the road to Balbina Village (PAS4), near the clover on BR-174, Amazonas, Brazil	2°03'57" S; 60°01'20" W	Pasture	20	20	0.45	5	304 ± 5	[61]

Table 1. Details of density, family abundance, and forms of seedlings that emerged from the seed bank in the terra firme forest of the Amazon rainforest. EA: Estimated age at the time of the study; N: Number of samples; A: Total area sampled (m²); D: Depth of the sample collected (cm); DS: Density of seedlings (m²) (mean ± standard deviation).

used in this study. The datasets involve different types of land use in the Brazilian Amazon rainforest, including (1) old-growth forests, with no evidence of anthropogenic changes in the last 60 years or more; (2) forest fragments with different historical changes; (3) forests with logging of wood species; (4) secondary forests with evidence of natural and anthropogenic changes and (5) agriculture areas.

Seedling density emerging from soil samples is used in all datasets as an indirect estimate of seed density in the seed bank [51–56]. In addition to the highly variation found in the seed banks, even at small distances [20, 54, 55], we see variation in the methods of soil sampling and sampled area [56], sampling depth and spread of sample in the nursery [15], all of which could influence both density and floristic composition. It should be noted that the tropical region lacks seedling identification guides or floras, making this activity largely dependent on the expertise of parobotanics and researchers involved in the field. It is well known that the seedling stage is one of the most difficult stages to identify, as reflected in the floristic composition of the seed bank. Even the division of seedlings into a life form, is difficult to position and categorize. To compile a file form database, we followed the categories proposed by the authors, but with minor changes. We chose to group emerged seedlings into four major categories, i.e., tree, herb, shrub, and support-dependent plants, which included lianas, epiphytes, and hemiepiphytes. Some species like *Miconia serialis* DC. can be shrubby to small trees; however, the small tree life form is the most common, and this species was placed in the tree categories.

3. Results

In general, the lower density of seedlings that emerged from the seed bank samples was observed in old-growth forests, while the highest density in seedlings emerged in agricultural areas (**Figure 1**). Seedling density in old-growth forests had less variability, with numbers varying between 94 and 913 seedlings per m² (**Table 1**). In the other classes of land use, the density of seeds in the soil was found to be higher and had high variation (**Figure 1** and **Table 1**).

Figure 1. Seedling density (m²) emerged from the seed bank in different classes of land use. The vertical bar shows the standard deviation when cited. The datasets used are those described in table 1.

Figure 2.
The proportion of seedlings emerged from seed banks of the ten most abundant families according to different types of land use. A: Old-growth forests, with no evidence of anthropogenic changes in the last 60 years or more; B: Forest fragments with different historical changes; C: Forests with logging of wood species; D: Secondary forests with evidence of natural and anthropogenic changes; E: Agriculture areas.

The type of land use promotes changes in floristic composition (**Figure 2**). Melastomataceae seedlings predominated in all land uses, except for agricultural areas where Rubiaceae seedlings were the most abundant (**Figure 2**). Melastomataceae was represented by the following genera: *Aciotis*, *Adelobotrys*, *Bellucia*, *Clidemia*, *Henriettea*, *Leandra*, *Maieta*, *Miconia*, and *Tococa*. Urticaceae was the second most abundant family in the old-growth forests and the forests with logging of wood species. It was the third most abundant in forest fragments with different historical changes (**Figure 2**). Here, the following genera predominated: *Cecropia*, *Coussapoa*, and *Pourouma*, with only *Cecropia* occurring in agricultural areas and with low density. The families Dilleniaceae (*Davilla*, *Doliocarpus*, and *Tetracera*), Goupiaceae (*Goupia glabra* Aubl.), Moraceae (*Ficus*, *Bagassa*, *Helicostylis*, and *Maquira*), and Araceae (*Philodendron*) were present among the ten most abundant families, but only for old-growth forests (**Figure 2**). Hypericaceae seedlings, as represented by *Vismia* species, were among the ten most abundant families for all types of land use, except for agricultural areas, and, similar to Urticaceae, they occurred at low density (**Figure 2**). Cannabaceae seedlings represented an important component in forest fragments. It was represented by a single species, *Trema micranta* (L.) Blume, with wide distribution, and it serves as an indicator of degraded areas under anthropic use. The Piperaceae family was among the ten most abundant families in the category of intermediate change. It was absent from old-growth forests and agricultural areas. Cyperaceae and Poaceae were configured as a common component of altered areas. Poaceae, however, is not among the ten most abundant families for forests with logging of wood species. Solanaceae, as well as Rubiaceae, was present in all forest types; however, the latter had greater abundance in secondary forests and agricultural areas. Asteraceae (*Chromolaena*, *Rolandra*, and *Vernonia*) and Cyperaceae (*Cyperus*, *Rhynchospora*, and *Fimbristylis*) had greater abundance in agricultural areas (**Figure 2**). Seedlings of Olacaceae (*Heisteria*) were among the ten most abundant families, but only for old-growth forests and forests with logging of wood species (**Figure 2**). Seedlings of Gentianaceae (*Coutoubea* and *Irlbachia*) were among the ten most abundant families, but only for forests with logging of wood species and agricultural areas. Muntingiaceae (*Muntingia*)

Figure 3.
The proportion of seedlings emerged from seed banks divided into life forms according to different types of land use.

was configured among the ten most abundant families only for forest fragments, Icacinaceae (*Dendrobangia*) only for forests with logging of wood species and Verbenaceae (*Stachytarpheta*) and Ochnaceae (*Lacunaria*, *Ouratea* and *Sauvagesia*) only for secondary forests. Euphorbiaceae (*Croton*), Phyllanthaceae (*Phyllanthus*) and Molluginaceae (*Mollugo*) were also among the ten most abundant families, but only for agricultural areas (**Figure 2**).

Tree seedlings predominated in all types of land use in the seed bank, except for agricultural areas (**Figure 3**). Herbs increased in frequency according to land use, with a high proportion in the seed bank in agricultural areas. Despite the low proportion of seedlings classified as support-dependent plants (lianas, epiphytes, and hemiepiphytes) they still showed a higher proportion in the old-growth forests. In the seed bank of agricultural areas, a suppression of other life forms was observed (**Figure 3**). In the seed bank of forests with logging of wood species, shrubs decreased, while the proportion of tree seedlings increased.

4. Discussion

The seed bank has been the subject of studies in different forest types. However, literature surveys carried out in the present study reveal that very few studies reporting on the Amazon rainforest have been published. This highlights the need to expand research on seed banks in natural and anthropized areas. The data used in this chapter account for regions close to the capitals of the states of Amazonas and Pará (**Table 1**), owing to easy access by highways, in addition to universities and research institutes with a long tradition in ecological studies.

Changing land use in the Brazilian Amazon threatens the extinction of a significant number of species and consequent loss of environmental functions and services of the largest tropical forest on the planet [35, 37, 62–64]. Despite repeated warnings and concerns of conservationists and the scientific community, deforestation continues at an accelerated rate [63, 65]. The replacement of the forest by pasture has been the main means of occupation and use of the land, as agriculture advances in the region [65–67]. The resilience of the forest and natural regeneration depends on several factors. Among them are type and intensity of the initial disorder, recurrence of disorders, topography, soil type, and the maintenance of accessible propagation sources [3, 36, 40, 68, 69]. The main mechanisms involved in the regeneration of these altered areas occur through the seed bank, dispersion of seeds from nearby areas, and vegetative regeneration, which includes surviving plants capable of sprouting from both the aerial part and the roots [3, 8, 69].

We generally do find a high density of seeds in the altered areas. Nevertheless, the type and intensity of disturbances and changes occurring around in forest areas contribute to corresponding changes in the floristic composition of the seed bank [5]. Moreover, invasive, or ruderal, species are common and cause the impoverishment of the seed bank [70–74]. Thus, understanding the effects of different types of land use on the seed bank is fundamentally essential to understand the evolution of the landscape, identify obstacles to the restoration of the forest, and, consequently, ensure the regeneration of forest environments and maintenance of environmental services [41, 64, 65, 69, 70, 74].

Our data support the results of other studies carried out in tropical regions where the density of seeds in the topsoil is highly variable [5, 10, 14, 21, 33, 34]. Seed density has increased from the old-growth forest to the altered areas (**Figure 1**). The observed variations in seed density in each class of land use (**Table 1**, **Figure 1**) reflect differences in forest typology, canopy opening, and sampling time among

the areas [9, 14, 19, 21]. In addition, intrinsic variations are associated with the seed bank [20, 54], as well as methodological differences [15, 52, 56].

The seed bank is characterized by the occurrence and dominance of a limited number of botanical families. These families contribute markedly to common species and genera in secondary forests or the early stages of forest regeneration. Among the ten most abundant families in the seed bank, the presence of a high number of seedlings belonging to the Melastomataceae family stands out. This family has high diversity in the Neotropics, with approximately 3000 species, being composed of shrubs, lianas, herbs, epiphytes, and trees [75]. In the Amazon basin, the family is mainly composed of small tree species and shrubs, and it occurs in high abundance and diversity in the forest understory [76–78].

The Melastomataceae family is an important component of the seed bank of the Amazon rainforest [7, 19, 60], as well as other forest types in the Neotropical region [9, 23, 79, 80]. Its high abundance can likely be attributed to the number of small seeds produced per individual [18, 81], longevity [82], and photoblastic seeds, favoring the recruitment of seedlings in environments with greater luminosity [83–86]. The Melastomataceae family is composed of pioneer species that require high to low light, as well as species tolerant to shading [86–88]. Given the great importance of this family to the seed bank, more detailed studies need to be performed in order to better understand the spectrum and functionality of this group in the process of ecological succession.

Urticaceae seedlings consist of *Cecropia*, *Coussapoa*, and *Pourouma* configured as an important component in forest types with low land-use intensity, such as old-growth forests, forest fragments with different historical changes, and forests with logging of wood species (**Figure 2**). The pioneer species of *Cecropia* stand out for colonizing secondary areas that have suffered low impact disturbances, those are more important in the succession processes of these areas [39–43].

In the present study, seedlings of tree species predominated in the seed bank, except for agricultural areas where herbs predominated (**Figure 3**). A decrease in tree seedlings and an increase in herbs can already be observed in secondary forests. Herbs increased density with intensity of disturbance, with low density in old-growth forests (**Figure 3**). In general, the forest seed bank is dominated by trees (49% on average), while cultivated areas and secondary forests are dominated by herbs (75% on average) [14]. The high density of herbs in secondary forests and forest fragments results from the occurrence of anthropized areas around these areas [5, 14, 22, 29, 33]. The importance of shrubs and small trees is little studied in successional processes in tropical forests. Most studies focus on changes in the structure and floristic composition of the woody layer [89–94], but such studies exclude many groups that occur in high density in the seed bank, groups which can play a relevant role in the mechanisms of ecological succession. These groups also respond to different time scales in biological attributes, such as lifetime, reproductive age, and rate of evolution [95].

Secondary forests in the Amazon may result from the abandonment of areas previously used for different purposes, such as shifting agriculture, pastures, and mining [63, 65, 96, 97], which rarely originate from natural disorders [46]. Abandoned pastures occur after years of grazing and cleaning, usually by fire [65, 69]. These areas usually have a seed bank with high density and composition mainly consisting of locally produced herb seeds [41, 65, 69]. This seed bank is very similar to that with established vegetation cover [39–44], which is not seen in old-growth forests [14, 98, 99]. Among the ten most abundant families in the seed bank, common herbs from high-impact degraded areas, such as Poaceae, Rubiaceae, Asteraceae, and Cyperaceae predominate. However, seedlings of typical families from the seed bank of old-growth forests do occur (**Figure 2**). Floristic composition

and seed density in agricultural areas suggest the need to use forest restoration techniques after abandonment, to facilitate and accelerate the return of the forest.

Forest fragments are stretches of forest inserted in a matrix of different types of land uses, typically of anthropic origin [38, 100–102]. The areas used in this study encompass a variety of forest fragments, requiring a more detailed analysis of the characteristics of each. Increase in seed density and changes in the floristic composition of the seed bank intensify in small fragments inserted in a matrix composed of pastures, as well as recurrence of disturbances in these forest fragments [5, 24, 34, 74, 100]. While large forest fragments over 100 ha have a density and floristic composition more similar to the seed bank of old-growth forests, the seed bank also contains species typical of anthropized areas [7, 19, 102, 103].

In the areas of forests with logging of wood species, we can find a mosaic of altered and unaltered areas [45, 57, 104–110] with marked differences between open canopy areas and those that suffered little or no impact [104, 107]. Thus, a greater number of seeds are found in the soil in the centers of exploration clearings and tractor trails [45, 57]. Later, with regeneration, seed density declines and approaches pre-exploratory conditions [45]. The density, as well as life forms, of these areas is closer to that of old-growth forests (**Figures 1 and 3**). For the three most abundant families in the seed bank, floristic composition is very similar to that of old-growth forests. On the other hand, in other families, such as Cyperaceae, Rubiaceae, and Piperaceae, we see higher density of seedlings characteristic of open areas (**Figure 2**).

The seed bank is directly related to forest resilience which contributes to a large number of regenerants, including species of ecological groups not present in the arboreal stratum of old-growth forests. This means that dramatic changes in the seed bank owing to the use and management of soil will, in turn, promote changes in floristic composition and density in a manner that favors the introduction of species not commonly found in the seed bank of old-growth forests. Ultimately, these conditions cause the impoverishment of the seed bank and consequent loss of its functionality. In extreme cases where total suppression of the seed bank has occurred, its absence completely alters the successional trajectory [39–44]. The seed bank is essential for resilience, forest regeneration, and forest diversity; therefore, any changes in its functionality compromise the diversity, regeneration, and maintenance of tropical forests.

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Conflict of interest

There are no conflicts of interest in the chapter entitled “Ecology of the seed bank in the Amazon rainforest” to be considered for publication in Open Access

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