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The Role of the Soil Seed Bank in the Recovery and Restoration of a Burned Amazonian *Terra Firme* Forest

Vynicius B. Oliveira [1], Mário A. G. Jardim [2], Maria Fabíola Barros [3], Danilo S. Silva [4], Ima C. G. Vieira [2] and Marcelo Tabarelli [5,*]

[1] Postgraduate Program in Environmental Sciences, Federal University of Pará, Belém 66075-110, Brazil; vynicius.oliveira@ig.ufpa.br
[2] Coordination of Botany, Museum Paraense Emílio Goeldi, Belém 66077-830, Brazil; jardim@museu-goeldi.br (M.A.G.J.); ima@museu-goeldi.br (I.C.G.V.)
[3] Vale Institute of Technology, Belém 66055-090, Brazil; mariafabiolabarros@gmail.com
[4] Postgraduate Program in Tropical Botany, Federal Rural University of the Amazon, Belém 66070-830, Brazil; souzas.danilo@live.com
[5] Department of Botany, Federal University of Pernambuco, Recife 50670-901, Brazil
[*] Correspondence: marcelo.tabarelli@ufpe.br

Abstract: Here, we examine the effects of wildfires on the soil seed bank of a *terra firme* forest in the eastern Amazon. This seed bank is described via community-level attributes across forest stands exposed to wildfires once or twice, as well as across unburned, old-growth forest stands. A total of 2345 seeds germinated (837.5 seeds/m^2). Across all three forest habitats, the soil seed bank was dominated by a small set of light-demanding species, with two to three species accounting for over 80% of all seeds. On the other hand, the seed bank of all habitats completely lacked seeds from the old-growth flora. Wildfires posed no effects relative to seed density and species richness. However, fire (1) reduced beta diversity, (2) caused an 8% increase in herb abundance and a 4% increase in the number of seeds produced by short-lived pioneers, and (3) resulted in a slight impact on taxonomic species composition. Our results suggest that the soil seed bank, while exhibiting high seed densities, is naturally species poor and, thus, relatively resistant to the first fire events. This implies that the recovery of fire-degraded forests will rely on vertebrate-dispersed seeds coming from any remaining well-preserved old-growth forest stands that are present in the landscape and are highly vulnerable to fire.

Keywords: forest degradation; forest regeneration; regeneration mechanism; tropical forest; resilience

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1. Introduction

Regardless of the role tropical forests play relative to biodiversity conservation and the provision of ecosystem services of both local and global relevance [1,2], these irreplaceable biotas continue to experience increasing levels of habitat loss and degradation imposed by human activities [3]. Across many regions, in fact, degradation scores have already exceeded those of deforestation via a combination of selective logging, edge effects, defaunation, wildfires, and intense droughts associated with climate change, i.e., El-Niño-related droughts [4,5]. The collapse of forest structure, biomass decline, taxonomic and functional changes on local assemblages (from plants to vertebrates), and biodiversity loss among sensitive groups (usually forest-dependent species [6,7]) represent the most conspicuous aspects of forest degradation as land-use changes and climate change continue [3].

In this context, wildfires associated with land use (logging and habitat fragmentation) and intense droughts have been recognized as key drivers of degradation with significant effects on the seed traits of tree communities [8] and affect not only disturbed forests but also old-growth forest stands [9,10]. In fact, previous disturbances favor wildfires via habitat desiccation, the accumulation of combustible materials [11,12], and activities that operate as an ignition source, such as slash-and-burn agriculture and pasture renovation [13,14]. But even large tracts of relatively undisturbed forests have experienced wildfires [15], particularly in the context of very intense droughts [10].

Increasing temperatures, more intense and more frequent droughts, and decreasing precipitation (as expected across some tropical forest regions) have established wildfires as a key topic across research agendas [16,17]. Briefly, wildfires are associated with slow and high tree mortality, biomass collapse, and canopy openness, which triggers a successional process towards pre-fire conditions [18] where additional fires or other disturbances do not occur [19]. In addition, they reduce soil microbiota diversity by promoting local extinction among particular groups of bacteria [20]. Thereby, wildfires promote a temporary decline in old-growth flora (i.e., shade-tolerant species) and the proliferation of light-demanding, fast-growing plant species associated with the early stages of forest regeneration [21,22].

In summary, whatever the intensity of the impacts imposed by wildfires, from temporary changes to almost irreversible forest degradation in the case of repeated fires [18,23,24], the outcome depends on the forest's ability to recover via regeneration mechanisms [25]. We refer to regeneration mechanisms such as seed rain, soil seed bank, seedling bank, and plant resprouting. Overall, the soil seed bank stores a small portion of the woody flora, in particular, pioneer species with dormant seeds [26,27], while it lacks a variable proportion of the recalcitrant seeds from shade-tolerant plant species, including tree species [28,29]. However, the seed bank has a key function in tropical forest regeneration in response to human disturbances, as it can guarantee the prompt recruitment of pioneer species and thus trigger the forest regeneration process [25]. Although the impacts of wildfires have received increased attention, little information is available on patterns of forest recovery and its underlying mechanisms, such as the role played by the soil seed bank. Apparently, wildfires reduce seed abundance and species richness in the soil seed bank, and thus seedling abundance, while promoting plant resprouting from trunks and roots in cases where forests are not exposed to frequent fires [30]. Seeds are damaged or destroyed by soil heating, particularly in the superficial layer, as fire-induced increases in soil temperature can reach up to five meters deep [31]. This implies (1) early forest regeneration is modulated by resprouting species and seedlings emerging from the remaining soil seed bank, as well as those seedlings that are resistant to fire [32], and (2) complete forest recovery depends on the arrival of old-growth flora via seeds from source areas.

Wildfires in the Amazon region have increased in frequency and extent in response to land-use intensification, particularly logging, habitat fragmentation, and climate change [33,34]. In 2020, fires were present across 17% of the entire region, including intentional fires used for forest clearing [35], while wildfires associated with intense and prolonged droughts occurred at least twice in recent decades [17,36]. Wildfires, frequently result from fires escaping from crop/pasture fields [9] and do not only burn logged forest stands and edge-dominated forest fragments but also immense tracts of old-growth forests, communal forests managed by traditional communities, and protected areas [37]. Accordingly, recurrent wildfires have been proposed to cause intense short- and long-term forest degradation [18,21] with tangible impacts on the forest's ability to retain biodiversity and deliver ecosystem services of local (i.e., forest products for traditional communities) and global (i.e., carbon balance and climate regulation) relevance [10,38]. Also, it is worth mentioning the forest biomass collapse, which has limited the forest's ability to store carbon and led to the emission of considerable amounts of carbon into the atmosphere [5].

In this context, our aim was to evaluate the effects of wildfires on the soil seed bank of a *terra firme* forest in the eastern Amazon that had burned during wildfire events some years previously. We describe the soil seed bank in terms of community-level attributes (taxonomic and functional dimensions) across a set of forest stands exposed to wildfires once or twice (during 2015 or 2015 and 2017), as well as across unburned, old-growth forest stands. This forest landscape has been protected and managed as an extractive reserve with the occurrence of intense wildfires in the last decade [37,39]. As in other lowland forests in the Amazon, the tree species flora is dominated by vertebrate-dispersed species, particularly those that benefit from gut dispersal [40] and those with medium to large seeds (>1.5 cm length), probably recalcitrant seeds, which are not expected to be part of the soil seed bank [41]. Thus, wildfires in old-growth forests (i.e., those experiencing their first fire event) are expected to result in low-density and more impoverished seed bank assemblages by eliminating those few seeds (i.e., small and less recalcitrant seeds) from the old-growth flora, which are eventually incorporated in the soil seed bank. The uncovered patterns are discussed in the light of the seed bank as a key factor in the recovery and restoration of fire-degraded forests.

2. Methods

2.1. Study Area

This study was carried out in the Tapajós-Arapiuns Extractive Reserve (hereafter Tapajós-Arapiuns ER), covering 647,611 hectares in the eastern Amazon, Brazil (Figure 1). This is a lowland landscape covered by flat lands, through which Yellow Oxisols predominate [42]. The climate is tropical and humid (Am according to Köppen climate system), as annual precipitation varies between 1287 and 2538 mm. The rainy season is between December and June, while the dry season occurs from August to November, and average annual temperatures vary between 26 and 27 °C [43]. The Tapajós-Arapiuns ER was originally covered by old-growth *terra firme* forest with a highly diverse flora, particularly tree species from the Fabaceae, Lauraceae, Moraceae, Lecythidaceae, and Sapotaceae families [44]. A substantial portion of this forest has been converted into a successional mosaic due to slash-and-burn agriculture, along with the exploitation of forest products by traditional communities and indigenous groups [37,45]. Currently, the Tapajós-Arapiuns ER is home to around 4800 families and 23,000 inhabitants, distributed across 74 traditional communities/villages [45]. Both the regenerating and the old-growth forest experienced wildfires in 2015 and 2017 due to the occurrence of an intense drought associated with the El Niño phenomenon. Around 1 million hectares (Mha) of forest was burned in this event [39].

2.2. Study Design and Soil Seed Bank

A total of 14 forest plots, each one covering 0.25 ha (10 m × 250 m), was established: five in once-burned (2015; BF1), six in twice-burned (2015 and 2017; BF2), and three in unburned (UF) forest (Figure S1). The selection of forest stands was carried out with the support of satellite images, followed by field validation for the presence of fire scars on standing and fallen trees, clearings, and information provided by the locals. Stands were separated by at least 500 m and distributed around four local villages. All stems $\geq$ 10 cm of DBH were recorded and tree species were identified by the parataxonomist of the Museu Paraense Emílio Goeldi (Pará, Brazil). The soil seed bank was recorded via a simple sample measuring 20 cm × 20 cm × 5 cm of depth [46]. In each forest plot and across the three habitats (i.e., burned once, burned twice, and unburned), five soil samples were taken at random points, once (December 2021), summing up a total of 70 soil samples (2.8 m^2 in total), 25 in habitats burned once, 30 in habitats burned twice, and 15 in habitats unburned.

Before collecting the soil, the litter layer was removed [47]. Samples were then collected and stored in plastic bags, labeled, and sent to a greenhouse at the Jacques Huber Botanical Garden of the Museu Paraense Emílio Goeldi. Each soil sample was spread in a tray (40 cm × 31.7 cm × 16.2 cm), which was covered with 3.5 cm deep vermiculite layer and perforated to avoid water retention [46]. The trays were placed into a greenhouse with a wooden structure entirely covered with a 50% shade cover and sides covered with plastic to avoid the impact of rain and the entry of contaminating seeds. This allowed sufficient illumination to stimulate seed germination and soil was kept moist. Seed germination was monitored daily for a six-month period from December 2021 to June 2022 [46]. After three months, soil was disturbed and the containers were reallocated inside the greenhouse. Seedlings were identified at species level by the parataxonomist of the Museu Paraense Emílio Goeldi. To check for contamination, six containers with sterilized sand were also monitored. Sample sufficiency was checked using a species accumulation curve with 1000 random permutations. Furthermore, we acknowledge that three stands of old-growth forest (i.e., unburned forest) would be considered a reduced number of replicates but, because of the wildfires, this habitat became almost inaccessible. Potential caveats are highlighted in the Discussion section.

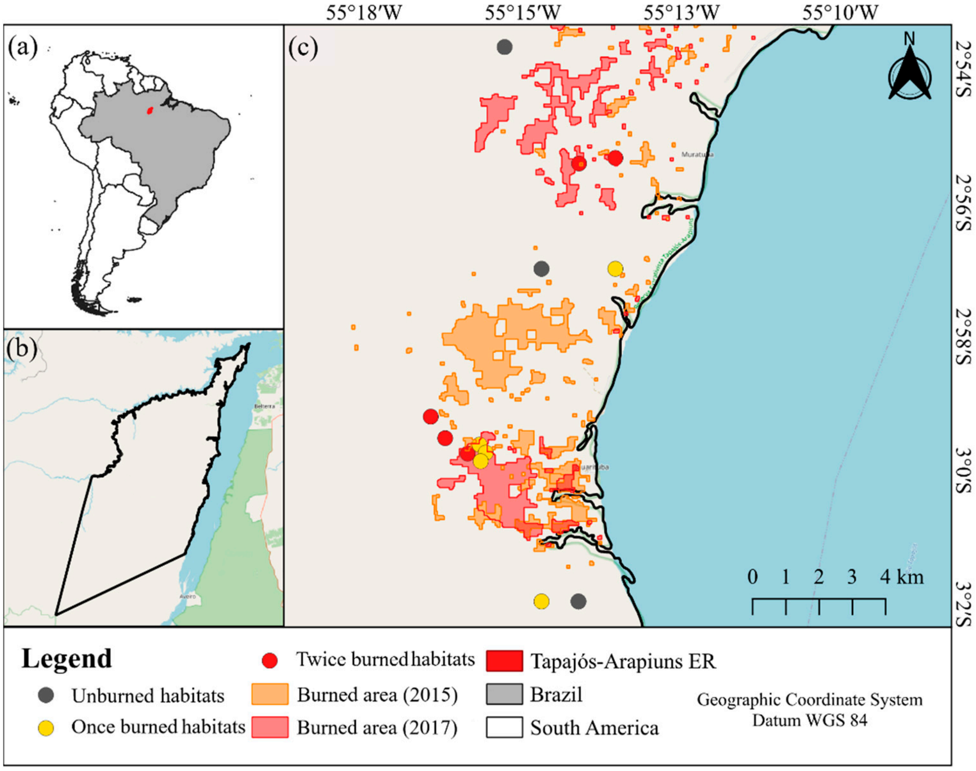

Figure 1. Location of the study area in the eastern Amazon (**a**), with emphasis on the Tapajós-Arapiuns Extractive Reserve (**b**), and location of the studied plots (**c**). Source for burned area data: Mapbiomas Fogo (2023).

2.3. Functional Composition of the Soil Seed Bank

All plant species recorded in the soil seed bank were classified into ecological groups as follows: (1) life form (tree, shrub, herbaceous, and liana following the database hosted at: http://floradobrasil.jbrj.gov.br/, accessed on 12 December 2023), (2) regeneration strategy (short- and long-lived pioneer by a parataxonomist of the Museu Paraense Emílio Goeldi and other specialists, as well as information from the literature), and (3) seed dispersal syndrome (abiotic and vertebrate seed dispersal following [48,49]). Species were classified into ecological groups to permit insights relative to (1) drivers relative to seed bank structure, (2) ecological impacts posed by wildfires, and (3) the contribution of the seed bank to forest recovery.

2.4. Data Analysis

Differences in seed density, taxonomic diversity (Hills numbers: q0, q1, and q2), and functional composition (Community Weighted Mean; CWM) across forest habitats were examined via one-way ANOVA (followed by Tukey post hoc tests to identify which groups differed from which) or Kruskal–Wallis following Shapiro–Wilk tests for normality, and Levene tests for homogeneity were checked. When examining the functional composition of the soil seed bank, we adopted plot-level analyses (via ANOVA) and treatment-level (i.e., pooling all samples from each forest habitat) analyses (via Qui-square tests). Taxonomic differences across forest habitats were examined via three complementary approaches. First, to check whether there was a difference in the taxonomic composition between the habitats, nonmetric multidimensional scaling (NMDS) was performed, based on species abundance (Bray–Curtis), followed by permutational multivariate analysis of variance (PERMANOVA). Second, an indicator species analysis (IndVal) was applied. Finally, we calculated the frequency of short-lived pioneer species from the soil seed bank recorded across all forest stands. To test the relationship between the frequency of short-lived pioneer species and the taxonomic composition (NMDS 1 axis), a linear regression was performed. Additionally, a Venn diagram was created to analyze the similarity of species among the above-ground vegetation, the soil seed bank of unburned forests, and the soil seed bank of burned forests (regardless of whether burned once or twice). All statistical analyses were performed using R (version 4.1.1) [50].

3. Results

During a span of 180 days, a total of 2345 seeds germinated (837.5 seeds/m^2), from 25 families, 33 genera, and 39 species (Table 1). The most species-rich families were Rubiaceae (5 species) and Poaceae (4), followed by Melastomataceae, Fabaceae, and Piperaceae (3). The germination peak across the three habitats took place in early January 2022, from the 10th to the 20th day, and in early April 2022, spanning from the 110th to the 140th day following soil overturning (Figure S2). Across the three habitats, a high-density seed bank emerged, with some samples exceeding 1000 seeds per m^2 (405 up to 1250 seeds m^2). Furthermore, wildfires had no effect on seed density ($F_{2,70}$ = 1.05; p = 0.38; Figure 2a). In contrast with seed density, the seed bank was species-poor (less than 26 species per m^2 in average) considering species richness (X^2 = 4.58; 2 df; p = 0.10; Figure 2b) and dominant and (X^2 = 3.49; 2 df; p = 0.17; Figure 2c) common species ($F_{2,70}$ = 1.74; p = 0.21; Figure 2d), with no effects by wildfires.

Table 1. Number of germinated seeds per m^2 identified and classified according to life form (LF), dispersal syndrome (DS), and regeneration strategy (short-lived pioneer (S) and long-lived pioneer (L); RS) in the soil seed bank of unburned (UF), once-burned (BF1), and twice-burned (BF2) habitats in the Tapajós-Arapiuns Extractive Reserve, Brazil.

Family	Species	LF	DS	RS	Number of Germinated Seeds (m^2)		
					UF	BF1	BF2
Fabaceae	*Amphiodon effusus* Huber	Tree	L. pioneer	Abiotica	0	0	1
Malvaceae	*Apeiba echinata* Gaertn.	Tree	L. pioneer	Abiotica	3	4	5
Poaceae	*Axonopus compressus* (Sw.) P. Beauv.	Herbaceous	S. pioneer	Abiotica	0	0	50
	Axonopus purpusii (Mez) Chase	Herbaceous	S. pioneer	Abiotica	0	0	10
Salicaceae	*Banara guianensis* Aubl.	Shrub	S. pioneer	Vertebrate	0	2	0
Rubiaceae	*Borreria latifolia* (Aubl.) K.Schum.	Herbaceous	S. pioneer	Abiotica	0	0	1
	Borreria verticillata (L.) G.Mey.	Herbaceous	S. pioneer	Abiotica	0	0	1
Malpighiaceae	*Byrsonima densa* (Poir.) DC.	Tree	S. pioneer	Vertebrate	5	7	4
Urticaceae	*Cecropia distachya* Huber	Tree	S. pioneer	Vertebrate	228	66	93
Asteraceae	*Chromolaena odorata* (L.) RMKing & H.Rob.	Shrub	S. pioneer	Abiotica	2	19	45
Menispermaceae	*Cissampelos pareira* L.	Liana	L. pioneer	Vertebrate	0	0	1
Melastomataceae	*Clidemia hirta* (L.) D. Don	Shrub	S. pioneer	Vertebrate	0	0	2
Polygonaceae	*Coccoloba mollis* Casar.	Tree	S. pioneer	Vertebrate	0	0	1
Plantaginaceae	*Conobea aquatica* Aubl.	Herbaceous	S. pioneer	Abiotica	3	0	16
Dilleniaceae	*Doliocarpus* dentatus (Aubl.) Standl.	Liana	L. pioneer	Vertebrate	0	2	0
Asteraceae	*Emilia sonchifolia* (L.) DC.	Herbaceous	S. pioneer	Abiotica	0	0	1

Table 1. *Cont.*

Family	Species	LF	DS	RS	Number of Germinated Seeds (m^2)		
					UF	**BF1**	**BF2**
Myrtaceae	*Eugenia patrisii* Vahl	Tree	S. pioneer	Vertebrate	17	8	1
Moraceae	*Ficus maxima* Mill.	Tree	L. pioneer	Vertebrate	3	0	1
Heliconiaceae	*Heliconia psittacorum* L.f.	Herbaceous	S. pioneer	Vertebrate	5	0	0
Convolvulaceae	*Ipomoea batatas* (L.) Lam.	Herbaceous	S. pioneer	Abiotica	0	6	0
Bignoniaceae	*Jacaranda copaia* (Aubl.) D. Don	Tree	L. pioneer	Abiotica	0	1	3
Euphorbiaceae	*Maprounea guianensis* Aubl.	Tree	S. pioneer	Abiotica	2	2	3
Melastomataceae	*Miconia ceramicarpa* (DC.) Cogn.	Shrub	S. pioneer	Vertebrate	17	35	83
	Miconia prasina (Sw.) DC.	Shrub	S. pioneer	Vertebrate	413	264	129
Rubiaceae	*Palicourea colorata* (Willd. ex Roem. & Schult.) Delprete & J.H.Kirkbr.	Shrub	S. pioneer	Vertebrate	8	1	0
	Palicourea guianensis Aubl.	Tree	S. pioneer	Vertebrate	13	49	39
Poaceae	*Panicum repens* L.	Herbaceous	S. pioneer	Abiotica	5	0	4
Piperaceae	*Piper carniconnectivum* C. DC.	Shrub	S. pioneer	Vertebrate	0	0	1
	Piper hostmannianum (Miq.) C. DC.	Shrub	S. pioneer	Vertebrate	73	23	70
	Piper marginatum Jacq.	Shrub	S. pioneer	Vertebrate	35	34	3
Fabaceae	*Pseudopiptadenia suaveolens* (Miq.) J.W.Grimes	Tree	L. pioneer	Abiotica	2	0	0
Rubiaceae	*Psychotria poeppigiana* Mull. Arg.	Shrub	S. pioneer	Vertebrate	12	0	3
Fabaceae	*Schnella guianensis* (Aubl.) Wunderlin	Liana	L. pioneer	Abiotica	2	0	0
Cyperaceae	*Scleria gaertneri* Raddi	Herbaceous	S. pioneer	Abiotica	2	18	8
Solanaceae	*Solanum schlechtendalianum* Walp.	Shrub	S. pioneer	Vertebrate	8	25	45
Poaceae	*Steinchisma laxum* (Sw.) Zuloaga	Herbaceous	S. pioneer	Abiotica	2	0	1
Eriocaulaceae	*Tonina fluviatilis* Aubl.	Herbaceous	S. pioneer	Vertebrate	2	1	2
Cannabaceae	*Trema micrantha* (L.) Blume	Tree	S. pioneer	Vertebrate	13	106	296
Rutaceae	*Zanthoxylum rhoifolium* Lam.	Tree	L. pioneer	Vertebrate	43	10	5
	Total				918	683	926

Moreover, the soil seed bank was dominated by a small set of species across the three habitats, with two to three species accounting for over 80% of all seeds (Figure S3), namely *Miconia prasina* (Sw.) DC. (Melastomataceae), *Cecropia distachya* Huber (Urticaceae), and *Trema micrantha* (L.) Blume (Cannabaceae). Species accumulation curves indicated a slight stabilization in the case of twice-burned forests and a higher beta diversity across the unburned forest and once-burned, i.e., twice as much as compared to the twice-burned forests (Figure 3). Despite this difference relative to beta diversity, habitats shared over 40% of all recorded species, with few species being exclusive to each habitat. Across the three habitats, our sampling effort captured over 90% of the species, regardless of the small number of unburned forest plots.

In terms of functional groups, the soil seed bank was dominated by seeds from shrubs (X^2 = 113.3; 2 *df*; $p < 0.01$; Figure 4a), those from short-lived pioneer species (X^2 = 22.5; 2 *df*; $p < 0.01$; Figure 4b), and those from vertebrate-dispersed species (X^2 = 84.6; 2 *df*; $p < 0.01$; Figure 4c). When pooling all samples per habitat, twice-burned forests supported more seeds from herbs (a 8% increase) and short-lived pioneers but fewer seeds from shrubs (a 20% decrease), long-lived pioneers, and those from vertebrate-dispersed species (a 14% decrease) as compared to unburned forests (Figure 4a–c). Lianas were almost completely absent across all habitats. On the other hand, there was no difference in the average functional composition across habitats (Figure S4), with all exhibiting the same predominance of shrubs and short-lived and vertebrate-dispersed species.

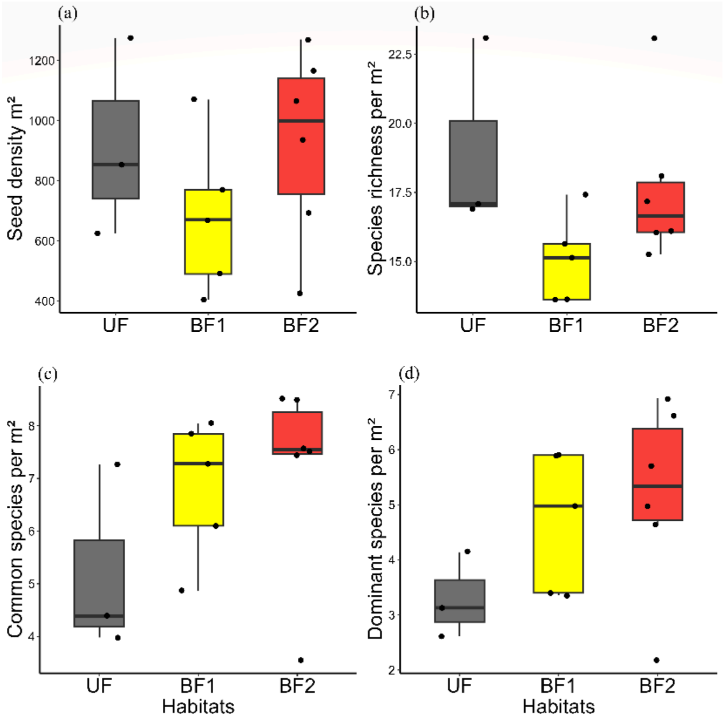

Figure 2. Seed density (**a**), species richness (**b**), common species (**c**), and dominant species (**d**) of unburned (UF), once-burned (BF1), and twice-burned (BF2) habitats in the Tapajós-Arapiuns Extractive Reserve, Brazil.

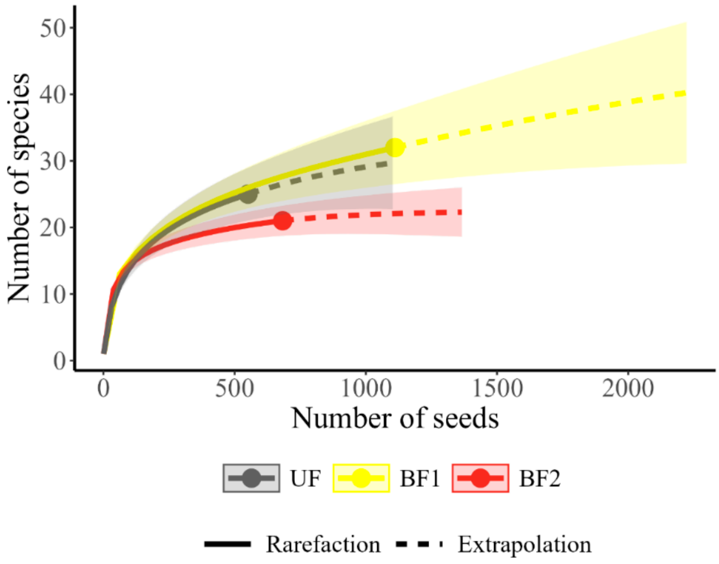

Figure 3. Species accumulation curves for seeds in unburned (UF), once-burned (BF1), and twice-burned (BF2) habitats in the Tapajós-Arapius Extractive Reserve, Brazil.

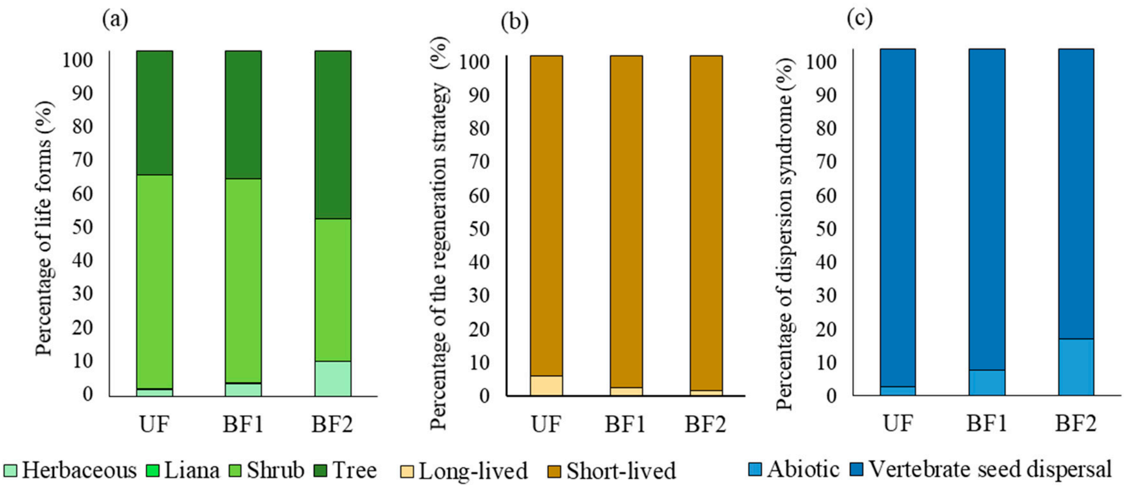

Figure 4. Frequency of seeds into categories of life forms (**a**), regeneration strategies (**b**), and dispersal syndromes (**c**) from the soil seed bank for unburned (UF), once-burned (BF1), and twice-burned (BF2) habitas in the Tapajós-Arapiuns Extractive Reserve, Brazil.

Regarding the taxonomic dimension, the NMDS resulted in three segregated clusters (Figure 5), with a taxonomic distinction supported by (1) a PERMANOVA ($F_{2,70} = 2.30$; $p = < 0.01$) and (b) the occurrence of indicator species. Namely, *M. prasina* (IndVal = 0.51; $p = 0.04$) and *Psychotria poeppigiana* Mull. Arg. (Rubiaceae; IndVal = 0.82; $p < 0.01$) were identified as indicators of the seed bank of unburned forests, while *Axonopus compressus* (Sw.) P. Beauv. (Poaceae; IndVal = 0.66; $p = 0.04$) were identified as indicator species for twice burned forests. Such taxonomic segregation via NMDS partially resulted from the relative abundance of seeds from short-lived pioneers ($R^2 = 0.31$; $p = 0.03$; Figure 6). Finally, the soil seed bank captured just an inexpressive portion of the flora by the adult tree assemblages regardless of the habitat, including the unburned forest, i.e., four species from a flora with more than 305 species (Figure S5). In other words, the seed bank completely missed the old-growth flora. We shall mention a small set of species shared by all habitats: *Eugenia patrisii* Vahl, *C. distachya* and *Palicourea guianensis* Aubl.

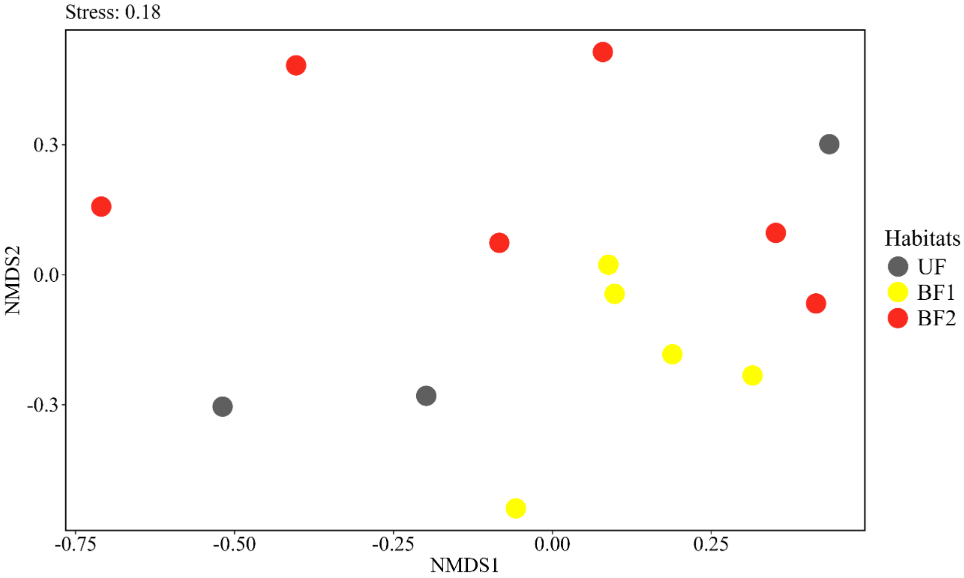

Figure 5. Nonmetric multidimensional scaling (NMDs) between the taxonomic composition of the soil seed bank from unburned (UF), burned-once (BF1), and burned-twice (BF2) habitats in the Tapajós-Arapiuns Extractive Reserve, Brazil.

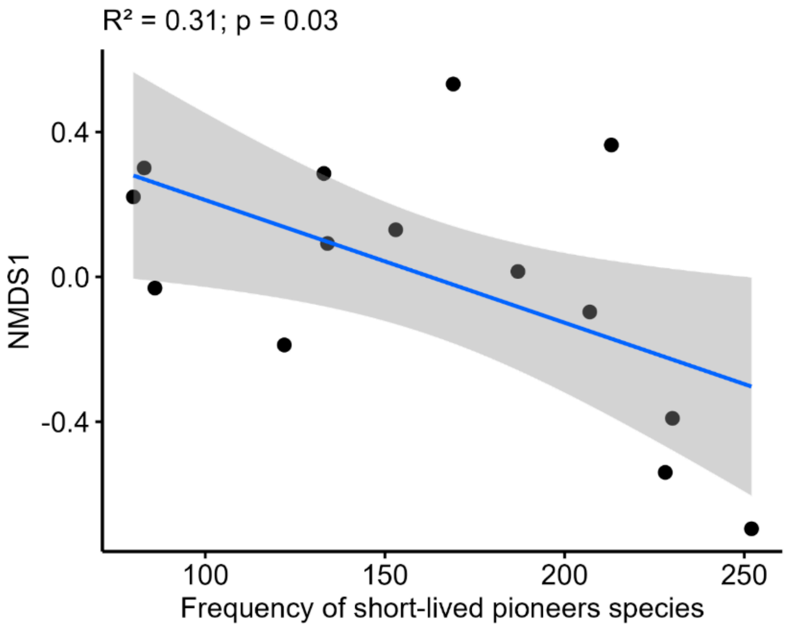

Figure 6. Simple linear regression between the NMDS1 (as a proxy for species' taxonomic composition) and the frequency of short-life pioneer species from the soil seed bank of the Tapajós-Arapiuns Extractive Reserve, Brazil.

4. Discussion

Our results suggest that the soil seed bank in Amazonian *terra firme* forest supports high-density but species-poor seed assemblages at the local and landscape scale. Seed assemblages are dominated by a small set of short-lived pioneer woody plant species across both old-growth and burned forests. In fact, the soil seed bank lacks any element from the old-growth flora, both taxonomically and functionally. We refer to long-lived, shade-tolerant tree species bearing vertebrate-dispersed species, i.e., the bulk of the old-growth *terra firme* flora. In addition to reduced species richness at the stand level, the soil seed bank also exhibits reduced beta diversity, as well as a reduced portion of the woody, especially tree flora, regardless of the forest habitat. Finally, seed germination responds quickly to soil disturbance, with germination occurring shortly after disturbance. In the context of old-growth forests, wildfires have limited impacts on the soil seed bank, slightly altering patterns of species dominance and taxonomic and functional composition (i.e., more seeds from herbs and short-lived species) of a naturally impoverished/species-poor seed bank by considering the diverse adult tree assemblage inhabiting the old-growth forest. Although we examined a limited number of unburned old-growth forest stands, the complete lack of the old-growth flora (i.e., large-seeded shade-tolerant tree species) in the soil seed bank, regardless of the habitat, suggests that it is a natural pattern, which limits the potential importance of fire-induced changes in the soil seed bank for forest regeneration.

The nature of the soil seed bank in tropical forests is highly dependent on the disturbance regime, both natural and human-induced [51–53], with most of the literature addressing the key role seed banks play in forest regeneration in the context of crop/pasture abandonment and in treefall gap dynamics. Seed banks in the context of wildfires is still a recent topic, which limits our ability to make generalizations. In this context, our findings support the notion that soil seed banks in tropical forests can be dense [54] but dominated by light-demanding, high-seed-producing species, species including herbs, shrubs, and tree species, particularly short-lived pioneers [46,55]. Please note that even those species dominating the seed bank in the unburned old-growth forest consisted of short-lived and small-statured pioneers. Light-demanding herbs are present even in the bank of unburned old-growth forests, but the relative contribution of this key ecological group tends to increase as disturbance increases, such as in landscapes dominated by pastures or forest patches that experience frequent fire events [22].

Although it is not a novelty that the old-growth flora (i.e., shade-tolerant species typical of old-growth forest patches) is an infrequent component of the soil seed bank [56], our findings suggest a complete lack of this group even in unburned old-growth forest that is situated in a landscape still dominated by old-growth forest cover. In our focal landscape, there are hundreds of shade-tolerant tree species (including understory, canopy, and emergent tree species), most of them with medium to large seeds depending on vertebrates for seed dispersal, including medium to large mammals [57], but also large-gaped birds (e.g., Cracidae and Cotingidae families). This disturbance-sensitive or forest-dependent ecological group [58] is numerically the dominant group of the regional tree flora (e.g., Sapotaceae, Lauraceae, Chrysobalanaceae, Annonaceae, and Lecythidaceae species), accounting for most of the ecosystem services provided by the old-growth flora, as it represents a substantial proportion of the forest biomass [59], as well as provisioning both timber and nontimber forest products.

The effects of fire in tropical forests have been documented to include changes in species density, richness, and species taxonomic composition, as well as increases in herb species as forests experience repeat fires [30,51,52,60]. Also, fire along with other forest disturbances favor small-seeded species and a high percentage of species and individuals dependent on animal dispersal [8]. In the long term, wildfires will completely change the taxonomic and ecological/functional composition of woody plant assemblages by (1) causing high mortality among the old-growth tree species, while favoring short-lived pioneers and those species that are resistant to fires via resprouting as the collapse of forest biomass creates more illuminated habitats [61]. In contrast, our findings suggest that the soil seed bank of old-growth forests submitted to the first fire events and surrounded by a forested landscape suffers a little impact from fire relative to seed density, species richness, and ecological composition. The response of the soil seed bank is restricted to changes in patterns of species dominance, taxonomic composition, and increases in herbs, short-life pioneers, and vertebrate-dispersed seeds. Moreover, a second fire event has no effect on the naturally high-density yet species-poor and functionally unrepresentative seed bank, as several functional groups from the old-growth flora are not present even in the old-growth unburned forest stands.

Such a naturally impoverished seed bank results from the fact that most of the medium to large seeds from the old-growth flora are recalcitrant with prompt germination as soon as seeds reach the soil, usually in the rainy season [26,51]. Seeds on the ground are also expected to suffer intense levels of predation by vertebrates and insects [62]. In contrast, small seeds from light-demanding species are likely to be rapidly covered by litter, incorporated in the soil bank, and thus remain protected from fire to some extent [63]. They also rely on generalist vertebrates for seed dispersal, such as small birds and bats [64,65]. It is also important to note that the wildfires occurred at the end of the dry season, a period that does not coincide with the fruiting season of fleshy fruit species [66]. Together, these processes help us to understand why wildfires apparently pose minimal impacts on the soil seed bank of *terra firme* forests in human-modified landscapes, such as those in forest extractive reserves.

In synthesis, the little information available so far suggests that wildfires do not change the main role played by the soil seed bank as a forest regeneration mechanism: supporting the recruitment of early-successional species and early-forest regeneration in the aftermath of fire events. On the other hand, the soil seedbank of repeated burned forests might be a source for the recruitment of species able to retard forest regeneration, such as grasses and ferns [67]. Anecdotal information from local residents suggests that tiririca grass (*Cyperus rotundus* L.) is highly effective at spreading fire and that fire is a trigger for the recruitment of the light-demanding palm *Attalea speciosa* Mart. present on the ground but also in the soil seed bank of regenerating forest stands (M. Tabarelli unpublished). A potential connection between wildfires and increased grass cover in the early-forest regeneration (e.g., *Axonopus compressus* (Sw.) P. Beauv.) has previously been documented, which is proposed to have negative impacts on regeneration [22,47,68]. In this context, fire-induced soil degradation, including the impoverishment of microbiota [20] is likely to favor such disturbance-adapted species by limiting sensitive species.

Finally, forest regeneration, long-term dynamics, and even the active restoration of fire-degraded forests rely on seedling recruitment from seeds actively dispersed by a myriad of vertebrate species. Such a scenario relies on the presence of seed sources in nearby old-growth forest patches in which the old-growth flora and their dispersers still persist [52,69]. Wildfires tend to eliminate the old-growth flora, at least in the immediate aftermath and during forest recovery/regeneration, including those supporting the frugivorous fauna, while wildfires reduce the abundance of medium to large vertebrates, the key seed dispersers but the cinegetic fauna in the Amazonian forests [30]. In our context of social forests (see [45]), the exploitation of both timber and NTFPs plus intense hunting are likely to reduce seed production but also the required seed movement from the old-growth patches towards fire-degraded forest and thus experiencing forest regeneration. Accordingly, we do not believe that a lack of the old-growth flora in the soil seed bank of our entire setup results from sample limitation. Hawes et al. [8] pointed out the importance of animal-mediated seed dispersal in disturbed and recovering forests, emphasizing the need to avoid defaunation or promote faunal recovery.

5. Conclusions

The soil seed bank of the *terra firme* forest of the eastern Amazon can be considered, to some extent, fire-resistant, given that the seed bank of unburned old-growth forest is naturally impoverished or species-poor as compared to the adult flora of old-growth forests. Forest resilience and recovery will be dependent on the persistence of well-preserved old-growth forest patches that can provide seed sources, as well as harboring irreplaceable seed dispersers such as mammals and large-gaped birds that provide gut-dispersal. The integrity of such source old-growth forest patches is not only vulnerable to climate change and wildfires but also to local populations that depend on the forest and may deplete the cinegetic fauna it provides.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15091513/s1, Figure S1: Sampling design of the plots in the Tapajós-Arapiuns Extractive Reserve, Brazil. The gray boxes represent the soil samples collected at random; Figure S2. Number of seeds germinated per day in the seed bank of unburned forests (UF) and forests burned once (BF1) and burned twice (BF2) forests in the Tapajós-Arapiuns Extractive Reserve, Brazil; Figure S3. Ranking and frequency of species germinated in the soil seed bank of unburned forests in the Tapajós-Arapiuns Extractive Reserve, Brazil. Habitats unburned (a), forests burned once (b), and forests burned twice (c); Figure S4. Mean (bar size) and standard deviation of seed frequency (%) by functional attribute: ((a) Life forms; (b) Regeneration strategy; (c) Dispersal syndrome)) in the unburned forest (UF), forests burned once (BF1) and forests burned twice (BF2) habitats in the Tapajós-Arapiuns Extractive Re-serve, Brazil; Figure S5. Venn diagram of species found in the soil seed bank of unburned forests, burned forests (once and twice) and above-ground vegetation of the Tapajós-Arapiuns Extractive Reserve, Brazil.

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