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Drastic impoverishment of the soil seed bank in a tropical dry forest exposed to slash-and-burn agriculture

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ABSTRACT

Forest ecosystems are increasingly threatened by unsustainable agricultural practices, especially by those that damage their regenerative potential. This can be the case of slash-and-burn agriculture – a farming method that can negatively impact the soil seed bank, potentially limiting the resilience of forest ecosystems. To test this hypothesis, and thus look for management practices aimed at enhancing forest recovery, we examined the impact of fire throughout an experiment of slash-and-burn agriculture on the soil seed bank of woody plants in the Caatinga tropical dry forest, northeast Brazil. We compared seed damage and viability, and the structure (seed density and diversity) and composition (taxonomic and functional) of seed bank assemblages before and after fire. We found a significant decrease in the frequency and proportion of intact (undamaged) seeds after fire, and a 3.6-fold decrease in the proportion of viable seeds. While seed density remained constant, species diversity drastically decreased after fire, especially the number of rare species. The compositional dissimilarity (β-diversity) between plots also dropped after fire, particularly its turnover component, thus causing the homogenization of seed assemblages across space. The functional composition of seed assemblages was also altered, with the relative frequency of shrub species increasing after fire, especially species with fleshy fruits and biotic dispersal. Taken together, our findings highlight the low resistance of the soil seed bank to this common farming method in tropical dry forests. Therefore, the recovery of this and potentially of other species-rich tropical forests exposed to slash-and-burn agriculture cannot rest on the soil seed bank, but on other processes such as seed dispersal and resprouting – an interesting avenue for future research.

1. Introduction

The ‘Anthropocene’ is characterized by an increasing conversion of forest ecosystems to agricultural lands (Malhi, 2017). Aside of forest loss (Hansen et al., 2020), such conversion has severe impacts on forest’s regenerative potential (Arroyo-Rodríguez et al., 2017; Malhi et al., 2014). This is particularly true for unsustainable agricultural practices that disrupt key ecological processes for forest regeneration (e.g. pollination, seed dispersal, seed bank formation) (Arroyo-Rodríguez et al., 2017; Malhi et al., 2014). Therefore, if we are to promote management practices aimed at enhancing the resilience of forest ecosystems, we need to understand the impact of agriculture on important sources of forest regeneration, such as the soil seed bank.

Forest regeneration after disturbance is usually faster and more predictable in recently modified landscapes, where remnant trees and the soil seed bank persist, and where well-preserved native forests are still present in the landscape (reviewed by Arroyo-Rodríguez et al., 2017). Therefore, the farming methods that eliminate the tree cover and disrupt the soil seed bank (“seed bank” hereafter) are expected to be particularly harmful for forest regeneration and resilience (Chazdon, 2014; Daïnou et al., 2011; Dalling et al., 1997; Plue and Cousins, 2013; Sousa et al., 2017; Wijdeven and Kuzee, 2000). This can be the case of slash-and-burn agriculture – a common farming method in tropical dry forests where billions of people depend on it for their subsistence (Curtis

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et al., 2018). The slash-and-burn agriculture involves the cutting down of the trees and other woody plants in an area to leave the downed vegetation (slash) to dry, and then burn the plant biomass (Fig. 1). Burning promotes a rapid incorporation of nutrients to the soil and the elimination of weeds in agricultural areas that are used for cultivation for up to 4 years before abandonment takes place and forest regeneration starts (Hauser and Norgrove, 2013; Ribeiro-Filho et al., 2015, 2013).

The fire can have direct negative effects on the seed bank (Fig. 1). The loss of adult trees and seed dispersers in burned lands can also limit the abundance and diversity of seeds in the seed bank through the so-called ‘seed source limitation’ (Clark et al., 1998) and ‘seed dispersal limitation’ (Howe and Smallwood, 1982; Fig. 1), which together limit potentially forest recovery after disturbance. We expect that fire increases the frequency and proportion of damaged (i.e. dehydrated and burned) seeds, and decreases the proportion of viable seeds. In addition, as the seed bank in tropical dry forests is naturally poor in terms of seed abundance and diversity of woody plants (e.g. da Silva et al., 2013; Garwood, 1989; Gomes et al., 2019; Skoglund, 1992), it is reasonable to expect a drastic impoverishment of the seed bank after fire, with a significant decrease in seed density and diversity, particularly the diversity of rare (less abundant) species (Mamede and Araújo, 2008). This is not only because of the incineration of seeds, but because of seed source and seed dispersal limitations caused by the loss of adult trees (Fig. 1).

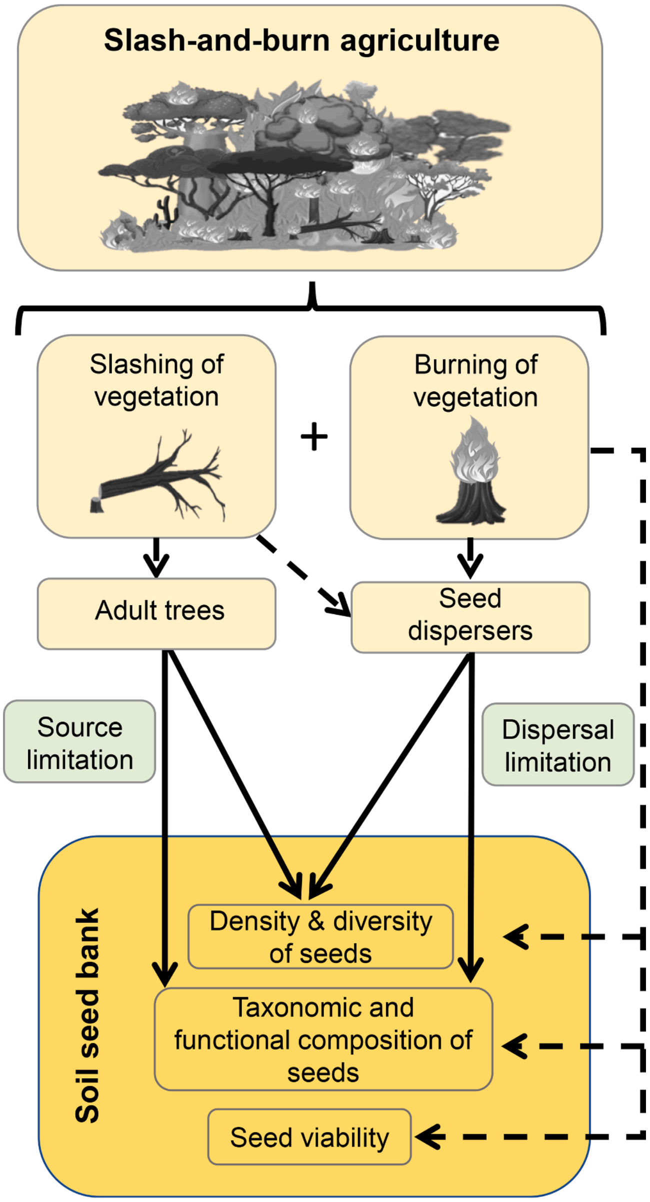

Fig. 1. Hypothesized effects of slash-and-burn agriculture on the soil seed bank. Positive associations are indicated with continuous arrows, and negative associations with dashed-line arrows. The loss of adult trees and seed dispersers in burned areas can cause limitations in seed source and seed dispersal, impoverishing seed assemblages in the soil. Fire can also have direct negative impacts on the seed bank, by dehydrating and/or incinerating the seeds and limiting its viability.

We can also expect that the strong environmental filtering imposed by fire should decrease the seed species turnover (β-diversity) between plots (floristic homogenization) after fire. The few remaining species after fire are predicted to be those with traits that confer tolerance to fire (Tangney et al., 2020, 2019), such as small size which makes it easier seed burial in the soil (Ferreira et al., 2014; Thompson et al., 1993). Dispersal mode can also be important, as dispersal limitation in disturbed forests is usually stronger in animal-dispersed than in wind-dispersed seeds (San-José et al., 2020). Another relevant trait includes a high seed hardness that favors physical dormancy – an attribute related to orthodox seeds inside dry fruits that could allow seeds to survive in soils exposed to high temperatures (Clark, 1991).

The slash-and-burn agriculture is widespread in the ‘Caatinga’ (Curtis et al., 2018; Kleinman et al., 1995) – a seasonally dry tropical forest endemic to Brazil (Silva et al., 2017). As other tropical dry forests, forest recovery after disturbance in this region is known to depend on plant resprouting (e.g. Barros et al., 2021; Kennard et al., 2002) and the seed bank; however, this later topic have been poorly investigated (reviewed by Meiado et al., 2012). About 75% of species in the Caatinga forest produces small seeds at the onset of the rainy season – a phenological synchronization that favors rapid seed germination for the successful establishment of seedlings (Meiado et al., 2012; Patrício and Trovão, 2020; Skoglund, 1992). Nevertheless, some species, particularly from the Fabaceae family, produce orthodox seeds that can remain in the soil for months or years until conditions become favorable for germination (Almeida-Cortez, 2004; Araújo-Neto et al., 2005; Barbosa et al., 2003; Gomes et al., 2019; Meiado, 2014; Nascimento and Meiado, 2016). The seed bank is generally dominated by herbaceous plants with a high dispersal ability (Mendes et al., 2015; Santos et al., 2013), which can reduce the compositional similarity between the seed bank and the local standing vegetation in regenerating forests (Gomes et al., 2019). Nevertheless, we only found one assessment of the effect of slash-and-burn agriculture on the seed bank, which demonstrates an 80% reduction of seed density and a 44% reduction of species richness following fire (Mamede and Araújo, 2008). However, the impact of fire on seed damage and viability, and on the taxonomic and functional composition of seed assemblages remains unknown. As the productivity and sustainability of this farming method strongly depend on the ability of the forest to recover after disturbance (Kukla et al., 2019; Sanchez, 2000), understanding the effect of slash-and-burn agriculture on the seed bank is valuable to inform management and conservation practices, particularly in seasonally dry tropical forests. Here, we assessed seed damage and viability, and the structure (seed density and diversity) and composition (taxonomic and functional) of seed assemblages in the seed bank in plots exposed to an experiment of slash-and-burn agriculture in the Caatinga dry forest, northeast Brazil.

2. Methods

2.1. Study area

This study was performed in the Catimbau National Park (8°23′17″-8°36′35″ S; 37°11′00″-37°33′32″W; ~600 m a.s.l.), a protected area covering 607 km^2 of Caatinga dry forest in northeastern Brazil. Flat lands covered by sandy soils predominate through the landscape, which is mostly exposed to a semi-arid climate (Koeppen’s classification Bsh).

Annual temperature averages 23 °C, and annual rainfall ranges from 650 to 1100 mm (Rito et al., 2017). The original vegetation consists of small-statured dry forest dominated by Fabaceae, Euphorbiaceae and Myrtaceae (Rito et al., 2017). Previous surveys reported at least 151 woody plant species (de Paula, 2017; Rito et al., 2017), but in the study plots (see below) we recorded 74 species. Most woody plant species are trees, almost 60% of which have dry fruits, and almost 50% have abiotic dispersal mode (see Fig. S1 in Supplementary material). Land use in this park include slash-and-burn agriculture (e.g. maize, cassava, beans) and free-ranging cattle, that convert the old-growth forest into a mosaic of different-aged secondary forests (Barros et al., 2021; Souza et al., 2019; Specht et al., 2019).

2.2. Slash-and-burn experiment

To assess the potential effect of slash-and-burn agriculture on the seed bank of woody plant species we adopted an experimental approach. At the end of the dry season (November-December) of years 2018, 2019 and 2020, we prepared 9 forest plots (three plots per year) of 20 × 50 m (0.1 ha each) for agriculture by local farmers (Fig. 2). These plots were located at least 400 m apart to minimize spatial dependence, after verifying with the information provided by local people that these forest stands were not submitted to recent agriculture.

The woody vegetation was completely cut with the help of axes and machetes. As they usually do, all high-density poles were immediately collected by farmers to be used as firewood, fences and other household facilities. The remaining plant biomass was left to dry naturally for a period of 20 days, piled into small amounts and then completely burned through a controlled fire that lasted between 20 and 40 min (Fig. 2). Following the methods described below, we collected the seed bank 30 days before vegetation cutting (i.e. 'before fire' treatment), and immediately (2–3 days) after burning the fields ('after fire' treatment).

2.3. Seed bank sampling

In each plot, we recorded the seed bank in 20 randomly located samples, 10 samples before fire and 10 samples after fire. Each sample consisted of a 0.2 × 0.2 m (0.04 m^2 each) metal grid, and we collected the litter and soil layer up to 5 cm depth (i.e. sample unit = 2000 cm^3). Soil samples were sieved to collect the seeds, which were counted and identified up to the lowest taxonomic level possible with the help of literature, seed specialists and a catalog of Caatinga seeds stored at the Applied Plant Ecology Laboratory (Universidade Federal de Pernambuco, Recife).

2.4. State of seeds

To assess the state of the seeds before and after fire, we classified the seeds as either: (1) undamaged seeds (i.e. intact seeds without any physical damage), (2) damaged seeds (i.e. dehydrated, and/or burned seeds), (3) predated (i.e. with signs of predation by bruchids), or (4) with signs of rotting by fungi (moldy seeds). We also assessed changes in seed viability using the tetrazolium method (sensu Moore, 1973). We selected this test because it is a reliable method to assess the physiological quality of seeds, in addition to offering measurements similar to those found in germination methods (Witkowski and Wilson, 2001). In particular, we first scarified each seed with a sandpaper to expose the endosperm, but avoiding any damage to embryo tissue. We then pre-conditioned the samples in deionized water for 12 h, and immersed them in tetrazolium (0.075%) at 25 °C for approximately 240 min. We also washed the seeds

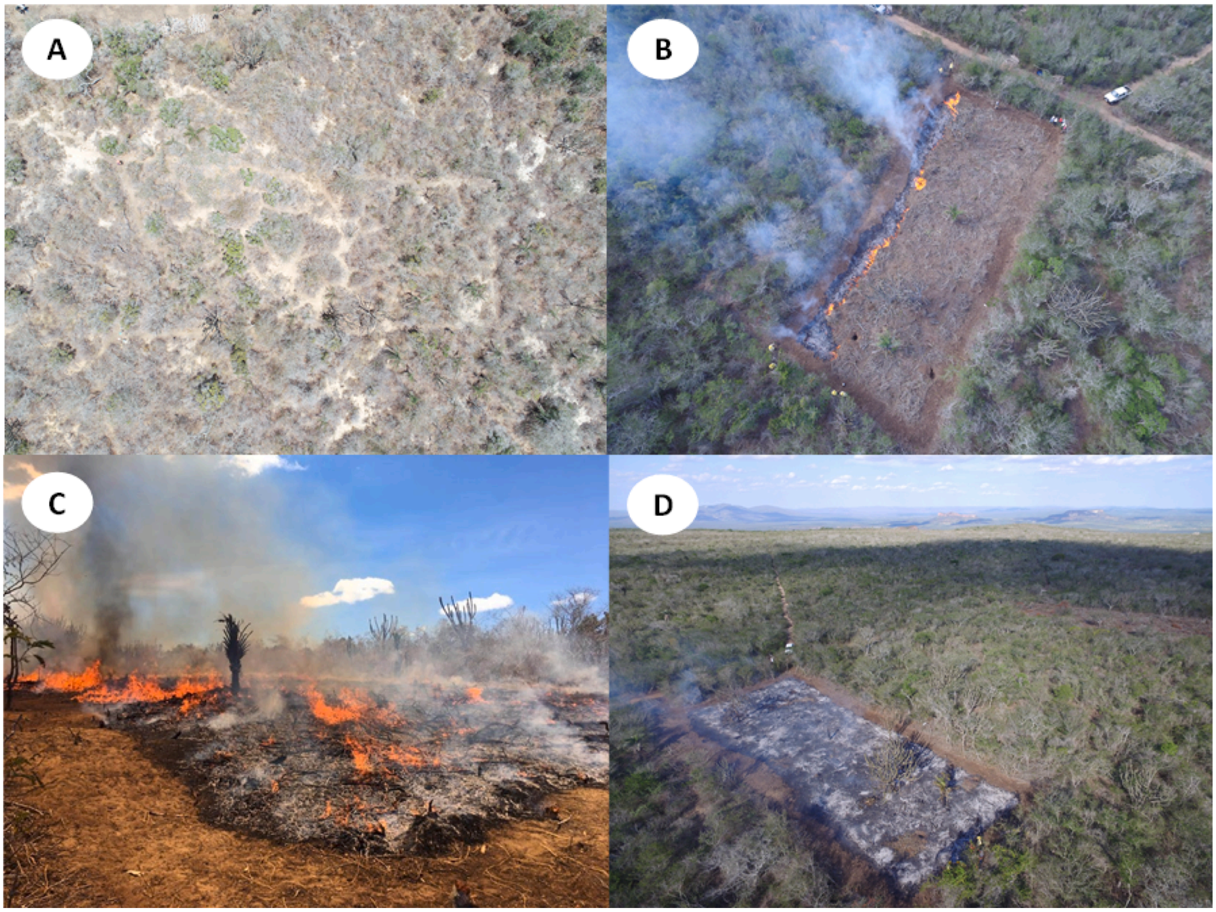

Fig. 2. The slash-and-burn experiment. In each plot, the native forest (A) was slashed and burned (B, C and D) to be converted into agricultural areas.

with running water and cut them longitudinally with the aid of a stylus and observed the color of the embryo tissues. A reddish color indicates the presence of living tissue (Moore, 1961; França-Neto and Krzyzanowski, 2019), while milky-white color means dead tissue. Thus, we considered the presence of living tissue in the embryo as a signal of seed viability, and estimated the proportion of viable seeds before and after fire.

2.5. *The structure and composition of seed assemblages*

As the seed bank refers to the seeds present in the soil that are able to germinate and become seedlings (i.e. viable seeds, Turnbull et al., 2000), the response variables and analyses that are described below include only the viable seeds. The structure of seed assemblages was described in each plot as the density and diversity of seeds summing up the information of the 10 samples per plot to avoid pseudoreplication problems. To estimate species diversity we used the Hill numbers of order 0 (^{0}D, species richness), 1 (^{1}D, exponential Shannon entropy) and 2 (^{2}D, inverse Simpson concentration) (Chao et al., 2014; Jost, 2006). ^{0}D is not sensitive to differences in seed abundance and it gives a disproportionate weight to rare species. ^{1}D weights each species according to its abundance in the community, without favoring rare or abundant species. ^{2}D favors very abundant species, and is therefore interpreted as the effective number of dominant species in the community. In particular, we calculated both α and γ diversities. α-diversity refers to the mean unweighted α-diversity per plot within each treatment, and was calculated with the "entropart" package (Marcon and Hérault, 2015), whereas γ-diversity is the accumulated diversity in all plots per treatment, and was calculated using the "iNEXT" package (Hsieh et al., 2016), for the R 3.3.0 software (R Core Team, 2016). To assess the accuracy of seed inventories in each plot, we estimated the sample coverage estimator (Chao and Jost, 2012), which vary from 0 to 1, and indicates the proportion of the total number of individuals in a community that belongs to the species found in the sample. Sample coverage was relatively high (>0.9) in all plots, suggesting that our sampling effort was adequate to assess changes in species diversity in all plots. However, to avoid any potential bias in our results due to differences in sample coverage among sites (see Chao and Jost, 2012), we considered not only the observed values of species richness, but also the expected values based on coverage-based rarefactions performed with the 'iNEXT' package (Hsieh et al., 2016).

To assess the differences in species composition between treatments, we calculated β-diversity between plots before and after fire with Hill numbers (Jost, 2006). We separately assessed β-diversity of all ($^{0}D_{\beta}$), typical ($^{1}D_{\beta}$) and dominant species ($^{2}D_{\beta}$) using the 'entropart' R package (Marcon and Hérault, 2015). These indices are interpreted as the effective number of completely different communities, and can vary between 1, when all plots are identical, and N communities, when all N plots are completely different from each other. To assess the mechanisms driving β-diversity patterns, we partitioned β-diversity into its turnover and nestedness components (Baselga, 2010) with the 'betapart' R package (Baselga and Orme, 2012). This procedure measures the overall dissimilarity (measured with the Sørensen dissimilarity index, β_{sor}), and partitions it into its turnover (β_{sim}) and nestedness resultant components (β_{sne}) (Legendre, 2014). These two components reflect (1) the replacement of some species by others as consequences of environmental filters or spatial and historical constraints (β_{sim}), and (2) the loss (or gain) of species across space causing a nested pattern (β_{sne}). We complemented these compositional analyses by assessing the differences in species abundances before and after fire with abundance-rank curves.

We also assessed the differences in functional composition of seed assemblages considering plant traits available in previous studies (de Paula, 2017; Rito et al., 2017). In particular, we considered traits potentially associated with seed resistance to fire and seed dispersal capacity, including (1) seed size (cm); (2) seed mass (g); (3) life form (tree or shrub); (4) fruit type (dry or fleshy); (5) seed dispersal mode (abiotic and biotic) and (6) seed type (orthodox or recalcitrant) (Díaz et al., 2016). Seed type was classified according to traits proposed by the literature, such as the presence of a hard coat (Turner, 2004). The abiotic dispersal syndrome includes species dispersed by wind, gravity and ballistic, whereas the biotic syndrome includes endozoochory and ectozoochory. We then calculated the community weighted mean (CWM) of each continuous trait (i.e. seed size and seed mass) in the plots before and after fire using the 'FD' R package for R, version 3.5 (Laliberté and Legendre, 2010). For the categorical traits, we calculated the relative abundance of seeds with each trait class.

2.6. *Data analysis*

We first tested whether the state of seeds (i.e. frequency of undamaged, damaged, predated and moldy seeds) was independent of the treatment (before and after fire) with a contingency table and an independence χ^2 test. The difference in the proportion of viable seeds before and after fire was tested using the prop.test function in R. However, given the paired nature of our experimental design, the difference in mean seed density and seed species diversity between treatments was tested with the non-parametric Wilcoxon signed-rank test. We did not use the parametric paired *t*-test because the residuals of several models did not meet the normality assumption. Regarding the functional composition of seed assemblages, we tested for differences between treatments in the frequencies of each categorical (binary) variable (i.e. life form, fruit type, dispersal mode, and seed type) with the Fisher's exact test for 2 × 2 contingency tables. For continuous variables (i.e. CWM of seed size and CWM of seed mass), we used the Wilcoxon test. We also tested for differences between treatments in total (γ) diversity comparing the mean values and 95% confidence intervals estimated for rarefied samples using the bootstrapping protocol described by Chao et al. (2014), and available in the 'iNEXT' package for R (Hsieh et al., 2016). Following Marcon et al. (2012), we also used 95% confidence intervals to test for changes in β-diversity between plots before and after fire using the bootstrap confidence intervals of diversity values provided by the 'entropart' package. Note that, as indicated above, all these statistical analyses were performed considering the viable seeds only.

3. Results

3.1. *Seed damage and viability*

In total, we recorded 449 seeds from 18 woody species belonging to 7 families. However, only 241 seeds (53%) were classified as undamaged, followed by predated (102 seeds, 23%), damaged (89 seeds, 20%), and moldy (17 seeds, 4%). Viable seeds belonged to 13 species, with Fabaceae and Euphorbiaceae representing 69% of species and 23% of viable seeds. Viable seeds mainly consisted of tree species (69% of all species) bearing dry fruits (84%) with abiotic dispersal (76%).

Seed state depended significantly on the treatment ($\chi^2 = 61.03$, df = 3, $p < 0.001$), with the observed frequency of undamaged seeds being higher than expected by chance before fire, but lower than expected after fire (Fig. 3). The frequency of damaged seeds followed the opposite pattern, with a higher frequency of damaged seeds after fire. The total number of viable seeds was 2.4 times higher before fire than after fire, and we found a 3.6-fold decrease in the proportion of viable seeds after fire (Table 1).

3.2. *Structure of seed assemblages*

Mean seed density did not differ significantly between treatments (Table 1). However, species diversity drastically decreased after fire, particularly the species richness ($^{0}D_{\alpha}$) (Table 1). This means that the negative impact of fire is stronger when considering rare species than when considering the number of typical ($^{1}D_{\alpha}$) or dominant species ($^{2}D_{\alpha}$) (Table 1). Considering the accumulated number of species in all plots

Fig. 3. Total frequencies of seeds (observed and expected values) within each seed state in 9 plots exposed to an experiment of slash-and-burn agriculture in the Catimbau National Park, Brazil. We tested for differences in frequencies between treatments (i.e. before and after fire) with a χ^2 test of independence ($p < 0.001$). Undamaged seeds are those without any physical damage, whereas the damaged ones are those dehydrated and/or burned.

Table 1
Description of seed assemblages in the seed bank of 9 plots exposed to an experiment of slash-and-burn agriculture in the Catimbau National Park, Brazil. The absolute and relative degree of seed viability is indicated, as well as the structure (seed density and diversity) and functional composition of seed assemblages before and after fire. When possible, we show mean values per plot and 95% confidence intervals.

Seed attributes	Before fire	After fire	Statistical test[b]
Total number of seeds	179	270	–
Number of viable seeds (total and %)	58 (32.4%)	24 (8.9%)	38.3**
Structure of seed assemblages			
Mean seed density (seeds/m^2)	16.11 (5.02–27.19)	6.66 (1.42–14.76)	28 ns
Mean species richness ($^{0}D_{\alpha}$)	2.33 (1.31–3.35)	0.77 (0.06–1.61)	21*
Mean number of typical species ($^{1}D_{\alpha}$)	1.91 (1.14–2.68)	0.71 (0.02–1.44)	33*
Mean number of dominant species ($^{2}D_{\alpha}$)	1.70 (1.06–2.34)	0.68 (0.01–1.37)	33*
Functional composition[a]			
Mean CWM - Seed size (cm)	0.21 (0.10–0.32)	0.30 (0.09–0.69)	2 ns
Mean CWM - Seed mass (g)	1.17 (0.11–2.45)	0.73 (0.67–2.12)	8 ns

[a] Only the two continuous traits are indicated, the community weighted mean (CWM) of seed size and seed mass, which indicates the mean trait value of all species present in the plots, weighted by their relative abundances.

[b] We tested for differences among treatments in the proportion of viable seeds with the prop.test function of R. The differences in the rest of variables were tested with the Wilcoxon test for dependent samples. *$p < 0.05$, **$p < 0.01$, ns $p > 0.05$.

(γ-diversity), species richness ($^{0}D_{\gamma}$) was 67% higher before fire than after fire, while the accumulated number of typical species ($^{1}D_{\gamma}$) was 69% higher before fire than after (Fig. 4a). In contrast, the accumulated number of dominant species ($^{2}D_{\gamma}$) did not differ between treatments (Fig. 4a).

3.3. *Taxonomic and functional composition of seed assemblages*

Forest stands before fire were dominated by two tree species (*Senna acurensis* and *Pityrocarpa moniliformis*) and a shrub species (*Croton tricolor*), together representing 66% of all viable seeds in these plots (Fig. 5; Table S1). Interestingly most species (75%) before fire were relatively rare, with nine species showing less than three seeds. In contrast, the plots after fire were composed of four similarly abundant species, three of them shrubs (*Croton tricolor, Byrsonima gardneriana* and *Senna rizzinii*), and only one tree species (*Pityrocarpa moniliformis*) (Fig. 5; Table S1).

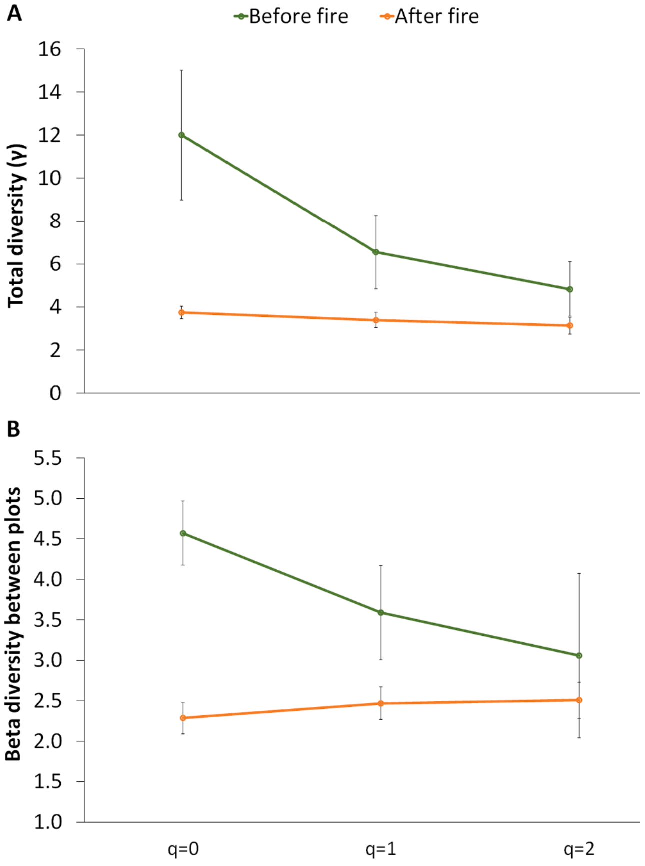

Fig. 4. Rarefied effective number of species (sample coverage = 0.91 in all cases) considering the total number of species ($^{0}D_{\gamma}$), the number of common species ($^{1}D_{\gamma}$), and number of dominant species ($^{2}D_{\gamma}$) before and after fire (A). Differences in species composition between plots (β-diversity) before and after fire is also indicated for $q = 0$, $q = 1$ and $q = 2$ (B). These measures of β-diversity indicate the effective number of completely different communities, and can vary between 1, if all plots ($n = 9$) are identical, and 9, if the plots are completely different from each other.

These compositional changes caused a significant decrease in β-diversity between plots (Fig. 4b). Considering all species ($^{0}D_{\beta}$), β-diversity was 50% higher before fire than after fire (Fig. 4b). Such differences between treatments decreased when considering the typical and dominant species (Fig. 4b), thus indicating that the loss of β-diversity was relatively stronger when considering rare species. Total β-diversity (i.e. β-JAC) was mainly caused by differences in species turnover among

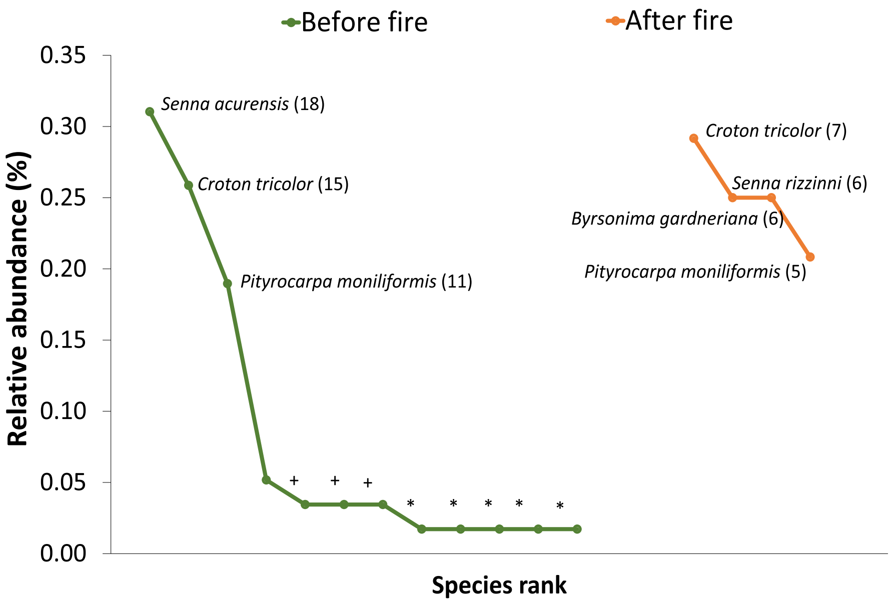

Fig. 5. Rank-abundance curves showing the relative abundance of viable seeds in nine 50 × 20-m plots (total sampling area = 0.9 ha) before (i.e. in forest stands) and after fire in a slash-and-burn experiment in the Catimbau National Park, Brazil. The species are ranked from highest to lowest abundance. The absolute abundance of the dominant species is also indicated (in parentheses), as well as those species with one (*singletons) and two (+doubletons) seeds. For further details see Table S1.

plots, but this component of β-diversity was slightly higher before fire (β-TUR = 0.91) than after fire (β-TUR = 0.73). The nestedness component of β-diversity followed the opposite pattern (β-NES before fire = 0.03; β-NES after fire = 0.22), thus indicating that there was a 7.3-fold increase in the relative contribution of nestedness to β-diversity after fire.

Functional composition of seed assemblages showed an increase in the frequency of shrubs after fire (Odds ratio, OR = 7.58, $p < 0.001$, Fig. 6a). The frequency of fleshy fruits also tended to increase after fire (OR = 0.22, p = 0.05, Fig. 6b), as did the frequency of seeds with biotic dispersal mode (OR = 0.07, $p < 0.001$, Fig. 6c). However, the relative frequency of recalcitrant and orthodox seeds did not differ between treatments (OR = 0, p = 1, Fig. 6d), and the two continuous seed traits (CWM of seed size and CWM of seed mass) were also similar before and after fire (Table 1).

4. Discussion

This study assessed the impact of experimental slash-and-burn agriculture on the soil seed bank in the Caatinga biome – a species-rich but vanishing tropical dry forest from northeastern Brazil. In agreement with previous studies (Mamede and Araujo, 2008), our findings support the hypothesis that this farming method promotes a drastic impoverishment of the seed bank. In particular, we found that fire: (1) increased seed damage and compromised seed viability; (2) decreased the diversity of seed species, particularly impacting rare species; (3) caused a significant homogenization (loss of β-diversity) of seed assemblages across space; and (4) changed its functional composition after fire. Together, these findings have critical applied implications that can be used to promote the sustainability of slash-and-burn agriculture in this and potentially other tropical dry forests.

As expected, we found evidence of strong deleterious effects of slash-and-burn agriculture on seed damage and viability. Thus, seeds of woody plants in this tropical forest are extremely vulnerable to this farming method. This is consistent with other studies that show the susceptibility of seeds to fire in the Caatinga forest (Mamede and Araújo, 2008) and other ecosystems (Auld and Denham, 2006; Kennard et al., 2002; Tarrega et al., 1992; Uhl et al., 1981), not only because fire can dehydrate the seeds, but also because it can overheat the embryo of seeds, causing the mortality of the seeds. Such negative impacts can be particularly important in the Caatinga biome, as unlike other fire-prone biomes such as the Brazilian Cerrado, the Caatinga's woody plants do not present adaptations to fire (Pivello et al., 2021).

We found a significant decrease in species diversity after fire. Such a loss of species diversity was evident at the local (α) and landscape (γ) scales. As the seed bank before and after fire was sampled with one month of temporal difference, the observed loss of species cannot be due to the loss of adult trees and seed dispersers in burned areas (i.e. seed source limitation and seed dispersal limitation, respectively), but simply to seed incineration by fire (Fig. 1). Importantly, the decline of species after fire was particularly evident when considering rare species, thus supporting previous evidence on the high susceptibility of rare tree species to forest disturbance in the region (Rito et al., 2017). In fact, our findings suggest that the most common species are likely less impacted by this farming method, as two dominant species in forest plots (i.e. *Croton tricolor* - Euphorbiaceae, and *Pityrocarpa moniliformis* - Fabaceae) remained dominant after fire. However, as other dominant species in forest plots (i.e. *Senna acurensis* - Fabaceae) were absent in burned plots, the effect of fire on dominant species needs to be investigated in more detail in the future.

Our finding also supports the hypothesis that, at the taxonomic level, this farming method homogenizes the composition of seed assemblages. This process of floristic homogenization can be associated with the loss of species discussed above, as the loss of β-diversity after fire was particularly evident when considering rare species ($^{0}D_{\beta}$), and these species were the most impacted by fire. Our assessment of the components of β-diversity also support the idea that floristic homogenization is mainly related to the loss of species in burned plots, as we found a 7.3-fold increase in the relative contribution of nestedness after fire, and this component is associated with the loss of species (Baselga, 2010). In contrast, species turnover – the substitution of species in one site by different species in another site – is usually related to species sorting (i.e. sites with different environmental conditions are occupied by different species; Baselga, 2010). Thus, the loss of β-diversity can also be partially

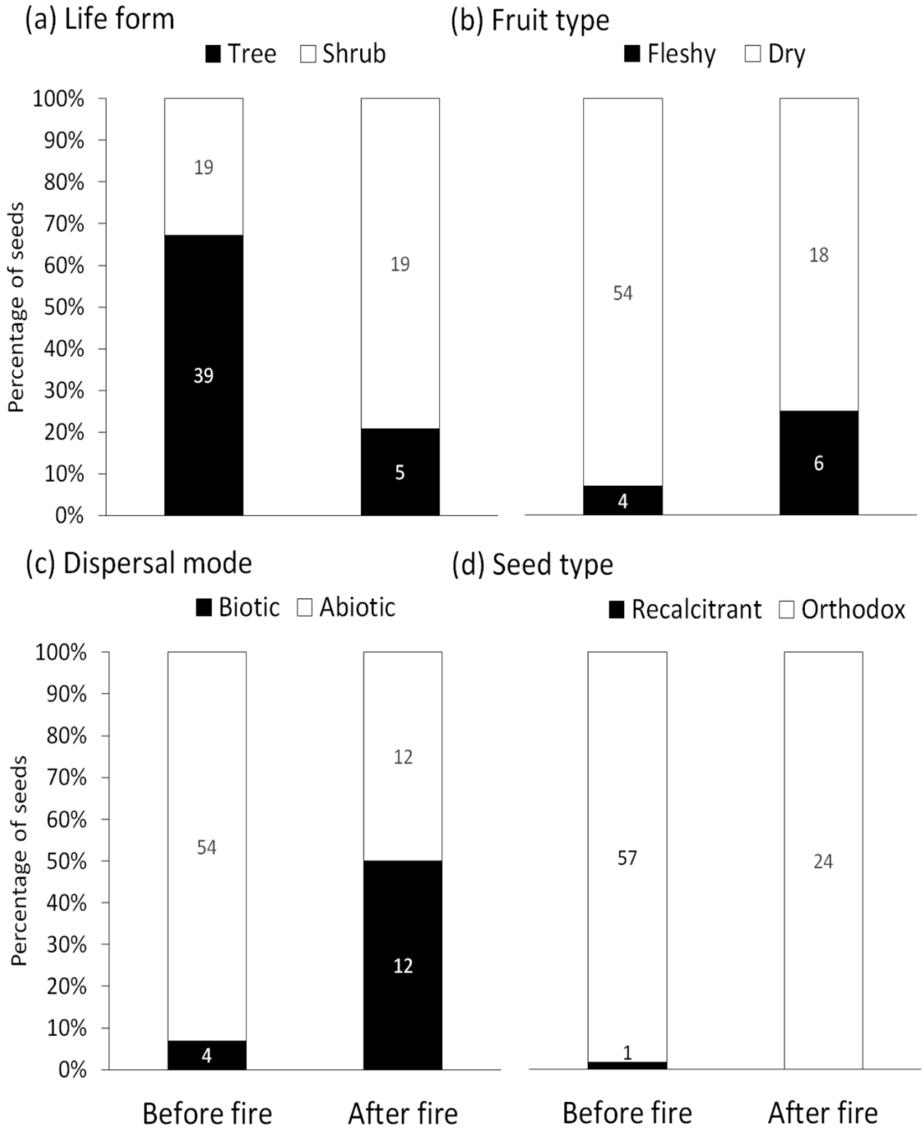

Fig. 6. Percentage of seeds (and absolute values within bars) per treatment, separately assessing different life forms (a), fruit types (b), dispersal modes (c), and seed types (d). The study plots were exposed to an experiment of slash-and-burn agriculture in the Catimbau National Park, Brazil, and we tested for differences between treatments (i.e. before and after fire) with a Fisher exact test for 2 × 2 contingency tables (see results in the main text).

related to the homogenization of environmental conditions after fire, which can cause the loss of species turnover in burned plots – a possibility supported by previous studies (Heydari et al., 2017).

4.1. Management implications

Taken together, these findings have important applied implications for the appropriate management and restoration of these (and potentially other) tropical dry forests. We not only found that slash-and-burn agriculture impoverishes the seed bank by decreasing α, β and γ diversity, but that this farming method causes severe physical damages on the remaining seeds after fire, compromising their viability. Importantly, as our sample plots are much smaller than the areas that are cultivated by the local population (i.e. slash-and-burn agriculture practiced in seasonally dry tropical forests usually involves crops of 0.5 to 5 ha; Lowder et al., 2016; Tanzito et al., 2020), we think that our assessment is conservative, as the impact of slash-and-burn agriculture should be more detrimental if extended over larger spatial extents.

From an applied perspective, our findings imply that forest recovery, and thus the productivity and sustainability of this farming method, cannot rely on the seed bank, but on other mechanisms of regeneration, such as seed dispersal. In fact, the seed bank could be replenished by seed dispersal from nearby areas, but we still do not know how long this could take. Thus, additional monitoring long-term studies are needed to fill this important knowledge gap. In any case, as this agricultural method is widespread in the region, a first and critical step to replenish the seed bank through seed dispersal and thus enhance forest recovery in sites exposed to slash-and-burn agriculture is to maintain a relatively high proportion of native old-growth forests in the surrounding landscape. This can increase the availability of seed sources, and thus enhance seed dispersal and plant colonization of regenerating stands (Piotto et al., 2021). Although we do not know exactly how much forest should be maintained in the landscape, there is evidence for other temperate and tropical forests that we should maintain at least 40% of landscape forest cover to prevent the extinction of most species (Arroyo-Rodríguez et al., 2020, 2021). Therefore, this could be used as reference data while we do not have specific information for the region.

Regarding the spatial configuration of old-growth forests in the landscape, we suggests that rather than preserving the 40% of forest cover in a single continuous forest, forest recovery is likely better if the remaining forest cover is preserved in many smaller forest patches scattered in the landscape (Arroyo-Rodríguez et al., 2020). We would suggest this because by increasing the number of relatively smaller old-growth forest patches in the landscape we can increase the probability that different patches have different environmental conditions (e.g. different precipitation regime), thus covering a wider range of environmental heterogeneity in the landscape (Arroyo-Rodríguez et al., 2020; Fahrig et al., 2019). This is important to increase the compositional dissimilarity (β-diversity) of plant assemblages in the region (Arroyo-Rodríguez et al., 2013; Liu and Slik, 2014; Rito et al. 2021). Furthermore, by increasing the number of small patches we can also reduce the isolation distance between agricultural lands and old-growth forest patches – a key strategy to improve landscape connectivity and prevent seed source and dispersal limitations (Arroyo-Rodríguez et al., 2017; Piotto et al., 2021). However, as we there is no available information on the relative importance of single-large vs several-small patches in preserving the seed bank in the Caatinga forest, this suggestion of preserving many smaller forest patches scattered in the landscape should be taken with care.

Finally, it is important to note that forest recovery can also depend on the ability of the plants to resprout – an important tolerance trait that enable plants to survive different disturbance regimes (Clarke et al., 2013). We particularly refer to the resprouting of tree stumps that survive the slashing and burning of vegetation, as well as the stumps and roots able to persist weeding and initiating forest regeneration (Barros et al., 2021; Dufumier, 2006; Vanderlei et al., 2021). Unlike fire-prone ecosystems, the ability to resprout in the Caatinga may be a strategy to overcome water stress or nutrient deficiencies (Costa et al., 2014; Souza et al., 2021), but also a source of regeneration that is less vulnerable to unsustainable agricultural practices such as slash-and-burn agriculture (Barros et al., 2021; Vanderlei et al., 2021). In fact, given the impoverished seed bank found in the present research, and the available evidence on the importance of resprouting for forest recovery (Barros et al., 2021; Vanderlei et al., 2021), we can hypothesize that forest recovery after slash-and-burn agriculture will largely depend on seed dispersal and resprouting – two interesting avenues for future research.

CRediT authorship contribution statement

Jakelyne S. Bezerra: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Víctor Arroyo-Rodríguez:** Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Jonathan M. Tavares:** Methodology, Investigation. **Adrielle Leal:** Methodology, Investigation. **Inara R. Leal:** Conceptualization, Investigation, Funding acquisition. **Marcelo Tabarelli:** Conceptualization, Funding acquisition, Methodology, Validation, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120185.

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