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Negative impact of slash-and-burn agriculture on the seed rain in a tropical dry forest

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ABSTRACT

Forest's recovery potential in human-modified landscapes is increasingly threatened by agricultural activities that disrupt critical sources of forest regeneration, such as the seed rain. Slash-and-burn agriculture is a good example. By slashing and burning the vegetation, this farming method can promote seed source and seed dispersal limitation, but this hypothesis remains poorly tested. Here, we sampled the seed rain during a complete year in nine plots exposed to slash-and-burn agriculture (i.e., burned plots) and in forest stands (control plots) in the Caatinga biome – a species-rich tropical dry forest endemic to Brazil that is increasingly threatened by slash-and-burn agriculture. We compared seed density, seed species diversity, and the taxonomic and functional composition of seed assemblages between burned and control plots. As expected, seed density was 15 times lower in burned plots than in control plots. Species diversity was also lower in burned plots, but only when considering the number of rare species. However, burned plots showed a higher β-diversity of rare species than forest plots, mainly caused by species replacement (i.e. species turnover) from plot to plot. Burned plots also showed 30% more species with dry fruits and abiotic dispersal than control plots, but this difference was not statistically significant. Taken together, our findings highlight the low tolerance of the seed rain to this dominant agricultural practice in tropical dry forests. This is likely related to the lack of seed sources and seed dispersers in burned plots. Therefore, increasing the availability of seed sources and ecological connectivity in the surrounding landscape are critical management strategies for enhancing seed dispersal and forest recovery in forest areas exposed to this farming method.

1. Introduction

We are amid a planetary emergency, largely pushed by extensive forest loss, which causes a myriad of cascading effects on biodiversity, including our own species (Ripple et al., 2017; Rockström et al., 2009). Forest loss is largely driven by agriculture worldwide, especially by large-scale (commercial) agriculture (FAO, 2020). However, small-scale agriculture, such as slash-and-burn agriculture, also leads to the loss and disturbance of forest ecosystems (Curtis et al., 2018). This farming method is widespread in tropical dry forests (FAO, 2020), and although it usually involves relatively small (0.5 to 5 ha) areas (Lowder et al., 2016; Tanzito et al., 2020), it can have major impacts on biodiversity patterns and processes (Bezerra et al., 2022; Klanderud et al., 2010; Oakley and Bicknell, 2022; Raman, 2001). In particular, it can threaten the resilience of forest ecosystems by altering key sources of regeneration (e.g., soil seed bank; Bezerra et al., 2022). However, our knowledge on this topic is far from complete, especially regarding the impact of slash-and-burn agriculture on the seed rain.

The seed rain is defined as all seeds falling on the soil surface of a particular site. Seed arrival to a site depends on the availability of fruits and seeds in the surrounding vegetation, and on active seed dispersal by frugivores or passive dispersal (e.g. gravity, wind) (Carriere et al., 2002; Huanca-Nuñez et al., 2021; Nathan and Muller-Landau, 2000; San-José et al., 2020; Schott and Hamburg, 1997). Animal seed dispersal is

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particularly important in the tropics (Carriere et al., 2002; Gentry, 1982; Howe and Smallwood, 1982), but wind-dispersed seeds can become dominant in defaunated areas (Martínez-Garza et al., 2009; San-José et al., 2020). Thus, the composition and structure of the seed rain can be highly variable among sites, with direct consequences for forest recovery (Arroyo-Rodríguez et al., 2017; Cole et al., 2010; Huanca-Nuñez et al., 2021; Pickett et al., 1987; Svenning and Wright, 2005).

The seed rain is paramount during early successional stages (Carriere et al., 2002; Cole et al., 2010; Huanca-Nuñez et al., 2021; Svenning and Wright, 2005). This is particularly true in areas exposed to slash-and-burn agriculture (e.g. Carriere et al., 2002), as the seed rain can replenish the seed bank and increase the regenerative potential of burned areas, which typically show few seed species in the soil seed bank that are generally damaged by fire (Bezerra et al., 2022). Such a critical functional role of the seed rain could be, however, jeopardized if slash-and-burn agriculture erodes the seed rain. Therefore, understanding the effect of this farming method on the seed rain has major ecological and applied implications.

Slash-and-burn agriculture is particularly common in the Brazilian Caatinga biome (Curtis et al., 2018; Silva et al., 2017). In this tropical dry forest, some plant species can resprout after fire (Barros et al., 2021; Kennard et al., 2002), providing some level of resilience to regenerating forests (Lawrence et al., 2010). However, as this regenerative potential is biased to few resprouting species (Barros et al., 2021; Ceccon et al., 2006; Cury et al., 2020), the recovery of major community attributes such as species diversity and composition in burned areas largely depends on the seed rain (Souza et al., 2014). Yet, slash-and-burn agriculture can negatively affect the seed rain through two alternative but non-exclusive paths (Fig. 1): (i) by decreasing the availability of trees and seeds (i.e. seed source limitation; Clark et al., 1998); and/or (ii) by decreasing the abundance (and diversity) of seed dispersers thereby limiting seed dispersal (Howe and Smallwood, 1982). As most species (≈70 %) in the Caatinga forest show abiotic dispersal (e.g. gravity, wind, and ballistic; Griz and Machado, 2001; Barbosa et al., 2003), the former path is likely more important than the latter. However, many plant species have small- and medium-sized berries or drupes (with seeds < 1 cm in length) primarily dispersed by ants, birds and bats (Griz and Machado, 2001; Leal et al., 2007, E. Bernard, personal communication), so the impact of slash-and-burn agriculture on animal dispersed seeds should not be overlooked.

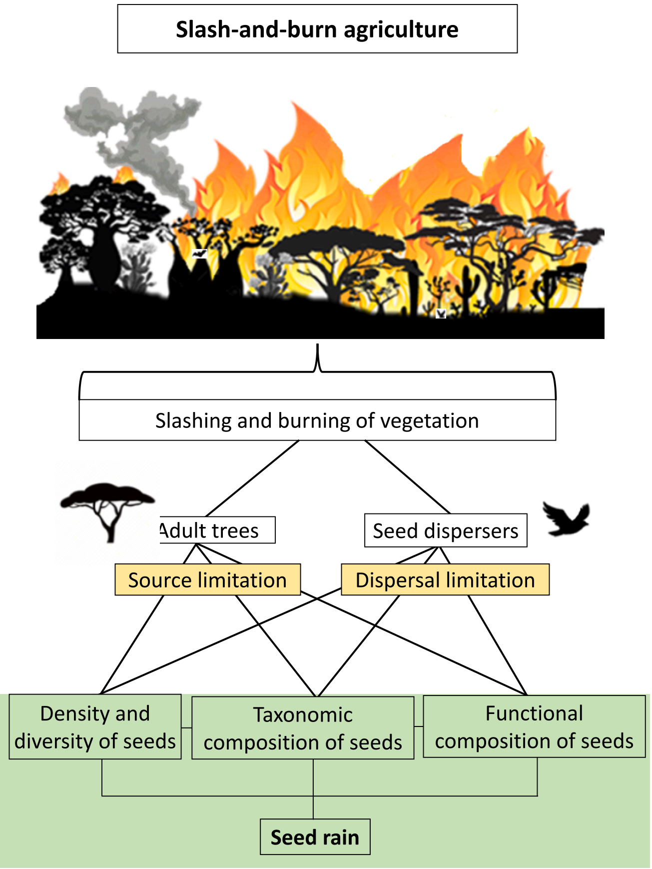

Fig. 1. Hypothesized effects of slash-and-burn agriculture on the seed rain. Adult trees and seed dispersers directly contribute to the structure and composition of seed rain through seed production and seed dispersal, respectively. Therefore, the loss of adult trees and seed dispersers after slashing and burning of vegetation can modify the structure and composition of seed assemblages through the so-called seed source and seed dispersal limitations.

In this study, we assessed for the first time the structure (seed density and diversity) and composition (taxonomic and functional) of seed assemblages in the seed rain in plots exposed to an experiment of slash-and-burn agriculture in the Caatinga dry forest. As this farming method can promote seed source and seed dispersal limitations (Fig. 1), it is reasonable to expect that the seed rain is extremely susceptible to slash-and-burn agriculture. In particular, compared to paired control plots (forest stands), we expected to find (i) a significantly lower number of seeds from a lower number of species in burned plots (i.e. areas exposed to slash-and-burn agriculture). We expected that this particularly affect rare species because forest loss in the region usually has stronger negative effects on adult trees of rare species than on common or dominant species (Rito et al., 2017). As burned plots are extremely homogeneous environments compared to forest plots, we also expected to find (ii) a lower β-diversity between burned plots (floristic homogenization) than between forest plots, especially the species turnover component of β-diversity. In addition, we predicted that (iii) the seed rain of burned plots would be composed of few species, particularly those with ecological traits that provide high dispersal ability (Trindade et al., 2020). Examples of such traits include small seeds with abiotic dispersal, which are commonly produced in large numbers by woody plants (Leishman, 2001); these traits are predicted to be particularly frequent in burned plots.

2. Methods

2.1. Study area

We carried out the study in the Catimbau National Park, northeastern Brazil (8°23′17″-8°36′35″ S; 37°11′00″-37°33′32″W; ~600 m a.s.l.). This protected area was created in 2002 and covers 607 km^2 of the Caatinga biome – a tropical dry forest endemic to Brazil. The climate is semi-arid (Koppen classification), with annual temperature averaging 25 to 30 °C, and annual rainfall ranging from 450 to 1100 mm, concentrated in a few (but variable) months (Nimer, 1972; Rito et al., 2021). Most (≈70 %) of the area is composed of litosol soils, and has been strongly impacted by human activities since the beginning of European colonization in the 16th century (Coimbra-Filho and Câmara, 1996). Small groups of farmers are still present within this national park, where they traditionally practice slash-and-burn agriculture to produce mainly beans, cassava, corn, and watermelon. Free-ranging cattle raising is also practiced, and both activities have converted old-growth forests 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

The study design was described elsewhere (Bezerra et al., 2022), but a summary is provided here. We adopted an experimental approach to assess the effects of slash-and-burn agriculture on the seed rain of woody plant species (i.e., trees and shrubs; Fig. 2). We selected nine blocks of two paired plots of 50 m × 20-m (0.1 ha) each, with no record of recent agricultural practices. One plot was exposed to slash-and-burn

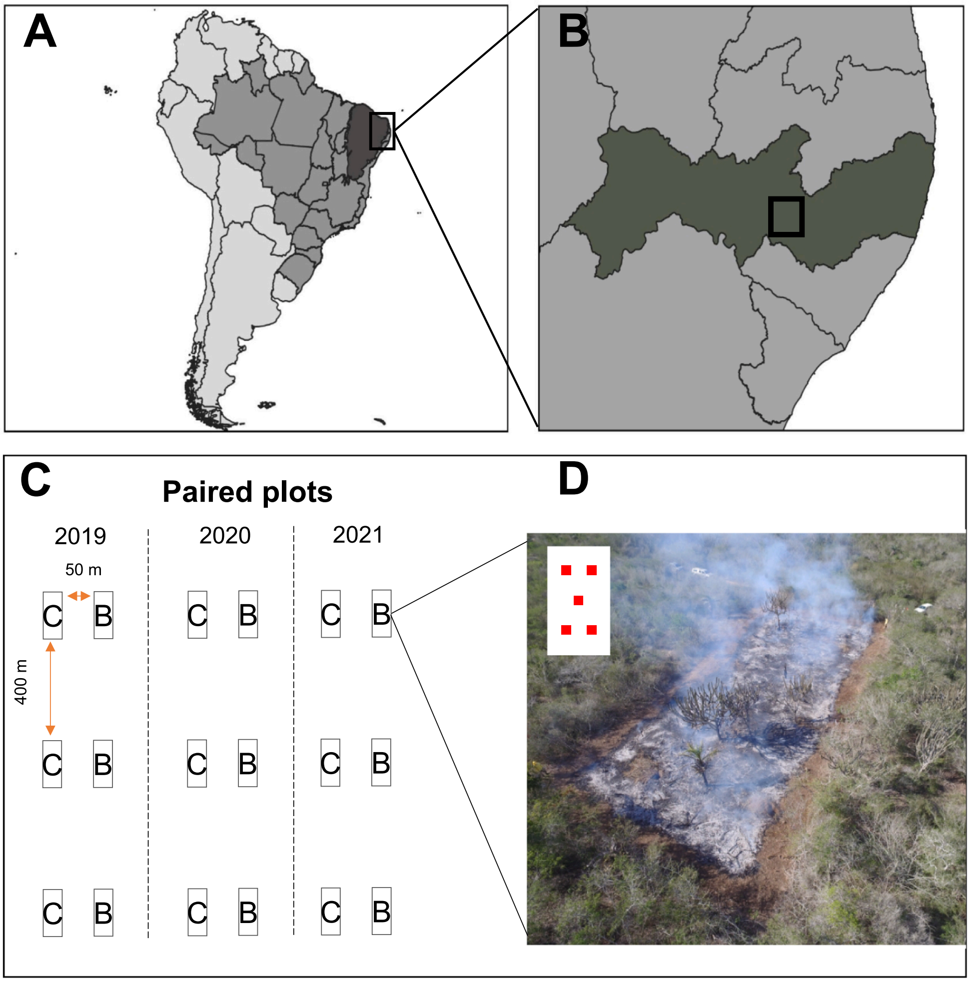

Fig. 2. Distribution of the Caatinga dry forest (dark gray area in A) and location of the Catimbau National Park (black square in B) within the Pernambuco state of Brazil (dark gray area in B), in which we sampled the seed rain using the experimental approach described in panels C and D. We sampled 9 paired (C = control; B = burned) plots in three different years (C) and sampled the seed rain along a complete year in 5 seed traps (red squares in D) within each plot. An example of burned plot is also indicated (D), courtesy of Jens Brauneck.

agriculture (i.e. burned plots), and as a reference (control), we located another plot in a forest area near (50 m apart) the burned plot. As all burned plots had the same size and were surrounded by forest, the isolation distance between sampling areas (i.e. the seed traps, see below) and the extant forest remained constant across burned plots (Fig. 2C), allowing us to control the potential effect of such a distance on the seed rain. The entire experiment was carried out with official permission from ICMBio (the Brazilian agency for protected areas). The information on historical land use was confirmed by the local community.

The blocks were located at an average distance of 400 m apart from each other to avoid spatial autocorrelation. The woody vegetation present in the nine plots exposed to slash-and-burn agriculture was completely cut by local farmers with the help of axes and machetes at the end of the dry season (November-December). Following the practices they usually do, all high-density poles were immediately collected by farmers, as they use them for 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 (during between 20 and 40 min) through a controlled fire by the park's fire brigade team (Fig. 2). After that, without further removal of the remaining debris, farmers seeded manually-three kilograms of each of the crop types commonly seeded by local farmers (i.e. beans, corn, and watermelon).

2.3. *Seed rain sampling*

We randomly placed five square (1 m × 1 m) seed traps of nylon mesh in each plot but keeping a minimum distance of 2.5 m from each other. Each trap was maintained 50 cm above the ground with plastic (PVC) poles. We collected the content of the traps every 30 d during a complete year. Three blocks (including burned and control plots) were sampled from February 2019 to February 2020, three additional blocks from February 2020 to February 2021, and three blocks from February 2021 to February 2022. This allowed us to have a more representative seed rain assemblage, as some species have triannual cycles of reproduction and can be overlooked if sampling all plots along a single year. Samples were sorted to separate leaves, flowers and/or fruits from the seeds of woody plant species (i.e., trees and shrubs), which were quantified and identified at species or genus level with the help of literature, seed specialists and a guide of Caatinga seeds available at the Applied Plant Ecology Laboratory (Universidade Federal de Pernambuco, Recife). It is important to note that annual rainfall during the sampling years (2019, 2020 and 2021) was 439 mm, 582 mm and 414 mm, respectively, which are normal values according to data collected by meteorological stations installed by the Long-Term Ecological Research Network (https://www.peldcatimbau.org.br) close to the study sites.

2.4. *Structure and composition of seed assemblages*

To avoid pseudoreplication, we combined (summed) the data from the five seed traps from each plot and considered each plot as an independent sample. To characterize the structure of seed assemblages in the seed rain, we calculated the total number of seeds (seed density hereafter) and seed species diversity. This later response variable was estimated with Hill numbers of order 0 (^{0}D, species richness), 1 (^{1}D, exponential Shannon entropy) and 2 (^2D, inverse Simpson concentration) (Chao et al., 2014; Jost, 2006). ^0D is not sensitive to differences in seed abundance, so it gives a disproportionately high weight to rare species. ^1D weights each species according to its relative abundance in the community, without favoring rare or abundant species, and thus it is considered a measure of the effective number of common or typical species (Jost, 2006). Finally, ^2D favors very abundant species, and is therefore interpreted as the effective number of dominant species in the community (Jost, 2006). To assess the accuracy of our seed inventories in each plot, we estimated the sample coverage index (C_n) proposed by Chao and Jost (2012). This index ranges from 0 to 1 and indicates the proportion of seeds in a plot that belongs to the species found in it. Sample coverage was very high ($C_n > 0.9$) in all plots, which suggests 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 carried out diversity analyses with coverage-based rarefied values of $^0D_\alpha$, $^1D_\alpha$ and $^2D_\alpha$, performed with the 'iNEXT' package for R, version 3.5. We also evaluated the patterns of β-diversity between control plots and between burned plots with Hill numbers (i.e. $D_\beta = D_\gamma / D_\alpha$; Jost, 2006). We assessed β-diversity considering all species ($^0D_\beta$), and focusing on typical ($^1D_\beta$) and dominant ones ($^2D_\beta$) using the 'entropart' R package (Marcon and Hérault, 2015). We calculated these three metrics using a function designed by Sfair et al. (2016) to construct a matrix that contained β-diversity values of each pairwise comparison within each treatment. Independently of order of q (i.e. $^0D_\beta$, $^1D_\beta$ and $^2D_\beta$), β-diversity values within the matrix could range between 1, when two plots were identical in composition, and 2, when both plots were completely different from each other. Then, following Sfair et al. (2016), we calculated the mean pairwise β-diversity values and 95 % confidence intervals to compare β-diversity between treatments. To assess to some extent the mechanisms driving β-diversity differences between treatments, we also assessed the species turnover and nestedness-resultant components of β-diversity with the metrics proposed by Baselga (2010) and calculated by the 'betapart' R package (Baselga and Orme, 2012). In particular, we calculated overall dissimilarity (measured as Jaccard dissimilarity, βJac) and partitioned it into its turnover (βSim) and nestedness (βSne) components (Legendre, 2014). βSim reflects the substitution of some species by others, usually associated with environmental filters and historical contractions, whereas βSne is related to the loss (or gain) of species through space in a nested pattern. We complemented our compositional analyses with abundance-rank curves to assess how the composition and dominance of species differed between control and burned plots. Finally, we assessed the functional composition of seed assemblages considering plant traits that can affect seed dispersal capacity, including (i) seed size (cm^3); (ii) life form (tree or shrub); (iii) fruit type (dry or fleshy); and (iv) seed dispersal mode (abiotic or biotic) (Díaz et al., 2016; Rito et al., 2017; Turner, 2004; Alexandre de Paula, unpublished data). For seeds identified only at the genus level, we considered the mean characteristics of all species within this taxon. For the continuous trait (seed size), we calculated the community weighted mean per plot with the 'FD' R package (Laliberté and Legendre, 2010). Following Bezerra et al. (2022), for categorical traits, we calculated the relative abundance of seeds with each trait class.

2.5. Data analyses

To test for differences in response variables between treatments (control and burned plots) we used parametric paired *t*-test after verifying that residuals of all models followed the normality assumptions (Shapiro-Wilk test): (i) seed density, (ii) total number of species ($^0D_\alpha$), (iii) number of typical species ($^1D_\alpha$), (iv) number of dominant species ($^2D_\alpha$), and (v) CWM of seed size. Following Bezerra et al. (2022), for categorical seed traits, we tested for differences between treatments in the total frequencies of each binary variable (i.e., life form, fruit type, dispersal mode, and seed type) with the Fisher's exact test for 2 × 2 contingency tables. Finally, the differences between treatments in pairwise β-diversity values were assessed by comparing mean and 95 % confidence interval values.

3. Results

3.1. Overview

In total, we found 8417 seeds belonging to 50 species, 37 genera and 18 families. The most abundant species was *Guapira graciliflora*, followed by *Croton heliotropiifolius*, and *Pityrocarpa moniliformis*, together representing 55 % of seeds. Most species (54 %) belonged to Fabaceae and Euphorbiaceae. Seed density averaged 467 seeds per plot (range = 6 to 3556 seeds), and the observed species richness averaged 10 species (range = 1 to 29 species). Seeds mainly consisted of tree species (76 % of all species) bearing dry fruits (70 %) with abiotic dispersal mode (62 %).

3.2. Structure of seed assemblages in burned and control plots

Both the total and the mean density of seeds were 15 times higher in control plots than in burned plots (Table 1). The total number of species was also 1.7-times higher in control plots (47 species) than in burned plots (27 species). Considering the rarefied values, seed species diversity was also significantly higher in control plots, but only when considering species richness ($^0D_\alpha$) (Table 1, Fig. 3). As the number of typical ($^1D_\alpha$) and dominant ($^2D_\alpha$) species did not differ between treatments, our findings indicate that the species that are lost in burned plots are relatively rare (with few seeds) (Table 1, Figs. 3 and 4).

3.3. Differences in taxonomic and functional composition of seed assemblages

Control plots were dominated by two species, a tree (*Guapira graciliflora*) and a shrub (*Croton heliotropiifolius*), together representing 46 % of all seeds in control plots (Fig. 4). Other common tree species in control plots were *Pityrocarpa moniliformis, Guapira laxa* and *Senegalia piauhiensis.* However, most species (46 %) in control plots were relatively rare (i.e. 23 species showed < 15 seeds; Fig. 4). In contrast, burned plots were by far dominated by a tree species (*Moquiniastrum oligocephalum*) that represented 43 % of all seeds recorded in these plots (Fig. 4). *Senegalia piauhiensis*, *Combretum leprosum*, *Cnidosculus bahianus*, and

Table 1
Structure of seed assemblages in the seed rain in 9 plots exposed to an experiment of slash-and-burn agriculture (i.e. burned plots) and 9 forest stands (i.e. control plots) in the Catimbau National Park, Brazil. The total number of seeds (i.e. summing all plots per treatment), as well as the mean (and range) values per plot are indicated. Significant differences between treatments are indicated with asterisks (*p < 0.05; **p < 0.01; ns p > 0.05).

Response variables	Control plots	Burned plots	test-value
Total number of seeds	7888	529	–
Total number of species	47	27	–
Structure of seed assemblages[a]			
Seed density (seeds/plot)	876.4 (74 – 3556)	58.7 (6 – 307)	2.32**
Species richness ($^0D_\alpha$)	9 (5 – 22)	4 (1 – 14)	8***
Number of typical species ($^1D_\alpha$)	4 (1 – 8)	3(1 – 12)	1.38 ^{ns}
Number of dominant species ($^2D_\alpha$)	3 (1 – 6)	3 (1 – 10)	0.14 ^{ns}
Functional composition			
CWM - Seed size (cm)[b]	0.54 (0.23 – 0.83)	0.56 (0.10 – 0.91)	− 0.52 ^{ns}

[a] Note that our unit of analysis is the plot (50 m × 20 m; 0.1 ha each), and that we sampled 5 m^2 per plot.

[b] The community weighted mean (CWM) of seed size is the mean value of all species per plot, weighted by their relative abundances.

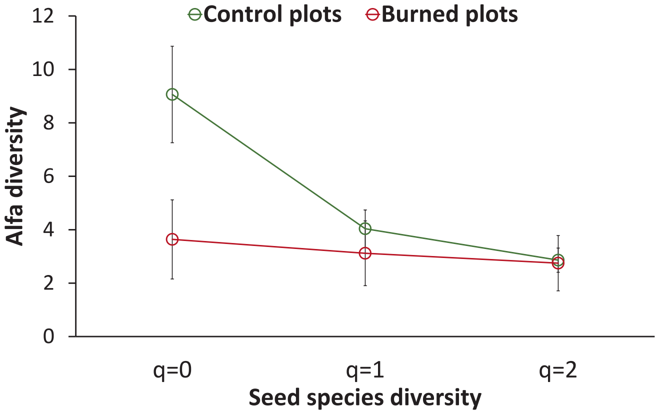

Fig. 3. Mean (±SE) rarefied effective number of species recorded in 9 plots exposed to slash-and-burn agriculture (burned plots) and 9 control (forest stands) plots in the Catimbau National Park, Brazil. We considered three orders of q ($^0D_\alpha$ = species richness; $^1D_\alpha$ = number of typical species, and $^2D_\alpha$ = number of dominant species).

Pityrocarpa moniliformis were also relatively common in burned plots, together representing 39 % of seeds. The rest of the species (78 %) in burned plots were rare (i.e. 21 species showed < 15 seeds).

β-diversity was significantly higher between burned plots than between control plots, but only when considering all species ($^0D_\beta$; Fig. 5). As β-diversity did not differ between treatments when assessing typical ($^1D_\beta$) and dominant species ($^2D_\beta$), our findings indicate that the relatively higher compositional differentiation between burned plots was driven by differences in rare species between plots. The partitioning of total β-diversity (β-Jac) in its turnover (β-Sim) and nestedness (β-Sne) components indicated that in both treatments β-diversity was mainly driven by species replacement from plot to plot (β-Sim), but the contribution (in percentage) of species turnover to total β-diversity was 90 % in burned plots and 92 % in control plots, whereas the nestedness component of β-diversity followed the opposite pattern (burned plots = 10 %; control plots = 8 %).

Regarding the functional composition of seed assemblages, we found that the seed rain in both control and burned plots was dominated by trees (77 % and 81 % of the species, respectively; Odds ratio = 0.75, p = 0.77, Fig. 6). Seed size varied more in control (0.03 to 2.43 g) than burned plots (0.03 to 1.74 g), but the community-level weighted mean (CWM) of seed size was similar in both treatments (Table 1). The percentage of species with dry fruits was 1.3-times (i.e. 30 %) higher in burned plots (85 % of species) than in control plots (68 %), but this difference was not significant according to Fisher's exact test (fleshy vs dry; OR = 2.66, p = 0.17, Fig. 6). Similarly, the percentage of species with abiotic dispersal was also 30 % higher in burned (78 %) than control (60 %) plots, but again the Fisher's test suggest this difference is not significant (biotic vs abiotic; OR = 2.35, p = 0.13).

4. Discussion

This study evaluates the impact of experimental slash-and-burn agriculture on the seed rain in the Caatinga biome – a species-rich but threatened tropical dry forest from northeastern Brazil. Our findings indicate that, as expected, this agricultural practice causes a drastic impoverishment of the seed rain, not only because seed density was 15 times lower in burned plots, but because seed species diversity was also significantly lower, particularly the number of rare species. Contrary to our expectations, β-diversity was significantly higher (not lower) in

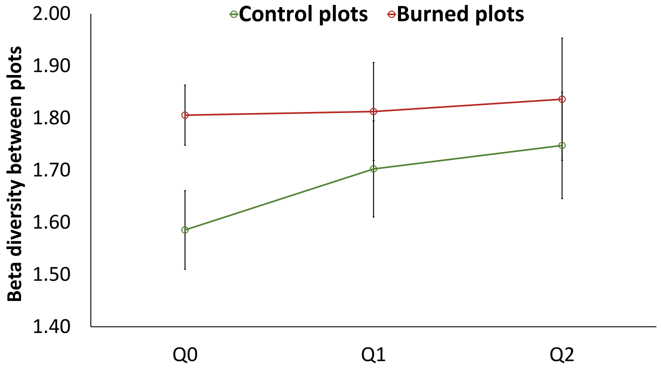

Fig. 5. Mean pairwise β-diversity values (and 95 % confidence intervals) between control and burned plots separately for different q orders (q = 0 assesses all species irrespective to their abundances, q = 1 focuses on typical species, and q = 2 focuses on highly abundant or dominant species). Note that these three β-diversity metrics can vary between 1 (if two plots are identical), and 2 (the plots are completely different from each other).

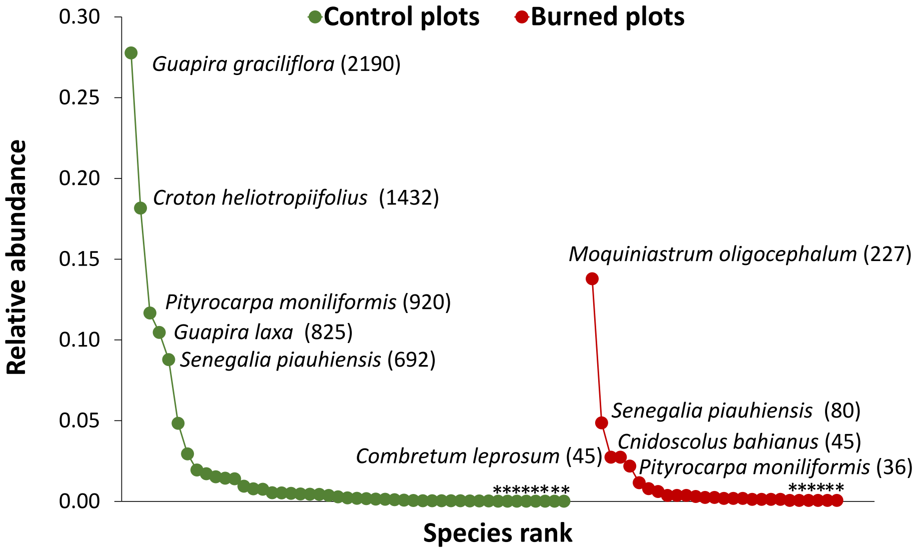

Fig. 4. Rank-abundance curves showing the proportion of seeds per species in control (forest stands) and burned plots in the Catimbau National Park, Brazil. The species are ranked from highest to lowest abundance, and we indicate the absolute abundance of each species in parentheses, as well as those species with one (* singletons) individuals.

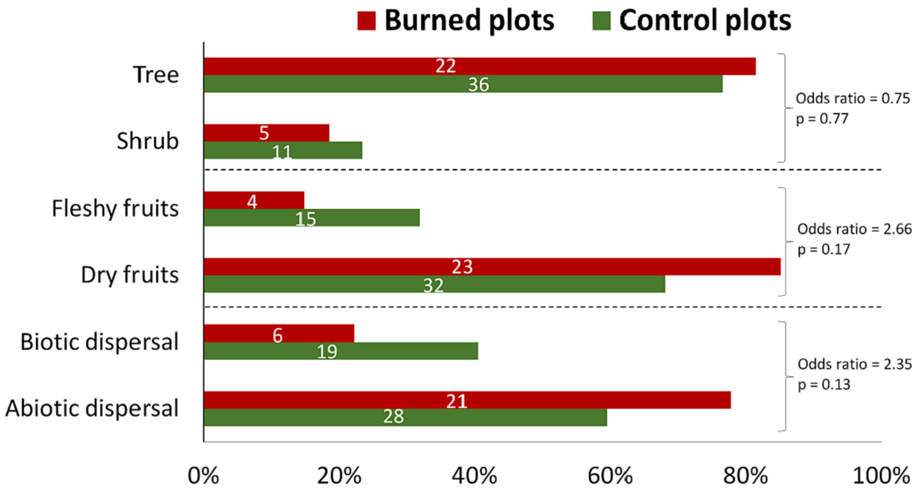

Fig. 6. Total percentage of species (and absolute frequency within bars) with different life forms (tree and shrub), fruit types (dry and fleshy) and dispersal modes (abiotic and biotic) in control and burned plots. The differences between treatments were tested with Fisher exact tests for 2 × 2 contingency tables, and the odds ratio and p-value of each test is indicated for each seed trait.

burned plots than in control plots, but only when considering rare species. Although the functional composition of seed rain did not differ significantly between treatments, we found some interesting trends that merit special attention. As discussed below, our findings can be explained by the lack of seed sources and seed dispersers in burned plots, which together limit the arrival of seeds to areas exposed to slash-and-burn agriculture. Therefore, we highlight some important applied implications for increasing the resilience of these degraded lands.

As expected, seed dispersal was extremely limited in burned plots. The significantly lower seed density and diversity in burned plots add to emerging evidence of the widespread impact this farming method has on different biodiversity patterns and processes (Bezerra et al., 2022; Klanderud et al., 2010; Oakley and Bicknell, 2022; Raman, 2001). For example, Rocha et al. (2021) and Cury et al. (2020) found that seed density and richness in the seed rain was significantly lower (up to two times) in burned forests than in control ones. This is likely caused by the removal of adult trees (and seeds) in burned sites (i.e. seed source limitation; Clark et al., 1998), especially in the Caatinga forests, where most plant species (≈70 %) have abiotic dispersal (e.g. gravity, wind, and ballistic; Barbosa et al., 2003; Griz and Machado, 2001), so they do not depend on animals for dispersing their seeds. Yet, the removal of adult trees not only causes seed source limitation, as it also increases the distance to seed sources, causing seed dispersal limitation (Piotto et al., 2019; Souza et al., 2014).

Slash-and-burn agriculture seems to be causing stronger negative impacts on rare species. This is consistent with previous studies of adult trees (Rito et al., 2017) and the soil seed bank (Bezerra et al., 2022) in the region, thus suggesting that rare species in the Caatinga forest are the most sensitive to human disturbances throughout ontogeny. This is not surprising, as the factors that limit seed dispersal in burned plots are expected to be even more limiting in species that have smaller populations (Pinho et al., 2022). What is likely more interesting is the fact that even relatively common plants in forest stands, such as *Croton heliotropiifolius* and *Senna macranthera*, showed a lower number of seeds in burned plots, and some of them (e.g. *Croton nepetifolius*) where actually absent in these plots. All these species have dry fruits with abiotic dispersal and are geographically restricted across the landscape, so the lack of seeds in burned plots could be simply caused by the removal of adult trees in burned plots, and/or by the absence of adult trees in the nearby forest. Nevertheless, as most tree species in this tropical dry forest are relatively rare (Bezerra et al., 2022; Pinho et al., 2022; Rito et al., 2017), and our findings suggest that they are exposed to strong dispersal limitations, the recovery of community attributes such as species diversity in the seed rain will be difficult.

Surprisingly, this farming method does not seem to promote the compositional homogenization (loss of β-diversity) of seed assemblages in burned plots, but rather the opposite. Our pairwise comparisons of β-diversity indicated that most burned plots were completely different from each other independently of species abundances (i.e. for all order q). This pattern is similar to that observed in adult trees in the region (Rito et al., 2021), likely because most species have abiotic dispersal and depend strongly on the composition of the remaining adult trees in the surrounding areas. Thus, such a relatively high β-diversity in adult trees and seeds is probably caused by the clumped spatial distribution of trees across the Caatinga forest (Pinho et al., 2022; Rito et al., 2021, 2017; Alexandre de Paula, unpublished data), which promotes a very high species replacement (turnover) from plot to plot. But why was β-diversity of rare species higher between burned plots than between control plots? The partitioning of β-diversity into its turnover and nestedness components suggests the answer is in both the loss and replacement of rare species from some burned plots to others. In addition to the aforementioned effects of tree spatial distribution on the turnover component of β-diversity, the loss of rare species in some burned plots can explain why the nestedness component of β-diversity was 2 % higher in burned plots, as this component is associated with the loss (or gain) of species from some plots to others (Baselga, 2010). In any case, our findings imply that because of the very high β-diversity between plots, each burned plot will follow different successional pathways after disturbance depending on the composition of surrounding adult trees (Arroyo-Rodríguez et al., 2017).

Our findings suggest that animal seed dispersal is not significantly impacted by this farming method. Previous studies in secondary (regenerating) tropical forests (Martínez-Garza et al., 2009) and fragmented tropical forests (San-José et al., 2020) suggest that seed dispersal limitation causes a proportionally stronger impact on animal-dispersed species than in species with abiotic dispersal. Yet, in our study the percentage of species with biotic and abiotic dispersal did not differ significantly between treatments, probably because burned plots were relatively small (0.1 ha), which would not be expected to have a major impact on seed-dispersing fauna. Alternatively (but not exclusively), our findings could be explained by centuries of overhunting and habitat degradation in the Caatinga forest. These processes have gradually defaunated the whole region (Alves et al., 2020, 2022; Bezerra et al., 2020), contributing to a generalized loss of animal-dispersed seeds across the ecosystem (Leal et al. 2014a, 2014b; Lins et al., 2022). It is worth noting, however, that the percentage of species with fleshy fruits and biotic dispersal was 30 % lower in burned plots – a non-negligible trend that might (to some extent) reflect the fact that the remaining fauna, although scarce, may avoid burned lands, either because these areas have fewer resources (e.g. food, shelter), or because they are perceived by animals as places of risk, and they avoid using them (see the "landscape of fear" conceptual framework; Frid and Dill, 2002). However, additional studies are needed to identify the composition and structure of animal assemblages, and their behaviors in burned lands to better understand the potential cascading effects of slash-and-burn agriculture on plant-animal interactions in the Caatinga.

All in all, our results have important implications. As argued in the introduction section, seed rain is paramount for replenishing the seed bank and thus increasing the resilience (regenerative potential) of burned areas, which usually have an impoverished soil seed bank (Bezerra et al., 2022). Therefore, the first and likely the most important implication of our findings is that such a critical functional role of the seed rain is likely compromised in burned plots, as the seed rain was significantly poorer in the number and diversity of seeds than in control (forest stands) plots. This finding is not trivial, as the study plots are smaller than the areas that are usually dedicated to this farming method in tropical dry forests (0.5 to 5 ha; Lowder et al., 2016; Tanzito et al., 2020). Therefore, as argued in previous studies (Bezerra et al., 2022), another important implication is that the impact of slash-and-burn agriculture on the seed rain is likely to be worse than that reported here (i.e. it should be more detrimental if extended over larger spatial extents). The third implication is that such impact is likely weaker on some dominant species, especially those with dry fruits and abiotic dispersal (e.g. *Senegalia piauhiensis*, *Moquiniastrum oligocephalum*). Yet, the presence and recruitment of rare species in burned plots will probably require effective management actions (see below). Finally, the very high β-diversity between burned plots implies that, after disturbance, the plots will follow multiple successional pathways (Arroyo-Rodríguez et al., 2017, 2022). This is good news, as it can contribute to maintaining this important component of species diversity and its critical role for preserving total (γ) diversity at the landscape and regional scales (Arroyo-Rodríguez et al., 2013; Flohre et al., 2011).

5. Management implications

The most important recommendation from enhancing seed dispersal and ecosystem resilience is preventing as much forest loss as possible. We understand that this is extremely challenging in a region where local people depend on slash-and-burn agriculture for subsistence (Souza et al., 2019). However, agricultural lands could at least be placed as far apart as possible from each other to leave old-growth forest patches between them so that seed sources can persist around the burned lands (Piotto et al., 2021). This is of critical importance because as discussed above, most plant species have passive dispersal modes, so they depend on nearby seed sources. Second, to promote the dispersal of rare tree species, which are the first to become extirpated from both the seed rain and the soil seed bank (see Bezerra et al., 2022), we must avoid losing adult trees of these species in the region. For this reason, when slashing the vegetation, we should avoid the removal of adult individuals of these species, not only within agricultural lands, but also outside these areas. Finally, we must recognize that in some places we may need to directly plant individuals of these rare species to enrich areas/regions of the forest where they are disappearing. In this sense, there are some successful restoration efforts in the Caatinga forest, which have increased the diversity of rare species and raised the species survival rate by 70 % in degraded agricultural lands in the National Forest Açu Federal Reserve, Rio Grande do Norte, Brazil (https://brazildry.wixsite.com/treediv). Taken together, these complementary management strategies can be valuable to promote the recovery of burned areas. Without these strategies, forest recovery will largely depend on plant resprouting, being biased to the few plant species that are able to resprout after fire (see Barros et al., 2021; Ceccon et al., 2006; Cury et al., 2020; Kennard et al., 2002), significantly limiting the future diversity and composition of this species-rich ecosystem.

CRediT authorship contribution statement

Jakelyne S. Bezerra: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Víctor Arroyo-Rodríguez:** Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Juan Manuel Dupuy:** Investigation, Writing – review & editing. **Inara R. Leal:** Conceptualization, Investigation, Funding acquisition, Supervision, Writing – review & editing. **Marcelo Tabarelli:** Conceptualization, Investigation, Funding acquisition, 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.

Data availability

Data will be made available on request.

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