Seed rain across fire-created edges in a neotropical rainforest

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Abstract Human-induced wildfires are increasing in frequency in tropical forests, and their deleterious consequences for biodiversity include decreases in seed rain, which may be affected directly by fire or indirectly by the creation of edges between forest and non-forest environments. Understanding seed rain is key to assess the potential for natural regeneration in plant communities. We assessed the impact of fire and fire-created edges on seed rain species richness, abundance, size, weight, and dispersal syndromes in Atlantic Forest remnants in Bahia, Brazil. We assessed seed rain at monthly intervals for an entire year along seven 300 m-long transects placed perpendicular to the edge. We installed seed traps at the edge and at 20, 40, 60, 80, 100, and 150 m into the burnt area and into the forest from forest edge. We recorded a total of 9050 seeds belonging to 250 morphospecies. We did not observe edge influence; however, we detected a lower abundance and proportion of animal-dispersed seeds in the burnt than in the unburnt areas. The seed abundance in the burnt areas was lower and seeds were smaller and lighter than those in the unburnt area. Seed rain in the burnt area was not greater near to the forest than far from it. The abundance and richness of seed rain was positively correlated with tree density. Our findings highlight the lack of seed rain in burnt areas and differences in community composition between the burnt and unburnt areas. Collectively, these results indicate negative consequences on natural regeneration, which can lead to permanent secondarization of the vegetation and challenges for early regeneration of burnt areas, which will initially have impoverished forests due to low seed richness.

Keywords Post-fire restoration, dispersal · Edge influence · Forest influence · Tropical forest

Introduction

Fires play a significant role in tropical ecosystems by influencing community structure and species composition (Bond and Keeley 2005). In tropical forests, the geographic extent of forests may be limited by fires as well as edaphic and climatic factors (Hoffmann and
Mature forest fragments near fire-affected areas are essential for seed inflow and may act as source areas for restoration (Rodrigues et al. 2009). Closer proximity to undisturbed forest edges may increase the dispersal of some vertebrate species, especially seed-dispersing birds (Casenavea et al. 1995; Ingle 2002). “Forest influence” occurs when a forest fragment affects biotic or abiotic variables in the adjacent disturbed area (Baker et al. 2013). Seed rain may be subjected to forest influence by a series of mechanisms. For example, fruiting plants at edges may be more abundant and attractive to some of the dispersing fauna, thus increasing animal movement along edges (Pollock et al. 2017) and consequently seed dispersal to the disturbed areas. Forest influence may thus improve the recolonization and establishment of viable populations in the disturbed area via seed dispersal from the forest edge or from surviving individuals within the burnt area (Baker et al. 2013).

In this study, we explored gradients in seed rain across fire-created edges in the Brazilian Atlantic Forest. Our main objectives were as follows: (i) to compare seed rain between the burnt and unburnt areas; (ii) to evaluate the existence of edge and forest influence on seed rain at fire edges; and (iii) to assess whether variation in seed rain can be explained by the structural characteristics of vegetation. We assessed seed rain by evaluating seed abundance and species richness, as well as different dispersal mechanisms.

We expected seed rain to differ between the burnt area and the remaining forest and to be affected by edge proximity, with a gradient from higher richness and abundance within the forest interior to lower richness and abundance within the burnt area. We also expected that zoochoric seeds would be more abundant than non-zoochoric seeds in unburnt areas, as previously recorded for tropical forests (Griz and Machado 1998; Jordano and Schupp 2000). We predicted that zoochoric seeds would be larger and heavier in the forest interior (Tabarelli et al. 2010), than in the burnt area, representing edge avoidance by large-bodied frugivores; and that non-zoochoric seeds would be more prevalent in the burnt area than in the intact forest.

Wildfires induce different levels of vegetation mortality, creating edges between stands of different structural characteristics according to the burn severity (Parkins et al. 2018) and between burnt and unburnt vegetation. These edges may alter community structure and dynamics, which can consequently cause edge influence (Murcia 1995; Harper et al. 2005). Partial burning of vegetation and organic matter at fire-created edges modifies abiotic attributes such as light, wind, and moisture (Harper et al. 2004, 2005). For example, edges between forest and non-forest vegetation alter wind speed (Laurance and Curran 2008), with possible consequences for seed dispersal by wind (anemochoric; Augsperger and Franson 1987). Furthermore, such edges may affect animal behavior by attracting animals (positive edge effect) or causing edge avoidance (negative edge effect, Potts et al. 2016). Consequently, fire-created edges may also affect seed dispersal by animals (zoochoric seeds; Freitas et al 2013; Ssali et al. 2018). Thus, seed rain is likely to be affected by forest edges (Capellesso et al. 2018; Vespa et al. 2014) and may consequently impact regeneration processes (Nathan et al. 2002).
Materials and methods

Study area

The study site is in a protected area, the Una Wildlife Refuge (Refugio de Vida Silvestre de Una—Revis-Una) (15°08’15" S, 39°00’39" W), which is in the municipality of Una in southern Bahia, North-Eastern Brazil. The area is affected by anthropogenic impacts mostly caused by illegal activities, such as deforestation for new agriculture fields, poaching, and extraction of wood and other plant products by local dwellers (GSCM, pers. obs.). The Revis-Una is 23,404 ha in size and has a humid to sub-humid climate without a defined dry period, an annual rainfall of 1600 to 1800 mm, and a mean yearly temperature of 23 °C (SEI-BA 1998). The soil is yellow oxisols (Santos et al. 2011) with a mostly sandy soil texture (pers. obs). The vegetation is 15 to 30 m tall and characterized by a large abundance of lianas and vertically stratified plants, including an herbaceous layer with many saplings and, in some areas, bamboos. The fires decreased tree number in burnt patches (958 tree/ha), compared to the surrounding unburnt forest (8360 trees/ha). In contrast, snag abundance was greater in the burnt area (449 trees/ha) than in the forest (145 trees/ha) (Menezes et al. 2019). A detailed comparison between the burnt and unburnt areas, based on the data from Menezes et al. (2019), is shown in Table 1.

The wildfires in the area are likely a result of the use of fire for management of agricultural areas within and around the Revis-Una, where fire can be used to prepare land for agriculture (Barlow et al. 2020). The area underwent accidental soil and surface fires between December 2015 and February 2016. The duration of each of the fires was approximately one month and the fires impacted different parts of the protected area (Menezes et al. 2019). The wildfires caused profound structural changes in burnt areas, which had lower basal area and density of trees, saplings, lianas, and herbaceous life-forms, but higher density of snags, logs (fallen trees), and pioneer species (such as Trema spp., Cecropia spp., Solanum spp.) as well as graminoids, than the surrounding unburnt forest. The bracken fern Pteridium arachnoideum (Kaulf.) Maxon dominated burnt areas, forming fronds with very high height and cover (Menezes et al. 2019). Sampling started approximately a year and a half after the fires ended.

Sampling design

Within the protected area, we selected three partially burnt forest patches (Fig. 1). All patches showed a clear edge between the forest and the burnt area (Fig. 1) and the sizes of the burnt areas were 28, 63.5, and 260 ha. Within these areas, we placed a total of seven transects, at least 100 m apart from each other, perpendicular to the edge and extending from 150 m into the forest to 150 m into the burnt area. Along each transect, we installed 13 seed collectors (Fig. 1): at the edge (determined by the presence of charcoal on the soil) and at 20, 40, 60, 80, 100, and 150 m into the forest and into the burnt area from the edge. Thus, we used a total of 91 seed traps at the seven transects.

They were made of a 1 m × 1 m square piece of polyester mesh, with a 1 mm mesh size, nailed on eight wooden sticks at a height of 1 m from the ground. This seed trap design is commonly used in seed rain studies (Melo et al., 2006; Rother et al., 2015), especially to capture wind-dispersed seeds and those dispersed by birds, bats, and primates, but not seeds dispersed by terrestrial vertebrates or invertebrates. The seed traps were visited monthly from September 2017 to August 2018, and all the material within them was taken to the lab for sorting. Next to each seed collector, we placed a 20 m × 4 m transect (long side parallel to the edge) to sample vegetation structure. In each transect, we measured the diameter at breast height (dbh) of all trees and snags with a dbh of at least 10 cm (detailed results for vegetation structure can be found in Menezes et al. 2019).

Sorting and classification of the collected material

In the lab, we first separated the fruits and seeds from the plant litter. We photographed the fruits and removed the pulp to store the seeds. We then weighed, measured the width, and took pictures of all seeds, separating them into morphotypes (which we treat here as morphospecies) where each new seed that was different from previously collected ones was classified as a new morphotype. The morphospecies were classified into dispersal types according to Van Der Pijl (1972) as follows: (a) zoochoric: seeds with characteristics of animal dispersal, especially fruits such as drupes or berries and seeds with aril; (b) anemochoric: seeds with structures for wind dispersal; and (c) autochoric: seeds with explosive
mechanisms. For data analysis, we grouped anemochoric and autochoric seeds into a single non-zoochoric category.

**Data analysis**

We analyzed the following response variables: total seed abundance (number of seeds per trap); mean seed species richness (mean number of morphospecies per month); total seed species richness (total number of different morphospecies observed at a seed trap throughout the study); mean seed width per seed trap; and mean seed weight per seed trap. We also calculated seed rain abundance and species richness separately for the dispersal categories (zoochoric and non-zoochoric species), as well as mean seed width per trap for zoochoric species and mean seed weight per trap for non-zoochoric species. We used seed width and seed weight because these traits are important for zoochoric seeds (Moles et al. 2005; Moran and Catterall 2010; Todeschini et al. 2020) and non-zoochoric seeds (Traveset and Rodríguez-Pérez 2008), respectively. When calculating mean seed weight and mean seed width per trap, we excluded two seed traps with no seeds. In some cases (0.2% of the total seeds collected), seed weight was below the detection limit of our scales so we assigned a value of 0.0001 g to the mean weight.

To assess differences between burnt and unburnt areas and the existence of edge-related gradients, we created different generalized linear and additive mixed models (Zuur et al. 2009), including transect as a random factor in all models. This analysis enabled us to simultaneously assess the differences between burnt and unburnt areas, the existence of edge-related gradients, and the shape of these gradients when present. Thus, we created six models for each response variable (Fig. 2): (1) a null (intercept-only) model representing the null hypothesis of no difference between the burnt and unburnt areas and no edge or

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**Table 1** Structural characteristics of the vegetation present at the sites of different areas, with trees, saplings, logs, and snags, for the forests burnt and forests unburnt plots, in Una, Brazil

| Area | Forest  | Attribute | Basal area (m²/ha) | Density (tree/ha) |
|------|---------|-----------|--------------------|-------------------|
| 1    | Burnt forest | Trees     | 7.74 ± 8.65       | 281.25 ± 233.09   |
| 1    | Unburnt forest | Trees     | 23.43 ± 14.41     | 828.12 ± 366.41   |
| 2    | Burnt forest | Trees     | 9.08 ± 8.66       | 322.92 ± 317.39   |
| 2    | Unburnt forest | Trees     | 30.61 ± 13.56     | 910.00 ± 294.3    |
| 3    | Burnt forest | Trees     | 13.45 ± 16.27     | 333.33 ± 281.15   |
| 3    | Unburnt forest | Trees     | 19.04 ± 13.74     | 673.61 ± 389.92   |
| 1    | Burnt forest | Saplings  | 2.33 ± 2.33       | 2068.7 ± 1463.07  |
| 1    | Unburnt forest | Saplings  | 8.28 ± 3.61       | 7500.0 ± 2906.84  |
| 2    | Burnt forest | Saplings  | 1.48 ± 1.20       | 2565.0 ± 1025.79  |
| 2    | Unburnt forest | Saplings  | 6.85 ± 2.11       | 7540.0 ± 3234.48  |
| 3    | Burnt forest | Saplings  | 1.91 ± 2.12       | 2272.7 ± 1965.39  |
| 3    | Unburnt forest | Saplings  | 8.11 ± 2.62       | 8600.69 ± 2366.02 |
| 1    | Burnt forest | Logs      | 18.75 ± 17.37     | 693.18 ± 496.61   |
| 1    | Unburnt forest | Logs      | 9.90 ± 9.74       | 262.50 ± 199.39   |
| 2    | Burnt forest | Logs      | 25.50 ± 22.25     | 945.00 ± 711.77   |
| 2    | Unburnt forest | Logs      | 14.13 ± 10.78     | 369.05 ± 225.26   |
| 3    | Burnt forest | Logs      | 11.38 ± 7.61      | 503.29 ± 242.26   |
| 3    | Unburnt forest | Logs      | 13.71 ± 11.42     | 366.94 ± 223.46   |
| 1    | Burnt forest | Snags     | 13.04 ± 11.91     | 333.33 ± 190.94   |
| 1    | Unburnt forest | Snags     | 6.85 ± 5.10       | 125.00 ± 0.00     |
| 2    | Burnt forest | Snags     | 24.14 ± 22.08     | 458.33 ± 194.99   |
| 2    | Unburnt forest | Snags     | 6.73 ± 6.11       | 160.71 ± 60.99    |
| 3    | Burnt forest | Snags     | 15.02 ± 10.89     | 455.88 ± 271.57   |
| 3    | Unburnt forest | Snags     | 7.53 ± 5.74       | 192.31 ± 208.01   |

Each number represents an area in Fig. 1. Basal area (m²/ha) and Density (trees/ha). Mean ± SD
forest influence; (2) a categorical model, with location (burnt area or unburnt forest) as an explanatory variable and with the edge being classified as unburnt forest; (3) a categorical model, with location as an explanatory variable, and with edge being classified as burnt area; (4) an additive model, with distance as an explanatory variable and the response variables modeled as a smooth function of distance; (5) an additive model that also included distance as an explanatory variable, with the edge being classified as unburnt forest; (6) an additive model that also included distance as an explanatory variable, with the edge being classified as burnt area. In the additive models, the optimal degree of smoothing was determined by cross-validation (Zuur et al. 2009), but we established a maximum smoothing of 4 effective degrees of freedom to avoid overfitting.

For count variables (abundance and total seed rain species richness), we used the negative binomial distribution. For average seed rain species richness, we used the Gaussian distribution; for mean weight and width we used the gamma distribution. We then calculated Akaike’s information criterion corrected for small sample size (AICc; Burnham and Anderson 2004) for each model, and, for each response variable, selected the simplest model among those with a $\Delta$AICc ≤ 2.0.

We also compared the mean values of the response variables between burnt and unburnt areas (excluding the collectors located at the edge) by means of a restricted-permutation t-test. The significance of the test was assessed by randomizing the label (“Fire” or “Forest”) between the collectors of each transect (Manly 2007). For this test, we first calculated the difference in the mean values between the burnt and unburnt areas, then randomized the data as explained above, and recalculated this difference for the randomized data. We used 9999 permutations in addition to the original data, used the absolute value of the difference between the mean values as the test statistic, and, for each permutation, calculated whether the absolute value of the difference between the mean values was less than or equal to the observed difference.
We performed a Non-metric Multidimensional Scaling analysis (NMDS) with two dimensions \((k = 2)\) to evaluate differences in species composition among areas (forests, edges, and burnt areas). We used seed abundance data and the Bray–Curtis dissimilarity index to perform the ordination based on similarities of species composition. We further performed a PERMANOVA using Bray–Curtis distances and 4999 permutations to assess whether the two areas differed significantly. To assess the effects of vegetation structure on seed rain, we performed Spearman correlations between seed abundance and seed rain species richness (average zoochoric and non-zoochoric) and two structural variables: number of live trees (dbh > 10 cm) and number of snags. We performed all analyses in R 3.4.4 (R Core Team).
2017) with the packages mgcv (Wood 2011), nlme (Pinheiro et al. 2017), bbmle (Bolker and R Development Core Team 2017), lme4 (Bates et al. 2015), gamm4 (Wood and Sheipl 2020), and vegan (Oksanen et al. 2009). The data and codes are available as supplementary material 1 and 2, respectively.

Results

We collected a total of 9050 seeds belonging to 295 morphospecies during the study year (12 months), with 4404 seeds (191 morphotypes) characterized as animal-dispersed and 4646 seeds (104 morphotypes) wind- or self-dispersed (autochoric). Seed abundance was highest in the unburnt forest, followed by the burnt area and the edge (143.7, 64.2, and 45.7 seeds/m², respectively, throughout the year) (Fig. 3a).

Mean seed width varied from 0.01 to 36.6 mm (Fig. 3c); 84% (7598) of the seeds were classified as small, 15% (1399) as medium, 0.5% (47) as large, and only 0.08% (7) as very large. Of the width zoochoric seeds (Fig. 6a), 47% (3564) of the seeds were classified as small, 19% (828) as mean, 0.5% (24) as large, and 0.1% (6) as very large. Seed mean weight varied from below our scales’ detection limit of 0.001 g to 30.47 g, with the largest seed being found 100 m inside the forest from the edge (Fig. 3b).

We observed significant differences between burnt and unburnt forest for all response variables, as the null model always presented ΔAICc > 6 (Table 2). Furthermore, the restricted permutations revealed differences between burnt and unburnt area for all variables (p < 0.02). All response variables had higher values in the unburnt forest than in the burnt area (Figs. 3, 4, 5). In the forest, independent from edge distance, there were 2.2 times more seeds than in the burnt area (2.4 and 2.1 times for total abundance of zoochoric and non-zoochoric seeds, respectively) (Table 2). Similarly, the average and total seed rain species richness in the forest were on average 2.5 times higher than in the burnt area (3 times for zoochoric and 2 times for non-zoochoric) (Table 2). Seed mean weight and seed weight was 1.3 times and 2.7 times, respectively, higher in the forest than in the burnt area (Table 2).

We did not observe evidence of edge influence, as the best model was categorical for all variables independent of distance from edge (Table 2). For the total abundance of non-zoochoric species, the best model was the additive and categorical, but the simpler categorical model had a ΔAICc higher than the null model, indicating that performance is similar to that of a more complex alternative (Burnham and Anderson 2004).

The comparison of two models, one in which edge was classified as unburnt forest and the other as burnt area, enabled us to assess to which environment the edge was more similar. The ΔAICc between these two models was higher for the null model (Table 2). The
seed abundance and average richness at the edge were more similar to the burnt area than the unburnt forest, but total richness at the edge was more similar to the unburnt forest. These results were consistent for all seeds, whether zoochoric or non-zoochoric (Table 2; Figs. 3 and 4). The mean seed weight and width and the mean weight of non-zoochoric seeds at the edge were more similar to the unburnt forest than the burnt area, but the mean width of zoochoric seeds was more similar to the burnt area than the forest (Table 2; Fig. 5).

The first two axes of the NMDS had a stress value of 0.20. The second axis showed a partial separation between the unburnt forest and burnt areas, whereas the group formed by the edge was more widely distributed (Fig. 6). We found a significant result in the PERMANOVA ($p < 0.001$), confirming the difference in species richness among groups and suggesting that species composition varied by location. The ordering axes of the seed rain species richness matrices segregated the unburnt forest, then the burnt areas, and the edges.

Total seed rain abundance was positively correlated with tree abundance ($r = 0.42$, $p < 0.001$). Furthermore, zoochoric and non-zoochoric seed abundance were strongly and positively correlated with live trees abundance ($r = 0.46$ and $r = 0.29$, $p < 0.001$, respectively). Seed rain species richness was also positively correlated with live tree abundance ($r = 0.56$, $p < 0.001$), as well as zoochoric and non-zoochoric seed richness ($r = 0.57$ and $0.48$, $p < 0.001$, respectively). There was no correlation between seed abundance and richness with snags ($r = 0.10$ and $r = 0.15; p > 0.05$, respectively).

### Discussion

Our results highlight a strong contrast in seed rain between intact forest and burnt areas. Seed rain

| Table 2 | Model selection results showing the differences in the corrected Akaike’s information criterion ($\Delta$AICc) values for each model for each response variable |
|--------|----------------------------------------------------------------------------------------------------------|
|        | Null | Categoric—edge as forest | Categoric—edge as fire | Gradient | Gradient and categoric—edge as forest | Gradient and categoric—edge as fire |
|--------|------|-------------------------|----------------------|----------|----------------------------------------|----------------------------------------|
| Total abundance | 20.36 | 6.77 | 0.00* | 16.11 | 11.25 | 3.43 |
| Total abundance—zoochoric | 13.90 | 4.11 | 0.00* | 8.71 | 8.08 | 4.51 |
| Total abundance—non-zoochoric | 16.62 | 6.90 | 0.68* | 16.82 | 9.59 | 0.00 |
| Average seed rain species richness | 44.06 | 6.54 | 0.00* | 14.21 | 10.57 | 4.53 |
| Average seed rain species richness—zoochoric | 50.94 | 8.59 | 0.00* | 10.26 | 7.74 | 2.04 |
| Average seed rain species richness—non-zoochoric | 17.90 | 2.53 | 0.00* | 14.71 | 5.33 | 1.39 |
| Total seed rain species richness | 46.34 | 0.00* | 6.29 | 24.72 | 4.24 | 9.49 |
| Total seed rain species richness—zoochoric | 47.74 | 0.00* | 4.71 | 23.23 | 2.45 | 5.86 |
| Total seed rain species richness—non-zoochoric | 29.76 | 0.00* | 4.74 | 16.80 | 3.86 | 9.19 |
| Mean width | 8.86 | 0.00* | 2.44 | 3.10 | 3.86 | 5.14 |
| Mean weight | 15.28 | 0.00* | 9.35 | 9.70 | 4.54 | 11.75 |
| Mean width—zoochoric | 6.40 | 3.01 | 0.00* | 4.90 | 6.81 | 4.59 |
| Mean weight—non-zoochoric | 12.67 | 0.00* | 10.06 | 5.36 | 2.77 | NA |

*Model selected for each response variable corresponding to the model with the lowest AICc
Fig. 4 Seed rain results showing seed rain species richness: mean seed rain species richness (a), total seed rain species richness (b), mean zoochoric seed rain species richness (c), total zoochoric seed rain species richness (d), mean non-zoochoric seed rain species richness (e), and total non-zoochoric seed rain species richness (f) recorded in each survey and for the seven transects in burnt and unburnt forest in the Atlantic Forest, Brazil. Surveys were performed monthly from September 2017 to August 2018. Negative and positive values represent the burnt areas and unburnt areas, respectively. Lines represent the mean value for each area.
species richness and seed abundance were higher in the unburnt forest than in the burnt areas, as well as seed size and width, independent of seed dispersal mode. Contrary to our expectations, we did not find a gradient in seed dispersal via seed rain from the edges to the interior of either the burnt areas or the unburnt forest, regardless of seed dispersal type, seed width, or seed weight. Interestingly, abundance and mean richness at edges were more similar to forest than burnt areas, but total richness at the edge was more similar to the burnt area than the unburnt forest. Collectively, our results may indicate that seed rain is compromised after fires, which can consequently impair initial natural unburnt forest regeneration after burning.

We found a two-fold (or more) decrease in abundance of seeds, both zoochoric and non-zoochoric, in the burnt areas as compared to the unburnt forest. This result is similar to what has been observed in other studies in the Atlantic Forest of southern Bahia (Martini and Santos 2007) and Amazonia (Cury et al. 2020). It is known that fire negatively affects sexual reproduction (and therefore seed production) even in fire-prone environments such as savannas (Dodonov et al. 2018; Hoffmann 1998), and this decrease is expected to be even greater in moist forest. In addition, we found that seed rain abundances (total, zoochoric and non-zoochoric) were positively correlated to vegetation structure, indicating that areas with higher tree density also have greater seed rain. This correlation reinforces the hypothesis that seed rain is reflecting forest structural changes promoted by fire. In the same burnt areas we investigated, a previous study revealed lower densities and basal areas of trees, saplings, and lianas, and also higher values of snag density, snag basal area, and log density than the unburnt contiguous forest areas (Menezes et al. 2019).

Seed rain in the burnt areas was impoverished, with fewer species, large and heavy seeds, and zoochoric seeds as compared to the unburnt forest. In fact, the morphospecies composition in the seed rain was

![Fig. 5](image_url)  
**Fig. 5** Zoochoric seed width (a) and non-zoochoric seed weight of (b) in burnt and unburnt forest, Una, Bahia, Brazil. In the x-axes, positive and negative values represent unburnt and burnt forest, respectively. The dots and lines represent transects and average values, respectively

![Fig. 6](image_url)  
**Fig. 6** Ordination diagram produced by Nonmetric multidimensional scaling (NMDS), with Bray–Curtis dissimilarity, for seed rain composition in unburnt forest, edges, and burnt area in Una Wildlife Refuge in southern Bahia, Brazil. The gray points labeled as edge refer to traps exactly on the boundary (i.e., 0 m) between the burnt areas (black points) and the surrounding unburnt forest (white points). STRESS value = 0.24, k = 2
different between the burnt and unburnt areas, indicating that generally seeds are not moving among areas. Hence, we can assume that seed rain is sourced from propagules of neighboring trees, with few exchanges between burnt and unburnt areas. Previous studies have revealed that forest interior areas had more medium and large sized seeds than forest edges (Melo et al. 2006; Piotto et al. 2019), which may be due to the autochthonous seed rain, representing the species found at each site. This probably occurs because the local composition of the vegetation may indicate the composition of the seed rain (Drake 1998; Jensen 1998), as most seeds fall near the parent plants (Burrows 1994). The few trees that were present in burnt areas produced many small seeds, which is characteristic of pioneer species (Levey 2005) that were responsible for most seed rain abundance.

The forest environments also had higher and heavier seeds than in the burnt area, generally related to zoochorous dispersal. In general, higher and heavier seeds are characteristic of late-successional plant species of the forest interior (Ehrlein and Lehtila 2002) and their dispersal might depend on forest specialist frugivores. Our observation of large seeds exclusively in the forest interior suggests there a mobility of large seeds to the burnt area, indicating that larger-bodied frugivorous birds tend to avoid open areas (Guariguata and Pinard 1998). The possible lack of birds capable of dispersing larger seeds may have also hindered the dispersal of these seeds beyond the forest edge (Galetti and Dirzo 2013; Tabarelli et al. 2004); however, the use of burnt areas by seed dispersers should be tested in future studies. In addition, it would be important to assess the use of burnt areas by medium and large terrestrial mammals that may also be important seed dispersers.

The lack of a gradient in seed rain from the edge to the unburnt forest was not expected, but 335 in the same areas (Menezes et al. 2019). This result differs from other studies that indicated edge influence on seed rain in the Atlantic Forest (Melo et al. 2006; Vespa et al. 2014). One important difference between these two studies and ours is that they were performed at maintained edges (sugarcane and commercial tree plantations, respectively), whereas our study was at a young but regenerating edge. Therefore, the lack of edge gradients observed in our study may be explained by forest edge age (burnt areas were approximately 2 years old), and it is possible that stronger gradients from the edge into the unburnt forests will be observed as the edge develops (Chabrerie et al. 2013; Harper et al. 2005). However, the opposite may also occur, with the unburnt forest and burnt area becoming more similar as the burnt area recovers from the disturbance. The absence of gradients within the burnt area may also be explained by avoidance of the burnt area by seed dispersers or from a lower flux of abiotic dispersed seeds from the unburnt forest to the burnt area because the strength of the winds within the unburnt forests is generally low. Forest structure affects wind flow, and dispersal distances in forests are considerably shorter than in open areas (Nathan et al. 2002; Vespa et al. 2018).

Even though we observed significantly more seeds in unburnt than burnt forests, our results showed that a relatively large number of seeds also reached the burnt areas, but they were mainly small and light, typically from pioneer species. This may be due to drastic structural change in the burnt areas, the presence of surviving trees post-fire, and post-fire regeneration of some pioneer and fast-growing species, such as Miconia mirabilis, Trema micranta, Cecropia sp., Solanum crinitum, and Henrietta succosa that were found throughout the burnt area (Menezes et al. 2019). These species are common in burnt areas and favored by disturbances such as fire because they are adapted to secondary forests and edges (Barlow and Peres 2004) and are present in early successional stages after fire (Martini and Santos 2007). They are characterized by high seed production and seeds dispersed by common generalist frugivorous species, such as bats or small birds (Laurance 2007), or wind (Whitmore 1983). The surviving trees can also provide shelter for the dispersing fauna and natural perches, which contribute to seed dispersal beneath tree canopies (Holl 2002). The NMDS results corroborate this idea as they indicate that morphospecies from seed rain have distinct composition in unburnt and burnt areas. These shifts in species composition can converge toward early successional communities (Berenguer et al. 2018) that can become functionally more similar to secondary forests over time (Arroyo-Rodríguez et al. 2017; Howe, 2016), especially if wildfires become more frequent.

Our findings reveal that edges were more similar to forests concerning abundance and mean richness but were more similar to the burnt area for total seed rain species richness. We previously discussed the lack of
edge gradient; however, we cannot exclude possible effects when distance to edge is equal to zero. Therefore, effects might be present very close to the edge and did not penetrate into the forest. Indeed, short-distance edge effects, limited to the first meters from the edge or even to the immediate edge, are not uncommon (Dodonov et al. 2013; Harper et al. 2005) and have been observed for some characteristics of vegetation structure at our study site (Menezes et al. 2019). In our study, such edge effects limited to the immediate edge were observed for total seed abundance, average seed rain species richness, and the mean width of zoochoric seeds, which may indicate that seed-dispersing fauna avoid the immediate edge as well as the burnt area.

Conclusion

In our study, seed rain was dominated by small and zoochoric seeds and was not affected by edge influence. We observed differences in abundance, richness, and seed dispersal syndromes between the unburnt forest and burnt areas. Our results indicate a decrease in large-seeded species and increase of small-seeded species in the burnt areas, which can impair or retard plant recruitment and restoration processes. Importantly, seed rain was not greater near remaining forest patches; instead, the decrease in seed rain was homogeneous throughout the burnt areas. Because forest fire disturbance reduces plant diversity, it compromises future forest regeneration, thus regeneration from seed rain to a burnt area may be less diverse. The decrease in seed diversity is of particular concern because trees are the major component of the diversity, structure, and function of tropical rain forests (Denslow 1987).

As we sampled seeds for a single year, we cannot account for possible inter-annual variation in seed rain. Furthermore, our sampling occurred only few years after fire, thus, our results are related to the early regeneration process and could differ with increased time-since-fire. Still, even with these limitations, the underrepresentation of large seeds in the study area suggests that initial regeneration in the burnt areas can be impoverished, with mostly small seeds of few species. Fires are an ever-increasing disturbance in tropical forests and burnt areas are more prone to new fires. The decrease in seed rain found in the study may indicate that active restoration actions might be needed for recovery of the burnt Atlantic forest areas.

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Data availability https://github.com/pdodonov/publications.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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