



The effect of forest fragmentation on the soil seed bank of Central Amazonia



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ABSTRACT

Deforestation of tropical forests has contributed to the formation of fragmented landscapes, surrounded mainly by a matrix of secondary forests, pastures and agriculture. In this study we evaluated the fragment-area effects on the density, diversity and composition of the soil seed bank. Fragments of primary forest of different sizes (1, 10 and 100 ha) and continuous primary forests were sampled in a region of terra firme forest in Central Amazonia. We collected 180 soil samples (45 samples per treatment), and monitored seedling emergence from the soil seed bank in a greenhouse for seven months. Density of emerged seedlings, floristic composition, richness and diversity of species were compared among treatments with Kruskal-Wallis non-parametric test, Mann-Whitney test, Fisher's Alpha diversity index and Non-metric multidimensional scaling (NMDS). Seedling density was inversely proportional to the size of the fragment, being higher in fragments of 1 ha, 10 ha, and lower in the primary forest and fragments of 100 ha. Diversity was higher in the fragments when compared to the primary forests. Melastomataceae was the most abundant family in all treatments. Species composition changed along the disturbance gradient, and is dominated, in the smaller fragments by species that are indicators of degraded environments. Results suggested that the area of the forest fragments affects the size and composition of the soil seed bank, and can significantly influence the potential resilience and regeneration of these sites in the event of natural or anthropic disturbance.

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1. Introduction

Deforestation of tropical forests, especially with the objective of introducing pasture and agriculture, promotes a reduction of biodiversity and the formation of fragmented landscapes (Laurance et al., 2011; Sandor and Chazdon, 2014; Santo-Silva et al., 2016). Accumulated deforestation of the Brazilian Legal Amazon from 1988 to 2015 was 413,882 km². In the year 2014 deforestation was 5012 km², approximately 60% of the deforested areas corresponded to pastures, 23% secondary forests and 6% agriculture (INPE, 2016a, 2016b). Forest fragmentation has been shown to modify micro-climate and wind regime, cause physical and ecological changes in the vegetation, increasing tree isolation and mortal-

ity rates, and interfere in the dispersion pattern of some species (Bierregaard et al., 1992; Laurance et al., 2002; Lovejoy et al., 1986; Pizo and Vieira, 2004). Floristic composition and richness are also changed with an increase of the abundance of pioneer and secondary species, within fragments and especially near the edges (Laurance et al., 2006; Mesquita et al., 2015; Santo-Silva et al., 2013).

Ecological changes due to forest fragmentation may be directly related to the size of the fragment and these are known as area effects. Smaller fragments tend to be affected more severely than larger ones, suffering a higher tree mortality and loss of species, including plants, primates, birds, insects, among others (Benítez-Malvido and Martínez-Ramos, 2003; Boyle and Smith, 2010; Laurance and Vasconcelos, 2009; Stouffer et al., 2009). The degradation of environmental conditions of small fragments tends to be favorable for secondary and invasive species (Scariot, 2001).

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Laurance et al. (2006) showed that fast growing trees of the genera *Bellucia*, *Cecropia* and *Vismia* increased significantly in density and basal area in forest fragments in Central Amazonia. In addition, there is also evidence of an increase in the abundance of lianas in these disturbed forests (Benítez-Malvido and Martínez-Ramos, 2003).

All these ecological changes promoted by deforestation and forest fragmentation can affect the potential for regeneration of the forests through the seed bank (Martins and Engel, 2007; Wilson et al., 2016). Soil seed bank is an important source of regeneration of these environments, especially for the pioneer species, which mostly form persistent seed banks (Dalling, 2002; Plue and Cousins, 2013). The input of seeds to the soil seed bank is determined by seed rainfall. The losses may be the result of the physio-

logical properties of the seeds, which will influence the germination, dormancy and viability. In addition, the death of the seed may also occur due to animal predation, pathogen attack, depth of burial or natural senescence. The balance between these inputs and outputs will control seed density, species composition and the genetic composition of soil seed stock (Baider et al., 1999; Dalling et al., 1998; Thompson, 2000).

To date, the impact of forest fragmentation has been mainly examined for plants starting at the seedling stage (Benítez-Malvido, 1998; Bernacci et al., 2006; Carmo et al., 2011), and mostly on established trees (e.g. Laurance et al., 1998; Santo-Silva et al., 2016). However, little is known about the effect of fragmentation on the seed bank of tropical forests and how the area of the fragments can influence its structure and dynamics, and none

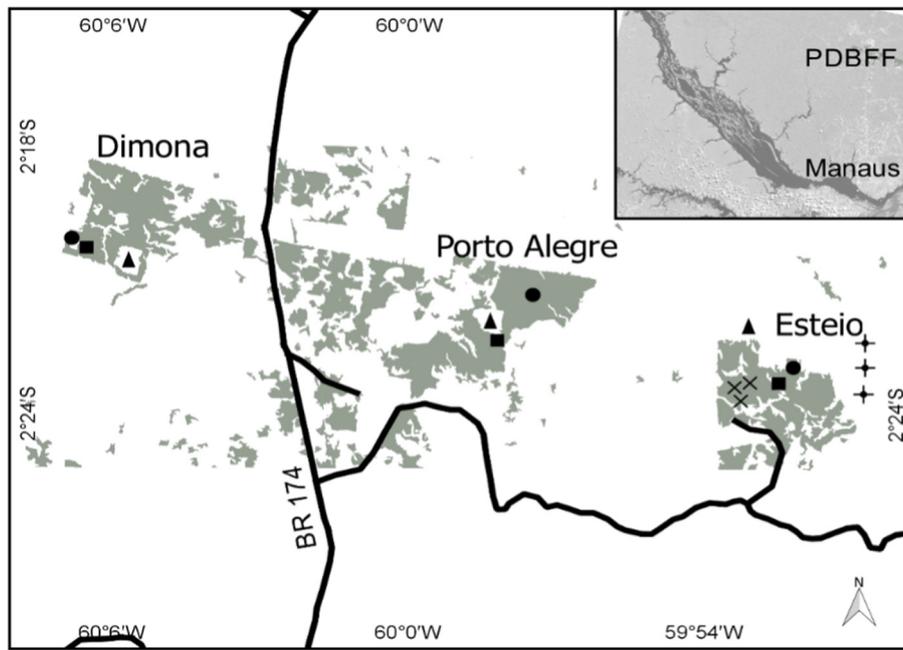


Fig. 1. Map of the experimental area of the Biological Dynamics of Forest Fragments Project (BDFFP), highlighted the ranches Dimona, Esteio, Porto Alegre and the collection areas of 1 ha fragments (black circles), 10 ha fragments (black square), 100 ha fragments (black triangle), and old growth forest (cross). White areas correspond to primary forests and gray to secondary forests.

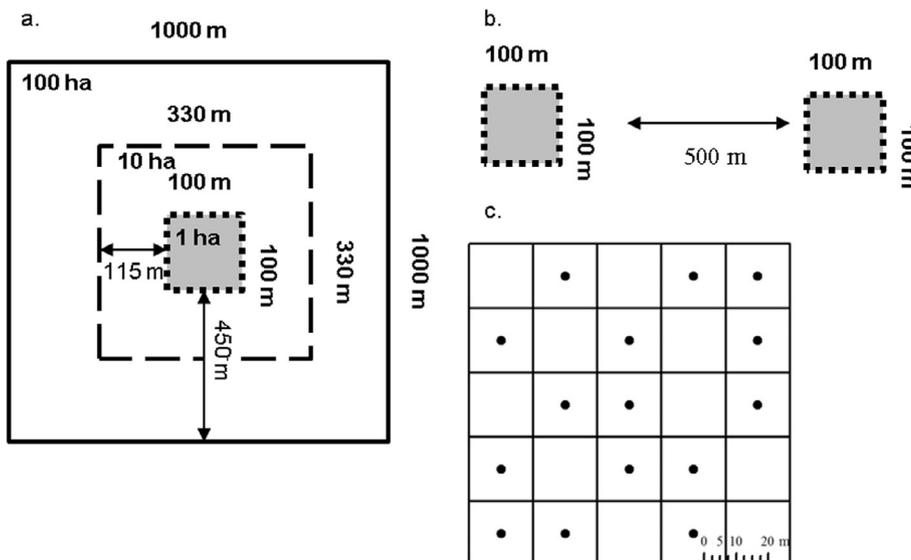


Fig. 2. Schematic drawing of location and sampling of the collection plots; a. Forest fragments, b. Old growth forest, c. Sample design of the seed bank in plots of 100 m × 100 m.

of the few studies to date (Alvarez-Aquino et al., 2005; Martins and Engel, 2007; Valenta et al., 2015) assessed this effect on Amazonian forests.

Most animal and plant taxa (including seedlings) studied so far were impoverished in fragments, proportionally to the fragment area (Benítez-Malvido and Martínez-Ramos, 2003; Ferraz et al., 2007; Scariot, 1999; Stratford and Stouffer, 1999). In this study we evaluated the fragment-area effect on the density, diversity and floristic composition of seedlings emerging from the seed banks of forest fragments (1, 10 and 100 ha) and old growth forest. Our hypothesis is that changes in these seed banks are dependent on fragment size, given the higher proportional border effect as fragment area decrease. A larger border effect implies lower humidity, higher light levels, and a shorter dispersal distance from the matrix around fragments, conditions that benefit pioneer species and increase the probability of invasion by non-forest species. Therefore, we predict that abundance of seeds in the soil seed bank will increase and species composition degrade, compared to old-growth forests, as fragment area decrease.

Understanding the role of the seed bank for the regeneration of tropical forests in the face of growing threats, mainly due to deforestation and changes in land-use, is essential not only to assess the vulnerability of forests, but especially to support strategies for the conservation and maintenance of biodiversity (Madawala et al., 2016; Williams-Linera et al., 2016).

2. Material and methods

2.1. Study area

This study was carried out in the reserves of the Biological Dynamics of Forest Fragments Project (BDFFP), on *terra firme* in tropical moist forest (Velooso et al., 1991), about 80 km north of Manaus city in the state of Amazonas, Brazil (2°25' S e 59°50' W). The BDFFP studies the environmental consequences of deforestation and fragmentation on the Amazon forest and is the largest and longest experimental study of forest fragmentation in the world (Laurance et al., 2002; Lovejoy et al., 1986). Climate in the study area is Af, tropical humid, in the Köppen classification, with an average annual temperature of 27 °C and precipitation between 1900 and 3500 mm per year, with higher rainfall occurring from February to April (Alvares et al., 2013; Fisch et al., 1998). Soils are dystrophic yellow latosols, poor in nutrients (Chauvel et al., 1987; Ranzani, 1980).

The study area encompasses three experimental sites consisting of ranches (Dimona, Esteio and Porto Alegre) that were clear-cut of primary forest in the early 1980s and abandoned or converted to pastures, with remaining isolated forest fragments of 1, 10 and 100 ha (Fig. 1). The ranches have different land use histories and are surrounded by extensive continuous primary forest with little or no human intervention. Some fragments were initially isolated by clear-cutting and the adjacent forest was not burned (Porto Alegre ranch) and regeneration of vegetation in these areas was dominated by *Cecropia* spp. On the other two farms (Dimona and Esteio), the surrounding forest was cleared and burned to maintain pastures, and these areas were dominated by *Vismia* spp. The dominance of these two genera generates differences in the diversity and composition of regenerating secondary forests, which are one of the sources of propagules for forest fragments (Mesquita et al., 2015).

2.2. Sampling and monitoring of the soil seed bank

The collection of the seed bank was carried out in areas (hereafter treatments) of old growth forest (OGF) at Esteio farm, and in forest fragments of 1, 10 and 100 ha of the Dimona, Esteio and

Porto Alegre farms. Each treatment had three replicates, totaling 12 collection sites. In each area three plots of 100 m × 100 m were delimited, and in the fragments of 1 ha the plot corresponded to the total area of the fragment. In the areas of continuous primary forest plots were set at a minimum distance of 500 m between them to ensure independence between the replicates, and in the forest fragments these plots were located in the center, aiming at reducing the edge effects (Fig. 2).

Fifteen soil seed bank sub-samples (15 cm × 15 cm and 3 cm depth) were collected at each plot, with a minimum distance of 20 m between them. The litter layer was removed before soil collection. Studies show that the depth of 0–3 cm corresponds to the layer of greater abundance, diversity and density of viable seeds in the soil (Dalling et al., 1994, 1998). Samples were collected during the rainy season, the period of greatest seed production in the region (Leal Filho et al., 2013), in 2014. Samples were packed in plastic bags, and immediately transported to a greenhouse, were exposed to natural light under 50% shade cloth, which allows for air circulation and reduces the probability of contamination by dispersed seeds from nearby areas.

Seed bank density and species identities were estimated with the seedling emergence technique (Simpson et al., 1989). Each sample was distributed with a maximum thickness of one centimeter on a substrate of sterilized sand and vermiculite (3:1), in rectangular plastic trays (20 cm × 30 cm × 7 cm) with perforated bottoms for water drainage. Ten control trays containing only sterilized sand and vermiculite were randomly distributed in the greenhouse to monitor the occurrence of possible external contam-

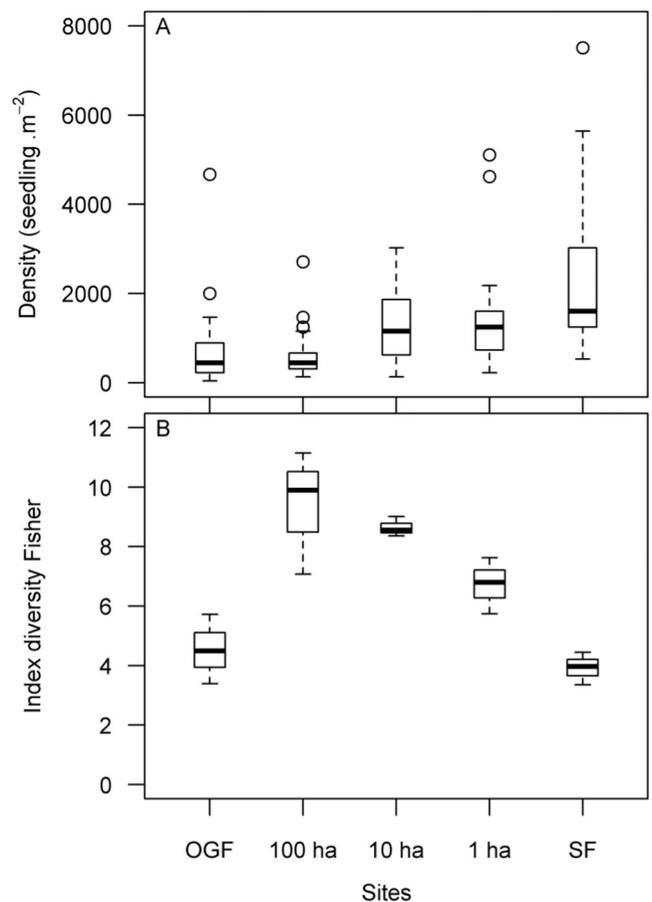


Fig. 3. A. Number of emerged seedlings per treatment. † One outlier count of 17,156 seedlings on a sample from 1 ha fragments is not shown in this graph. B. Fisher diversity index per treatment.

ination, but no germination was recorded. Samples were monitored daily for seven months, from March to September, after this period no more seedlings emerged. Taxonomic identification was performed with the aid of parataxonomists, experts and specialized literature. The number of species, morphospecies, genera and families were reported per site, and classified per life form (tree, shrub, herb and liana).

2.3. Data analysis

The mean density of emerged seedlings was compared between treatments using Kruskal-Wallis non-parametric test, followed by the Mann-Whitney test to determine differences between treatments. The diversity of species in the seed bank was estimated for each area using Fisher's Alpha diversity index. This index is based on abundance distributions and relates the number of spe-

cies to the number of individuals in a community. Non-metric multidimensional scaling – NMDS, was used to analyze the variation of the species composition among the studied areas. Ordinations were based on a Bray-Curtis dissimilarity matrix, after standardization of original data by row totals. All analysis of this work were performed in the statistical program R version 3.1.1 (R Core Team, 2013).

3. Results

After 214 days of monitoring in greenhouse, throughout all the plots, a total of 4289 seedlings emerged in the soil trays, of which 78% were identified to genus and species/morphospecies level, 22% of seedlings died before they could be identified. We recorded 28 families, 37 genera and 64 species/morphospecies in the soil seed bank. In all sites the seed bank consisted mostly of trees and

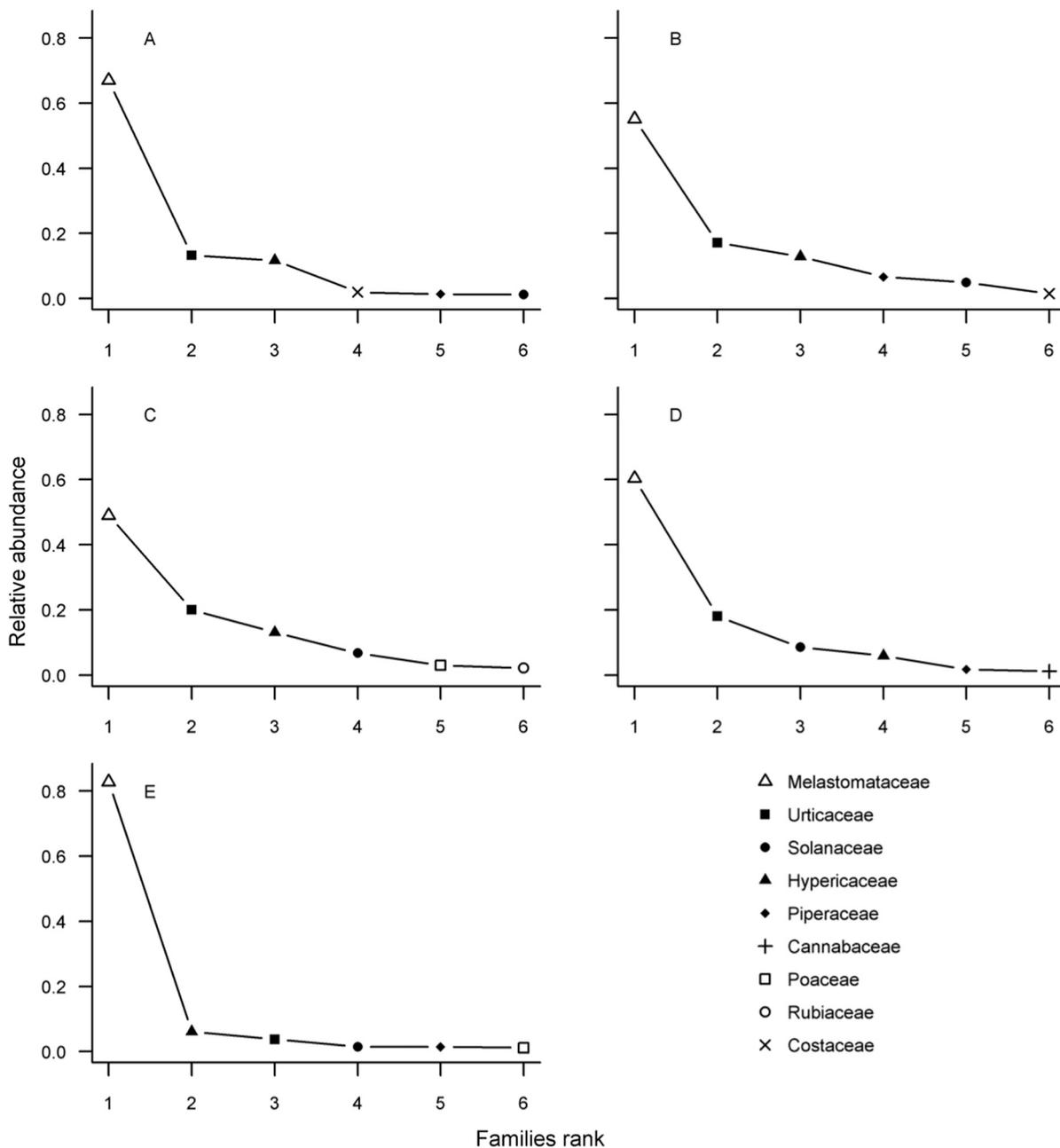


Fig. 4. Rank abundance curve of the six most abundant families in the soil seed bank; A. Old growth forest, B. 100 ha fragments, C. 10 ha fragments, D. 1 ha fragments.

shrubs, with a tree composition of 58% in 1 ha and 10 ha fragments, 71% in 100 ha fragments and 65% old growth forest.

Seedling density increased with forest degradation intensity (Fig. 3A), that is in fragments of smaller size, and is significantly higher in 1 ha fragments (1690 ± 2530 seedlings·m⁻²), followed by 10 ha fragments (1309 ± 787 seedlings·m⁻²), old growth forest (662 ± 741 seedlings·m⁻²) and 100 ha fragments (576 ± 450 seedlings·m⁻²) (Kruskal-Wallis, $\chi^2 = 52.71$, $df = 3$, $p < 0.0001$). The mean density of emerged seedlings in the 1 ha fragments approximately three times higher when compared to the 100 ha fragments and the old growth forest. There was also a greater variation of density within 1 ha fragments, where an outlier with more than 26 times the average number of seedlings of the primary forest was found. Fisher diversity index was higher in the fragments ($\bar{X} = 8.24$) than in the primary forest ($\bar{X} = 4.53$) (ANOVA, $F = 8.37$, $df = 3$, $p < 0.007$) (Fig. 3B).

The number of species/morphospecies was higher in the 1 ha (44) and 10 ha fragments (42), when compared to 100 ha fragments (25) and old growth forest (28) (ANOVA, $F = 4.02$, $df = 3$, $p = 0.05$). The number of families also increased from smaller to the larger fragments (1 ha: 13, 10 ha: 14, 100 ha: 7, OGF: 9 families, “Supplementary material”). *Cecropia sciadophylla* Mart. was the most abundant species in 1, 10 and 100 ha fragments (16%, 16% and 14%, respectively), while *Bellucia grossularioides* (L.) Triana was the most abundant species (28%) on old growth forest (“Supplementary material”). Melastomataceae was the family with greatest richness and abundance of individuals, corresponding to 20% of the total species/morphospecies and 57% of the total of seedlings identified. The abundance of Melastomataceae increased with disturbance intensity, from 257 seedlings·m⁻² in 100 ha fragments to 799 in 1 ha fragments. Melastomataceae, Urticaceae and Hypericaceae were the most frequent families in the soil seed bank. The six most common families represented, on average, 95% of the total individuals. Poaceae, a family characteristic of altered areas, was among the six most abundant families in the 10 ha fragments. The steeper relative abundance curve in the old growth forests and 1 ha fragments indicate greater dominance of a single family (Melastomataceae) in the soil seed bank, corresponding to a total of 67% and 60%, respectively (Fig. 4).

NMDS ordination in one dimension captured 35% of the variance in the original Bray–Curtis distances among plots, and shows that the composition of the old growth forest differ from the fragments (Fig. 5). A direct ordination of plots along the disturbance gradient shows the change in floristic composition from left (old growth forest - less disturbance) to the right (1 ha fragments -

greater disturbance). Old growth forest and large fragments (100 ha) have a smaller assembly of pioneer species, while small fragments (1 ha and 10 ha) have a large diversity of pioneers and species indicative of degraded environments such as *Istertia hypoleuca* Benth. and *Trema micrantha* (L.) Blume, the herb *Pleurostachys sparsiflora* Kunth, two Poaceae and some Solanaceae (Fig. 6).

4. Discussion

We have shown that smaller fragments (1 and 10 ha) of an Amazonian forest had higher seed density, higher species richness, and a differentiated species composition, including the presence of ruderal species. This result indicates a significant effect of forest fragmentation on the Amazon forest seed bank, smaller fragments being more intensely affected than larger ones.

Sites with a history of frequent disturbances, greater canopy openness and subject to edge effects tend to have larger seed bank (Alvarez-Aquino et al., 2005; Melo et al., 2007). Martins and Engel (2007) recorded lower seed density (589 seeds·m⁻²) in fragments of semi-deciduous tropical forest with lower disturbance when compared to fragments with more intense disturbances (800 seeds·m⁻²). But this trend was not clearly evidenced in the study by Alvarez-Aquino et al. (2005), in which tropical montane cloud forest fragments with different levels of disturbance were studied and fragments with intermediary levels of disturbance showed higher density in the soil seed bank. Values of seed density estimated in this study were slightly higher than those reported for old growth tropical forests, ranging from 137 to 447 seeds·m⁻² (Garwood, 1989; Vieira and Proctor, 2007), but similar to those observed in disturbed fragments by Martins and Engel (2007). The higher seed density recorded in smaller fragments directly reflects the changes in the post-fragmentation relative species abundance and composition, with an increase in the density of pioneer plants at the edge of the fragments. The increase in tree mortality rate near the edge of the fragments increases the amount of gaps which consequently leads to high establishment of pioneer species (Laurance et al., 2000, 2006), which grow fast and have large seed production (Thompson, 2000). Nascimento and Laurance (2006) have shown that the increase in the density of pioneers was three times higher in the first 300 m of fragment borders than in the fragment interior. The BDFFP 1-ha forest fragments are approximately 100 m × 100 m and those of 10 ha are 330 m × 330 m, which means that most of the fragment area is composed of borders. Light in the understory also increases due to the borders and the increased frequency of gaps (Camargo and Kapos, 1995; Lovejoy et al., 1986). The combination of higher light levels and abundant sources of pioneer seeds result in a large seed bank, but this is dominated by the seeds of these pioneers. It is often difficult to separate area and edge effects, as samples from small fragments are naturally closer to the edge than those collected in large fragments (Laurance and Vasconcelos, 2009).

In the current study the seed bank was dominated by pioneer species, mainly from the Melastomataceae family in all the studied environments, as also reported by Leal Filho et al. (2013). Generally, the seed bank is composed of pioneer species that efficiently disperse and are capable of producing a large number of seeds that remain viable and dormant in the forest soil for long periods (Dalling, 2002; Garwood, 1989; Mönaco et al., 2003). The proportion of life forms in the seed bank may vary according to the level of disturbance (Dalling and Denslow, 1998). Higher disturbance tends to shift the composition towards herbs and herbaceous vines (Grombone-Guaratini et al., 2004; Martins and Engel, 2007; Maza-Villalobos et al., 2011), mostly short-lived species. Contrary to this expectation, there was no change in this proportion in fragments (areas of higher disturbance); all of our sites were dominated by

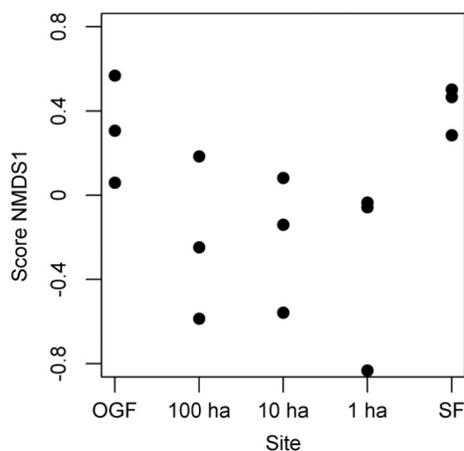


Fig. 5. NMDS ordination of species composition of forest fragments (1, 10 and 100 ha), old growth forest (OGF).

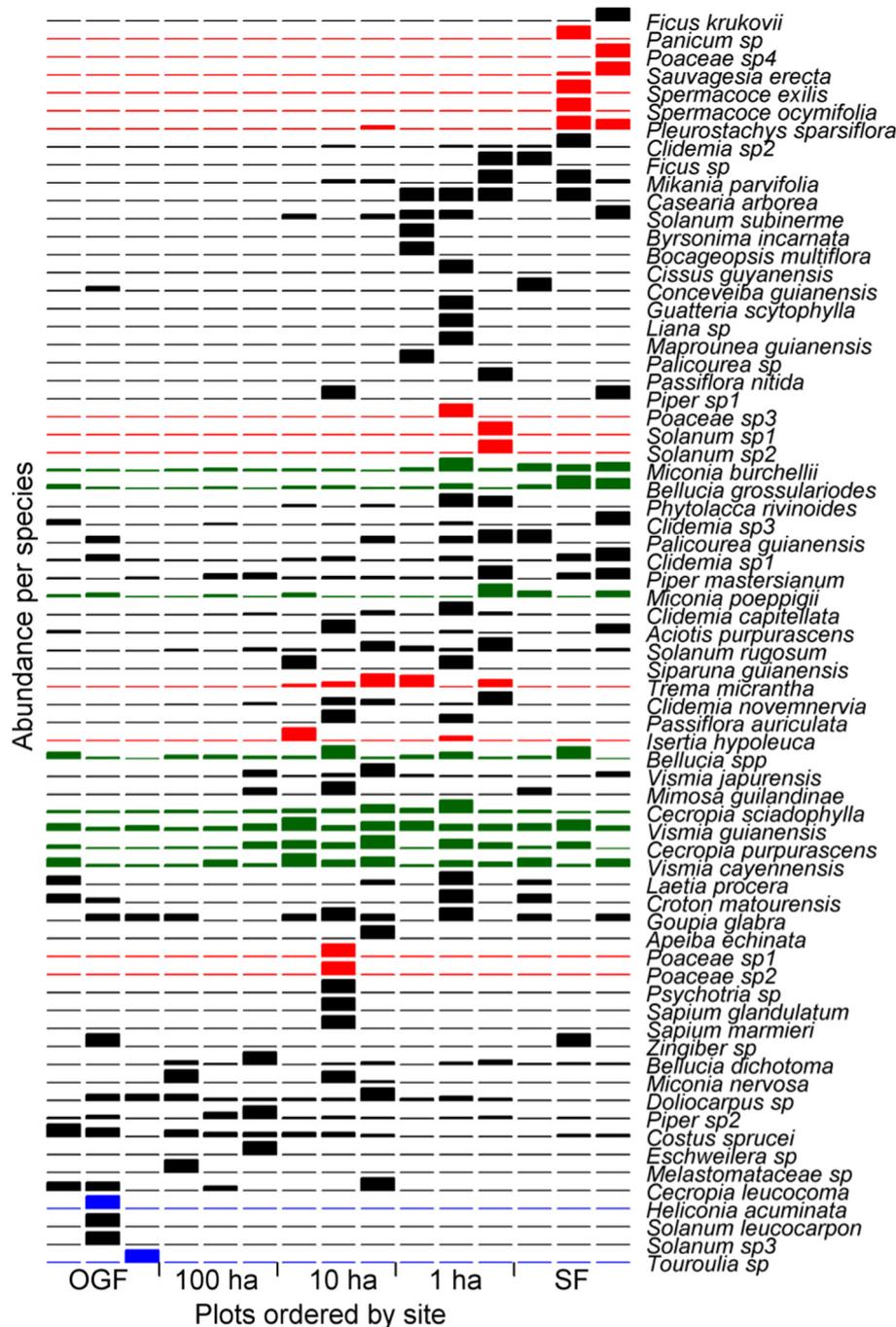


Fig. 6. Ordination of plots along the disturbance gradient. The sites indicated from left to right correspond to old growth forest, 100 ha fragments, 10 ha fragments, 1 ha fragments. The height of bars represents the abundance relative to the total number of individuals for the species. The colors of the bars indicate which species occur only in old growth forest (Blue); only in small (1 and 10 ha) fragments (Red); in all sites (Green); without a clear pattern of preference for sites (Black). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

trees and shrubs. This suggests that the levels of disturbance experienced by our forest fragments is moderate, in comparison to those studied in other regions.

Forest fragmentation can lead to significant changes in the composition of tree communities in the Amazon (Laurance et al., 2006; Nascimento and Laurance, 2006), mainly due to the proliferation of fast-growing pioneer species. In terms of composition of seed bank, we detected higher species diversity in the fragments. Valenta et al. (2015) found no differences in richness and diversity between fragments and continuous areas of semi-deciduous dry forest. However, a study of fragments in montane cloud forest recorded

greater diversity in fragments with high to intermediary disturbance (Alvarez-Aquino et al., 2005). In current study, the higher species richness in forest fragments is due to the addition of pioneers, grasses and ruderals that do not occur naturally in mature forests. Species indicative of anthropic alteration, such as *Trema micrantha* and *Isertia hypoleuca*, grasses and ruderals common in agricultural fields and pastures were found exclusively in the smaller fragments, as also found in altered forests fragments in Mexico (Alvarez-Aquino et al., 2005). Since most non-pioneer species do not form a seed bank, old growth forests had smaller richness and composition reflecting that of the pioneers normally found

within the forest. The higher density of the seed bank and the presence of ruderal species in the smaller fragments are indicative of the effect of community fragmentation and impoverishment in these areas, which may result in the susceptibility of these forests to invasion by exotic or non-forest species and, also a decrease in regeneration potential.

5. Conclusions

Very few studies have evaluated the effect of forest fragmentation on the soil seed bank (Alvarez-Aquino et al., 2005; Martins and Engel, 2007; Valenta et al., 2015), and none specifically addressed the influence of fragment area. Here we detected a clear change of seed banks on small fragments below 100 ha. Forest fragmentation led to a higher density of seeds and a change in floristic composition of the seed bank of small fragments, which included grasses and other ruderal species. The presence of these ruderals is of concern, because they can easily spread in the event of natural or anthropic disturbance, and hold back the successional process. Therefore, connecting of small fragments to nearby forest seed sources seems to be essential for impeding their complete degradation. Moreover, it demonstrates the urgent need to avoid the creation of small fragments. Larger fragments (~100 ha) behaved more similarly to old growth forests and may signal the minimum size limit above which regeneration from seed banks is safe in this Amazonian region.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.03.020>.

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