



Effects of lightgaps and topography on Amazon secondary forest: Changes in species richness and community composition



Tony Vizcarra Bentos^{a,*}, Henrique E.M. Nascimento^a, Marisângela dos Anjos Vizcarra^a, G. Bruce Williamson^{b,c}

^a Instituto Nacional de Pesquisas da Amazônia, Coordenação de Biodiversidade, C.P. 478, 69011-970 Manaus, AM, Brazil

^b Dept. of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803-1705, USA

^c Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA) and Smithsonian Tropical Research Institute, Manaus, AM 69067-375, Brazil

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ABSTRACT

Secondary succession on abandoned pastures in the Amazon is characterized by low diversity and slow turnover of plant species in the early decades. Here we present the results of a 6-year experiment in order to evaluate the effects of artificially created forest gaps established in 20-year old *Vismia*-dominated secondary forests in Central Amazonia. Plant diversity and composition of trees ≤ 5 cm DBH were assessed in 21,100-m² lightgaps evenly distributed in three topographic positions (plateau, slope, and bottomland). These empirical results were compared with four uncut, control plots nearby the experimental plots. There were no topographic effects on plant density and species richness for either the two size classes analyzed (seedlings <1 cm DBH and saplings 1–5 cm DBH). Irrespective of topographic level, tree density varied significantly before and six years after lightgap formation, for the both size classes. At six years after gap creation, the number of species increased by 30% for the seedlings, despite of the fact that the density declined significantly following creation of the lightgaps. As a result, there was a more rapid species accumulation than prior to lightgap creation. However, for the saplings the increase in species richness could be explained by the increase in the number of individuals over the six-year period. There were no significant changes in tree density and species richness for either size class for the control plots. Species composition diverged greatly from before to six years after cutting, for both size classes, as revealed by the NMDS ordinations. Moreover, for seedlings there was greater floristic similarity among plots before lightgap creation in comparison to evident divergence six years later. In contrast, for saplings floristic composition among plots was more similar after six years than prior to lightgap formation. There was little difference in floristic composition before lightgap formation and control plots. Lack of seed dispersal can be an important obstacle to natural regeneration of degraded pastures in the tropics. However, the lightgaps showed a marked increase in old-growth species originating from surrounding mature forests six years later. On intensely used sites where succession is slow, small-scale disturbance represent a feasible management tool to accelerate natural regeneration. Forest regeneration on abandoned pastures will depend on the regional pool of species and their successful establishment in secondary forest.

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1. Introduction

Tropical secondary forest covers an estimated area of 2.4×10^6 km² across Latin America and may uptake around 8.5 pentagrams of carbon in the next four decades (Chazdon et al., 2016). The rate of regeneration of secondary forest may vary globally with climate (Becknell et al., 2012), regionally with land use intensity (Purata, 1986; Saldarriaga et al., 1988; Uhl et al., 1988; Mesquita et al., 2001, 2015; Gehring et al., 2005; Norden et al.,

2010; Jakovac et al., 2015), and locally with soil properties (Becknell and Powers, 2014). In the central Amazon, secondary forests established on abandoned pastures, which have been subjected to intensive use and annual prescribed burning, follow a different successional pathway from those established on clearings abandoned immediately after deforestation (Mesquita et al., 2001; Williamson et al., 2014). The latter quickly exhibit a canopy of mixed pioneer trees, usually dominated by the genus *Cecropia* (mainly *C. sciadophylla* Mart. and *C. purpurascens* C.C.Berg) with a rich understory of herbs and shrubs characteristic of the prior forest. In contrast, secondary forests on abandoned pastures are slow to develop and are dominated by the genus *Vismia* (mainly *V.*

* Corresponding author.

E-mail address: vbtonyco@gmail.com (T.V. Bentos).

cayennensis (Jacq.) Pers.; *V. guianensis* (Aubl.) Choisy and *V. japuren-sis* Reichardt) with a depauperate understory.

Inhibition of forest development may result from reduced seed availability, often a consequence of intensive land use, and from pioneer species tolerance of degraded landscapes (Nepstad et al., 1990, 1996; Finegan, 1996; Mesquita et al., 2001; Martínez-Garza and Howe, 2003; Mônico et al., 2003; Hooper et al., 2004; Norden et al., 2010). Further, after an initial canopy of *Vismia* develops, seeds that depend on red and infra-red light may not germinate (Vásquez-Yanes et al., 1990), and newly emerging seedlings of other pioneer species may be inhibited by the low level of light penetration into the understory (Mônico et al., 2003; Bentos et al., 2013). During the process of succession, just as in mature forests, disturbances are essential for the maintenance of heterogeneity in structure and diversity. The formation of lightgaps, generally from the fall of one or several trees, is an important mechanism of disturbance that generates variability in microhabitats through availability of light and nutrients (Brokaw, 1985; Denslow, 1987; Whitmore, 1989). However, canopy openings in secondary forests tend to be relatively small, so light is a scarce resource for recruitment and establishment (Saldarriaga et al., 1988; Yavitt et al., 1995; Montgomery and Chazdon, 2001; Bebbier et al., 2002; Dupuy and Chazdon, 2006). In secondary forests originating from abandoned pastures in the Amazon, Bentos et al. (2013) showed that seedling emergence from the seed bank increased substantially in six-month old, experimental lightgaps relative to closed canopy, control plots. However, over a longer period, the processes of recruitment, including survival of initial seed bank recruits and of subsequent germinations from seed rain, remain unknown.

Given that secondary succession in abandoned pastures is characterized by low diversity and slow turnover of plant species, we present here a long-term study of the effects of experimental lightgaps six years after their creation, the same gaps initially monitored six-months after creation (Bentos et al., 2013). Specifically, our hypothesis is that through this longer period, species richness of regeneration in the artificial gaps will have increased relative to the uncut controls and that the floristic composition of lightgap plots will have diverged from each other relative to similarity prior to the lightgaps creation. Such a hypothesis emerges from the fact that lightgaps may allow the establishment of more species and the high-diverse seed rain from nearby mature forests will result in a more diverse composition among lightgaps. Our hypothesis presumes that the recruitment of viable seeds from mature forests can be favored because of the increase in light availability and decrease in belowground competition created by the gaps.

Topography can also exercise a strong effect on the distribution of plants and the structure of vegetation, as it influences physical and chemical soil properties in the Central Amazon (Costa et al., 2005). For example, soils on plateaus generally have high clay and low nutrient content relative to bottomland soils with high sand and organic content (Luizão et al., 2004; Toledo et al., 2011). Topography also affects the angle of light penetration and the amount of light reaching the soil. Bentos et al. (2013) showed that bottomlands had higher densities of seedlings than upland areas, suggesting the potential benefit of increased soil moisture as well as nutrients, despite having lower light levels. Our lightgap experiment was performed across a topographic classes, so we hypothesize that the gain in species richness in lightgaps will be greater on bottomlands than on slopes or on plateaus.

2. Materials and methods

2.1. Study area

The study was conducted on the Esteio ranch, one of the experimental areas of the Biological Dynamics of Forest Fragments Pro-

ject (PDBFF). Esteio is located about 80 km north of Manaus, Amazonas, Brazil (2°30'S, 60°W). The mean annual temperature is 27 °C with a mean monthly minimum of 19 °C and a monthly maximum of 36 °C. Mean annual precipitation is 2500 mm, with two well defined seasons - a wet season from November to June during which rainfall may reach 300 mm/month and a dry season from July to October when rainfall occasionally drops below 100 mm/month (Lovejoy and Bierregaard, 1990). Soils are clays, classified as yellow latosols (Ultisol) and red-yellow podzols (Oxisol) (Ranzani, 1980). In general, the soils are acidic and poor in nutrients, especially phosphorous, calcium, magnesium, sodium and potassium (Chauvel et al., 1987; Toledo et al., 2011). Topography of the region is lightly rolling hills, interrupted by upland plateaus and bottomlands; elevation is 40–140 m.s.n.m. Soil properties follow topography with high clay content on the plateaus and high sand content in the bottomlands (Chauvel et al., 1987; Toledo et al., 2011).

Three ranches (Dimona, Porto Alegre and Esteio) of PDBFF contain replicated forest fragments of 1, 10 or 100 ha. The fragments were isolated in the early 1980's after the mature forest was cleared for agronomic activity, principally pastures (Lovejoy and Bierregaard, 1990). Following 4–5 years of cattle grazing and annual prescribed burning to maintain the grassland, pastures were gradually abandoned because of decreased productivity. Forest regeneration commenced in abandoned pastures with scattered patches of trees, mostly *Vismia* species that survived the fires. However, other portions of the ranches that were never converted to pasture, reforested quickly from advanced regeneration - surviving stump sprouts, seedlings and germinations from the seed bank. The two types of regeneration, derived from different land use histories, have different dynamics, although they occur intermingled in the matrix around the original forest fragments. The study here was conducted only in one type, the abandoned pastures dominated by *Vismia* (Mesquita et al., 1999; Nascimento et al., 2006). When the experimental lightgaps were created in 2009, the secondary vegetation was around 20 years old since abandonment.

2.2. Experimental design

In April of 2009 at the end of the rainy season, 25 plots of 100 m² (10 × 10 m) were located in an 8 km² area of secondary forest with a closed canopy dominated by *Vismia* species at the Esteio ranch. As the study was to include artificial lightgaps, plots were chosen on the following criteria: (1) To ensure a minimum distance (200 m) between plots, (2) To avoid plots with recent natural lightgaps, and (3) To avoid obviously unrepresentative patches of the 20-year old secondary forest. Unrepresentative patches included those with severe soil erosion, completely open canopies or vine entanglements. Subsequently, in May of 2009, 21 plots were converted into artificial lightgaps by cutting and removing all the plants, including seedlings, trees and vines, as well as coarse woody debris. Adult plants were cut at the base of the trunk with a chainsaw, while small individuals were cut with a machete. Four uncut plots were left intact to serve as controls [see Bentos et al. (2013) for more details on the study area and experimental design].

In order to determine the effects of three topographic classes, the 21 plots were distributed evenly, seven plots per position across plateaus, slopes and bottomlands, whereas the four control plots were located on plateaus. For each plot, physical data were collected (TBV, unpublished data). Elevation on plateau plots (135.4 ± 1.8 m.s.n.m, mean ± standard error) was greater than plots on slopes (126.7 ± 0.5) and those on bottomlands (113.3 ± 0.8). Sand content of the soil was lower on plateaus (126.4 ± 35.1 g kg⁻¹) than on slopes (225.4 ± 40.2) or on bottomlands (383.2 ± 63.6). In addition, there were some topographic

differences in macro and micronutrient contents of the soils: phosphorous (P), calcium (Ca), iron (Fe) and magnesium (Mg) were lower on plateaus ($P = 2.76 \pm 0.95$; $Ca = 26.57 \pm 8.79$; $Fe = 166.64 \pm 34.99$ and $Mg = 11.93 \pm 2.98$ mg/kg) and on slopes ($P = 2.77 \pm 0.66$; $Ca = 26.07 \pm 10.08$; $Fe = 170.64 \pm 41.83$ e $Mg = 12.50 \pm 3.18$ mg/kg) than on bottomlands ($P = 3.73 \pm 0.85$; $Ca = 35.64 \pm 16.65$; $Fe = 196.79 \pm 32.79$ e $Mg = 15.29 \pm 3.83$ mg/kg). Soil moisture was lower on plateaus (45.5%) than on slopes (50.64%) and on bottomlands (51.36%).

Here we report the results of the 21-lightgap plots inventoried before (April 2009) and nearly six years after creation of the lightgaps. In both censuses, all individuals with $DBH \leq 5$ cm (height of 1.30 m) were identified and measured. These individuals present after 6 years in the experimental plots are new stems originating from seed or from sprouts of cut stems.

2.3. Data analyses

Two size classes of recruitment are defined for comparisons in this study. The first is composed of stems with $DBH < 1$ cm, hereafter called “seedlings”. They represent the community of small recruits early in establishment. The second class includes stems DBH in 1–5 cm, hereafter called “saplings”. They represent larger, established individuals. Both seedlings and saplings were established by seed, either from the seed bank or seed rain, or by sprouting from rootstock, because all the original seedlings, saplings, and trees were cut when the lightgaps were created in 2009. A one-factor mixed ANOVA, in which the ‘within-subject’ factor was the time period (before and six years after creation of the lightgaps) and the ‘between-subject’ factor was the topography position (bottomland, slope, and plateau), was utilized to evaluate the effects of both time and topographic position on the density of plants for each size class. A paired t test was performed to test the time effect on the density of plants for the control plots. Rarefaction (Gotelli and Colwell, 2001) was used to generate the number of species at the two sampling times and three topographic positions. The species number was generated by rarefaction of the individuals to minimize confounding effect of sample size on species richness. Freeware Past 3.13 (Hammer et al., 2001) was utilized to construct rarefaction curves.

Non-metric multi-dimensional (NMDS) ordination, which reduces the dimensionality of the original species composition matrices, was employed in order to visualize community differences between sampling times (before and after the lightgaps creation) and between size classes. The Bray-Curtis index, weighted by percent abundance per plot, was used to construct matrices of pairwise distances among plots for the ordinations. Distance-based tests for homogeneity of multivariate dispersions of the null hypothesis of no difference in beta diversity among two or more groups were run to assess for differences in beta diversity between size classes and sampling times within each size class (Anderson, 2006). For these analyses, the Bray-Curtis dissimilarities were used and p -values were obtained by permuting the least square residuals (9999 permutations). Moreover, inferential tests using multiple analysis of variance (MANOVA) were performed to test for differences between size classes and sampling times. Statistical analyses were performed using the R environment (R Core Team, 2016) with two packages: *vegan* (Oksanen et al., 2017) and *MANOVA.RM* (Friedrich et al., 2016).

3. Results

3.1. Density

Topography had no effect ($F_{2,18} = 0.083$, $p = 0.92$) on the density of seedlings per plot ($DBH < 1$ cm); likewise it had no effect

($F_{2,18} = 0.62$, $p = 0.55$) on the density of saplings ($1 \leq DBH \leq 5$ cm). However, time had a significant effect on the density of both seedlings and saplings ($F_{1,18} = 26.49$, $p < 0.001$ and $F_{1,18} = 43.94$, $p < 0.001$, respectively). While the density of seedlings showed a decline from before and six years after lightgaps (mean \pm sd = 64.4 ± 24.9 and 34.3 ± 12.6 , respectively, Fig. 1A), the density of saplings doubled over the same time interval (33.1 ± 8.3 and 77 ± 27.8 , respectively, Fig. 1B). Meanwhile, control plots showed only minor changes, but no significant differences, in density for seedlings ($t = 2.01$, $p = 0.14$; paired t test) or saplings ($t = -0.77$, $p = 0.49$) (Fig. 1C).

3.2. Diversity

The total number of species recorded varied little among the three topographic levels for either size class ($DBH < 1$ cm: lowlands = 92 species, slopes = 96, plateau = 93; $1 \leq DBH \leq 5$ cm: lowlands = 104, slopes = 100, plateau = 94). Likewise, rarefaction curves showed little difference among topographic classes for both seedlings and saplings (Fig. 2A and B, respectively). However, the number of species increased substantially over the six years fol-

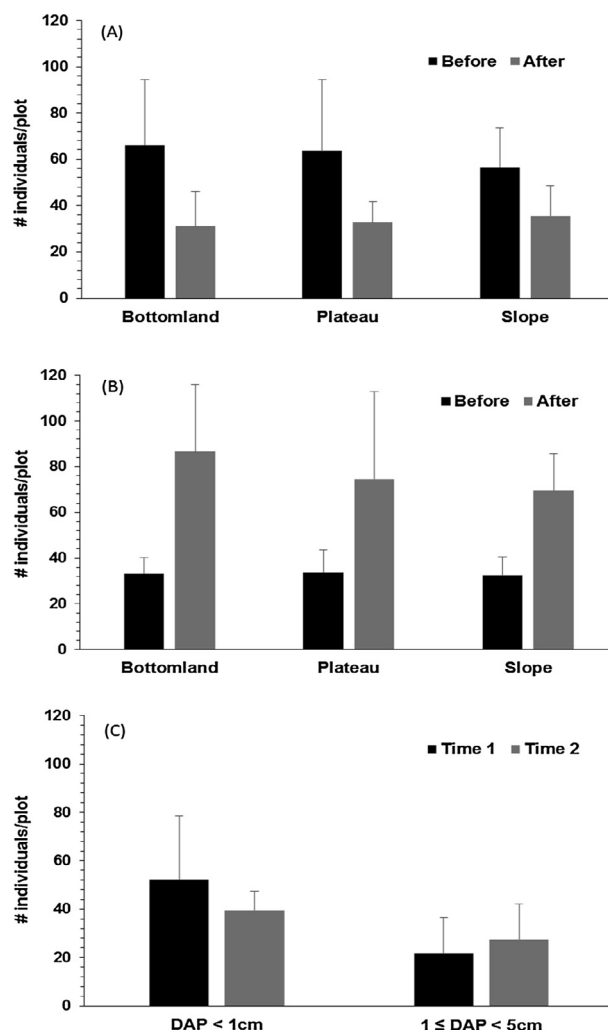


Fig. 1. Variation in the density (mean \pm st. dev.) before and six years after the creation of experimental lightgaps as a function of topographic position for two size classes of trees, seedlings <1 cm DBH (A) and saplings $1 \leq DBH \leq 5$ cm (B). Similarly, for the two sizes classes in the control plots without lightgaps, measured before (Time 1) and six years after (Time 2) (C). Time 1 and Time 2, shown in figure, correspond to before and six years after gap creation, but no gaps were created in the control plots.

lowing creation of the lightgaps, varying from 95 species before gap creation to 123 species six years afterwards, for the seedlings, even though the density of seedlings declined significantly. The rarefaction curves for the seedlings clearly demonstrated a more rapid accumulation at six years after gap creation than prior to it (Fig. 2C). Also, over the six years total richness increased for the

saplings, from 106 to 121 species, although the increase could be attributed to the increase in the number of individuals, as shown by the species accumulation curve (Fig. 2D). For the control plots there were no significant changes in species richness between before (Time 1) and six years after (Time 2) gap formation, for either size class (Fig. 2E and F).

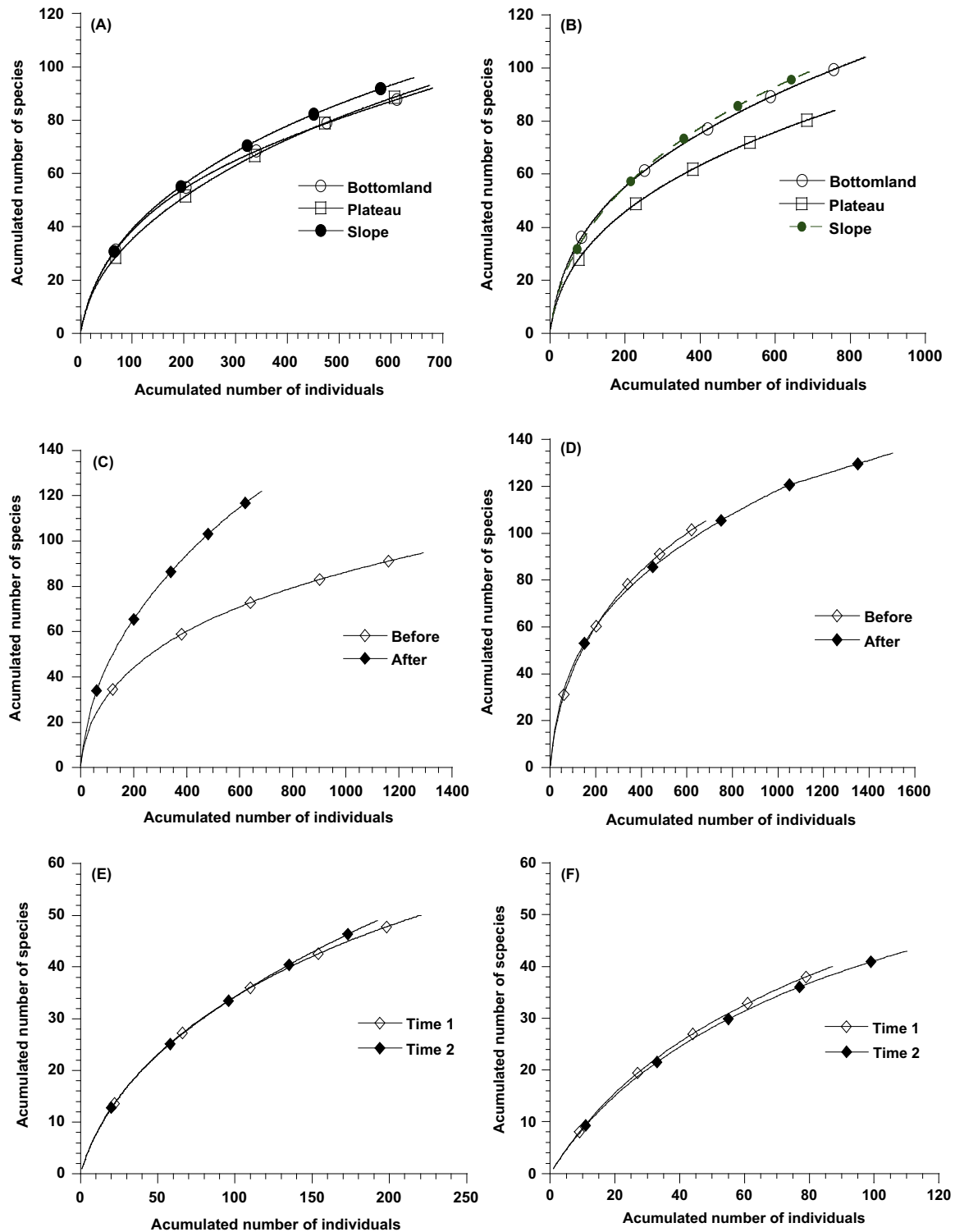


Fig. 2. For the lightgap plots, species accumulation curves as a function of the accumulation of individuals for the topographic classes for seedlings <1 cm DBH (A); for saplings $1 \leq \text{DBH} \leq 5$ cm (B); before and six years after lightgap creation for seedlings (C) and saplings (D). For the control plots, accumulation curves for seedlings (E) and saplings (F) at time 1 (before lightgaps) and time 2 (six years after lightgap creation).

3.3. Species composition

For the NMDS, randomization tests ($n = 50$ runs) revealed that the first two axes explained significant variation ($p < 0.02$ in all cases). The final stress values (Standardized Residual Sum of Squares < 0.23) indicated that the ordination matrix distances reflected those in the original distance matrix.

The NMDS ordination with the two dimensions explaining most of the variance among plots in floristic composition showed clearly the separation of the two size classes prior to creation of lightgaps, principally along the first axis (Fig. 3A, Pillai-Trace = 0.702, $F_{2,39} = 46.01$, $p < 0.001$). This axis explaining 39.2% of the variance in the original matrix was positively correlated with several species of saplings that dominate the canopy of the study area (*Vismia japurensis* Reichardt, *Bellucia dichotoma* Cogn., *Bellucia grossularioides* (L.) Triana). Likewise, the axis was negatively correlated with *Guatteria scytophylla* Diels, the most common species in the seedlings stage. Also, it is noteworthy that for saplings there was significantly greater beta diversity (dispersion) among plots than for seedlings ($F_{1,40} = 9.84$, $p = 0.003$).

The ordinations (Fig. 3B and C) revealed temporal variation in the species composition before and six years after the opening of the lightgaps for each size class analyzed separately (seedlings: Pillai-Trace = 0.807, $F_{2,39} = 81.54$, $p < 0.001$; saplings: Pillai-Trace = 0.539, $F_{2,39} = 22.83$, $p < 0.001$). Although not significant, there was greater floristic similarity among plots for seedlings before lightgap creation in comparison to evident divergence six years later ($F_{1,40} = 2.98$, $p = 0.095$). The opposite pattern appears for saplings whose floristic composition among plots was significantly more similar after six years than prior to lightgap formation ($F_{1,40} = 5.66$, $p = 0.022$). When the control plots were compared to the lightgap plots (only plateau plots), there was little difference in floristic composition before lightgap formation and substantial difference after formation for seedlings (Fig. 3D) and saplings (Fig. 3E).

For seedling species identified in both inventories (156 species), 21% (33 species) were found exclusively prior to lightgap formation and 39% (61 species) exclusively six years later. For saplings (164 species), 26% (43 species) were exclusive to plots prior to lightgap formation and 35% (58 species) exclusive six years later. Exclusivity, separate for pioneer species and non-pioneers (old-growth species from mature forest) species, increased from before the creation of lightgaps to the six-year inventory for both pioneer species and for mature forest species, being more marked in seedlings (from 27 to 45 species for mature species) than in the saplings (40 to 49 species) (Fig. 4).

4. Discussion

This study aimed to evaluate how three community attributes – density, diversity and community composition – may be influenced by artificial gaps created in a 20-year old secondary forest that originated from intensive land use. The division into tree size classes, although arbitrary, allowed us to glimpse in greater detail the dynamics of regeneration in two different life stages over six years. An important aspect of our study is that information on the three attributes was obtained prior to the lightgaps creation, thereby allowing a thorough assessment of the effects of openings on tree regeneration over the six-year period. Moreover, all live aboveground biomass was removed, including the seedling layer, so all regeneration and tree establishment occurring after the gap creation originated as germination from the original seed bank or recent seed rain (dispersal) and as sprouting from root stocks. Generally, species turnover (Norden et al., 2010) and species accumulation (Williamson et al., 2014) in young stands are much slower in

Vismia-dominated secondary forests than in nearby *Cecropia*-dominated secondary forests. Such differences in species accumulation and turnover explain the convergence in floristic composition in *Vismia*-dominated forests because of the persistence of a few dominant pioneer species throughout the succession (Longworth et al., 2014). The novel findings of our study are that experimental six-year old lightgaps, established in 20-year old *Vismia*-dominated stands, effected an increase in local diversity compared to 26-year old control plots without gaps, and the lightgap plots showed increasing dissimilarity through time, as demonstrated by NMDS ordinations. Therefore, six years after gap creation, the net gain in species per plot also resulted in an increase in regional diversity.

In general, successful forest regeneration should depend on the seed and seedling bank, plus any viable seed rain. However, in the initial year of succession, Amazonian secondary forests regenerating in pastures are dominated strongly by resprouts of *Vismia* spp., to the detriment of regeneration from the seed and seedling bank (Jakovac et al., 2015). Further, seed and seedling banks, characteristic of older forests, are exhausted by annual burning of pastures prior to abandonment. Thus, the accumulation of tree species in these forests may be subject to species' availability via dispersal from adjacent forests to replenish the seed bank. Plant recruitment after six years of gap creation necessarily originated from the seed bank (20 years old at gap formation), sprouting of cut stems, and ongoing seed rain from old-growth species from surrounding primary forests. Given the large influx of mature forest species, measured here, lightgap stimulated germinations from seed bank and seed rain necessarily played a role.

However, the recruitment by seed of mature forest species appears to contradict earlier studies in *Vismia*-dominated secondary forests. In the plots studied here, just six months after gap creation, the dominant canopy pioneer species, namely *Vismia*, *Bellucia*, *Miconia* and *Cecropia*, comprised 90% of the emerging seedlings that established (Bentos et al., 2013), but the six-month period may have been insufficient for recruitment of primary forest species. Earlier, Wieland et al. (2011), who quantified the seed rain in *Vismia*-dominated secondary forest, found that virtually all seeds found in seed traps were early pioneer species already present in secondary vegetation, not propagules arriving from adjacent primary forest. However, primary forest seeds generally are dispersed by mammals and large birds, so Wieland et al. (2011) may have failed to catch these seeds as their seed traps were suspended above ground. Availability of nearby primary forests is characteristic of the PDBFF, where secondary forests are enmeshed in a continuous landscape of uncut Amazonian old growth. Therefore, mature forest seed sources and their dispersers are readily available to facilitate colonization of adjacent secondary forests, as shown by recruitment of mature species over our six-year study.

Seed dispersal during the 20 years of secondary succession may have been crucial to the differences in floristic composition between the two tree size classes before the lightgaps were created (Fig. 4A). In a separate study conducted in the same gaps before their creation, one of us (TVB, unpublished data) reported that the composition of adult individuals (DBH > 5 cm), dominated by pioneer species, was closer to seed bank composition than the seedling bank (DBH < 1 cm), demonstrating the importance of local and external dispersal as determinants of composition of seeds and seedlings, respectively, in our study site. Therefore, we can assume that dispersal is no longer a limiting factor after two decades of natural regeneration in our study site, but survival and growth seem to be influencing the differentiation in composition between tree size classes. While individuals of local dispersal (mainly pioneer species) are able to reach the canopy, the growth of individuals from external dispersal (mainly primary forest species) seems to be limited by the adverse environmental conditions as a

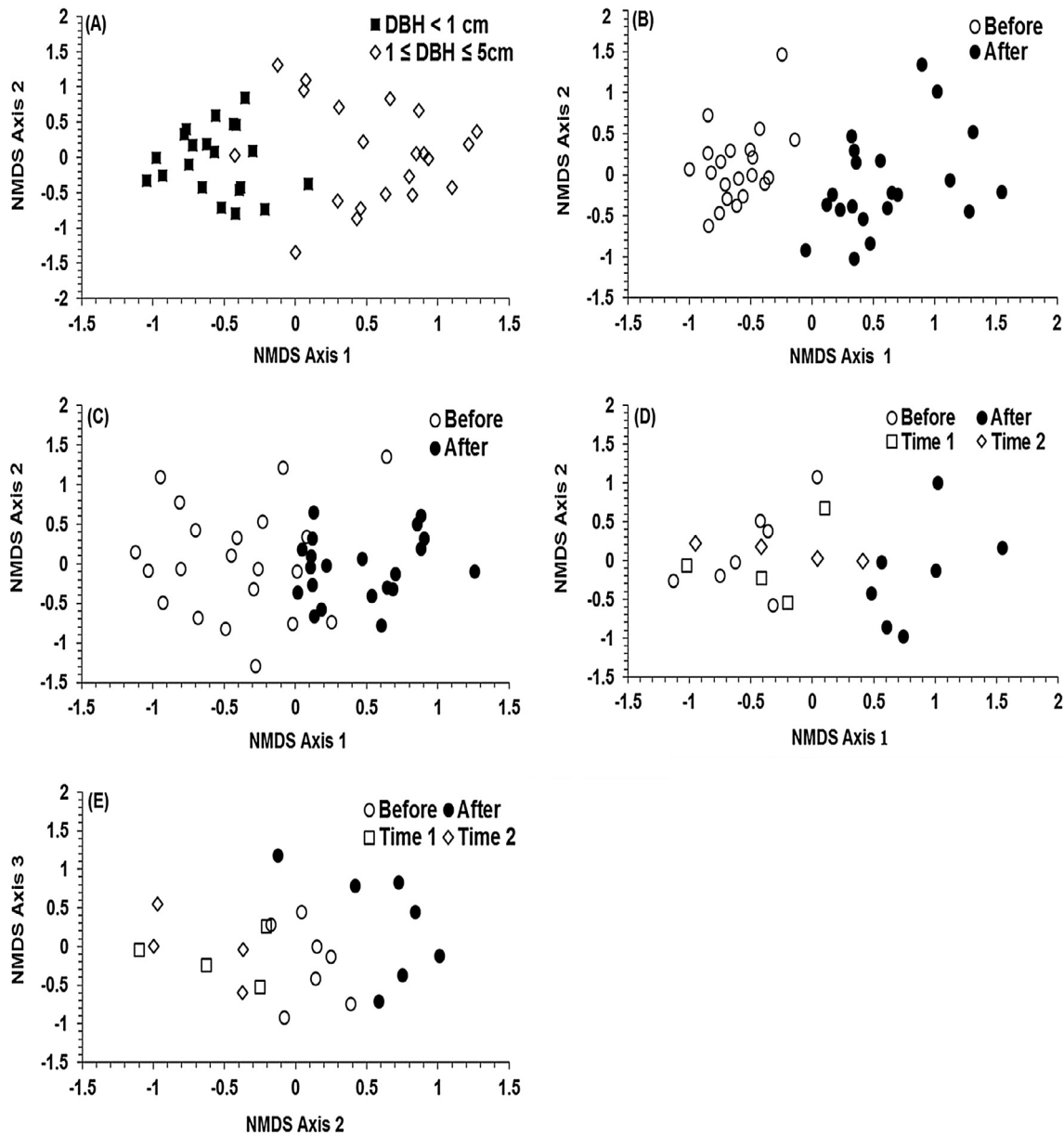


Fig. 3. Ordination diagrams from non-metric multi-dimensional scaling (NMDS) based on floristic composition of (A) the two size classes before lightgap formation, (B) seedlings <1 cm de DBH before and six years after lightgap formation, (C) saplings 1–5 cm DBH before and six years after lightgap formation, (D) the control plots (time 1 and time 2) and plateau lightgap plots (before and after) for seedlings <1 cm DBH, and (E) the control plots and plateau lightgap plots before and six years after lightgap formation for saplings 1–5 cm DBH.

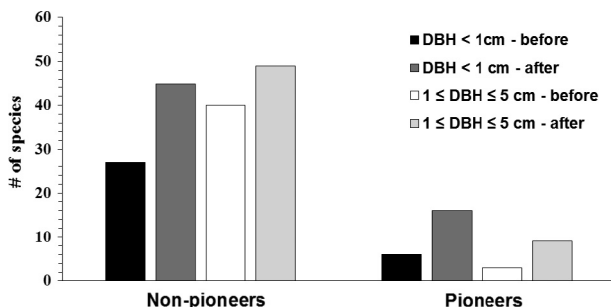


Fig. 4. Number of species exclusive to sampling date (before vs six-years after lightgap formation), separately by ecological group and by tree size class.

consequence of impediment of growth under closed canopy and intense belowground competition. Before gap creation, the greater floristic differentiation among gaps for the 1–5 cm size class indicates that as succession proceeds, plot composition becomes more variable, whereas in the <1 cm size class plot composition tends to be more similar. However, six year later several changes in biological and environmental variables may have occurred, primarily light availability and belowground competition. As a result, temperature and nutrient availability will also change with variation in light (Brokaw, 1985; Denslow, 1987). Gaps create different microsites in terms of light, moisture and nutrient availability favoring the establishment of species, which resulted in a greater dissimilarity in the composition among gaps after six years for the <1 cm size class as a consequence of the increase in local diversity and recruitment of new species (Figs. 3B and 4). Jakovac et al. (2014) planted 990 seedlings of nine tree species and found that

the relative growth rate over 17 months was higher in *Cecropia*-dominated forests than in *Vismia*, even although the photosynthetically active radiation reaching the ground was lower in the former (Jakovac et al., 2014). Thus, nutrient limitation and/or below-ground competition may be negatively influencing the establishment and growth of tree species in *Vismia*-dominated secondary forests, so physical and biological changes in the environment like those created by gaps appear crucial for successful recruitment and establishment of tree species.

Will gaps become more dissimilar floristically or tend to converge over the time? Our results showed a floristic convergence after six years for the $1 \leq \text{DBH} \leq 5$ cm class (Fig. 3C), mainly as a result of a widespread recruitment and growth of pioneer species. The high density of individuals in the $1 \leq \text{DBH} \leq 5$ cm size class after six years portends an accelerated canopy closure because of the rapid growth of these species. In fact, the 10 most abundant species in this size class are typically dominant pioneers in the study area, which comprised about 64% of individuals recruited after six years. On the other hand, the relative high divergence in plot composition for the <1 cm DBH class after six years, as a consequence of new primary species and low dominance of the most common canopy species, may suggest that over the years these newly recruited species may dominate the canopy. However, the fate of the small primary forest trees recruited during the six years after gap formation is uncertain given the high competitive ability of large pioneer species (Jakovac et al., 2015), although thinning of canopy trees may facilitate the survival and growth of recruits in the experimental lightgaps, as was the case in Costa Rica (Dupuy and Chazdon, 2008).

There was no topographic effect on density or diversity for both size classes, although diversity in the bottomlands tended to be slightly lower than in plateaus and slopes. These results contradict those of Bentos et al. (2013), who recorded higher emergence and initial growth of seedlings in the bottomlands six months after lightgap creation. That particular six-month period coincided with the drought of the 2010 El Niño. The lack of differences after six years may reflect the return to normal rainfall after 2010. Also, seeds of secondary species are very small (Wieland et al., 2011; Bentos et al., 2014), so germination is best in the soil surface layer, where mortality due to desiccation can occur rapidly (Bewley and Black, 1982; Ashton, 1992). Thus, germination and initial growth of pioneer species can be favored in moist sites (Daws et al., 2008). However, later in succession after canopy closure, soil moisture becomes less of a limiting factor for seedling survival, whereas light becomes crucial to plant establishment and growth.

5. Conclusions

In this study, we showed that artificial lightgaps influenced the successional dynamics in *Vismia*-dominated secondary forests originated from abandoned pastures in Central Amazonia. Our 6-year experiment provided strong evidence that on lands with high intensive use, such as abandoned pastures, lightgaps increased local species diversity in the gaps and contributed to an increase in regional diversity. Seed sources from the seed bank and dispersal from the surrounding vegetation may limit species richness in the first few years after regeneration, but after two decades of abandonment competition for primary resources, probably supersedes propagule limitation. In an era of increasing demand for restoration of highly degraded lands, artificial lightgaps may represent a cost-effective silvicultural treatment.

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