Long-term effect of selective logging on floristic composition: A 25 year experiment in the Brazilian Amazon

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ABSTRACT

Selective logging is one of the most prominent land uses in tropical forests and although it involves harvesting a limited number of trees, the impact on forest structure, composition and aboveground biomass can be significant. Although these impacts are well documented, what is little known is the extent to which selective logging affects tree floristic composition and its recovery process. Understanding how floristic composition is affected by logging activities is essential for determining subsequent cutting cycles, for the maintenance of carbon stocks and for biodiversity conservation. This research investigates the effect of logging on long-term trends on the recovery of species composition in a tropical forest using a unique logging experiment where measurements have been taken annually over a period of 25 years. Changes in 12 long-term 1-hectare (ha) permanent plots were assessed where different selective logging intensities occurred. In the first years after logging, floristic composition differed widely between intact and selectively logged forests, with exploited areas deviating from pre-logged composition. Over time, exploited areas shifted towards the original composition, with more pronounced changes in this trend after ~13 years. Shifts in floristic composition were caused mainly by a significant increase in light-demanding fast-growing pioneer species and their subsequent continuous high mortality rates after 13 years of the recovery process. In contrast, the control plots showed similar shifts in composition over time, suggesting external factors such as long-term climate changes may be driving these shifts. The results suggest that 25 years after an experimental selective logging has taken place, floristic composition tends to recover closer to the pre-logged status. Thus, in the absence of further human disturbances, experimental selectively logged forests in low to moderate intensities are compatible with biodiversity conservation, at least during the first cycle of exploitation. Reconciling conservation strategies with the recovery of stocks of commercial timber species would be greatly improved by using these results and lead towards more sustainable forest management plans.

1. Introduction

Amazonian forests are of one of the most diverse ecosystems on earth (Gentry, 1988; ter Steege et al., 2013) and play an important role in the global carbon cycle (Malhi and Grace, 2000; Malhi et al., 2006). However, the strong anthropogenic pressure on these forests threatens their role in mitigating climate change and biodiversity loss due to increasing deforestation and forest degradation. In particular, logging is one of the main drivers of current land use change with nearly 20% of tropical forests under timber extraction (Asner et al., 2009; Tyukavina et al., 2017) and impacting at least 15 000 km² of Amazonian forests

per year (Asner et al., 2005). Although illegal logging plays a major role on the proportion of forest loss (Monteiro et al., 2012) aboveground biomass can decline up to 40% in areas under selective logging through harvesting of selected commercial tree species (Nepstad et al., 1999). Specifically, in the Brazilian Amazon, roughly 2 Mha yr⁻¹ were logged between 1999 and 2002, which is equivalent to the annual deforestation during this period (Asner et al., 2005), highlighting the high ecological impact of managed forests and consequently on ecosystem processes and services.

In selective logging, a small proportion of timber tree species is harvested. However, because the removal of large trees can cause

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collateral damage to the remaining and adjacent trees (Magnusson et al., 1999; Nepstad et al., 1999; Gourlet-Fleury et al., 2005; Griscom et al., 2018), understory vegetation (Costa et al., 2002; Kembel et al., 2008) and soils (Olander et al., 2005), selective logging can have considerable impact on forest structure and composition. Logging activities can also increase the number of fallen and damaged trees, and tree recruitment, causing long-term changes in forest structure (Nepstad et al., 1999; Hall et al., 2003; Cazzolla Gatti et al., 2014). Due to harvesting of large trees and collateral damage to non-timber species, carbon stocks are sharply reduced, independent of logging regime, though smaller impacts are detected at lower intensities (Higuchi et al., 1997; Chambers et al., 2004; Gourlet-Fleury et al., 2013; Griscom et al., 2018; Otani et al., 2018). Despite this notable initial decrease, recovery rates of above-ground biomass are relatively fast and proportional to the disturbance intensity (Gourlet-Fleury et al., 2013; Piponiot et al., 2016; Otani et al., 2018). For instance, in a Central African silvicultural experiment, Gourlet-Fleury et al. (2013) found that above-ground biomass sufficiently recovered after 24 years following logging activities. This harvesting impact on biomass losses varies widely from 3% to 53% (Putz et al., 2012) and is followed by shifts in species richness and composition (Silva et al., 1995; Magnusson et al., 1999; Lima et al., 2002; Cazzolla Gatti et al., 2014).

Not all species are equally affected by selective logging. Specifically, logging activities focus on a few commercial large timber species, of high wood density and long life-cycles (da Silva et al., 2002; Gourlet-Fleury et al., 2005; Keller et al., 2007). Removal of these trees changes forest diversity and structure by reducing the number of stems, increasing the number of large canopy gaps and consequently changing microclimatic conditions. Thus, after forest disturbances there is an initial decrease in species richness (Griscom et al., 2018) with community composition shifting in favour of light-wooded and fast growing tree species (Baraloto et al., 2012; Baker et al., 2016). Although this initial decline in species richness is well documented (Baraloto et al., 2012; Griscom et al., 2018), how the whole community composition changes over longer time scales and how long it takes to recover to pre-logging conditions remains to be evaluated.

Therefore, this study investigates the long-term impact of different selective logging intensities on tree community composition in tropical forests by using a unique long-term forest management experiment under low, medium, and high harvesting intensities and adjacent control areas from 1987 to 2012 (Higuchi et al., 1985; Higuchi et al., 1997). All plots were monitored annually. Specifically, the study asks: (i) does floristic composition differ among control plots and across treatments with different logging intensities?, (ii) do control and selectively logged areas shift similarly over time? and, (iii) can floristic composition recover to pre-logged status after 25 years?

2. Methods

2.1. Study area

The study was conducted at the Experimental Station of Forest Management (EEST) managed by Forest Management Laboratory of the National Institute of Amazonian Research, Manaus, Amazonas, Brazil (Fig. 1). The area is covered by closed canopy old-growth *terra-firme* forest with high tree species diversity and dense understory (i.e. more than 800 species on 61 families) (Marra et al., 2014; Fontes et al., 2018). Soils are predominantly dystrophic, with low levels of phosphorus, calcium, magnesium, sodium, and potassium and high levels of aluminium (Quesada et al., 2010). Annual temperature is roughly 26 °C and average annual rainfall is 2000–2400 mm year^{-1} with mean monthly precipitation exceeding 300 mm during the rainy season from December to May (Sombroek, 2001; Higuchi et al., 2011).

2.2. Experimental design

The selective logging experiment implemented in the EEST contains 3 blocks with 24 ha distributed in 5 different treatments and 1 control, encompassing a total area of 72 ha (Higuchi et al., 1985). For this study we used repetitions of 3 different levels of wood exploration treatments and control plots with the experiment being divided into 12 randomly distributed plots (Fig. 1). Plots with different logging intensities were 4 ha (200 × 200 m). Monitoring was conducted in permanent 1 ha plots (100 × 100 m) established in the center of each treatment, preventing edge effects (Laurance et al., 2002). The 3 silvicultural treatments applied were: T1, low intensity, where logging removed an average of 1/3 of the basal area of timber species (34 m^3/ha); T2, intermediate intensity, where 50% of the basal area of timber species were removed (49 m^3/ha) and T3, high intensity, that removed 2/3 of the basal area of timber species (67 m^3/ha). Despite the specified logging intensity applied in the different treatments, the absolute impact varied widely due to the collateral damage in each permanent plot. Further details on the methods are given elsewhere (Higuchi et al., 1985, 1997, 2004).

2.3. Data collection

Permanent plots were installed in 1980; selective logging occurred in 1987 and re-censuses were carried out on a yearly basis. The study uses data from 25 censuses from the pre-logging status in 1987 until 2012. All living trees and palms greater than 10 cm diameter (dbh, measured at 1.3 m height or above any buttress or deformity) were recorded in the first census. During each remeasurement, surviving trees were measured, dead trees were documented, and new trees with ≥10 cm dbh were recorded. In each census all individual trees were identified by experienced botanists using a vernacular name based on vegetative characteristics. Between 2011 and 2012 botanical vouchers of individual trees for all species were collected for taxonomic checking. Tree species were identified using INPA's and the Biological Dynamics of Forest Fragments Project's herbarium reference collections and also by consulting specialists. Botanical identification followed the "Angiosperm Phylogeny Group – APG" (APG III, 2009) classification system. Voucher specimens were deposited in the INPA Herbarium located in Manaus (please see Appendix 1 for deposit number). All the individuals that died between the initial and final census and the additional 6% of non-collected trees had their given vernacular name carefully associated with a correspondent scientific name following strict criteria (see SI for details). Spellings, synonyms, and taxonomic issues were checked and standardized using the Taxonomic Name Resolution Service, including TROPICOS (Boyle et al., 2013).

2.4. Data analyses

To analyse the changes in floristic composition, the 25 years (1987–2012) of annually collected floristic data were used. We used Principal Coordinates Analysis (PCoA) to reduce the dimensionality of the high number of species into two main axes of variation (McCune and Grace, 2002). Ordinations were based on the relative abundances (standardization of the original data by the total number of individuals in the plots) and Bray-Curtis distance. These first two axes of the ordination space were used to generate a visual representation of differences within and among treatments and the trends in compositional changes (Espirito-Santo et al., 2009; Feeley et al., 2011a). Differences in floristic composition among treatments were tested through multivariate Analyses of Covariance (MANCOVA) on the first two axes of the PCoA and both years and replicate sites were used as covariates.

The directions of shifts in community composition were investigated further. To test whether observed shifts in floristic composition in logged areas over the years were random or followed a unidirectional trajectory, 500 shifts in random directions for each plot in each of the 25 years of monitoring were simulated. For each census interval, the
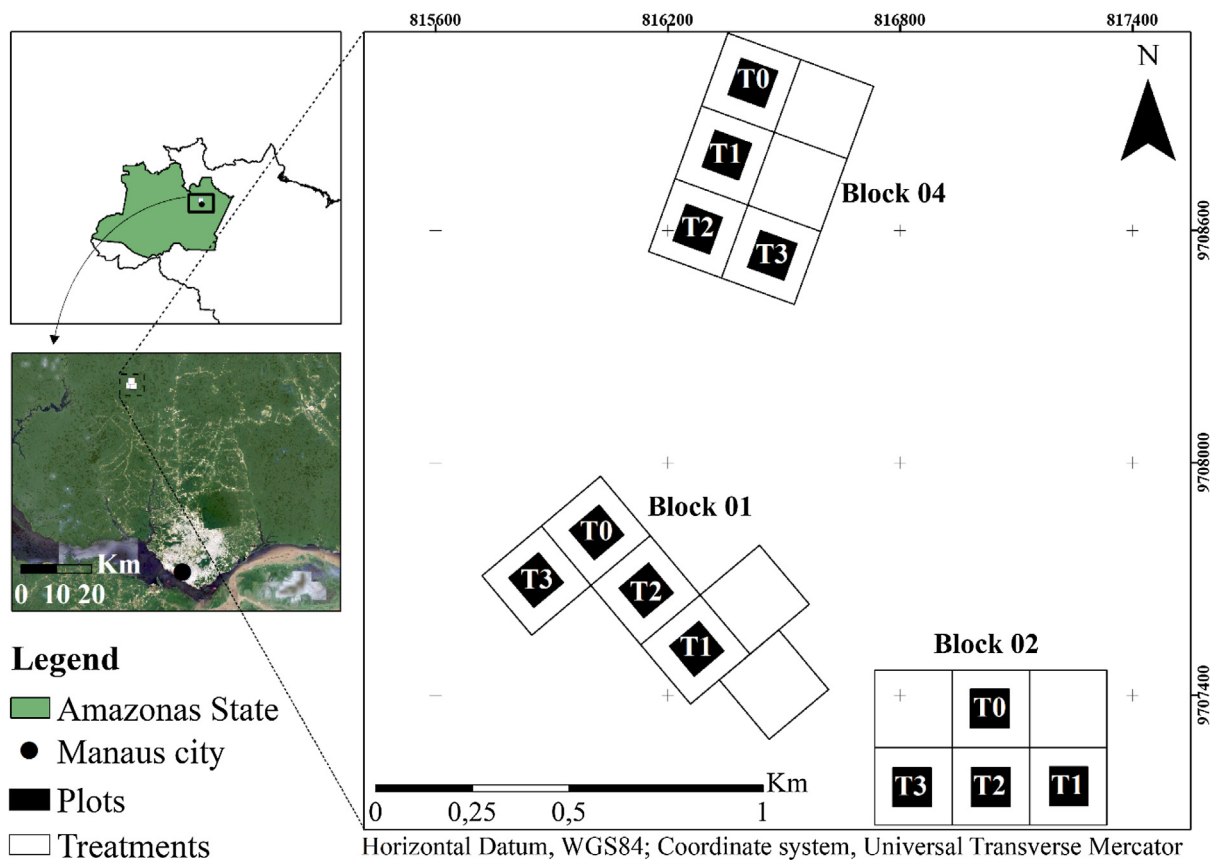
Fig. 1. Map of the Experimental Station of Forest Management (EEST) where the logging experiment is located. Groups of white squares correspond to the different blocks and the smaller black squares the different treatments: T0 the control plots, T1 low logging intensity, T2 intermediate intensity, and T3 high intensity. Please see methods for further details.

Euclidian distance between the initial and the final year of each plot was calculated from the bi-dimensional ordination space to estimate the average shift per plot. Because across different treatments the distribution of measured distances was a negative exponential, simulated shifts were constrained to the distance values within this distribution and in the range of the observed values, but were not constrained in their directions. To determine if shifts in community composition were random or followed a directional trajectory, the simulated distances were compared with actual data. The proportion of times in which simulated values were greater than empirical distances gave the significance of the change for each plot: when the proportion of simulated distances were smaller or equal to the observed, shifts in floristic composition were random, whilst simulated distances greater than observed indicated changes that were significantly more directional than expected by chance. All analyses were conducted in the R 3.1.1 platform (Team, 2014).

3. Results

Over the 25 years of forest monitoring 11,338 stems ≥ 10 cm dbh, from 709 species belonging to 242 genera and 58 families were inventoried. In the last year (2012), 169 species (2.3% of stems and 23.8% of species) were considered rare and represented by a single individual, whilst eight species were highly abundant in the area, encompassing 15% of the total number of individuals: *Eschweilera wachenheimii* (Benoist) Sandwith, *Micrandropsis scleroxylon* (W.A.Rodrigues) W.A.Rodrigues, *Protium hebetatum* Daly, *Croton matourensis* Aubl., *Eschweilera romeu-cardosoi* S.A.Mori, *Eschweilera truncata* A.C.Sm., *Eschweilera coriacea* (DC.) S.A.Mori and *Rinorea paniculata* (Mart.) Kuntze. However, when considering the entire time period

(1988–2012), the most abundant species was *Cecropia sciadophylla* Mart. (n = 284), an early successional and short-lived tree quickly recruited after logging, although dying in large numbers during the 25 years of forest monitoring.

Floristic composition varied widely during the study period and species composition in different years was summarized by the ordination analysis along two main axes of variation (Fig. 2). The first two axes explained 25.24% of the variation in community composition and were used to visualize shifts between treatments and control plots over 25 years. This low variance captured by the first two axes is associated with the high species diversity and a disproportional number of rare species in the study area.

Overall, there was a clear difference in floristic composition between intact and selectively logged forests, independent of the year of forest monitoring. These differences were detected both between treatments (MANOVA: Pillai-Trace = 1.26; $F_{3,293}$ = 169.65; $p < 0.001$) and plots (MANOVA: Pillai-Trace = 0.67; $F_{2,293}$ = 75.16; $p < 0.001$). However, despite notable dissimilarity in species composition among control plots, differences were more prominent among sites under selective logging. Throughout the monitoring period, control plots were grouped to one side of the second PCoA axis due to greater similarity in species composition within controls, whilst plots with different logging intensities were clustered at the other extreme. One of the low intensity logged plots (T1_B2) showed a very distinct floristic composition compared to the other sites (Fig. 2), with strong positive loadings for species from more humid environments (e.g. *Mollia* cf. *lepidota* Spruce ex Benth., *Croton urucurana* Baill., *Eperua duckeana* R.S.Cowan, *Caraipa punctulata* Ducke, *Virola pavonis* (A.DC.) A.C.Sm., *Iryanthera macrophylla* (Benth.) Warb. and *Inga paraensis* Ducke). In particular, 15% of the total number of species identified in
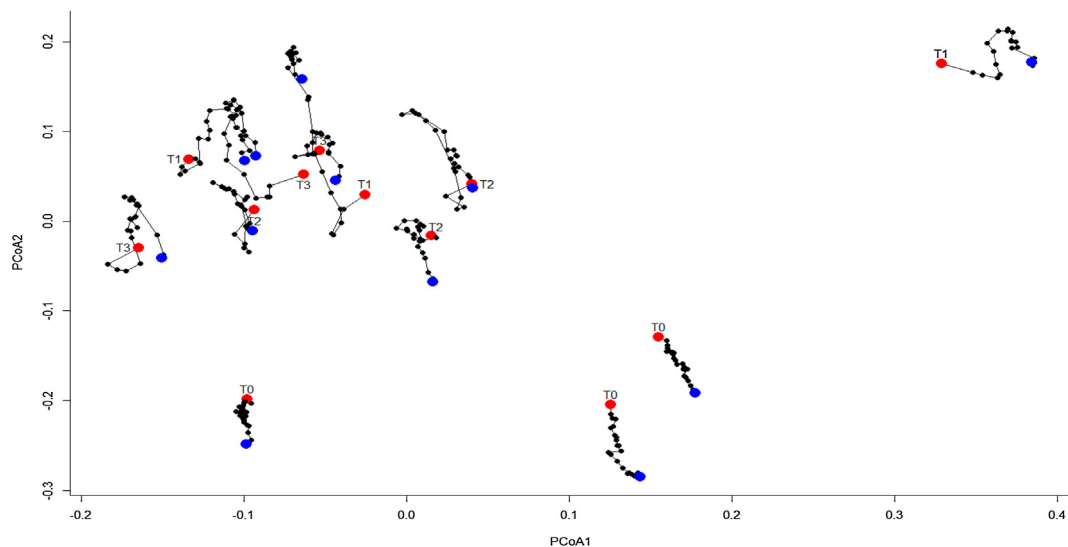
Fig. 2. Trends in composition change for each 1 ha plot (N = 12 plots) over time based on their species composition reduced by PCoA (red, first year pre-logged; blue, last year after logging; black, all 23 intervening years). T0, control plots; T1; forest plots under low selective logging intensity; T2, moderate intensity; T3, high intensity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the area were restricted to this specific site. Thus, rather than differences among treatments, the first PCoA axes captured a natural variation in floristic composition.

In contrast to the natural variation reflected along the first axis, the second PCoA axis shows large differences in taxonomic composition between intact and logged sites (Fig. 2). Immediately after logging, the logged and control plots had very different taxonomic composition, independent of logging intensity. Overall, logged sites were grouped in the positive part of the second PCoA axis, with strong positive loadings for pioneer species with very low wood density and short life cycles: *Vismia* spp., *Cecropia purpurascens* C.C.Berg, *C. sciadophylla*, *Croton matourensis* and *Miconia* spp. Control plots were clustered at the other extreme of the second axis, with strong negative loadings for species of late successional stages: *Pterocarpus rohrii* Vahl, *Pouteria fimbriata* Baehni, *Gustavia elliptica* S.A.Mori, *Swartzia corrugata* Benth., *Micropholis guyanensis* (A.DC.) Pierre and *Ocotea percurrens* Vicent.

Community composition varied widely across yearly censuses and compositional changes are clearly observed in the two dimensional PCoA ordination space during the 25-years (Figs. 2 and 3). There were marked differences in the trajectories trends between control and selective logged areas. Comparisons between plots show that because shifts in species composition in control and logged plots were in distinct directions, there were no differences across years when both control and logged forests were considered together (MANOVA: Pillai-Trace = 0.01; $F_{1,293} = 1.93$; p = 0.14). In contrast, when considering only plots under different logging intensities, floristic composition varied widely over the years, both between blocks (MANOVA: Pillai-Trace = 0.67; $F_{2,293} = 75.16$; p < 0.001) and treatments (MANOVA: Pillai-Trace = 1.26; $F_{3,293} = 169.65$; p < 0.001).

Across different logging treatments, forest plots under moderate logging intensity (Fig. 3g–i) showed greater ability to recovery when compared to plots under either low (Fig. 3d–f) or high logging intensity (Fig. 3j–l). On average, 11 years after logging, the floristic composition of plots under moderate intensity tended to return to a pre-logged status as estimated by the inflexion point in the floristic trajectories, compared to 13 and 15 years after logging for low and high intensity respectively. However, collateral damage in the low intensity treatment was higher than the other treatments: effectively while medium and high intensity treatments had a 35% higher impact than planned, the true damage impact was 93% higher in the low intensity treatment (i.e. of the 34 m³ trunk volume that was planned to be removed during logging, 65.76 m³ was actually lost during harvesting due to collaterally damaged trees).

Over time, control sites followed a unidirectional shift in species composition with similar and consistent trends across the three one-hectare replicates (Fig. 3a–c). Specifically, among control plots, there is no clear tendency to return to the initial floristic composition. This unidirectional trajectory in forest plots not under selective logging is marked by an increase in the abundance of late successional species (e.g. *Protium hebetatum* Daly, *Eschweilera truncata* A.C.Sm.) and recruitment of late successional species not present in the original census (e.g. *Erisma floribundum* Rudge, *Virola mollissima* (A.DC.) Warb., *Copaifera multijuga* Hayne e *Dipteryx odorata* (Aubl.) Willd.). This result is shown in the second PCoA axes, where the direction of compositional change for control plots vary from positive to negative loadings (Fig. 3a–c).

In contrast to the unidirectional trajectory followed by control plots, logged forests tended to change their trajectory direction over time (Fig Fig. 3d–l, p = 0.02). In particular, community composition deviated from the pre-logged status during the early years of forest recovery (Fig. 3d–l). After selective logging, community composition shifted towards more positive values on the second PCoA axis due to the logging of old-growth and high density timber species, followed by a notable increase in the abundance of early successional pioneer species (e.g. *C. sciadophylla*, *Croton matourensis*, *Byrsonima duckeana* W.R.Anderson, *M. minutiflora* (Bonpl.) DC. and *Bellucia grossularioides* (L.) Triana. Secondary species such as *Mabea angularis* Hollander and *M. speciosa* Müll. Arg. also showed a gradual increase over the years in logged areas (Fig. 4). Additionally, early successional pioneer species not initially occurring in the sites (*C. purpurascens* C.C.Berg, *Pourouma velutina* Mart. ex Miq., *P. villosa* Trécul, *P. cucura* Standl. & Cuatrec., *Miconia longispicata* Triana, *M. hypoleuca* (Benth.) Triana, *M. pyrifolia* Naudin, *M. punctata* (Desr.) DC., *Vismia cayennensis* (Jacq.) Pers., *V. macrophylla* Kunth, e *V. guianensis* (Aubl.) Choisy) colonized the canopy gaps created by logging activities. The sharp increase in pioneers and early stage species was accompanied by a gradual decrease in shade-tolerant species such as *Rinorea paniculata* e *Kutchubaea insignis* Fisch. ex DC. (Fig. 4).

Despite the initial shift in favour of pioneer species, logged plots inverted their trajectory of compositional change after 11–17 years (an average of 13 years), reverting towards the initial composition prior to logging. The distances between initial and final taxonomic composition scores (Fig. 3d–l) were smaller than expected by chance, and the simulation of trajectories of change indicated that this tendency to return to the pre-logged status is greater than expected for random trajectories
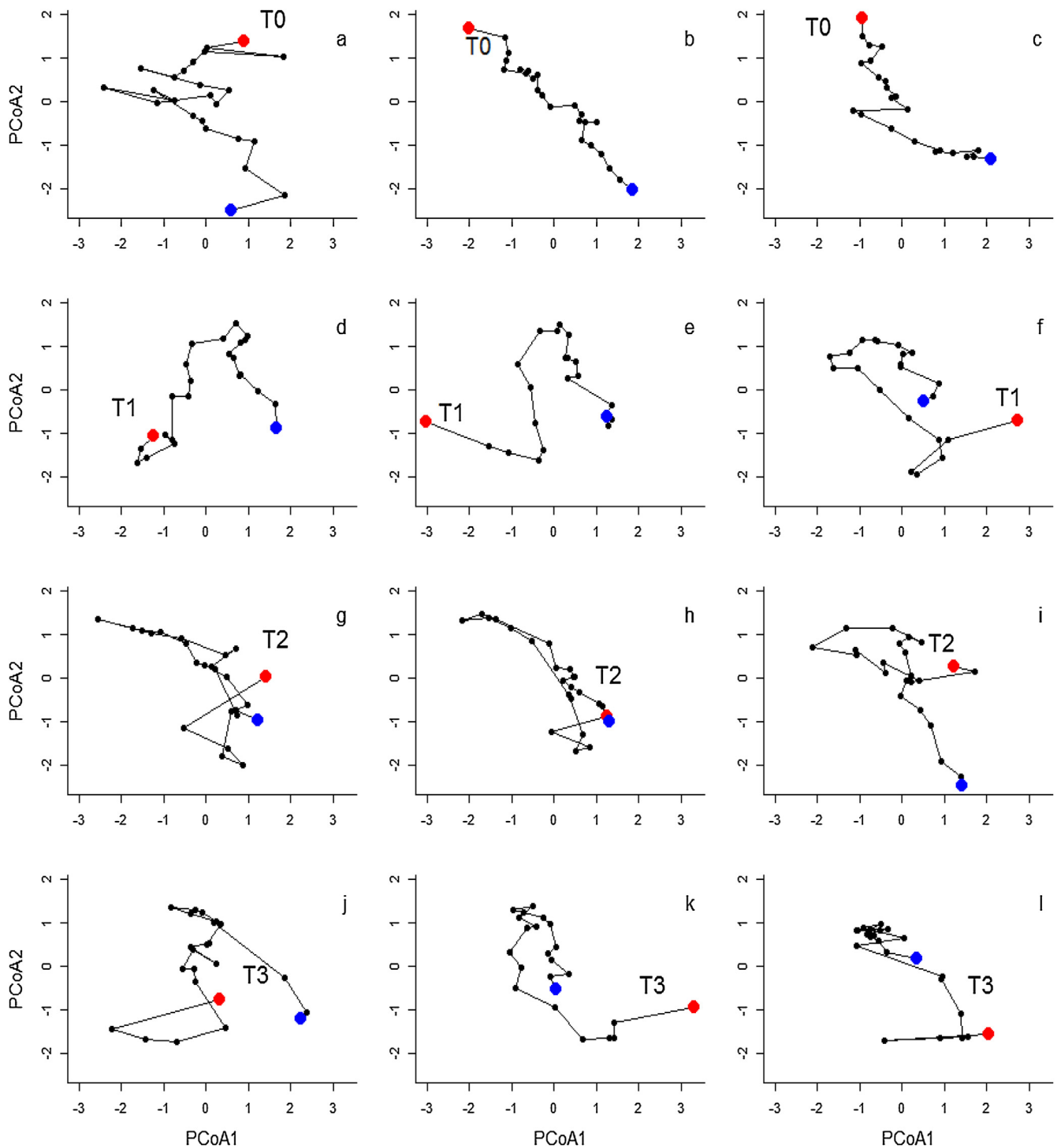
Fig. 3. Detailed trajectories of change in floristic composition in the first two ordinations axes (PCoA) for each 1 ha plot. Control plots (T0) and area under different selective logging intensities: T1 (low intensity), T2 (medium), T3 (high) and B referring to replicates of each treatment in the different blocks: B1 (block 1), B2 (block 2) and B3 (block 3). Yearly community composition is represented by a dot, where red dots represent the initial floristic composition pre-logged, blue dots the final floristic composition and all the 23 yearly inventories between 1987 and 2012 in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(p = 0.02).

Overall, late successional and non-timber species experienced little or no change in abundance over the years after logging, suggesting an apparent stability in their dynamics over time. The pervasive decrease in some late successional species may be explained by the collateral damage of selective logging. For instance, late successional species, such as *Geissospermum argenteum* Woodson, *Hevea guianensis* Aubl. and

Swartzia reticulata Ducke, were particularly affected by wood exploitation and had their abundance reduced slightly after logging (Fig. 4). In contrast, commercial timber species highly abundant in the area, such as *Scleronema micranthum* (Ducke) Ducke, *Brosimum rubescens* Taub., *Minquartia guianensis* Aubl. (Fig. 4), *Corythophora rimosa* W.A.Rodrigues, *Goupia glabra* Aubl., *Lecythis prancei* S.A.Mori, *Mezilaurus itauba* Taub. ex Mez and *Zygia racemosa* (Ducke) Barneby &
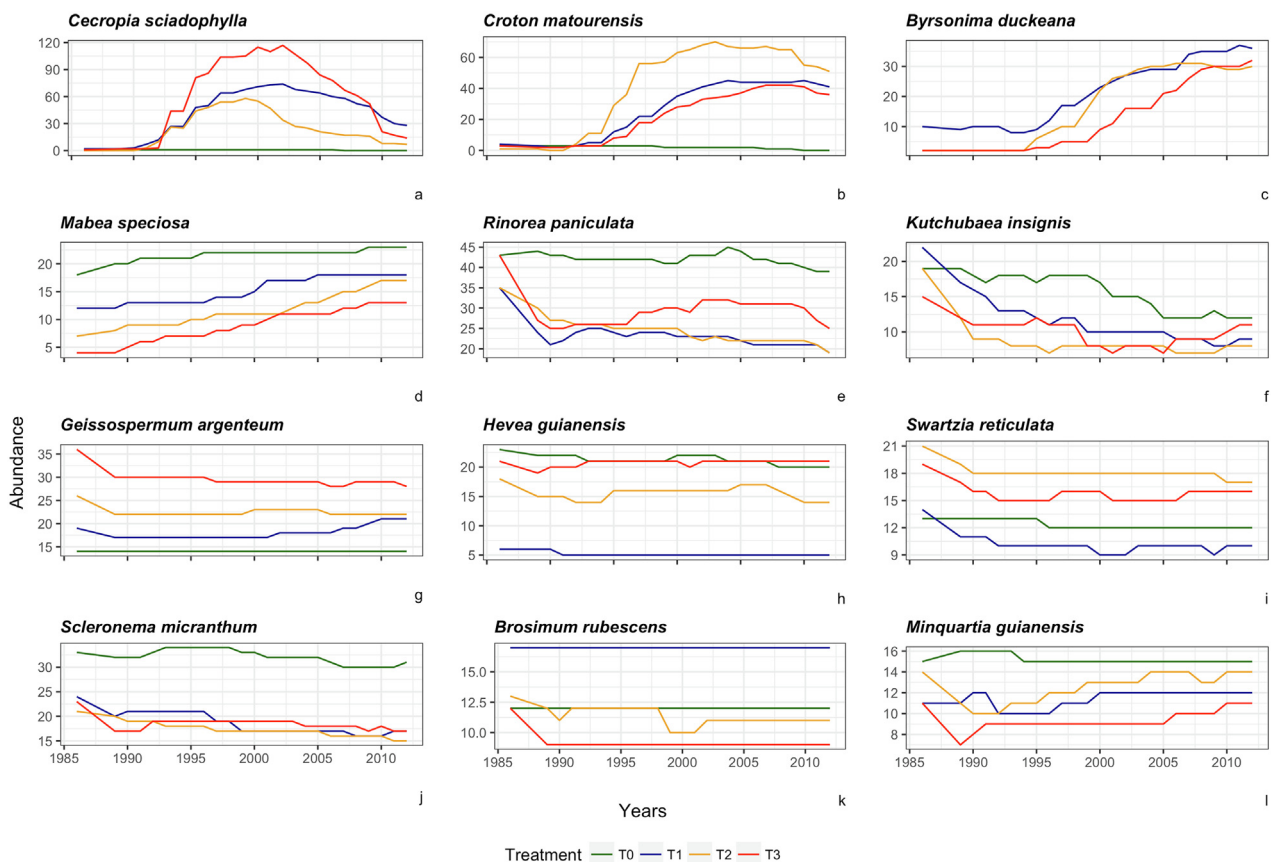
Fig. 4. Trends in compositional changes for individual species between 1988 and 2012 across 12 1 ha plots, summarized here by treatments. Control plots (T0), low intensity (T1), moderate (T2) and high intensity (T3) logging.

J.W.Grimes, significantly decreased in abundance following harvesting. After the initial decline caused by wood exploitation, commercial timber species in logged plots stabilized, similar to those observed in the control plots (Fig. 4).

Despite an overall stable abundance in exploited commercial species after selective logging, they showed low recruitment rates throughout the study period, with few individuals recruited between 10 and 25 cm and not achieving the minimum diameter that can be harvested. In turn, abundance of shade tolerant and late successional species support the overall finding that observed compositional changes were mainly driven by the direct harvesting of commercial timber species and the increase of early successional and pioneer species following selective logging and their subsequent decline.

4. Discussion

Our results show a clear trend in floristic compositional recovery after selective logging (Figs. 2 and 3d–l). Across plots under different logging intensities, harvesting prompted gap opening, leading to a striking increase in the abundance of early successional pioneer species (Fig. 4a–c). In contrast, harvesting had little effect on unfelled late successional species over the 25 years period (Fig. 4j–l). These results suggest that the overall trend in compositional changes over time is mainly driven by (1) the direct harvesting of commercial timber species and, (2) the striking increase and subsequent decline after ~13 years of short-lived pioneer species.

Overall, despite pronounced compositional shifts, floristic composition did not reach the exact pre-logged status. Although biodiversity recovery rate is slower in tropical as compared to temperate systems (Meli et al., 2017), we show that in tropical forests in the absence of further human disturbances, floristic composition tends to recover after

25 years following logging. Recovery rates are much faster in temperate ecosystems, where diversity seems to recover completely after ~15 years (Wu et al., 2018). This disparity in recovery rate is likely associated with large species pool in tropical forests (e.g. > 300 species greater than 10 cm diameter in a single hectare plot; Valencia et al., 1994) as compared to temperate zones that are simpler in structure and composition, not achieving 50 species per hectare (Latham et al., 1993).

Recovery in community composition was mainly driven by the reduction in the abundance of pioneer species, though even 25 years after logging the abundance of pioneers hasn't returned back to their original numbers. The resulting conditions created by the initial recruitment of pioneers with great colonization ability tended to favour a distinct suite of species and consequently a high mortality of those pioneers and light demanding species.

Our results are in accordance with previous findings in logged forests. The sharp increase in the abundance of pioneer species drives the differences in floristic composition between unexploited forests and forest communities under different logging intensities (Silva et al., 1995; Frederickson and Mostacedo, 2000). Following forest disturbance species grew rapidly and filled the canopy gaps, slowly recovering the forest microclimate to a pre-disturbance condition (Schliemann and Bockheim 2011; Espirito-Santo et al., 2009; Soamandaugh, 2017). In contrast, logging intensity had a negligible impact on shade tolerant species (Fig. 4e-f). Importantly, the recruitment and mortality of many rare species did not influence the general patterns observed here.

Topographic and/or soil environment may affect recovery after logging. We had only one plot where change in composition did not tend towards pre-logged status. This plot originally differed widely from the others, and was located in a slope transitioning to a valley, characterized by a greater sand content and lower nutrient availability

in comparison to all other forest plots (Figs. 2; 3d). Variation in topography, soil texture and fertility is strongly associated with variation in floristic composition (Vormisto et al., 2000; Tuomisto et al., 2003, 2016; Zuquim et al., 2012; Figueiredo et al., 2018). Differences in soil fertility, texture and drainage are also important for determining forest structure and dynamics (Phillips et al., 2004; de Castilho et al., 2010; Quesada et al., 2012; Schietti et al., 2014; de Toledo et al., 2012) which may have had a direct impact on the composition of this specific plot. Valleys with sandy soils in central Amazonia tend to have higher natural disturbance levels (de Toledo et al., 2012), which may further increase when externally disturbed by logging. Although the evidence here is based on only one plot, this suggests that logging should be avoided in sloping terrain and valleys, where recovery may be significantly slower or may even not occur.

Post logging recovery was faster for plots under moderate logging intensity, and slower for low and high intensities: 11, 13 and 15 years respectively (Fig. 3d–l). Although collateral damage can be reduced by up to 50% in selectively logged forests (Pinard and Cropper, 2000) the absolute impact for low intensity was much greater than planned (93%), which may explain the slower recovery time in relation to the moderate intensity. Slower recovery of moderately exploited plots was likely associated with collateral damage: a greater volume of trees was lost during harvesting besides the targeted commercial trees. The logging impact on each treatment was planned based on the amount of wood to be extracted. This timber extraction volume is similar to the established in the current Brazilian Legislation for sustainable forest management (IN 05/2006). For instance, an average of $34 m^3$ was harvested in the low intensity treatment and according to the Brazilian regulation forest harvest limit is of maximum $30 m^3$/ha (Brasil, 2006). However, the volume of trees damaged incidentally during harvesting and extraction under selective logging is much greater then the planed impact. In this study, we show that the absolute impact accounting for trees that were brought down unintentionally was slightly greater in the low intensity in comparison to moderate intensity ($65.76 m^3$/ha and $64.5 m^3$/ha respectively). Therefore, forest plots under moderate harvesting intensity provided the smallest absolute impact, supporting faster recovery for the moderate in relation to low and high intensities. These results corroborate previous findings on the importance of accounting for the unconsidered volume lost through harvesting (Oliveira and Braz, 1995; Sist, 2000; Soamandaugh, 2017) and highlights the need to minimize collateral damage during felling operations in order to ensure forest management occurs on a sustainable basis.

In contrast to forest plots under different harvesting intensities, control plots changed their floristic composition unidirectionally (Figs. 2; 3a–c). These clear and consistent unidirectional changes in floristic composition may be associated with climate induced shifts, supporting previous findings that show pervasive compositional changes associated with increase in atmospheric CO_2 (Laurance et al., 2004), increase in frequency and intensity of extreme droughts (Enquist and Enquist, 2011; Fauset et al., 2012) or higher temperatures (Feeley et al., 2011a; Feeley et al., 2011b). Additionally, the observed trend towards species of a latter successional stage (i.e. second PCoA axes varying from positive to more negative loadings – Fig. 3a–c) can also be associated with forest succession due to forests recovering from past disturbances. Although control plots were not directly affected by selective logging, an indirect impact on their composition may be possible due to the proximity to logged plots. Therefore, the drivers of observed unidirectional trajectory in control forest plots cannot be unequivocally established here and need to be investigated further.

The tendency to return to the pre-logged status show the resilience of these forests and indicate their ability to recover following low to moderate levels of disturbance. Our results support the growing literature suggesting that in the absence of further human disturbances selectively logged tropical forests retain important environmental values and despite the environmental impacts of tree harvesting, these forests are important for biodiversity conservation (Clark et al., 2009; Berry et al., 2010; Baraloto et al., 2012; Putz et al., 2012; Laurance and Edwards, 2014).

For all the different logging intensities, 25 years after harvesting were not sufficient for the complete recovery of species composition to a pre-logged status. As there is no substitute for primary forests (Gibson et al., 2011), we do not advocate for an expansion of logged areas, but highlight that these logged forests can have important conservation values. Complete protection of primary forests seems very unrealistic in light of economic needs, similarly to temperate, tropical forests will have to be properly managed in order to reduce the impact on the biodiversity. Moreover, although the remaining commercially valuable tree species with trunk diameter greater than 40 cm guarantee a new cutting cycle, small or moderate levels of forest disturbance without the complete recovery of canopy gaps may deplete current stocks.

Overall, the results of the study show that 25 years after selective logging there is a general trend towards the recovery of floristic composition close to pre-logged status. However, although these results advance our understanding on the effect of selective logging on tree species composition, further studies are needed to support sustainable forest management that goes beyond the first cutting cycle. The ecological impacts of logging are highly variable and depend on the environmental conditions of the logged forests (Darrigo et al., 2016). To better understand the impact of selective logging and its viability, future studies would largely benefit from including distinct environmental conditions when investigating changes in floristic composition. Moreover, despite the general trend of floristic composition to return to the pre-logged status, the recovery in volume of commercial timber species should also be considered in management plans, in order to guarantee the sustainable cycles of timber harvesting and promote the conservation of the world's largest tropical forest.

Author contributions

Higuchi, N. designed the experiment and led the long-term data collection. Gaui, T.D., collected 2011-2012 data, conducted data analyses and wrote the manuscript. Higuchi, N.; Costa, F.R.C.; and Souza, F.C., supervised data analyses and contributed to the text. Amaral, M.R.M., Carvalho D.C., Reis, F.Q., participated on data collection and botanical identification. All co-authors commented and/or approved the manuscript.

Conflicts of interest

The authors declare no conflict of interest.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://

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