Tropical forest management altered abundances of individual tree species but not diversity

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A B S T R A C T

In this study, we evaluated tree species abundance distribution in a Brazilian Amazon forest following reduced-impact logging and unlogged plots over two decades. A large body of literature shows changes in species abundance distributions (SADs) after disturbances in many systems and suggests that SADs are a useful tool for monitoring community recovery after impacts. We used Poisson lognormal distribution to described SAD, which has sigma and correlation parameters, for comparing species diversity before logging and over time. Sigma is a measure of alpha diversity and correlation expresses similarity between communities. Contrary to our expectations, we detected no changes for sigma, but correlation showed a decreasing trend, particularly after the first decade. Those changes were due to the increase in the abundance of pioneers and little recruitment of commercial species. Mortality was mainly attributed to the accidental death of non-targeted individuals. Because of the dominant role of random accidental tree deaths, the signature of logging operations was not detected immediately after logging using sigma. Forest management did not cause changes in the abundance structure of communities if we disregard species composition. However, considering species composition, and particularly, which species were common or rare, we did detect changes over time. The trends we have detected might be an early warning of a stronger long term tendency, which could affect abundance distributions. Due to the long lifecycle of trees and their slow growth rate, longer-term studies are needed to understand the impacts of logging on tropical forests.

1. Introduction

Tropical forests are important sources of timber for the world (Sabogal et al., 2006; Poudyal et al., 2018). In Brazil, Amazon forests have been exploited mainly by conventional logging practices with little operational planning to minimize impacts (Lentini et al., 2005). Reduced-impact logging (RIL) has been proposed since 1990s to attenuate such unintended damages and to make possible the sustainable forest management (Putz et al., 2008). Nevertheless, although few trees are harvested, 3 to 9 trees per hectare in the Amazon, (Verissimo et al., 1992), any logging activity strongly affects gap dynamics in tropical forests, as non-targeted trees are accidentally killed during the operations due to the falling trees, road building, trails, and log landing (Johns et al., 1996; Pereira et al., 2002). Therefore, even reduced-

impact logging has putative effects on the abundance and composition of tree species that make up the Amazon forest, which may, in turn, affect the long-term functioning of the forest and the sustainability of timber harvesting itself. In terms of species richness, previous studies have produced varying results: reduction of tree species (Clark and Covey, 2012); little impact (Carreño-Rocabado et al., 2012); fast recovery of species richness (Xu et al., 2015); and changes in species composition (Xu et al., 2015; de Avila et al., 2015; Poudyal et al., 2018; Hu et al., 2018). It is still challenging to detect changes at the community level and to predict the consequences of these changes over time. In this study, we used species abundance distributions to evaluate changes in tree diversity in the context of tropical forest management.

The abundance structure of communities is summarized through species abundance distribution (SADs) models, which are probability

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functions that use few but highly interpretable parameters (Tokeshi, 1993; McGill et al., 2007; McGill, 2011; Magurran, 2013). Since their origin, models for SADs have also included the effects of sampling, i.e. they are independent of sample size (Fisher et al., 1943; Pielou, 1975), which allows one to draw valid statistical inferences about abundance structures in communities from samples (Green and Plotkin, 2007; Sæther et al., 2013). Changes in probabilistic distributions fitted to empirical SADs have been widely used to characterize the effects of disturbances from samples taken from communities (Tokeshi, 1993; Diserud and Engen, 2000; Ugland et al., 2007; Sæther et al., 2013; Matthews et al., 2014). According to this approach, disturbances can affect mortality rates, birth rates and carrying capacities of all or of some species, which, in turn, may change the shape of the SAD and thereby the parameters of the fitted models (Gray, 1981; Ugland and Gray, 1982; Tokeshi, 1993; Hågvar, 1994; Hill et al., 1995; Diserud and Engen, 2000; Ugland et al., 2007; Dornelas et al., 2009; Dornelas, 2010; Dornelas et al., 2011; Sæther et al., 2013; Matthews et al., 2014).

Disturbances might also change the relative abundance of several species without changing the shape of the SAD (Dornelas, 2010). For instance, if the SAD expresses a resource partitioning rule (Tokeshi, 1993), a disturbance might shift the resource share among species without changing the partition structure. In this case, only compositional similarity would decrease with the disturbance. The bivariate Poisson lognormal distribution is a model that allows for the description of changes in the shapes of two SADs along with their compositional similarities (Engen et al., 2002, 2008, 2011; Grøtan et al., 2012; Sæther et al., 2013). The model also includes a Poisson sampling process, and thus provides a synthetic approach to assessing changes in relative abundance and species composition at two points in time or space, independent of sampling size (Grøtan et al., 2012).

Changes in species abundance distributions (SADs) following disturbances have been widely used to monitor community recovery after impacts. In this context, logging can change the shape of SADs by decreasing the abundance of targeted trees and of accidentally killed trees (see the 'Study Site' section below). The rationale of reduced-impact techniques is to allow for the recovery of the tree community abundance structure between harvesting cycles (Putz et al., 2008). Therefore, an integrated approach to assess changes in the abundance structure and composition of tropical forests caused by logging contributes to improving our knowledge of the effects of reduced-impact logging. We used the Poisson lognormal model as an integrative approach to comparing changes in the shape of SADs and in tree community composition caused by reduced-impact logging in tropical rainforests.

2. Materials and methods

2.1. Study site

The study site consists of a tropical forest located in the Amazon, in the Paragominas municipality, in Pará State, Brazil (3°17'S 47°13'W). In 1993, two permanent plots were established, totaling 5.25 hectares each. All trees with a diameter at breast height greater than or equal to 10 cm (DBH⩾10 cm) were measured and identified. After this first initial survey, forest management (reduced-impact logging) was performed in one of the plots and the other was mantained without logging as a control. The plots were sequentially surveyed again in 1994, 1998, 2000, 2006, 2009 and 2014 and all new individuals were identified according to the inclusion criteria.

This study used a before-after control-impact (BACI) design, i.e., a single site was surveyed multiple times (Smith, 2002). Measurements were taken in the control and in the impact treatment plots before and after the activity (Smith, 2002). Our inferences rely on the comparison of each plot to itself before and after logging. The unlogged plot was used for addressing what would be expected in terms of changes over time in an unlogged forest, i.e., the natural variation due to forest

Table 1
Density of living trees with DBH⩾ 10 cm in each experimental plot before logging (1993) and mortality one year after logging (1994). The total volume extracted is also provided.

	Unlogged	Reduced-Impact
Trees.ha^{-1} in 1993	441	463
Species richness in 1993	149	141
Extracted volume m^3.ha^{-1}	–	38.6
Mortality of tress⩾ 10 cm (1993–1994)	3.3%	21.3%
Mortality of tress⩾ 25 cm (1993–1994)	1.9%	9.1%

dynamics.

The dataset used in this paper is part of a landmark performed in the Amazon which is available at Schepaschenko et al. (2019). More information about this experiment is also available at: Johns et al. (1996), Barreto et al. (1998), Vidal et al. (2002), Vidal (2004), Valle et al. (2006), Schulze et al. (2008), Macpherson et al. (2010), West et al. (2014), Vidal et al. (2016). These plots were randomly deployed within a larger area. In their supplementary material, West et al. (2014) explored the limitation of the sample design experiment, due to each treatment having only one replicate. Through (1) a comparison of pre-logging forest characteristics, (2) geostatistical analyses of pre-logging aboveground biomass and (3) a comparison of post-logging growth rates, West et al. (2014) concluded that there were no pre-existing conditions that would be confounded with treatment effects.

All practices that are indicated in RIL were conducted, such as the cutting of all vines with DBH⩾2 cm before logging, directional felling, road planning, and training of workers to reduce damage to juvenile commercial trees (Johns et al., 1996; Barreto et al., 1998; Vidal et al., 2016). Table 1 shows information about the 1993 survey (before logging) and the number of dead trees. Mortality refers to the amount of logged trees, plus accidentally killed trees and naturally dead trees. In the reduced-impact logging scenario, for each tree harvested, 17 additional trees were killed.

In the reduced-impact treatment, 23 commercial species were harvested within a minimum merchantable size (DBH⩾45 cm; Supplementary material). We denoted as commercial species those selected to be harvested according to the local forest management plan, and these commercial species were not an ecological nor a homogeneous group in any sense. It is important to mention that those species were merchantable in 1993, but some of them may not be anymore. In contrast, several other species without commercial interest in the past are now generating more interest for management purposes. We do not intend to discuss each species one by one (population level), although we think this is a key point for forest management. In this study, we are focusing on changes and patterns at the community level.

2.2. Statistical methods

The Poisson lognormal (PLN) distribution was used to describe the SAD of each treatment in each year (Preston, 1948; Grundy, 1951; Bulmer, 1974). The choice of this distribution is justified by its wide use in the description of biological communities (Hubbell, 2001) and by the possibility of accessing temporal and/or spatial similarity between communities (Engen et al., 2002, 2011; Engen et al., 2008; Grøtan et al., 2012; Sæther et al., 2013; Olesen et al., 2016). The PLN distribution has two parameters, representing the mean (μ') and variance (σ^2) of log abundances. The sigma parameter (σ^2) is the same shape parameter of the sampled lognormal community and is not affected by sampling intensity (Grundy, 1951; Bulmer, 1974). The estimate of the sigma parameter (σ^2), derived from fits of SADs to the Poisson lognormal, can be interpreted as a measure of species dominance, or an inverse measure of species diversity (Engen et al., 2011; Grøtan et al., 2012; Sæther et al., 2013).

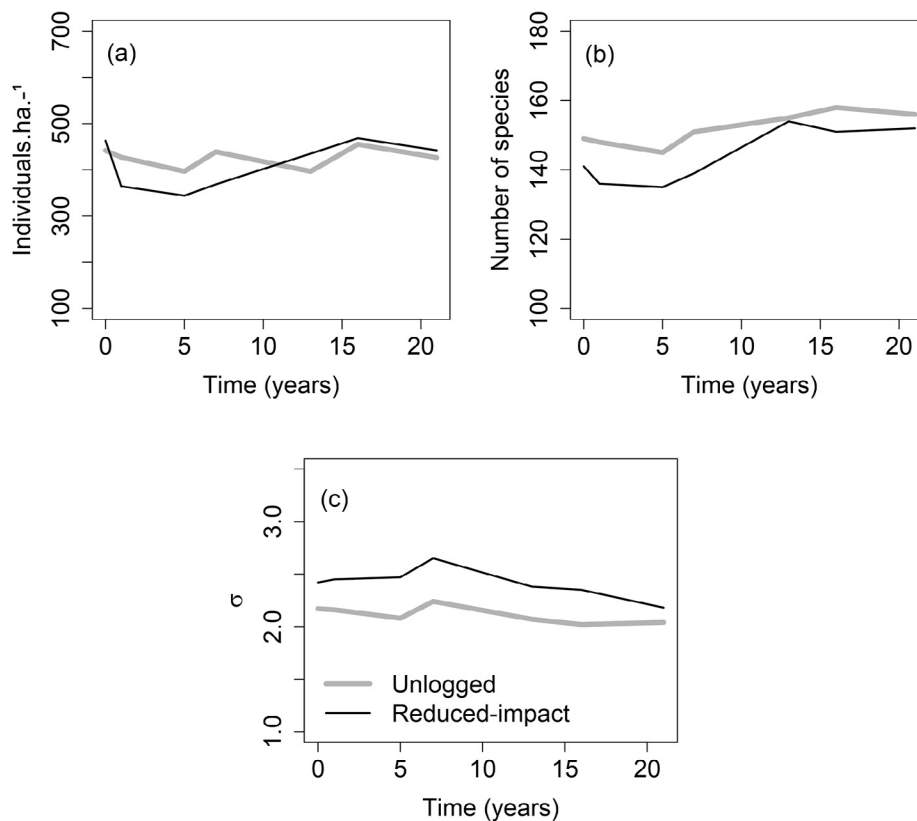The parameters are estimated through a numerical minimization of

Fig. 1. Time series of diversity descriptors of forest plots that have been logged by reduced-impact methods and unlogged plot. At year zero (1993) all plots were surveyed before logging. The descriptors are: (a) Number of individuals; (b) Number of species; (c) Estimate of parameter σ of the Poisson lognormal model fitted to the species abundance distributions.

the negative log-likelihood function (Bulmer, 1974; Bolker, 2008). A goodness of fit test was performed by comparing the likelihood of the data with likelihoods of simulated data sets based on the estimated parameters (Grøtan and Engen, 2008). The PLN distribution provided reasonable descriptions for these data.

The minimization of the log-likelihood function gives us the maximum likelihood estimates (MLEs) of the parameters, but there is an uncertainty surrounding the parameter estimates. We used the log-likelihood surface to compare the PLN parameter estimates among years in each treatment. This is the region around the MLEs where any value is equally likely to occur according to a certain limit. This limit is defined as log(8) or 2.07, and is derived from the likelihood ratio, as a canonical criterion (in a similar way that the confidence interval is defined as 95% in frequentist statistics). If the surfaces are overlapped according to this limit, we can use the same estimates to describe the data, i.e., there is no relevant difference between the models (Edwards, 1992; Hilborn and Mangel, 1997; Burnham and Anderson, 2001; Bolker, 2008).

SADs could have no changes, but these patterns could be obtained by different species composition, as well as the same species, but in different position on the ranking of abundance, i.e., common species becoming rare and/or rare species becoming common. We used the bivariate Poisson lognormal distribution to describe pairs of observations at different times (Engen et al., 2002, 2008, 2011; Grøtan et al., 2012; Sæther et al., 2013). This distribution has the correlation parameter (ρ), which represents similarity between communities, considering species composition and relative abundance, independently of sampling size (Engen et al., 2011). If the relative abundance of any specie is the same in both communities, i.e., the same species are common in both communities and the same species are rare in both communities, the correlation is equal to 1 (Grøtan et al., 2012).

Mortality was mainly attributed to the accidental death of non-targeted trees. For each tree harvested, 17 additional trees were killed (total number of trees killed/ total number of harvested trees, considering the 1993–1994 period). This accidental death could seem similar to a random removal of individuals, because it is not correlated to species identity and SAD models consider sampling effects (Poisson process) (Fisher et al., 1943; Bulmer, 1974). We simulated the random death of 15%, 25 % and 50% of individuals and compared those simulated communities to the ones before logging (1993), using the PLN correlation parameter.

The community in the last survey (2014) is composed of survivors of pre-harvest and recruits, considering as a recruit the individual recorded in 2014 (21 years postharvest) but not in 1993 (pre-harvest). Therefore SAD is a mix of these two assemblages. We analyzed the community of recruits in the last survey (2014). All analyses were performed using R 3.3.1 R Core Team (2016), and the following packages: *sads* Prado et al. (2016), *poilog* Grøtan and Engen (2008) and *bbmle* Bolker and Team (2016).

3. Results

The number of recorded individuals and the estimated parameters of the Poisson lognormal fitted to the SADs returned values close to those recorded before logging (Fig. 1a and Fig. 1 c). The number of recorded species overcompensated the losses in the reduced-impact logging by a small amount, but a slight increase in species richness also occurred in the unlogged plot (Fig. 1b).

Species abundance distributions (SADs) in reduced-impact logging also showed a trend of recovering their original shapes after 21 years (Fig. 2 above). Accordingly, the log-likelihood surfaces of the parameters of the Poisson lognormal overlapped extensively, although slightly less so for the estimates made one year after harvesting in the reduced-impact logging (Fig. 2 below). This trend was not observed in
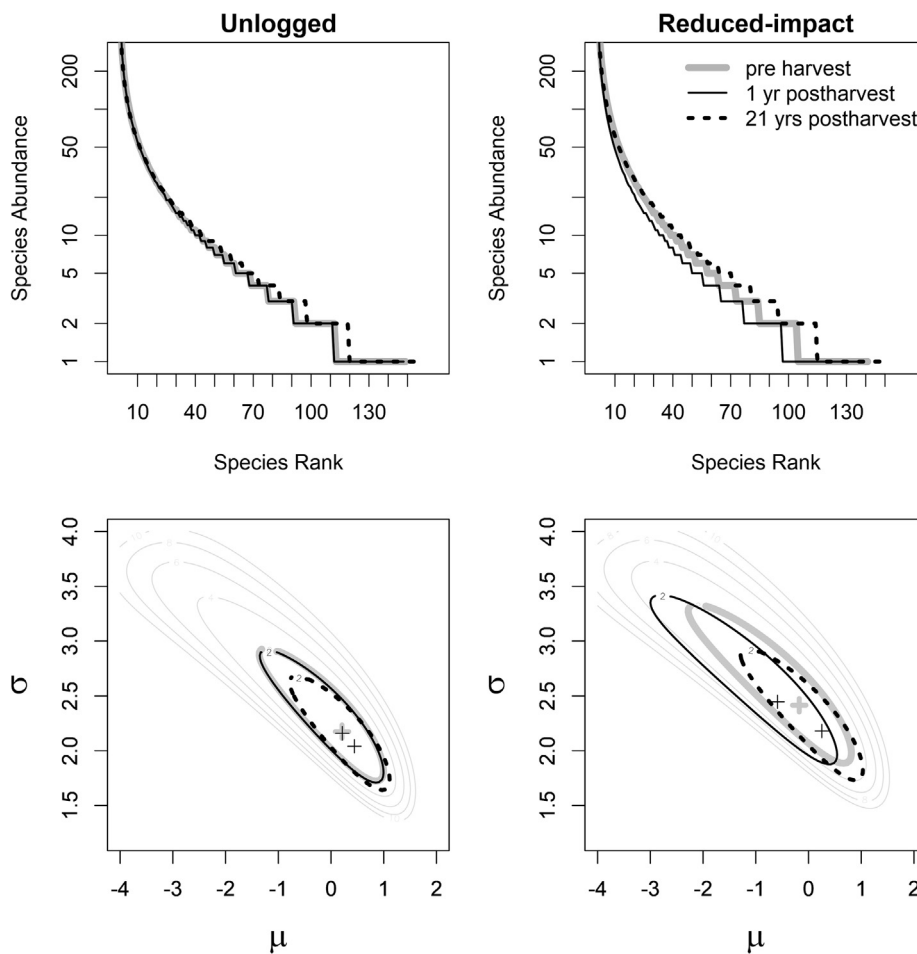
Fig. 2. Species abundance distributions of each forest plot before and after logging.**Above:** rank abundance distribution (RADs). **Below:** Log-likelihood surface for the two parameters of the Poisson lognormal distribution fitted to the species abundance distributions. The cross-points show the maximum-likelihood estimates of the parameters, while the lines delimit the log-likelihood region $\leqslant \log(8)$.

the unlogged plot, but changes are too small to be considered statistically relevant.

Logging killed about 20% of the trees recorded before the interventions in the reduced-impact logging (Fig. 3 above), but the correlation parameter (ρ) of the bivariate Poisson lognormal distribution fitted to the SADs remained close to one from the first to the seventh year after logging (1994 – 2000, Fig. 4a). A simulated removal of the same proportion of individuals at random reproduced the same correlation patterns observed between pre and post-harvest SADs (Fig. 3 below). Accidental deaths were about twenty times more frequent than logged trees, and they were not correlated to species identity. Thus, the remaining trees are a random sample of the tree community before logging.

On the other hand, we observed a decreasing trend for the correlation parameter of the pre-harvest SAD and the SADs recorded in the last two surveys (Fig. 4a). This decreasing trend of the correlation parameter in the reduced-impact logging was mainly caused by the increase in abundance of some rare species over time (rare in the sense that they were not abundant, having few or no individuals before logging). Four of these species are typical pioneer species in tropical forests, and are common in gaps and degraded areas, but are absent or rare in primary forests: *Cecropia obtusa* Trécul, *Cecropia* sp., *Vismia guianensis* (Aubl.) Choisy and *Byrsonima aerugo* Sagot (Uhl and Jordan, 1984; Uhl et al., 1988; Parrotta and Knowles, 1999). Those species had few individuals in the pre harvest, but 21 years postharvest they were the most abundant species recorded (see Fig. 4b).

The community sampled 21 years after logging (2014) was

composed of trees recorded before logging (1993) that endured ('survivors') and individuals recorded in 2014 but not in 1993 ('recruits') (Fig. 5). The species with the largest number of recruits in the unlogged plot was *Sagotia racemosa* Baill. with 61 incoming individuals (6.5% of recruits), while in RIL the most recruited species was *Cecropia obtusa*, with 133 individuals (12% of recruits), highlighting the presence of overly- dominant species in RIL compared to the unlogged plot. All four pioneer species had few individuals in the pre harvest survey in all communities, but this group had the larger share of recruits after reduced-impact logging, although these short-lived pioneers are starting to die out. Moreover, the group of harvested species had few recruits in the reduced-impact (Fig. 5 below) compared to the unlogged plot. As a consequence of all these differences, there was a poorer match between the abundances of trees 21 years after logging compared to the initial community, which impacted the correlation parameter of the bivariate Poisson lognormal distribution (Fig. 4).

4. Discussion

The bivariate Poisson lognormal model provided an integrated but synthetic account of changes in abundance and composition of tree species in the Amazon forest within the first two decades after logging. By coupling two SADs using a correlation term with this model, we have shown that logging caused, at least in the first decades, more variation in the position of the species on the abundance ranking, than a change in abundance distributions. The changes were caused by an increase in the relative abundances of pioneer species. Such changes in
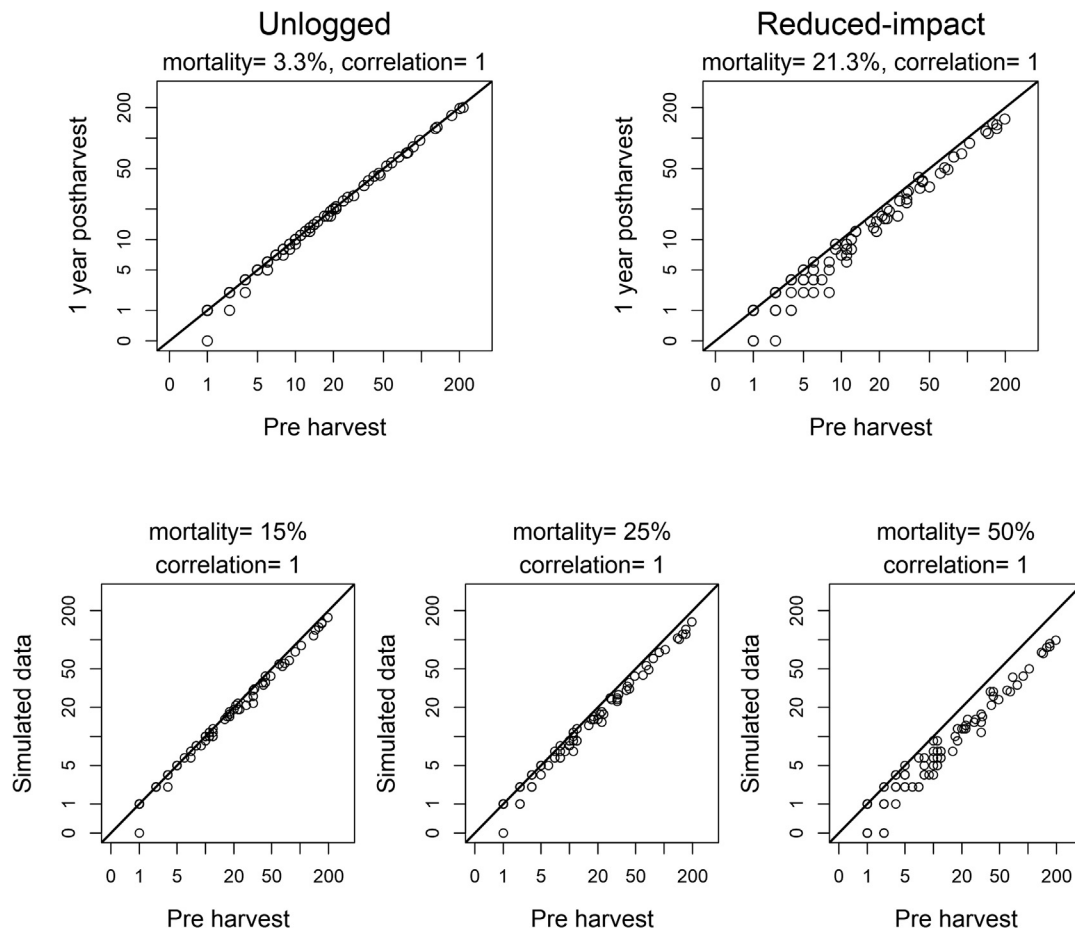
Fig. 3. Above: Abundance of each species recorded one year after harvest as a function of their abundances before harvest (1993). Each plot has an equivalence line (1;1) for reference **Below:** Mortality simulation. Abundance of each species in the 1993 survey (pre harvest) and simulated data, considering 3 levels of mortality (15, 25 and 50% of the individuals). Correlation is the parameter ρ of the bivariate PLN.

species composition could be detected by the census methods only a decade after logging took place.

Models of species abundance distributions (SADs) have been advocated as useful tools to assess the effects of disturbances on ecological communities (Hill and Hamer, 1998; Dornelas et al., 2011; Matthews and Whittaker, 2015) through changes in the shape of the distributions. However, such disturbance-related changes in SADs have not been found in the few studies available for trees in tropical forests (Nummelin, 1998; Filho et al., 2002; Francez et al., 2007; Hu et al., 2018). We also found that logging impacts were not detectable in the SAD immediately after logging, because of the dominant role of accidental deaths of non-targeted trees. For the Poisson lognormal distribution, a random sampling of a fraction p of the community changes only the scale parameter μ to $\mu + \log p$ (Bulmer, 1974). In our case, logging removed about 20% of the trees and thus assuming random sampling, the parameter μ would decrease by $\log 0.8 = -0.19$, a small amount when compared to the uncertainty of its estimate (likelihood interval between -2 and 1). More generally, a random sample re-scales SADs by a constant scaling factor, but even distributions that do not include an explicit sampling effect such as Poisson lognormal or Fisher's logseries achieve this effect (Pielou, 1977; Dewdney, 1998; Green and Plotkin, 2007). By definition, this re-scaling has little or no effect on the shape of distributions that have separated parameters for scale and shape, such as many used fit model SADs. We thus provide a simple instance of a weak or non-existing relationship between disturbance and change in the shape of SADs. As noted by Watt (1998) however, the strength of such a relationship is contingent on characteristics of the disturbance. For instance, a strong departure from randomness in tree

deaths can change the shape of SADs. This can happen if accidental felling were a small fraction of tree deaths or if tree deaths were markedly aggregated in space. In the first case, the selectivity of logging would change relative abundances and in the former case the sampled community would depart from a Poisson sample, causing a change in the shape of the SADs (Green and Plotkin, 2007).

While the shape of SADs changed little, some species with few or no individuals became increasingly common and some others became rarer after reduced-impact logging, particularly in the last survey, as shown by the decreasing trend of the correlation parameter from the bivariate Poisson lognormal distribution. Among the species that became common were *Cecropia* spp., *Vismia guianensis* and *Byrsonima aerugo* (Uhl and Jordan, 1984; Parrotta and Knowles, 1999; d'Oliveira, 2000). These pioneers typically colonize large gaps and are recognized among the main over-abundant species in logged forests in the Amazon, but these are generally absent or occur in low abundance in primary forests (Uhl et al., 1988; Thiollay, 1992; Felton et al., 2006). In contrast, most of the harvested species are recovering their original abundances slowly, possibly due to different causes as commercial species in our survey are not an ecological nor a homogeneous group in any sense. Amongst the commercial species we have secondary and climax ones, different pollination and dispersal syndromes, and species of marked differences in wood density (Darrigo et al., 2016). The regeneration process for many of them is still unknown (Verissimo et al., 1992), and several of them are shade-intolerant when they are young, having slow growth rates and few seedlings and saplings (Uhl et al., 1991; Grogan and Galvão, 2006; Darrigo et al., 2016). It is important to highlight that this was not a substantial change in species composition, but by changes
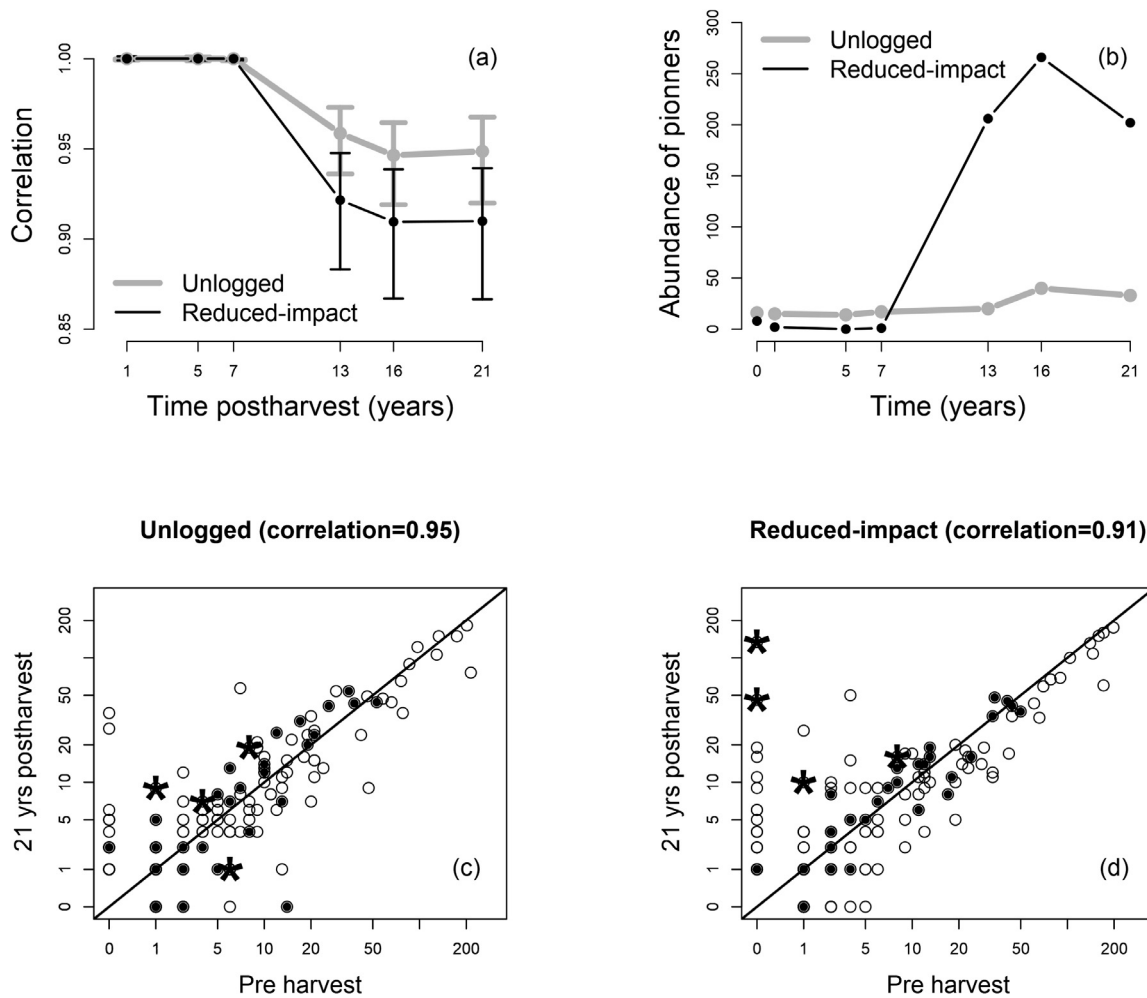
Fig. 4. Species abundance distributions of each forest plot before and after logging. (a) Correlation parameter (ρ) of the bivariate Poisson lognormal distribution fitted to the distributions of abundances of each plot before and after logging. Bars are the log-likelihood interval (delimited by log-likelihood $\leqslant$ log(8)). (b) Abundance of four pioneer species over time (*Cecropia obtusa* Trécul, *Cecropia* sp., *Vismia guianensis* (Aubl.) Choisy and *Byrsonima aerugo* Sagot). (c, d) Abundance of each species recorded in the plots 21 years after logging as a function of their abundances before logging. Each plot has an equivalence line (1;1) for reference. Black points: commercial species, gray points: non-commercial species, stars denote the four pioneer species.

in the relative abundances, e.g., pioneers were already there before logging and commercial species had fewer recruits compared to unlogged, but did not disappear. Overall, the main effect of the first two decades of logging was a gradual increase in the abundance rankings of gap colonizers while the abundance distribution changed little.

The compositional changes described above were mainly caused by an increase in the abundance of pioneer trees, which grew fast (d'Oliveira, 2000), but still became more abundant in our survey only approximately two decades after harvest, after they had reached the DBH inclusion criterion. At this moment, at least half of the trees recorded before harvesting were still alive. Within the share of recruited trees, a few fast-growing pioneer species were overrepresented while harvested species remained underrepresented. However, the temporal scales of surveys of tree communities seldom encompass even a single generation of forest trees, and our study is no exception (tree turnover was no more than 50% after 21 years). This shortcoming combined with the DBH inclusion criterion (DBH $\geqslant$ 10 cm) greatly affects the perception of long-term disturbance effects, as in other communities of long-lived organisms (Sousa, 1984). Indeed, most of the evidence for changes in SAD related to disturbances have been gathered from assemblages of organisms with short life cycles: benthic communities (Gray et al., 1979; Gray and Mirza, 1979; Lambshead et al., 1983; Warwick, 1986); insects (Hågvar, 1994; Hill et al., 1995; Nummelin, 1998; Mouillot and Lepretre, 2000; Bellier et al., 2014); and other types of invertebrates

(Syrek et al., 2006; Tang et al., 2010; Kim et al., 2013); weed communities (Nummelin, 1998; Dornelas et al., 2009); and rodents (Thibault et al., 2004).

The main change observed in tree communities subjected to forest management was not species abundance distribution (disregarding species identities) neither species composition, but rather the fact that some species with few individuals became over-abundant and others became less abundant, which was reflected in the correlation parameter. In this sense, we propose that the small changes in the correlation parameter we have detected might be an early warning of a trend that will be strongly expressed in the future (Thibault et al., 2004; Magurran, 2007), which could jeopardize community integrity (Magurran et al., 2018). Although we cannot state this is the case, we think it is the most precautionary inference we can draw for management purposes, in the absence of more complete information. Two decades might not be enough time for detecting major changes caused by forest logging in tropical tree communities, despite being a considerable research effort. It is important to highlight the need for longer-term studies in permanent plots, to follow possible changes for the communities and populations (eg. recruits occupying gaps where pioneers are dying), which would imply a better understanding of the forest dynamic and, thus, improve predictions to ensure management sustainability.
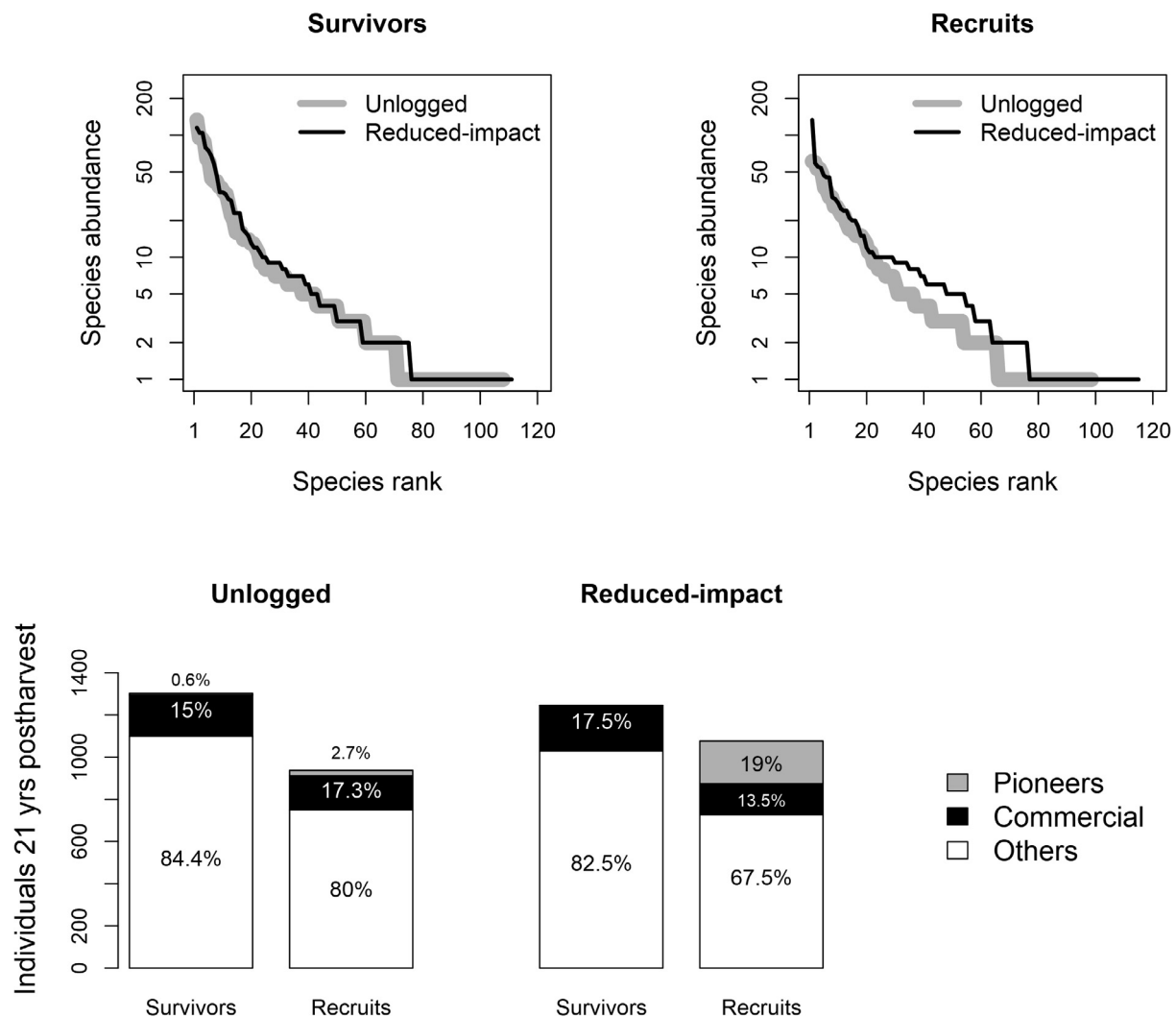
Fig. 5. Individuals in 2014, composed of survivors and recruits. Above: Rank-abundance distributions of the trees recorded 21 years after logging in each plot that had been recorded before logging ('survivors', left) and that had not been recorded before ('recruits', right). Below: numbers and proportions of pioneer species, commercial species and other species among survivors and recruits at each plot 21 years after harvesting.

CRediT authorship contribution statement

Rafaela Pereira Naves: Methodology, Formal analysis, Writing - original draft. **Vidar Grøtan:** Methodology, Writing - review & editing, Formal analysis. **Paulo Inácio Prado:** Methodology, Writing - review & editing, Formal analysis. **Edson Vidal:** Investigation, Resources, Project administration, Writing - review & editing. **João Luís Ferreira Batista:** Conceptualization, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2020.118399.

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