Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests

Erika Berenguer1,2 | Toby Alan Gardner3,4 | Joice Ferreira5 | Luiz E. O. C. Aragão6,7 | Ralph Mac Nally8,9 | James R. Thomson8 | Ima Célia Guimarães Vieira10 | Jos Barlow2,10

1Environmental Change Institute, University of Oxford, Oxford, UK; 2Lancaster Environment Centre, Lancaster University, Lancaster, UK; 3Stockholm Environment Institute, Stockholm, Sweden; 4International Institute for Sustainability, Rio de Janeiro, Brazil; 5Embrapa Amazônia Oriental, Belém, Brazil; 6College of Life and Environmental Sciences, University of Exeter, Exeter, UK; 7Tropical Ecosystems and Environmental Sciences Group (TREES), Remot Sensing Division, National Institute for Space Research - INPE, São José dos Campos, Brazil; 8Institute for Applied Ecology, University of Canberra, Bruce, ACT, Australia; 9R. E. O. C. Aragão, 10Jos Barlow

Correspondence
Erika Berenguer
Emails: erikaberenguer@gmail.com, e.berenguer@lancaster.ac.uk

Funding information
Natural Environment Research Council, Grant/Award Number: NE/F015356/2, NE/F016141/1, NE/G000816/1, NE/K016431/1 and NE/I018123/1; Empresa Brasileira de Pesquisa Agropecuária, Grant/ Award Number: SEG:02.08.06.005.00; Svenska Forskningsrådet Formas, Grant/ Award Number: 2013-1571; The Nature Conservancy; Banco Santander; Darwin Initiative, Grant/Award Number: 17-023; Australian Research Council, Grant/ Award Number: DP120100797; Lancaster University; Instituto Nacional de Ciência e Tecnologia – Biodiversidade e Uso da Terra na Amazônia, Grant/Award Number: CNPq 574008/2008-0; CNPq; CAPES

Handling Editor: Gabriela Bielefeld Nardoto

Abstract
1. Most of the world's remaining tropical forests have been affected by either selective logging, understorey fires, fragmentation or are regrowing in areas that were previously deforested. Despite the ubiquity of these human-modified forests, we have a limited knowledge of their potential to recover key traits linked to ecosystem processes and consequent services.

2. Here we present data from 31,095 trees and saplings distributed across 121 plots of undisturbed and disturbed primary forests as well as secondary forests in the eastern Amazon. We examined the post-disturbance recovery trajectory of an important plant functional trait, wood density. We tested whether human-modified Amazonian forests are experiencing a rapid or a slow, or even impeded, recovery of this trait, which is associated with the provision of a fundamental ecosystem service—carbon storage.

3. As expected, we found that the plot-level wood density of trees and saplings in disturbed primary and secondary forests was significantly lower than in undisturbed forests. However, there was no significant difference in the average wood density of saplings between disturbed primary and secondary forests, possibly indicating a process of secondarization. We also found evidence that the recovery of wood density in human-modified forests is being severely disrupted due to edge effects (in the case of disturbed primary forests) and high liana densities (in the case of both disturbed primary and secondary forests). Surprisingly, these two factors were more important predictors of wood density recovery than the time elapsed since the disturbance event.

4. Synthesis. Plant communities in human-modified Amazonian forests appear to not be recovering a key functional property—wood density, which in turn may affect...
their ability to store carbon in the future. If the aim of conservation programs in tropical forests is to maintain existing rates of ecosystem functions, processes and services, then they must concentrate efforts on avoiding anthropogenic disturbance in areas of currently undisturbed forests. It is also vital to prevent further disturbance in human-modified forests to avoid disrupting even more their recovery.

**KEYWORDS**

Amazon, degradation, edge effects, lianas, recovery, succession, wood density

## 1 | INTRODUCTION

In a world under intense human pressure, it is crucial to understand how ecosystems and the services they provide recover after human disturbance (Steffen et al., 2015). This is particularly important in human-modified tropical forests, which are an increasingly prevalent feature of the humid tropics (Asner, Rudel, Aide, Defries, & Emerson, 2009; Lewis, Edwards, & Galbraith, 2015), occupying over 500 million hectares (ITTO, 2002). Human-modified tropical forests include both disturbed primary forests (i.e. forest stands that have never been clear-felled, but have experienced human-induced disturbance such as selective logging or understory fires) and secondary forests (i.e. forest regrowth in areas that have been completely cleared). These forests are often embedded in agricultural landscapes devoid of undisturbed vegetation, and play an essential role in the provision of locally, regionally and globally important ecosystem services, including carbon storage, biodiversity conservation and climate regulation (Barlow et al., 2016; Berenguer et al., 2014; Parrotta, Wildburger, & Mansourian, 2012). However, it is unclear to what extent these human-modified forests are maintaining or recovering pre-disturbance functions and associated ecosystem services (Davidson et al., 2012).

Our current knowledge of post-disturbance recovery of tropical forests remains limited mainly because of four main reasons. First, very few studies in disturbed areas have access to long-term datasets or accurate information on disturbance history. This is important because post-disturbance recovery depends on the nature, timing, frequency and intensity of the disturbance event (Bonnell, Reyna-Hurtado, & Chapman, 2011; Chazdon et al., 2009; Gardner et al., 2009; Mesquita, Massoca, Jakovac, Bentos, & Williamson, 2015). Second, most studies either address only secondary forests (Piotto, Montagnini, Thomas, Ashton, & Oliver, 2009; Poorter et al., 2016) or only specific forms of primary forest disturbance, such as selective logging (Rutishauser et al., 2015) or fire (Brando, Oliveria-Santos, Rocha, Cury, & Coe, 2016), not considering the full suite of disturbances that commonly co-occur in human-modified tropical forests. Third, the majority of studies investigating the rates of forest recovery tend to focus on large stems (≥10 cm diameter at breast height—DBH), which include many long-lived relics that have survived disturbance events, but that may not successfully reproduce and persist in the future (Metzger et al., 2009; Rigueira, Rocha, & Mariano-Neto, 2013). As such, these studies ignore the small-stemmed vegetation that reflects patterns of post-disturbance dispersal and recruitment, and therefore provides greater insights into the process of post-disturbance succession (Williamson, Bentos, Longworth, & Mesquita, 2014). Last, the majority of studies have focused only on taxonomic or biomass changes following human impacts (e.g. Imai et al., 2012; Letcher & Chazdon, 2009; Poorter et al., 2016). However, a narrow focus on taxonomic changes may mask underlying functional shifts in the studied system if, for example, a whole functional group is lost or severely reduced due to human-induced disturbances (Chillo, Anand, & Ojeda, 2011). To better understand the post-disturbance recovery of tropical forests it is thus critical to directly assess changes in specific traits that underlie key ecosystem functions (Asner et al., 2017) and whose impairment can have profound impact on the future provision of critical ecosystem services (Bello et al., 2010).

Here, we address these knowledge gaps by investigating the extent to which tropical forests are recovering from human-induced disturbances, including selective logging, understory fires (i.e. disturbed primary forests), and clear-felling (i.e. secondary forests). We analyse a unique dataset comprising 31,095 stems measured in 121 forest plots in an agricultural frontier region of the eastern Brazilian Amazon, combined with an assessment of forest disturbance history based on a 22-year chronosequence of satellite images. This time-scale is relevant to provide novel insights into tropical forest recovery in dynamic landscapes, where new anthropogenic disturbances are likely to occur in intervals shorter than 20 years. For example, in the Amazon, most selective logging is illegal, with cutting cycles shorter than the 30 years stipulated by law (Monteiro, Cardoso, Conrado, Verissimo, & Souza, 2013); extreme drought events are becoming more common (Lewis, Brando, Phillips, Heijden, & Nepstad, 2011), reducing the return intervals of large-scale understory fires (Alencar, Brando, Asner, & Putz, 2015); and most secondary forests are <5 years old before being converted again for agriculture (Neeff, Lucas, Dos, Brondizio, & Freitas, 2006). As such, human-modified tropical forests are unlikely to experience a recovery process free from new disturbances in time-scales longer than 20–30 years, a challenge that must be considered in any conservation program.
held in non-protected areas if we wish for these forests to resemble undisturbed ones.

To enhance our understanding of the functional recovery of human-modified forests, we used wood density, a key plant functional trait, as an indicator. Variation in wood density is linked to tree growth and mortality rates, carbon investment per unit area, cavitation avoidance in the xylem, resistance to splitting and elasticity to bending (Chave et al., 2009). Consequently, wood density is closely related to important ecosystem functions and services, such as drought and mechanical resistance, provision of timber stocks and carbon storage (Baker, Phillips, & Malhi, 2004; Bello et al., 2010; Phillips et al., 2009; van Gelder, Poorter, & Sterck, 2006). We make inferences about forest recovery by focusing on the saplings (stems < 10 cm DBH), which respond much faster than large trees (stems ≥ 10 cm DBH) to human-induced disturbance (Barlow, Peres, Lagan, & Haugaasen, 2003; Laurance et al., 2006). We make inferences about forest recovery by focusing on the saplings (stems < 10 cm DBH), which respond much faster than large trees (stems ≥ 10 cm DBH) to human-induced disturbance (Barlow, Peres, Lagan, & Haugaasen, 2003; Laurance et al., 1997; Rüegger et al., 2013), and effectively represent the future of a forest stand—although not all saplings will survive to become trees, the opposite is not true; all trees were indeed once saplings that have successfully passed through the environmental filters present at the time they were growing. Specifically, we address three questions:

1. What are the differences between the average plot-level wood density of trees and saplings in either disturbed primary or secondary forests when compared to undisturbed forests? We expect to find a higher average wood density in the trees and saplings of undisturbed forests where low-wood density pioneer species are less abundant (Laurance, Nascimento, Laurance, Andrade, Fearnside, et al., 2006; Park, Justiniano, & Frederiksen, 2005).

2. Within each forest disturbance class, what are the differences between the average plot-level wood density of trees and saplings? We expect that these differences will vary according to each forest class: in undisturbed forests the average wood density of trees and saplings is likely to be very similar, but statistically lower in saplings. This is expected because, although recruitment into the understory will largely mirror the average trait values of the established trees (Wright, Muller-Landau, Condit, & Hubbell, 2003), the understory may hold a larger number of low-wood density pioneers (Hubbell et al., 1999; Poorter & Bongers, 2006) that will likely die before reaching the canopy (Wright et al., 2010). In secondary forests, we predict that saplings will have a higher average wood density than trees as a consequence of the successional process, with more high-wood density species represented in the saplings than in the larger stems (Piottot et al., 2009). Finally, we expect no significant differences between the average wood density of trees and saplings in disturbed primary forests where the time elapsed since the disturbance event varies from 0 to 25 years: this is because of a gradual stand replacement in the trees, with delayed mortality of old-growth individuals (Barlow et al., 2003; Vellend et al., 2006) and recruitment of pioneers into the larger size classes (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006), accompanied by the successional processes in the saplings (Park et al., 2005).

3. Using the average plot-level wood density of saplings in undisturbed forests as our baseline, can we infer whether human-modified Amazonian forests are experiencing either a rapid trajectory of recovery (cf. Poorter et al., 2016) or a very slow or even impeded recovery following disturbance (cf. Flores, Fagoaga, Nelson, Holmgren, & Barlow, 2016; Tymen et al., 2016)? If secondary forests are following a rapid trajectory of recovery, we would expect a consistent increase in the average wood density of saplings over time (Letcher & Chazdon, 2009; Liebsch, Marques, & Goldenberg, 2008; Piottot et al., 2009). In the case of disturbed primary forests, we would expect to observe an initial sharp reduction in the average wood density of saplings, due to the rapid recruitment of low-wood density pioneer species within the first years (D’Oliveira & Ribas, 2011; Park et al., 2005), which would then be followed by a gradual recruitment of old-growth (high-wood density) species (Bonnell et al., 2011), with a consistent trend towards levels of wood density found in undisturbed forests. In contrast, if disturbed primary or secondary forests are not recovering from human disturbance, we expect that the average wood density of saplings will level off at lower values than those found in undisturbed forests, and wood density would be linked to potential sources of impeded recovery, being lower close to forest edges (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006; Santos et al., 2008), at high liana densities (Heijden, Schnitzer, Powers, & Phillips, 2013; Schnitzer, Dalling, & Carson, 2000) or in landscapes with little remaining forest cover (Muñiz-Castro, Williams-Linera, & Benayas, 2006; Nepstad, Uhl, Pereira, & Silva, 1996).

2 | MATERIALS AND METHODS

2.1 | Study area

Sampling was conducted in the municipality of Paragominas in eastern Amazon (Figure 51a). Paragominas was founded in 1965, with little human occupancy prior its foundation. The municipality currently covers an area of 1.9 million ha with c. 60% of remaining forest cover. Most forests in the region have been selectively logged at varying levels of intensity, as Paragominas was one of the world’s largest timber extraction centres during the 1980s (Verissimo, Barreto, Mattos, Tarifa, & Uhl, 1992). Currently, Paragominas is a mosaic of agricultural land, pastures, Eucalyptus plantations and human-modified forests, with no remnant areas of undisturbed forests but those in reserves. Although deforestation has largely decreased in the region (INPE, 2016a), illegal logging and understory fires are still widespread, affecting the remaining areas of forest (INPE, 2016b). This dynamic landscape is similar to many others in the Amazon, where deforestation is somewhat controlled, but in which human impacts on standing forests continue to be rampant (Aragão et al., 2018).
We selected 18 study catchments across the region (c. 5,000 ha each), distributed along a gradient of remaining forest cover (6%–100%; Figure S1b). In each catchment, we randomly distributed our study plots (10 × 250 m) in forested areas, with a maximum density of 1 plot per 400 ha (Figure S1c). Plots were located ≥1,500 m apart from one another and, whenever possible, ≥100 m away from the nearest forest edge (Gardner et al., 2013). We sampled a total of 121 plots located in undisturbed primary forests (n = 13), disturbed primary forests (n = 88) and secondary forests (n = 20). We did not find any evidence of pre-Columbian settlements (e.g. terra preta) in any of our study plots.

2.2 Vegetation sampling and wood density estimates

All live trees (≥10 cm DBH) in our study plots were identified to species level. In each plot, we established five subplots (5 × 20 m) in which we inventoried saplings (2-10 cm DBH). In total we sampled 13,982 trees and 17,113 saplings (Figure S1d). Wood density of both trees and saplings was obtained from the Global Wood Density Database (Zanne et al., 2009), using values only from South America tropical regions. When data on a given species were not available, we used the average wood density of the next taxonomic level with existing data (Table S1). Although it would be ideal to have locally validated estimates of wood density for all sampled species, this was complicated by the large number of plant species we sampled in the region (n = 619 tree and 686 sapling species). In addition, wood density values change during the lifetime of a plant (Castro, Williamson, & Jesus, 1993), being unsuitable for direct comparisons between trees and saplings. Therefore, to perform our analyses, we used values from the Global Wood Density Database, instead of precise estimates for each measured stem, assigning the same density value for a given tree or sapling when they belonged to the same species.

2.3 Variable selection

We used both disturbance-related (i.e. time-since disturbance, stand age, distance to edge and amount of surrounding forests) and natural variables (i.e. liana density, plot slope and soil clay content) to evaluate determinants of forest recovery. Time-since the last disturbance (in the case of disturbed primary forests) and stand age (in the case of secondary forests) were obtained through a visual analysis of a chronosequence (1988–2010) of georeferenced Landsat images with 30-m spatial resolution (Table S2). This remote-sensing approach was combined with a ground assessment of past disturbance in the primary forest plots. In the occasions in which we found physical evidence of past disturbance in the ground assessment (e.g. logging stumps, charcoal, charred stems), but not in the satellite images, we attributed an arbitrary value of 25 years since disturbance, assuming that the event occurred before the earliest image (n = 18 plots). We used a 2010-(sampling year) classified Landsat image to estimate the average distance of all pixels that comprise a plot to the nearest forest edge surrounding it (hereafter distance to edge) and the per cent of remaining primary forest in a 500-m buffer around each study plot (hereafter percentage of surrounding forest). Although study catchments had between 6–100% forest cover, at the 500-m buffer scale forest cover varied between 40% and 100% (Table S2). All remote-sensing analyses were conducted in ArcGIS 9.3.

For the natural variables, we used a digital elevation model (STRM 90 m) to estimate mean plot slope. Both liana density and soil clay content were evaluated through ground assessments. Lianas (diameter 2-10 cm at 1.3 m from the main rooting point) were sampled at the same subplots in which we inventoried saplings (i.e. five subplots of 5 × 20 m within each study plot; Figure S1d). In total we measured 2,845 lianas. To estimate clay content, we took 45 composite soil samples (0–30 cm) in every plot from a total of five different sampling points separated by 50 m (Figure S1d). Clay content (g/kg) was determined by the densimeter method (Camargo, Moniz, Jorge, & Valadares, 2009) and averaged for each plot. No other natural factors known to considerably slow or even impede the recovery of tropical forests were present in our plots, such as high density of bamboos (Griscom & Ashton, 2003; Guilherme, Oliveira-Filho, Appolinário, & Bearzoti, 2004), ferns (Douterlungne, Levy-Tacher, Golicher, & Dañobeytia, 2010; Slocum, Aide, Zimmerman, & Navarro, 2004), grasses (Sarmiento, 1997) or understorey palms (Denslow, Newell, & Ellison, 1991; Schnitzer et al., 2000), and therefore were not analysed here.

2.4 Data analysis

For each study plot we calculated the abundance-weighted average wood density for trees and saplings separately. We pooled together data for the five subplots in each study plot to avoid pseudo-replication in the analyses of saplings. Given that we used saplings to make predictions about the future trees in a forest stand, we excluded from analyses all species that are restricted to the understory and will never reach a DBH of 10 cm (n = 34 individuals from 10 species; Table S3). To first assess whether in fact the average wood density of saplings mirror that of trees in undisturbed forests, we ran a Spearman’s rank correlation test.

To evaluate if there were significant differences in average plot-level wood density between forest classes, we performed Kruskal-Wallis tests followed by post-hoc Dunn tests, first considering only trees and then considering only saplings. In addition, we used Wilcoxon Signed-rank tests to evaluate differences between average wood density of trees and saplings within each forest class.

To examine the two alternative trajectories of forest recovery (i.e. either fast or slow), we averaged wood density of saplings over all undisturbed forest plots and then subtracted from this average the mean wood density of each human-modified plot. We used these values to model plot-level variability in mean wood density, building two sets of models using Random Forests with 10,000 decision trees each. One set of models contained only disturbed primary forests and the other only secondary forests. Predictor variables included time-since the last disturbance (for models of disturbed primary forests) or stand age (for models of secondary forests), distance to edge, liana density, percentage of surrounding...
so these variables were excluded. After models were built, we assessed the relative importance of all variables in each model set. We also built partial plots to analyse the effect of each individual variable on wood density when partialling out the effect of all other modelled variables. Last, we used Wilcoxon—Mann–Whitney tests to compare the mean wood density of saplings between undisturbed forests and study plots that reached a plateau in recovery of wood density. All analyses were conducted in R version 3.2.0, using both the "dunn.test" (Dinno, 2015) and the "randomForest" (Liaw & Wiener, 2002) packages.

3 | RESULTS

3.1 | Wood density of trees and saplings across human-modified tropical forests

We found a strong positive relationship between plot-level average wood density of trees and saplings in undisturbed forests (rho = 0.67, p < .05), even though average wood density varied very little (Figure S2). The average wood density of both large trees and saplings was lower in human-modified forests than in undisturbed sites. When considering only trees, the average plot-level wood density was significantly different among all forest classes (Figure 1a), with undisturbed forests having the highest average wood density, followed by disturbed primary and secondary forests (H (2) = 43.32, p < .001; Dunn tests, all p < .001; Figure S3). Saplings in both disturbed primary forests and secondary forests had significantly lower wood density than saplings in undisturbed forests (H (2) = 34.39, p < .001; Dunn tests, both p < .001; Figure 1b), but there was no difference in average wood density of saplings between disturbed primary and secondary forests (p = .23).

3.2 | Wood density of trees and saplings within each forest disturbance class

In undisturbed forests, there was a significant difference between the average plot-level wood density of trees and saplings (V = 0, p < .001), with marginally higher values in the trees than in the saplings (Figure 1c). However, these differences were very small (Figure S4), and the averaged values were just 4% lower in the saplings. In disturbed primary forests we found no significant difference between the average wood density of trees and saplings (V = 1,842, p = .63; Figure 1c); while in secondary forests saplings had significantly higher wood density than trees (V = 210, p < .001; Figure 1c, Figure S4).
3.3 | Recovery trajectories of plot-level wood density

There were nonlinear positive relationships between wood density of saplings in disturbed primary forests (Figure 2) and in secondary forests (Figure 3) with time-since disturbance and stand age respectively. These variables were highly important in influencing the recovery of wood density (Random Forest importance value of time since disturbance = 70%, importance value of stand age = 37%). In disturbed primary forests, rates of increase in wood density appeared to stabilize 19 years after human disturbance (Figure 2a). However, this result should be interpreted with caution because the sites that experienced either selective logging or fire at least 25 years ago had a large variation in recovery rates.

FIGURE 2 Expected (left) and observed (right) differences from undisturbed forests in average plot-level wood density of saplings in disturbed primary forests across gradients of (a) time-since anthropogenic disturbance, (b) distance to the nearest forest edge (in a log scale), (c) liana density, and (d) amount of surrounding forest in a 500-m buffer. Expected differences can either indicate a rapid (dark grey line) or an impeded recovery following disturbance (dotted line). The zero line is indicated in light grey (baseline). The observed differences are in the logit scale and show the effect of each of the predictor variables on the response when holding constant all the other predictors presented. The black solid line is the model result, while the grey dots are the observed data.
In secondary forests, the wood density of saplings appeared to stabilize after just 12 years following the commencement of forest regeneration (Figure 3a). In both primary and secondary forests, the wood density of saplings plateaued long before they reached values similar to those of undisturbed forest plots (both $W = 0$, $p < .001$, Figure 4a).

Edge effects and a high density of lianas were both associated with lower plot-level values of wood density in human-modified Amazonian forests (Figures 2b,c and 3b). In disturbed primary forests, distance to the nearest forest edge was more important than time-since disturbance in explaining the observed variance of average wood density of saplings (importance value = 78%). In plots located within 160 m from edges, the recovery trajectory appeared impeded (Figure 2b) and a closer look showed that such plots had a significantly lower average wood density than the baseline ($W = 4$, $p < .001$; Figure 4b). Liana density was the third most important factor in disturbed primary forests (importance value = 37%) and the most important in secondary forests (importance value = 40%). The influence of liana density appeared to level off at 600 stems/ha in disturbed primary forests (Figure 2c) and at 950 stems/ha in secondary forests (Figure 3b). Subsequent Wilcoxon–Mann–Whitney tests showed that disturbed primary forests with ≥600 liana stems/ha and secondary forests with liana densities ≥950 stems/ha presented significantly lower levels of wood density than undisturbed forest plots (disturbed primary forests: $W = 4$, $p < .001$; secondary forests: $W = 0$, $p < .01$; Figure 4c). The percentage of surrounding forest was of lower importance in both disturbed primary forests (importance value = 20%) and secondary forests (importance value = 3%), not showing any strong relationships with wood density (Figures 2d, 3c). Finally, our remaining natural covariate (soil clay content) was also of limited importance in the models (Random Forest importance value = 11% and 17% in disturbed primary and secondary forests, respectively; Figure S5).
4 | DISCUSSION

4.1 | Seeing the woods through the saplings

In undisturbed Amazonian forests, canopy and emergent trees can live up to 1,400 years (Chambers, Higuchi, & Schimel, 1998) and, as a result, conventional floristic analyses, which focus only on large trees (i.e. ≥10 cm DBH), can provide valuable insights into the current and future ecological states of a forest stand. However, the same assumptions do not necessarily hold for either disturbed primary or secondary forests, which are highly dynamic, presenting elevated levels of tree mortality and greater abundances of short-lived, pioneer species (Barlow et al., 2003; Brando et al., 2012; Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006; Piotto et al., 2009). In addition, these forests often have long-lived relics, trees that remained in the land even after logging or clearance, but that are not successfully reproducing and thus will not leave offspring (Metzger et al., 2009; Rigueira et al., 2013). Therefore, to examine the likely future state of a human-modified forest stand, it is essential to survey the saplings (i.e. <10 cm DBH), as they effectively constitute the future of the forest canopy—although not all individual sapling will make to the canopy, all canopy trees were once saplings; their survival thus reflecting the environmental filters that were at work during the post-disturbance recovery process of a forest. This recovery, however, is likely to be often disrupted and suffer a reset in human-modified Amazonian forests—these forests are the most vulnerable to further human impacts in the decades after the initial disturbance event, due to changes in microclimate (Camargo & Kapos, 1995; Uhl & Kauffman, 1990), increased fuel loads on the forest floor (Gerwing, 2002; Keller, Palace, Asner, Pereira, & Silva, 2004) and the newly acquired ease of access (Asner et al., 2006; Laurance, Goosem, & Laurance, 2009). Hence, to make any estimates of recovery beyond 25–30 years in these systems is probably unrealistic. Using wood density levels in sapling communities as an indicator of forest recovery, our findings reveal the following new insights:

4.1.1 | Human-modified forests are functionally different from undisturbed forests

Our expectation that both disturbed primary and secondary forests would have lower wood densities when compared to undisturbed forests was supported. Plot-level wood density of trees and saplings in disturbed primary forests were, respectively, 19% and 17% lower than in undisturbed forests; while in secondary forests these differences were 33% for trees and 18% for saplings. These significant differences in average wood density highlight that not only are current human-modified Amazonian forests different from undisturbed ones, but also that in the future this difference is likely to persist. It is worthwhile pointing out that these results are probably conservatively—as human-modified forests are more prone to additional disturbances (Asner et al., 2006; Siegert, Ruecker, Hinrichs, & Hoffmann, 2001), these differences in wood density are expected to become even more accentuated after new disturbance events.

FIGURE 4 | Comparison between the average wood density of saplings in undisturbed forest plots and (a) disturbed primary forests that experienced either selective logging or understory fires ≥19 years prior sampling, and secondary forests ≥12 years old; (b) disturbed primary forests within 160 m from a man-made edge; (c) disturbed primary forests with liana density ≥600 stems/ha and secondary forests with liana density ≥950 stems/ha. Error bars indicate standard error. Asterisks represent $p < .001 (***)$ and $p < .01 (**)$ in relation to undisturbed plots, following Wilcoxon–Mann–Whitney tests.
4.1.2 Convergence of disturbed primary and secondary forests

Our results also indicate that in the future, disturbed primary forests and secondary forests are likely to have similar wood density values, as there was no significant difference in average sapling wood density between these forests. This apparent convergence between disturbed primary and secondary Amazonian forests, a process called secondary arization (Malhi, Gardner, Goldsmith, Silman, & Zelazowski, 2014), has already been observed both in terms of carbon stocks (Berenguer et al., 2014) and forest structure (Xaud, Martins, & SRV, Santos Jr dos, 2013), but this is the first time to be highlighted in terms of a plant functional trait.

4.1.3 A slowdown in the recovery trajectory of wood density may negatively impact carbon storage

Tropical forests are expected to take ≥12 years to return to original levels of biomass following selective logging (Rutishauser et al., 2015) and ≥6 years following clearance (Hughes, Kauffman, & Jaramillo, 1999; Letcher & Chazdon, 2009; Poorter et al., 2016), although biodiversity recovery can take much longer (Chazdon et al., 2009; Mesquita et al., 2015). Recovery rates can vary depending on disturbance type, frequency and intensity (in the case of disturbed primary forests); previous land-use management (in the case of secondary forests); and on differences in soil fertility, landscape configuration and the presence of organisms that can either accelerate or hamper the recovery process (Chazdon, 2003; Imai et al., 2012; Mesquita et al., 2015; Schnitzer et al., 2000; Zarín et al., 2005). Our results show that the recovery of sapling wood density appears to either stop or dramatically slow down after only 19 years in disturbed primary forests and after 12 years in secondary forests. Average wood density in each case levelled off at values significantly lower than those found in undisturbed forests, indicating that disturbed and secondary Amazonian forests are either experiencing a very slow rate of recovery or are in a state of impeded succession with respect to this key plant functional trait. We cannot differentiate which is the case, whether these forests are undergoing a process of step-change recovery (Norden, Letcher, Boukili, Swenson, & Chazdon, 2012) that we could not detect within our time frame of 25 years, or whether their recovery has been arrested and they are currently trapped into an alternative stable state as seen in burned Amazonian floodplains (Flores et al., 2016). Regardless, both alternatives are alarming: because they can undermine the provision of a crucial ecosystem service—carbon storage. For example, an individual tree with 30-cm DBH from a common low-wood density pioneer species in the region, such as Jacaranda copia, is estimated to store 0.43 Mg C, while a tree of the same size from an abundant high-wood density canopy species, such as Eschweileria coriacea, stores 1.03 Mg C; a difference of 139% in carbon storage capacity. It is thus critical to identify the factors that may be negatively influencing the recovery of wood density in disturbed and regenerating Amazonian forests, in order to develop measures to revert this process.

4.1.4 Forest edges matter

Forest-edge environments are affected by a variety of changes in abiotic aspects: lower air and soil moisture, increased wind disturbance, and higher above and below-ground temperatures (Camargo & Kapos, 1995; Ewers & Banks-Leite, 2013). These microclimatic alterations lead to biotic changes, such as proliferation of invasive and disturbance-adapted plant and animal species, increased tree mortality and subsequent gap formation, lower biomass, thicker understorey and elevated litter fall; all of which then contribute to further modification of microclimatic conditions (Broadbent et al., 2008; Laurance et al., 2002). Ultimately, these forests experience a drastic structural change and become fire-prone (Alencar, Nepstad, Diaz, & Vera, 2006), which is atypical of undisturbed tropical rainforests (Archibald, 2013). Given the proximity to agricultural land uses and the increased vulnerability to fire, forest-edge environments are more likely to burn and to be subjected to frequent human disturbance, such as logging and hunting (Cochrane & Laurance, 2002). Our findings shed new light on the pervasive impacts of fragmentation in tropical forests, showing that edge effects can negatively interfere with the recovery of key functional groups, such as high-wood density species. As already 40% of all Amazonian forests are within 2 km of a forest edge (Haddad et al., 2015) and deforestation rates are currently going up (INPE, 2016a), it is expected that more remaining forests will become closer to edges, severely affecting the ability of these forests to recover their pre-disturbance levels of wood density. Finally, small (≤8 ha—i.e. ≤160 m radius if round) or narrow forest fragments, although important for increasing landscape connectivity and conserving a subset of fauna and flora species (Barlow et al., 2010; Lees & Peres, 2008), are unlikely to maintain all existing ecosystem functional attributes and processes in the long term if edge effects hampers the recovery of wood density.

4.1.5 High liana densities are detrimental for forest recovery

Lianas out-compete saplings of high-wood density tree species and favour the establishment of pioneers in naturally occurring treefall gaps (Heijden et al., 2013; Schnitzer et al., 2000). However, these effects have been reported only at small spatial scales and in areas with no human disturbance. A better understanding of the ecological consequences of liana infestation on ecosystem functioning is crucial since neotropical forests are experiencing a widespread increase in the abundance of small diameter lianas, both in undisturbed (Schnitzer & Bongers, 2011) and in human-modified forests (Berenguer et al., 2014; Laurance et al., 2014). Our finding showed that plots with a high density of lianas (i.e. ≥600 liana stems/ha, compared to c. 400 stems/ha in undisturbed forests) had lower average wood density of saplings in both disturbed primary and secondary forests, suggesting a potentially important role of lianas in locking forests into an early successional state, as has been found for treefall gaps in Central America (Schnitzer et al., 2000) and in forest fragments in the Atlantic Forest (César et al., 2016).
4.1.6 | Surrounding primary forest cover seems of less importance

Surprisingly, we found little influence of the percentage of primary forest cover in the surrounding landscape on the average wood density of saplings—we had expected that plots surrounded by greater forest cover would present a higher recruitment of high-wood density species. However, this result should be interpreted with caution: given that there was ≥40% primary forest cover in the buffer zone surrounding each plot, we do not know whether lower amounts of surrounding forest could negatively affect wood density recovery. It is very unlikely that human-modified forests will recruit old-growth tree species in a landscape devoid of both seed sources and seed dispersers (Muñiz-Castro et al., 2006; Nepstad et al., 1996; Rigueira et al., 2013).

4.2 | Research challenges for understanding ecosystem functioning in human-modified tropical forests

The establishment and periodic monitoring of permanent study plots in undisturbed tropical forests has, for the past 20 years, greatly increased our understanding of how edaphic, climatic and topographic patterns influence the functioning of forests in the humid tropics (Baraloto et al., 2011; Girardin, Malhi, & Aragão, 2010; Lewis et al., 2013; Malhi et al., 2009; Quesada et al., 2012). These long-term datasets have also been used to highlight changes in ecosystem processes following extreme climatic events, such as the 2005 and the 2010 droughts in the Amazon, when affected forests shifted from acting as carbon sinks to carbon sources (Lewis et al., 2011; Phillips et al., 2009). It is now critical to expand these permanent plot networks into human-modified tropical forests to provide much-needed information on the recovery dynamics following human disturbance and, in particular, the extent to which successional processes may have been impaired or are just currently experiencing very slow step changes.

To achieve this understanding, our work demonstrates that sampling protocols must incorporate the monitoring of saplings and lianas, components that are often neglected in vegetation surveys and subsequent analyses, but that clearly play vital roles in forest recovery. Other locally abundant plant forms that have the potential to disrupt the recovery of disturbed primary and secondary forests should also be monitored, including bamboos, ferns, grasses and understorey palms (Douterlunge et al., 2010; Guillerme et al., 2004; Sarmento, 1997; Schnitzer et al., 2000). Currently we do not fully understand whether the role of lianas and other plant forms may change as succession continues and, as such, studies focusing exclusively on these organisms could considerably improve our knowledge about their influence on the post-disturbance recovery of tropical forests.

4.3 | Perspectives for the future of human-modified tropical forests

At the beginning of the 21st century, it was estimated that 500 million hectares of tropical rainforests were already modified by humans in some way (ITTO, 2002). Since then, this figure has increased: new studies show that 80% of forests in Borneo and Brunei have been either logged or cleared (Bryan et al., 2013), while in the Brazilian Amazon 10 million hectares were selectively logged between 2007 and 2013 (INPE, 2015) and vast forested areas burned during the 2015–16 El Niño event (INPE, 2016b). The total extent of secondary forests in the tropics is harder to measure, as regenerating stands might just be temporary fallows between deforestation cycles. Still, in 2,000 around 23.5 million hectares of the world’s humid tropics were occupied by secondary forests (Asner et al., 2009), from which 15 million hectares were found in the Brazilian Amazon alone (Almeida et al., 2016). The combination of a continued dependence on fire for much of tropical agriculture (Aragão et al., 2018; Carmenta, Vermeylen, Parry, & Barlow, 2013), unsustainable timber extraction practices (Monteiro et al., 2013) and widespread fragmentation in the wake of ongoing agricultural expansion (Hansen et al., 2013), indicate that the area of tropical forest unaffected by human activity is rapidly diminishing. Contrary to recent reports that regenerating tropical forests have a high level of resilience (Pooper et al., 2016; Rutishauser et al., 2015) our findings highlight that a key ecological trait may in fact recover very slowly, and might not regain pre-disturbance levels in decadal time-scales. Our results are also likely to be conservative, given that human-modified tropical forests are more susceptible to additional human-driven disturbances, thereby setting back the recovery process. Although changes in wood density levels in the sapling community is just an indicator of forest recovery, it is one more piece of the puzzle on our understanding of whether tropical forests can bounce back from human impacts. The literature now abounds with examples of human-modified tropical forests being trapped in alternative states, supporting a much impoverished set of species and performing ecosystem processes at rates that are significantly different from undisturbed forests (Barlow et al., 2016; Flores et al., 2016; Gibson et al., 2011; Laurance et al., 2011; Riutta et al., 2018). It seems therefore imperative to effectively protect areas of remaining undisturbed forests, while also avoiding further human impacts in already disturbed areas. Achieving these goals requires a step change in the priorities of conservation research, practice and policy, recognizing forest disturbance as a comparable concern to the maintenance of key ecosystem functions and services as deforestation.

ACKNOWLEDGEMENTS

We are grateful to the following for financial support: Instituto Nacional de Ciência e Tecnologia—Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0), Empresa Brasileira de Pesquisa Agropecuária—Embrapa (SEG:02.08.06.005.00), the UK government Darwin Initiative (17-023), The Nature Conservancy, and UK Natural Environment Research Council (NERC; NE/ F01614X/1 and NE/G000816/1). E.B. was supported by a university scholarship from Lancaster University and a research grant.
from Santander. E.B. and J.B. also acknowledge the support of a NERC grant (NE/K016431/1). T.A.G. was funded by the by Swedish Research Council Formas (2013-1571). L.E.O.C.A. was supported by the CNPq and CAPES science without Borders Program’s Fellowship and by two NERC grants (NE/F015356/2 and NE/I018123/1). R.M. and J.R.T. were partially supported by an Australian Research Council Discovery Grant (DP120100797). We are deeply grateful to our numerous field and laboratory assistants, particularly to our parabotanists Nelson Rosa and Manoel Cordeiro. We also thank the farmers and workers unions of Paragominas and all collaborating private landowners for their support. This paper is number #50 in the Rede Amazônia Sustentável publication series.

AUTHORS’ CONTRIBUTIONS

E.B., T.A.G., J.F. and J.B. designed the study. E.B. performed data collection, with contributions on sampling design from T.A.G., J.F., L.E.O.C.A., I.C.G.V. and J.B. E.B. conducted all statistical analyses, with contributions from R.M.N. and J.R.T. E.B. and J.B. wrote the manuscript with critical inputs from all authors.

DATA ACCESSIBILITY

Data available from Figshare: https://doi.org/10.6084/m9.figshare.6068693 (Berenguer et al., 2018). Data on wood density come from The Global Wood Density Database (Zanne et al., 2009).

ORCID

Erika Berenguer http://orcid.org/0000-0001-8157-8792
Toby Alan Gardner http://orcid.org/0000-0002-4007-2936
Luiz E. O. C. Aragão http://orcid.org/0000-0002-4134-6708
Ralph Mac Nally http://orcid.org/0000-0002-4473-1636
Ima Célia Guimarães Vieira http://orcid.org/0000-0003-1233-318X
Jos Barlow http://orcid.org/0000-0003-4992-2594

REFERENCES

Alencar, A. A., Brando, P. M., Asner, G. P., & Putz, F. E. (2015). Landscape fragmentation, severe drought, and the new Amazon forest fire regime. Ecological Applications, 25, 1493–1505. https://doi.org/10.1890/14-1528.1
Alencar, A., Nepstad, D. C., Díaz, M., Vera, C., & (2006). Forest understory fire in the Brazilian Amazon in ENSO and non-ENSO years: Area burned and committed carbon emissions. Earth Interactions, 10, 1–17. https://doi.org/10.1175/1523-3269(2006)010<0001:FUIFIL>2.0.CO;2
Aragão, L. E. O. C., Anderson, L. O., Fonseca, M. G., Rosan, T. M., Vedovato, L. B., Wagner, F. H., ... Barlow, J. (2018). 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. Nature Communications, 9, 536. https://doi.org/10.1038/s41467-017-02771-y
Archibald, S. (2013). Defining pyromes and global syndromes of fire regimes. Proceedings of the National Academy of Sciences of the United States of America, 110, 6442–6447. https://doi.org/10.1073/pnas.1211466110
Asner, G. P., Broadbent, E. N., Oliveira, P. J. C., Keller, M., Knapp, D. E., & Silva, J. N. M. (2006). Condition and fate of logged forests in the Brazilian Amazon. Proceedings of the National Academy of Sciences of the United States of America, 103, 12947–12950. https://doi.org/10.1073/pnas.0604093103
Asner, G. P., Martin, R. E., Knapp, D. E., Tupayachi, R., Anderson, C. B., Sinca, F., ... Llactayo, W. (2017). Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. Science, 355, 385–389. https://doi.org/10.1126/science.aaj1987
Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R., & Emerson, R. (2009). A contemporary assessment of change in humid tropical forests. Conservation Biology, 23, 1386–1395. https://doi.org/10.1111/j.1523-1739.2009.01333.x
Baker, T., Phillips, Q., & Malhi, Y. (2004). Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology, 10, 545–562. https://doi.org/10.1111/j.1365-2486.2004.00751.x
Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., ... Fine, P. V. (2011). Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. Global Change Biology, 17, 2677–2688. https://doi.org/10.1111/j.1365-2486.2011.02432.x
Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., ... Parry, L. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature, 535, 144–147. https://doi.org/10.1038/nature18326
Barlow, J., Louzada, J., Parry, L., Hernandez, M. I., Hawes, J., Peres, C. A., ... Gardner, T. A. (2010). Improving the design and management of forest strips in human-dominated tropical landscapes: A field test on Amazonian dung beetles. Journal of Applied Ecology, 47, 779–788. https://doi.org/10.1111/j.1365-2664.2010.01825.x
Barlow, J., Peres, C., Lagan, B., & Haugaasen, T. (2003). Large tree mortality and the decline of forest biomass following Amazonian wildfires. Ecology Letters, 6, 6–8. https://doi.org/10.1046/j.1461-0248.2003.00394.x
Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H., Bardgett, R. D., ... da Silva, P. M. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. Biodiversity and Conservation, 19, 2873–2893. https://doi.org/10.1007/s10531-010-9850-9
Berenguer, E., Ferreira, J., Gardner, T. A., Aragão, L. E. D., Camargo, P. B., Cerri, C. E., ... Barlow, J. (2014). A large-scale field assessment of carbon stocks in human-modified tropical forests. Global Change Biology, 20, 3713–3726. https://doi.org/10.1111/gcb.12627
Berenguer, E., Gardner, T., Ferreira, J., Aragão, L., Nally, R., Thomson, J., ... Barlow, J. (2018). Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. Figshare, https://doi.org/10.6084/m9.figshare.6068693
Bonnell, T. R., Reyna-Hurtado, R., & Chapman, C. A. (2011). Post-logging recovery time is longer than expected in an East African tropical forest. Forest Ecology and Management, 261, 855–864. https://doi.org/10.1016/j.foreco.2010.12.016
Brando, P. M., Nepstad, D. C., Balch, J. K., Bolker, B., Christman, M. C., Coe, M., & Putz, F. E. (2012). Fire-induced tree mortality in a neotropical forest: The roles of bark traits, tree size, wood density and fire behavior. Global Change Biology, 18, 630–641. https://doi.org/10.1111/j.1365-2486.2011.02533.x
Brando, P. M., Oliveira-Santos, C., Rocha, W., Curry, R., & Coe, M. T. (2016). Effects of experimental fuel additions on fire intensity and severity: Unexpected carbon resilience of a neotropical forest. Global Change Biology, 22, 2516–2525. https://doi.org/10.1111/gcb.13172
Broadbent, E., Asner, G., Keller, M., Knapp, D., Oliveira, P., & Silva, J. (2008). Forest fragmentation and edge effects from deforestation
primary productivity and its allocation in Bornean tropical forests. Global Change Biology, 1-16. https://doi.org/10.1111/gcb.14068

Rutishauser, E., Hérault, B., Baraloto, C., Blanc, L., Descroix, L., Sotta, E. D., de Oliveira, L. C. (2015). Rapid tree carbon stock recovery in managed Amazonian forests. Current Biology, 25, R787–R788.

Santos, B. A., Peres, C. A., Oliveira, M. A., Grillo, A., Alves-Costa, C. P., & Tabacchelli, M. (2008). Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. Biological Conservation, 141, 249–260. https://doi.org/10.1016/j.biocon.2007.09.018

Sarmiento, F. Q. (1997). Arrested succession in pastures hinders regeneration of Tropaeanean forests and shrubs mountain landscapes. Environmental Conservation, 24, 14–23. https://doi.org/10.1017/S0376892997000052

Schnitzer, S., & Bongers, F. (2011). Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. Ecology Letters, 14, 397–406. https://doi.org/10.1111/j.1466-0265.2011.01590.x

Schnitzer, S. A., Dalling, J. W., & Carson, W. P. (2000). The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. Journal of Ecology, 88, 655–666. https://doi.org/10.1046/j.1365-2745.2000.00489.x

Sieger, P., Ruecker, G., Hinrichs, A., & Hoffmann, A. A. (2001). Increased damage from fires in logged forests during droughts caused by El Niño. Nature, 414, 437–440. https://doi.org/10.1038/35106547

Slocum, M. G., Aide, T. M., Zimmerman, J. K., & Navarro, L. (2004). Natural regeneration of subtropical montane forest after clearing fern thickets in the Dominican Republic. Journal of Tropical Ecology, 20, 483–486. https://doi.org/10.1017/S0266467404001646

Steffen, W., Richardson, K., Rockstrom, J., Cornell, S. E., Fetzer, I., Bennett, E. M., ... Folke, C. (2015). Planetary boundaries: Guiding human development on a changing planet. Science, 347, 1259855-1-1259910. https://doi.org/10.1126/1259855

Tymen, B., Réjou-Méchain, M., Dalling, J. W., Fauset, S., Feldpausch, T. R., Norden, N., ... Chave, J. (2016). Evidence for arrested succession in a liana-infested Amazonian forest. Journal of Ecology, 104, 149-159. https://doi.org/10.1111/1365-2745.12504

Uhl, C., & Kauffman, J. (1990). Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. Ecology, 71, 437-449. https://doi.org/10.2307/1940299

van Gelder, H. A., Poorter, L., & Sterck, F. J. (2006). Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. New Phytologist, 171, 367-378. https://doi.org/10.1111/j.1469-8137.2006.01757.x

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., & Hermy, M. (2006). Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology, 87, 542-548. https://doi.org/10.1890/05-1182

Verissimo, A., Barreto, P., Mattos, M., Tarifa, R., & Uhl, C. (1992). Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: The case of Paragominas. Forest Ecology and Management, 55, 169–199. https://doi.org/10.1016/0378-1127(92)90099-U

Williamson, G. B., Bentos, T. V., Longworth, J. B., & Mesquita, R. C. G. (2014). Convergence and divergence in alternative successional pathways in Central Amazonia. Plant Ecology & Diversity, 7, 341–348. https://doi.org/10.1016/j.pl-ed.2012.735714

Wright, S. J., Kitajima, K., Kraft, N. J., Reich, P. B., Wright, I. J., Bunker, D. E., ... Engelbrecht, B. M. (2010). Functional traits and the growth-mortality trade-off in tropical trees. Ecology, 91, 3664–3674. https://doi.org/10.1890/09-2335.1

Wright, S., Muller-Landau, H., Condit, R., & Hubbell, S. (2003). Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology, 84, 3174–3185. https://doi.org/10.1890/02-0038

Xaud, H. A. M., Martins, F. D. S. R. V., dos Santos, J. R. (2013). Tropical forest degradation by mega-fires in the northern Brazilian Amazon. Forest Ecology and Management, 294, 97-106. https://doi.org/10.1016/j.foreco.2012.11.036

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., ... Chave, J. (2009). Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository, https://doi.org/10.5061/dryad.3.34

Zarin, D. J., Davidson, E., Brondizio, E., Vieira, I. C., Sá, T., Feldpausch, T., ... Ducey, M. J. (2005). Legacy of fire slows carbon accumulation in Amazonian forest regrowth. Frontiers in Ecology and the Environment, 3, 365–369. https://doi.org/10.1890/1540-9295(2005)003[365:LOFSCA]2.0.CO;2

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Berenguer E, Gardner TA, Ferreira J, et al. Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. J Ecol. 2018;106:2190–2203. https://doi.org/10.1111/1365-2745.12991