RESEARCH ARTICLE

Large-scale impacts of selective logging on canopy tree beta-diversity in the Brazilian Amazon

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Abstract

1. Selective logging is one of the largest drivers of tropical forest degradation. While logged forests often retain high alpha-diversity of tropical trees at local spatial scales, understanding how selective logging impacts tree beta-diversity and community composition across far larger spatial scales remains a key unresolved question.

2. We leverage large datasets of more than 155,000 adult trees over 35 cm DBH covering 3100 ha of Amazonian rainforest to inform simulations of selective logging harvests across a gradient of logging intensity (0–40 m^3 ha^{-1}). These simulations incorporate real world price data, account for all forest damage throughout the harvest process and assume preferential harvest of the most valuable stems. We use the simulations to assess how selective logging affects canopy tree beta-diversity and composition across large spatial scales, whether nestedness or turnover of species best explains variation in communities across space, and how the spatial scale of sampling influences observed beta-diversity effects.

3. Selective logging had minimal impacts on beta-diversity across the canopy tree community, but caused substantial subtractive heterogenization in community composition for larger trees, in particular very large trees over 110 cm DBH. Turnover is the dominant component of tree beta-diversity in unlogged and logged forests. Increasing the spatial grain of sampling reduced the observed importance of logging in explaining patterns of beta-diversity in very large tree communities.

4. *Synthesis and applications*. Minimal impacts on tree beta-diversity across large spatial scales points towards the retention of substantial conservation value in logged tropical forests. Strong subtractive heterogenization in very large trees indicates the breakdown of broad scale patterns of composition with potential negative consequences for recruitment processes, fauna reliant upon emergent trees, and other ecosystem functions and services. Avoiding large-scale erosion of very large tree community composition in the Amazon requires stronger conservation policies, including enforced retention or maximum cutting diameters.

KEYWORDS
Amazon, beta-diversity, biodiversity, forest degradation, selective logging, tree diversity, tropical forest

1 | INTRODUCTION

Tropical forests support extensive biodiversity (Pimm & Raven, 2000) and maintain globally significant carbon stocks (Pan et al., 2011). Yet these forests are subject to widespread selective logging (Blaser et al., 2011), which is the primary driver of tropical forest degradation (Hosonuma et al., 2012; Pearson et al., 2017). Selective logging involves the harvesting of commercially valuable species of a minimum cutting size, leaving behind non-commercial species, smaller individuals, and a degraded forest structure with a fragmented canopy and patches of intense sunlight (Bousfield et al., 2020). Despite this disturbance, selectively logged forests often retain most of their biodiversity and ecosystem services relative to primary forest (Edwards, Tobias, et al., 2014; Putz et al., 2012) and are much more biodiverse than competing land-uses, especially agriculture (Gibson et al., 2011).

Harvest intensity plays an important role in determining the severity of logging impacts on biodiversity, with higher intensities resulting in greater losses of tree species richness (Martin et al., 2015). Large, valuable trees targeted by selective logging are vulnerable to local population collapses (Richardson & Peres, 2016), yet play irreplaceable ecological roles in tropical forests (Lindenmayer et al., 2012; Pinho et al., 2020). They provide food and habitat for a multitude of organisms, giving structure that provides humid, dark, cool microclimates, and account for a large proportion of total forest biomass and carbon (Nascimento & Laurance, 2002). Selective logging thus also drives losses of favourable microclimates in the short term (Mollinari et al., 2019) and large tree biomass and above-ground carbon over longer timescales (Sist et al., 2014).

Understanding of the impacts of selective logging on tree diversity has tended to focus on alpha diversity (i.e. local species richness) and associated changes in community composition measured at small spatial scales (Cazzolla Gatti et al., 2015; Gourlet-Fleury et al., 2013; Martin et al., 2015). However, focusing on species richness across small areas within a few relatively small plots (1 ha or smaller) risks underestimating the impacts of selective logging at larger spatial scales. Logging activity is not evenly distributed across a forest, often creating a heterogenous mosaic of patches that undergo different levels of disturbance (Cannon et al., 1994). Such heterogeneity in local conditions could lead to shifts in landscape-level community composition and diversity that are not detected by local-scale assessments (Berry et al., 2008), with observed community responses to disturbance being heavily impacted by the spatial scale of sampling (Dumbrell et al., 2008; Hill & Hamer, 2004). Furthermore, the spatial grain of sampling (i.e. size of sampling units) can influence observed variation in community composition (Barton et al., 2013). A key question, therefore, is how selective logging impacts tree community composition over large areas and across varying spatial grains.

Beta diversity—the component of regional (gamma) diversity that accumulates due to variations in local species assemblages (Socolar et al., 2016)—could be impacted by selective logging through two processes. Firstly, heterogenization, whereby communities become increasingly different from each other, as the same set of high-value shared species is consistently targeted by logging across the entire landscape. Alternatively, homogenization, whereby communities become increasingly similar as the same species are left behind. Furthermore, beta-diversity can be partitioned into two separate components, turnover and nestedness, which could both be impacted by selected logging (Baselga, 2010). Turnover occurs when species are present at one site, but lost at another where they are replaced by different species. Alternatively, nestedness occurs when one site contains only a subset of the species present at another site.

Our understanding of these potential impacts of selective logging on tree beta-diversity is limited. In Borneo, logged forests had higher levels of beta-diversity and increased turnover of species across large spatial scales compared to unlogged forests, suggesting logging-induced heterogenization (Berry et al., 2008). In the Amazon, similar patterns were observed at small scales ~10 years after logging, but tree community composition recovered towards a pre-logging state within 25 years (Gaui et al., 2019). However, these studies relied on a small number of 1 ha plots (30 and 12, respectively) dispersed across the landscape, which fails to capture both the substantial turnover of species in these hyperdiverse communities and the large heterogeneity of disturbances that could affect beta-diversity patterns across entire landscapes, particularly when different sampling scales are considered. Understanding the impacts of selective logging on beta-diversity across large contiguous areas of forest is thus of high importance to policy and conservation efforts aiming to maintain ecological diversity at larger scales (Socolar et al., 2016).

In this study, we tackle the key question of how logging impacts tree beta-diversity at large spatial scales. We do so by leveraging detailed tree distribution maps containing information on more than 155,000 large trees (DBH >35 cm) across 3100 ha of continuous tropical forest within an Amazonian logging concession. The Amazon has hyperdiverse tree communities (Ter Steege et al., 2013), including some highly valuable timber species (e.g. big-leaf mahogany- *Swietenia*, ipê- *Tabebuia*, and jatobá- *Hymenaea*; Schulze et al., 2008), and contains the largest unexploited tropical timber stocks globally (Merry et al., 2009). Within the Brazilian Amazon, the Brazilian Forestry Service (Serviço Florestal Brasileiro; SFB) has been undertaking an ambitious programme since 2006 to create a network of long-term legal timber concessions within National and State Forests (FLONAs and FLOTAs). In combination with other areas designated for sustainable use, up to 35–50 million hectares is potentially available for harvest in the coming decades (de Marques et al., 2016; Sist et al., 2021). Ensuring that logging does not erode diversity patterns at scale is thus a key issue. We generate harvest simulations across a gradient of logging intensity to ask, for both the wider canopy tree community and across different tree size classes: (1) whether tree beta-diversity and composition is affected by selective logging across large spatial scales and through which mechanism this occurs (i.e. heterogenisation or homogenization); (2) whether nestedness or turnover are primarily responsible for explaining community change; and (3) how does the spatial scale of sampling influence the beta-diversity effects observed.

2 | MATERIALS AND METHODS

2.1 | Study site

The study area consists of the wet tropical lowland forest of the northern Amazon Basin and within the Guianan Shields, in the Vale do Jari region, Pará, Brazil (1°13′12″S 52°33′36″W). The site was granted to the Grupo Orsa Florestal forestry company as a 'reduced-impact logging' (RIL) concession for sustainable forest management by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA). Between 2001 and 2003, a complete forest census was undertaken, spatially mapping within a 5-m positional accuracy all large tree stems ≥35 cm in diameter at breast height (DBH), each of which was identified to species level by a team of highly experienced parabotanists. This team of five people was led by Mr. Domingos Sanches, an expert tree parabotanist who had been working at the site since the mid-1980s and was completely familiar with the local tree flora.

The accuracy of species-level field identifications at Jari was enhanced by cross-referencing either fertile or infertile vouchers collected in situ with those deposited at the herbaria of Embrapa Amazônia Oriental and Museu Paraense Emílio Goeldi, and later the Herbarium Felisberto Camargo of the Universidade Federal Rural da Amazônia. The credibility of species-level tree identifications at this concession was further strengthened by collections of wood samples that were cross-referenced at the Jari Xylotheque, which houses 4672 wood samples of over 397 canopy tree species (Ferreira, 2009).

Spatial mapping was conducted manually, operating within 12.5 m width bands, covering a total area of 5083 ha of undisturbed forest that excluded riparian forest areas. Fieldwork permission was not required for this study. The tree inventory data on which this study is based was carried out within Annual Production Units (UPAs) 1 and 2, which spanned an area of 1635 and 3448 ha, respectively, and included a total of 291,027 identified and mapped individual trees ≥35 cm DBH representing 377 species, 196 genera, and 56 families. Species nomenclature was standardised to adhere to The Plant List database (TPL, 2013). Before harvest, the study site had a mean canopy tree (DBH >35 cm) density, basal area, and standing volume of 49.7 ± 9.2 stems ha^{-1}, 10.46 ± 2.35 m^3 ha^{-1}, and 81.2 ± 27.2 m^3 ha^{-1}, respectively, with a mean DBH of 49.2 ± 16.2 cm and maximum DBH of 254 cm.

2.2 | Creating plots for pairwise comparisons

To create a network of sampling plots, we overlaid a 3-ha grid of plots across the 5100-ha forest landscape. We then increased the number of plots by manually shifting and/or rotating grid cells in order to fit within the irregular shaped boundaries of the concession. This resulted in a sampling network of 1036, 3-ha plots (total sample area = 3108 ha) with a mean tree density of 151 (range = 48–244), containing 156,601 individual trees ≥35 cm DBH (Figure 1).

2.3 | Simulating logging of the forest

We tested the influence of selective logging on tree beta-diversity across two levels of logging intensity. The first, a lower-intensity logging scenario, whereby logging occurred at an average intensity of 20 m^3 ha^{-1}, which represents the typical logging intensity of legal forestry concessions in the Brazilian Amazon. The second was a higher-intensity logging scenario, where logging occurred at an average intensity of 40 m^3 ha^{-1}, thus exceeding the legal limit of 30 m^3 ha^{-1} and representing a scenario where high-intensity logging is conducted beyond legal limits.

To generate a landscape of plots that had either been logged (at high or low intensity) or left unlogged, we randomly allocated one third of the 1036 plots to each of the three logging treatments (Figure 1). To account for any impact of random allocation on the tree communities found for each logging treatment type, we repeated harvest simulations over 999 random iterations in which a new suite of plots were randomly allocated to each logging class.

To simulate a typical logging cycle within logged plots, we used financial data from Bousfield et al. (2021) to estimate the value of each individual tree within the logged plots (accounting for the estimated volume of each tree, and species-specific processing yields and selling prices). Assuming loggers would preferentially log the most valuable stems first, we then ranked all trees within the logged plots (≥50 cm DBH following legal limits) based on their estimated value. We then assigned the most valuable trees to be logged until the cumulative volume of logged trees met the logging quota (either 20 m^3 ha^{-1} in lower-intensity logged forest or 40 m^3 ha^{-1} in higher-intensity logged forest).

2.4 | Simulating residual damage of the forest

To account for the residual damage that occurs when a tree is logged and removed from a forest, we used the linear model ($r = 0.83$, $p < 0.01$) developed by Sist and Ferreira (2007) based on empirical field measurements of residual damage in a Brazilian logging concession that implemented Reduced Impact Logging (RIL) techniques. For each 3-ha plot, the total number of trees logged were calculated, and the resulting percentage of the original tree stand killed by residual damage was estimated as:

$$y = 1.9x + 2.7,$$

where y represents the percentage of the original tree stand destroyed through residual damage and x represents the logging intensity in the plot (in trees ha^{-1}). We assumed that each logged tree could only kill trees that were smaller or equal in size, and within a 20 m radius of the logged tree. Trees fitting these criteria were considered under threat of mortality by residual damage, before a random sample matching the estimated proportion of trees killed (Equation 1) was taken, with all trees that were selected assumed to have died from residual damage during the logging harvest.
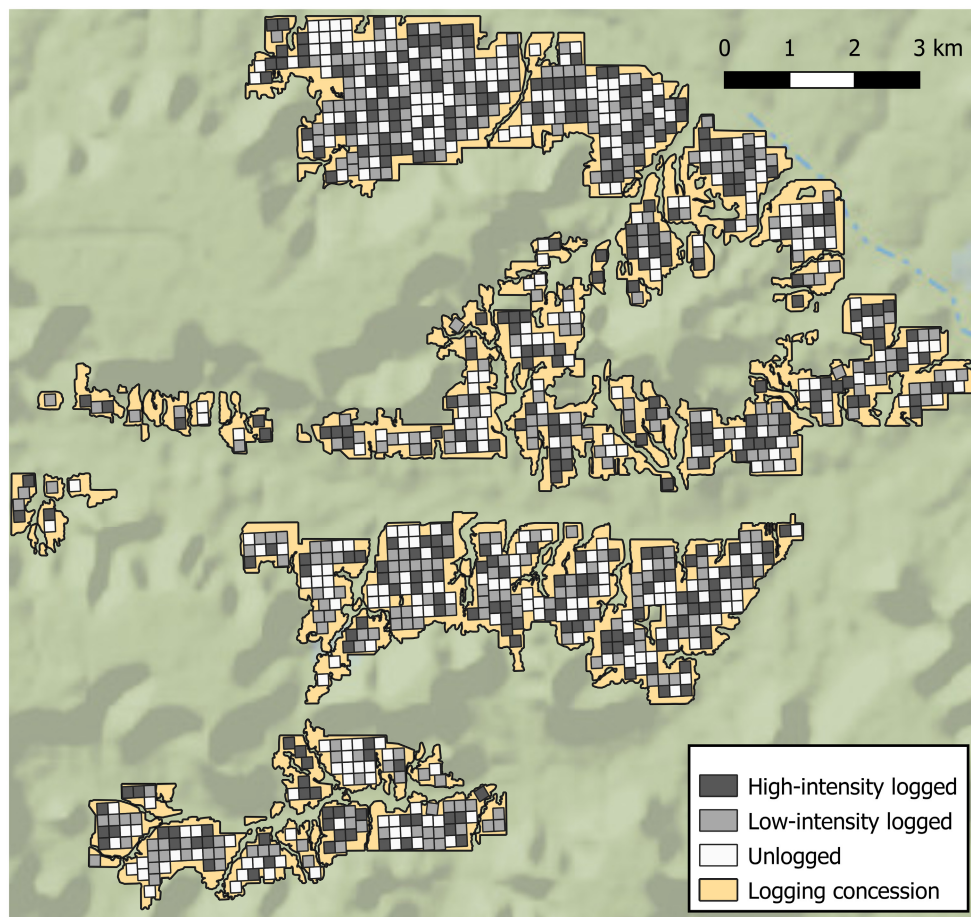
FIGURE 1 The forest inventory of Vale do Jari, Pará, Brazil. The concession was divided in 1036 three-ha plots, which were randomly assigned 1 of 3 treatments (Unlogged, Low-intensity logging, and High-intensity logging), to generate a contiguous area of forest that had undergone different levels of logging. The colours represent the treatment assignments of a single simulation.

2.5 | Simulating road network and skid trail damage

To account for the destruction of trees caused by the creation of a road network to facilitate the extraction of timber from the forest, we adopted the methods of Bousfield et al. (2022), which used detailed road maps provided by a sustainable logging company (AMATA based in Rondônia) to estimate the typical extent of road networks required in Brazilian logging concessions. The total combined extent of road and log deck construction was thus estimated as 1.82% of the logged area, in line with other estimates in Brazil (Carvalho et al., 2017) and the global median of 1.7% (Kleinschroth & Healey, 2017). To account for the damage this would cause to the tree community, we randomly allocated 1.82% of the area of each logged plot as being lost to road construction and deemed any trees inside this area to be killed during the logging process.

To account for the impact of skid trails during harvest, we used detailed skid trail maps from the same concession (AMATA) to estimate the area extent of skid trails required for harvest. Using these

maps, we estimated a skid trail cover of 1.6% of concession area at a harvest intensity of $12\,m^3\,ha^{-1}$ (again close to previous estimates; Carvalho et al., 2017). Readjusting to the higher logging intensities simulated here, we estimated skid trails to cover 2.66% and 5.32% of land logged at low ($20\,m^3\,ha^{-1}$) and high ($40\,m^3\,ha^{-1}$) intensity, respectively. To account for this damage, we randomly allocated this proportion of land in each logged plot to skid trails, and assumed all smaller trees ($35\,cm \leq DBH < 50\,cm$) in this area to be killed through skid trail construction. As per standard practice by logging concessionaries, we assumed large trees (i.e. $DBH > 50\,cm$) located on a skid trail would simply be avoided due to the large financial costs and labour requirement involved in removing them, and did not assign them as killed during skid trail construction. As a precaution, we conducted a reanalysis whereby all trees of any size in a skid trail were destroyed, but this had minimal impact on the results (Figure S7). After simulating the logging extraction, residual damage and damage through road and skid trail construction across all plots, we were left with a continuous network of forest plots that depicted the surviving canopy tree community after varying levels of logging harvests had occurred.

2.6 | Harvest assumptions

All further analysis of the beta-diversity impact of selective logging on Amazonian canopy tree communities are based on the results of our simulated logging harvests. Conclusions are therefore made in the context of the assumptions and caveats contained within our harvest simulation models, which are:

- Large trees only—our data is limited to trees with DBH values >35 cm, thus focusing on the largest trees most important for biodiversity and carbon storage, and the group specifically targeted by logging. Our simulations thereby exclude stems that are <35 cm DBH. Because these stems are not directly targeted by logging, but may suffer residual damage from felling and extraction, their beta-diversity may be differentially impacted compared to the canopy tree community.

- First harvest using RIL—due to data limitations, we simulate the first logging harvest of a primary old-growth forest, conducted under RIL techniques. Additional timber harvests (after the 30–35 year minimum cycle time) and those conducted using Conventional Logging techniques will cause further damage to the tree canopy community not simulated here.

- Preference for large, valuable trees—our harvest model assumes that trees are harvested preferentially in order of their value, which typically results in the largest individuals of commercial species being harvested first. Beta-diversity impacts will therefore be skewed towards trees in larger size classes, although to structure logging around smaller or less-valuable species would likely be uneconomic (Bousfield et al., 2021).

- Road and skid trail damage—our simulations of the damage caused by road and skid trail creation are conservative. In many concessions, road creation may deliberately miss the largest trees, while skid trails will likely avoid trees in the 35–50 cm DBH class.

2.7 | Logging impacts on tree beta-diversity in Amazonian tropical forests

To analyse beta-diversity patterns across gradients of logging intensity, we employed generalised dissimilarity modelling (Ferrier et al., 2007) in *R* version 4.1.0 using the GDM package (Fitzpatrick et al., 2021). The GDM method is an extension of matrix regression, designed specifically to accommodate two common types of non-linearity found in larger-scaled ecological data sets: (1) the curvilinear relationship between increasing ecological distance, and observed compositional dissimilarity between sites; and (2) the variation in the rate of compositional turnover at different positions along environmental gradients (Ferrier et al., 2007). This approach fits non-linear functions to each predictor variable using flexible *i*-splines, which are then combined to estimate the 'ecological distance' between a pair of cells. The maximum height of each *i*-spline thus indicates the amount of compositional turnover

associated with each variable while holding all other variables constant. The GDM allowed us to quantify the importance of selective logging in driving beta-diversity patterns, while holding other variables (.g. geographic separation) constant, and to assess how the impact of selective logging changes along a gradient of logging intensity (from 0 to 40 m^3 ha^{-1}).

We used pairwise Bray–Curtis dissimilarity between pairs of plots as our dissimilarity measure (>500,000 comparisons), and included logging intensity and geographic distance between plots as predictors. We then fitted a GDM using three *i*-spline basis functions per predictor and quantified the importance of each variable in explaining beta-diversity by randomising each variable's position in the dissimilarity matrix in turn for 50 permutations and noting the loss in explanatory power. We also tested dissimilarities in community composition using the Jaccard index, square root transformed, presence-absence transformed data and basal area. We present the raw abundance-based results (i.e. number of individual trees) of Bray–Curtis dissimilarity as all measures resulted in similar outcomes (see Figures S3–S6 for comparison).

To ascertain how the impacts of selective logging on beta-diversity vary across different tree size classes, we grouped trees into the following three classes: medium (35 cm ≤ DBH <50 cm), large (50 cm ≤ DBH <110 cm), and very large (DBH ≥110 cm), resulting in communities with overall species richness of 339, 336 and 59, respectively. The above analysis was then repeated separately for tree communities within each size class.

2.8 | Does nestedness or turnover best explain observed beta-diversity patterns in unlogged and logged forests?

To estimate the proportion of beta-diversity attributable to either turnover or nestedness for each logging type (unlogged, low-intensity logged and high-intensity logged), for all trees, and each size class, we used the *bray.part* function from the BETAPART package (Baselga et al., 2021). Here, logging treatments were conducted across the entirety of the logging concession, such that there were three repeats of the original logging concession that each underwent a different logging treatment. Pairwise comparisons of all plots from the same treatment concession were then made, and the levels of Bray–Curtis dissimilarity, and its constituent parts (nestedness and turnover) were calculated.

2.9 | How does the spatial scale of sampling influence the beta-diversity effects observed?

To test how the spatial scale of sampling impacts the patterns observed, we repeated the GDM analysis for plots at 5 different spatial scales: 1, 3, 5, 10 and 25 ha. The same method was adopted to create each set of plots, by imposing a grid over the forest landscape and allocating as a plot all grids that were bounded entirely within the

concession. The number of plots used in analysis for each plot size thus varied, but the total area of forest assessed remained constant.

3 | RESULTS

Harvest simulations resulted in the felling and harvesting of 4.1 ± 0.2 and 13.1 ± 0.3 trees ha^{-1} under low-intensity ($20 \text{m}^2 \text{ha}^{-1}$) and high intensity ($40 \text{m}^2 \text{ha}^{-1}$) harvests, respectively. This represents a mean basal area of 2.3 ± 0.02 and $4.9 \pm 0.04 \text{m}^2 \text{ha}^{-1}$ for low- and high-intensity harvests, respectively (i.e. 22% and 47% of the total basal area of trees >35 cm DBH before logging). These harvests thus accurately represent real-world harvest intensities that occur within the Amazon (Figure S1). Residual damage resulted in the loss of 4.4 ± 0.2 and 11.4 ± 0.3 trees ha^{-1}, for low- and high-intensity scenarios, respectively, representing 8.9 ± 0.4 and $22.9 \pm 0.5\%$ of the canopy tree community.

3.1 | Impact of selective logging on tree beta-diversity and composition in Amazonian forests

Across the canopy tree community, selective logging had a significant but relatively small impact on community composition, accounting for $22.4 \pm 1.3\%$ of the explained variation between unlogged and logged plots, compared to the $77.6 \pm 1.3\%$ explained by geographic separation. However, when considering only very large tree communities (DBH ≥110 cm), selective logging was the dominant driver of changes in beta-diversity between unlogged

and logged forest, accounting for $89.2 \pm 2.2\%$ of explained community variation compared to only $10.8 \pm 2.2\%$ explained by geographic distance (Figure 2). Similarly, for large tree communities (50 cm ≤ DBH <110 cm), selective logging accounted for $72.4 \pm 3.4\%$ of the explained variation in community composition compared to the $27.6 \pm 3.4\%$ explained by geographic distance. For medium-sized tree communities (DBH < 50 cm), there was an effect of logging on beta-diversity, but this effect was very small and only accounted for $7.5 \pm 0.8\%$ of explained community variation. Logging intensity was found to be a significant predictor of canopy tree community composition across all tree size classes (mean harmonic p-value < 0.001; Wilson, 2019, see Table S1 for model summaries).

In all scenarios, the impact of selective logging on beta-diversity increased along the logging-intensity gradient. For the whole canopy tree community, there was no effect of low-intensity logging (i.e. <20 m^3 ha^{-1}), but a small effect that increased in size at higher logging intensities (i.e. >30 m^3 ha^{-1}; Figure 2). For very large emergent trees, logging strongly altered community composition even at low logging intensities (<20 m^3 ha^{-1}), but at high intensity the shift in community composition attributable to logging was ~15% larger. Logging up to 20 m^3 ha^{-1} had little impact on beta-diversity in large trees, but at higher intensities (>20 m^3 ha^{-1}) logging started to cause stronger changes in community composition (Figure 2). Logging had little effect on beta-diversity of medium-sized trees across the entire intensity gradient. Removing the effect of residual damage from harvest simulations led to similar patterns, but with a slightly reduced impact of logging on beta-diversity (Figure S2).

When considering species basal area instead of abundance, the impact of selective logging on community turnover was greater for
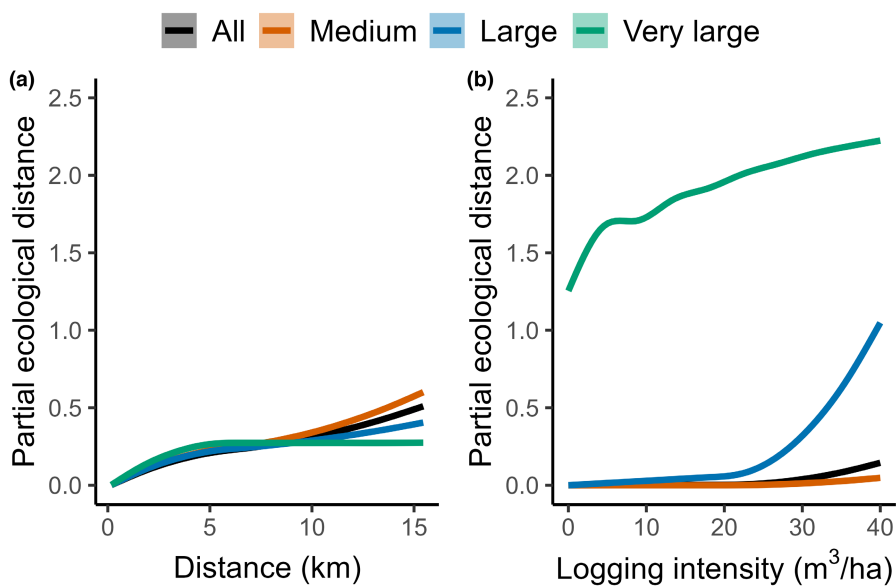

FIGURE 2 *I*-splines from GDM indicating the relative role of geographic separation (a) and logging intensity (b) in accounting for community turnover (partial ecological distance) between sites for all canopy trees, and medium-, large-, and very large-sized trees. The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable while holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).

all canopy trees and in medium-sized canopy trees, but the effect size remained relatively low, and did not change in large and very large tree communities (Figure S3). Different measures of beta-diversity also demonstrated similar patterns to the Bray-Curtis results presented here (Figures S4–S6).

3.2 | Does nestedness or turnover best explain observed beta-diversity patterns in unlogged and logged forests?

The dominant component of beta-diversity in unlogged forest tree communities was turnover, with little nestedness present between plots. The same pattern was observed in both lower- and higher-intensity logged tree communities (Figure 3a). There was a small increase in average Bray–Curtis dissimilarity between plots logged at the highest intensities, suggesting only slight heterogenization due to selective logging (Figure 3 and Figure S8).

In very large tree communities in unlogged forests, turnover remained the dominant component of beta-diversity, although nestedness accounted for a larger proportion of beta-diversity than it did for medium and large tree communities. However, very large tree communities in logged forest (both low and high intensity) demonstrated extremely high turnover and little to no nestedness compared to unlogged forest (Figure 3d). Total beta-diversity of very large trees increased after logging (Figure S8). In both medium and large tree

communities, turnover was the main component of beta-diversity in all forest types, with total beta-diversity increasing slightly along the logging gradient (Figure 3b,c).

3.3 | How does the spatial scale of sampling influence the beta-diversity effects observed?

For all, medium and large canopy trees, the importance of geographic separation in explaining changes in the canopy tree community composition remained relatively constant up to 10 ha before dropping in 25 ha plots (Figure 4a). By contrast, for very large trees the importance of geographic separation increased as sampling plots became larger (Figure 4c). For all canopy trees, geographic separation explained $69.4 \pm 3.1\%$ of the explained community variation in 1-ha plots compared to $61.4 \pm 9.2\%$ in 25-ha plots, whereas in very large trees, it accounted for $17.7 \pm 5.7\%$ in 1-ha plots compared to $41.3 \pm 11.3\%$ in 25-ha plots. Geographic separation remained a significant predictor of beta-diversity at all spatial grains across the canopy tree community and all size classes (mean harmonic p-value < 0.001, see Table S2 for model summaries).

For the whole canopy tree community (Figure 4b), as well as for medium and large canopy trees (Figure S9), the observed influence of logging intensity on tree beta-diversity was relatively stable across plot sizes, whereas the observed effect of logging was consistently weakened in larger plots for very large tree communities. For all canopy trees, logging intensity accounted for $30.6 \pm 3.1\%$ of the explained community variation between 1-ha plots compared to $38.6 \pm 9.2\%$ in 25-ha plots, while in very large trees it accounted for $82.3 \pm 5.7\%$ of the community variation between 1-ha plots compared to only $58.7 \pm 11.3\%$ in 25-ha plots (Figure 4d). Logging intensity remained a significant predictor of beta-diversity at all spatial grains across the whole canopy tree community and all size classes (mean harmonic p-value < 0.001).

4 | DISCUSSION

Selective logging is a primary driver of tropical forest degradation, occurring across vast areas, yet a key question is how logging impacts tree diversity across large spatial scales. Focusing on a ~3100 ha forest landscape in the Brazilian Amazon, we show that logging across a range of intensities had minimal effect on composition of the canopy tree community, with turnover the principal component of beta-diversity in both unlogged and logged forest. However, selective logging was the key driver of beta-diversity changes between unlogged and logged forests in very large tree communities (DBH ≥110 cm) and, to a lesser extent, large tree communities (50 cm ≤ DBH < 110 cm). Given the critical ecological importance of very large trees to forest ecosystems, improved conservation policies are required to prevent logging-induced large-scale shifts in their community composition across the Amazon.
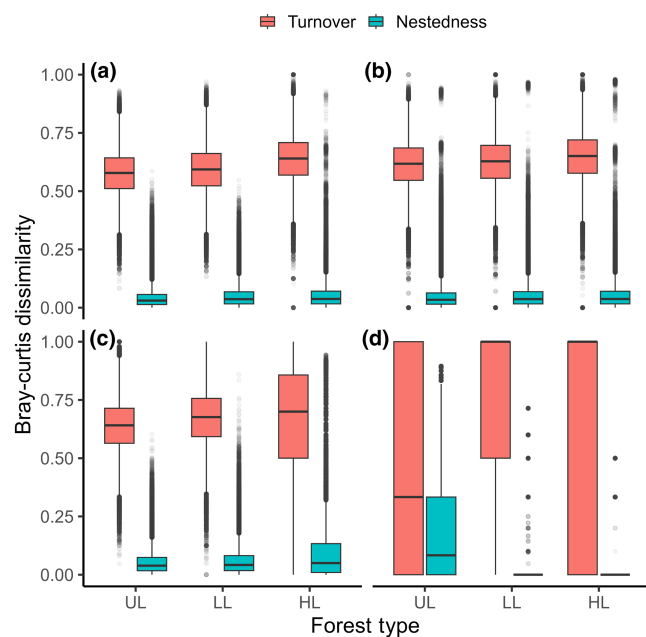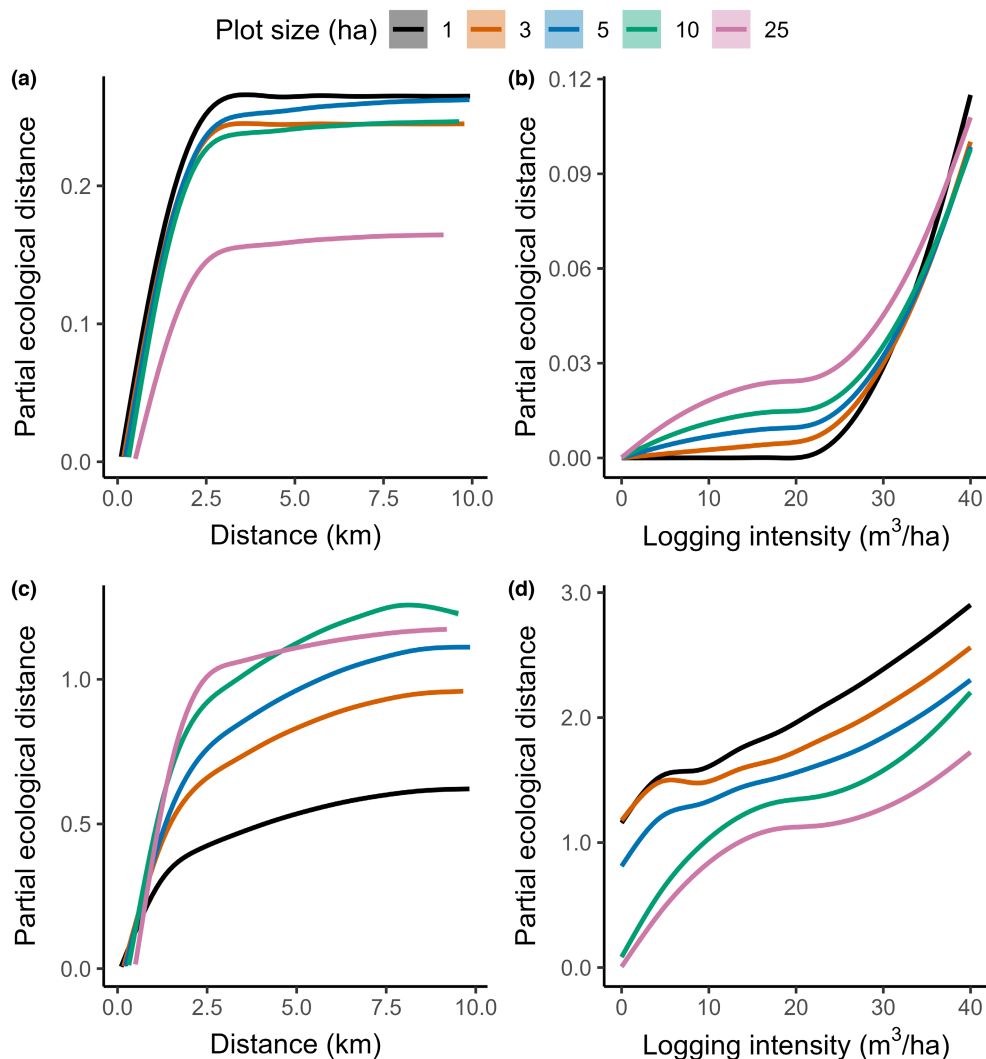

FIGURE 3 Pairwise Bray–Curtis dissimilarity of tree communities across all canopy trees (a), medium- (b), large- (c) and very large- (d) sized trees attributable to turnover and nestedness in unlogged (UL), low-intensity logged (LL) and high-intensity (HL) logged forest plots. Central bar shows median, box shows upper and lower quartiles, whiskers extend to 1.5× the inter-quartile range, and outliers are presented as dots.

FIGURE 4 *I*-splines from GDM indicating the relative role of geographic separation (a, c) and logging intensity (b,d) in accounting for community turnover between sites for all canopy trees (a, b) and very large trees (c, d) for 1, 3, 5, 10 and 25-ha plots. The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable while holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).

4.1 | Selective logging has minimal impacts on the beta-diversity of the wider canopy tree community

The small effect of logging on beta-diversity as a whole suggests that under current intensities (typically <20 m³ ha⁻¹), logging is not driving any large-scale change in Amazonian canopy tree community composition (≥35 cm DBH) in the short term. These conclusions are supported by longer-term, small-scale experimental plots that demonstrate recovery towards pre-logging species composition in the Amazon within 25 years (Gaui et al., 2019). By contrast, logged forests in Borneo have higher beta-diversity than unlogged forest, suggesting logging-induced heterogenization (Berry et al., 2008), but here logging can occur at intensities of ~150 m³ ha⁻¹ (Fisher et al., 2011) resulting in a far more disturbed landscape. Indeed, under RIL regimes (as simulated here), Bornean logged forest tree

communities more closely resembled unlogged forests than conventionally logged forests (Imai et al., 2012). Our results thus point to the high conservation value of selectively logged Amazonian forests across large spatial scales.

Partitioning beta-diversity into its constituent parts indicates that in both unlogged and logged Amazonian forest, changes in canopy tree community composition across the forest landscape are primarily a result of species turnover (Baselga, 2010). High turnover between plots suggests that to maintain a diverse canopy tree community, conservation efforts protecting larger forest areas would be more beneficial than targeting a few of the most species-rich sites (Socolar et al., 2016). Given that low-intensity logging (<20 m³ ha⁻¹) had little impact on the wider canopy tree community composition, and that logged and unlogged plots had similarly high levels of turnover, our results suggest that land-sharing style logging (Edwards,

Gilroy, et al., 2014) would be less detrimental to maintaining tree species diversity across a large forest landscape than land sparing, supporting similar conclusions from a theoretical study (Ramage et al., 2013). While such an approach would also be more profitable (Bousfield et al., 2021), it could be damaging for other important biological groups such as birds and dung-beetles (Edwards, Gilroy, et al., 2014; França et al., 2017), thus highlighting a trade-off in forest management.

Although logging had limited impact on tree beta-diversity at lower intensities, the increased impact on beta-diversity as logging intensity increases above legal limits (30 m^3 ha^{-1}) is cause for concern given the prevalence of extensive illegal logging occurring at high intensities across the Amazon (Brancalion et al., 2018; Finer et al., 2014). Although we show limited impacts of even high-intensity logging on tree beta-diversity, this would amount to a sizeable effect given the huge footprint of illegal logging in the Amazon (Matricardi et al., 2020), particularly if illegal harvests occur at higher intensities than we simulated. Furthermore, selective logging alters community composition in Amazonian butterflies (Montejo-Kovacevich et al., 2018), bats (Peters et al., 2006), and dung beetles (França et al., 2017), with Neotropical fauna apparently more sensitive to logging disturbance than their analogues in Afrotropical and Indomalayan forests (Burivalova et al., 2014). Logging-induced shifts in community composition across the ecosystem are complex and a wide range of taxa must be considered when assessing logging impacts across entire communities.

While the range of logging intensities simulated here is contextually relevant to the Amazon (Martin et al., 2015), the world's largest store of as-of-yet unexploited tropical timber (Merry et al., 2009), in the context of the global tropics they are relatively low. Commercial species availability and Brazilian law restrict harvests to 30 m^3 ha^{-1}, yet logging intensities in South-East Asia have regularly exceeded 100 m^3 ha^{-1} (Martin et al., 2015). In Borneo, selectively logged forests demonstrate increased tree species turnover and differ significantly in species composition when compared with primary forest (Berry et al., 2008). Furthermore, logging intensities in tropical Africa range from 5 to 100 m^3 ha^{-1} (Martin et al., 2015), with logging at higher intensities leading to a marked reduction in tree species richness and changes to the vertical forest structure that persist for decades (Cazzolla Gatti et al., 2015). Understanding how selective logging impacts tropical tree beta-diversity in other tropical regions where forest damage is generally higher (Putz et al., 2012) is thus an important area for future research.

4.2 | Selective logging primarily affects beta-diversity of larger, emergent trees

Selective logging in the Amazon targets primarily large, commercially valuable tree species (Richardson & Peres, 2016), and there was a strong signal of subtractive heterogenization after logging in these communities (Socolar et al., 2016). Along the logging intensity gradient, very large and large logged canopy tree communities became increasingly different from one another compared to unlogged communities, likely a result of increased turnover through logging-induced loss of highly prized shared species. This was particularly the case in very large tree communities, which were less species-rich than medium- and large-sized classes, making them more susceptible to greater changes in beta-diversity as large trees of highly valued species are removed from the forest. Furthermore, while the logging impact on large tree communities was limited until high logging intensities (>20 m^3 ha^{-1}), logging-induced subtractive heterogenization of very large emergent tree communities was evident even at low logging intensities typical in the Brazilian Amazon (<20 m^3 ha^{-1}), making this a concern for most forestry operations.

Very large trees have high ecological importance (Lindenmayer et al., 2012; Pinho et al., 2020), harbouring important forest biodiversity, biomass, and carbon stocks (Sist et al., 2014), and take centuries to replace through regeneration (Cannon et al., 2022). Our study provides further ecological support for restricting the harvest of these emergent trees (Mazzei et al., 2010; Sist et al., 2014). Despite potential short-term financial losses of protecting very large trees given their economic value, current logging intensities mean Brazilian timber concessions cannot support timber yields beyond the first harvest cycle (Piponiot et al., 2019; Sist et al., 2021). Retention of a significant proportion of the larger trees beyond the first harvest would reduce the impact of logging on these tree communities and associated ecosystem functions and services, while also contributing towards more sustainable economic production across future harvests.

Where the effect of logging on beta-diversity was strong (i.e. for very large trees), increasing the spatial grain of sampling (from 1 to 25 ha plots) consistently reduced the importance of logging intensity in explaining beta-diversity patterns. Sampling extent influences observed impacts of disturbance on community composition (Dumbrell et al., 2008; Hill & Hamer, 2004) and beta-diversity tends to decrease with increasing spatial grain of sampling, because larger sampling units observe greater proportions of the total community increasing their similarity to one another (Barton et al., 2013; Steinbauer et al., 2012). We extend this thinking by demonstrating that the spatial grain of sampling also influences the observed importance of ecological disturbances (here selective logging) in driving beta-diversity changes, highlighting the need to consider a range of spatial extents and sampling grains when assessing the impacts of disturbance on communities.

Our results have four caveats. First, the logging census only recorded trees ≥35 cm DBH. While trees of this size account for more than half of above-ground biomass (Cummings et al., 2002; Peres et al., 2016), we cannot make conclusions on the beta-diversity impact of logging on smaller trees (<35 cm DBH) that can constitute >66% of species and ~98% of individuals in Amazonian tree communities (Valencia et al., 2004). Although smaller trees are not directly harvested through logging, tree death through road construction and residual damage is typically high (Pinard & Putz, 1996) and could drive greater erosion of beta-diversity than for the canopy tree

community. Second, our simulations did not consider post-logging regrowth or colonisation from pioneer species exploiting logging gaps (Berry et al., 2008). Our results thus represent a snapshot of conditions immediately after logging; however, our focus was on large to very large trees which mature on multi-decadal to centennial timescales. Third, our estimates of residual damage are based on field data from RIL harvests, which can significantly reduce impacts on the surrounding canopy (Pereira Jr et al., 2002; Sist & Ferreira, 2007). For "hit-and-run" logging operations using conventional logging techniques that cause greater damage, the impact of selective logging on tree beta-diversity could be larger. Finally, we simulate logging across only one timber harvest, but in Brazilian concessions a second logging harvest is permitted within 35 years (Sist et al., 2021). At current typical harvest rates (~20 $m^3 ha^{-1}$), timber production cannot be maintained beyond the first harvest (Sist & Ferreira, 2007; Sist et al., 2021). Without significant reform to long-term concession management, subsequent harvests may cause increased damage to canopy tree communities and erosion of beta-diversity across the smaller size classes as trees that remained after the first harvest are targeted for logging.

5 | CONCLUSIONS

Our simulations found selective logging to have minimal impact on large-scale beta-diversity in the canopy tree community as a whole in a large Amazonian forest concession, but that logging causes increasingly strong subtractive heterogenization in very large tree communities. Logging-induced shifts in the community composition of very large trees is cause for concern given the widespread extent of unregulated selective logging in the Amazon (Asner et al., 2005; Sist et al., 2021) and the vital ecological roles such trees fulfil (Lindenmayer et al., 2012; Pinho et al., 2020). Targeted harvesting of the largest, most valuable trees over multiple harvest cycles thus risks large-scale canopy tree community shifts, thereby calling for improved conservation and protection of these very large tree communities during logging. This could be achieved through the introduction of a maximum cutting diameter or the enforced retention of a greater proportion of the largest trees of each species within the forest (Bousfield et al., 2021; Mazzei et al., 2010; Sist et al., 2014). Such measures would aid in preventing logging-induced shifts in Amazonian canopy tree community composition, while protecting the longer-term sustainability of timber harvests, the structural integrity of logged forests and the biodiversity and carbon they support.

AUTHOR CONTRIBUTIONS

Christopher G. Bousfield, David P. Edwards and Mike R. Massam conceived the ideas and designed methodology; Carlos A. Peres obtained the data; Christopher G. Bousfield and Mike R. Massam analysed the data; Christopher G. Bousfield led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing conflict of interest.

DATA AVAILABILITY STATEMENT

The data used in this study were made confidentially available to Carlos A. Peres by Jari Florestal. Due to its sensitive nature, we are unable to make this publicly available, as openly available geo-location data of all commercially valuable trees, including threatened and CITES-listed species, could leave the concession vulnerable to exploitation.

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SUPPORTING INFORMATION

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

Table S1. GDM model summaries for all canopy trees, medium, large and very large tree communities. Significance values are the harmonic mean p values of the 999 iterations of each model where a different suite of sample plots were allocated to each logging treatment. Values displayed are the means from the 999 iterations and standard deviations are shown. Bold coefficients represent the most important predictor of beta-diversity for that size class.

Table S2. GDM model summaries for all canopy trees, medium, large and very large tree communities with sampling plots 1, 3, 5, 10 and 25 ha in size. Significance values are the harmonic mean p values of the 999 iterations of each model where a different suite of sample plots were allocated to each logging treatment. Values displayed are the means from the 999 iterations and standard deviations are shown. Bold coefficients represent the most important predictor of beta-diversity for that size class.

Figure S1. Harvest intensities (trees ha^{-1}) reported under the simulated low and high intensity harvests from this study, compared with those reported from post-harvest field data in the literature ($n = 12$).

Figure S2. *I*-splines from GDM indicating the relative role of geographic separation (a) and logging intensity (b) in accounting for community turnover (partial ecological distance) between sites for all canopy trees, and medium-, large-, and very large-sized trees, without accounting for residual damage. The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable whilst holding all others constant, and the shape of

the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. Both geographic distance and logging intensity were found to be significant predictors of canopy tree community turnover across all trees and all individual size classes (mean harmonic $p < 0.001$). *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).

Figure S3. *I*-splines from GDM indicating the relative role of logging intensity in accounting for canopy tree community turnover between sites using species abundances (a) and basal area (b). The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable whilst holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).

Figure S4. *I*-splines from GDM using alternative beta-diversity metrics (Bray-Curtis, Jaccard, square-rooted Bray-Curtis and presence-absence Bray-Curtis) indicating the relative role of geographic separation (a) and logging intensity (b) in accounting for canopy tree community turnover between sites. The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable whilst holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).

Figure S5. *I*-splines from GDM using alternative beta-diversity metrics (Bray-Curtis, Jaccard, square-rooted Bray-Curtis and presence-absence Bray-Curtis) indicating the relative role of geographic separation in accounting for community turnover between sites for medium (a), large (b) and very large (c) sized trees. The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable whilst holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).

Figure S6. *I*-splines from GDM using alternative beta-diversity metrics (Bray-Curtis, Jaccard, square-rooted Bray-Curtis and presence-absence Bray-Curtis) indicating the relative role of selective logging in accounting for community turnover between sites for medium (a), large (b) and very large (c) sized trees. The maximum height of each

i-spline indicates the amount of community turnover attributable to that variable whilst holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).

Figure S7. *I*-splines from GDM indicating the relative role of geographic separation (a) and logging intensity (b) in accounting for community turnover (partial ecological distance) between sites for all canopy trees, and medium-, large-, and very large-sized trees, where all trees located on a skid trail were considered destroyed. The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable whilst holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging, and high-intensity logging).

Figure S8. Pairwise Bray-Curtis dissimilarity of tree communities across all canopy trees (a), medium- (b), large- (c) and very large- (d) sized trees, demonstrating total Bray-Curtis diversity and the portions attributable to turnover and nestedness in unlogged (UL), low-intensity logged (LL) and high-intensity (HL) logged forest plots. Central bar shows median, box shows upper and lower quartiles, whiskers extend to 1.5× the inter-quartile range, and outliers are presented as dots.

Figure S9. *I*-splines from GDM indicating the relative role of geographic separation (a, c) and logging intensity (b, d) in accounting for community turnover between sites for medium (a, b) and large trees (c, d) for 1, 3, 5, 10 and 25 ha plots. The maximum height of each *i*-spline indicates the amount of community turnover attributable to that variable whilst holding all others constant, and the shape of the *i*-spline demonstrates how the rate of turnover changes across the ecological gradient. *I*-splines shown are aggregated from the *i*-splines produced by 999 random permutations of selective logging, whereby each plot was randomly assigned one of three logging treatments (no logging, low-intensity logging and high-intensity logging).