

Functional resistance to a selective logging disturbance in Amazonian forests

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Abstract

Tropical forests bring numerous benefits for humanity, but they suffer from increasing human disturbance that can lastingly modify their functioning. In this study we evaluate the effect of selective logging, one of the most widespread human disturbances in tropical forests, on Amazonian forests' functional composition. We develop a model of post-logging trajectory of community weighted mean traits and calibrate it in a Bayesian framework using data from 12 experimentally logged sites (264 ha total) spread over the Amazon biome. We test the effect of the initial composition and functional diversity as well as the precipitation seasonality and stem turnover rate on the functional resistance to a logging disturbance (i.e. the maximum relative change in functional composition after logging).

Our results show that, contrary to expectations, the initial composition and functional diversity have no significant effect on the functional resistance in our plots. The stem turnover rate was the best predictor of post-logging resistance for two traits, namely the 95th percentile of a species diameter distribution (as a proxy of adult tree stature) and wood density. Forests with high turnover rates were predicted to be the more resistant to logging. Overall, adult tree stature and SLA seem to be more resistant to logging, while seed mass and wood density show consistent decreases after a logging disturbance. Forests in northeastern Amazonia are predicted to experience the strongest decreases in wood density after logging (-10%). These forests are especially important for water cycles and carbon sequestration, and a decrease in wood density may lower their ability to provide these benefits.

Introduction

Tropical forests are crucial for most global ecological cycles. They hold 230 Pg of carbon, around 11% of the total carbon in terrestrial ecosystems (Baccini et al. 2012) and intact tropical forests are estimated to have sequestered an

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annual 1.19 ± 0.41 Pg of carbon between 1990-2007 (Pan et al. 2011), about 15% of total anthropogenic carbon emissions, thus playing a major role in climate change mitigation (IPCC 2014). Tropical forests are also key in the global water cycle, recycling rainfall through vegetation evapotranspiration and thus buffering droughts in adjacent regions (Staal et al. 2018). Moreover, tropical forests harbor an exceptional biodiversity (Jenkins, Pimm, and Joppa 2013, Slik et al. (2015)), providing species to surrounding regions through biotic interchanges (Antonelli et al. 2018). The state of tropical forests thus largely determines the functioning of global ecosystems, and hence human well-being.

The future of tropical forests is however highly uncertain: during the past three centuries, humans activities have triggered rapid changes in global ecosystems, causing massive species extinctions and accelerating climate change through increased carbon emissions (Crutzen 2002). During the past century these changes are particularly intense in the tropics, where forests are being clearcut for agricultural or mining purposes at unprecedented rates, and where most remaining forests have or will be heavily impacted by human activities (Malhi et al. 2014).

One predominant human activity in tropical forests is the selective logging of a few merchantable trees: around 400 million hectares of tropical forests are designated for timber production (Blaser et al. 2011), and ca. 20% of tropical forests were affected by selective logging between 2000 and 2005 (Asner et al. 2009). Because selective logging focuses on a few individual trees (typically 5-10 trees per hectare), 65-95% of the forest cover is maintained after logging operations (Cannon et al. 1994, Pereira et al. (2002)). Damage to the forest is concentrated in logging gaps created by tree felling, and in infrastructure (skid trails and, to a lesser extent, roads and log decks) (Pereira et al. 2002, Asner, Keller, and Silva (2004)).

Disturbances such as selective logging, droughts, fires, or hunting, are increasing in intensity and frequency (Lewis, Edwards, and Galbraith 2015). Human disturbances alter the composition and dynamics of tropical forests by provoking a higher-than-normal tree mortality, which can affect some trees more than others. Large trees of commercial value with good mechanical properties are the focus of loggers; trees with low-density wood are more vulnerable to droughts (Mcdowell et al. 2018, Aleixo et al. (2019)), and trees with thick bark are more resistant to fires (Brando et al. 2012). Directional mortality has a straight-forward effect on forest composition and structure. The indirect effect of disturbance is the higher recruitment of light-demanding species in canopy gaps (Carreño-Rocabado et al. 2012): these changes in tree species composition can last for several decades (Avila et al. 2015).

Changes in composition and their effects on forest functioning can be quantified with functional traits (Chapin III et al. 1997, Lavorel and Garnier (2002)). Functional traits are measures of an individual's features that impact its growth, reproduction and survival, and hence its overall fitness (Violle et al. 2007). In tropical forests, at least four major functional axes have been described: (i) the leaf economic spectrum (short-lived low-investment leaves vs. tough leaves) (Wright et al. 2004), the wood economic spectrum (fast-growing low-density

vs. long-lived high-density wood) (Chave et al. 2009), adult tree stature and height (canopy vs. understory trees) linked to light capture (Poorter et al. 2003) and survival strategy (Johnson et al. 2018), and the seed dispersal strategy (large, zoochorous and resource-rich seeds vs. light anemochorous seeds) (Poorter and Rose 2005). Together, these four axes explain most of the functional variation observed in forest ecosystems (Baraloto, Hardy, et al. 2012, Costa-Saura et al. (2019)).

Disturbances such as selective logging change local conditions by creating canopy gaps and thus increasing the quantity of light that gets to the soil. The new light conditions favor the germination and rapid growth of small-seeded, light-wooded species (Poorter and Rose 2005, Baraloto, Hérault, et al. (2012), Baker et al. (2016), Poorter et al. (2019)). These light-demanding pioneer species have high growth rates but generally poor resistance to drought (Aleixo et al. 2019). It has also been shown that selective logging can decrease the canopy height, and consequently total carbon storage (Rutishauser et al. 2016). Understanding the long-term effects of disturbances on a community’s functional composition will thus be key to predict the future of tropical forests in the context of rapid changes in disturbance regimes (Wright 2005).

Ecosystem resilience is a measure of an ecosystem’s ability to cope with disturbances (Holling 1973). It is a key concept to understand the long-term changes in forest composition and dynamics following a disturbance. The notion of resilience can be defined with two essential components: the change in state (or resistance to disturbance), and the time to return to a pre-disturbance state (or recovery) (Hodgson, McDonald, and Hosken 2015). Resilience, and in particular its change-in-state component, depends strongly on the disturbance frequency and intensity. Additionally, ecological memory of past disturbances is a key component of forest resilience (Johnstone et al. 2016, Ciemer et al. (2019)). Ecological memory translates into the presence and diversity of trees and seeds of species with life-history traits adapted to disturbances, which in turn can shape forest demographics, and especially vegetation turnover rates (Lavorel and Garnier 2002, (???)). Environmental constraints such as water limitations have also been shown to affect the functional resistance of Neotropical forests to disturbances (???).

In Amazonia, the largest tropical forest biome on Earth (600 million hectares), at least two large gradients explain regional patterns of forest dynamics (Johnson et al. 2016). Vegetation productivity is strongly correlated to the precipitation regime (Fauset et al. 2019), being higher in northwestern forests with high levels of precipitation and lower in southeastern forests which suffer from a long dry season (Davidson et al. 2012, Johnson et al. (2016)). Stem turnover rates describe a Northeast-Southwest gradient (???), mainly driven by soil stability (Quesada et al. 2012), and the frequency and intensity of natural disturbances such as windstorms (Espírito-Santo et al. 2014, Negrón-Juárez et al. (2018)) and droughts (Phillips et al. 2010). Understanding how these gradients structure the forest response to a logging disturbance can help improve predictions of Amazonian forests vulnerability to future increases in disturbance regimes.

Here we assess the resistance of four functional traits (namely wood density,

seed mass, specific leaf area and maximum tree diameter) to selective logging in Amazonia. Our research questions are: (i) how is the functional composition of Amazonian forests affected by disturbances such as selective logging? (ii) are some functional traits more resistant than others? (iii) what is the effect of initial functional composition and diversity on the functional resistance? and (iv) how does functional resistance vary across Amazonia, and is it related to regional patterns of natural disturbances?

To bring light on these questions, we modeled the post-disturbance trajectory of four key community mean traits within an original Bayesian hierarchical model. We calibrated the model using data from 161 permanent forest plots from 12 long-term experimentally logged sites (264 ha total) spread over Amazonia. We tested the effect of the initial (pre-disturbance) trait value and functional diversity, and of regional patterns of forest demographics (stem turnover rate as a proxy of natural disturbance regimes) and precipitation seasonality.

Methods

Study sites

Our study includes data from twelve long-term (8–35 year) experimental forest sites located in the Amazon Basin and the Guiana Shield (Figure 1) (Sist et al. 2015). All sites are located in tropical forests with mean annual precipitation ≥ 1000 mm. In each site, permanent forest plots (3–56.25 ha per site) were logged, and censused at least once before and twice after logging.

For each site, we extracted the precipitation seasonality from Worldclim database (bioclimatic variable 15) (Fick and Hijmans 2017), at a 2.5 arc-minute resolution. Annual stem turnover rates (as a % of live stems) were based on data from unlogged plots inside our sites. For the 5 sites in which no unlogged plot was available, stem turnover rates were extracted from a map based on the metadata from Johnson and colleagues (Johnson et al. 2016) (extracted from the ForestPlots database (Lopez-Gonzalez et al. 2011)) and interpolated with the R package gstat (Pebesma 2004) on a 1° resolution grid. Site coordinates, precipitation seasonality and stem turnover rates are reported in Table 1.

Data compilation

For sites with plots ≤ 1 ha, data from those with the same treatment were aggregated to mitigate the small plot effect on the variation in density of large trees. In each census, all trees ≥ 10 cm diameter at breast height (dbh) were marked, measured and identified to the lowest taxonomic level (84% to species, 14% to genus).

Median values of functional traits were calculated at the species level. Four functional traits were chosen, as proxies of complementary ecosystem functions in tropical forests: (i) the DBH 95th percentile as a proxy of adult tree stature and light demand (Poorter et al. 2003), (ii) the seed mass (log-transformed) as a proxy of the dispersal strategy (Poorter and Rose 2005), (iii) the specific leaf area as a proxy of the assimilation strategy and leaf economic spectrum

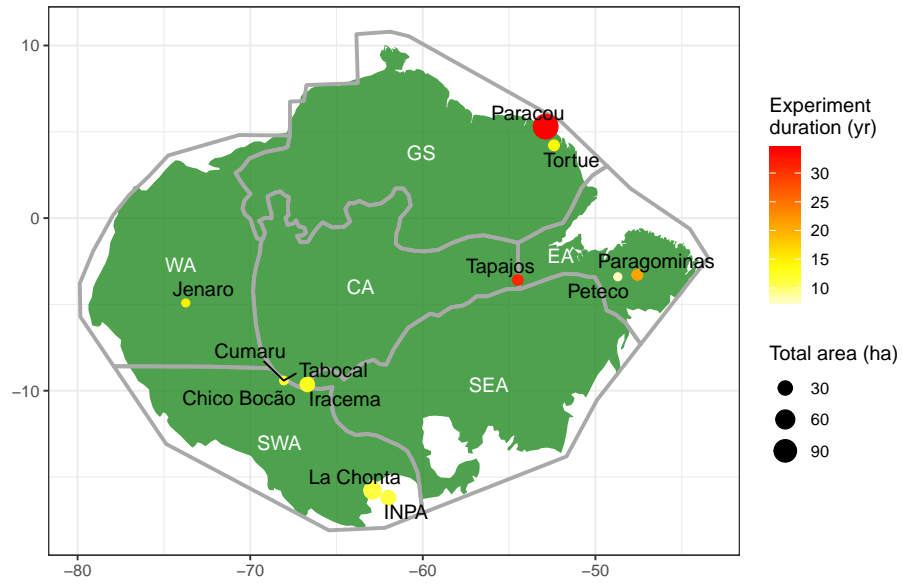


Figure 1: Location of the 12 experimental permanent forest sites used in this study: the size of the points represents the total monitored area, and the color (from yellow to red) represents the total length of the experiment, as the time interval (in years) between the first and the last census. Grey boundaries define 6 ecoregions and were retrieved from Ter Steege et al., 2013 (Ter Steege et al. 2013), CA: central Amazonia, EA: eastern Amazonia, GS: Guiana shield, SEA: southeastern Amazonian, SWA: southwestern Amazonia, and WA: western Amazonia. Green areas define the Amazonian biome.

(Wright et al. 2004) and (iv) the stem wood density as a proxy of growth rate and mechanical support (Chave et al. 2009).

The DBH 95th percentile was chosen because it is more robust than the maximum DBH which is too sensitive to sampling size. The DBH 95th percentile was calculated for all species for which at least 20 individuals were censused in our permanent forest plots. Seed mass and specific leaf area measurements were retrieved from the TRY database (Kattge et al. 2011) (datasets citations xx). Wood density measurements were retrieved from the global wood density database (Chave et al. 2009, Zanne et al. (2009)).

Median trait values were calculated per species and genus. Each individual tree in our permanent sample plots was then attributed a value for each trait at the lowest available taxonomic level. Trees with no available species- or genus-specific trait value were given their plot's median trait value. The aboveground biomass of each individual was estimated using the R package BIOMASS (Réjou-Méchain et al., n.d.).

Selective logging typically targets large trees belonging to a small group of species with commercial value. Those species usually have particular functional trait values, such as large maximum diameters. The functional composition of the largest trees is thus artificially modified because of the selectivity of harvests. Because we are more interested in the indirect effects of selective logging disturbance on the functional composition, i.e. the functional changes induced by tree felling and canopy openings, we excluded large trees with DBH > 35 cm from the analysis.

For each functional trait k (either $DBH95$, $\log SeedMass$, SLA , or WD), we computed the community's mean biomass-weighted trait (CMT) value at census c in plot p in site s as:

$$CMT_{k,c,p,s} = \frac{\sum_{i \in I_{c,p,s}} (T_{k,i} \cdot agb_i)}{\sum_{i \in I_{c,p,s}} (agb_i)} \quad (1)$$

with $T_{k,i}$ the value of trait k for individual tree i , agb_i the aboveground biomass of individual tree i , and $I_{c,p,s}$ all live trees with DBH ≥ 10 cm and ≤ 35 cm at census c in plot p in site s . Mean trait values were weighted by aboveground biomass to reflect the importance of larger trees in forest functioning (e.g. carbon cycling).

The distance of a trait value to its initial (pre-logging) value was estimated as:

$$dCMT_{k,c,p,s} = \frac{CMT_{k,c,p,s} - CMT0_{k,p,s}}{CMT0_{k,p,s}} \quad (2)$$

The functional diversity $FD_{k,c,p,s}$ for a given trait k was calculated as the similarity-based diversity of order 1 of all trees with dbh between 10 and 35 cm at census c in plot p and site s , and was calculated with the function Dqz in the R package *entropart* (Marcon and Hérault 2015).

Model calibration

The model presented here aims at capturing the changes in the community's mean biomass-weighted traits (CMT) after the disturbance, as well as their recovery. For each trait k , the change in CMT at census c in plot p and site s was modeled as:

$$dCMT_{k,c,p,s} \sim \mathcal{N}\left(\mu_{k,c,p,s}, \left(\frac{\sigma_k}{size_p}\right)^2\right) \quad (3)$$

where

$$\mu_{k,c,p,s} = \Delta_{k,p,s} \cdot \left(\frac{t_c}{tmax_{k,p,s}} \cdot \exp\left(1 - \frac{t_c}{tmax_{k,p,s}}\right)\right)^{\theta_{k,p,s}} \quad (4)$$

with t_c the time since logging (in years) at census c ; $size_p$ is the size of plot p ; $\Delta_{k,p,s}$ is the maximum post-disturbance change (negative if the CMT decreases, and positive if it increases). $tmax_{k,p,s}$ is the time taken to reach $\Delta_{k,p,s}$; when $t_c > tmax_{k,p,s}$, the CMT starts to get closer to its initial value, entering the recovery phase which is in some plots not yet observed. θ_k is a shape parameter that controls the width of the hump; when it increases, the hump is narrower.

Parameters $\Delta_{k,s,p}$ and $tmax_{k,p}$ were modeled with a normal distribution:

$$tmax_{k,p,s} \sim \mathcal{N}(\mu m1_{s,k}, \sigma m1^2) \quad (5)$$

where $\sigma m1$ is the standard deviation of $tmax$ and $\mu m1_{s,k}$ is the mean of $tmax$ for trait k in site s . To benefit from the information from sites with long experiment duration and help infer $tmax$ in sites where it had not been reached during the experiment duration (i.e. no observed return to initial CMT because of short experiment duration), we added one hierarchical level to $tmax$:

$$\mu m1_{s,k} \sim \mathcal{N}(\mu m2_k, \sigma m2^2) \quad (6)$$

with $\mu m2_k$ and $\sigma m2$ the mean and standard deviation of $\mu m1_{s,k}$.

$\Delta_{k,p,s}$ is the maximum change of trait k after the disturbance: its absolute value is expected to increase with disturbance intensity. We thus modeled it as:

$$\Delta_{k,p,s} \sim \mathcal{N}\left(loss_p \cdot (\lambda_{0,k} + \sum \lambda_{m,k} Cov_{m,k,p,s}), \sigma_\Delta^2\right) \quad (7)$$

where $loss_p$ is the relative aboveground biomass loss after logging in plot p , as a proxy of the disturbance intensity; it is estimated as the difference between the pre-logging aboveground biomass and the minimum biomass in the first 4 years after logging, divided by the pre-logging aboveground biomass (similar to Piponiot et al. (2016)). $Cov_{m,k,p,s}$ is the value of covariate m for trait k in plot p in site s . Covariates are (i) the stem turnover rate, (ii) the precipitation seasonality (both defined for each site from Amazonian-wide maps), (iii) the initial community mean trait and (iv) the initial functional diversity, both defined for each trait and plot with pre-logging censuses. σ_Δ is the standard deviation of Δ for trait k in site s .

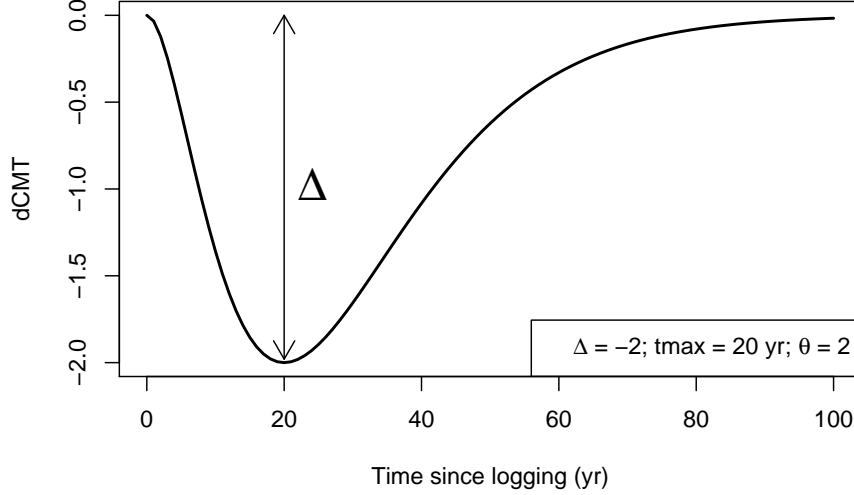


Figure 2: Example of predicted relative CMT change (dCMT) after a disturbance.

Bayesian hierarchical models were inferred through MCMC methods using an adaptive form of the Hamiltonian Monte Carlo sampling using the R language (R Development Core Team 2018) and the Rstan package (Carpenter et al. 2017). A detailed list of priors is provided in Table XXX (informative priors?).

Predictions

Predictions of maximum CMT change after the disturbance were made at the Amazonian level on a 1° grid, i.e. the coarsest resolution of input maps, and errors were propagated with the following steps:

1. For each cell j of the grid: (i) a value of stem turnover was taken from the map of stem turnover fitted with the data from (Johnson et al. 2016) (see (Piponiot et al. 2019)); (ii) a value of precipitation seasonality was taken from the distribution of pixel values in the Worldclim map (Fick and Hijmans 2017) that were inside the cell.
2. Parameters $\lambda_{0,k}$ and $\lambda_{m,k}$ were taken from their posterior distribution.
3. For each trait k and grid cell j , predictions of maximum CMT change $\Delta_{k,j}$ after a disturbance were calculated using a biomass loss of $loss = 40\%$:

$$\Delta_{k,j} = loss \cdot (\lambda_{0,k} + \sum \lambda_{m,k} Cov_{m,j}) \quad (8)$$

These steps were repeated 1000 times and summary statistics were calculated for each 1° grid cell.

Results

Predictions of functional trajectories and parameters

The estimated time to reach the maximum trait change is similar between traits (Figure 3) and is estimated to be between [5, 36] yr (95% confidence interval).

The maximum relative trait change (Δ) was between [-11, 7]%, with large differences between traits and sites (Figure 3). The community mean adult tree stature (*DBH95*) decreased after the disturbance in almost all sites except the two sites in Bolivia: La Chonta and, to a lesser extent, INPA (Figure 3). The community mean seed mass (*logSeedMass*) decreased in most sites after the disturbance ($\Delta \in [-19, 3]\%$), except for two sites in western Amazonia, Cumaru and Chico Bocão. The community mean specific leaf area (*SLA*) increased or stayed close to its initial value in most sites after the disturbance, except in INPA, Bolivia (see full trajectories in supplementary Figure 7). The increase in the community mean SLA was especially high in Tapajos where it gained +12% compared to its initial value. The community mean wood density (*woodDensity*) decreased in most sites after the disturbance ($\Delta \in [-12, 1]\%$), except for three sites: INPA, Peteco and Tabocal, where it stayed close to its initial value.

Effect of covariates on functional resistance

The intercept λ_0 is significantly different from zero for all traits except for *DBH95* (Figure 4). A site with average stem turnover rate and precipitation seasonality is thus predicted to have a small non-significant decrease in *DBH95* (as a proxy of tree stature). Both the seasonality of precipitations and the stem turnover rate have a significant positive effect on mean *DBH95*: highly seasonal forests with high turnover rates are predicted to favor larger trees (on average) after a logging disturbance, while forests with low precipitation seasonality and turnover rates are predicted to have a decrease in mean *DBH95*. The initial functional composition (*CMT*) and diversity (*FD*) have no significant effect on post-disturbance *DBH95* changes. The intercept is significantly negative for *logSeedMass* and positive for *SLA*, but no significant covariate effect was detected for either of these traits (Figure 4): seed mass is predicted to decrease and SLA is predicted to increase after a logging disturbance. For *woodDensity*, the intercept is significantly negative: wood density is predicted to decrease after a logging disturbance (Figure 4). The effect of precipitation seasonality is significantly negative and the effect of stem turnover rate and the initial wood density (*CMT*) have a significantly positive effect on post-disturbance wood density change. A forest with high precipitation seasonality, low stem mortality and low initial wood density is thus predicted to have a stronger decrease of mean wood density after a logging disturbance.

Predictions of regional variability in functional resistance

Functional resistance is predicted to vary strongly between traits and across the Amazonian biome (Figure 5). *DBH95* is predicted to decrease strongly

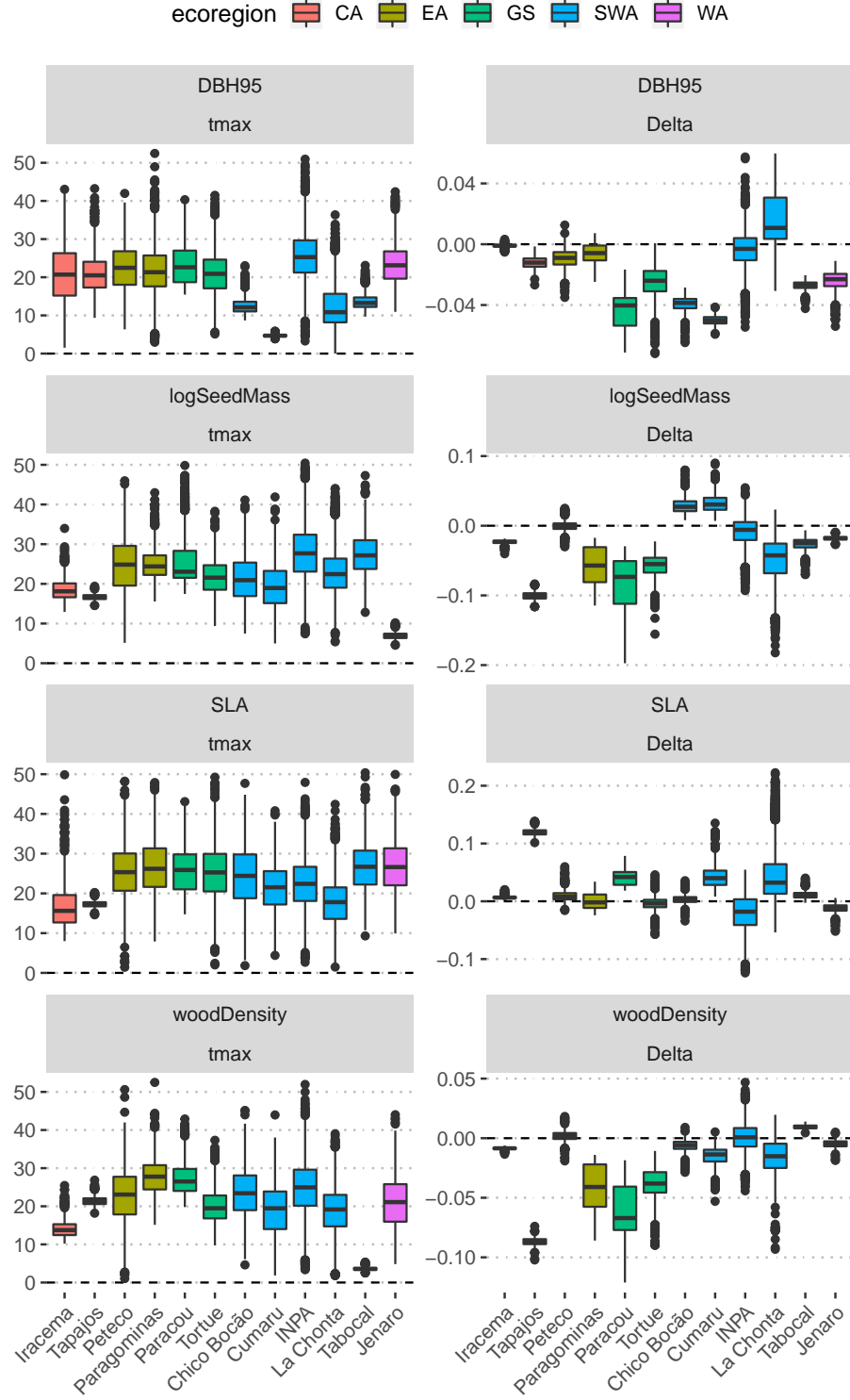


Figure 3: Posterior distribution of parameters t_{max} (left panels) and Δ (right panels) per site (x-axis) and trait (top to bottom panels). The wider the posterior, the larger the uncertainty on its estimation. Functional traits are: $DBH95$ community mean 95th percentile of the diameter at breast height (a proxy of the adult stature); \logSeedMass community mean seed mass (log-transformed); SLA community mean specific leaf area; $woodDensity$ community mean wood density. Ecoregions (as defined in Ter Steege et al., 2013) are: CA: central Amazonia, EA: eastern Amazonia, GS: Guiana shield, SWA: southwestern Amazonia and WA: western Amazonia.

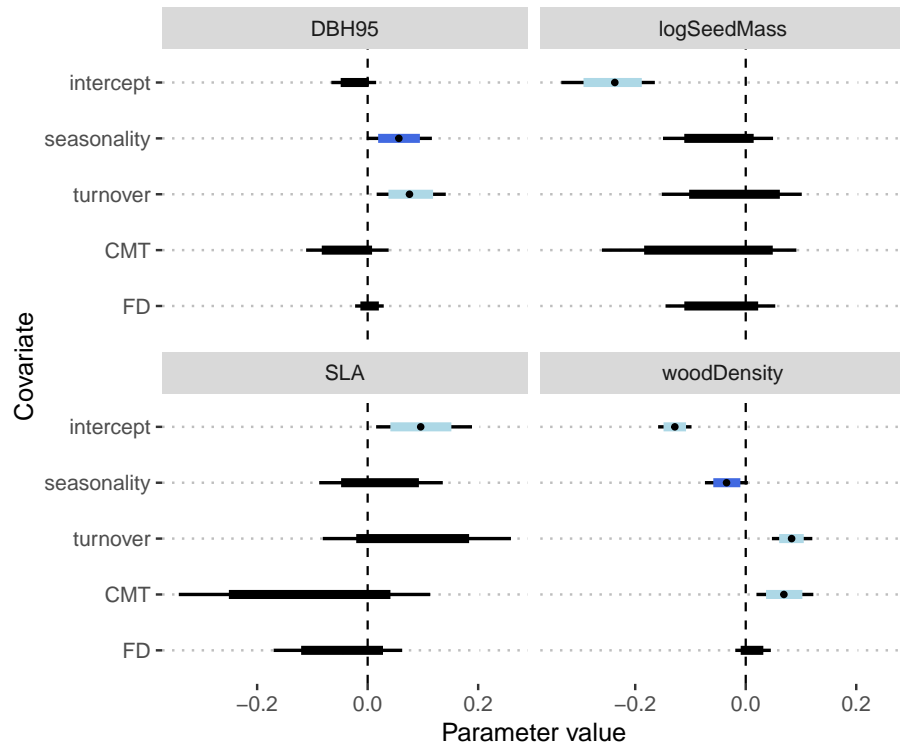


Figure 4: Covariates effect on maximum relative CMT change per trait. *intercept* is the value when all covariates are null; *seasonality* is the effect of the precipitation seasonality; *turnover* is the effect of the stem turnover rate; *CMT* is the effect of the initial community wbiomass-weighted mean trait; and *FD* is the effect of the initial functional diversity. Dots represent the median value, and the segments are the 95% confidence intervals. All covariates were scaled and centered. Colours indicate if zero is in the confidence interval: black when zero is in the 80% interval, dark blue when its in the 95% interval but not the 80% interval, and light blue when its in neither.

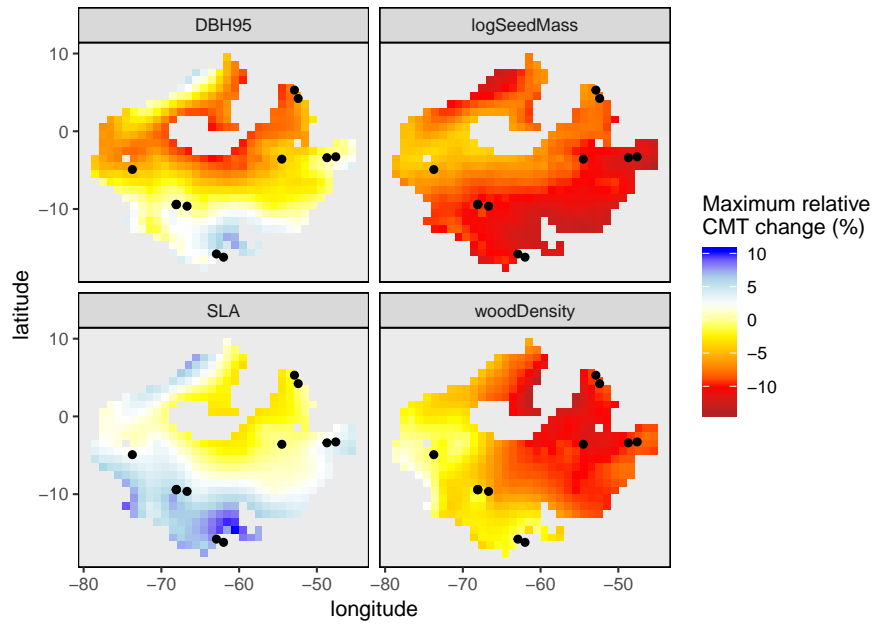


Figure 5: Prediction maps of maximum relative community mean trait (CMT) change (i.e. resistance to disturbance) by trait. Warm colors (from yellow to red) show a decreases in CMT; blue colors show an increase in CMT. Black dots are study sites location.

in northern regions of Amazonia (up to -rxx), and to increase slightly in the most southern regions of Amazonia (Figure 5a). Seed mass is predicted to strongly decrease everywhere in Amazonia after selective logging, and especially in southeastern regions (Figure 5b). SLA is predicted to increase, and in particular in southern Amazonia, except in northern regions where it is expected to decrease slightly (Figure 5c). Wood density is predicted to decrease everywhere in Amazonia after logging, and especially in northeastern and eastern Amazonia (Figure 5d).

Discussion

Model structure and limitations

This study presents, to our knowledge, the first explicit model of post-disturbance stand-level functional trajectory in tropical forests. This model describes two phases of the trajectory: first a change in the functional composition ($t_c \in [0, tmax]$) triggered by an increase light availability that favors fast-growing pioneer trees, and second a progressive return to initial functional composition ($t_c > tmax$) once the canopy gaps have closed and pioneer trees start to die. The advantage of this framework is that it relies on a small set of parameters to describe the trajectory, while accurately predicting observations (see supplementary figure ??). This makes the predictions more robust, limiting the risks of over-fitting. One other advantage is that results are easier to interpret. Δ (i.e. the maximum change in CMT) can be interpreted as the functional resistance of the forest to logging; $tmax$ is the time taken to reach this maximum change; θ is a non-dimensional rate of recovery : the higher the value of θ , the faster the return to the initial CMT value during the recovery phase ($t_c > tmax$). Together, these three parameters summarize the functional resilience to logging. This framework could be applied to describe and predict the resilience of ecosystems to other disturbance types.

One major problem of this study is the lack of long-term data that hampers our ability to correctly predict the long-term recovery of functional traits. The time to reach the maximum trait change (median value: 22 yr) is higher than the total experiment duration in several of our sites. The maximum trait change was therefore not always observed in the data, resulting in large uncertainties over the estimated parameters in our models (Figure 3). The hierarchical structure of our model can partially offset this lack of long-term data in some of our sites by integrating information from other sites where the information is available, but cannot replace real observations. One other issue with short experiment duration is that we cannot be sure that changes are not permanent and that functional traits will recover their initial value where this recovery has not been observed. This issue could be more serious with ongoing climate changes and increasing disturbance intensity that can cause a shift to another state of the forest and a new composition (Hirota et al. 2011, Johnstone et al. (2016)). Unfortunately, long-term permanent forest plots are scarce in the tropics, mainly because they are expensive to repeatedly re-census (Verburg and Eijk-Bos 2003). Investing

in long-term experiments (> 20 years) such as the forest plots used in this study will be extremely valuable to validate our results, and more generally to greatly improve the understanding of tropical forest resilience to disturbances and climate change.

In our framework we decided to use data only from trees < 35 cm to avoid interpreting the direct (and artificial) effects of tree selection on the functional composition. Nonetheless, trees > 35 cm dbh constitute on average 57 % of the biomass in our plots and have thus a large weight in forest functioning (e.g. carbon cycling refxx). In the supplementary material, we show plotted the trajectory of CMT for trees > 35 cm dbh (supplementary figure xxx). These trajectories were highly variable and showed no consistent pattern. [en rajouter? pas très convaincant xx]

Finally, there is a high uncertainty around functional trait estimation. To estimate the community's weighted mean trait, each individual was given a species-specific trait value (or the lowest taxonomic level available) retrieved from global databases (Kattge et al. 2011). High intra-specific variations in trait value have been observed (e.g. for SLA (Derroire et al. 2018)) due to local environmental conditions (e.g. soil or light environment), ontogeny, or differences in measurement protocols (e.g. SLA measured in leaves with or without the petiole and rachis). Tropical forests have high species richness, and extensive trait measurements are expensive, so for most species there are only a few (< 5) measurements of each trait in the database. This is a potential source of error in the data that is difficult to control for. We thus believe that overall trends provide some valuable information, but that individual plot trajectories should not be interpreted in too much detail.

A consistent functional response to logging disturbance

The changes in functional traits after logging are consistent with what has already been described in tropical forests. Community mean seed mass and wood density are the most affected by selective logging in our data (Figure 4): their decrease after a logging disturbance has been reported in previous studies (Poorter and Rose 2005, Verburg and Eijk-Bos (2003), Baraloto, Hérault, et al. (2012)) and correspond to specific strategies of the pioneer species that appear after a disturbance. It is interesting to note that across the Amazon biome, the response to logging relies on a small group of genres (*Cecropia* and *Inga* in northern and central Amazonia, *Urera* in southwestern Amazonia) that have developed a similar opportunist strategy to colonize logging gaps, that reflects on functional traits.

Seed mass is inversely correlated to the number of seeds that an individual can produce: small-seeded species can produce a lot of seeds that will easily be dispersed by wind, but that have a lower tolerance for shady and generally resource-limited environments during the establishment phase (Muller-Landau 2010). Small-seeded species usually develop an opportunistic strategy by being able to spread dormant seeds efficiently that germinate in high-light environments such as logging gaps where they are highly competitive (Poorter and Rose 2005).

This explains the sharp decrease in mean seed mass observed in most of our plots after logging.

The increase in the abundance of light-wooded species after logging is also consistent with results from previous studies (Verburg and Eijk-Bos 2003, Baraloto, Hérault, et al. (2012), Both et al. (2018)). The relationship between wood density and individual growth and mortality rates has been well established in tropical forests (Poorter et al. 2008, Chave et al. (2009)): light-wooded species grow and die faster, and are thus particularly competitive in environments with high resource availability. In most Amazonian forests the limiting resource is light (???), and light-wooded species are thus particularly competitive in logging gaps. The main exception in our data is the site INPA in southern Bolivia (Figure 1) where wood density is particularly high prior to logging and increases slightly after a logging disturbance (Figure 3). This may be explained by the fact that this site is located in a transitional forest that is particularly constrained by water rather than light availability (???). Because light-wooded species have a lower resistance to water stress (Aleixo et al. 2019), they may not be favored in such environmental conditions.

The observed increase in SLA can be interpreted as an increase in the light-acquisition potential (Wright et al. 2004). Species with high SLA can rapidly grow low-investment and efficient leaves in conditions of high light availability, which is typical of an opportunistic pioneer strategy and has already been described in other logged tropical forests (Both et al. 2018). In some sites the community mean SLA decreases after logging (e.g. La Chonta in Bolivia and Jenaro in Peru). This variability of post-logging SLA changes may be caused either by differences in species strategies or inconsistencies in SLA measures. Indeed, SLA has been shown to present high intraspecific variation (Derroire et al. 2018) and is particularly sensitive to ontogeny and measurement protocols.

Community pre-logging characteristics explain little of the functional resistance to logging

Contrary to expectations, the initial CMT and functional diversity had little to no effect on the functional resistance to a logging disturbance (Figure 4). The only exception is the effect of the initial community weighted wood density (Figure 4d), but even this effect might be overestimated: in fact, when the model is calibrated only with the initial CMT and functional diversity as covariates (no turnover rate nor precipitation seasonality), there is no significant covariate effect (see supplementary material xxx). These results are particularly surprising if compared to ecological theory (Oliver et al. 2015,(???)) and previous studies showing that the pre-disturbance functional composition affects post-disturbance ecosystem dynamics (Bernhardt-Römermann et al. 2011,(???)).

[explanations? not enough precision to detect the effect of initial composition? so why do we detect the effect of spatially-explicit variables?]

Functional response to logging is spatially structured in Amazonian forests

Precipitation seasonality has only a relatively weak effect on the functional resistance of tree stature (*DBH95*) and wood density to logging (Figure 4). [other

studies? expectations? xx] Stem turnover rate has a much stronger effect on the response of those two traits to logging. For both traits, the median intercept is negative and the effect of the stem turnover rate is positive. This means that forests with high turnover rates show lower decreases in wood density and tree stature after logging. In other terms, forests with high turnover rates seem to be more functionally resistant to logging. Stem turnover rates are a proxy of natural disturbance regimes: forests with high turnover rates have a history of natural disturbances, that may have selected for species adapted to disturbances, thus explaining the higher resistance to a logging disturbance (Johnstone et al. 2016).

-> wood density and stem turnover (Fauset et al. 2019)

Even though the SLA is expected to increase (Figure 4), the predicted variations in Amazonia are limited (Figure 5c). In contrast, the seed mass is expected to decrease sharply after logging (Figure 4 and 5b), as well as tree stature and wood density in northern and western Amazonian forests (Figure 5).

-> vulnerability of wood density in highly seasonal forests (+more exposure to climate change and disturbances in SE Amazonia)

Conclusion

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Supplementary material

TmFO sites: covariates values

Parameters priors

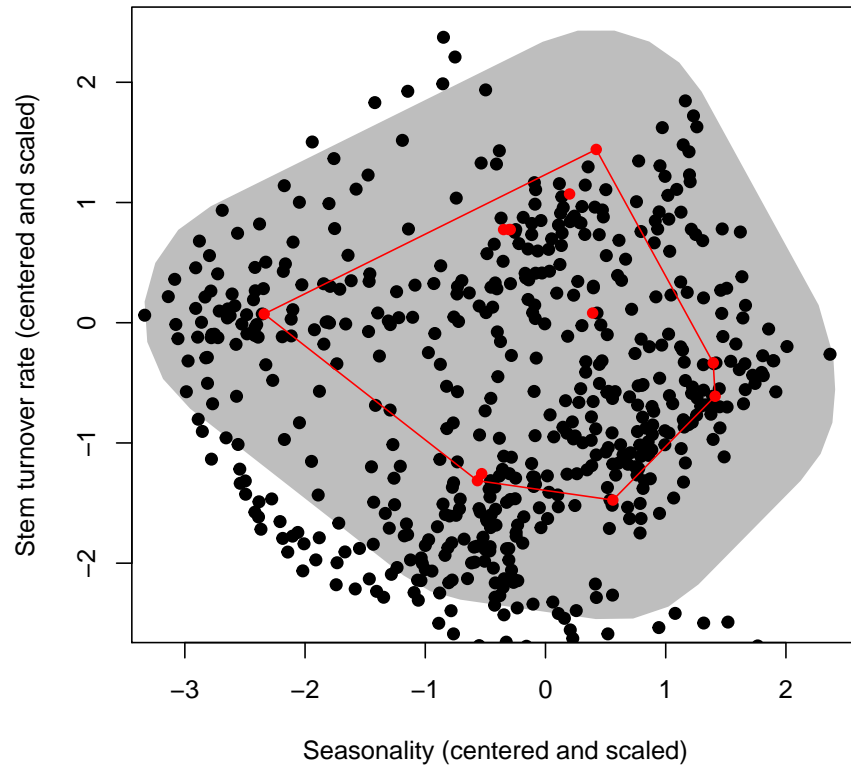
Choice of pixels on prediction maps

goal: represent only pixels that have covariates values close enough to our range of calibration (i.e. TmFO sites conditions).

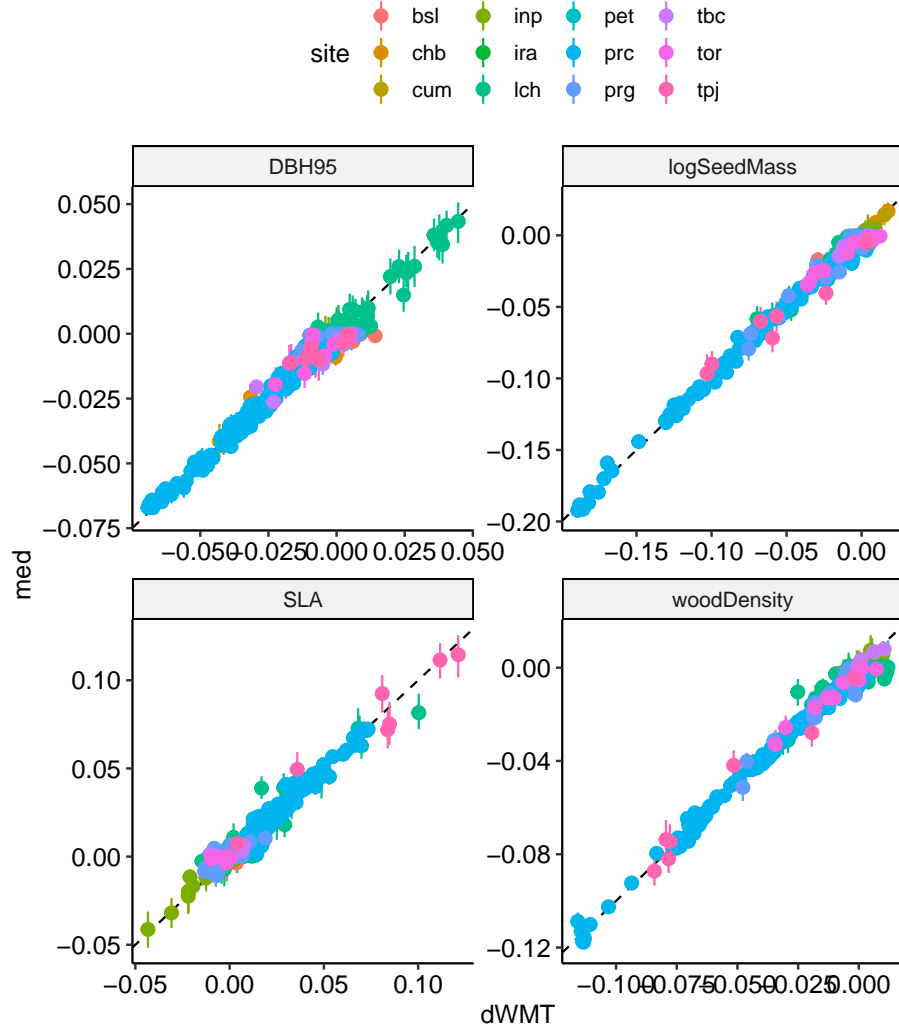
Table 1: Summary table of sites' location and covariates value.

| Site | Longitude | Latitude | Precipitation seasonality (%) | Stem turnover rate (%) |
|-------------|-----------|----------|-------------------------------|------------------------|
| Jenaro | -73.73 | -4.92 | 23 | 2.26 |
| Chico Bocão | -68.10 | -9.44 | 51 | 2.59 |
| Cumaru | -68.09 | -9.39 | 52 | 2.59 |
| INPA | -62.00 | -16.20 | 59 | 2.73 |
| Iracema | -66.69 | -9.64 | 62 | 2.26 |
| La Chonta | -62.92 | -15.78 | 62 | 2.91 |
| Peteco | -48.70 | -3.40 | 77 | 1.93 |
| Paracou | -52.88 | 5.30 | 49 | 1.63 |
| Paragominas | -47.57 | -3.28 | 76 | 2.06 |
| Tabocal | -68.05 | -9.41 | 52 | 2.59 |
| Tortue | -52.40 | 4.22 | 48 | 1.60 |
| Tapajos | -54.50 | -3.58 | 64 | 1.52 |

Scaled covariates -> convex hull around TmFO sites values -> buffer of 1 (scaled: equivalent to 1 standard deviation) -> all points outside this buffer were removed.



Goodness of predictions



Predictions

Large trees' CMT trajectories

Here we tested the effect of removing one site on final parameter posteriors. All sites were removed sequentially and the model was re-calibrated with this new subset of the original data. Covariates effects (intercept, *seas*: seasonality of precipitations and *smort*: stem turnover rate) are reported for each site removal (y axis), for each trait.

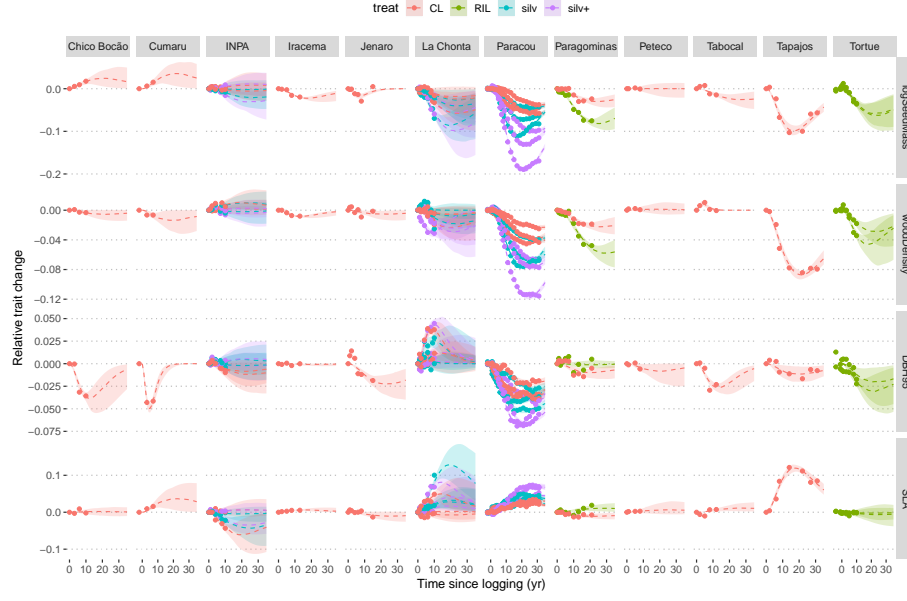


Figure 6: Observed values against trajectories of CMT predicted with our model.

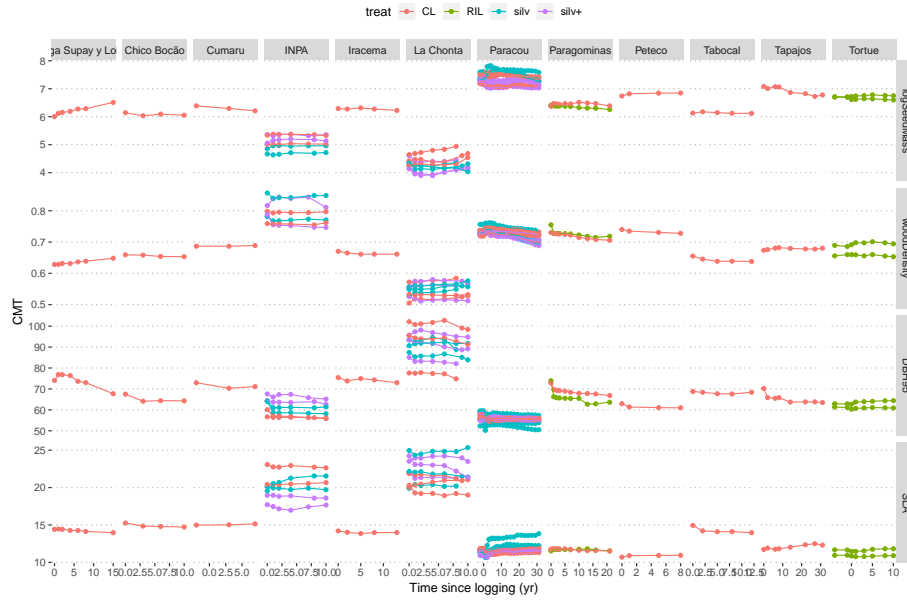
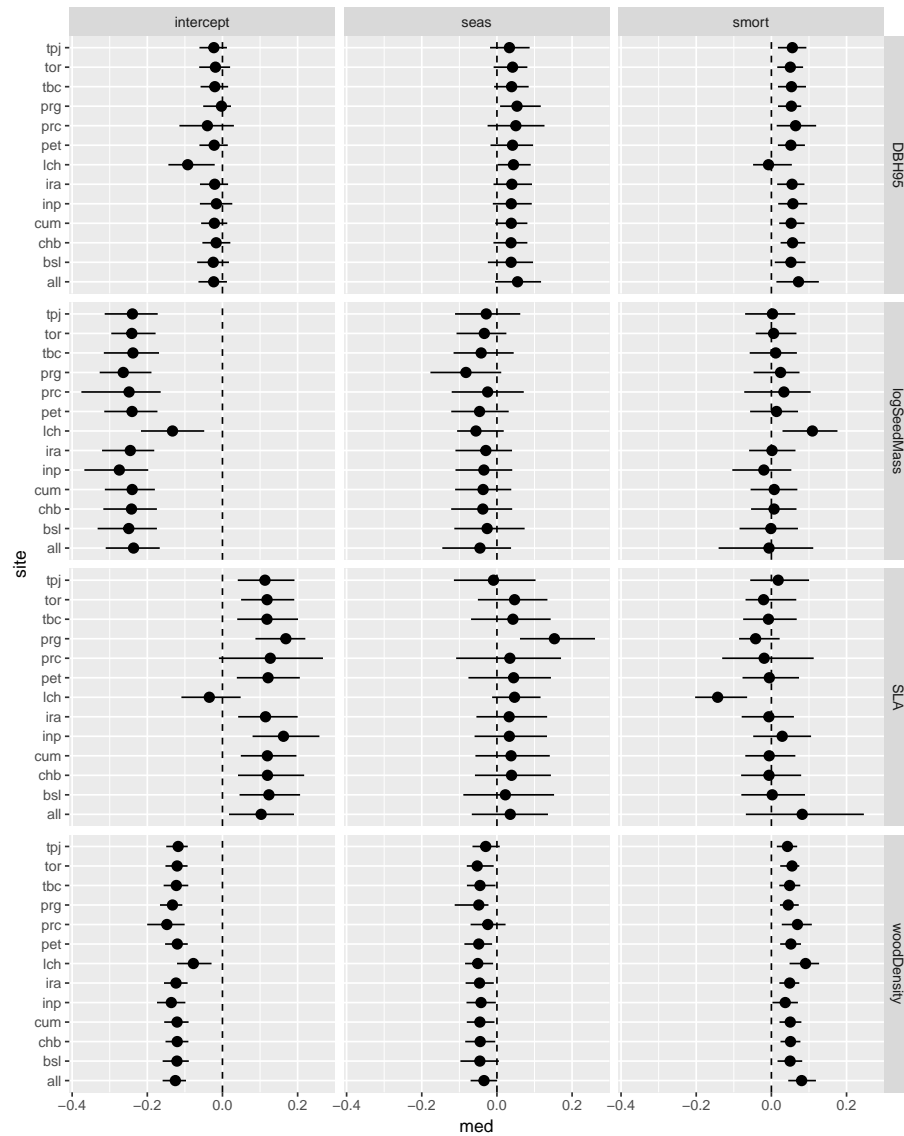


Figure 7: Observed CMT trajectories of large trees (> 35 cm dbh).



References

Aleixo, Izabela, Darren Norris, Lia Hemerik, Antenor Barbosa, Eduardo Prata, Flávia Costa, and Lourens Poorter. 2019. "Amazonian rainforest tree mortality driven by climate and functional traits." *Nature Climate Change*. doi:10.1038/s41558-019-0458-0.

Antonelli, Alexandre, Alexander Zizka, Fernanda Antunes Carvalho, Ruud Scharn, Christine D. Bacon, Daniele Silvestro, and Fabien L. Condamine. 2018.

“Amazonia is the primary source of Neotropical biodiversity.” *Proceedings of the National Academy of Sciences* 115 (23): 6034–9. doi:10.1073/pnas.1713819115.

Asner, Gregory P., Michael Keller, and JNM Silva. 2004. “Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon.” *Global Change Biology* 10 (5): 765–83. doi:10.1111/j.1529-8817.2003.00756.x.

Asner, Gregory P., Thomas K. Rudel, T. Mitchell Aide, Ruth Defries, and Ruth Emerson. 2009. “A contemporary assessment of change in humid tropical forests.” *Conservation Biology* 23 (6): 1386–95. doi:10.1111/j.1523-1739.2009.01333.x.

Avila, Angela Luciana de, Ademir Roberto Ruschel, João Olegário Pereira de Carvalho, Lucas Mazzei, José Natalino Macedo Silva, José do Carmo Lopes, Maristela Machado Araujo, Carsten F. Dormann, and Jürgen Bauhus. 2015. “Medium-term dynamics of tree species composition in response to silvicultural intervention intensities in a tropical rain forest.” *Biological Conservation* 191. Elsevier B.V.: 577–86. doi:10.1016/j.biocon.2015.08.004.

Baccini, a., S. J. Goetz, W. S. Walker, N. T. Laporte, M. Sun, D. Sulla-Menashe, J. Hackler, et al. 2012. “Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps.” *Nature Climate Change* 2 (3). Nature Publishing Group: 182–85. doi:10.1038/nclimate1354.

Baker, Timothy R., Dilys M. Vela Díaz, Victor Chama Moscoso, Gilberto Navarro, Abel Monteagudo, Ruy Pinto, Katia Cangani, et al. 2016. “Consistent, small effects of treefall disturbances on the composition and diversity of four Amazonian forests.” *Journal of Ecology*. doi:10.1111/1365-2745.12529.

Baraloto, Christopher, Olivier J Hardy, C E Timothy Paine, Kyle G Dexter, Corinne Cruaud, Luke T Dunning, Mailyn-Adriana Gonzalez, et al. 2012. “Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities.” *Journal of Ecology* 100 (3): 690–701. doi:10.1111/j.1365-2745.2012.01966.x.

Baraloto, Christopher, Bruno Hérault, C. E Timothy Paine, Hélène Massot, Lilian Blanc, Damien Bonal, Jean-François François Molino, Eric A. Nicolini, and Daniel Sabatier. 2012. “Contrasting taxonomic and functional responses of a tropical tree community to selective logging.” *Journal of Applied Ecology* 49 (4): 861–70. doi:10.1111/j.1365-2664.2012.02164.x.

Bernhardt-Römermann, Markus, Alan Gray, Adam J. Vanbergen, Laurent Bergès, Andreas Bohner, Rob W. Brooker, Luc De Bruyn, et al. 2011. “Functional traits and local environment predict vegetation responses to disturbance: A pan-European multi-site experiment.” *Journal of Ecology* 99 (3): 777–87. doi:10.1111/j.1365-2745.2011.01794.x.

Blaser, Juergen, Alastair Sarre, Duncan Poore, and Steven Johnson. 2011. “Status of Tropical Forest Management 2011.” Vol. 38. http://www.itto.int/news/{_}releases/id=2663.

Both, Sabine, Terhi Riutta, C. E. Timothy Paine, Dafydd M. O. Elias, R. S. Cruz, Annuar Jain, David Johnson, et al. 2018. “Logging and soil nutrients independently explain plant trait expression in tropical forests.” *New Phytologist*, September. doi:10.1111/nph.15444.

Brando, Paulo M., Daniel C. Nepstad, Jennifer K. Balch, Benjamin Bolker,

- Mary C. Christman, Michael Coe, and Francis E. Putz. 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 (2): 630–41. doi:10.1111/j.1365-2486.2011.02533.x.
- Cannon, Chuck H, David R Peart, Mark Leighton, Kuswata Kartawinata, Mark Leighton, and R Peart David. 1994. “The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia.” *Forest Ecology and Management* 67 (1-3): 49–68. doi:10.1016/0378-1127(94)90007-8.
- Carpenter, Bob, Andrew Gelman, Matthew D. Hoffman, Daniel Lee, Ben Goodrich, Michael Betancourt, Marcus Brubaker, Jiqiang Guo, Peter Li, and Allen Riddell. 2017. “Stan : A Probabilistic Programming Language.” *Journal of Statistical Software* 76 (1). doi:10.18637/jss.v076.i01.
- Carreño-Rocabado, Geovana, Marielos Peña-Claros, Frans Bongers, Alfredo Alarcón, Juan Carlos Licona, and Lourens Poorter. 2012. “Effects of disturbance intensity on species and functional diversity in a tropical forest.” *Journal of Ecology* 100 (6): 1453–63. doi:10.1111/j.1365-2745.2012.02015.x.
- Chapin III, F. S., F S Chapin, B H Walker, R J Hobbs, D U Hooper, J H Lawton, O E Sala, and D Tilman. 1997. “Biotic control over the functioning of ecosystems.” *Science* 277 (5325): 500–504. doi:10.1126/science.277.5325.500.
- Chave, Jerome, David Coomes, Steven Jansen, Simon L Lewis, Nathan G Swenson, and Amy E Zanne. 2009. “Towards a worldwide wood economics spectrum.” *Ecology Letters* 12: 351–66. doi:10.1111/j.1461-0248.2009.01285.x.
- Cierner, Catrin, Niklas Boers, Marina Hirota, Jürgen Kurths, Finn Müller-Hansen, Rafael S. Oliveira, and Ricarda Winkelmann. 2019. “Higher resilience to climatic disturbances in tropical vegetation exposed to more variable rainfall.” *Nature Geoscience* 12 (March). Springer US. doi:10.1038/s41561-019-0312-z.
- Costa-Saura, José M., Antonio Trabucco, Donatella Spano, and Simone Mereu. 2019. “A height-wood-seed axis which is preserved across climatic regions explains tree dominance in European forest communities.” *Plant Ecology* 0123456789. doi:10.1007/s11258-019-00928-x.
- Crutzen, Paul J. 2002. “Geology of mankind.” *Nature* 415 (6867): 23. doi:10.1038/415023a.
- Davidson, Eric a., Alessandro C. de Araújo, Paulo Artaxo, Jennifer K. Balch, I. Foster Brown, Mercedes M. C. Bustamante, Michael T. Coe, et al. 2012. “The Amazon basin in transition.” *Nature* 481 (7381): 321–28. doi:10.1038/nature10717.
- Derroire, Géraldine, Jennifer S. Powers, Catherine M. Hulshof, Luis E. Cárdenas Varela, and John R. Healey. 2018. “Contrasting patterns of leaf trait variation among and within species during tropical dry forest succession in Costa Rica.” *Scientific Reports* 8 (1): 1–11. doi:10.1038/s41598-017-18525-1.
- Espírito-Santo, Fernando D.B., Manuel Gloor, Michael Keller, Yadvinder Malhi, Sassan Saatchi, Bruce Nelson, Raimundo C Oliveira Junior, et al. 2014. “Size and frequency of natural forest disturbances and the Amazon forest carbon balance.” *Nature Communications* 5 (March): 3434. doi:10.1038/ncomms4434.
- Fauset, Sophie, Manuel Gloor, Nikolaos M. Fyllas, Oliver L. Phillips, Gregory P. Asner, Timothy R. Baker, Lisa Patrick Bentley, et al. 2019. “Individual-

Based Modeling of Amazon Forests Suggests That Climate Controls Productivity While Traits Control Demography.” *Frontiers in Earth Science* 7 (April). doi:10.3389/feart.2019.00083.

Fick, Stephen E, and Robert J Hijmans. 2017. “WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas.” *International Journal of Climatology* 4315 (May): 4302–15. doi:10.1002/joc.5086.

Hirota, M., M. Holmgren, E. H. Van Nes, and M. Scheffer. 2011. “Global Resilience of Tropical Forest and Savanna to Critical Transitions.” *Science* 334 (6053): 232–35. doi:10.1126/science.1210657.

Hodgson, Dave, Jenni L. McDonald, and David J. Hosken. 2015. “What do you mean, ‘resilient’?” *Trends in Ecology and Evolution* 30 (9). Elsevier Ltd: 503–6. doi:10.1016/j.tree.2015.06.010.

Holling, C S. 1973. “Resilience and Stability of Ecological Systems.” *Annual Review of Ecology and Systematics* 4 (1): 1–23. doi:10.1146/annurev.es.04.110173.000245.

IPCC. 2014. *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. New York, NY.

Jenkins, C. N., S. L. Pimm, and L. N. Joppa. 2013. “Global patterns of terrestrial vertebrate diversity and conservation.” *Proceedings of the National Academy of Sciences* 110 (28): E2602–E2610. doi:10.1073/pnas.1302251110.

Johnson, Daniel J., Jessica Needham, Chonggang Xu, Elias C. Massoud, Stuart J. Davies, Kristina J. Anderson-Teixeira, Sarayudh Bunyavejchewin, et al. 2018. “Climate sensitive size-dependent survival in tropical trees.” *Nature Ecology and Evolution* 2 (9): 1436–42. doi:10.1038/s41559-018-0626-z.

Johnson, Michelle O., David Galbraith, Manuel Gloor, Hannes De Deurwaerder, Matthieu Guimberteau, Anja Rammig, Kirsten Thonicke, et al. 2016. “Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: implications for dynamic global vegetation models.” *Global Change Biology* 22 (12): 3996–4013. doi:10.1111/gcb.13315.

Johnstone, Jill F., Craig D. Allen, Jerry F. Franklin, Lee E. Frelich, Brian J. Harvey, Philip E. Higuera, Michelle C. Mack, et al. 2016. “Changing disturbance regimes, ecological memory, and forest resilience.” *Frontiers in Ecology and the Environment* 14 (7): 369–78. doi:10.1002/fee.1311.

Kattge, J., S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönsch, E. Garnier, et al. 2011. “TRY - a global database of plant traits.” *Global Change Biology* 17 (9): 2905–35. doi:10.1111/j.1365-2486.2011.02451.x.

Lavorel, Sandra, and Eric Garnier. 2002. “Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail.” *Functional Ecology* 16 (5): 545–56. doi:10.1046/j.1365-2435.2002.00664.x.

Lewis, Simon L, David P Edwards, and David Galbraith. 2015. “Increasing human dominance of tropical forests.” *Science* 349 (6250): 827–32. doi:10.1126/science.aaa9932.

Lopez-Gonzalez, Gabriela, Simon L Lewis, Mark Burkitt, and Oliver L Phillips. 2011. “ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data.” *Journal of Vegetation Science* 22 (4):

610–13. doi:10.1111/j.1654-1103.2011.01312.x.

Malhi, Yadvinder, Toby A. Gardner, Gregory R. Goldsmith, Miles R. Silman, and Przemyslaw Zelazowski. 2014. “Tropical Forests in the Anthropocene.” *Annual Review of Environment and Resources* 39 (1): 125–59. doi:10.1146/annurev-environ-030713-155141.

Marcon, Eric, and Bruno Hérault. 2015. “entropart : An <i>R</i> Package to Measure and Partition Diversity.” *Journal of Statistical Software* 67 (8). doi:10.18637/jss.v067.i08.

Mcdowell, Nate, Craig D. Allen, Kristina Anderson-Teixeira, Paulo Brando, Roel Brien, Jeff Chambers, Brad Christoffersen, et al. 2018. “Drivers and mechanisms of tree mortality in moist tropical forests.” *New Phytologist*. doi:10.1111/nph.15027.

Muller-Landau, H. C. 2010. “The tolerance-fecundity trade-off and the maintenance of diversity in seed size.” *Proceedings of the National Academy of Sciences* 107 (9): 4242–7. doi:10.1073/pnas.0911637107.

Negrón-Juárez, R.I., JA Holm, D Magnabosco Marra, SW Rifai, WJ Riley, JQ Chambers, CD Koven, et al. 2018. “Vulnerability of Amazon forests to storm-driven tree mortality.” *Environmental Research Letters* 13: 054021. doi:10.1088/1748-9326/aabe9f.

Oliver, Tom H., Matthew S. Heard, Nick J B Isaac, David B. Roy, Deborah Procter, Felix Eigenbrod, Rob Freckleton, et al. 2015. “Biodiversity and Resilience of Ecosystem Functions.” *Trends in Ecology & Evolution* 30 (11). Elsevier Ltd: 673–84. doi:10.1016/j.tree.2015.08.009.

Pan, Yude, Richard a Birdsey, Jingyun Fang, Richard Houghton, Pekka E Kauppi, Werner a Kurz, Oliver L Phillips, et al. 2011. “A large and persistent carbon sink in the world’s forests.” *Science (New York, N.Y.)* 333: 988–93. doi:10.1126/science.1201609.

Pebesma, E.J. 2004. “Multivariable geostatistics in S: the gstat package.” *Computers & Geosciences* 30: 683–91.

Pereira, Rodrigo, Johan Zweede, Gregory P Asner, and Michael Keller. 2002. “Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para , Brazil.” *Forest Ecology and Management* 168: 77–89. doi:10.1016/S0378-1127(01)00732-0.

Phillips, Oliver L., Geertje van der Heijden, Simon L. Lewis, Gabriela López-González, Luiz E O C Aragão, Jon Lloyd, Yadvinder Malhi, et al. 2010. “Drought-mortality relationships for tropical forests.” *New Phytologist* 187 (3): 631–46. doi:10.1111/j.1469-8137.2010.03359.x.

Piponiot, Camille, Antoine Cabon, Laurent Descroix, Aurélie Dourdain, Lucas Mazzei, Benjamin Ouliac, Ervan Rutishauser, Plinio Sist, and Bruno Hérault. 2016. “A methodological framework to assess the carbon balance of tropical managed forests.” *Carbon Balance and Management* 11 (1). Springer International Publishing: 15. doi:10.1186/s13021-016-0056-7.

Piponiot, Camille, Edna Rödig, Francis E Putz, Ervan Rutishauser, Plinio Sist, Nataly Ascarrunz, Lilian Blanc, et al. 2019. “Can timber provision from Amazonian production forests be sustainable?” *Environmental Research Letters*

14 (6). IOP Publishing: 064014. doi:10.1088/1748-9326/ab195e.

Poorter, L, F Bongers, F J Sterck, and H Wöll. 2003. "Architecture of 53 rain forest tree species differing in adult stature and shade tolerance." *Ecology* 84 (3): 602–8. [http://www.esajournals.org/doi/abs/10.1890/0012-9658\(2003\)084\[0602:AORFTS\]2.0.CO;2](http://www.esajournals.org/doi/abs/10.1890/0012-9658(2003)084[0602:AORFTS]2.0.CO;2).

Poorter, L, S J Wright, H Paz, D D Ackerly, R Condit, G Ibarra-Manriquez, K E Harms, et al. 2008. "Are functional traits good predictors of demographic rates? Evidence from five neotropical forests." *Ecology* 89 (7): 1908–20. doi:10.1890/07-0207.1.

Poorter, Lourens, and Simmoné A. Rose. 2005. "Light-dependent changes in the relationship between seed mass and seedling traits: A meta-analysis for rain forest tree species." *Oecologia* 142 (3): 378–87. doi:10.1007/s00442-004-1732-y.

Poorter, Lourens, Danaë M. A. Rozendaal, Frans Bongers, Jarcilene S. de Almeida-Cortez, Angélica María Almeyda Zambrano, Francisco S. Álvarez, José Luís Andrade, et al. 2019. "Wet and dry tropical forests show opposite successional pathways in wood density but converge over time." *Nature Ecology & Evolution*. doi:10.1038/s41559-019-0882-6.

Quesada, C. a., O. L. Phillips, M. Schwarz, C. I. Czimczik, T. R. Baker, S. Patiño, N. M. Fyllas, et al. 2012. "Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate." *Biogeosciences* 9 (6): 2203–46. doi:10.5194/bg-9-2203-2012.

R Development Core Team. 2018. "R: A Language and Environment for Statistical Computing." *R Foundation for Statistical Computing*, Lecture notes in physics,. Berlin, Heidelberg: Springer Berlin Heidelberg. doi:10.1007/978-3-540-74686-7.

Réjou-Méchain, Maxime, Ariane Tanguy, Camille Piponiot, Jérôme Chave, and Bruno Hérault. n.d. "BIOMASS: An R Package for estimating above-ground biomass and its uncertainty in tropical forests." *Methods in Ecology and Evolution*.

Rutishauser, Ervan, Bruno Hérault, Pascal Petronelli, and Plinio Sist. 2016. "Tree Height Reduction After Selective Logging in a Tropical Forest." *Biotropica* 48 (3): 285–89. doi:10.1111/btp.12326.

Sist, Plinio, Ervan Rutishauser, Marielos Peña-Claros, Alexander Shenkin, Bruno Hérault, Lilian Blanc, Christopher Baraloto, et al. 2015. "The Tropical managed Forests Observatory: A research network addressing the future of tropical logged forests." *Applied Vegetation Science* 18: 171–74. doi:10.1111/avsc.12125.

Slik, J W Ferry, Víctor Arroyo-Rodríguez, Shin-ichiro Aiba, Patricia Alvarez-Loayza, Luciana F Alves, Peter Ashton, Patricia Balvanera, et al. 2015. "An estimate of the number of tropical tree species." *Proceedings of the National Academy of Sciences* 112 (24). doi:10.1073/pnas.1423147112.

Staal, Arie, Obbe A. Tuinenburg, Joyce H. C. Bosmans, Milena Holmgren, Egbert H. van Nes, Marten Scheffer, Delphine Clara Zemp, and Stefan C. Dekker. 2018. "Forest-rainfall cascades buffer against drought across the Amazon." *Nature Climate Change* 8 (June). Springer US: 1. doi:10.1038/s41558-018-0177-y.

Ter Steege, Hans, Nigel C a Pitman, Daniel Sabatier, Christopher Baraloto, R. P. Salomao, Juan Ernesto Guevara, O. L. Phillips, et al. 2013. "Hyper-

dominance in the Amazonian Tree Flora.” *Science* 342 (6156): 1243092–2. doi:10.1126/science.1243092.

Verburg, René, and Clara van Eijk-Bos. 2003. “Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest.” *Journal of Vegetation Science* 14 (1): 99–110. doi:10.1111/j.1654-1103.2003.tb02132.x.

Violle, Cyrille, Marie-laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène Hummel, and Eric Garnier. 2007. “Let the concept of trait be functional!” *Oikos* 116 (5): 882–92. doi:10.1111/j.2007.0030-1299.15559.x.

Wright, Ian J., Peter B. Reich, Mark Westoby, David D. Ackerly, Zdravko Baruch, Frans Bongers, Jeannine Cavender-Bares, et al. 2004. “The worldwide leaf economics spectrum.” *Nature* 428 (6985): 821–27. doi:10.1038/nature02403.

Wright, S. Joseph. 2005. “Tropical forests in a changing environment.” *Trends in Ecology and Evolution* 20 (10): 553–60. doi:10.1016/j.tree.2005.07.009.

Zanne, A. E., G. Lopez-Gonzalez, D.A. A Coomes, J. Ilic, S. Jansen, Simon L S.L. Lewis, R.B. B Miller, N.G. G Swenson, M.C. C Wiemann, and Jerome Chave. 2009. “Global wood density database.” Vol. 235. doi:10.5061/dryad.234.