Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract
Understand the maintenance of forests biodiversity structure, functioning and dynamics is urgent to anticipate their fate in the global changing context. Communities diversity structure is assumed to rely on a constant regime of disturbance and peak at intermediate intensity. For tropical forests this intermediate disturbance hypothesis (IDH) remain debated as well as the completeness of forests resilience in all taxonomic and functoinal facets. To disentangle the ecological processes driving forests dynamics we examined the the trajectories over 30 years after a gradient of logging and thinning disturbance, focusing on communities taxonomic and functional composition and diversity. Specifically we analysed the trajectories of communities taxonomic richness and evennes and functional composition, diversity and redundancy based on 7 key functional traits assessing species ecology. We highlighted a decoupling between functional and taxonomic trajectories, translating a fast recovery of communities functioning while their taxonomic recovery was slowed by the recruitment of infrequent species specific to mature forests. The IDH consistently predicted communities functional trajectories but poorly reflected the taxonomic ones, blurried by changes in the functional redundancy entailing competitive exclusion. Although communities consistently recovered their functioning after 30 years, initially infrequent species proved long to recover which impacted the taxonomic structure and functoinal redundancy over several decades. Our results acknowledged the need of decades-long recovery cycles to restore the resilience of the community and prevent species loss in the long term.

Keywords
Taxonomic and Functional Biodiversity, Neotropical Forests, Disturbance Trajectories, Intermediate Disturbance Hypothesis, Long-term Resilience

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1. Introduction

The large areas covered with tropical forests worldwide hold crucial environmental, economic and social values. They provide wood and multiple non-timber forest products, shelter a diversified fauna, regulate the local climate, support the carbon, water and nutrient cycles, and ensure cultural and human well-being. The simultaneous increased demand in forests products and the substantial climatic changes currently heighten the pressure on remaining forests (Gibson *et al.*, 2011; Morales-Hidalgo *et al.*, 2015), threatening the maintenance of communities structure, composition and functioning and their dynamics in space and time (Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015).

In tropical forest, ecological communities are constantly re-shaped by natural disturbance events that change both abiotic environment, through the fluxes of light, heat and water (Goulamoussène *et al.*, 2017), and biotic interactions like competition among species (Hérault & Piponiot, 2018). The cornerstone of tropical forests ecology is to understand the mechanisms and the determinants of ecosystems response to disturbance (White & Jentsch, 2001; Chazdon, 2003).

For now, this has been largely studied through structural parameters, rapid and convenient to measure, as above-ground biomass, tree height or stem density (Piponiot *et al.*, 2016; Rutishauser *et al.*, 2016). These structural parameters were thereafter sucessfully modeled, giving important insights into the maintenance of ecosystems processes and services (Denslow & Guzman, 2000; Blanc *et al.*, 2009). However the response of forests diversity in tree species remains unclear, albeit it determines the productivity, stability and functioning of ecosystems (Tilman *et al.*, 2014, Liang *et al.* (2016)) and would be most probably impacted by the changes following disturbance (Baraloto *et al.*, 2012).

In the short-term disturbance demonstrated negligible or even positive impacts on communities diversity, which have been formalized by the intermediate disturbance hypothesis (IDH) stating a maximized species diversity at intermediate disturbance intensity (Molino & Sabatier, 2001; Kariuki *et al.*, 2006; Berry *et al.*, 2008). Still, validations of the IDH remain scarce in the long term and mainly rely on species richness analyses that give limited or misleading information on forests recovery and functioning (Martin *et al.*, 2015; Chaudhary *et al.*, 2016). More releveant monitoring would encompass communities composition, crucial for conservation issues, and complete diversity profiles integrating both species richness and evenness, to reveal the ecological rules structuring communities (Magurran, 1988; Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Furthermore, the functional approach that accounts for species biological attributes and role in the ecosystem would be essential to understand the correlations between ecosystems biodiversity, functioning and environmental constraints (Violle *et al.*, 2007; Moretti *et al.*, 2009; Baraloto *et al.*, 2012; Scheiter *et al.*, 2013). The functional trait-based approach focused on major traits related to species ecology and performance was sucessfully adopted (Díaz *et al.*, 2005; Villéger *et al.*, 2008), for example in highlighting deterministic processes in tropical rainforests that foster fast growing species with efficient resources acquisition after disturbance (Molino & Sabatier, 2001; Haddad *et al.*, 2008; Rüger *et al.*, 2009). Communities then shifted from a dominance of "conservative" slow-growing species dealing with scarce resources to "acquisitive" fast-growing species with rapid and efficient use of abundant resources (TerSteege & Hammond, 2001; Reich, 2014; Hérault *et al.*, 2011). This shift translated into consistent trajectories for key functional traits related to resource acquisition (leaf area, density and chlorophyll content, and stem specific gravity and bark thickness), tree growth and reproduction and life history traits (seed mass and maximum height) (Wright *et al.*, 2004; Westoby & Wright, 2006; Chave *et al.*, 2009).

A combination of taxonomic and functional approaches are essential to fully assess communities response to disturbance and differences in their respective trajectories are insightful of underlying mechanisms (Lohbeck *et al.*, 2015; Guariguata & Ostertag, 2001). Although taxonomic and functional diversity are complementary and sometimes decouples, they are combined in the measure of communities functional redundancy that quantifies the amount of shared trait values among species (Carmona *et al.*, 2016). Func-tional redundancy is determinant of communities resilience as high redundancy, like in highly diverse tropical forests (Bellwood *et al.*, 2006), mitigates the impacts of species removal on ecosystem functioning (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

Grasp all facets of communities response to disturbance comes to examine the taxonomic and functional trajectories in diversity and composition. These trajectories would highlight the ecological rules constraining or not communities dynamics towards the recovery of initial composition, diversity and functioning. They would therefore clarify the tenants in the long term of the debated Intermediate Disturbance Hypothesis for tropical forests, a cruicial point for future adaptive conservation strategies (Adler *et al.*, 2007). Here we monitored over 30 years the response of 75 ha of forests plots set up on a gradient of disturbance intensity, from 10 to 60% of ecosystem biomass removed. We made use of a large functional traits database browsing major leaf, stem and seed functional traits and species maximum height to draw the trajectories over time of communities taxonomic and functional composition and diversity. Specifically, we (i) questioned the coupling between taxonomic and functional response to disturbance and identified the underlying assembly processes, which allowed to (ii) clarify the validity of the IDH in the long term for tropical forest and (iii) question the completeness of communities recovery regarding their functional redundancy.

2. Material and Methods

2.1 Study site

Paracou station in French Guiana (5°18'N and 52°53'W) is located in a lowland tropical rain forest in a tropical wet climate with mean annual temperature of 26°C, mean annual precipitation averaging 2980 mm.y^{-1} (30-y period) and a 3-month dry season (< 100 mm.month^{-1}) from mid-August to mid-November, and a one-month dry season in March (Wagner *et al.*, 2011). Elevation ranges between 5 and 50 m and soils correspond to thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains.

The experiment is a network of twelve 6.25ha plots that underwent a gradient of three logging, thinning and fuel-wood cutting treatments (Table 1). Disturbance treatments were attributed according to a randomized plot design with three replicate blocks of four plots. The disturbance corresponds to averages of 10 trees removed per hectare with a diameter at 1.3 m height (DBH) above 50 cm for treatment 1 (T1), 32 trees/ha above 40 cm DBH for treatment 2 (T2) and 40 trees/ha above 40 cm DBH for treatment 3 (T3). Treatments T2 and T3 besides included the thinning of trees by poison girdling (Schmitt & Bariteau, 1989; Blanc *et al.*, 2009). The disturbance intensity was measured as the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984 and five years after disturbance (ref to be found) measured with the BIOMASS R package (Réjou-Méchain *et al.*, 2018).

Table 1. Intervention table, summary of the disturbance intensity for the 4 plot treatments in Paracou.

Treatment	Timber	Thinning	Fuelwood	%AGB lost
Control				0
T1	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha			$[12\% - 33\%]$
T2	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha	DBH $\geq$ 40 cm, non-valuable species, $\approx$ 30 trees/ha		$[33\% - 56\%]$
T3	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha	DBH $\geq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha	40 cm $\leq$ DBH $\leq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha	$[35\% - 66\%]$

2.2 Inventories protocol and dataset collection

The study site corresponds to a tropical rainforest with a dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae botanical families. In the twelve experimental plots of the experiment, all trees above 10 cm DBH are mapped and measured annually since 1984. Trees are first identified during inventories with a vernacular name assigned by the field team, and afterward with a scientific name assigned by a botanist during regular botanical campaigns. In 1984, specific vernacular names are given to 62 commercial or common species whereas more infrequent ones were identified under general identifiers only distinguiching trees and palm trees. From 2003 botanical campaigns were conducted every 5 to 6 years to identify all trees at the species level but identification practices still varied among plots and campaigns.

This variability of protocols raised methodological issues as vernacular names usually correspond to different botanical species. It resulted in significant taxonomic uncertainties that had to be propagated to composition and diversity metrics. The uncertainty propagation was done through a Bayesian framework reconstituting complete inventories at genus level from real incomplete ones on the basis of vernacular/botanical names association. Vernacular names were replaced through multinomial trials $M_v\left([s_1, s_2, \ldots, s_N], [\alpha_1, \alpha_2, \ldots, \alpha_3]\right)$ based on the association probability $[\alpha_1, \alpha_2, \ldots, \alpha_3]$ observed across all inventories between each vernacular name v and the species $[s_1, s_2, \ldots, s_N]$. See appendix 1 and Aubry-Kientz *et al.* (2013) for the detailed methodology.

The functional approach used a dataset of 6 functional traits representing leaf economics (leaves thickness, toughness, total chlorophyll content and specific leaf area, the leaf area per unit dry mass) and wood economics (wood specific gravity and bark thickness), and life history traits (maximum specific height and seed mass). The trait database came from the BRIDGE project [1] where trait values were assessed from a selection of individuals located in nine permanent plots in French Guiana, including two in Paracou, and comprised 294 botanical species pertaining to 157 botanical genera.

[1] http://www.ecofog.gf/Bridge/

Missing trait values were filled using multivariate imputation by chained equation (mice) from the mice R package (van Buuren & Groothuis-Oudshoorn, 2011). Imputations were restricted within genus, or family when samples wre too scarce, in order to account for the phylogenetic signal of the functional traits. Whenever a species inventoried was not in the dataset, it was attributed a set of traits values randomly sampled among species of the same next higher taxonomic level (same genus or family). As seed mass information corresponds to a classification into mass classes, no data filling process was applied and analysis were restricted to the 414 botanical species recorded.

All composition and diversity metrics corresponded to the average obtained after 50 iterations of the taxonomic uncertainty propagation framework and of the filling process of missing trait values.

2.3 Composition and diversity metrics

To counter taxonomic uncertainties due to the variability of botanical identification protocols (see [#protocols]), the taxonomic composition and diversity analysis were conducted at the genus level, *i.e.* referring to the genus of observed or trialed botanical names. Trajectories of communities taxonomic and functional variations in composition after disturbance were followed in a two-dimensional ordination space the 30 years monitored. Two NMDS were conducted to map either taxonomic flora inventories or communities functional composition based on the 7 leaf, stem and life history traits (without seed mass classes). In both cases the NMDS were performed using occurrence-based (Jaccard) and abundance-based (Bray-Curtis) dissimilarity measures. Trajectories along time in the plan were reported through the euclidean distance of successive inventories to the reference inventories in 1989, 5 years after disturbance, when the uncertainty degree did not exceed 30% of undetermined trees. The trajectories of the leaf and stem and life traits were also visualized with the community weighted means (CWM), representing the average trait value in a community weighted by relative abundance of the species carrying each value (Díaz *et al.*, 2007; et al. Garnier, 2004). To compensate the intrinsinc difference among plots the trajectories

corresponded to the differences along time with the reference inventory in 1989. Species seed mass corresponded to 5 classes of increasing mass, seed mass trajectories were therefore reported as the proportion of each class in the inventories.

The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973). These three indices belong to the set of HCDT or generalized entropy, respectively corresponding to the 0, 1 and 2 order of diversity (q), recomended for diversity studies (Patil & C., 1982; Tothmeresz & Tóthmérész, 1995). The functional diversity was reported using the Rao index of quadratic entropy which combines species abundance distribution and average pairwise dissimilarity based on all functional and life traits.

The impacts of initial disturbance were first tested with the spearman rank correlation between the extremum of taxonomic and functional metrics reached over the 30 years and the initial %AGB removed. Then they were analysed through the linear correlations between Simpson and Rao diversities and the initial %AGB removed at 10, 20 and 30 years after disturbance.

The functional redundancy was measured as the overlap among species in communities' functional space (Carmona *et al.*, 2016). The samples of the trait database were first mapped in a 2-dimensional plan from a PCA analysis. Then, multivariate kernel density estimator associated with individual trees returned species traits probability distribution (TDP). Species TDP weighted by species abundance were eventually summed for each community: the functional redundancy was the sum of TDPs overlap, expressed as the average number of species that could be removed from without reducing the functional space (see appendix I for a more comprehensive sheme).

3. Results

3.1 Communities Diversity

In the inventories from 1989 (5 years after disturbance) to 2015 (31 years after disturbance), 828388 trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. Communities taxonomic diversity trajectories were examined through the Richness, Shannon and Simpson diversities at genus level, in relation to the 1989 inventories (5 years after disturbance) (See annexe I). For undisturbed plots the Richness, Shannon and Simpson diversities remained stable over the 30 years monitored. In disturbed communities the taxonomic richness increased after low disturbance intensity, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2) while it followed unimodal trajectories after intense disturbance, decreasing for ten years before recovering predisturbance values. In all disturbed plots the taxonomic evenness (Shannon and Simpson diversities) increased, following unimodal trajectories with a maximum, reached after around 20 years, positively correlated to the disturbance treatment ($\rho_{spearman}^{Shannon} = 0.86$, and $\rho_{spearman}^{Simpson} = 0.89$). Return towards initial evenness values was beginning after 30 years except for two T3 plots (plots 8 and 12) which evenness still increased, suggesting similar but delayed trajectories [1].

Trajectories of communities functional diversity were examined through the Rao diversity based on the 7 leaf, stem and life history traits (to the exception of seed mass). The plot 7 from treatment 1 displayed a constantly outlying diversity and was removed from the graphical representation for better readability (see appendix for full graphs). In undisturbed plots the functional diversity remained stable along the 30 years while in disturbed plots it followed unimodal trajectories with a return towards initial values that strated around 20 years after disturbance.

The impact of disturbance was examined specifically through the linear correlation between the intial %AGB removed and the Simpson and Rao diversities (diversities of order 2) after 10, 20 and 30 years [1]. The correlation with disturbance intensity was weak for the Simpson diversity ($R^2 < 0.25$) and only valid from 20 years after disturbance but it was much stronger for the Rao diversity ($0.60 < R^2 < 0.75$) for all the time studied. Slope of linear correlations, reflecting the impact of disturbance, was the highest 20 years after disturbance.

3.2 Communities composition

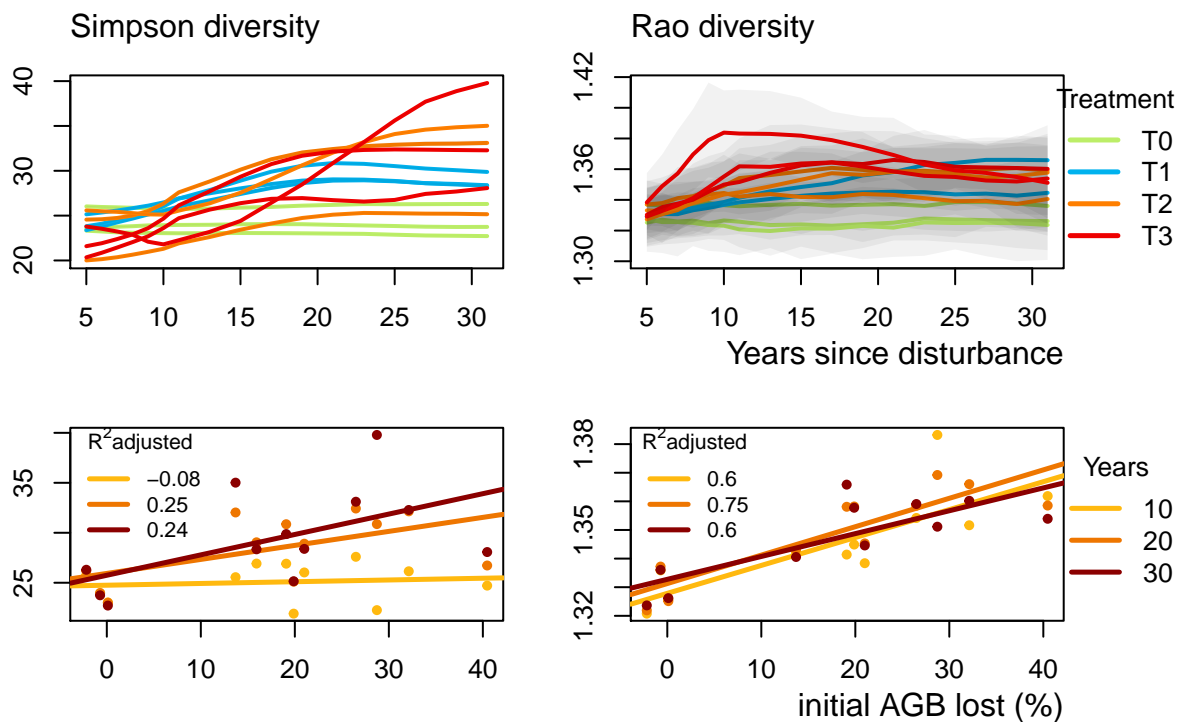### 3.2.1 Taxonomic and functional trajectories

The trajectories of taxonomic and functional composition were visualized in a two dimensional ordination space mapping the successive inventories according to their flora and corresponding traits. Classifications were performed using either abundance-based Bray-Curtis (Figure 2) or incidence-based Jaccard dissimilarity, both giving similar results only analysis using Bray-Curtis dissimilarity are discussed.

While both taxonomic and functional composition remained stable in undistrubed communities, they followed consistent trajectories over time after disturbance which revealed significant compositional changes. According to the mapping of functional traits (see appendix I) these compositional changes corresponded to shifts towards species with more acquisitive functional strategies, from communities with high average WD to high average SLA and chlorophyll content. For disturbed communities the distance of successive inventories to the 1989 reference inventory followed unimodal trajectories translating cyclic compositional changes with a recovery of the initial composition (Figure 2). The maximum dissimilarity with the initial state was positively correlated to the disturbance treatment for both taxonomic and functional composition ($\rho_{spearman}^{taxonomic} = 0.91$ and $\rho_{spearman}^{functional} = 0.96$ respectively) and the time at maximum was reached around 26 years after disturbance for taxonomic composition and 22 years for functional composition.

3.2.2 Traits community weighted means (CWM)

The changes observed in plots functional composition went hand to hand with consistent trajectories of the 8 functional and life history traits visualized with the trajectories of community weighted means (CWM) of leaves economics (leaves thickness, chlorophyll content, toughness and specific area), wood economics (wood specific gravity, bark thickness), and life history traits (seed mass and maximum adult height) (Figure 3).

Figure 1. Upper panels, Trajectories of the Simpson taxonomic diversity **(a)** and Rao functional diversity **(b)** over 30 years after disturbance, corresponding to the median and 0.025 and 0.975 percentile observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1,orange for T2 and red for T3. Lower panels, Relationship between the initial %AGB removed and the median values of Simpson **(c)** and Rao **(d)** diversities at three times after disturbance. Solid lines colors represent the time, 10 years (yellow), 20 years (orange) and 30 years (brown) after disturbance.
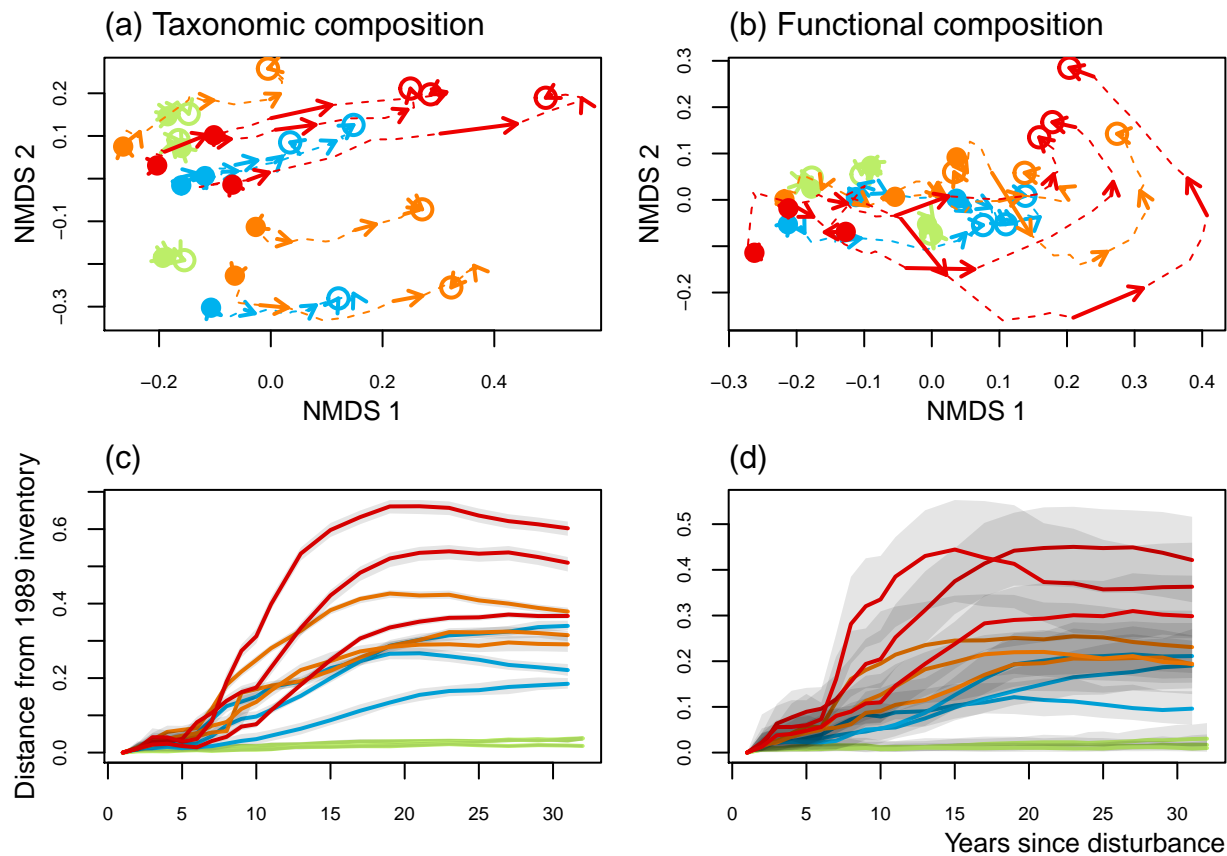
Figure 2. Trajectories of the plots in terms of flora composition (left panels **(a)** and **(c)**) and functional composition (right panels **(b)** and **(d)**) regarding the 6 leaf and stem functional traits, the maximum allometric height and seed mass class. Plots trajectories are first represented in the two-dimensional space from the NMDS performed for the 30 years after disturbance based on Bray-Curtis dissimilarity measures between successive inventories (Upper panels **(a)** and **(b)**). Then the lower panels (**(c)** and **(d)**) represent the euclidean distance to initial condition along the 30 sampled years. Line colors represent the disturbance treatment (green for control, blue for T1,orange for T2 and red for T3). The 0.025 and 0.975 percentile correspond to the variance observed for 50 iteration of the taxonomic uncertainty propagation and functional trait filling processes.

Except for leaf chlorophyll content, which continued to increase for some T3 and T2 plots 30 years after disturbance, all traits and seed mass proportions followed unimodal trajectories either stabilizing or returning towards their initial values. Thirty years after disturbance the weighted means of communities specific maximum height at adult stage (*Hmax*), leaf toughness (*L_toughness*) and wood specific gravity (*WD*) remained significantly lower than their initial value (Figure 3). The weighted means of bark thickness (*Bark_thick*) similarly remained substantially higher than initially for all disturbed plots while the specfic leaf area (*SLA*) had almost recovered its initial value. For all traits the maximum difference to initial state was correlated to the disturbance intensity ($\rho_{spearman}^{L_{thickness}} = 0.67$, $\rho_{spearman}^{L_{chloro}} = 0.45$, $\rho_{spearman}^{L_{toughness}} = -0.43$, $\rho_{spearman}^{SLA} = 0.93$, $\rho_{spearman}^{WD} = -0.78$, $\rho_{spearman}^{Bark-thickness} = 0.88$, $\rho_{spearman}^{Hmax} = -0.48$).

3.2.3 Functional redundancy
Communities functional redundancy was measured as the sum within communities the species weighted functional overlap based on the 7 leaf, stem, and maximum height traits (see appendix I for PCA details). Communities functional redundancy remained stable in control plots but after disturbance the redundancy trajectories were quite variable (See appendix I) and apparently independently of the initial disturbance. Globally after most intense disturbance (plots T2 and T3) communities redundancy decreased at first place before increasing to edge, recover or exceed the initial value.

Considering the functional redundancy restricted to the functional space of the initial inventory, all disturbed plots followed similar decreasing humped shaped trajectories (@ref(fig:RedFun_rest)). The maximum redundancy loss was positively correlated with the disturbance intensity (XX spearman to be measured) and the initial value had not recovered for any disturbed communities.

4. Discussion

4.1 Decoupled taxonomic and functional trajectories
Both communities taxonomic and functional diversity and composition proved resilient, following similar humped shaped trajectories returning towards initial values. The resilience of communities functional structure, that is the most direct link between biodiversity and ecosystem functioning (Díaz *et al.*, 2005), meant a consistent recovery of ecosystem processes in the long term (Guariguata & Ostertag, 2001). The resilience of communities taxonomy meant the maintenance of their initial differences in composition and diversity, suggesting the existence of multiple stable equilibria as assumed for highly diverse and productive ecosystems (Chase, 2003), and the dependency of recovery trajectories on the initial composition to be recovered that would the the asymptot of the humped shaped dynamics (Hubbell *et al.*, 1999; Molino & Sabatier, 2001; Anderson, 2007; Baraloto *et al.*, 2012).

Although both communities taxonomic and functional characteristics proved resilient and followed similar humped shaped trajectories, the taxonomic recovery systematically lagged behind the functional one. The decoupling between functional and taxonomic dynamics has already been observed for grasslands (Tilman, 1997; Mouillot *et al.*, 2011) and more recently for tropical forests (Lohbeck *et al.*, 2015; Guariguata & Ostertag, 2001). According to the "vegetation quantity effect" (Grime, 1998) functional trajectories rely on the pool of dominant species, which diversity and evenness increased after disturbance but rapidly recovered their initial functional structure. Although the pool of dominant species recovered quickly, communities evenness remained high so infrequent species still missed to the taxonomic recovery. Taxonomic recovery was then all the more longer that unrecovered species would be functionally redundant and probably underwent selective competition processes.

4.2 A validation of the intermediate disturbance hypothesis
In accordance with the IDH the trajectories confirmed the increase of communities diversity after disturbance with the favored growth of otherwise less favored species. However, although it was clear for the functional diversity this tendency was more blurry regarding communities taxonomic structure.

The taxonomic richness was enhanced after low disturbance but it was weakly or negatively impacted by intense disturbance, as observed on several post logging surveys (Cannon, 1998; Baraloto *et al.*, 2012). The taxonomic evenness also increased after disturbance, but the correlation between the disturbance intensity and the diversity increase remained weak and valid only after 20 years (*i.e.* Simpson diversity).

Contrastingly the functional diversity increase after disturbance was determined by the disturbance intensity all along the 30 years monitored. We already demonstrated that disturbance primarily entailed turnover of specific within communities, either among pre-disturbance survivors or among newly recruited trees. It wasdemonstrated that the composition of old-growth survivors proved to mirror initial communities (Hérault & Piponiot, 2018), so disturbance rather impacted trees recruitment with the enhanced growth and survival of previously infrequent species and functional types. Consistently disturbance resulted in an increase of the taxonomic dissimilarity between communities and their pre-disturbance composition, and in significant functional shifts towards resource-acquisitive strategies (sharp increase in the SLA, leaf thickness and bark thickness and decrease in wood density, leaf toughness and maximum height) (Westoby, 1998; Wright *et al.*, 2004; Reich, 2014). Disturbance entailed a reorganization of the typical high dominance structure of hyperdiverse mature forests benefiting to pioneers and light demanding species: the changes in abiotic environment and competitive pressure favored pioneers which outcompete other species in non limiting resources but were excluded in mature forests by long-lived, more resistant and shade tolerant species. Corroborating the IDH, the trajectories after disturbance relied on the environmental niches made available and filled by species from a restrictied functional range. Recruited species therefore differed from pre-disturbance ones, constituting a community all the more diverse that the disturbance was intense (Molino &

Community Weighted Means
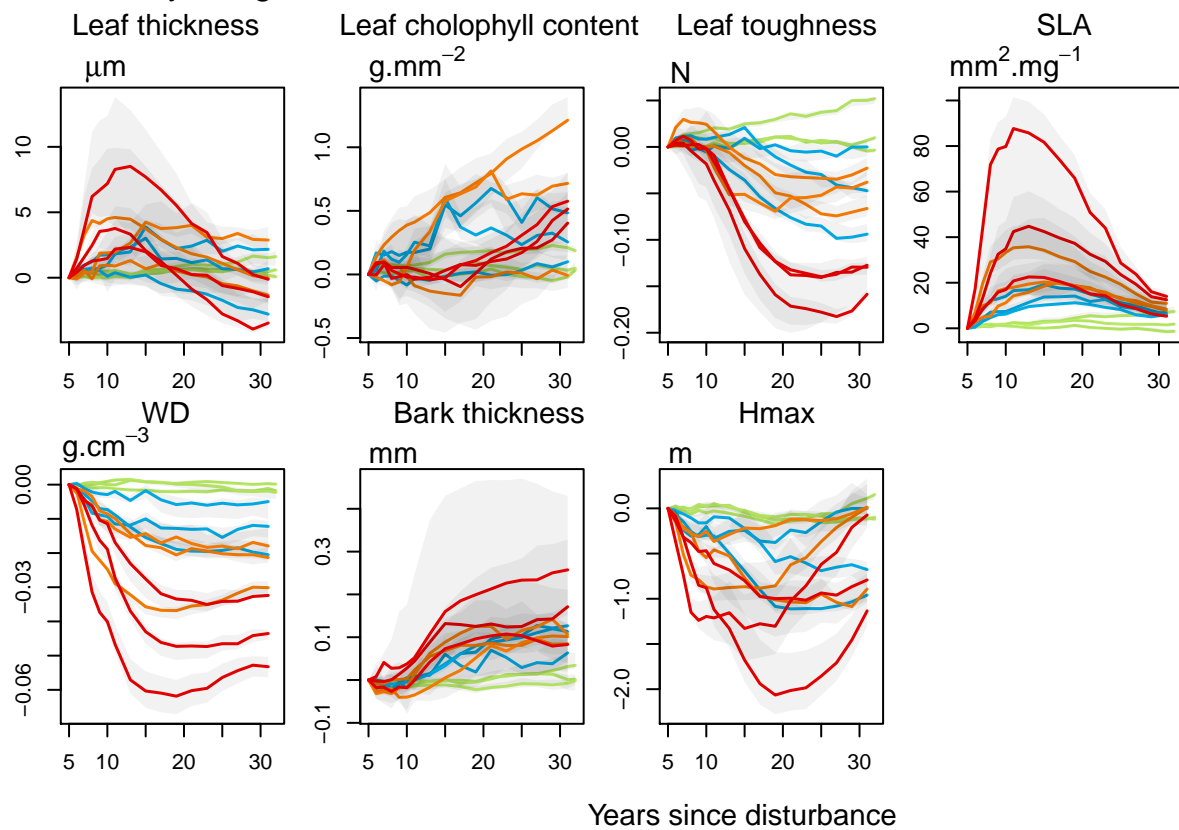
Figure 3. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, *L_thickness*, chlorophyll content, *L_chloro*, toughness, *L_toughness* and specific area, *SLA*), 2 stem traits (wood specific gravity, *WD*, and bark thickness, *Bark-thick*) and one life trait (Specific maximum height at adult stage, *Hmax*). Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1,orange for T2 and red for T3.
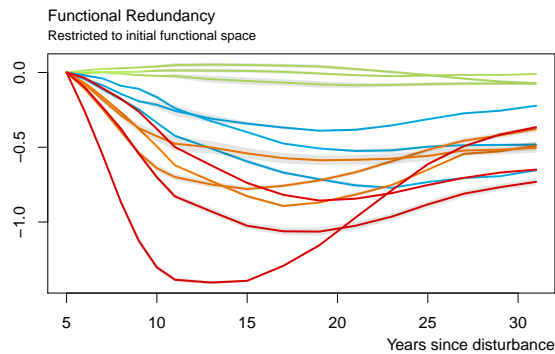
Figure 4. Trajectories of the functional redundancy within the initial cpùùunities functional space over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1,orange for T2 and red for T3. (#fig:RedFun_rest)

Sabatier, 2001).

4.3 The functional redundancy, key of communities resilience

Both the lag between taxonomic and functional recovery and the middling consistency of the IDH regarding communities taxonomic diversity were explained by the incomplete recovery of communities functional redundancy, which besides implies that communities resilience remained altered 30 years after disturbance (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

Functional redundancy mitigates the loss of species on communities functional structure (Carmona *et al.*, 2016), and therefore reduces the impact on disturbance. The functional redundancy itself however might be reduced or reorganized within the functional space and alter communities resilience. Although the functional redundancy considered in the whole commnities functional space did not follow consistent trajectories after disturbance, the redundancy restricted to the functional space of the initial community clearly followed humped shaped trajectories. This restricted redundancy first decreased, all the more so that the disturbance was intense, and then returned towards the initial value but this had not recovered for any disturbed community after 30 years. After disturbance communities then differently occupied the functional space, as it was suggested by the shifts observed for the functional diversity and traits trajectories, before recovering the specific highly redundant initial functional space. This increasing redundancy along the trajectory explained the hampered recovery of infrequent species specific to old-growth forests, as they were likely functionally redundant and therefore underwent competitive pressures limiting species functional similarity (Mayfield & Levine, 2010). The unachieved recovery of the functional redundancy meant a decreased resilience of pre-

disturbance communities and an increased of disturbance-specific communities (corresponding to lower richness and higher dominance of pioneer species). After disturbance the chances were therefore higher to have long lasting or self-maintained compositional changes in favor of disturbance resistant species, lianas or epiphytes (Haddad *et al.*, 2008; Burslem *et al.*, 2000; Martin *et al.*, 2013). The recovery was not complete until the functional redundancy and resilience of the initial communities remained altered. Specificaly, such incomplete recovery would threaten the maintenance of species contingent to undisturbed forests and increase the risk of cornerstone species loss and unexpected ecological consequences (Jones *et al.*, 1994; Chazdon, 2003; Díaz *et al.*, 2005; Gardner *et al.*, 2007).

5. Conclusions

Our study defined the decoupled functional and taxonomic trajectories of tropical rainforests after disturbancethat demonstrated a rapid functional recovery but a slower and more variable taxonomic one. Consistently with the IDH, functional trajectories were driven by deterministic processes favoring pioneers and light-demanding species after disturbance. The following functional shifts entailed a reorganization of communities functional redundancy in the functional space that proved long to recover and explained the more variable and longer taxonomic trajectories as shade tolerant species of old-growth forests faced functional redundancy and limiting similarity processes. The resilience of tropical forests then proved long in the face of quite intense disturbance and did not preclude the settling of a persistent disturbanc-specific community (Gourlet-Fleury *et al.*, 2005). Within the mechanisms of this resilience the recruitment processes proved central, in accordance with the IDH, and would deserve closer focus to specify their ecological drivers. The disturbance range however stayed within the spectrum of selective logging, with a forest cover remaining all along the experiment, and the response mechanisms would probably be much different after harder disturbance.

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