Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract
Résumé de l'article.

Keywords
mot-clés, séparés par des virgules

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1. Introduction

The large areas covered with tropical forests worldwide hold crucial economic, social and cultural value. 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 increase of forests products demand and substantial climatic changes currently heighten the pressure on the remaining forests (**??**). It threatens the maintenance of communities structure, composition and functioning and the underlying dynamics in space and time (**??**).

In tropical forest, ecological communities are contantly re-shaped by the natural disturbance events that changes the abiotic environment, through the fluxes of light, heat and water, and the biotic interaction and competitive pressure (**?**). The cornerstone of tropical forests ecology is then to understand the underlyings of ecosystem response to disturbance, its mechanisms and drivers (**??**). For now, this has been largely studied through structural parameters, rapid and convenient to measure, as aboveground biomass, tree height or stem density (**??**). These structural parameters have then been sucessfully modeled and allowed to assess the maintenance of ecosystems processes and services (**??**). However the response of tree species diversity remains unclear, also it is determinant of ecosystems productivity, stability and functioning (**?, ?**) and would be most probably impacted by post-disturbance environmental changes (**?**).

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 (**???**). Validations of the IDH in the long term, however, remain scarce and mainly rely on the analysis of the rough species richness that gives limited or misleading information on forests recovery and functioning (**??**). More releveant monitoring would encompass communities composition, that is crucial for conservation issues, and diversity profiles, that reveals ecological rules underlying communities' structure (**???**). Furthermore, the functional approach accounting for differenes species biological attributes would be insightful as it reveals the species role in the post-disturbance trajectory of ecosystems functioning (**????**). In that respect major functional traits related to species ecology and performance were largely adopted through an integrative framework (**??**). The functional trait-based approach, for example, highlighted in tropical rainforests the environmental filters fostering disturbance resistant species with rapid growth and efficient resources acquisition (**??**). In disturbed tropical rainforests, this framework translates into the fostering of disturbance resistant species with rapid growth and efficient resources acquisition (**??**). It results in a shift from "conservative" slow-growing species dealing with scarce resources that dominate before disturbance, to "acquisitive" fast-growing species with rapid and efficient use of abundant resources (**???**). It was mirrored by shifts in key functional traits related to resource acquisition (leaf area, density and chlorophyll content, and stem specific gravity and bark thickness), tree growth and reproduction life history traits (seed mass and maximum height) (**???**).

A proper monitoring of communities response should therefore encompass taxonomic and functional diversity and composition measures to test the validity of the IDH in the long term for tropical forests, and clarify the resilience of communities evenness, composition, and also functioning. The trajectories followed by all these facets would high-

light the role of deterministic processes, like competitive exclusion or abiotic selection, and the communities' convergence maintaining intrinsinc differences in diversity and composition,which is as much insgights for future adaptive conservation strategies (**?**).

Here we investigated 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 traits and species maximum height to draw the trajectories over time of communities taxonomic and functional composition and diversity. Specifically, we (i) tested the validity of the IDH in the long term for tropical hyperdiverse forest and highlighted the ecological rules shaping their response to disturbance, (ii) clarified the different facets of communities resilience in terms of communities composition, diversity and functioning *????(iii) questioned the completeness of communities recovery given the altered 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 corresponding to a tropical wet climate with mean annual precipitation averaging 2980 mm.y^{-1} (30-y period) with a 3-month dry season (< 100 mm.month^{-1}) from mid-August to mid-November, and a one-month dry season in March (**?**). Elevation ranges between 5 and 50 m and mean annual temperature is 26°C. Soils correspond to thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains. The experiment corresponds to a network of twelve 6.25ha plots that have undergone a gradient of three logging, thinning and fuelwood treatments (Table **??**). 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 above 40 cm DBH for treatment 3 (T3). Treatments T2 and T3 besides included the thinning of trees by poison girdling (**?**).

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 were mapped and measured annually since 1984. During inventories, trees were first identified 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 were given to 62 commercial or common species whereas other less common species were identified under two identifiers only separating trees and palm trees. The botanical campaigns carried every 5 to 6 years to identify all trees at the species level only started in 2003 and identification practices varied among plots and successive campaigns. This raised methodological

issues as vernacular names usually correspond to different botanical species, resulting in significant taxonomic uncertaities that had to be propagated to composition and diversity metrics through a Bayesian framework. The uncertainty propagation was done by the replenishment of inventories completed 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 observed association probability $[\alpha_1, \alpha_2, \ldots, \alpha_3]$ between each vernacular name v and the species $[s_1, s_2, \ldots, s_N]$ recorded in the inventory. See appendix 1 and **?** for the detailed methodology.

The functional diversity metrics used a dataset for 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. Missing trait values were filled using multivariate imputation by chained equation (mice) restricted to samples pertaining to the next higher taxonomic level, in order to account for the phylogenetic signal of the functional traits. The dataset comprised 294 botanical species pertaining to 157 botanical genera.

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. As seed mass information corresponds to a classification into mass classes, no data filling process was applied so analysis were performed considering the 414 botanical species of the seed mass dataset. 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 the remaining taxonomic uncertainty, plots taxonomic composition and diversity were analysed at the genus level, *i.e.* referring to the genus of observed or trialed botanical names. Variations in plots taxonomic and functional composition after disturbance was visualized by their trajectories in a two-dimensional ordination space over 30 years. Two NMDS were conducted, either from taxonomic flora inventories or from plots functional composition based on the 8 leaf, stem and life history traits. Plots trajectories along time was reported comparatively to the inventories in 1989, 5 years after disturbance, which corresponded to first inventory with a sufficient degree of uncertainty (<30% of undetermined trees). The inventories dissimilarity compared to the reference 1989 inventory was reported using occurrence-based (Jaccard) and abundance-based (Bray-Curtis) similarity measures. The trajectory of inventories along time was visualized with the euclidean distance in

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

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	$[35\% - 66\%]$

the two-dimensional ordination space to the 1989 inventory. 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 (**??**). 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 (**?**). These three indices belong to the set of HCDT or generalized entropy, respectively corresponding to the 0, 1 and 2 order of diversity (q), which proved well suited for diversity studies (**??**). 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 functional redundancy was measured as the overlap among species in communities' functional space (**?**). The samples of the trait database were first located with a PCA analysis in a two-dimensional functional space summarizing the 8 functional traits considered. We choose to summarize species functional space through a PCA because functional traits considered were already somehow redundant and allows not to overweight the role of one trait. Then, multivariate kernel density estimator associated with individual trees were summed to give the distribution of traits probabilites of each species. For each community the trait probability distributions of corresponding species were combined and weighted by species abundance. Eventually communities functional redundancy was measured as the sum of overlap between species weighted functional density. Communities functional redundancy is expressed as the average number of species that could be removed from the community without reducing the functional space.

3. Results

3.1 Disturbance impacts on communities composition and average functional traits values

3.1.1 Composition trajectories

Over time, 828388 trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. Taxonomic and functional plots trajectories were examined through the trajecotries in a two dimensional ordination space of successive inventories from 1989 (5 years after disturbance) to 2015 (31 years after disturbance). Classifications were performed using either abundance-based Bray-Curtis (Figure **??**) or incidence-based Jaccard dissimilarity, this last having given similar results (data not shown).

Both taxonomic and functional composition of disturbed plots followed consistent trajectories over time, translating compositional changes while control plots remained stable. The addition of functional traits in the two dimensional space revealed a shift of plots composition towards more acquisitive functional strategies (disturbed plots changed from high average WD to high average SLA and chlorophyll content). The dissimilarity of the successive inventories for disturbed plots compared to their respective reference inventory in 1989 followed unimodal trajectories (AppendixI, Figure A2). The maximum dissimilarity of plot strajectories was positively correlated to the disturbance intensity for taxonomic ($\rho^{taxonomic}_{spearman} = 0.91$) as well as functional composition ($\rho^{taxonomic}_{spearman} = 0.96$). The time at maximum dissimilarity for taxonomic composition was reached around 26 years after disturbance while it was 22 years for functional composition. All trajectories returned towards the initial composition and translated cyclic compositional changes as visualized in figure (Figure **??**).

3.1.2 Traits community weighted means

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

Except for leaf cholorphyll content, which continued to

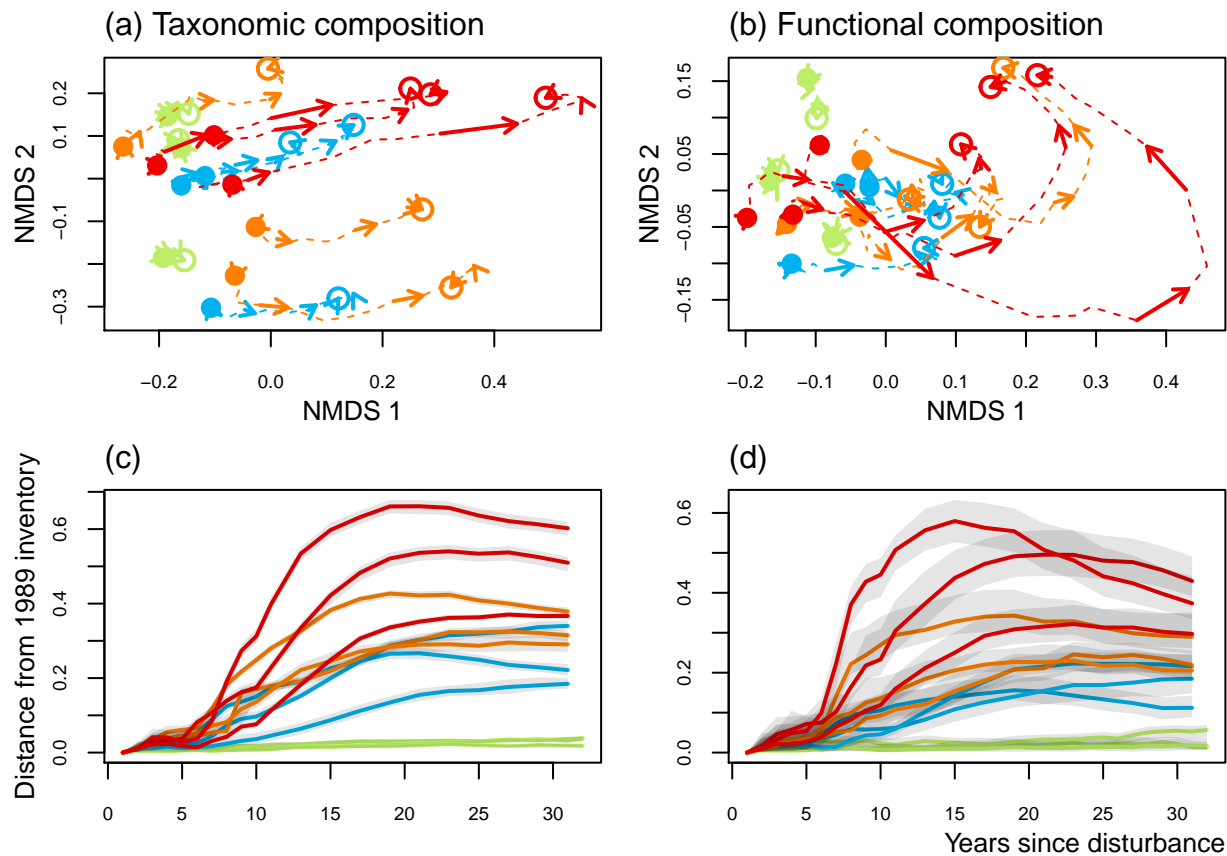**Figure 1.** Trajectories of the plots in terms of flora composition (left panels **(a)** and **(c)**) and functional composition (right panels **(b)** and **(d)**) regarding the 6 leaf and stem functional traits, the maximum allometric height and seed mass class. Plots trajectories are first represented 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.

increase for some T3 and T2 plots 30 years after disturbance, all traits and seed mass proportions displayed a unimodal trajectories. 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 and than these of the control plots (Figure **??**). The weighted means of bark thickness (*Bark_thick*) similarly remained substantilly higher than initially for all disturbed plots while the specfic leaf area (*SLA*) had almost recovered its initial value and this of the undisturbed plots at the end of the experiment. Once again 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 Trajectories of communities diversity after disturbance

3.2.1 Communities taxonomic and functional diversity

Trajectories of Richness, Shannon and Simpson taxonomic diversity were examined at genus level in relation to the 1989 inventories (5 years after disturbance) (Figure **??**).

For undisturbed plots the Richness, Shannon and Simpson diversities remained stable over the 30 years monitored. After low disturbance intensity the richness increased, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2). After intense disturbance however, the taxonomic richness followed a unimodal decrease with a return to pre-disturbance values. The taxonomic evenness (Shannon and Simpson diversities) increased after disturbance, whenever its intensity. The evenness followed a unimodal trajectory with a just beginning return towards initial values and a maximum value, reached around 20 years, positively correlated to the disturbance intensity ($\rho_{spearman}^{Shannon} = 0.86$, and $\rho_{spearman}^{Simpson} = 0.89$). Only two T3 plots (plots 8 and 12) were still increasing 30 years after disturbance **??**), suggesting a similar be much delayed unimodal trajectory.

Communities functional diversity trajectories were examined through the Rao diversity based on the 7 leaf, stem and life history traits (the seed mass was excluded as a qualitative variable). The plot 7 from treatment 1 that displayed a constantly outlying diversity was removed from the graphical representation for better readability, see figure A3 in appendix for full graph. The functional diversity of all undisturbed communities remained stable along the 30 years monitored. For all disturbed communities the functional diversity followed unimodal trajectories with a marked return towards the initial state (5 years after disturbance) with values comparable to those of control plots.

The impact of disturbance was examined more accurately at 10, 20 and 30 years after disturbance through the linear correlation between the initial percentage of AGB removed and the value of communities Simpson and Rao diversities (both diversities of order 2).

The functional redundancy was measured as the sum of weighted overlap among species in communities' functional space. Functional space were defined in the main two-dimensional space of a PCA analysis based on all leaf and stem and maximum height traits (see appendix I for PCA

details). Plots functional redundancy compared to the initial value after logging so that only communities dynamics are followed apart from the impact of logging itself. Communities functional redundancy remained stable in control plots but after disturbance the redundancy trajectories were quite variable (See appendix I). Globally after most intense disturbance (plots T2 and T3) communities redundancy decreased at first place and then increased to edge, recover or even exceed the initial value. Considering the functional redundancy restricted to the functional space of the initial inventory, though, all disturbed plots followed similar decreasing humped-shaped trajectories (@ref(fig:RedFun_rest)). The maximum redundancy loss observed was positively correlated with the disturbance intensity (XX spearman to be measured) and none of the disturbed plots had recovered the functional redundancy within their initial functional space.

4. Discussion

4.1 A validation of the intermediate disturbance hypothesis

The monitoring of disturbed forest communities confirmed a limited negative impact of disturbance on species richness, as observed on several post logging surveys (**??**). Thirty years after disturbance, the genus richness was restored to initial plot values after high disturbance intensity while it substantially increased after low disturbance intensity, reaching a gain of almost 12 genera for some plots.

Both richness and evenness followed asymptotic trajectories after disturbance, sharply increasing for 15 years before stabilizing at higher values than those of control plots. An increase of communities evenness stems from a higher homogeneity of species distribution. After disturbance, communities are made of the old, pre-disturbance survivors and the newly recruited trees: changes in composition and abundance distribution are to be found in the recruitment processes and in the pre-disturbance survivors mortality. Because the composition of old survivors proved to mirror the initial community (**?**), a specific turnover was expected among recruited trees with enhanced growth and survival of previously infrequent species. Indeed, the increase in taxonomic diversity was accompanied by an increase of taxonomic dissimilarity with plots initial state and a functional shift towards resource-acquisitive strategies (sharp increase in the SLA, leaf thickness and bark thickness and decrease in wood density, leaf toughness and maximum height) (**???**). Disturbance then causes a reorganization of the typical high dominance structure of hyperdiverse mature forests after disturbance, benefiting to pioneers and light demanding species. Likely, the changes in abiotic environment and competitive pressure favored pioneers which outcompete others in non limiting resources but are excluded in mature forests by long-lived, more resistant and shade tolerant species.

As stated by the IDH, communities dynamics after disturbance relied on species functional strategy and corresponding ability to fill the environmental niches made available by disturbance. Recruited species then mixed with pre-disturbance ones, from which they differed, and constituted a community all the more diversified that the disturbance
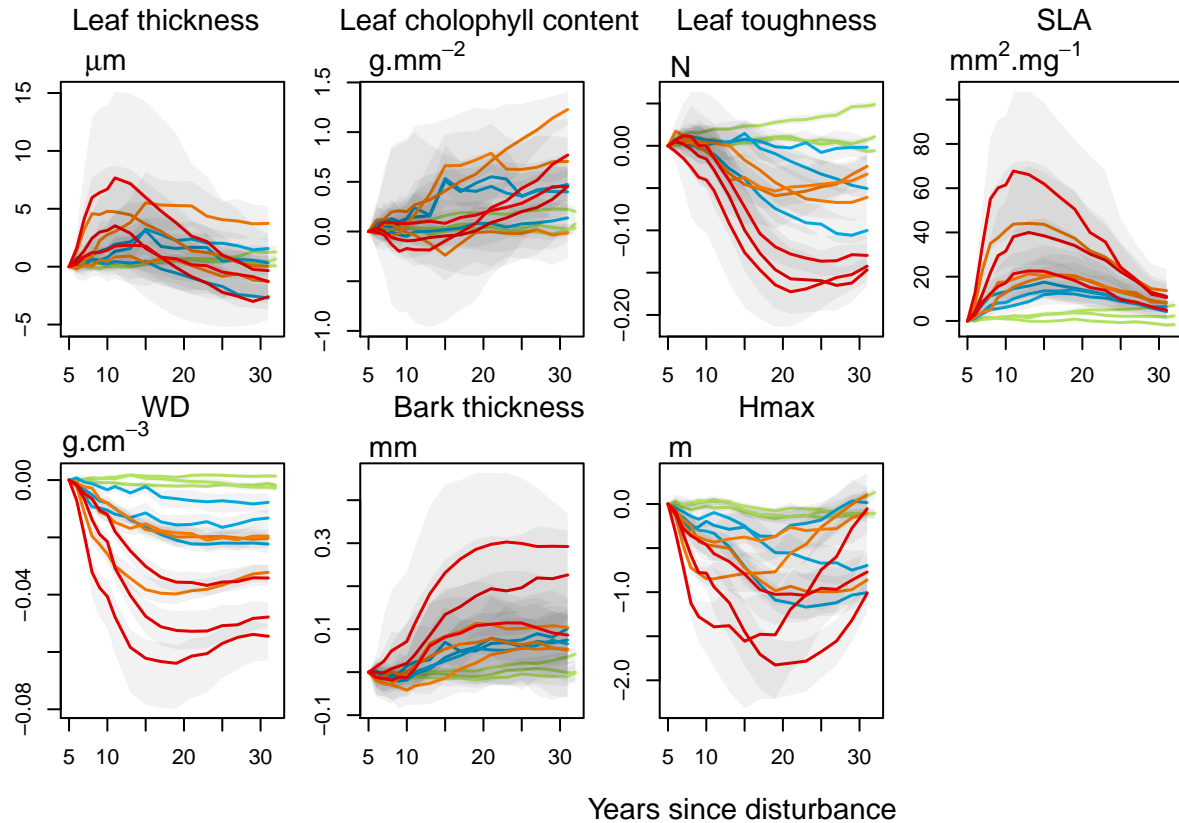
Community Weighted Means

Figure 2. 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.
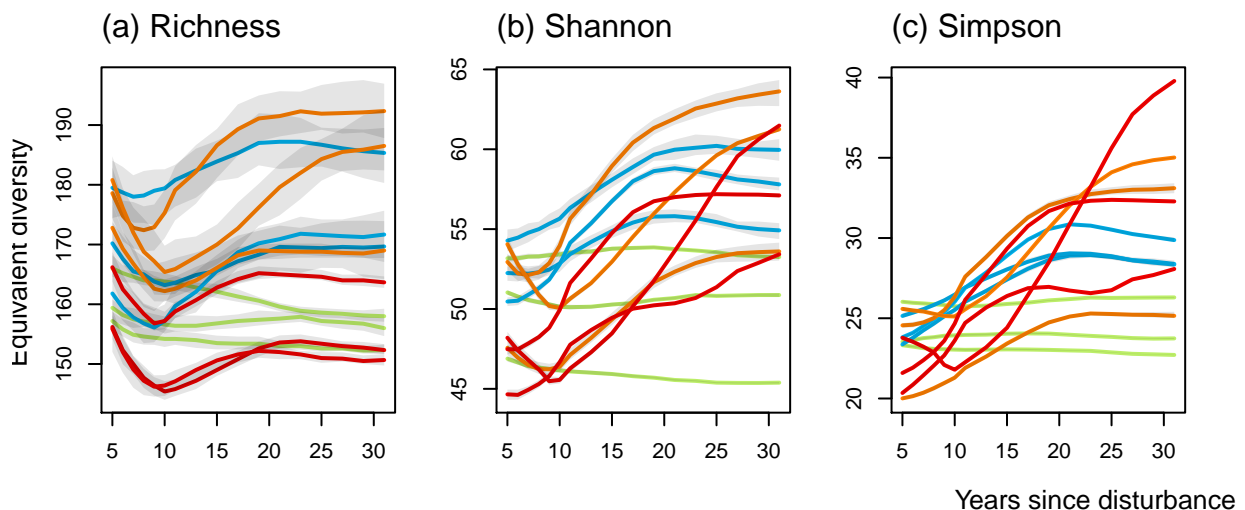

Figure 3. Trajectories of the difference to the 1989 inventories (5 years after disturbance) over 30 years after disturbance of plots communities **(a)** Richness, **(b)** Shannon and **(c)** Simpson diversities. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation. Initial treatments are represented by solid lines colors with green for control, blue for T1,orange for T2 and red for T3.
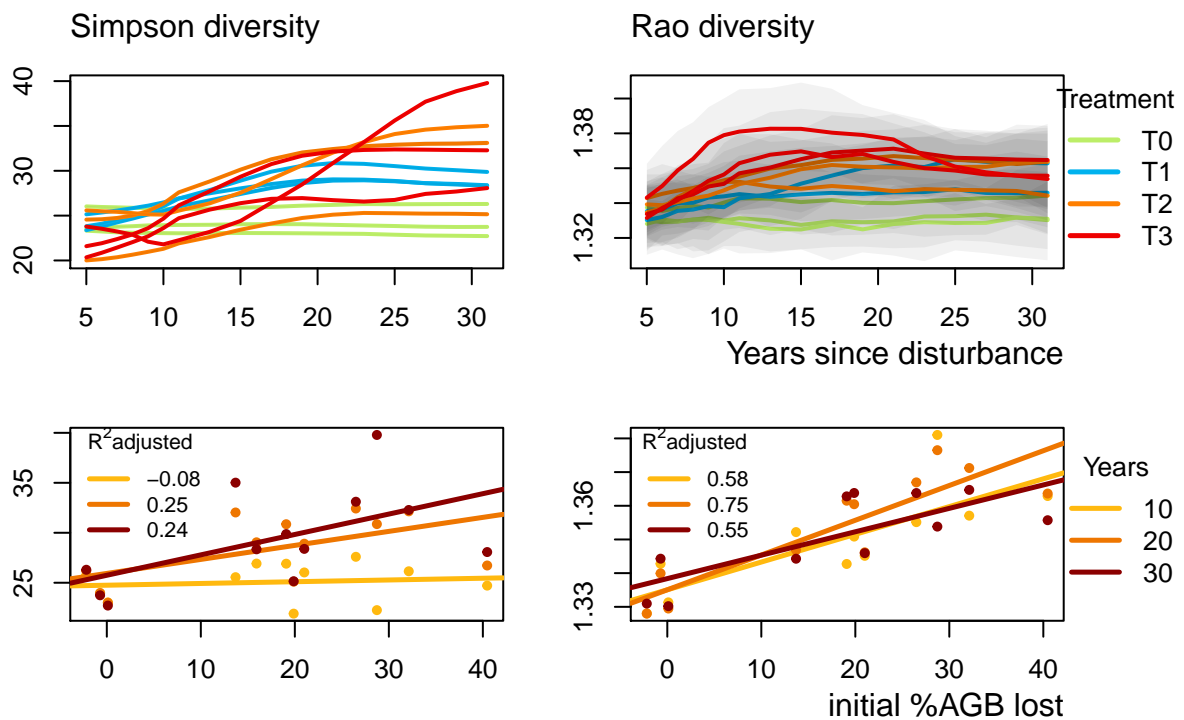
Figure 4. Upper panels, Trajectories of the Simpson taxonomic diversity **(a)** and Rao functional diversity **(b)** over 30 years after disturbance, corresponding to the median and 0.025 and 0.975 percentile observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value 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.
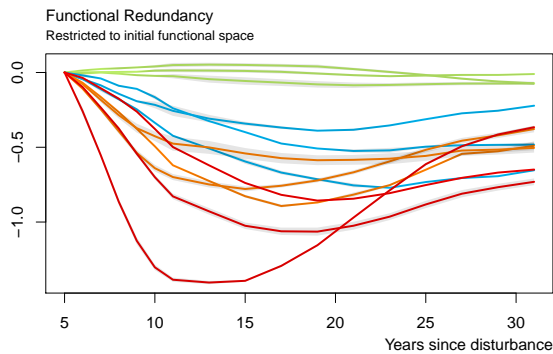
Figure 5. Trajectories of the functional redundancy within the initial cpùùunities functional space over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and 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)

was intense (**?**).

4.2 On the recovery of disturbed communities

All diversity and composition trajectories followed similar hump-back trajectories returning towards their initial values. Communities trajectories therefore illustrated their taxonomic and function resilience.

Because functional traits and functional diversity are the most direct link between biodiversity and ecosystem functioning (**?**), their resilience meant a consistent recovery of ecosystem processes in the long term (**?**). The resilience of the taxonomic diversity and composition similarly translated the recovery of communities such as before disturbance. This resilience meant the maintenance of communities initial differences in composition and supported the idea of their convergence towards a determined state (**???**). If all plots followed similar hump-back trajectories, though, some significant differences emerged. To name but one, the taxonomic evenness of one plot displayed an extensive increase until 30 years after disturbance. The differences trajectories maxima and time path, along with the fact intrinsinc communities differences are maintained, suggested that the trajectories depend on the initial plots composition or on some abiotic parameters (**?**).

4.3 Functional redundancy of disturbed ecosystems

Despite the recovery of pre-disturbance state there was a time lag between the trajectories followed by communities taxonomic and functional characteristics. The trajectory of taxonomic composition and evenness had a longer time-path and remained altered while communities functional composition and diversity had already recovered.

Such delay between functional and taxonomic dynamics was already observed for grasslands (**??**) and more recently

for tropical forests (**??**). According to the "vegetation quantity effect" (**?**), the functional diversity of communities rely on the dominant species. Communities functional trajectories were then driven first by the increase in diversity and evenness of dominant species, which restored the predisturbance functional characteristics. Then, the functional trajectories were driven by the recruitment of species resembling the old pre-disturbance community, which reduced the overall diversity. At that time, the taxonomic composition and diversity remained altered: the still missing species were then the initially infrequent and functionally redundant ones. The functional redundancy, the functional overlap between species that is typical of the huge biodiversity of tropical forests (**?**), was then not restored 30 years after disturbance and this is major to consider as it defines forests' resilience (**???**).

Besides the long-term alteration of functional redundancy, there was probably persistent compositional changes favoring disturbance resistant species (**?**), lianas or epiphytes (**?**) and environmental changes, like in the soils nutrient cycling and compaction (**?**). These persistent changes highly question forest's resilience (**?**). New conditions would not only be longer lasting but self-maintained as tied to disturbance regime (**?**). Specificaly, this would impair species contingent to undisturbed forests, threatening their maintenance, and run the risk to loose cornerstone species and trigger unexpected ecological consequences (**???**).

5. Conclusions

Our study showed the significant impact of disturbance on tropical forests communities and validated the consistency of the IDH in the long term. It revealed the contrasting response of communities taxonomic and functional characteristics, with persisting impacts on the species abundance distibution while the functional diversity and dominant functional strategies were restored. Communities recovery therefore remained unachieved but consistent for the range of disturbance studied here. The length of the recovery, however, severly questioned the sustainability of intense selective logging and advocated felling cycle much longer than 30 years (**?**).