Hal xxx
DOI xxxx

Post-Disturbance Tree Community Trajectories in a Neotropical Forest

Ariane MIRABEL[1*]
Eric Marcon[1]
Bruno Hérault[2 3]

Abstract
Résumé de l'article.

Keywords
mot-clés, séparés par des virgules

[1]UMR EcoFoG, AgroParistech, CNRS, Cirad, INRA, Université des Antilles, Université de Guyane.
Campus Agronomique, 97310 Kourou, France.
[2]Cirad, Univ montpellier, UR Forests & Societies.
Montpellier, France.
[3]INPHB, Institut National Polytechnique Félix Houphouet-Boigny
Yamoussoukro, Ivory Coast.
*Corresponding author: ariane.mirabel@ecofog.gf, http://www.ecofog.gf/spip.php?article47

Contents

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 for 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 heightened the pressure on the remaining forests (**??**) and threatened the maintenance of communities structure, composition and functioning and their underlying dynamics (**??**).

In tropical forests communities are shaped by a constant range of disturbance that changes the abiotic environment, as the light, the heat and water fluxes, and the biotic interaction and competitive pressure. The cornerstone of tropical forests ecology is then to understand their response to disturbance and its mechanisms (**??**). Forests response 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, which is determinant of ecosystems productivity, stability and functioning (**?**) and would be most probably impacted by post-disturbance environmental changes (**?**), remains unclear.

In the short-term diversity dynamics demonstrated negligible or even positive impacts of disturbance on communities diversity, which have been formalized by the intermediate disturbance hypothesis (IDH) stating a maximized species diversity at intermediate disturbance intensity (**???**). However, validations of the IDH in the long term remain scarce and mainly rely on the analysis of 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 evenness, that reveals ecological rules underlying communities' structure (**???**). Furthermore, the functional approach accounting for species biological attributes would be insightful as it reveals species fitness and ecosystems functioning (**????**). In that respect major functional traits related to species ecology and performance were largely adopted through a relevant 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 (**??**). This translated by shifts from "conservative" slow-growing species dealing with scarce resources, 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 highlight 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 hiperdiverse 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. >>revoir la fin

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 uncertainties 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 $M_v\Big([s_1,s_2,\ldots,s_N],[\alpha_1,\alpha_2,\ldots,\alpha_3]\Big)$ 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 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 intrinsic difference among plots the trajectories corresponded to the differences along time with the reference inventory in 1989. Species seed

[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	$[35\% - 66\%]$

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. 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.

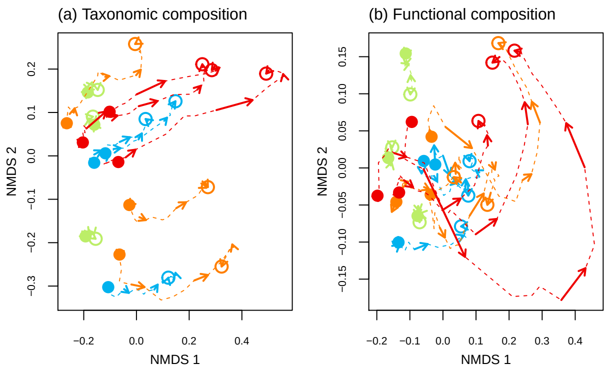

Figure 1. Trajectories of the plots in terms of **(a)** flora composition and **(b)** functional composition regarding the 6 leaf and stem functional traits,the maximum allometric height and seed mass class in the two-dimensional space from the NMDS performed for the 30 years after disturbance. Distance matrix for NMDS were computed from the Bray-curtis dissimilarity between successive inventories. Line colors represent the disturbance treatment (green for control, blue for T1,orange for T2 and red for T3).

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 (Leaf thickness, chlorophyll content, toughness and specific area, wood specific gravity and bark thickness and seed mass and maximum adult height) visualized with plots community weighted means (CWM) (Figure **??**).

Except for leaf cholorphyll content, which continued to 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 Taxonomic 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 monitored years. After disturbance the richness increased when the disturbance intensity was low, with a maximum increase of 14 botanical genera (plot 3 from treatment 2). When the disturbance was intense however, plots taxonomic richness followed a unimodal decrease with a return to initial values after intense disturbance. The taxonomic evenness (Shannon and Simpson diversities) significantly increased irrespective of the disturbance intensity. The evenness followed a unimodal trajectory with a just beginning return towards initial values and a maximum reached around 20 years and 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, remained increasing 30 years after disturbance **??**), suggesting a similar be much delayed unimodal trajectory.

3.2.2 Functional diversity

The functional diversity trajectories of plots based on the 8 leaf, stem and life history traits was examined through the Rao diversity. For all undisturbed plots the functional diversity remained comparable to the reference values 5 years after disturbance (1989 inventories). For all disturbed plots the functional trajectories followed a unimodal trajectory with a maximum positively correlated to disturbance intensity ($\rho_{spearman} = 0.73$) (Figure **??**). The plot 7 from treatment 1 that displayed a constantly outlying diversity was removed from the graphical representation for better readability, see appendix for full graph. Thirty years after disturbance all plots, whenever the initial disturbance intensity, regained diversity values similar to their initial value and to those of control plots.

The functional redundancy was measured as the sum of weighted overlap among species in the communities. Species 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 more details). Plots functoinal redundancy was followed in comparison to their initial value right after logging so that only communities dynamics are followed apart from the impact of logging itself. While the functional redundancy of control plots remained stable along the 30 years it systematically decreased after disturbance (**??**). The decrease of functional redundancy was comparable between all disturbed plots but started later for the most disturbed plots. Plots recovery did not seemed correlated to the initial disturbance, for five out of nine disturbed plots the initial functional redundancy was had recovered while it was still decreasing or stabilized at lower values for the fou other plots.

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.

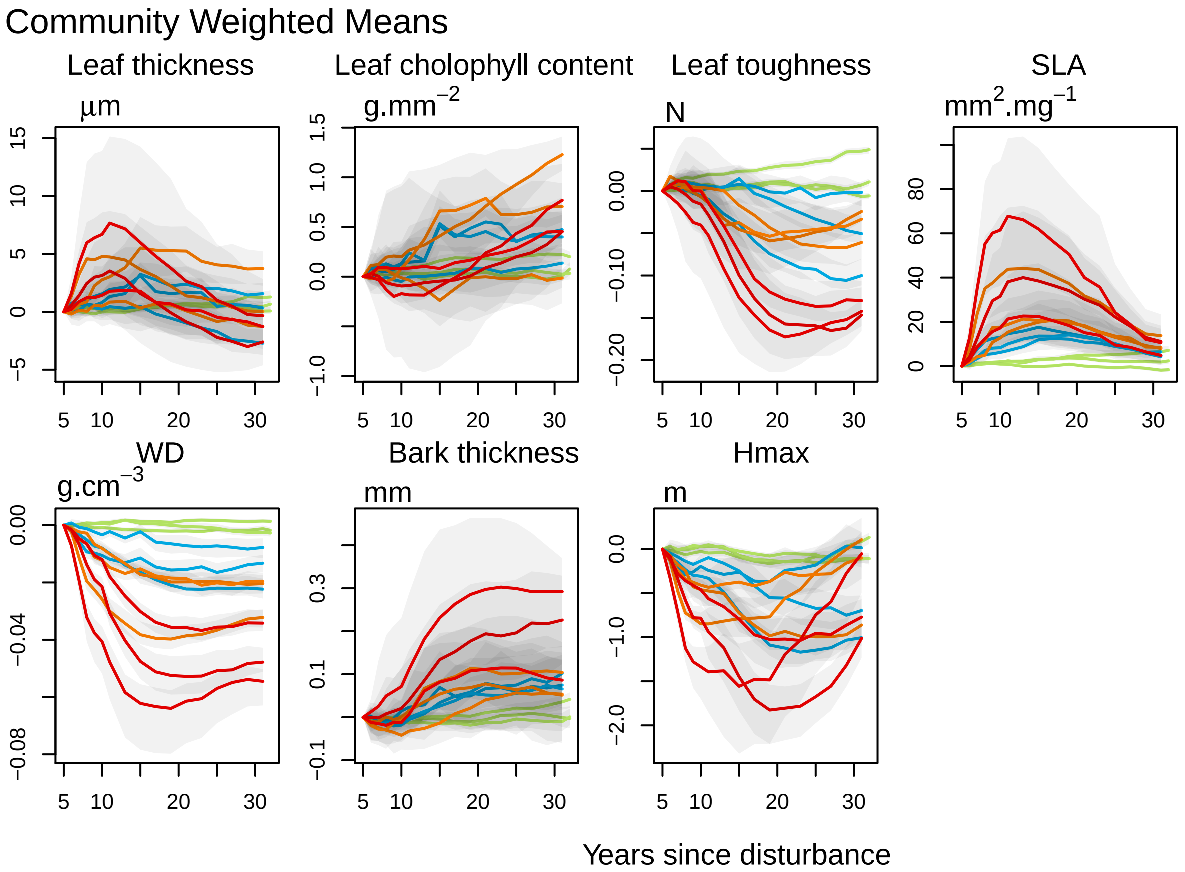

Figure 2. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, *L_thickness*, chlorophyll content, *L_chloro*, toughness, *L_toughness* and specific area, *SLA*), 2 stem traits (wood specific gravity, *WD*, and bark thickness, *Bark-thick*) 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.

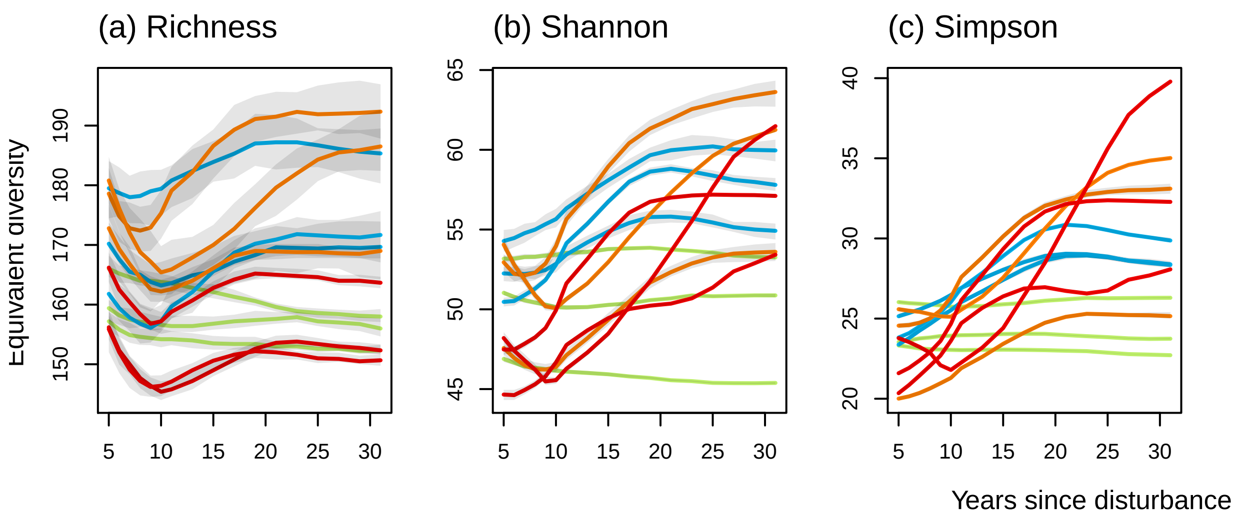

Figure 3. Trajectories of the difference to the 1989 inventories (5 years after disturbance) over 30 years after disturbance of plots communities **(a)** Richness, **(b)** Shannon and **(c)** Simpson diversities. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray 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.

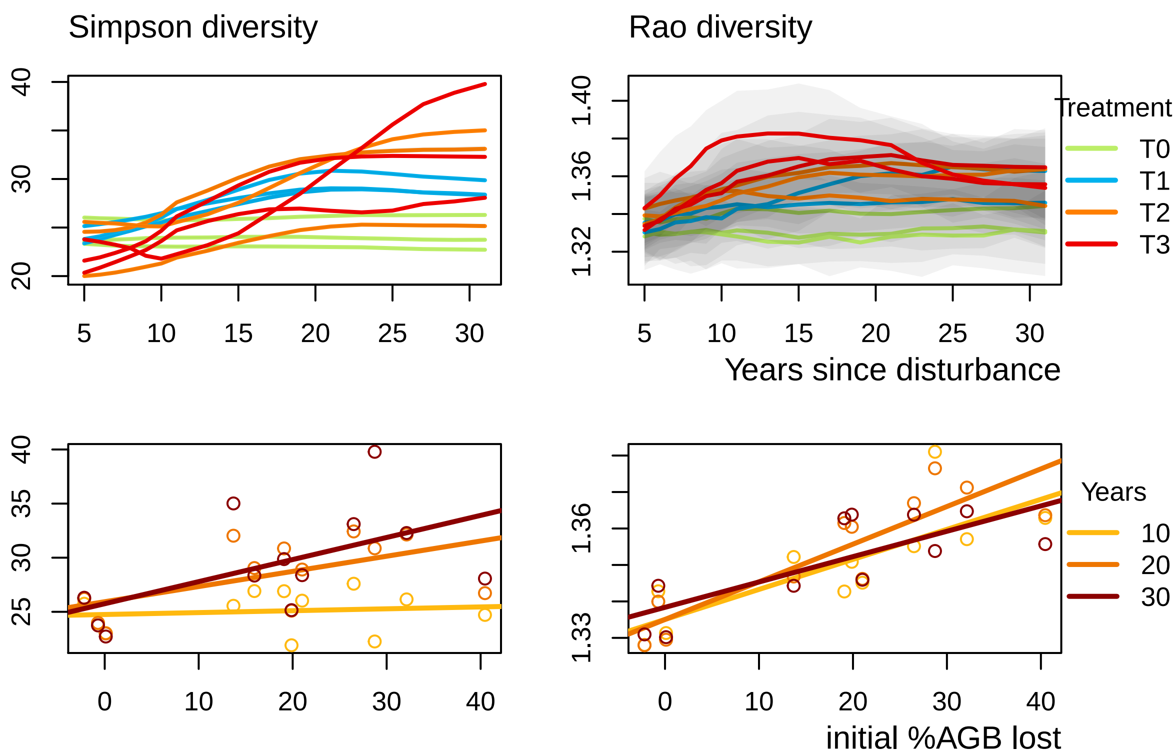

Figure 4. Upper panels, Trajectories of the Simpson taxonomic diversity **(a)** and Rao functional diversity **(b)** over 30 years after disturbance, corresponding to the median and 0.025 and 0.975 percentile observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value 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 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.

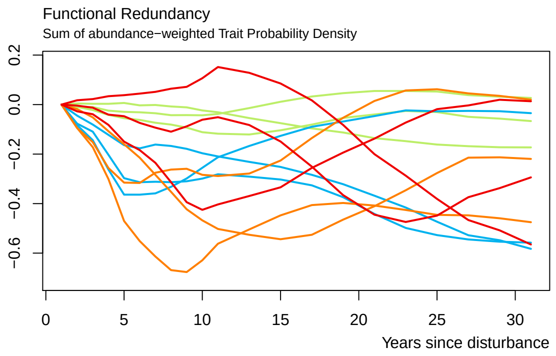

Figure 5. Trajectories of the functional redundancy over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes.Initial treatments are represented by solid lines colors with green for control, blue for T1,orange for T2 and red for T3.

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 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 pre-disturbance 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 presistent 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 (**?**).