Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract
Résumé de l'article.

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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 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, 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 the corresponding mechanisms (**??**). Forests response to disturbance 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 assessed the maintenance of ecosystems processes and services (**???**). However the response of tree species diversity although it is determinant of ecosystems productivity, stability and functioning (**?**) and it would be most probably impacted by the biotic and abiotic changes after disturbance (**?**).

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 are crucial for conservation issues, and evenness, that revealing 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 functonial 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-months dry season (< 100 mm.months^{-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 throught a Bayesian framework. The uncertainty propagation was done by the replenishment of

inventories completed at genus level from real incomplete ones on the basisof 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.

To avoid remaining identification caveats and consider complete inventories, the simulated inventories were then reported at genus. 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 traits 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.

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

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

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	$[35\% - 56\%]$

(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 1984 (5 year after disturbance). 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 (**?**). >>To tackle the unequal number of recruited trees among treatments the indices bias corrected estimator were used, following (**??**).

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.

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 ordination in a two dimensional ordiantion 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
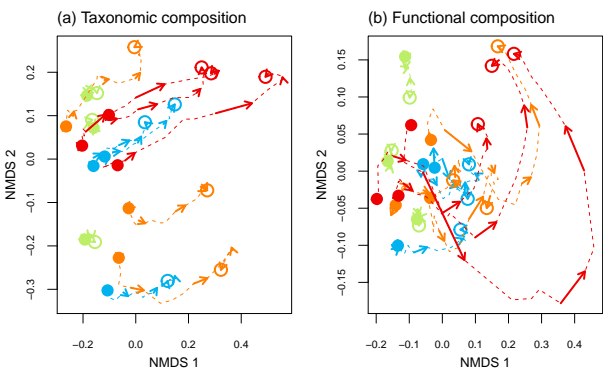

Figure 1. Trajectories of the plots in terms of **(a)** flora composition and **(b)** functional composition regarding the 6 leaf and stem functional traits,the maximum allometric height and seed mass class in the two-dimensional space from the NMDS performed for the 30 years after disturbance. Distance 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).

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 ($\rho_{spearman}^{taxonomic} = 0.91$) as well as functional composition ($\rho_{spearman}^{taxonomic} = 0.96$). 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 barck thickness and seed mass and maximum adult height) visaualized 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 ($\rho_{spearman}^{L_t hickness} = 0.67, \rho_{spearman}^{L_{chloro}} = 0.45, \rho_{spearman}^{L_t oughness} = -0.43, \rho_{spearman}^{SLA} = 0.93, \rho_{spearman}^{WD} = -0.78, \rho_{spearman}^{Bark_{thick}} = 0.88, \rho_{spearman}^{Hmax} = -0.48$).

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 diversity 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 genuses (plot 3 from treatment 2). When the disturbance was intense however, plot staxonomic richness followed a unimodal decrease with a return to initial values after intense disturbance. The taxonomic evenness (Shannon and Simpson diversities) significantly increased whenever 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 ($\rho_{spearman} = XX$) (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 avule

and to those of control plots.

4. Discussion

4.1 A validation of the intermediate disturbance hypothesis

The monitoring 30 years of disturbed forest communities confirmed the limited direct impact of low disturbance on species richness as it was found for impact survey of selective logging (**??**). Only the most disturbed plots had not fully achieved the ongoing recovery of genus richness, although all had already reached equivalent levels as those of some control plots. Such long time richness recovery had already been observed in several logging experiments, which also highlighted the role of random disturbance damage in the richness decrease (**??**).

The evenness of all disturbed plots and the richness of low disturbance plots on the other hand mainly followed an asymptotic growth sharply increasing until 15 years after disturbance. Such increased evenness is explained by a much more homogeneous species distribution after disturbance. Communities composition after disturbance is either due to the old, pre-disturbance survivors or to the recruited trees. The composition of old survivors proved to mirror the initial community (**?**), the observed composition turnover would stem from an enhanced the growth and survival of previously infrequent species which, along with the IDH, reorganizes the typical high dominance structure of hyperdiverse mature forests. This increase in taxonomic diversity was accompanied by an increased taxonomic dissimilarity to initial state along time, translating a a taxonomic turnover benefiting to pioneers and light demanding species, as illustrated by the communities 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) (**???**). Post-disturbance changes in abiotic environment and competitive pressure then well favored pioneers outcompeting other species when abiotic resources are abundant but otherwise excluded in mature forests by long-lived, resistant and shade tolerant species. The trajectories of proportions among seed mass classes besides revealed the enhanced growth of small seeded, large dispersive, species and therefore the importance of species reproductive strategy which further supported the role of species dispersion and demographic strategy for the post-disturbance dynamics, as suggested by the IDH (**???**).

4.2 On the recovery of disturbed communities

The functional diversity followed a hump-back trajectory which maximum was positively correlated to the disturbance intensity ($\rho_{spearman} =$) and after 30 years, all disturbed plots had recovered diversities close to their initial values. Similar hump-back trajectories were followed by all leaf and stem functional traits and life history traits, to the exception of leaf chlorophyll content. Although the return to initial values was still ongoing the recovery of functional diversity and average communities trait values was undeniable. This translated the recovery of ecosystems processes (**?**), as functional traits are the most direct link between biodiversity
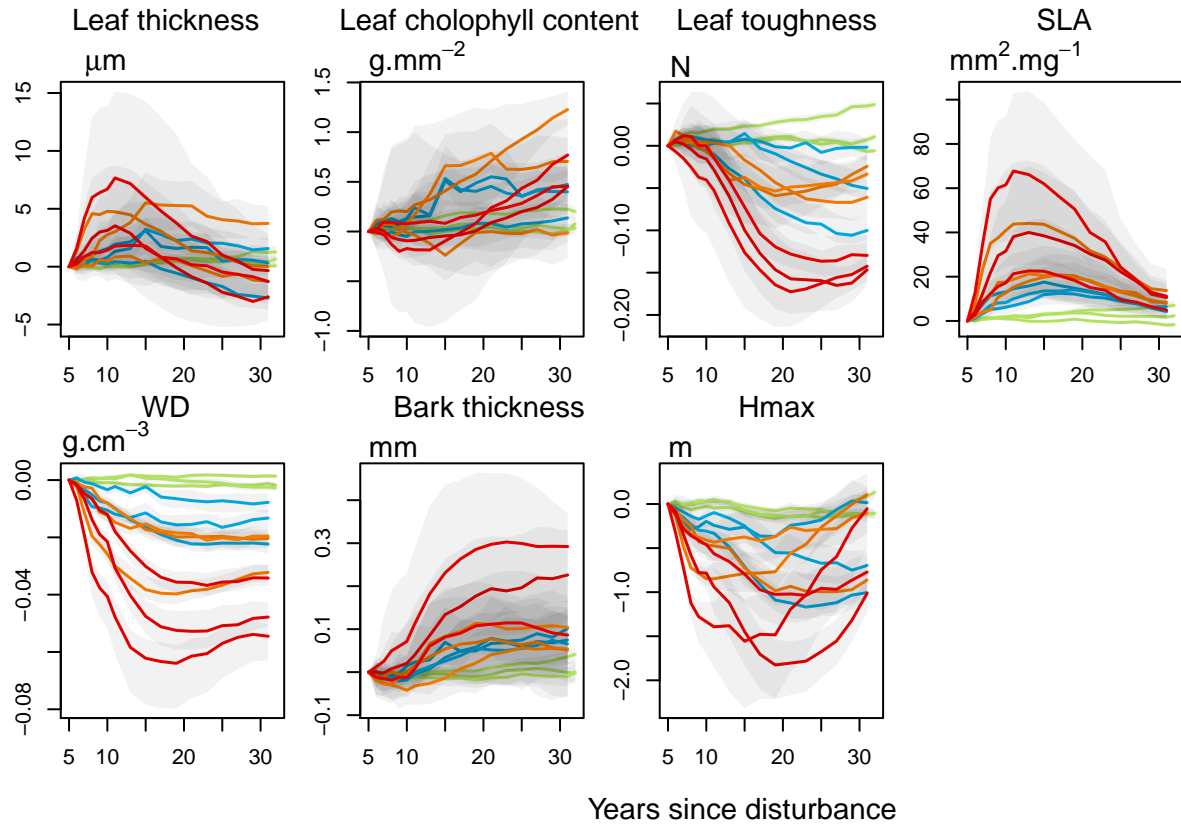
Community Weighted Means

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 colorswith green for control, blue for T1,orange for T2 and red for T3.
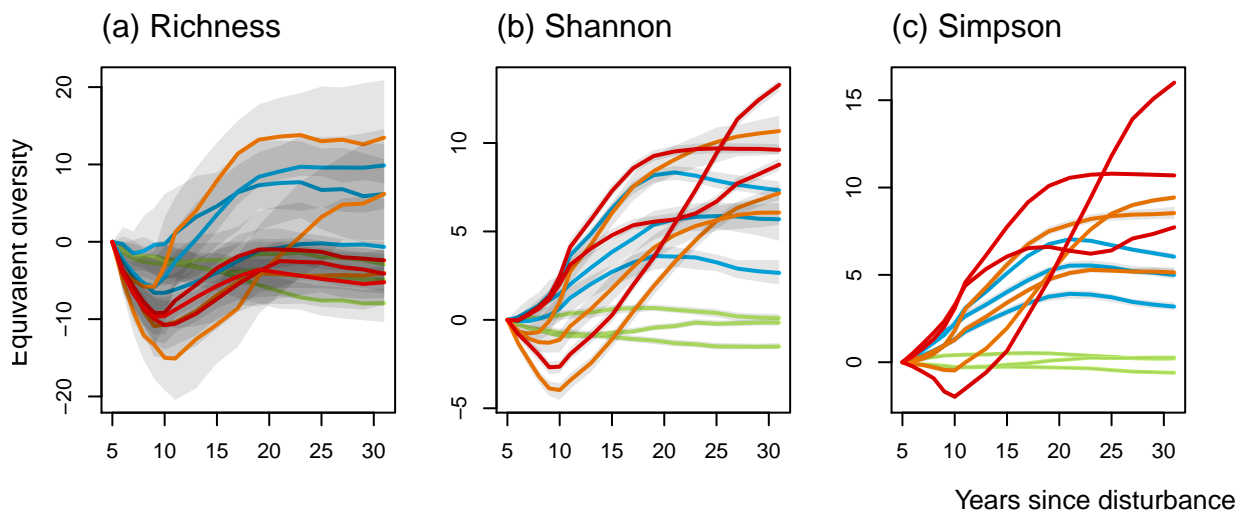

Figure 3. Trajectories of the difference to the 1989 inventories (5 years after disturbance) over 30 years after disturbance of plots communities **(a)** Richness, **(b)** Shannon and **(c)** Simpson diversities. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray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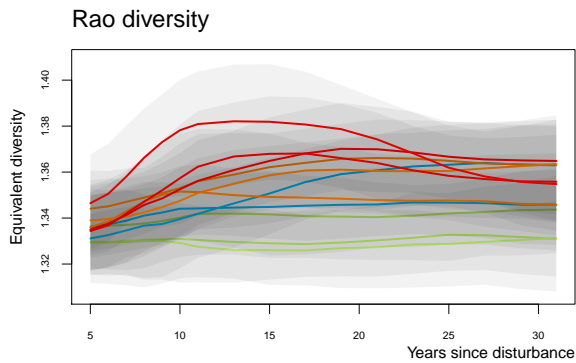
Rao diversity

Figure 4. Trajectories of the Rao functional diversity 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. Initial treatments are represented by solid lines colorswith green for control, blue for T1,orange for T2 and red for T3.and the missing trait value filling processes.

and ecosystem functioning (**?**). Same recovery trajectories were followed by taxonomic and functional composition which argued for communities convergence and the maintenance of plots initial difference (**???**). These compositon difference, and probably also some abiotic parameters, besides strongly determined the maximum and time path of the trajectories which, despite an homogeneous trend were quite variable among plots.

4.3 Functional redundancy of disturbed ecosystems

Despite the consistent recovery of initial diversity and composition there was a time lag between the communities taxonomic and functional characteristics. Taxonomic composition had longer time path and while communities had recovered their functional diveristy, their taxonomic composition and evenness remained higher than before disturbance. This delay between functional and taxonomic dynamics was already observed for grasslands (**??**) and more recently for tropical forests (**??**). Communities functional diversity rely, according to the "vegetation quantity effect" (**?**), on the functional strategy of dominant species. Communities functional trajectory is then first driven by the increase of dominant species diversity and evenness following disturbance and then by the emergence of recruitment of species progressively resembling the old pre-disturbance community which decreased the diversity. Dominant species then restored the functional diversity and the dominant functional type of the community although the functional and taxonomic composition remained altered and the infrequent species of initial communities are still missing to plots recovery. The functional traits trajectories suggest that those species would match the dominant functional type therefore increasing communities functional redundancy. The functional overlap between species is typical of the huge biodiversity of tropical forests (**?**), and proved far from recovery 03 years after

disturbance. It is though a determinant of forests resilience and should be accounted for (**???**).

Long-term alteration of functional redundancy besides came along with persistent compositional changes which most probably impact disturbance resistant species (**?**) and probably lianas or epiphytes (**?**), and the modification of environmental conditions like soils nutrient cycling and compaction (**?**) forest resilience remains under question (**?**). 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. The subsequent diversity trajectories confirmed the intermediate disturbance hypothesis debated for tropical forests through their correlation with disturbance intensity. Besides it revealed the contrasting response of taxonomic and functional characteristics, specifically the decoupling between communities taxonomic evenness and their functional diversity and dominant functional traits values. The long-term disturbance trajectories observed highlighted the unachieved but consistent recovery of communities assembly for the lowest disturbance intensity but questioned it after higher disturbance.