Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract
Understanding the ecological rules underlying the maintenance of tropical forests biodiversity, structure, functioning and dynamics is urgent to anticipate their fate in the global changing context. The huge diversity of tropical forests is often assumed to be shaped by constant regime of disturbance yielding a diversity peak at intermediate intensity, but for tropical forests this intermediate disturbance hypothesis (IDH) remains debated, and this controversy also questions the extent of communities resilience regarding their functional and taxonomic facets is also to be clarified. To disentangle the ecological processes driving communities response to disturbance we analysed the taxonomic and functional diversity trajectories following a logging and thinning disturbance gradient. Specifically we examined over 30 years the trajectories of communities taxonomic richness and evenness and functional composition, diversity and redundancy based on 7 leaf, stem and life history traits. Trajectories highlighted the cyclic recovery of communities taxonomic composition, maintaining the pre-disturbance differences, as well as functional composition and diversity. The IDH predicted communities functional response to disturbance that resulted from competition processes determined by the disturbance intensity. The IDH however poorly represented the taxonomic response that relied upon lottery recruitment and recruitment limitation which hampered the recovery of infrequent, shade tolerant species. After disturbance communities functioning followed a cyclic recovery and the initial composition differences among plots were maintained. Although consistent the recovery of communities functioning and taxonomic composition and diversity remained unachieved after 30 years which acknowledged the need of decades-long recovery cycles to ensure a complete recovery, and questioned communities sustainability after repeated disturbance.

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, and the carbon, water and nutrient cycles, and ensure cultural and human well-being. The growing demand in forests products together with current climatic changes increases the pressure on remaining forests (**??**) and threatens the maintenance and dynamics in space and time of communities structure, composition and functioning (**??**).

In tropical forests, ecological communities are constantly re-shaped by natural disturbance events that change both the abiotic environment, through the fluxes of light, heat and water (**?**), and the biotic interactions like competition among species (**??**). One of the cornerstone of tropical forest ecology is to understand the processes and drivers of

ecosystems response to disturbance (**??**). For now, this has been largely studied through forest structural parameters, rapid and convenient to measure, as aboveground biomass, tree height or stem density (**??**). These structural parameters were thereafter sucessfully modeled, giving important insights into the recovery of ecosystems processes and services (**?**). However the response of forests diversity is still unclear, albeit it determines the productivity, stability and functioning of ecosystems (**?, ?**) and would be most probably impacted by the changes induced by disturbance (**?**). In the short-term, moderate disturbance may lead to positive impacts on communities diversity, which have been formalized by the intermediate disturbance hypothesis (IDH) stating a maximized species diversity when the disturbance regime is moderate but significant (**???**). Along time the IDH would translate into a variety of post-disturbance trajectories shaped by the different ecological processes at stake.

Validations of the IDH though remain scarce in the long term and mainly rely on the analysis of species richness. Species richness though gives limited or misleading information on forests recovery and functioning (**??**): more complete analysis would encompass communities composition that is crucial for conservation issues, and abundance distribution that reveals the ecological processes involved (**???**). Furthermore, a functional approach accounting for species biological attributes and assessing their role in the ecosystem would directly link communities diversity to the ecosystem functioning and to its environmental constraints (**????**). In that respect, the functional trait-based approach that focused on major traits related to species ecology and performance was sucessfully adopted (**??**). For example the functoinal approach revealed in tropical rainforests the deterministic processes fostering fast growing species with efficient resources acquisition after disturbance (**???**). Disturbance therefore entails a functional shift 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 (**???**). This shift is translated into consistent trajectories of 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) (**????**). Eventually a complete overview of communities response to disturbance would encompass the changes in functional redundancy, that quantifies the amount of shared trait values among species (**?**). High functional redundancy like in the very diverse tropical forests (**?**) mitigates the impacts of species removal on ecosystem functioning and determines the resilience of communities (**???**). High functional redundancy also increases the functional overlap among species and would foster neutral stochastic processes (**?**).

To grasp all facets of communities response to disturbance we examined here the taxonomic and functional trajectories in terms of richness, evenness, composition and redundancy (**??**). These trajectories would highlight the recovery of communities initial characteristics and the underlying ecological processes, and provide indications for future adaptive conservation strategies (**?**). They would clarify the tenants of the Intermediate Disturbance Hypothesis in the long term, debated in tropical forests, and explicit the variety of post-disturbance trajectories defined by the disturbance intensity. We monitored over 30 years the response of 75 ha of neotropical forest 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, richness, evenness and redundancy. Specifically, we (i) questioned the recovery of communities taxonomic and functional characteristics and identify the underlying assembly processes, (ii) clarified the validity of the IDH in the long term for tropical forest and elucidated its declination into different trajectories, and (iii) questioned the length of complete communities recovery.

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 (**?**). 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 fuelwood cutting treatments (Table **??**) 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 (**??**). The disturbance intensity was measured as the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984 and five years after disturbance (**?**) estimated with the BIOMASS R package (**?**).

2.2 Inventories protocol and dataset collection

The study site corresponds to a tropical rainforest typical of the Guiana Shield 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 have been mapped and measured annually since 1984. Trees are first identified during inventories with a vernacular name assigned by the forest worker team, and afterward with a scientific name assigned by botanists 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 distinguishing

trees and palm trees. From 2003, botanical campaigns have been conducted every 5 to 6 years to identify all trees at the species level but identification levels 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 based on the association probability $[\alpha_1, \alpha_2, \ldots, \alpha_3]$ observed across all inventories between each vernacular name v and the species $[s_1, s_2, \ldots, s_N]$:

$$M_v\Big([s_1, s_2, \ldots, s_N], [\alpha_1, \alpha_2, \ldots, \alpha_3]\Big)$$

See appendix 1 and **?** for the detailed methodology.

Six 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) came from the BRIDGE project [1]. Traits 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. Missing trait values were filled using multivariate imputation by chained equation (**?**). Imputations were restricted within genus, or family when samples were 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 were 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 levels (in space) and protocols (in time), 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 NMDS ordination space of 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 abundance-based (Bray-Curtis) dissimilarity measures. Trajectories

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

along time were reported through the distance between successive inventories and the reference inventories in 1989, *i.e.* 2-3 years after disturbance, when the uncertainty degree did not exceed 30% of undetermined trees. for the taxonomix composition trajectories were measured by the euclidean distance between inventories in the multivariate space of all inventories species. For the functoinal composition trajectories were measured by the sum for all traits of the euclidean distances between the traits density distributions of successive inventories. To compensate the intrinsinc difference among plots, the trajectories corresponded to the euclidean differences along time with the reference inventory in 1989. Univariate trajectories of the leaf, stem and life-history traits were also visualized with the community weighted means (CWM) (**??**). 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 reported through species richness and the evenness, *i.e* the Hill number translation of the Simpson index (**?**). These two indices belong to the set of HCDT or generalized entropy, respectively corresponding to the 0 and 2 order of diversity (q), recomended 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 impacts of initial disturbance were tested with the spearman rank correlation between the extremum of taxonomic and functional metrics reached over the 30 years and the initial %AGB removed. The were besides 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 community functional space (**?**). 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 richness and evenness

From 1989 (2-3 years after disturbance) to 2015 (28-29 years after disturbance), 828388 individual trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. For undisturbed plots taxonomic Richness and Evenness (Simpson diversity) remained stable over the 30 years monitored. In disturbed communities after low disturbance intensity the taxonomic richness increased, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2). After intense disturbance the taxonomic richness followed unimodal trajectories, decreasing for ten years after disturbance before recovering to pre-disturbance

values. In all disturbed plots the taxonomic evenness (Simpson diversity) followed unimodal trajectories with first an increase until a maximum reached after around 20 years that was positively correlated to the disturbance treatment ($\rho_{spearman}^{Shannon} = 0.86$, and $\rho_{spearman}^{Simpson} = 0.89$). The return towards initial values of communities evenness was beginning after 30 years except for two T3 plots (plots 8 and 12) which evenness still increased, suggesting similar but delayed trajectories 1.

The plot 7 from treatment 1 displayed a constantly outlying functional evenness and was removed from the graphical representation for better readability (see appendix for full graphs). In undisturbed plots the functional evenness remained stable along the 30 years while in disturbed plots it followed unimodal trajectories with a return towards initial values starting 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 **??**. 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

While both taxonomic and functional composition remained stable in undisturbed communities (Figure 5), 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 5). 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)

Changes in functional composition trajectories went hand to hand with consistent trajectories of the 8 functional traits (Figure 6). 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 6). 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

In control plots the functional redundancy remained stable but in undisturbed plots it was quite variable and independent of the disturbance intensity (See appendix I). 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 ($\rho_{spearman} = 0.50$) and the initial value had not recovered for any disturbed communities.

4. Discussion

4.1 Communities cyclic recovery

Communities taxonomic and functional composition and functional evenness proved resilient, following similar humped-shaped trajectories starting to return towards pre-disturbance composition and functioning after 30 years.

The taxonomic differences among communities, marked before disturbance by the distinct starting points of the NMDS, were maintained throughout communities recovery trajectories. More than commonly thought post-disturbance trajectories depended on communities initial composition, that partly determined the pool of recruitable species and that constrained the converge towards the recovery of the initial composition (**????**). The resilience of communities taxonomy suggested the existence of multiple stable equilibria, here the pre-disturbance communities, as assumed for highly diverse and productive ecosystems (**?**).

Communities functional composition followed similar trajectories that were not so distinct in the functional space. The trajectories of functional evenness as well were similar among communities Communities functional characteristics are the most direct link between biodiversity and ecosystem functioning and their resilience here meant the recovery of ecosystem processes and services ona cycle of several decades (**??**).

4.2 Another view of the intermediate disturbance hypothesis

The IDH consistently predicted communities functional response to disturbance and the functional trajectories in time highlighted the underlying ecological mechanisms, but the theory was diproved regarding communities taxonomic richness and evenness.

With the studied range of intensity, disturbance enhanced communities functional evenness but did not have

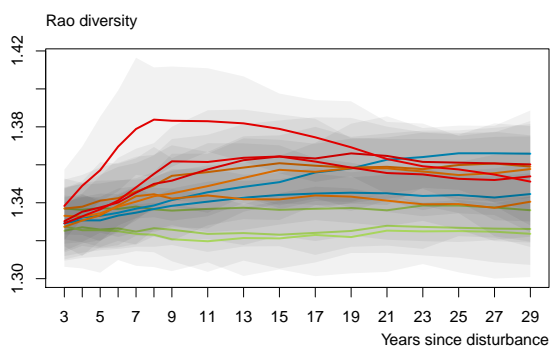## (a) Richness
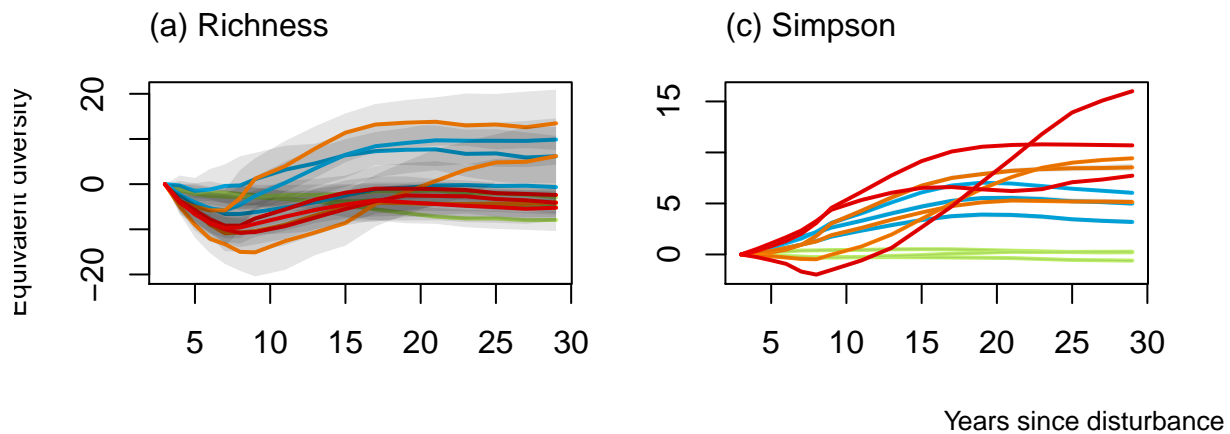
(c) Simpson

Figure 1. 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 2. Trajectories of the Rao functional diversity over 30 years after disturbance. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals.

clear impact on taxonomic richness or evenness. The IDH proved a good predictor of the disturbance impact on communities functioning but not on their taxonomic richness or evenness.

The humped-shaped trajectories of communities along time illustrated the processes enhancing the functional evenness and the changes in functional composition following disturbance before communities return towards initial composition and lower evenness. Disturbance entailed significant variability in the communities through the emergence of ecological processes different from thoses involvemnt before disturbance, in accordance with the IDH. The increase in functional evenness went with 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) (**???**). Because the pre-disturbance survivor trees mirror the initial communities (**?**), the functional changes relied upon recruited trees and the enhanced growth and survival of previously infrequent species and functional types. Disturbance vacated environmental niches of high light, space and nutrient availability, filled by competitive pioneers that became dominant and determined the functional characteristics of the community (**?**). Before disturbance and over communities recovery time though, these species would be excluded by long-lived, more resistant and shade tolerant species.

In contrast the taxonomic richness and evenness were decoupled from the disturbance intensity, questioning the consistency of the IDH as already observed in the Guiana Shield (**?**) and in Bornean tropical forests (**?**). The recovery of communities functional characteristics, that mostly rely on dominant species according to the "vegetation quantity
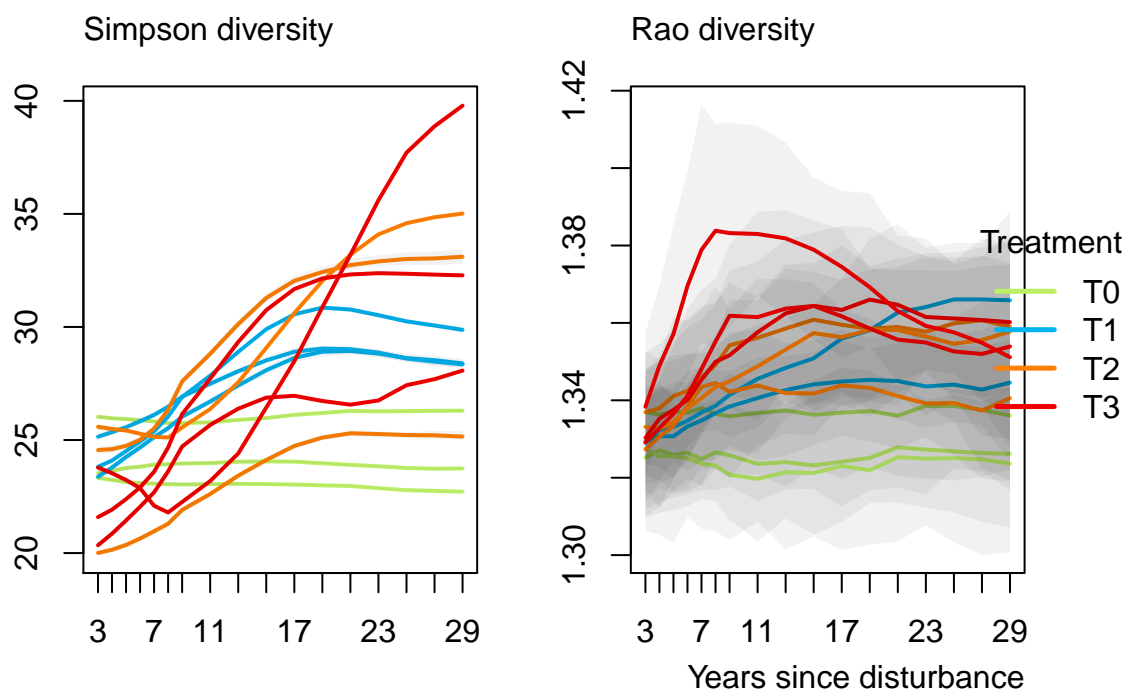
Figure 3. Upper panels, Trajectories of the taxonomic evenness (Simpson diversity) **(a)** and Rao functional diversity **(b)** over 30 years after disturbance. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals. Lower panels, Relationship between the initial %AGB removed and Simpson **(c)** and Rao **(d)** diversities 10, 20 and 30 years after disturbance.
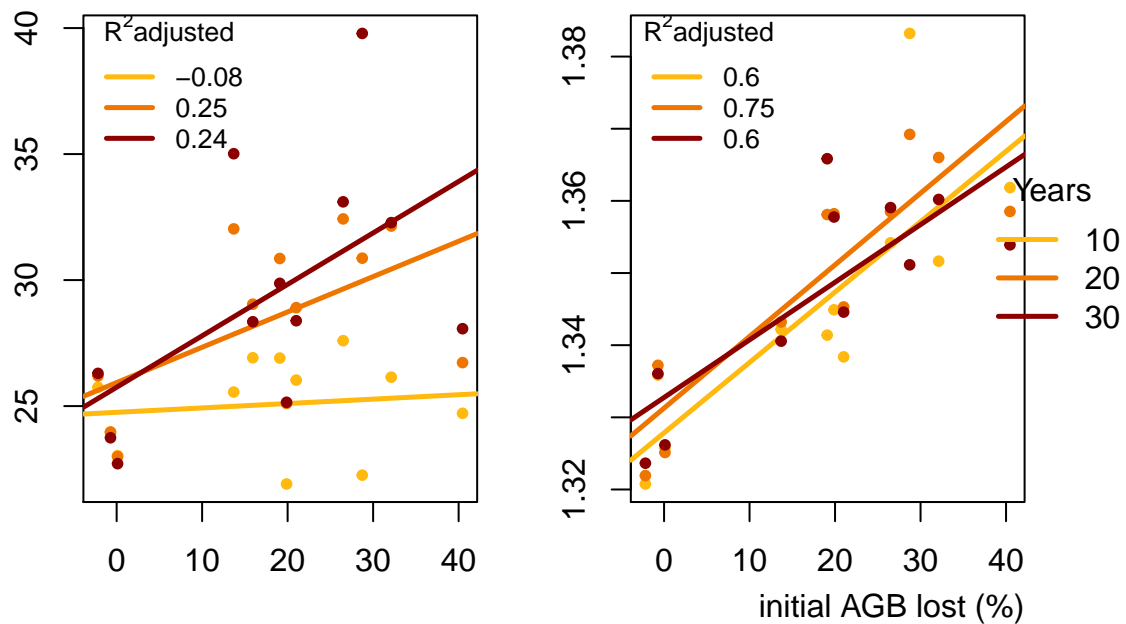
Figure 4. Upper panels, Trajectories of the taxonomic evenness (Simpson diversity) **(a)** and Rao functional diversity **(b)** over 30 years after disturbance. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals. Lower panels, Relationship between the initial %AGB removed and Simpson **(c)** and Rao **(d)** diversities 10, 20 and 30 years after disturbance.
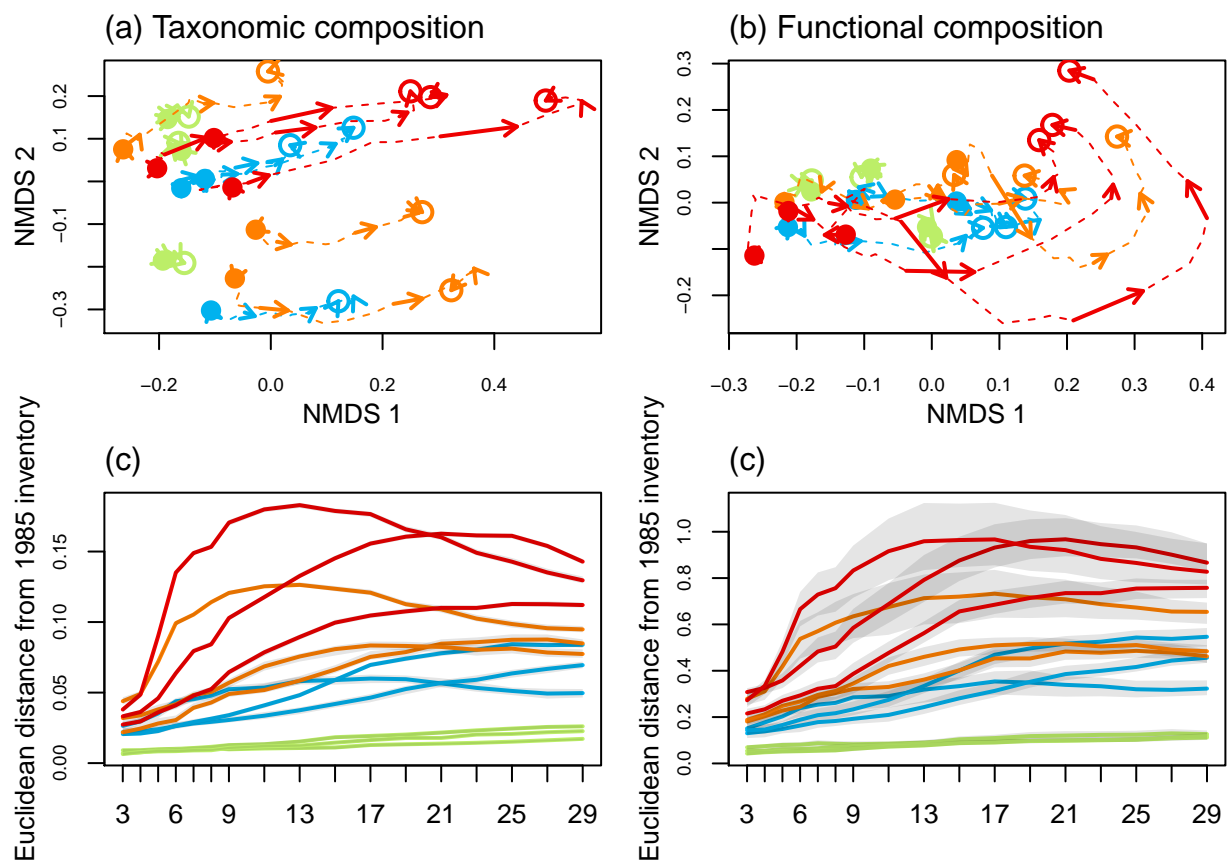
**Figure 5.** Plot trajectories in terms of flora composition (left panels (**a**) and (**c**)) and functional composition (right panels (**b**) and (**d**)) in a two-dimensional NMDS space. Lower panels ((**c**) and (**d**)) represent the euclidean distance to initial condition along the 30 sampled years. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals
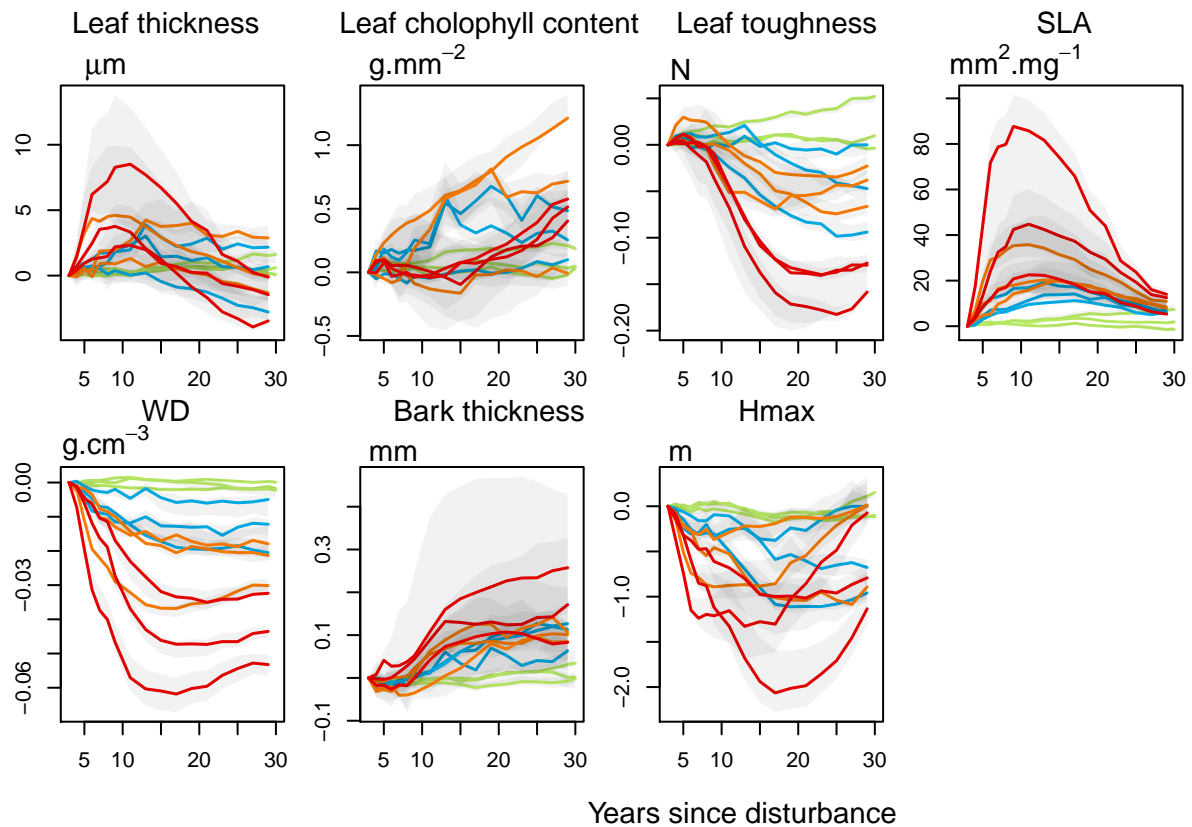
Figure 6. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, *L_thickness*, chlorophyll content, *L_chloro*, toughness, *L_toughness* and specific area, *SLA*), 2 stem traits (wood specific gravity, *WD*, and bark thickness, *Bark-thick*) and one life history trait (Specific maximum height at adult stage, *Hmax*). Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals.
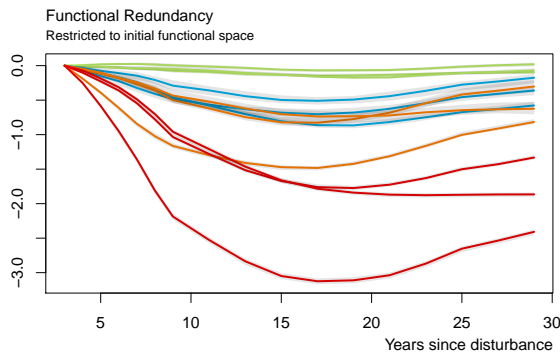
Figure 7. TTrajectories of functional redundancy within the initial functional space over 30 years after disturbance. Colors are disturbance treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals.
(#fig:RedFun_rest)

effect" (**?**), suggested a similar recovery of the dominant species (**?**). Still, the taxonomic trajectories were blurried by the hampered recovery of infrequent species that entailed after disturbance a decrease in the taxonomic richness and an increase of the evenness (**??**). The disturbance therefore porrly predicted commuties taxonomic richnessa and evennes that rely upon different ecological processes.

4.3 The functional redundancy, key of the taxonomic resilience

The recovery of the most infrequent species followed the lottery recruitment rules (**?**) and was hampered by the increasing competition among species, implying long term recovery (**???**).

Following disturbance the space and resources made available corresponded to a rapid decrease of the functional redundancy within the initial functional space. The high light, space and nutrient niches were rapidly filled by species, mainly the most dominant and frequent ones. Thereafter competitive exclusion emerged following the filling of the niches and limited the recruitment of infrequent species (**?**). The recovery of communities taxonomic richness and evenness relied upon the recovery of the initial functional redudancy. Although underway 30 years after disturbance the recovery remained unachieved and after 30 years the recovery it was underway but remained unachieved. This alteration of the functional redundancy meant a lower resilience of pre-disturbance communities and higher chances to see the persistence of disturbance-specific communities, with less species and more pioneers (**???**). Besides the slowed recovery of rare species increased the risks to loose cornerstone specie, with unexpected ecological consequences (**????**). Apart from the functional characteristics considered here, infrequent species mighthave unique functions i nthe ecosystem or be a key for some fauna.

5. Conclusions

Our study revealed communities cyclic recovery after disturbance allowing the resilience of their functioning and taxonomic composition with the maintenance of initial differences among communities. Communities functional evenness was enhanced for 20 years after disturbance through the enrichment of the communities with pioneers and light-demanding species,in accordance with the IDH. The IDH, though, poorly predicted the disturbance impact on communities taxonomic richness and evenness that were blurried by the emergence of competitive exclusion along time. The resilience of tropical forests proved consistent although spread over several decades. Still, the disturbance impact on communities redundancy cautioned against the risks of infrequent species loss and the persistence of disturbance-specific communities (**?**). As the trajectories highlighted the recruitment processes proved central for communities response to disturbance and closer focus on demographical drivers of communities response would clarify the fate of the future forests.

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