

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 communities taxonomic resilience, maintaining their initial differences in composition, and functional resilience through fast functional trajectory common to all communities in the functional space. The IDH consistently predicted communities functional trajectories according to the disturbance intensity, but poorly represented their taxonomic trajectories, blurred by the alteration of the functional redundancy and the recruitment of infrequent, shade tolerant species slowed by competitive exclusion processes. Although communities functioning had recovered after 30 years their taxonomic diversity and composition in infrequent species and their functional redundancy remained altered. these results acknowledged the need of decades-long recovery cycles to ensure communities complete resilience, and questioned communities maintenance 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 forest, 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 successfully 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 at intermediate disturbance intensity (???). Still, validations of the IDH remain scarce in the long term and mainly rely on the analysis of species richness that gives limited or misleading information on forests recovery and functioning (??). More complete analysis would besides encompass communities composition that is crucial for conservation issues, and abundance distribution to reveal the ecological rules structuring communities (???). Furthermore, a functional approach accounting for species biological attributes and role in the ecosystem directly links ecosystems biodiversity, functioning and environmental constraints (????). The functional trait-based approach focused on major traits related to species ecology and performance was successfully adopted (??), for example to reveal in tropical rainforests the deterministic processes that foster after disturbance the fast growing species with efficient resources acquisition (???). This basic deterministic process 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) (????). Besides communities functional composition and diversity, a last key aspect of communities response to disturbance is the changes in functional redundancy that quantifies the amount of shared trait values among species (?). High functional redundancy, as in the very diverse tropical forests (?), mitigates the impacts of species removal on ecosystem functioning and determines communities resilience (???). 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 diversity and composition (??). These trajectories would highlight the recovery of communities initial composition, diversity and functioning and the underlying ecological processes. They would clarify the tenants in the long term of the Intermediate Disturbance Hypothesis debated in tropical forests, and provide indications for future adaptive conservation strategies (?). 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 and diversity. Specifically, we (i) questioned the coupling between taxonomic and functional response to disturbance and identified the underlying assembly processes, (ii) clarified the validity of the IDH in the long term for tropical forest and (iii) questioned the completeness of communities recovery regarding communities functional redundancy.

2. Material and Methods

2.1 Study site

Paracou station in French Guiana (5°18'N and 52°53'W) is located in a lowland tropical rain forest in a tropical wet climate with mean annual temperature of 26°C, mean annual precipitation averaging 2980 mm.y⁻¹ (30-y period) and a 3-month dry season (< 100 mm.month⁻¹) from mid-August to mid-November, and a one-month dry season in March (?). 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 $[\alpha_1, \alpha_2, \dots, \alpha_3]$ observed across all inventories between each vernacular name v and the species $[s_1, s_2, \dots, s_N]$:

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

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 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. Taxonomic trajectories were measured through the euclidean distance between inventories in the multivariate space of all inventories species. Functional trajectories were measured through

the sum of euclidean distances among traits density distributions between inventories. To compensate the intrinsic 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 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), recommended 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 first tested with the spearman rank correlation between the extremum of taxonomic and functional metrics reached over the 30 years and the initial %AGB removed. Then they were analysed through the linear correlations between Simpson and Rao diversities and the initial %AGB removed at 10, 20 and 30 years after disturbance.

The functional redundancy was measured as the overlap among species in 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 scheme).

3. Results

3.1 Communities Diversity

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 Richness and taxonomic evenness (Shannon and Simpson diversities) remained stable over the 30 years monitored. In disturbed communities the taxonomic richness increased after low disturbance intensity, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2) while it followed unimodal trajectories after intense disturbance, decreasing for ten years before recovering to pre-disturbance values. In all disturbed plots the taxonomic evenness (Shannon and Simpson diversities) increased, following unimodal trajectories with a maximum, reached after around 20 years, positively correlated to the disturbance treatment ($\rho_{\text{Spearman}}^{\text{Shannon}} = 0.86$, and $\rho_{\text{Spearman}}^{\text{Simpson}} = 0.89$). Return towards initial evenness values was beginning after 30 years except for two T3 plots (plots

¹<http://www.ecofog.gf/Bridge/>

8 and 12) which evenness still increased, suggesting similar but delayed trajectories 1.

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

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

3.2 Communities Composition

3.2.1 Taxonomic and functional trajectories

While both taxonomic and functional composition remained stable in undisturbed communities (Figure 2), they followed consistent trajectories over time after disturbance which revealed significant compositional changes. According to the mapping of functional traits (see appendix I) these compositional changes corresponded to shifts towards species with more acquisitive functional strategies, from communities with high average WD to high average SLA and chlorophyll content. For disturbed communities the distance of successive inventories to the 1989 reference inventory followed unimodal trajectories translating cyclic compositional changes with a recovery of the initial composition (Figure 2). The maximum dissimilarity with the initial state was positively correlated to the disturbance treatment for both taxonomic and functional composition ($\rho_{\text{Spearman}}^{\text{taxonomic}} = 0.91$ and $\rho_{\text{Spearman}}^{\text{functional}} = 0.96$ 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 3). 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 (H_{max}), leaf toughness ($L_{\text{toughness}}$) and wood specific gravity (WD) remained significantly lower than their initial value (Figure 3). The weighted means of bark thickness ($Bark_thick$) similarly remained substantially higher than initially for all disturbed plots while the specific leaf area (SLA) had almost recovered its

initial value. For all traits the maximum difference to initial state was correlated to the disturbance intensity ($\rho_{\text{Spearman}}^{L_{\text{thickness}}} = 0.67$, $\rho_{\text{Spearman}}^{L_{\text{chloro}}} = 0.45$, $\rho_{\text{Spearman}}^{L_{\text{toughness}}} = -0.43$, $\rho_{\text{Spearman}}^{SLA} = 0.93$, $\rho_{\text{Spearman}}^{WD} = -0.78$, $\rho_{\text{Spearman}}^{Bark_thickness} = 0.88$, $\rho_{\text{Spearman}}^{H_{\text{max}}} = -0.48$).

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 ($\rho_{\text{Spearman}} = 0.50$) and the initial value had not recovered for any disturbed communities.

4. Discussion

Si on met que richesse et evenness,
pour fonctional c'est de l'evenness
(Rao = order2)

4.1 Communities cyclic recovery

Both taxonomic and functional composition proved resilient and followed similar humped-shaped trajectories starting to return towards initial values 30 years after disturbance.

The taxonomic NMDS revealed differences in the composition of initial communities that proved maintained throughout the recovery trajectories after disturbance. More than commonly though, communities trajectories after disturbance was specific to the initial composition and converged towards its recovery (????). The resilience of communities taxonomy suggested the existence of multiple stable equilibria, corresponding here to communities initial composition, as assumed for highly diverse and productive ecosystems (?).

Contrastingly communities functional composition and diversity proved more homogeneous among communities and communities functional trajectories were similar in the functional space. Communities functional characteristics are the most direct link between biodiversity and ecosystem functioning (?) so their resilience meant the recovery of ecosystem processes in the long term (?).

4.2 Another view of the intermediate disturbance hypothesis

The initial disturbance intensity determined the maximum functional diversity increase, confirming the IDh within this range of disturbance. Regarding communities communities along time, the humped-shaped trajectories of the functional diversity following disturbance demonstrated the positive impact of disturbance that enhanced the diversity before a return to initial lower diversity levels. In accordance with the IDH disturbance entailed ecological processes different than in undisturbed communities and a temporal variability correlated to the intensity of the disturbance. The functional

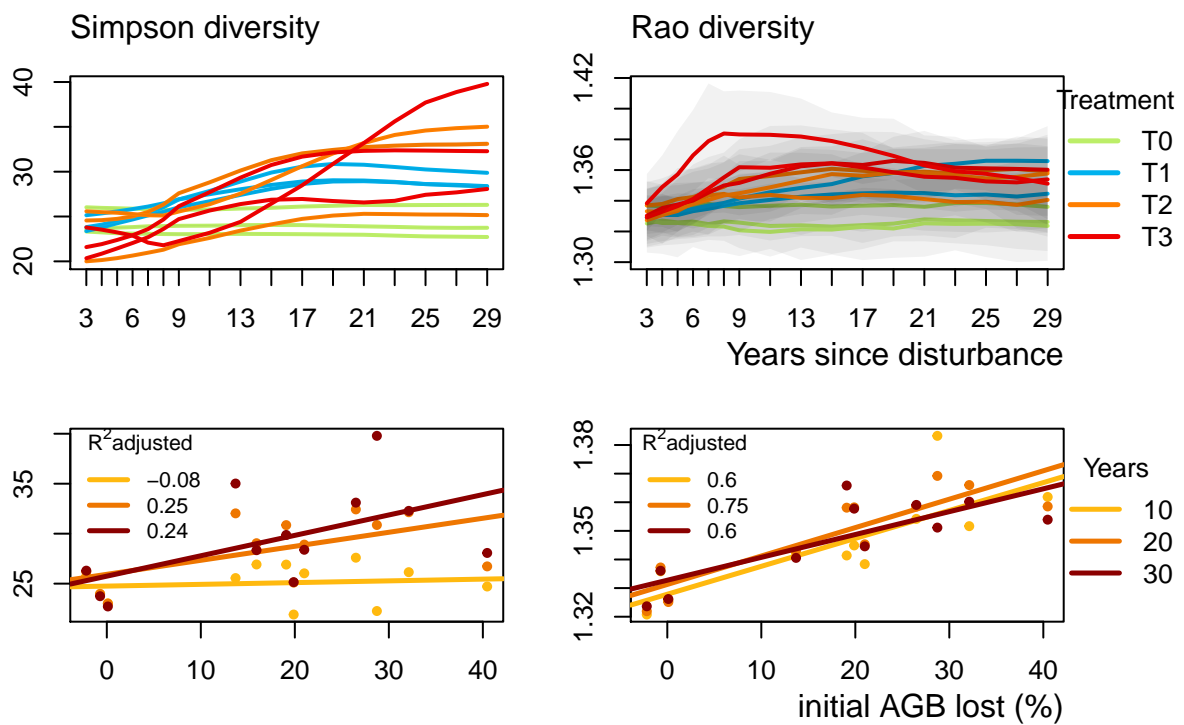


Figure 1. Upper panels, Trajectories of the Simpson taxonomic diversity (a) and Rao functional diversity (b) over 30 years after disturbance. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals. Lower panels, Relationship between the initial %AGB removed and Simpson (c) and Rao (d) diversities 10, 20 and 30 years after disturbance.

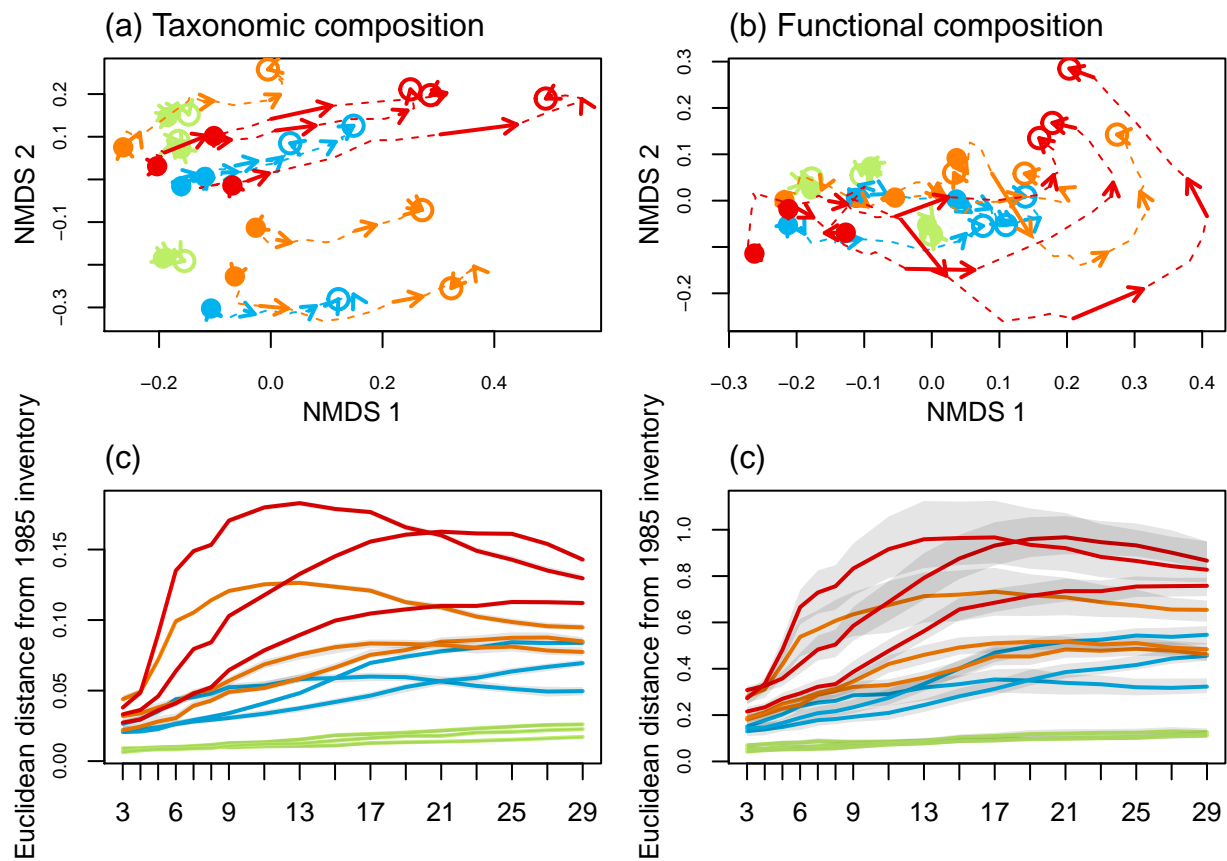


Figure 2. Plot trajectories in terms of flora composition (left panels (a) and (c)) and functional composition (right panels (b) and (d)) in a two-dimensional NMDS space. Lower panels ((c) and (d)) represent the euclidean distance to initial condition along the 30 sampled years. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals

Community Weighted Means

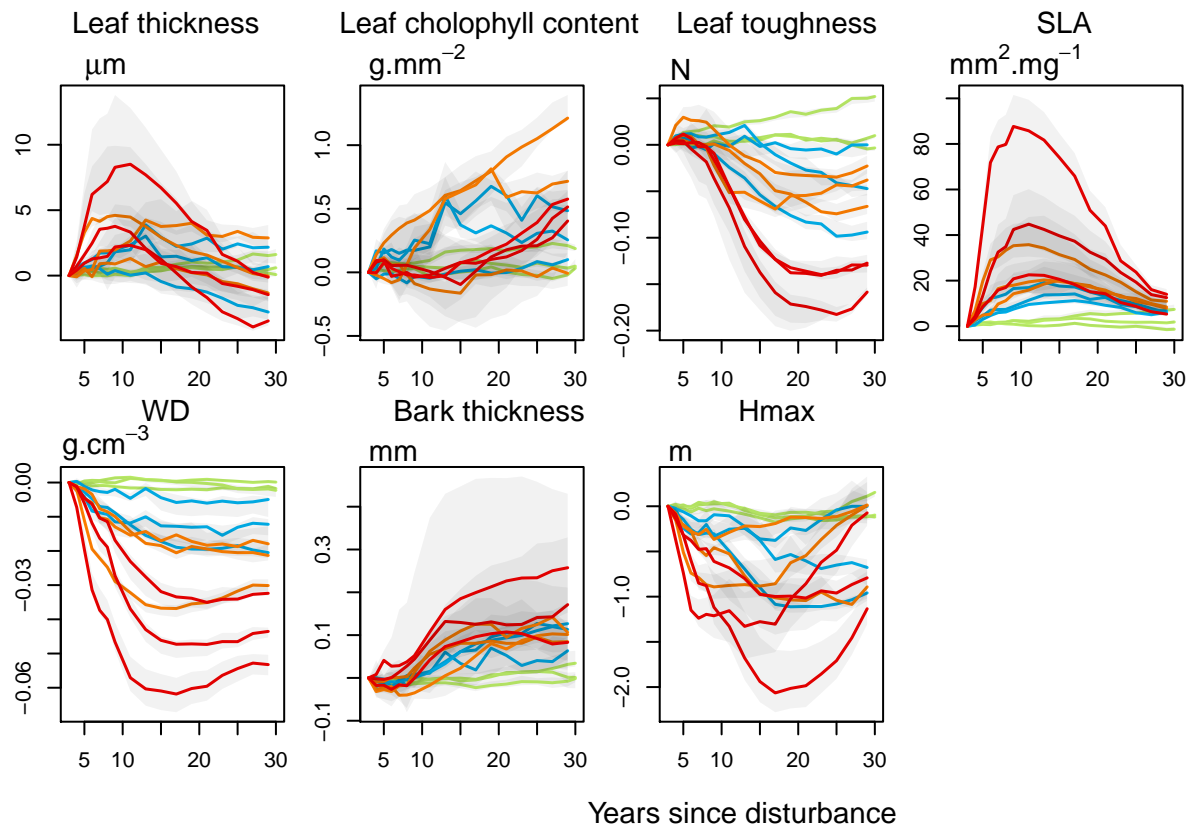


Figure 3. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, $L_{thickness}$, chlorophyll content, L_{chloro} , toughness, $L_{toughness}$ and specific area, SLA), 2 stem traits (wood specific gravity, WD , and bark thickness, $Bark-thick$) and one life 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.

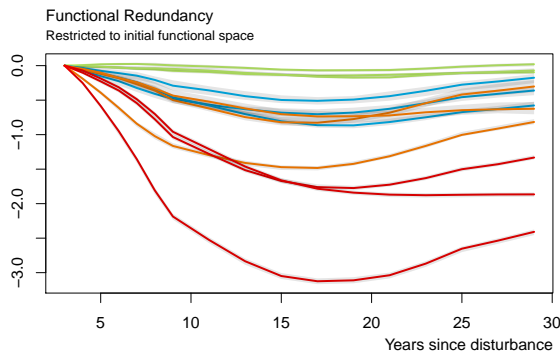


Figure 4. Trajectories of functional redundancy within the initial functional space over 30 years after disturbance. Colors are disturbance treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals.

(#fig:RedFun_rest)

diversity increase paralleled the 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) (???). As the old-growth, pre-disturbance survivor trees proved mirroring the initial communities (?) the functional trajectories and taxonomic turnover rather relied upon the pool of newly recruited trees driven by the enhanced growth and survival of previously infrequent species and functional types. The changes in abiotic environment and competitive pressure favored pioneers which outcompeted other species in non limiting light resources but were excluded in mature forests by long-lived, more resistant and shade tolerant species. >> Not clear Disturbance trajectories therefore relied upon the environmental niches made available and filled by species from a restricted functional range that became dominant and structured the functional characteristics of the community (?).

In contrast the trajectories of taxonomic richness and evenness were decoupled from the disturbance intensity, questioning the consistency of the IDH to predict communities taxonomic diversity, as already observed in the Guiana Shield (?) and in Bornean tropical forests (?).

In the most disturbed plots the taxonomic richness did not exceed this of the initial communities but the taxonomic evenness significantly increased, revealing the loss of most infrequent species. Dominant species fastly recovered and restored the communities functional characteristics that mostly rely on dominant species, according to the “vegetation quantity effect” (?), while the recovery of more infrequent species was hampered. >> Not clear The intermediate disturbance hypothesis was suitable to predict communities functional diversity and pool of dominant species (?), but it poorly represented the whole taxonomic structure that was hampered by the slow recovery of rare species (??).

4.3 The functional redundancy, key of communities resilience

The recovery of the most infrequent species was hampered by the competition among species, in accordance with the lottery recruitment (?) and entailed long term recovery cycles (???).

The progressive increase of the functional redundancy within the initial functional space, that had first sharply decreased, explains the lottery recruitment that first allow an easy taxonomic recovery and then a progressive slow down. functional redundancy restricted to the functional space of the initial community clearly followed. After disturbance communities differently occupied the functional space, following the observed shifts in traits trajectories and functional composition, and the redundancy in the initial functional space decreased according to the disturbance intensity. After 30 years the recovery of the initial redundancy structure was consistent but remained unachieved.

unclear The persistent alteration of functional redundancy meant a lower resilience of pre-disturbance communities and an higher resilience disturbance-specific communities (corresponding to lower richness and higher dominance of pioneer species) so chances to observe self-maintained compositional changes in favor of disturbance resistant species, lianas or epiphytes were increased after disturbance (???).

unclear (cornerstone?) This decades-long recovery specifically increased the risks of losing cornerstone species, with unexpected ecological consequences (???). Indeed the flora-fauna relationship and the functional traits studied are not exhaustive and key function might be lost. specifically for the fauna-flora relationships.

5. Conclusions

Our study defined the decoupled functional and taxonomic trajectories of tropical rainforests after disturbance demonstrating a rapid functional recovery but a slower and more variable taxonomic one. Consistently with the IDH, functional trajectories were driven after disturbance by enrichment of the system with pioneers and light-demanding species.

unclear The following functional shifts entailed a re-organization of communities functional redundancy that proved long to recover and explained the more variable and longer taxonomic trajectories as shade tolerant species of old-growth forests faced

functional redundancy and limiting similarity processes.

The resilience of tropical forests then proved long in the face of quite intense disturbance and did not preclude the settling of a persistent disturbance-specific community (?). 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.

unclear The disturbance range however stayed within the spectrum of selective logging, with a forest cover remaining all along the experiment, and the response mechanisms would probably be much different after harder disturbance.

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