

Post-Disturbance Tree Community Trajectories in a Neotropical Forest

Ariane MIRABEL^{1*}

Eric Marcon¹

Bruno Hérault^{2 3}

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 change context. The huge diversity of tropical forests is often assumed to be regularly reshaped by natural disturbance yielding a diversity peak at intermediate intensity, but this intermediate disturbance hypothesis (IDH) remains debated, and this controversy also questions the extent of communities resilience regarding their functional and taxonomic facets. To disentangle the ecological processes driving community response to disturbance, we analysed the taxonomic and functional diversity trajectories following a disturbance gradient. Specifically, we examined, over 30 years, the functional and taxonomic community trajectories with regards to diversity, composition and redundancy. Functional trajectories were drawn based on 7 leaf, stem and life-history traits. We highlighted the cyclic recovery of community taxonomic and functional composition. The pre-disturbance taxonomic differences were maintained over time while the functional composition trajectories were quite similar. The IDH did predict communities functional diversity response while taxonomic diversity remained poorly sensitive to disturbance intensity. Although consistent, the recovery of community composition, diversity and redundancy remained unachieved after 30 years. This acknowledged the need of decades-long cycles with no disturbance to ensure a complete recovery, and questioned tropical forest community resilience after repeated disturbance.

Keywords

Taxonomic and Functional Biodiversity, Neotropical Forests, Disturbance Trajectories, Intermediate Disturbance Hypothesis, Long-term Resilience

¹UMR EcoFoG, AgroParistech, CNRS, Cirad, INRA, Université des Antilles, Université de Guyane.
Campus Agronomique, 97310 Kourou, France.

²Cirad, Univ Montpellier, UR Forests & Societies.
Montpellier, France.

³INPHB, Institut National Polytechnique Félix Houphouët-Boigny
Yamoussoukro, Ivory Coast.

*Corresponding author: ariane.mirabel@ecofog.gf, <http://www.ecofog.gf/spip.php?article47>

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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 and regional climates, the carbon, water and nutrient cycles, and ensure cultural and human well-being. The growing demand in forests products together with current global changes increases the pressure on remaining natural forests (Gibson *et al.*, 2011; Morales-Hidalgo *et al.*, 2015) and threatens the maintenance and dynamics in space and time of communities structure, composition and functioning (Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015).

In tropical forests, ecological communities are regularly re-shaped by natural disturbance events changing both the abiotic environment, through the fluxes of light, heat and water (Goulamoussène *et al.*, 2017), and the biotic interactions such as competition among species (Chesson, 2000; Hérault & Piconiot, 2018). One of the cornerstone of tropical forest ecology is to understand the processes and drivers of ecosystems response to disturbance (White & Jentsch, 2001; Chazdon, 2003). For now, this has been

largely studied through forest structural parameters such as aboveground biomass, tree height or stem density (Piponiot *et al.*, 2016; Rutishauser *et al.*, 2016) that are rapid and convenient to measure. These structural parameters have been successfully modeled, giving important insights into the recovery of ecosystem processes and services (Héroult & Piponiot, 2018). However the response of forests diversity and composition is still unclear, albeit it determines the productivity, stability and functioning of ecosystems (Tilman *et al.*, 2014; Liang *et al.*, 2016). In the short-term, moderate disturbance may lead to positive impacts on communities diversity, an idea formalized by the intermediate disturbance hypothesis (IDH) stating a maximized species diversity when disturbance intensity is not too high (Molino & Sabatier, 2001; Kariuki *et al.*, 2006; Berry *et al.*, 2008).

Validations of the IDH though remain scarce in the long-term and mainly rely on the analysis of taxonomic richness (Molino & Sabatier, 2001). Taxonomic richness alone, though, gives limited or misleading information on forests recovery and functioning (Martin *et al.*, 2015; Chaudhary *et al.*, 2016). More ecological-meaningful analysis would couple richness with (i) evenness that would reveal underlying ecological processes and (ii) composition that is crucial for conservation issues (Magurran, 1988; Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Furthermore, a functional approach accounting for species biological attributes would directly link communities diversity, composition and redundancy to ecosystem functioning and to its environmental constraints (Violle *et al.*, 2007; Moretti *et al.*, 2009; Baraloto *et al.*, 2012; Scheiter *et al.*, 2013). In that respect, the functional trait-based approach that focus on major traits related to species ecology and mediate species performance in a given environment was successfully adopted (Díaz *et al.*, 2005; Villéger *et al.*, 2008). For instance, the functional approach revealed in tropical rainforests the deterministic processes entailing, after disturbance, 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 (TerSteege & Hammond, 2001; Reich, 2014; Héroult *et al.*, 2011). This shift is translated into the trajectories of key functional traits related to resource acquisition (leaf and stem traits) and life-history traits (seed mass, maximum size) (Wright *et al.*, 2004; ter Steege *et al.*, 2006; Westoby & Wright, 2006; Chave *et al.*, 2009). 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 (Carmona *et al.*, 2016). The high functional redundancy of hyperdiverse tropical forests (Bellwood *et al.*, 2006) mitigates the impacts of species removal on ecosystem functioning and determines the resilience of communities after disturbance (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

In this study, 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 aboveground biomass (AGB) loss. We made use of a large functional traits database encompassing major leaf, stem and

life-history traits in order to draw the taxonomic and functional trajectories in terms of richness, evenness, composition and redundancy (Lohbeck *et al.*, 2015; Guariguata & Ostertag, 2001). Specifically, we (i) questioned the recovery of communities taxonomic and functional characteristics and identified the underlying assembly processes, (ii) clarified the validity of the IDH in the long term for tropical forest and elucidated its translation into different trajectories, and (iii) questioned community recovery time.

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 (Wagner *et al.*, 2011). 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 disturbance 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 (Schmitt & Bariteau, 1989; Blanc *et al.*, 2009). The disturbance intensity was measured as the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984 and five years after disturbance (Piponiot *et al.*, 2016) estimated with the BIOMASS R package (Réjou-Méchain *et al.*, 2018).

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. In the twelve experimental plots, all trees above 10 cm DBH have been mapped and measured annually since 1984. Trees are first identified 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 were 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 in time 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 all 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 Aubry-Kientz *et al.* (2013) for the detailed methodology.

Six functional traits representing leaf economics (leaves thickness, toughness, total chlorophyll content and specific leaf area) and stem economics (wood specific gravity and bark thickness), and life-history traits (maximum specific height and seed mass) came from the BRIDGE project¹. Trait values were assessed from a selection of individuals located in nine permanent plots in French Guiana, including two in Paracou, and comprised 294 species pertaining to 157 genera. Missing trait values (10%) were filled using multivariate imputation by chained equation (van Buuren & Groothuis-Oudshoorn, 2011). Imputations were restricted within genus or family when samples were too scarce, in order to account for the phylogenetic signal. Whenever a species was not in the dataset, it was attributed a set of trait values randomly sampled among species of the next higher taxonomic level (same genus or family). As seed mass information was classified into classes, no data filling process was applied and analyses were restricted to the 414 botanical species recorded.

All composition and diversity metrics were obtained after 50 iterations of the uncertainty propagation framework.

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. Taxonomic and functional trajectories of community composition were followed in a two-dimensional NMDS ordination space. Two NMDS using abundance-based (Bray-Curtis) dissimilarity measures were conducted to map either taxonomic or functional composition, the later based on the 7 leaf, stem and life history traits (without seed mass classes). Trajectories along time were reported through the euclidean distance between the target inventories and the reference inventories in 1989, *i.e.* 2 years after disturbance. Univariate trajectories of the leaf, stem and life-history traits were also visualized with the community weighted means (CWM) (Díaz *et al.*, 2007; Garnier *et al.*, 2004). 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 (Supp Mat XX).

The taxonomic diversity was reported through species richness and evenness, *i.e.* the Hill number translation of

the Simpson index (Hill, 1973). These indices belong to the set of HCDT or generalized entropy, respectively corresponding to the 0 and 2 order of diversity (q), recommended for diversity studies (Patil & Taillie, 1982; Tothmeresz & Tóthmérész, 1995; ?). The functional diversity was reported using the functional richness and functional evenness, *i.e.* Rao index of quadratic entropy which combines species abundance distribution and average pairwise dissimilarity based on species functional traits.

The impacts of initial disturbance were tested with the spearman rank correlation between the extrema of taxonomic and functional metrics reached over the 30 years and the initial %AGB loss. They were besides analysed through polynomial regression between (i) taxonomic and functional richness and evenness and (ii) the initial %AGB loss at 10, 20 and 30 years after disturbance.

The functional redundancy was measured as the overlap among species in community functional space (Carmona *et al.*, 2016). The samples of the trait database were first mapped in a 2-dimensional plan with 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. Community 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 richness and evenness

From 1989 (2 years after disturbance) to 2015 (28 years after disturbance), 828 388 individual trees and 591 botanical species pertaining to 223 genus and 64 families were recorded. For undisturbed plots, taxonomic Richness and Evenness 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 a more complex trajectory, decreasing for ten years after disturbance before recovering to pre-disturbance values. The maximum richness loss or gain after disturbance was positively correlated to the disturbance intensity ($\rho_{\text{spearman}}^{\text{Richness}} = 0.50$). In all disturbed plots the taxonomic evenness first increased until a maximum reached after around 20 years. This maximum was positively correlated to the disturbance intensity ($\rho_{\text{spearman}}^{\text{Evenness}} = 0.77$). The evenness then stabilized except for two T3 plots (plots 8 and 12) for which evenness kept increasing.

The plot 7 from treatment 1 displayed constantly outlying functional richness and evenness and was removed from the graphical representation for better readability. In undisturbed plots both functional richness and evenness remained stable along the 30 years. In disturbed plots, functional richness and evenness trajectories depended on the disturbance intensity with their maximum positively correlated to %AGB loss $\rho_{\text{spearman}}^{\text{Richness}} = 0.76$ and $\rho_{\text{spearman}}^{\text{Evenness}} = 0.60$. Functional richness and evenness displayed for low dis-

¹<http://www.ecofog.gf/Bridge/>

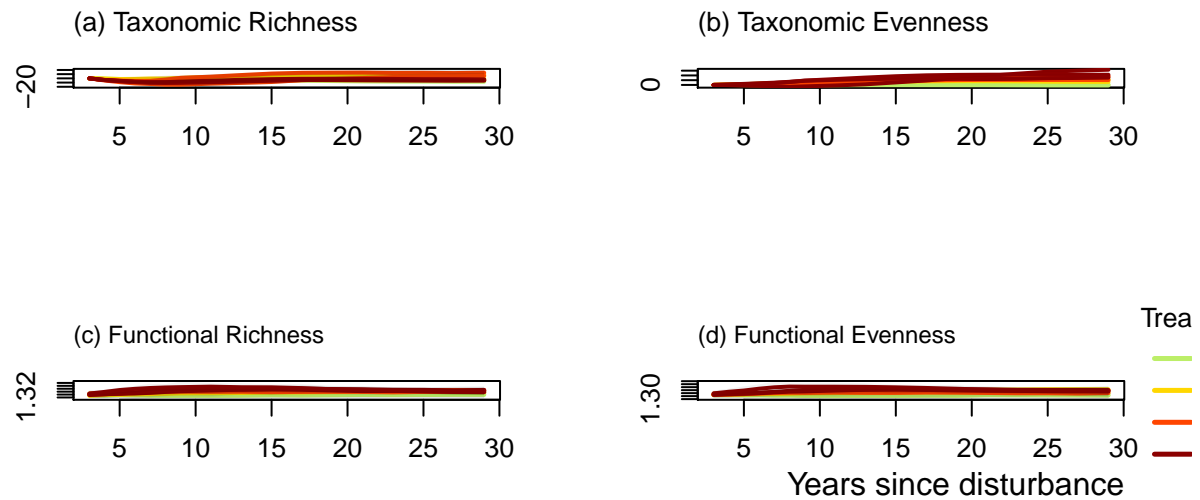


Figure 1. Trajectories over 30 years of the difference with the 1989 inventory (2 years after disturbance) of community taxonomic (a) richness, (b) taxonomic evenness, (c) functional richness, and (d) functional evenness. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals

turbance intensity a low but long-lasting increase up to a maximum reached after 20–25 years, and for high intensity, a fast but short increase followed after 10 years by a slow decrease towards the initial values.

The second-degree polynomial regressions between (i) the %AGB loss and (ii) taxonomic and functional richness and evenness after 10, 20 and 30 years best predicted the hump-shaped curve of the disturbance impact along the disturbance intensity gradient 2. The relationship between the disturbance impact and its intensity was more markedly hump-shaped for the taxonomic richness than for the taxonomic evenness. For both functional richness and evenness the relationship was almost linear. The regression model better predicted the functional richness and evenness ($0.55 < R^2_{\text{FunctionalRichness}} < 0.72$, and $0.60 < R^2_{\text{FunctionalEvenness}} < 0.81$) than the taxonomic richness and evenness ($0.21 < R^2_{\text{TaxonomicRichness}} < 0.4$, and $-0.15 < R^2_{\text{TaxonomicEvenness}} < 0.43$ respectively)

3.2 Communities Composition

While both taxonomic and functional composition remained stable in undisturbed communities (Figure 3), they followed marked and consistent trajectories over post-disturbance time. In disturbed communities, these compositional changes corresponded to shifts towards species with more acquisitive functional strategies, from communities with high average WSG to high average SLA and chlorophyll content (see appendix I). For functional composition, this translated into cyclic compositional changes with an unachieved recovery of the initial composition (Figure 3). The maximum dissimilarity with the initial state was positively correlated to the disturbance intensity for both taxonomic and functional composition ($\rho_{\text{spearman}}^{\text{taxonomic}} = 0.87$ and $\rho_{\text{spearman}}^{\text{functional}} = 0.90$ respectively). The maximum value was reached around 26

years after disturbance for taxonomic composition and 22 years for functional composition.

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.

Maximum height at adult stage (H_{max}), leaf toughness ($L_{\text{toughness}}$) and wood specific gravity (WSG) first decreased and then slightly increased but remained significantly lower than their initial value (Figure 4). On the other side, Bark thickness (B_{thick}) and specific leaf area (SLA) increased and while B_{thick} remained substantially high after 30 years, SLA had almost recovered its initial value. For all traits, the maximum difference to initial value was correlated to the disturbance intensity ($\rho_{\text{spearman}}^{L_{\text{thickness}}} = 0.76$, $\rho_{\text{spearman}}^{L_{\text{chloro}}} = 0.60$, $\rho_{\text{spearman}}^{L_{\text{toughness}}} = -0.53$, $\rho_{\text{spearman}}^{SLA} = 0.93$, $\rho_{\text{spearman}}^{WSG} = -0.75$, $\rho_{\text{spearman}}^{B_{\text{thickness}}} = 0.71$, $\rho_{\text{spearman}}^{H_{\text{max}}} = -0.40$).

3.3 Functional redundancy

All disturbed plots had lower functional redundancy than control plots and followed similar hump-shaped trajectories (@ref(fig:RedFun_rest)). The maximum redundancy loss was positively correlated with the disturbance intensity ($\rho_{\text{spearman}} = 0.47$) and the initial value had not recovered for any disturbed communities after 30 years.

4. Discussion

4.1 A cyclic recovery of community composition

Communities taxonomic and functional composition appeared resilient, following similar hump-shaped trajectories starting to return towards pre-disturbance composition after 30 years. The taxonomic differences among communities,

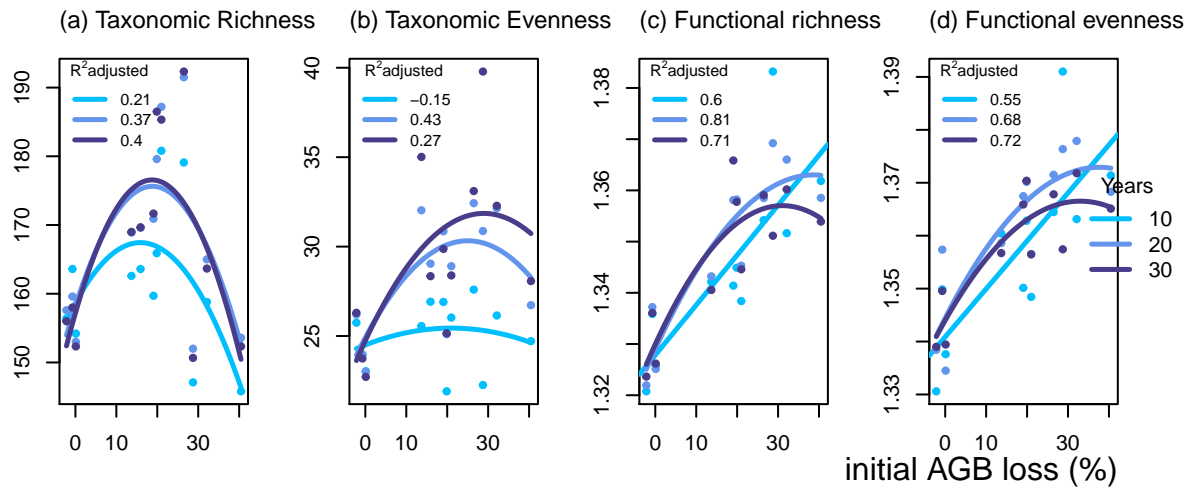


Figure 2. Relationship between the initial %AGB loss and community taxonomic richness (a), taxonomic evenness (b), functional richness (c), and functional evenness (d) at 10, 20 and 30 years after disturbance. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals

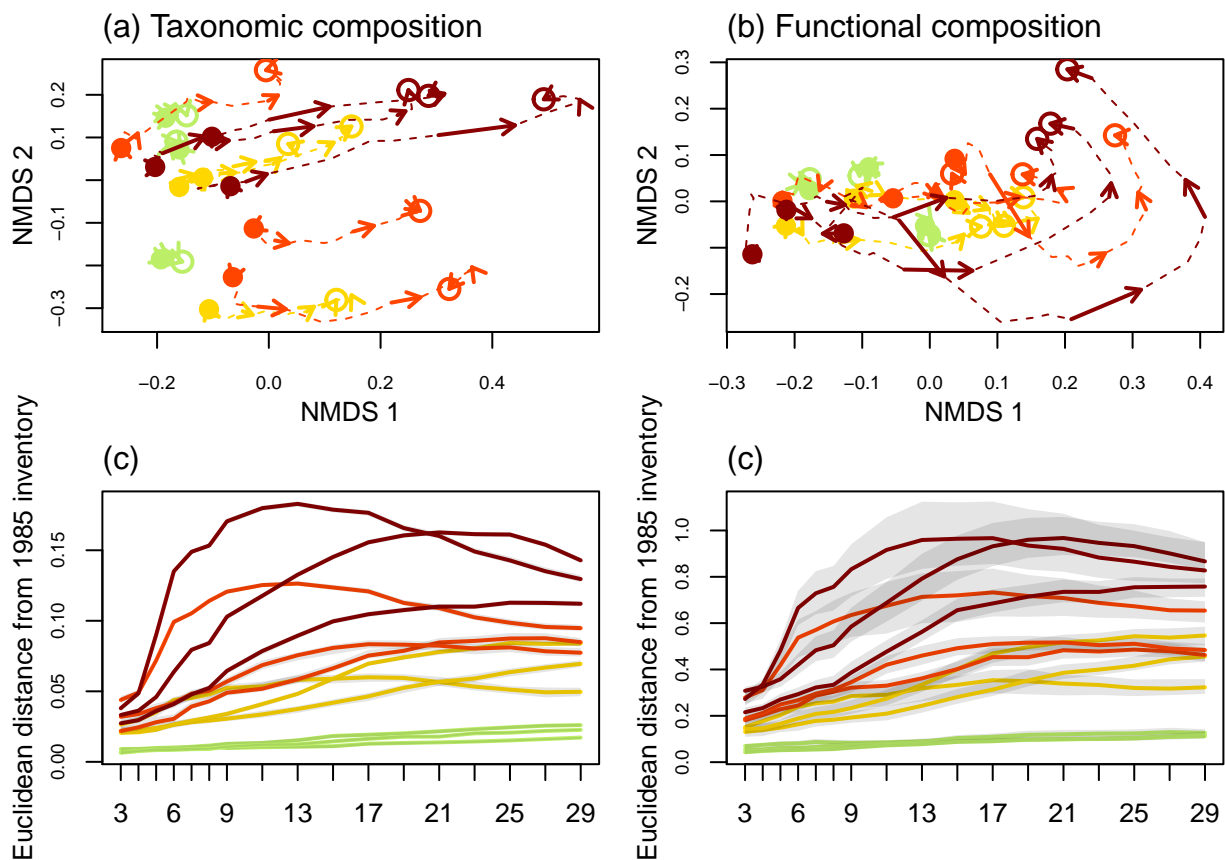


Figure 3. Plot trajectories in terms of flora composition (left panels (a) and (c)) and functional composition (right panels (b) and (d)) in a two-dimensional NMDS space. Lower panels ((c) and (d)) represent the euclidean distance to initial condition along the 30 sampled years. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals

Community Weighted Means

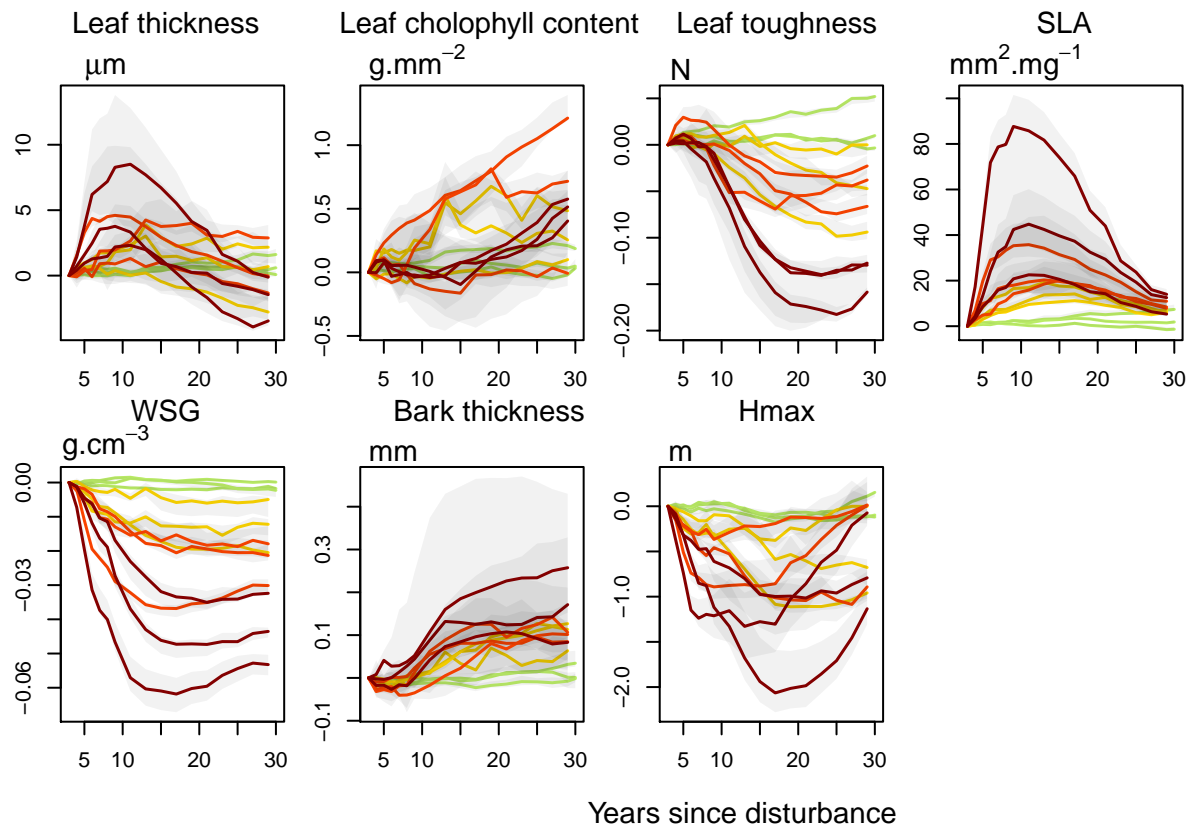


Figure 4. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, $L_{thickness}$, chlorophyll content, L_{chloro} , toughness, $L_{toughness}$ and specific area, SLA), 2 stem traits (wood specific gravity, WSG , and bark thickness, $Bark-thick$)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

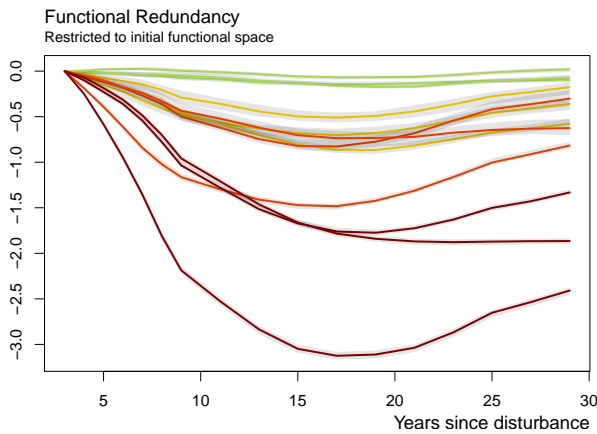


Figure 5. Trajectories of the functional redundancy within the initial functional space over 30 years after disturbance. Colors are disturbance treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals.
(#fig:RedFun_rest)

marked before disturbance by the distinct starting points on the NMDS axis 2, were maintained throughout recovery trajectories. More than commonly thought, post-disturbance trajectories depended on community initial composition, that partly determined the pool of recruited species and constrained the trajectories towards the initial composition. The high resilience of communities taxonomy revealed that species not belonging to the pre-disturbance community were hardly recruited because of the commonness of dispersal limitation among tropical tree species (SVENNING & Wright, 2005).

Trajectories of community functional composition appeared similar in time and close in terms of functional composition. Because pre-disturbance surviving trees mirror the initial community (Hérault & Pioniot, 2018), changes in functional composition relied upon the recruitment of species or functional types infrequent or absent before disturbance. Competitive pioneers became dominant in filling the environmental niches of high availability of light, space and nutrient made available by the disturbance. It changed community functional composition in the same way for all communities, towards more resource-acquisitive strategies (Grime, 1998; Westoby, 1998; Wright *et al.*, 2004; Reich, 2014). Later during the community recovery long-lived, more resistant and shade-tolerant species, would exclude those pioneers and restore the pre-disturbance composition.

4.2 Another perspective on the intermediate disturbance hypothesis

Disturbance appeared to enhance community taxonomic richness until an intensity threshold (20-25% of initial AGB loss), while the taxonomic evenness was somewhat decoupled from the disturbance intensity as already observed in the Guiana Shield (Baraloto *et al.*, 2012) and in Bornean tropical forests (Cannon, 1998). The IDH well predicted the disturbance impact on community taxonomic richness and to some extent on taxonomic evenness. The disturbance intensity determines the balance in the community between

pre-disturbance surviving trees and the trees recruited afterward. In the Guiana Shield, the pool of true pioneer species specifically recruited after disturbance is restricted to a few common genera (e.g. *Cecropia* spp., *Vismia* spp.). Below the intensity threshold the size of the surviving community maintains its pre-disturbance taxonomic richness and the recruitment of pioneers, infrequent or absent before disturbance, increases both community taxonomic richness and evenness. Beyond the intensity threshold the taxonomic diversity of the surviving trees decreases and is not offset by the taxonomic enrichment of pioneers. The disturbance impact was similar but slighter for community taxonomic evenness, that is less sensitive to the loss of rare species and rather represents the increased dominance of pioneers that balanced the usual hyper-dominance of tropical forest. While below the intensity threshold pioneers species increase the diversity of dominant or common species, beyond the threshold they become in turn highly dominant.

Conversely the IDH was disproved to predict the disturbance impact on community functional diversity. Pioneer species were functionally highly different from the pre-disturbance community composition, so their recruitment increased the community functional richness and evenness whenever its intensity.

Along time, the post-disturbance taxonomic richness trajectories showed first a similar drop following the species loss during disturbance, and then a species gain determined by the disturbance intensity. Until an intensity threshold the gain in taxonomic richness increased with the disturbance intensity through the establishment of long-lived pioneers enhancing community taxonomic richness and evenness in the long term. These long-lived pioneers were functionally quite different from the functional composition and their establishment entailed a progressive and long-lasting increase of the functional diversity. Beyond the intensity threshold a few short-lived pioneers occupied the vacated environmental space and prevented further species establishment. These short-lived pioneers were functionally very different from the pre-disturbance community and rapidly and significantly increased the functional diversity. Already after 10 years, though, they started to decline and the functional diversity started to decrease. Likely the establishment of long-lasting pioneers will follow and we expect the taxonomic and functional trajectories to catch up with those observed after intermediate disturbance.

4.3 The functional redundancy, key of the community resilience

For 15 years the species loss during disturbance, determined by the disturbance intensity, commensurately decreased the functional redundancy within the pre-disturbance functional space. At first place the pioneers recruited, functionally different from the pre-disturbance functional composition did not compensate for the redundancy decrease. Progressively though, first establish species were replaced by more competitive long-lived pioneers or late-successional species resembling more the pre-disturbance functional composition and restoring the functional redundancy. This replacement was stochastic and followed the lottery recruitment rules, that ease the recovery for the first recruited species but then

increasingly hamper it with the emergence of interspecific competition due to increasing functional redundancy (?). Along time the recovery of infrequent species is increasingly difficult, and the recovery of the functional redundancy that was just initiated after 30 years in some communities is difficult to estimate (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

The long-term impact of disturbance on community functional redundancy meant a lower resilience of pre-disturbance communities and higher chances to see the persistence of disturbance-specific species at the expense of late-successional ones (Haddad *et al.*, 2008; Burslem *et al.*, 2000; Martin *et al.*, 2013). Besides the long-term recovery of infrequent species increases the risks to loose cornerstone species, with unexpected ecological consequences (Jones *et al.*, 1994; Chazdon, 2003; Díaz *et al.*, 2005; Gardner *et al.*, 2007). Apart from the functional characteristics considered here, infrequent species might indeed have unique functions in the 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 blurred by the emergence of competitive exclusion along time.] The resilience of tropical forests proved consistent although several decades-long. Still, the disturbance impact on communities redundancy cautioned against the risks of infrequent species loss and the persistence of disturbance-specific communities (Gourlet-Fleury *et al.*, 2005). 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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