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 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. This intermediate disturbance hypothesis (IDH), though, remains debated and the resilience of community taxonomic and functional diversity and composition remains controversial. To disentangle the ecological processes driving community response to disturbance, we analyzed tree community trajectories following a disturbance gradient in a Neotropical forest. We examined community diversity, composition and redundancy trajectories over 30 years, considering both taxonomic and functional trajectories based on 7 leaf, stem and life-history traits. We highlighted the cyclic recovery of community taxonomic and functional composition. While pre-disturbance taxonomic differences were maintained over time, functional composition trajectories were quite similar among communities. The IDH did predict community taxonomic diversity response while functional diversity was enhanced whatever the 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 disturbances.

Keywords
Community Ecology, Community Diversity Determinants, Disturbance Trajectories, Intermediate Disturbance Hypothesis, Mid-term Resilience, Neotropical Forests, Taxonomic and Functional Biodiversity

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Contents

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, however, increase the pressure on remaining natural forests (Morales-Hidalgo *et al.*, 2015). This changing context alters the natural disturbance regime that shape and maintain tree community structure, composition and functioning (Schnitzer & Carson, 2001; Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015), so anticipate the fate of tropical forests requires to understand community response to disturbance. Disturbance initiate ecological succession comprising a suit of changes in community structure and functioning over time, which rate, endpoint an duration depend on the disturbance intensity (**?**Willig & Presley, 2018). Regarding tropical forests, community response to disturbance would be secondary succession, starting with an intact soil and a consistent seed bank, from which we aim would be to highlight predictable trajectories and their underlying ecological processes.

Disturbance change both community abiotic and biotic environments, through modifications in the fluxes of light, heat and water (Goulamoussène *et al.*, 2017), and modifications in species interactions, mainly through modifications of species density (Chesson, 2000). For now, post-disturbance response has been largely studied through forest structural parameters, rapid and convenient to measure, such as aboveground biomass, tree height or stem density (Piponiot *et al.*, 2016; Rutishauser *et al.*, 2016). Thereafter, models based on the observed trajectories after disturbance gave important insights into community recovery and resilience (Hérault & Piponiot, 2018). Regarding community diversity and composition, however, post-disturbance trajectories have not been as thoroughly understood. A leading idea on how the impacts of disturbance on community diversity is the Intermediate Disturbance Hypothesis (IDH) (Connell, 1978). The IDH assumes biodiversity changes in relation to disturbance intensity and frequency, with diversity peaks for intermediate intensity and at intermediate time after disturbance. At intermediate level of disturbance, the fluctuation of environmental conditions entails deterministic processes favoring both competitively superior species and fast colonizers, hence preventing competitive exclusion (Shea *et al.*, 2004; Pulsford *et al.*, 2016).

The IDH then assumes both predictable trajectories depending on the disturbance intensity, and, without additional disturbance, the recovery of pre-disturbance state defined by the dominance of late-successional species (Rees *et al.*, 2001; Sheil & Burslem, 2003; Willig & Presley, 2018). In highly diverse tropical forests, however, the validation of the IDH remains controversial (Fox, 2013; Sheil & Burslem, 2013) and observed post-disturbance trajectories are often blurry compared to theoretical expectations (**?**Randall Hughes *et al.*, 2007; Norden *et al.*, 2015, 2017). Empirical evidence generally rely on the analysis of a single diversity metric, often the taxonomic richness (Molino & Sabatier, 2001), which might give limited or misleading information on community disturbance response. The IDH pattern of diversity peak under an intermediate disturbance regime can indeed result from various ecological processes (Sheil & Burslem, 2003). To disentangle these various processes and grasp the different facets of community response to disturbance it is crucial to combine a suitable range of approaches (Shea *et al.*, 2004). More ecological-meaningful analysis would first couple taxonomic richness and evenness, which reveals the changes in species abundance distribution and hence in the underlying ecological processes (Chaudhary *et al.*, 2016). Analysis would as well include taxonomic composition, which is crucial for conservation issues (Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Eventually, including a functional approach accounting for species biological attributes would be highly revealing of ecological process involved in community response to disturbance. The functional trait-based approach indeed directly links community diversity, composition and redundancy to ecosystem functioning and environmental constraints (Violle *et al.*, 2007; Baraloto *et al.*, 2012). In that respect, a vast literature allowed recognizing major traits related to species ecology and mediating species performance in a given environment (Díaz *et al.*, 2005). Specifically in tropical forests, the functional approach revealed the post-disturbance deterministic processes entailing a shift from a dominance of "conservative" slow-growing species dealing with scarce resources, to a dominance of "acquisitive" fast-growing species with rapid and efficient use of abundant resources (Reich, 2014; Hérault *et al.*, 2011). This shift is translated into the trajectories of average community value of key functional traits related to resource acquisition (leaf and stem traits) and life-history strategy (seed mass, maximum size) (Wright *et al.*, 2004; Díaz *et al.*, 2005; ter Steege *et al.*, 2006; Westoby & Wright, 2006; Chave *et al.*, 2009). The functional approach would eventually be completed with the analysis of functional redundancy that quantifies the amount of shared trait values among species (Carmona *et al.*, 2016). The high functional redundancy of hyper-diverse tropical forests (Bellwood *et al.*, 2006) mitigates the impacts of species removal on ecosystem functioning and determines the resilience of communities after disturbance (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. Specifically, we elucidateed (i) the community taxonomic and functional recovery and (ii) the ecological processes underlying community post-disturbance trajectories and discussed the validity and the extent of the IDH, and (iii) examined 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 which produces lateral drainage during heavy rains.

The experiment is a network of 12 6.25 ha plots that underwent a disturbance gradient of three logging, thinning and fuelwood cutting treatments (Table 1) according to a randomized plot design with three replicate blocks of four plots. The disturbance corresponds to an intensity gradient. For treatment 1 (T1) 10 trees of commercial species (of a diameter at 1.3 m height (DBH) equal or above 50 cm) were felled per hectare. For treatment 2 (T2) 10 trees/ha of commercial species (DBH $\geq$ 50 cm) were felled and 30 trees/ha of non-valuable species (DBH $\geq$ 40 cm) were removed by poison girdling. For treatment 3 (T3) 10 trees/ha of commercial species (DBH $\geq$ 50 cm) were felled and 30 trees/ha of non-valuable species (15 with DBH $\geq$ 50 cm and 15 with DBH $\geq$ 40 cm) were removed by poison girdling (Schmitt & Bariteau, 1989). 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 12 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 palms. 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. This resulted in significant taxonomic uncertainty 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 $[\alpha_1, \alpha_2, ..., \alpha_V]$ observed across all inventories between each vernacular name v and all species $[s_1, s_2, ..., s_N]$:

$$M_v\Big([s_1, s_2, ..., s_N], [\alpha_1, \alpha_2, ..., \alpha_V]\Big)$$

See Supplementary Materials -Fig. S1 and Aubry-Kientz *et al.* (2013) for the detailed methodology.

Six functional traits representing leaf economics (leaf 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 project [1]. 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.

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

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

2.3 Composition and diversity metrics

Because of the variability in the precision of botanical identification efforts, we were constraint to conduct the taxonomic composition and diversity analysis at the genus level. Taxonomic and functional trajectories of community composition were followed in a two-dimensional NMDS ordination plan. Two NMDS using abundance-based (Bray-Curtis) dissimilarity measures were conducted to map either taxonomic or functional composition, the latter based on the seven 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). Species seed mass were given in 5 mass classes. Seed mass trajectories were therefore reported as the proportion of each class in the inventories (Supplementary materials).

The taxonomic diversity was reported through species richness and the Hill number translation of the Simpson index (Hill, 1973). These metrics allowed assessing the taxonomic richness as well as evenness, through the comparison between richness and Simpson diversity. R.esults will thus be discussed directly in terms of taxonomic richness and evenness. Both 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 (Marcon, 2015). The functional diversity was reported using the functional richness and functional evenness, *i.e* the Rao index of quadratic entropy. The Rao index combines species abundance distribution, and the average pairwise functional dissimilarity between species computed by the gower distance.

The impacts of initial disturbance were tested with the Spearman rank correlation between the extremes of taxonomic and functional metrics reached over the 30 years and the initial %AGB loss. They were besides analyzed 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.

Functional redundancy was measured as the overlap among species in community functional space (Carmona *et al.*, 2016). First, the individuals of the trait database were mapped in the plane of the two first axes from a PCA analysis. Then, for each species, the traits probability density (TPD) were computed through two-dimension kernel density estimators. Second, for each community, the TDB weigthed by species abundance were summed accross the functional space. Third, the functional space was divided into a 100 x 100 grid and the number of species with a positive TDP was counted in each cell. The average count across cells minus 1 returnedthe Community Functional Redundancy, which was the average number of species in the community that share the same trait values.

Table 1. Intervention table, summary of the disturbance intensity for the 4 plot treatments in Paracou.

Treatment	Timber	Thinning	Fuelwood	%AGB lost
Control	-	-	-	0
T1, low	$DBH \geq 50$ cm, commercial species, $\approx 10\ trees.ha^{-1}$	-	-	$[12-33]$
T2, intermediate	$DBH \geq 50$ cm, commercial species, $\approx 10\ trees.ha^{-1}$	$DBH \geq 40$ cm, non-valuable species, $\approx 30\ trees.ha^{-1}$	-	$[33-56]$
T3, high	$DBH \geq 50$ cm, commercial species, $\approx 10\ trees.ha^{-1}$	$DBH \geq 50$ cm, non-valuable species, $\approx 15\ trees.ha^{-1}$	$40\text{ cm} \leq DBH \leq 50$ cm, non-valuable species, $\approx 15\ trees.ha^{-1}$	$[35-56]$

3. Results

3.1 Community Composition

From 1989 (2 years after disturbance) to 2015 (28 years after disturbance), 828 388 individual trees and 591 botanical species pertaining to 223 genera and 64 families were recorded.

While both taxonomic and functional composition remained stable in undisturbed communities (Fig. 1), 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 mean WSG to high mean SLA and chlorophyll content (see appendix I). For functional composition, this translated into cyclic compositional changes with an incomplete recovery of the initial composition (Fig. 1). The maximum dissimilarity with the initial state was positively correlated with the disturbance intensity for both taxonomic and functional composition ($\rho^{Taxonomic}_{Spearman} = 0.87$ and $\rho^{Functional}_{Spearman} = 0.90$ respectively). The maximum dissimilarity with the initial was reached for taxonomic composition between 15 to 25 years, for most of the plots, and around 22 years for functional composition.

Community CWM average value of all traits and seed mass proportions followed unimodal trajectories, either stabilizing or returning towards their initial values, to the exception of leaf chlorophyll content, which continued to increase for some T3 and T2 plots 30 years after disturbance.

Community CWM average value of Maximum height at adult stage (*Hmax*), leaf toughness and wood specific gravity (*WSG*) first decreased and then slightly increased but remained significantly lower than their initial value (Fig. 2). On the other side, bark thickness and specific leaf area (*SLA*) increased and while bark thickness remained substantially high after 30 years, *SLA* had almost recovered to its initial value. For all traits, the maximum difference to initial value was correlated to the disturbance intensity. Positive correlations were observed for Leaf thickness, chlorophyll content, SLA and bark thickness ($\rho^{Leafthickness}_{Spearman} = 0.76$, $\rho^{Chlorophyllcontent}_{Spearman} = 0.60$, $\rho^{SLA}_{Spearman} = 0.93$, $\rho^{Barkthickness}_{Spearman} = 0.71$). Negative correlation was observed for Leaf toughness, WSG and Hmax ($\rho^{Leaftoughness}_{Spearman} = -0.53$, $\rho^{WSG}_{Spearman} = -0.75$, $\rho^{Hmax}_{Spearman} = -0.40$) The proportions of the three lightest seed mass classes increased in all disturbed plots, and decreased after 30 years for the lightest class while it stabilized for the two other (Supp. Mat. - Fig. S2).

3.2 Community taxonomic and functional diversity

For undisturbed plots, taxonomic richness and Simpson diversity remained stable over the 30 years of monitoring. 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 with the disturbance intensity ($\rho^{Richness}_{Spearman} = 0.50$). In all disturbed plots the Simpson diversity first increased until a maximum reached after around 20 years. This maximum was positively correlated with the disturbance intensity ($\rho^{Simpson}_{Spearman} = 0.77$). The Simpson diversity then stabilized except for two T3 plots (plots 8 and 12) for which it kept increasing (Fig. 3).

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

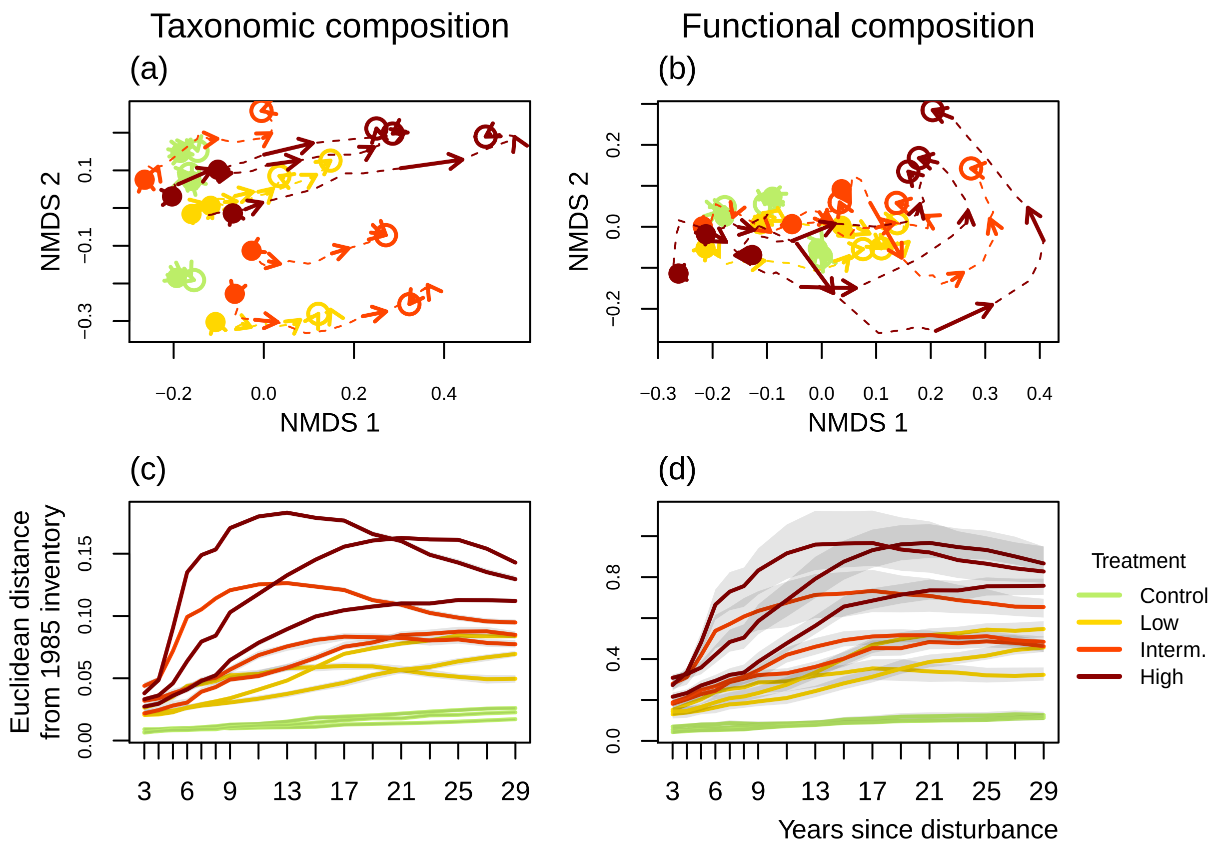

Figure 1. Plot trajectories in terms of taxonomic composition ((**a**) and (**c**)) and functional composition ((**b**) and (**d**)) in a two-dimensional NMDS plan. Lower panels ((**c**) and (**d**)) represent the Euclidean distance to initial condition along the 30 sampled years. Shaded areas are the credibility intervals.

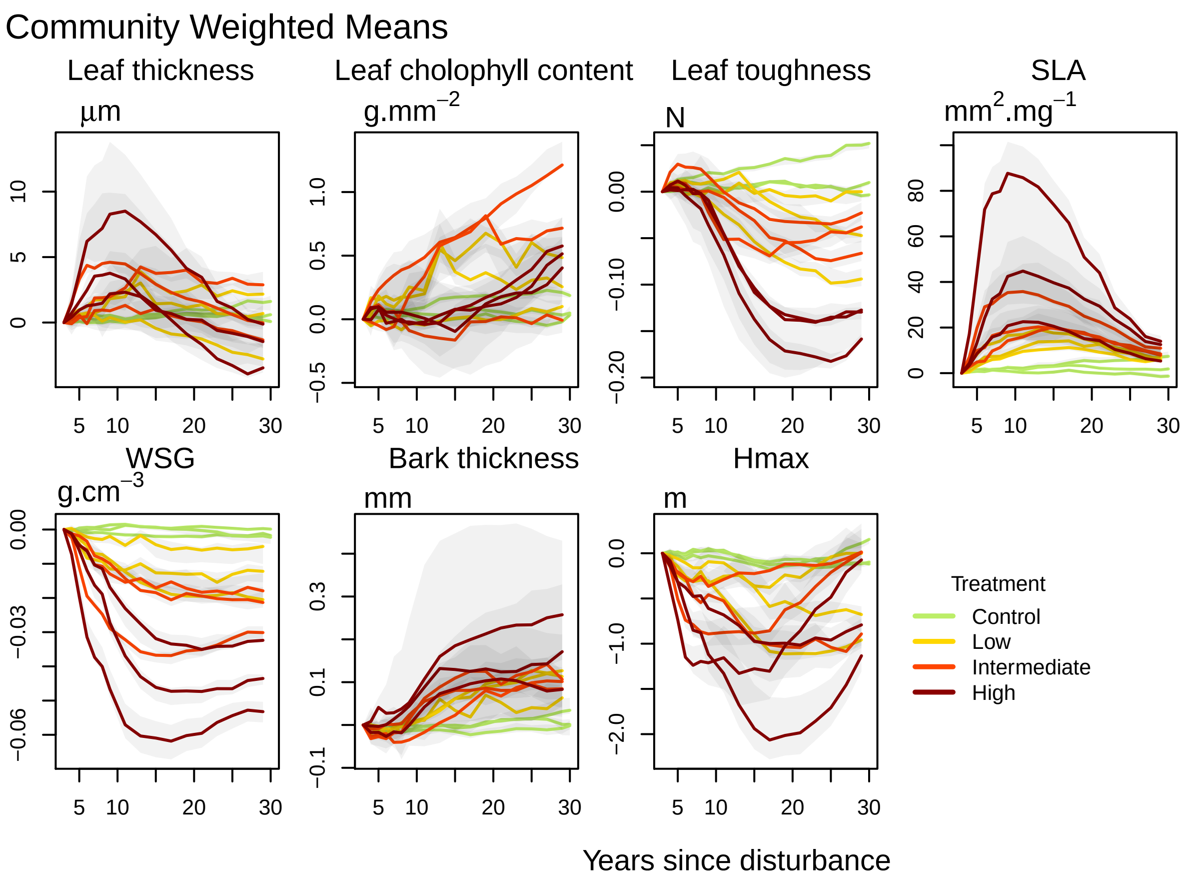

Figure 2. Trajectories of community weighted means over 30 years after disturbance of four leaf traits (Leaf thickness, chlorophyll content, toughness, and specific area), two stem traits (wood specific gravity, and bark thickness) and one life history trait (Specific maximum height at adult stage).

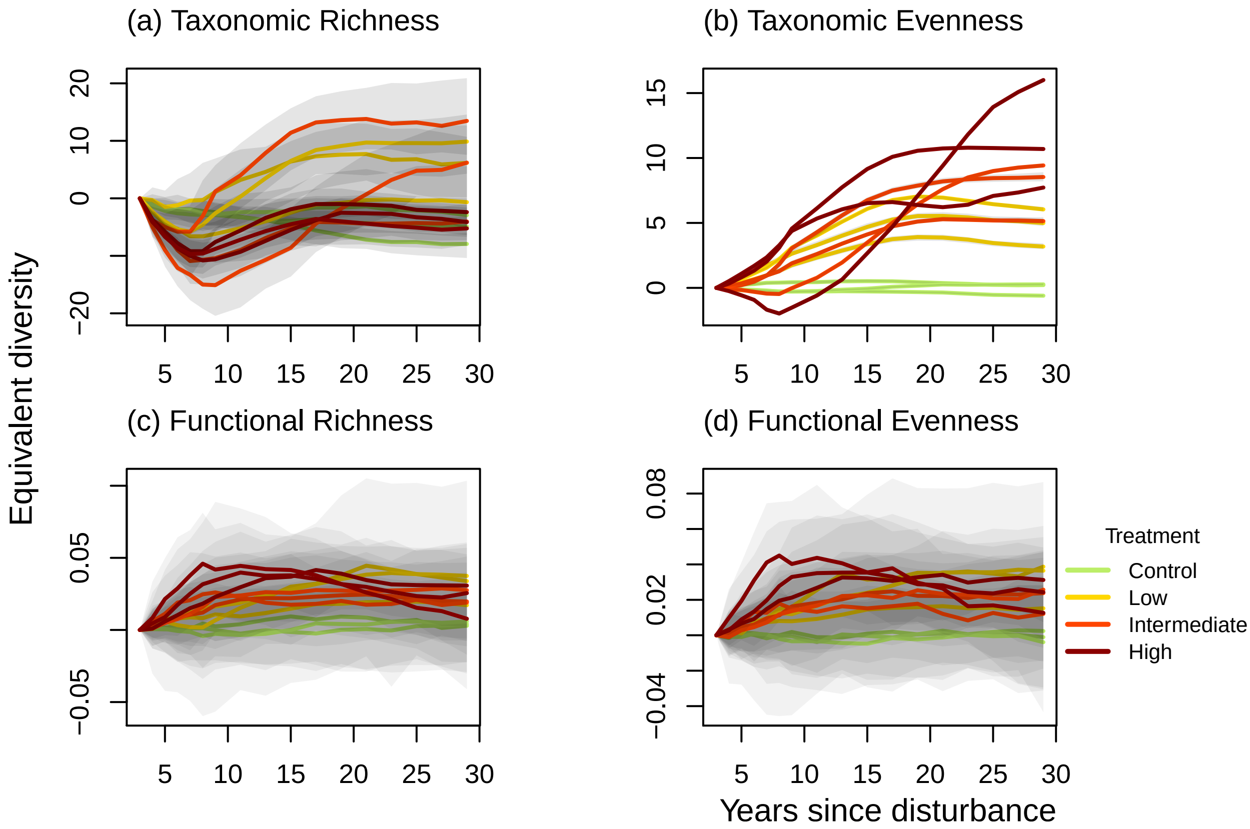

Figure 3. Trajectories over 30 years of the difference with the 1989 inventory (2 years after disturbance) of community taxonomic richness **(a)**, Simpson diversity **(b)**, functional richness **(c)**, and Rao diversity **(d)**. Shaded areas are the credibility intervals

the percentage AGB loss and (ii) taxonomic and functional diversity after 10, 20 and 30 years best predicted the hump-shaped curve of the disturbance impact along the disturbance intensity gradient 4. The relationship between the disturbance impact and its intensity was more markedly hump-shaped for the taxonomic richness than for the Simpson diversity. For both functional richness and Rao diversity the relationship was almost linear. The regression model better predicted the functional richness and Rao diversity ($0.55 < R^2_{FunctionalRichness} < 0.72$, and $0.60 < R^2_{FunctionalRao} < 0.81$) than the taxonomic richness and evenness ($0.21 < R^2_{TaxonomicRichness} <$ 0.4, and $-0.15 < R^2_{TaxonomicSimpson} < 0.43$ respectively).

3.3 Functional redundancy

All disturbed plots had lower functional redundancy than control plots and followed similar hump-shaped trajectories (5). The maximum redundancy loss was positively correlated with the disturbance intensity ($\rho_{Spearman} = 0.47$) and the recovery had not attained initial values for any disturbed communities after 30 years.

4. Discussion

4.1 A cyclic recovery of community composition

The hump-shaped trajectories of community composition returned towards pre-disturbance state after 30 years, highlighting community resilience in terms of taxonomic and functional composition.

Before disturbance, there were already taxonomic differences among local communities, as revealed by the distinct starting points on the NMDS axis 2. These initial differences were maintained throughout the trajectories following disturbance, so community initial state influenced the trajectories following disturbance more than commonly thought. The initial composition indeed partly determined the pool of species recruited, and hence shaped the composition trajectories and drove them towards the recovery of the initial composition. This taxonomic recovery, although it was not fully achieved after 30 years, suggested the resilience of community taxonomic composition and the maintenance of community initial differences (Folke, 2006). Species not belonging to the pre-disturbance community were then rarely recruited, probably because of the common dispersal limitations among tropical tree species (Svenning & Wright, 2005).

Functional composition trajectories were, conversely, highly similar among disturbed communities. As the composition of pre-disturbance surviving trees is representative of the initial community (Hérault & Piponiot, 2018), changes in functional composition relied upon the recruitment of species or functional types that were infrequent or absent before disturbance. Competitive pioneers became dominant in filling the environmental niches vacated by the disturbance, with a high availability of light, space and nutrients. This recruitment of pioneers similarly changed the functional composition of all communities, whenever the disturbance intensity. The functional composition went towards more resource-acquisitive strategies, translated in the functional plan (Fig. 1) by a displacement on the right along the first axis (Westoby, 1998; Wright *et al.*, 2004; Reich, 2014). Thereafter, the pioneers first recruited were progressively excluded by long-lived, more resistant and shade-tolerant species. The commpunity functional composition then returned towards more resource-conservative strategies, suggesting the recovery of the initial community composition and translated in the functional plan by a displacement left along the first axis and upward along the second axis (Fig. 1).

In the light of these taxonomic and functional composition trajectories, community response to disturbance proved simultaneously deterministic and stochastic at different levels of community organization. Taxonomic trajectories were shaped by dispersal limitations maintaining the stochastic differences among communities due to historical contingency. Functional trajectories were shaped by trait-based processes resulting the the convergence of community functional composition (Fukami *et al.*, 2005).

4.2 A new perspective on the intermediate disturbance hypothesis

Community taxonomic richness and evenness trajectories were determined by the disturbance intensity, ranging from a limited and temporary impact to significant and persistant alterations of community diversity. The taxonomic trajectories markedly changed above an intensity threshold for which community response corresponded to a maximized richness and a resilience of the evenness. The disturbance intensity determined the balance in the community between pre-disturbance surviving trees, and trees recruited afterward. Below a 20%-25% AGB loss, the trees surviving after disturbance remained numerous enough to maintain the high taxonomic richness of the pre-disturbance community (Bongers *et al.*, 2009). The recruitment of pionners, infrequent or absent before disturbance, then increased the taxonomic richness all the more so that the disturbance was intense (**?**Chaudhary *et al.*, 2016). As these pioneers became more dominant they besides temporarily balanced the usual hyper-dominance of tropical forests, hence temporarily increasing the taxonomic evenness (Baraloto *et al.*, 2012). Above the intensity threshold, the taxonomic richness of surviving trees was too low to be offset by the recruitment of pioneers. In the Guiana shield indeed, the pool of true pioneers specifically recruited after disturbance is restricted to a few common genera (e.g. *Cecropia* spp., *Vismia* spp.) (Guitet *et al.*, 2018). The richness trajectories following intense disturbance then decreased, all the more so that the disturbance intensity was high (Molino & Sabatier, 2001). At the same time, pioneers became persistently dominant and prevented a return towards the initial evenness and the recovery of hyper-dominant shade-tolerant species.

Observed trajectories supported the IDH in highlighting a threshold disturbance intensity, expressed as percentage of AGB removed, marking a change in post-disturbance trajectories. Taxonomic trajectories besides highlighted, below the intensity threshold, an intermediate time after when the taxonomic evenness was maximized. This time corresponded to the intermediate between the generation time of pionneers, first to dominate the post-disturbance recruitment, and the time for competitive exclusion, leading

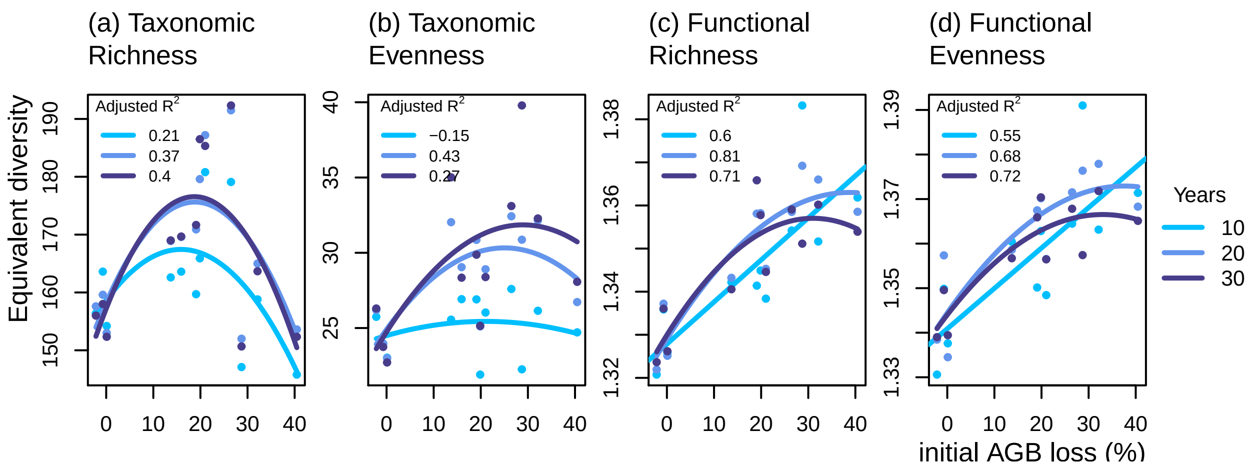

Figure 4. Relationship between the initial %AGB loss and community taxonomic richness **(a)**, taxonomic evenness **(b)**, functional richness **(c)**,and functional evenness **(d)** at 10, 20 and 30 years after disturbance

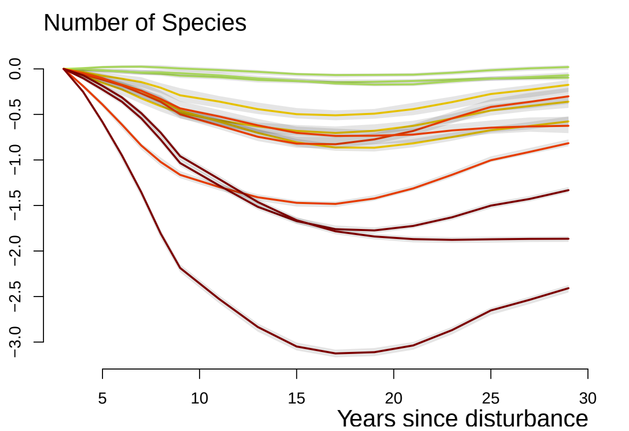

Figure 5. Trajectories of the functional redundancy within the initial functional space over 30 years after disturbance. Shaded areas are the credibility intervals.

to the dominance of late-successional species. As already observed in the Guiana shield (Baraloto *et al.*, 2012) and in Borenan tropical forests (Cannon, 1998), taxonomic evenness followed humped-shaped trajectories with a peak when the recruitment was balanced between pioneers and late-successional species.

Regarding community functional trajectories in contrast, there was neither intermediate disturbance intensity nor time to disturbance, which dismissed the IDH. The functional response according to disturbance intensity did not display the characteristic hump-shaped trajectories. Whenever the disturbance intensity, both community functional richness and evenness increased with the recruitment of pioneers that were functionally highly different from the species of the pre-disturbance community (Denslow, 1980; Molino & Sabatier, 2001). Above the intensity threshold however, for the most intense disturbance, community functional richness and evenness started to decrease after 15 to 20 years. The vacated environmental space was then occupied by short-lived species which prevented the establishment of other species. The decline of these short-lived pioneers decreased the functional richness and evenness, but we suggest that the establishment of long-lasting pioneers will follow and the taxonomic and functional trajectories will catch up with those observed for intermediate disturbance (Walker & del Moral, 2009).

The IDH then translated into community taxonomic response, with markedly different trajectories below and above an intensity threshold, and with an intermediate time to disturbance when the intensity remained below the threshold. It was however not tangible regarding the functional response, with functional trajectories decoupled from taxonmic ones.

4.3 The functional redundancy, key of community resilience

The decoupling between taxonomic and functional trajectories was explained by a decrease in the functional redundancy within the pre-disturbance functional space, due to the loss of species following disturbance. The recruitment of pioneers, functionally different from the pre-disturbance functional composition, did not compensate the decrease of functional redundancy in the first place. Progressively though, the functional redundancy was restored through the replacement of the first established species by more competitive, long-lived pioneers or late-successional species that were functionally closer to the pre-disturbance community. This replacement followed the lottery recruitment rules, implying a recruitment easy for the first recruited species but increasingly hampered by the emergence of interspecific competition (Busing & Brokaw, 2002). The functional redundancy then relied upon stochastic processes and its recovery, depending on the recruitment of infrequent species constrained by the increasing competition, was increasingly slow and difficult to anticipate (Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

The impact of disturbance on community functional redundancy meant a lower resilience of the pre-disturbance communities, with higher chances to see the persistence of disturbance-specific species at the expense of late-successional ones (Haddad *et al.*, 2008). Besides, the stochastic recovery of infrequent species increases the risks to lose keystone species, with unexpected ecological consequences (Jones *et al.*, 1994; Chazdon, 2003; Díaz *et al.*, 2005). Apart from the functional characteristics considered here, infrequent species might indeed have unique functions in the ecosystem or be a key for some fauna (Schleuning *et al.*, 2016).

5. Conclusions

Our study highlighted the combination of deterministic and stochastic processes determining the succession of recruited species and shaping community response to disturbance. The deterministic recruitment of pioneers shaped functional trajectories convergent in the functional space, while dispersal limitations shaped stochastic taxonomic trajectories maintaining community divergence in taxonomic composition. In accordance with the IDH, community taxonomic diversity was maximised for intermediate disturbance intensity, before reaching an intensity threshold beyond which the taxonomic richness decreased and the taxonomic evenness remained persistently higher. Conversely, functional trajectories proved decoupled from the taxonomic ones and did not follow the hypothesis of the IDH as no distinct trajectories emerged with increasing disturbance intensity. The decoupling between taxonomic and functional disturbance was explained by a decrease of community functional redundancy mitigating the functoinal impact of disturbance. The resilience of tropical forests, defined in terms of recovery to pre-disturbance state, proved tangible but requiring several decades. Still, the disturbance impact on community redundancy cautioned against the risks of infrequent species loss and the persistence of disturbance-specific communities (Hérault & Piponiot, 2018).

6. Acknowledgement

We are in debt with all technicians and colleagues who helped setting up the plots and collecting data over years. Without their precious work, this study would have not been possible and they may be warmly thanked here.

7. Author's contributions

AM, EM & BH designed the study, developed the analysis framework, interpreted the results and wrote the manuscript. All authors gave final approval for publication.

8. Data availability

This article is based upon the dataset of the Paracou station, which is part of the Guyafor permanent plot network in French Guiana (Cirad-CNRS-ONF). The dataset is available upon request to the scientific director (https://paracou.cirad.fr).

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