Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract
Anticipate the impact of the global change context on tropical forests is now urgent. This calls to highlight the taxonomic and functional facets of tree community post-disturbance trajectories and the underlying processes. It also calls to clarify the link between biodiversity and disturbance, specifically the scope of the Intermediate Disturbance Hypothesis (IDH) that is debated in tropical forests. In this study, we analyzed the tree community trajectories following a disturbance gradient in a Neotropical forest over 30 years. We considered community taxonomic and functional diversity, composition and redundancy trajectories. We based on the annual botanical inventories of 75 ha of a Neotropical forest and on large trait datasets comprising 7 leaf, stem and life-history traits. We highlighted a decoupling between taxonomic trajectories, that differed among communities, and functional trajectories, remained similar and convergent. We explained this decoupling by the variations in community functional redundancy that mitigated the functional impact of disturbance. Post-disturbance trajectories clarified the scope of the Intermediate Disturbance Hypothesis that was validated regarding taxonomic diversity, with an intensity threshold of 20-25%, but not regarding functional diversity.The IDH applied around 20 years after disturbance when the recruitment of pioneers and late-successionals were balanced. Although consistent, the recovery of community composition, diversity and redundancy remained unachieved after 30 years. This acknowledged the need of decades-long cycles without disturbance to ensure a complete recovery, and questioned tropical forest community resilience after repeated disturbances.

Keywords
Community Ecology, 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, and ensure cultural and human well-being. They regulate as well the local and regional climates, and the carbon, water and nutrient cycles. However, the growing demand in forests products together with current global changes increase the pressure on remaining natural forests (Morales-Hidalgo *et al.*, 2015). These threats affect the disturbance regime that naturally shapes and maintains the structure, composition and functioning of tree communities (Schnitzer & Carson, 2001; Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015). To anticipate the fate of tropical forests in the current context it is then urgent to understand the response of communities to disturbance and the underlying processes. Disturbance impact forest communities in changing both abiotic and biotic environments, through modifications in the fluxes of light, heat and water (Goulamoussène *et al.*, 2017). Although in the tropical context the forest environment is maintained after disturbance, there is a succession of changes in the structure and functioning of communities constituting a post-disturbance secondary succession. For now, this succession has been largely studied through trajectories of forest structural parameters such as aboveground biomass, tree height or stem density (Piponiot *et al.*, 2016; Rutishauser *et al.*, 2016). Models based on observed trajectories assessed community time to recovery and identified some of the determinants of post-disturbance trajectories, like forest structure, forest composition, environmental parameters and disturbance characteristics (Hérault & Piponiot, 2018). Regarding community diversity and composition however, post-disturbance trajectories have not been as thoroughly understood (Guitet *et al.*, 2018; Molino & Sabatier, 2001). Given the variety of species response to disturbance and the huge diversity of tropical forests, manifold post-disturbance biodiversity trajectories might emerge (Lindenmayer *et al.*, 2012; Garcia Florez *et al.*, 2017). It is then essential to anticipate post-disturbance trajectories and highlight the link between biodiversity and disturbance, specifically the link between disturbance intensity and frequency and the rate, endpoint and duration of the trajectories (Chazdon, 2003; Willig & Presley, 2018).

An early conceptual basis of the linkage between biodiversity and disturbance is the Intermediate Disturbance Hypothesis (IDH). The IDH assumes a relationship between community diversity and the intensity and frequency of disturbance events, stating that community diversity peaks at intermediate level of disturbance (Connell, 1978). The theory assumes that the environmental fluctuations following disturbance foster both competitively superior species and fast colonizers and thus prevent competitive exclusion (Shea *et al.*, 2004; Pulsford *et al.*, 2016). In tropical forests, however, observations of the IDH often diverge from theoretical expectations (Randall Hughes *et al.*, 2007; Sheil & Burslem, 2003; Norden *et al.*, 2017), and the validation of the theory remains controversial (Hubbell, 2001; Fox, 2013; Sheil & Burslem, 2013). The link between biodiversity and disturbance might be complicated by the huge diversity of tropical communities and a variety of ecological processes may underlie the IDH (colonisation, facilitation, coexistence, etc)(Lindenmayer *et al.*, 2012; Garcia Florez *et al.*, 2017). There is a need to clarify the scope of the IDH in terms of the different facets of community diversity that are taxonomic richness, species abundance distribution and community functioning. Besides, there is a need to delineate the scope of the IDH in time, and highlight the moment when the conditions for the IDH emerge (Sheil & Burslem, 2003; Shea *et al.*, 2004).

Analysing community response to disturbance requires a set of metrics, to grasp all aspects of community changes (Sheil & Burslem, 2003; Shea *et al.*, 2004; Mayfield & Levine, 2010). The analysis should first consider community composition, which is crucial for conservation issues and which reveals the species fostered by the disturbance (Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Then, diversity metrics encompassing taxonomic richness and evenness should be considered to assess the changes in community abundance distribution. Besides, a functional approach that accounts for species biological attributes and ecological strategy would directly link 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 that represent species ecological strategy and determine how they respond to changing conditions (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 (Rees *et al.*, 2001; 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; ter Steege *et al.*, 2006; Westoby & Wright, 2006; Chave *et al.*, 2009). The functional approach also encompasses the analysis of functional redundancy, that quantifies the amount of shared trait values among species (Carmona *et al.*, 2016). The typical high functional redundancy of hyper-diverse tropical forests (Bellwood *et al.*, 2006) mitigates the impacts of species removal on ecosystem functioning and determines communities resilience 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 above-ground 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, (i) we defined taxonomic and functional post-disturbance trajectories and examined the underlying ecological process, (ii) we discussed the scope of the IDH regarding the different facets of community diversity and the time after disturbance, and (iii) we analyzed community resilience and time to recovery.

2. Material and Methods

2.1 Study site

Paracou station in French Guiana (5°18'N and 52°53'W) is located in a lowland tropical rain forest in a tropical wet climate with mean annual temperature of 26°C, mean annual precipitation averaging 2980 $mm.y^{-1}$ (30-y period) and a 3-month dry season (< 100 $mm.month^{-1}$) from mid-August to mid-November, and a one-month dry season in March (Wagner *et al.*, 2011). The mean annual temperature is 26°C. Elevation ranges from 5 to 50 m. Across all plots the topography mainly corresponds to hilltops or hillsides, while bottomlands cover less than 1 % of the area. Plots are shallow ferralitic acrisols over a layer of transformed saprolite with low permeability and lateral drainage. Soil conditions are homogeneous, to the exception of the highest hilltops where the thick surface allows a free vertical drainage (Gourlet-Fleury *et al.*, 2004).

The experiment is a network of twelve 6.25 ha plots (Table 1) that underwent three disturbance treatments in 1987 according to a randomized plot design (Gourlet-Fleury

et al., 2004).
The experiment comprised three replicates of three sylvicultural treatments (hereafter plots T1, T2 and T3) and three control plots (T0). All treatments T1, T2 and T3 comprised the logging of 10 trees/ha with 50 cm minimum DBH that belonged to a set of 58 commercial species (Gourlet-Fleury *et al.*, 2004). Treatment T2 additionally comprised a thinning treatment by poison-girdling of non-commercial, randomly selected species with an average 30 trees/ha with 40 cm minimum DBH. Treatment T3 additionally comprised the logging of 15 trees /ha with 40 cm minimum DBH and the poison-gidling of 20 trees/ha with a 50 cm minimum DBH, all belonging to non-commercial species. Considering the silvicultural treatments and the following damage, 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). The three treatments constituted a disturbance intensity gradient with increasing of aboveground biomass (AGB) lost and surface disturbed.

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.

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 constrained 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 plane. 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, and seed mass trajectories were 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 these two metrics.: results will 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.

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

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 cm $\leq$ DBH $\leq$ 50 cm, non-valuable species, $\approx 15\ trees.ha^{-1}$	$[35-56]$

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 first two axes from a PCA analysis, which lowered the weight of correlations among traits as the PCA axes were combinations of most decoupled traits. For each species, the traits probability density (TPD) were computed from the mapping of individuals through two-dimension kernel density estimators. Second, for each community, the TPD 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 TPD was counted in each cell. The average count across cells minus 1 returned the Community Functional Redundancy, which was the average number of species in the community that share the same trait values.

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 the taxonomic composition changed towards more species with acquisitive functional strategies. This translated into a switch from high mean WSG in the community to high mean SLA and chlorophyll content (see appendix I). The functional composition of disturbed communities corresponded to 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 state 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*) 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*) both increased. Bark thickness remained substantially high after 30 years, and *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. After 30 years the proportion of lightest seed mass class decreased while it stabilized for the two other lightest seed mass classes (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.

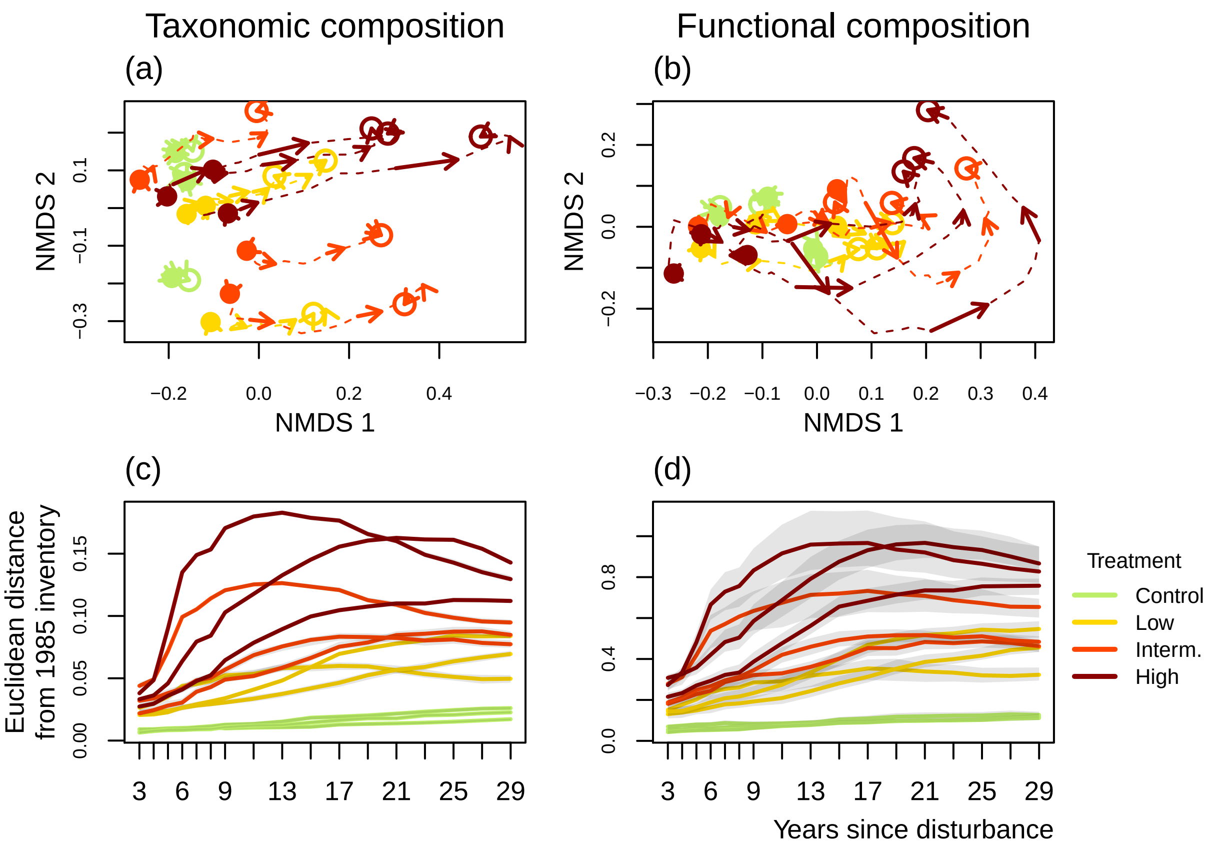

Figure 1. Plot trajectories in terms of taxonomic composition ((**a**) and (**c**)) and functional composition ((**b**) and (**d**)) in a two-dimensional NMDS plane. Lower panels ((**c**) and (**d**)) represent the Euclidean distance to initial condition along the 30 sampled years. Shaded areas are the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

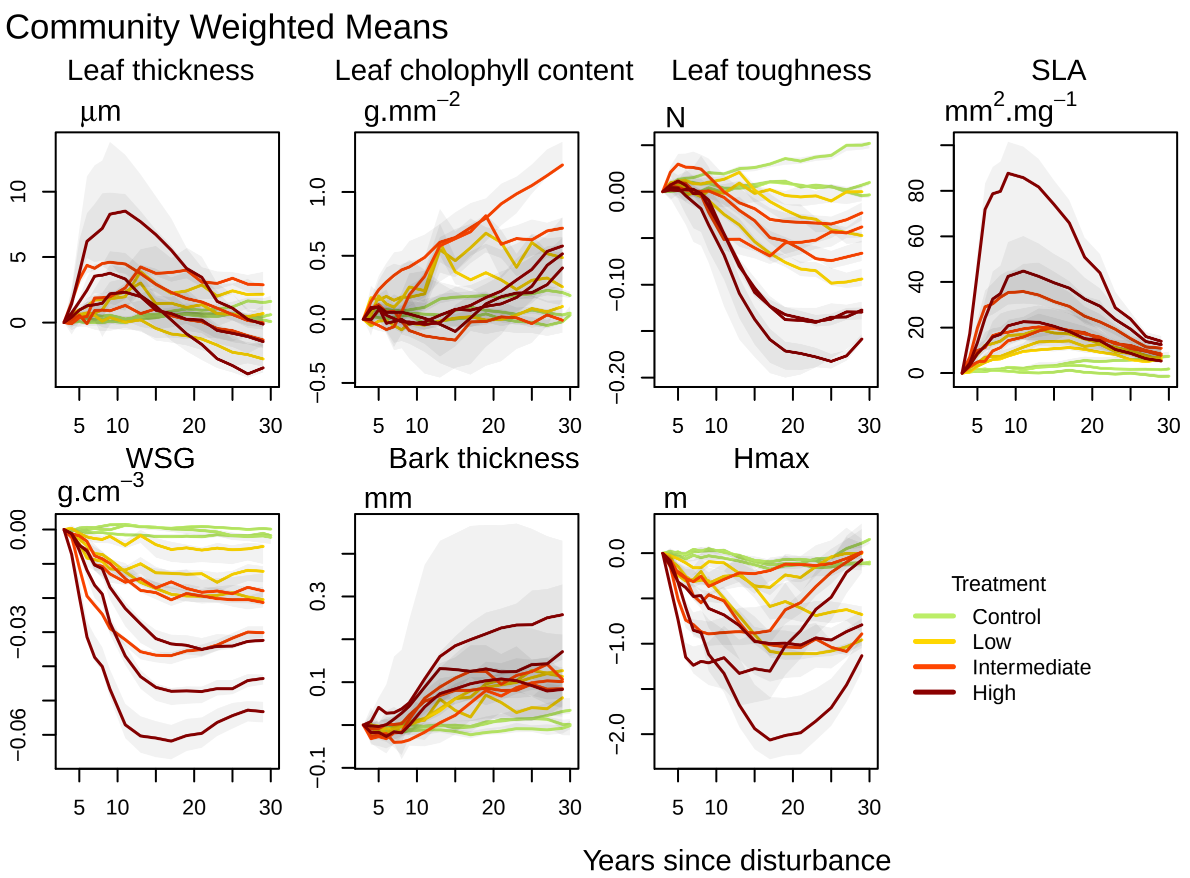

Figure 2. Trajectories of community weighted means over 30 years after disturbance of four leaf traits (Leaf thickness, chlorophyll content, toughness, and specific area), two stem traits (wood specific gravity, and bark thickness) and one life history trait (Specific maximum height at adult stage).

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. Following high intensity, they displayed 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 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 (Fig. 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 Decoupled taxonomic and functional trajectories

Before disturbance, the different communities had different taxonomic compositions, visualized by their distinct starting points on the NMDS axis 2. These initial differences were maintained all along the 30 years following disturbance, with the disturbance leading a displacement on the NMDS axis 1. The taxonomic compositional changes following disturbance were similar among communities, which may correspond to the recruitment of a group of pioneers common to all communities whenever their initial differences and the intensity of disturbance (Denslow & Guzman, 2000; Bongers *et al.*, 2009). Taxonomic trajectories continued with a recovery of the initial composition which, althought not fully achieved after 30 years, suggested the resilience of the taxonomic composition resilience and the maintenance of the initial differences among communities (Folke, 2006). The return towards initial taxonomic composition showed that species not belonging to the pre-disturbance community were rarely recruited, probably because of the common dispersal limitations among tropical tree species (Svenning & Wright, 2005).

Regarding functional composition, initial communities were similar and trajectories were confounded in the functional space. Following disturbance, the functional composition of pre-disturbance surviving trees is believed to be the same as this of the initial community (Hérault & Piponiot, 2018). The changes in functional composition following disturbance then relied upon the recruitment of species or functional types previously infrequent or absent. These species were probably competitive pioneers becoming dominant as the most efficient to benefit from the light, space and nutrients made available by the disturbance. This recruitment of pioneers led similar functional composition trajectories for all plots, whenever the disturbance intensity. The composition first went towards more resource-acquisitive strategies, which was translated by a displacement to the right along the first axis in the functional plane (Westoby, 1998; Wright *et al.*, 2004; Reich, 2014). Thereafter, the pioneers recruited primarily were progressively excluded by long-lived, more resistant and shade-tolerant species. The community functional composition then returned towards more resource-conservative strategies, suggesting the recovery of the initial functional composition. This recovery translated in the functional plane by a displacement left along the first axis and upward along the second axis (Fig. 1).

Both taxonomic and functional composition trajectories initiated a return towards pre-disturbance state after 30 years, which highlighted the taxonomic and functional resilience of communities. Taxonomicand functional trajectories however appeared decoupled: while taxonomic trajectories maintained the initial differences among communities, the functional trajectories where similar and convergent in the functional space (Fukami *et al.*, 2005).

4.2 The scope of 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 at which the taxonomic richness was maximized and the taxonomic evenness remained resilient. The disturbance intensity impacted the balance in the community between pre-disturbance surviving trees, and trees recruited afterward. On the one hand, 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 pioneers, infrequent or absent before disturbance, then increased the taxonomic richness all the more so that the disturbance was intense (Martin *et al.*, 2015; Chaudhary *et al.*, 2016). As these pioneers became more dominant they balanced the usual hyper-dominance of tropical forests, hence temporarily increasing the taxonomic evenness (Baraloto *et al.*, 2012). On the other hand, above the intensity

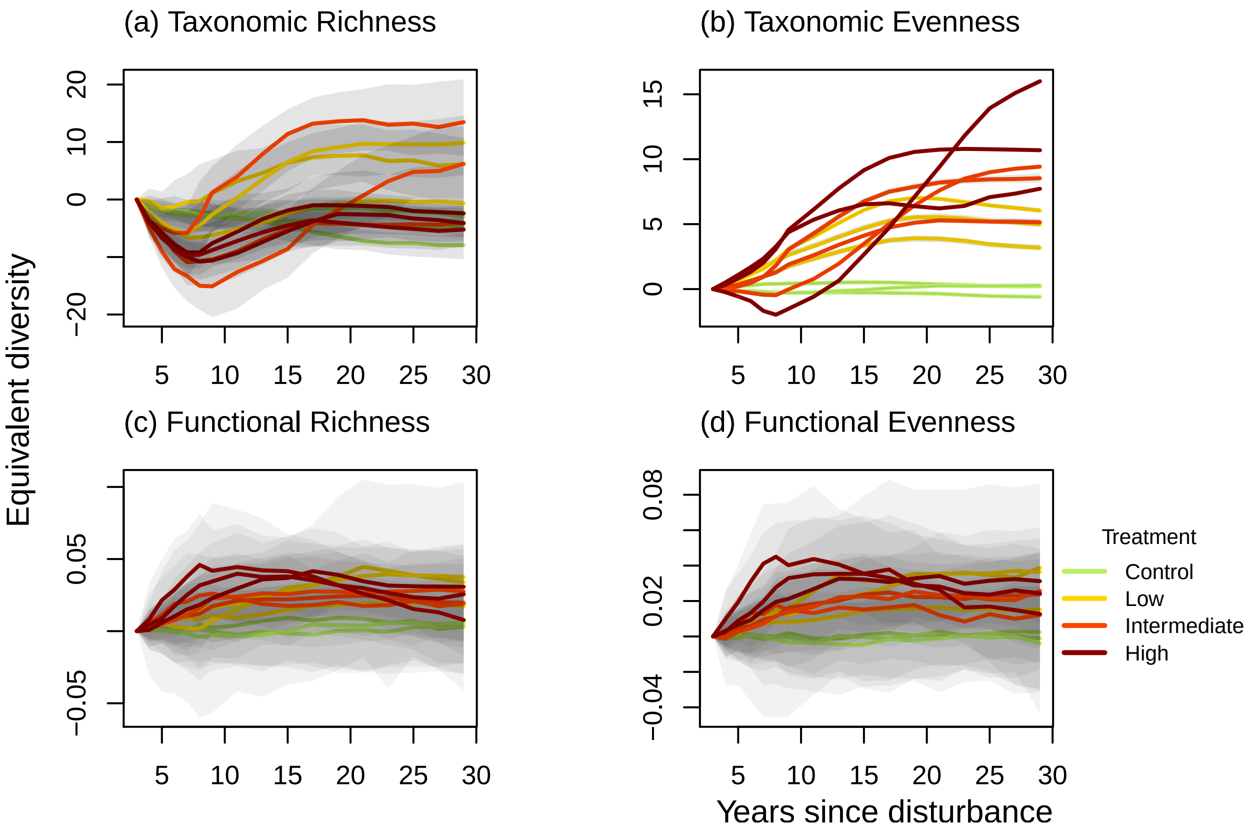

Figure 3. Trajectories over 30 years of the difference with the 1989 inventory (2 years after disturbance) of community taxonomic richness **(a)**, Simpson diversity **(b)**, functional richness **(c)**, and Rao diversity **(d)**. Shaded areas are the credibility intervals

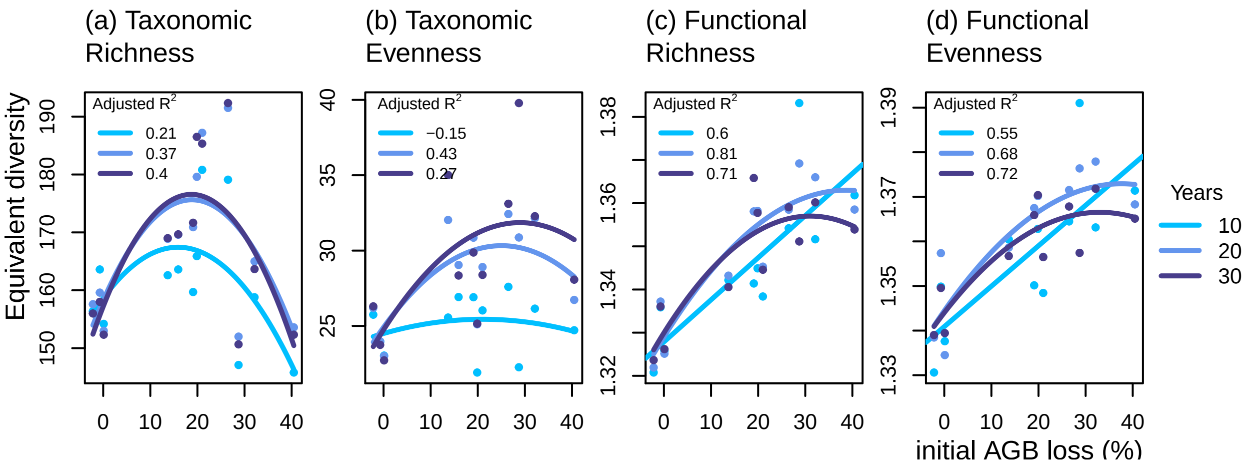

Figure 4. Relationship between the initial %AGB loss and community taxonomic richness **(a)**, taxonomic evenness **(b)**, functional richness **(c)**,and functional evenness **(d)** at 10, 20 and 30 years after disturbance

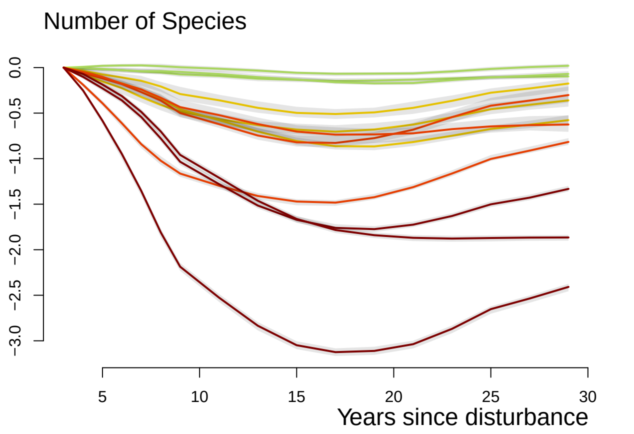

Figure 5. Trajectories of the functional redundancy within the initial functional space over 30 years after disturbance. Shaded areas are the credibility intervals.

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 taxonomic richness then decreased following intense disturbance, 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.

Taxonomic trajectories following disturbance of intermediate intensity besides highlighted an intermediate time after disturbance, around 15-20 years, for which the taxonomic evenness was maximized. As already observed in the Guiana shield (Baraloto *et al.*, 2012) and in Bornean tropical forests (Cannon, 1998), taxonomic evenness followed hump-shaped trajectories with a peak when the recruitment was balanced between pioneers and late-successional species. This intermediate time corresponded to the match between the generation time of pionneers, dominating first the post-disturbance recruitment, and the time for competitive exclusion to emerge, leading afterwards to the dominance of late-successional species.

Regarding community functional trajectories in contrast, there was neither intermediate disturbance intensity nor intermediate time after disturbance, which dismissed the IDH. Neither functional richness nor functional evenness displayed a humped-shaped pattern, but both rather increased with the recruitment of pioneers that were functionally highly different from 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. Right after disturbance, short-lived species benefited from the resources made available and 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 that the trajectories will catch up with those observed for intermediate disturbance (Walker & del Moral, 2009).

The IDH then translated into community taxonomic response, with post-disturbance trajectories changing markedly below and above an intensity threshold of 25 % AGB loss. The IDH was also valid at an intermediate time after disturbance, when the recruitment of early- and late-successional species were balanced. Functional trajectories, however, remained decoupled from taxonomic ones and dismissed the IDH.

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 an easy recruitment for the first species but becoming increasingly hampered by the emergence of interspecific competition (Busing & Brokaw, 2002). The recovery of the functional redundancy then relied upon the random process of species recruitment and 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 disturbed communities, with higher chances to see the settltement of pioneers and early-successional species at the expense of late-successional ones (Haddad *et al.*, 2008). Besides, the random 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). Infrequent species might indeed have unique functional characteristics, apart from those considered here, in the ecosystem or be a key for some fauna (Schleuning *et al.*, 2016).

5. Conclusion

Community post-disturbance trajectories in compositon and diversity were shaped by the recruitment of a determined pool of pioneers identical among communities and disturbance intensity. Nevertheless, taxonomic and functional composition trajectories appeared decoupled. While functional trajectories remained similar in the functional space and converged towards the recovery of a comparable initial state, taxonomic trajectories showed initial differences in community composition that were maintained along time. This decoupling was explained by a decrease of the functional redundancy that mitigated the functional impact of disturbance. Community functional and taxonomic diversity response to disturbance was contrasted as well. While the functional trajectories remained similar whenever the disturbance intensity, taxonomic trajectories were markedly different above a threshold of 20-25% AGB removed for which taxonomic richness was maximized and taxonomic eveness remained resilient. The Intermediate Disturbance Hypothesis applied to the linkage of disturbance with the taxonomic diversity, but not with the functional diversity. Taxonomic diversity was maximized following a disturbance of intermediate intensity, that was the threshold of 25% AGB removed, and at an intermediate time after disturbance, that was around 25 years after disturbance when the recruitment of early- and late-successional species were balanced. Whenever the disturbance intensity, community resilience (in terms of recovery of the pre-disturbance state) was tangible but required several decades and relied upon the random lottery recruitment of rare species. Although resilient, the functional redundancy was lower for more than 30 years after disturbance which 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 and interpreted the results. AM wrote the manuscript with contributions by EM & BH. 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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