Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract

Résumé de l'article.

Keywords

mot-clés, séparés par des virgules

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1. Introduction

The large areas covered with tropical forests worldwide hold crucial economic, social and cultural values. They provide wood and multiple non-timber forest products, shelter a diversified fauna, regulate the local climate, support the carbon, water and nutrient cycles, and ensure cultural and human well-being. The simultaneous increase of forests products demand and the substantial climatic changes currently heighten the pressure on remaining forests (Gibson *et al.*, 2011; Morales-Hidalgo *et al.*, 2015), threatening the maintenance of communities structure, composition and

functioning and their dynamics in space and time (Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015).

In tropical forest, ecological communities are constantly re-shaped by the natural disturbance events changing both abiotic environment, through the fluxes of light, heat and water, and biotic interactions and competitive pressure (Goulamoussène et al., 2017). The cornerstone of tropical forests ecology is to understand the mechanisms and the determinants of ecosystems response to disturbance (White & Jentsch, 2001; Chazdon, 2003). For now, this has been largely studied through structural parameters, rapid and convenient to measure, as aboveground biomass, tree height or stem density (Piponiot et al., 2016; Rutishauser et al., 2016). These structural parameters were thereafter consistently modeled and gave important insights into the maintenance of ecosystems processes and services (Denslow & Guzman, 2000; Blanc et al., 2009). However the response of forests diversity in tree species remains unclear, albeit it determines the productivity, stability and functioning of ecosystems (Tilman et al., 2014, Liang et al. (2016)) and would be most probably impacted by the changes following disturbance (Baraloto et al., 2012).

In the short-term disturbance demonstrated negligible or even positive impacts on communities diversity, which have been formalized by the intermediate disturbance hypothesis (IDH) stating a maximized species diversity at intermediate disturbance intensity (Molino & Sabatier, 2001; Kariuki et al., 2006; Berry et al., 2008). Still, validations of the IDH remain scarce in the long term and mainly rely on species richness analyses that gives limited or misleading information on forests recovery and functioning (Martin et al., 2015; Chaudhary et al., 2016). More releveant monitoring would encompass communities composition, crucial for conservation issues, and complete diversity profiles encompassing species evenness in addition to their richness,

that reveals ecological rules shaping communities (Magurran, 1988; Lavorel & Garnier, 2002; Bellwood et al., 2006). Furthermore, account for species biological attributes and role in the ecosystem is essential to understand the correlations between ecosystems biodiversity, functioning and environmental constraints (Violle et al., 2007; Moretti et al., 2009; Baraloto et al., 2012; Scheiter et al., 2013). In that respect functional approaches based on major traits related to species ecology and performance was largely adopted (Díaz et al., 2005; Villéger et al., 2008), for example highlighting in tropical rainforests the environmental filters fostering fast growing species with efficient resources acquisition after disturbance (Molino & Sabatier, 2001; Haddad et al., 2008). Post-disturbance trajectories then corresponded to a shift from "conservative" slow-growing species dealing with scarce resources dominating before disturbance, to "acquisitive" fast-growing species with rapid and efficient use of abundant resources (TerSteege & Hammond, 2001; Reich, 2014; Hérault et al., 2011). This shift translated into consistent trajectories for key functional traits related to resource acquisition (leaf area, density and chlorophyll content, and stem specific gravity and bark thickness), tree growth and reproduction and life history traits (seed mass and maximum height) (Wright et al., 2004; Westoby & Wright, 2006; Chave et al., 2009).

Functional and taxonomic trajectories are both essentiall to fully assess communities response to disturbance. Both relate to distinct ecological rules and processes and might then be decoupled as it was observed already in tropical forests (Lohbeck et al., 2015; Guariguata & Ostertag, 2001). Although taxonomic and functional diversity are complementary, they are combine into communities functional redundancy that measures the amount of species sharing same trait values (Carmona et al., 2016). Functional redundancy then explicits the link between otherwise decoupled taxonomic and functional diversities and is central for communities description. Besides, functional redundancy determines communities resilience as high redundancy, like in highly diverse tropical forests (Bellwood et al., 2006), mitigates the impacts of species removal on ecosystem functioning (Trenbath, 1999; Elmqvist et al., 2003; Díaz et al., 2005).

Grasp all facets of communities response to disturbance amount to disentangle the taxonomic and functional trajectories in diversity and composition. These trajectories would highlight the ecological rules constraining, or not, communities dynamics towards a recovery of initial composition, diversity and functioning. They would therefore clarify the tenants in the long term of the debated Intermediate Disturbance Hypothesis for tropical forests, which would be as much insights for future adaptive conservation strategies (Adler et al., 2007). Here we monitored over 30 years the response of 75 ha of forests plots set up on a gradient of disturbance intensity, from 10 to 60% of ecosystem biomass removed. We made use of a large functional traits database browsing major leaf, stem and seed traits and species maximum height to draw the trajectories over time of communities taxonomic and functional composition and diversity. Specifically, we (i) questioned the coupling

between taxonomic and functional response to disturbance and identified the underlying assembly processes, which allowed to (ii) clarify the validity of the IDH in the long term for tropical forest and (iii) question the completeness of communities recovery regarding their functional redundancy.

2. Material and Methods

2.1 Study site

Paracou station in French Guiana (5°18'N and 52°53'W) is located in a lowland tropical rain forest in a tropical wet climate with mean annual temperature of 26°C, mean annual precipitation averaging 2980 mm.y⁻¹ (30-y period) and a 3-month dry season (< 100 mm.month⁻¹) from mid-August to mid-November, and a one-month dry season in March (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 gradient of three logging, thinning and fuelwood cutting treatments (Table 1). Disturbance treatments were attributed 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 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 (ref to be found) measured 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 with a dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae botanical families. In the twelve experimental plots of the experiment, all trees above 10 cm DBH are mapped and measured annually since 1984. Trees are first identified during inventories with a vernacular name assigned by the field team, and afterward with a scientific name assigned by a botanist during regular botanical campaigns. In 1984, specific vernacular names are given to 62 commercial or common species whereas more infrequent ones were identified under general identifiers only distinguiching trees and palm trees. From 2003 botanical campaigns were conducted every 5 to 6 years to identify all trees at the species level but identification practices still varied among plots and campaigns.

This variability of protocols raised methodological issues as vernacular names usually correspond to different botanical species. It resulted in significant taxonomic uncertainties that had to be propagated to composition and diversity metrics. The uncertainty propagation was done through a Bayesian framework reconstituting complete inventories at genus level from real incomplete ones on the basis of

Treatment	Timber	Thinning	Fuelwood	%AGB lost
Control				0
T1	DBH \geq 50 cm, commercial species, \approx 10 trees/ha			[12% – 33%]
T2	DBH \geq 50 cm, commercial species, \approx 10 trees/ha	DBH \geq 40 cm, non-valuable species, \approx 30 trees/ha		[33% – 56%]
Т3	DBH \geq 50 cm, commercial species, \approx 10 trees/ha	DBH \geq 50 cm, non-valuable species, \approx 15 trees/ha	$40 \text{ cm} \leq \text{DBH} \leq 50$ cm, non-valuable species, ≈ 15 trees/ha	[35% – 66%]

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

vernacular/botanical names association. Vernacular names based on the association probability $[\alpha_1, \alpha_2, \dots, \alpha_3]$ observed across all inventories between each vernacular name v and the species $[s_1, s_2, \dots, s_N]$. See appendix 1 and Aubry-Kientz et al. (2013) for the detailed methodology.

The functional approach used a dataset of 6 functional traits representing leaf economics (leaves thickness, toughness, total chlorophyll content and specific leaf area, the leaf area per unit dry mass) and wood economics (wood specific gravity and bark thickness), and life history traits (maximum specific height and seed mass). The trait database came from the BRIDGE project ¹ where trait values were assessed from a selection of individuals located in nine permanent plots in French Guiana, including two in Paracou, and comprised 294 botanical species pertaining to 157 botanical genera. Missing trait values were filled using multivariate imputation by chained equation (mice) from the mice R package (van Buuren & Groothuis-Oudshoorn, 2011). Imputations were restricted within genus, or family when samples wre too scarce, in order to account for the phylogenetic signal of the functional traits. Whenever a species inventoried was not in the dataset, it was attributed a set of traits values randomly sampled among species of the same next higher taxonomic level (same genus or family). As seed mass information corresponds to a classification into mass classes, no data filling process was applied and analysis were restricted to the 414 botanical species recorded.

All composition and diversity metrics corresponded to the average obtained after 50 iterations of the taxonomic uncertainty propagation framework and of the filling process of missing trait values.

2.3 Composition and diversity metrics

To counter taxonomic uncertainties due to the variability of botanical identification protocols (see [#protocols]), the taxonomic composition and diversity analysis were conducted at the genus level, i.e. referring to the genus of observed or trialed botanical names. Trajectories of communities

taxonomic and functional variations in composition after were replaced through multinomial trials $M_{\nu}([s_1, s_2, \dots, s_N], [\alpha_1 \phi i s_2 \psi r ban \alpha_2])$ were followed in a two-dimensional ordination space the 30'years monitored. Two NMDS were conducted to map either taxonomic flora inventories or communities functional composition based on the 7 leaf, stem and life history traits (without seed mass classes). In both cases the NMDS were performed using occurrence-based (Jaccard) and abundance-based (Bray-Curtis) dissimilarity measures. Trajectories along time in the plan were reported through the euclidean distance of successive inventories to the reference inventories in 1989, 5 years after disturbance, when the uncertainty degree did not exceed 30% of undetermined trees. The trajectories of the leaf and stem and life traits were also visualized with the community weighted means (CWM), representing the average trait value in a community weighted by relative abundance of the species carrying each value (Díaz et al., 2007; et al. Garnier, 2004). To compensate the intrinsinc difference among plots the trajectories corresponded to the differences along time with the reference inventory in 1989. Species seed mass corresponded to 5 classes of increasing mass, seed mass trajectories were therefore reported as the proportion of each class in the inventories.

> The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973). These three indices belong to the set of HCDT or generalized entropy, respectively corresponding to the 0, 1 and 2 order of diversity (q), which proved well suited for diversity studies (Patil & C., 1982; Tothmeresz & Tóthmérész, 1995). The functional diversity was reported using the Rao index of quadratic entropy which combines species abundance distribution and average pairwise dissimilarity based on all functional and life traits.

> The impacts of initial disturbance were first tested with the spearman rank correlation between the extremum of taxonomic and functional metrics reached over the 30 years and the initial %AGB removed. Then they were analysed through the linear correlations between Simpson and Rao diversities and the initial %AGB removed at 10, 20 and 30 years after disturbance.

The functional redundancy was measured as the overlap

¹http://www.ecofog.gf/Bridge/

among species in communities' functional space (Carmona et al., 2016). The samples of the trait database were first mapped in a 2-dimensional plan from a PCA analysis. Then, multivariate kernel density estimator associated with individual trees returned species traits probability distribution (TDP). Species TDP weighted by species abundance were eventually summed for each community: the functional redundancy was the sum of TDPs overlap, expressed as the average number of species that could be removed from without reducing the functional space (see appendix I for a more comprehensive sheme).

3. Results

3.1 Communities Diversity

In the inventories from 1989 (5 years after disturbance) to 2015 (31 years after disturbance), 828388 trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. Communities taxonomic diversity trajectories were examined through the Richness, Shannon and Simpson diversities at genus level, in relation to the 1989 inventories (5 years after disturbance) (See annexe I). For undisturbed plots the Richness, Shannon and Simpson diversities remained stable over the 30 years monitored. In disturbed communities the taxonomic richness increased after low disturbance intensity, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2) while it followed unimodal trajectories after intense disturbance, decreasing for ten years before recovering predisturbance values. In all disturbed plots the taxonomic evenness (Shannon and Simpson diversities) increased, following unimodal trajectories with a maximum, reached after around 20 years, positively correlated to the disturbance treatment ($\rho_{spearman}^{Shannon} = 0.86$, and $\rho_{spearman}^{Simpson} = 0.89$). Return towards initial evenness values was beginning after 30 years except for two T3 plots (plots 8 and 12) which evenness still increased, suggesting similar but delayed trajectories 1.

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

The impact of disturbance was examined specifically through the linear correlation between the intial %AGB removed and the Simpson and Rao diversities (diversities of order 2) after 10, 20 and 30 years 1. The correlation with disturbance intensity was weak for the Simpson diversity ($R^2 < 0.25$) and only valid from 20 years after disturbance but it was much stronger for the Rao diversity (0.55 < $R^2 < 0.75$) for all the time studied. Slope of linear correlations, reflecting the impact of disturbance, was the highest 20 years after disturbance.

3.2 Communities composition

3.2.1 Taxonomic and functional trajectories

The trajectories of taxonomic and functional composition were visualized in a two dimensional ordination space mapping the successive inventories according to their flora and corresponding traits. Classifications were performed using either abundance-based Bray-Curtis (Figure 2) or incidence-based Jaccard dissimilarity, both giving similar results only analysis using Bray-Curtis dissimilarity are discussed.

While both taxonomic and functional composition remained stable in undistrubed communities, they followed consistent trajectories over time after disturbance which revealed significant compositional changes. According to the mapping of functional traits (see appendix I) these compositional changes corresponded to shifts towards species with more acquisitive functional strategies, from communities with high average WD to high average SLA and chlorophyll content. For disturbed communities the distance of successive inventories to the 1989 reference inventory followed unimodal trajectories translating cyclic compositional changes with a recovery of the initial composition (Figure 2). The maximum dissimilarity with the initial state was positively correlated to the disturbance treatment for both taxonomic and functional composition ($\rho_{spearman}^{taxonomic} = 0.91$ and $\rho_{spearman}^{functional} = 0.96$ respectively) and the time at maximum was reached around 26 years after disturbance for taxonomic composition and 22 years for functional composition.

3.2.2 Traits community weighted means (CWM)

The changes observed in plots functional composition went hand to hand with consistent trajectories of the 8 functional and life history traits visualized with the trajectories of community weighted means (CWM) of leaves economics (leaves thickness, chlorophyll content, toughness and specific area), wood economics (wood specific gravity, bark thickness), and life history traits (seed mass and maximum adult height) (Figure 3).

Except for leaf chlorophyll content, which continued to increase for some T3 and T2 plots 30 years after disturbance, all traits and seed mass proportions followed unimodal trajectories either stabilizing or returning towards their initial values. Thirty years after disturbance the weighted means of communities specific maximum height at adult stage (Hmax), leaf toughness ($L_toughness$) and wood specific gravity (WD) remained significantly lower than their initial value (Figure 3). The weighted means of bark thickness ($Bark_thick$) similarly remained substantially higher than initially for all disturbed plots while the specfic leaf area (SLA) had almost recovered its initial value. For all traits the maximum difference to initial state was correlated to the disturbance intensity ($\rho_{spearman}^{L_{thickness}} = 0.67$, $\rho_{spearman}^{L_{chloro}} = 0.45$, $\rho_{spearman}^{L_{toughness}} = -0.43$, $\rho_{spearman}^{SLA} = 0.93$, $\rho_{spearman}^{WD} = -0.78$, $\rho_{spearman}^{Bark_{-thickness}} = 0.88$, $\rho_{spearman}^{Hmax} = -0.48$).

3.2.3 Functional redundancy

Communities functional redundancy was measured as the sum within communities the species weighted functional overlap based on the 7 leaf, stem, and maximum height

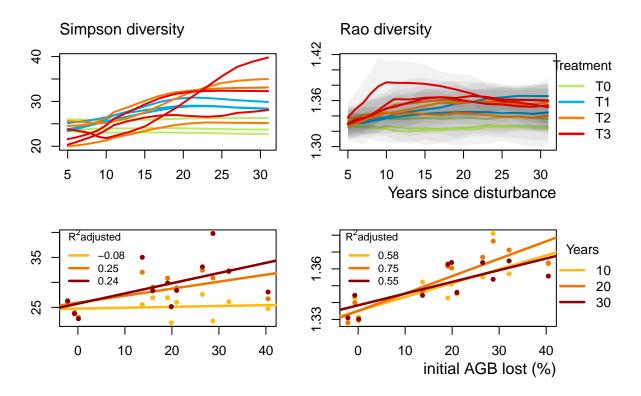


Figure 1. Upper panels, Trajectories of the Simpson taxonomic diversity (**a**) and Rao functional diversity (**b**) over 30 years after disturbance, corresponding to the median and 0.025 and 0.975 percentile observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1, orange for T2 and red for T3. Lower panels, Relationship between the initial %AGB removed and the median values of Simpson (**c**) and Rao (**d**) diversities at three times after disturbance. Solid lines colors represent the time, 10 years (yellow), 20 years (orange) and 30 years (brown) after disturbance.

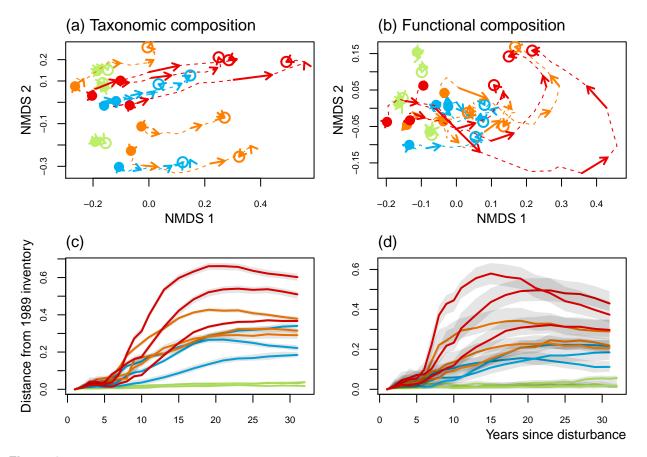


Figure 2. Trajectories of the plots in terms of flora composition (left panels (a) and (c)) and functional composition (right panels (b) and (d)) regarding the 6 leaf and stem functional traits, the maximum allometric height and seed mass class. Plots trajectories are first represented in the two-dimensional space from the NMDS performed for the 30 years after disturbance based on Bray-Curtis dissimilarity measures between successive inventories (Upper panels (a) and (b)). Then the lower panels ((c) and (d)) represent the euclidean distance to initial condition along the 30 sampled years. Line colors represent the disturbance treatment (green for control, blue for T1, orange for T2 and red for T3). The 0.025 and 0.975 percentile correspond to the variance observed for 50 iteration of the taxonomic uncertainty propagation and functional trait filling processes.

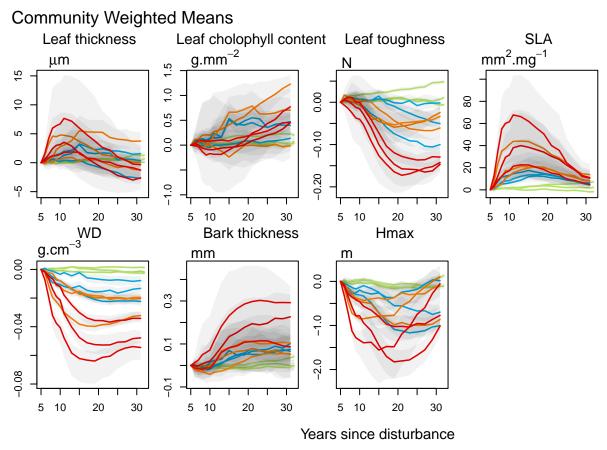


Figure 3. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, *L_thickness*, chlorophyll content, *L_chloro*, toughness, *L_toughness* and specific area, *SLA*), 2 stem traits (wood specific gravity, *WD*, and bark thickness, *Bark-thick*) and one life trait (Specific maximum height at adult stage, *Hmax*). Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1, orange for T2 and red for T3.

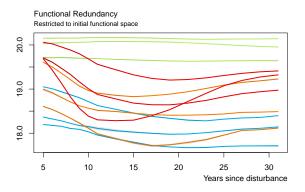


Figure 4. Trajectories of the functional redundancy within the initial cpùùunities functional space over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1, orange for T2 and red for T3. (#fig:RedFun_rest)

traits (see appendix I for PCA details). Communities functional redundancy remained stable in control plots but after disturbance the redundancy trajectories were quite variable (See appendix I) and apparently independently of the initial disturbance. Globally after most intense disturbance (plots T2 and T3) communities redundancy decreased at first place before increasing to edge, recover or exceed the initial value.

Considering the functional redundancy restricted to the functional space of the initial inventory, all disturbed plots followed similar decreasing humped-shaped trajectories (@ref(fig:RedFun_rest)). The maximum redundancy loss was positively correlated with the disturbance intensity (XX spearman to be measured) and the initial value had not recovered for any disturbed communities.

4. Discussion

4.1 Decoupled recovery of communities taxonomic and functional characteristics

Both communities taxonomic and functional diversity and composition proved resilient, following similar humped-back trajectories with a return towards initial values. The resilience of communities functional characteristics, the most direct link between biodiversity and ecosystem functioning (Díaz *et al.*, 2005), meant a consistent recovery of ecosystem processes in the long term (Guariguata & Ostertag, 2001). The resilience of communities taxonomic characteristics, in turn, meant the maintenance of their initial differences in composition and structure. It suggested that communities response to disturbance were somehow constraint to converge towards determined compositions (Hubbell *et al.*, 1999; Molino & Sabatier, 2001; Anderson, 2007; Baraloto *et al.*, 2012).

Although both communities taxonomic and functional

characteristics proved resilient and followed similar humpedback trajectories, the taxonomic recovery systematically lagged behind the corresponding functional dynamics. Such delay between functional and taxonomic dynamics has already been observed for grasslands (Tilman, 1997; Mouillot et al., 2011) and more recently for tropical forests (Lohbeck et al., 2015; Guariguata & Ostertag, 2001). According to the "vegetation quantity effect" (Grime, 1998) functional trajectories rely on the pool of dominant species, which diversity and evenness were enhanced after disturbance, and which rapidly restored the functional diversity and composition. However, communities evenness remained high so infrequent species still missed to the taxonomic recovery that mechanically lagged behind, all the more so that unrecovered species would be functionally redundant and probably undergo competition processes.

4.2 A validation of the intermediate disturbance hypothesis

Validating the IDH, communities trajectories confirmed the diversity increase after disturbance through an enhanced growth of otherwise less favored species. This was however completely clear regarding the functional diversity but much more blurry for communities taxonomic characteristics.

The taxonomic richness was weakly or negatively impacted by intense disturbance, as observed on several post logging surveys (Cannon, 1998; Baraloto et al., 2012), while it substantially increased after low intensity disturbance. Disturbance also enhanced taxonomic evenness, but its intensity was only weakly and lately correlated to communities eveness (i.e. Simpson diversity). Contrastingly, disturbance intensity consistently predicted the significant increase of communities functional diversity for 30 years. Disturbance impacts involve specific turnover within communities, either among pre-disturbance survivors or among newly recruited trees. As the composition of old-growth survivors proved to mirror initial communities (Hérault & Piponiot, 2018), disturbance would impact trees recruitment through the enhanced growth and survival of previously infrequent species and functional characteristics. Consistently, disturbance resulted in increasing taxonomic dissimilarity compared to pre-disturbance communities and functional shifts towards resource-acquisitive strategies (sharp increase in the SLA, leaf thickness and bark thickness and decrease in wood density, leaf toughness and maximum height) (Westoby, 1998; Wright et al., 2004; Reich, 2014). Disturbance then caused a reorganization of the typical high dominance structure of hyperdiverse mature forests after disturbance, benefiting to pioneers and light demanding species. Likely, the changes in abiotic environment and competitive pressure favored pioneers which outcompete others in non limiting resources but are excluded in mature forests by long-lived, more resistant and shade tolerant species. Therefore, consistently with communities dynamics after disturbance relied on species functional strategy and corresponding ability to fill the environmental niches made available by disturbance. Recruited species then mixed with pre-disturbance ones, from which they differed, and constituted a community all the more diversified that the disturbance was intense (Molino & Sabatier, 2001).

4.3 The functional redundancu and the resilience of communities

Both the lag between taxonomic and functional recovery and the middling consistency of the IDH regarding communities taxonomic diversity entail a central role of functional redundancy. Functional redundancy, determinant of communities resilience (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005), seemed not to have recovered 30 years after disturbance.

Although disturbance would be mitigated by communities functional redundancy, we expect the redundancy itself to be reduced or re-organized within the functional space. Globally, disturbed communities did not follow consistent trajectories after disturbance and 30 years after disturbance, irrespective of the intensity, disturbed communities displayed lower, similar or higher functional redundancy. The redundancy within the functional space of the initial community however clearly followed humped-back trajectories which decrease was determined by the disturbance intensity and which return to initial state was not observed for any disturbed community. Not only did the functional redundancy and hence the resilience of pre-disturbance community decrease, but also did the ones of disturbance-specific communities increase. It means higher chances to have long lasting or self-maintained compositional changes towards disturbance resistant species, lianas or epiphytes (Haddad et al., 2008; Burslem et al., 2000; Martin et al., 2013) and thus highly question forest's resilience (Chazdon, 2003). Specificaly, this would impair species contingent to undisturbed forests, threatening their maintenance, and run the risk to loose cornerstone species and trigger unexpected ecological consequences (Jones et al., 1994; Díaz et al., 2005; Gardner et al., 2007).

5. Conclusions

our study disentangled tropical forests functional and taxonomic decoupled response to disturbance, with a rapid recovery of communities functioning but slower and more variable taxonomic dynamics. Consistently with the IDH functional trajectories were constrained by environmental pressures favoring pioneers and light-demanding species after disturbance, but taxonomic dynamics were more stochastic as they involved infrequent species functionally redundant with the dominants and thus under competitive pressure. While communities functioning rapidly recovered, taxonomic trajectories, although consistent and converging towards full recovery, were much slower and entailed persisting alteration of communities functional redundancy. the trajectories therefore suggested a potential sustainability of tropical forests in the face of quite intense disturbance but only when followed by long recovery periods, longer than 30 years (Gourlet-Fleury et al., 2005). This study besides highlighted the central role of recruitment processes underlying the IDH mechanisms and holding the whole community response to disturbance.

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