

# Diverging taxonomic and functional trajectories following disturbance in a Neotropical forest

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## Abstract

In the current global change context, it is urgent to anticipate the fate of tropical forests. This means understanding tree community response to disturbance and the underlying processes. In that respect, we aim here to clarify taxonomic and functional post-disturbance trajectories, and determine the scope of the Intermediate Disturbance Hypothesis (IDH) that remains debated in tropical forests. We analyzed community trajectories following a disturbance gradient from 10 to 60% of above-ground biomass loss in a Neotropical forest over 30 years. We considered trajectories along time of community taxonomic and functional trajectories in terms of richness, evenness, composition, and redundancy. We based on the annual botanical inventories of 75 ha of a Neotropical forest and on large trait datasets comprising seven leaf, stem, and life-history traits. We identified a decoupling between taxonomic composition, differing among communities, and functional composition, similar among communities and convergent in the functional space. The taxonomic diversity followed humped-shaped trajectories along time after disturbance depending on the initial disturbance intensity, which validated the IDH (Intermediate Disturbance Hypothesis). The functional diversity trajectories, however, were homogeneous among plots and dismissed the IDH. We explained this decoupling by the variations in community functional redundancy that mitigated the functional impact of disturbance. Although consistent, the recovery of community composition, diversity, and redundancy remained unachieved after 30 years. These results acknowledged the need of decades-long cycles without disturbance to ensure community complete recovery.

## Keywords

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

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## 50 1. Introduction

51 The large areas covered with tropical forests worldwide hold crucial environmental, economic, and social values. They  
52 provide wood and multiple non-timber forest products, shelter a diversified fauna, and ensure cultural and human well-  
53 being. They regulate local and regional climates, as well as carbon, water and nutrient cycles. However, the growing  
54 demand in forests products together with current global changes increase the pressure on remaining undisturbed forests  
55 (Morales-Hidalgo *et al.*, 2015). **These threats may change the frequency and magnitude of the natural disturbance regime**  
56 **that defines and maintains the structure, composition, and functioning of tree communities** (Schnitzer & Carson, 2001;  
57 Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015). To anticipate the fate of tropical forests, it is urgent to understand tree  
58 community response to disturbance, and the underlying ecological processes. The forest cover is generally maintained  
59 following disturbance, but modifications in the fluxes of light, heat, and water (Goulamoussène *et al.*, 2017) change

community abiotic and biotic environments. These changes translate into post-disturbance community trajectories that have 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). Some of the determinants of post-disturbance biomass trajectories are already identified, like the structure and composition of the pre-disturbance community, or the post-disturbance environmental parameters (Hérault & Piponiot, 2018). Community diversity and composition trajectories, however, have not been as thoroughly understood (Guitet *et al.*, 2018; Molino & Sabatier, 2001), and manifold biodiversity trajectories might emerge given the variety of species response to disturbance and the diversity of tropical forests (Lindenmayer *et al.*, 2012; Garcia Florez *et al.*, 2017).

An early conceptual basis of the linkage between biodiversity and disturbance is the Intermediate Disturbance Hypothesis (IDH). The IDH states a relationship between the community diversity and the intensity and frequency of disturbance events, and postulates a diversity peak at intermediate level of disturbance (Connell, 1978). This is based on the fluctuations of community environment following disturbance that foster both competitively superior species and fast colonizers, and prevents competitive exclusion (Shea *et al.*, 2004; Pulsford *et al.*, 2016). In tropical forests, some studies advocate community deterministic response to disturbance, as for example in the dry and wet forests in Ghana (Bongers *et al.*, 2009) or in the guianese rainforests (Molino & Sabatier, 2001), where intermediate disturbance proved to increase the community richness by increasing the proportion of pioneers or heliophilous species in the community while maintaining the richness in old-growth forest species. In other cases, however, observations of the IDH diverge from theoretical expectations (Randall Hughes *et al.*, 2007; Sheil & Burslem, 2003; Norden *et al.*, 2017). Some studies refute the role of disturbance intensity, as observed in forest gaps in Panama where no difference in species richness was found between forest gaps and undisturbed areas (Hubbell, 2001), or in costa-rican forests where forests that did not follow deterministic convergence display stochastic trajectories (Norden *et al.*, 2015).

The high diversity of tropical forests may foster the emergence of numerous facilitation, adaptation, and inter- and intra-specific competition following disturbance (Garcia Florez *et al.*, 2017; Bongers *et al.*, 2009). These interactions can result in miscellaneous responses to disturbance (Lindenmayer *et al.*, 2012), which question the validity of the IDH in tropical forests (Hubbell, 2001; Fox, 2013; Sheil & Burslem, 2013).

Analysing community response to disturbance and grasp all aspects of community changes requires a wide array of metrics (Sheil & Burslem, 2003; Shea *et al.*, 2004; Mayfield & Levine, 2010). The analysis should first consider community composition, which is crucial for conservation issues and reveals the pool of species fostered or hampered by disturbance (Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). This should be completed with diversity metrics encompassing both community richness and evenness to assess the changes in community abundance distribution. Besides,

functional approaches have been shown to usefully complement pure taxonomic approaches as they shed light on the species biological attributes directly linking community diversity, composition, and redundancy to ecosystem functioning (Violle *et al.*, 2007; Baraloto *et al.*, 2012). In that respect, a vast literature allowed recognizing major traits representing species ecological strategy and determining how they respond to changing conditions (Díaz *et al.*, 2005). Specifically, in tropical forests, the functional approach revealed the emergence of deterministic processes following disturbance. Such deterministic processes entailed 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, as leaf and stem traits, and life-history strategy, as seed mass and 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 community resilience after disturbance (Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

Here, 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 drew taxonomic and functional post-disturbance trajectories and examined the underlying ecological processes, (ii) we discussed the scope of the IDH regarding taxonomic and functional facets of community diversity, and (iii) we analyzed community resilience and time to recovery. We hypothesized that community functional and taxonomic trajectories might not track each other, given the high functional redundancy in tropical forests. While functional diversity would be enhanced by the environmental changes following disturbance, specifically the increase in light availability, taxonomic trajectories would only increase until a disturbance intensity threshold, as pioneers recruited following disturbance are not as diverse as late-successional species. Community taxonomic and functional would hence follow different rates of 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, and mean annual precipitation averaging 2980 mm.y<sup>-1</sup> (30-y period). The

climate comprises a 3-month dry season ( $< 100 \text{ mm} \cdot \text{month}^{-1}$ ) from mid-August to mid-November, and a one-month dry season in March (Wagner *et al.*, 2011). Across all plots, elevation ranges from 5 to 50 m, and the topography mainly corresponds to hilltops or hillsides, while bottomlands cover less than 1 % of the area. Plots are shallow ferrallitic 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, distributed over a 400ha area (Table 1, Supp. Mat. Fig. S1), that undergone three disturbance treatments in 1987 according to a randomized plot design (Gourlet-Fleury *et al.*, 2004).

The experiment intended to simulate logging intensities and distinguished the treatments for non-commercial commercial species, logged at 40cm DBH to simulate thinning operations. The experiment comprised three replicates of three silvicultural treatments (hereafter plots T1, T2, and T3), and three control plots (T0). Control plots are set in mature forest stand that did not undergone any logging nor intense anthropic activities activities for the last 500 years. 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 commercially exploited species (Gourlet-Fleury *et al.*, 2004). Treatment T2 additionally comprised a thinning treatment by poison-girdling of non-commercially exploited species randomly selected with an average of 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-girdling of 20 trees/ha with a 50 cm minimum DBH, all belonging to non-commercially exploited 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.*, 2017). Tree diameter are provided in the experimental dataset, wood density is extracted from global wood density (GWD) database (Zanne *et al.*, 2009), and tree height is retrieved from a generic H-D model based on a single bioclimatic predictor (eqn 6a in (Chave *et al.*, 2014)). The AGB is measured from the generalized allometric model eqn 4 of (Chave *et al.*, 2014). The three treatments were then transformed into a continuous disturbance intensity gradient with increasing above-ground biomass (AGB) loss.

## 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 common or commercially exploited species. More infrequent species were identified under general identifiers only distinguishing trees and palms. From 2003, botanical campaigns have been conducted every 5 to 6

**Table 1.** Intervention table, summary of the disturbance intensity for the 4 plot treatments in Paracou. Treatment intensities are defined by the minimum logging DBH (Diameter at Breast Height), the type of logged species (commercially exploited or not), the density of logged trees, and the total AGB (Above Ground Biomass) lost after treatment.

Treatment	Timber	Thinning	Fuelwood	%AGB lost
Control	-	-	-	0
T1, low	DBH $\geq$ 50 cm, commercially exploited species, $\approx$ 10 <i>trees.ha</i> <sup>-1</sup>	-	-	[12 – 33]
T2, intermediate	DBH $\geq$ 50 cm, commercially exploited species, $\approx$ 10 <i>trees.ha</i> <sup>-1</sup>	DBH $\geq$ 40 cm, non-commercially exploited species, $\approx$ 30 <i>trees.ha</i> <sup>-1</sup>	-	[33 – 56]
T3, high	DBH $\geq$ 50 cm, commercially exploited species, $\approx$ 10 <i>trees.ha</i> <sup>-1</sup>	DBH $\geq$ 50 cm, non-commercially exploited species, $\approx$ 15 <i>trees.ha</i> <sup>-1</sup>	40 cm $\leq$ DBH $\leq$ 50 cm, non-commercially exploited species, $\approx$ 15 <i>trees.ha</i> <sup>-1</sup>	[35 – 56]

149 years to identify all trees at the species level. In 2015, however, identification levels still varied among plots and campaigns.

150 This variability of protocols in time raised methodological issues as vernacular names usually correspond to various  
 151 botanical species. This resulted in significant taxonomic uncertainty that had to be accounted for in the measure of composi-  
 152 tion and diversity metrics. Uncertainty propagation was implemented within a Bayesian framework using vernacular/botanical  
 153 names associations to reconstitute complete inventories at genus level from real incomplete ones. Vernacular names were  
 154 replaced through multinomial trials based on the association probability  $[\alpha_1, \alpha_2, \dots, \alpha_V]$  observed across all inventories  
 155 between each vernacular name  $v$  and all species  $[s_1, s_2, \dots, s_N]$ :

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

156 See Supplementary Materials -Fig. S2 and Aubry-Kientz *et al.* (2013) for the detailed methodology.

157 Six functional traits representing the leaf economics (*i.e.* leaf thickness, toughness, total chlorophyll content, and  
 158 specific leaf area), and the stem economics (*i.e.* wood specific gravity and bark thickness) were obtained from the BRIDGE  
 159 project <sup>1</sup>. Trait values were assessed from a selection of individuals located in nine permanent plots in French Guiana,  
 160 including two in Paracou, and comprised 294 species belonging to 157 genera. Whenever a species was in the dataset  
 161 but missed some trait values (10% of the species), missing values were filled using multivariate imputation by chained  
 162 equation (van Buuren & Groothuis-Oudshoorn, 2011). To account for the phylogenetic signal in the imputation process,  
 163 imputations were based on samples of species from the same genus or from the same family. Whenever a species was  
 164 not in the dataset, it was attributed a set of trait values randomly sampled among species of the next higher taxonomic  
 165 level (same genus or family). Two life-history traits, maximum specific height and seed mass, came from the Mariwenn  
 166 database <sup>2</sup>. The database compiles information from a vast literature on the flora of French Guiana (Ollivier *et al.*, 2007)  
 167 and comprises 362 species belonging to 188 genera. As seed mass information was classified into classes, no data filling  
 168 process was applied and analyses were restricted to the botanical species recorded.

169 Confidence intervals of the composition and diversity metrics were computed after 50 iterations of the uncertainty  
 170 propagation framework.

### 171 2.3 Composition and diversity metrics

172 Because of the variable precision of botanical identification efforts, we had to conduct the taxonomic composition and  
 173 diversity analysis at the genus level. Functional composition, diversity, and redundancy measures were conducted at  
 174 species level. Taxonomic and functional trajectories of community composition were drawn in a two-dimensional NMDS

<sup>1</sup><http://www.ecofog.gf/Bridge/>

<sup>2</sup><https://www.ecofog.gf/mariwenn/>

ordination plane. Two NMDS using abundance-based (*i.e.* 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 1984 pre-disturbance inventories of reference. 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 and functional trajectories were analysed from the 1984 pre-disturbance inventories of reference. The taxonomic diversity was reported through species richness and the Hill number translation of the Simpson index (Hill, 1973). The comparison between these two metrics assesses community taxonomic richness and evenness: thereafter, results will be discussed directly in terms of taxonomic richness and evenness. Both indices are recommended for diversity studies (Marcon & Hérault, 2015), and belong to the set of Tsallis or generalized entropy corresponding, respectively, to the 0 and 2 order of diversity ( $q$ ). Diversity metrics were measured using the Hqz function from the entropart package (Marcon & Hérault, 2015). The functional diversity was reported using the functional richness and functional evenness. Both functional richness and evenness were measured through a distance-based dissimilarity matrix built with the daisy function of the cluster R package (Maechler *et al.*, 2019), using the Gower distance between species, similar to Hérault & Honnay (2007), Hérault (2007). The functional diversity was measured through the Rao index of quadratic entropy. The Rao index combines the community abundance distribution, from species relative abundance, and the average pairwise functional dissimilarity between species computed by the Gower distance. The comparison between these two metrics assesses community functional richness and evenness: thereafter, results will be discussed directly in terms of functional richness and evenness.

The impacts of the initial disturbance levels on the maximum gain or loss in richness and evenness were tested with the Spearman rank correlation tests. Richness and evenness trajectories were besides analyzed through polynomial regression or simple linear models between (i) taxonomic and functional richness and evenness, and (ii) the initial %AGB loss at 10, 20, and 30 years after disturbance. The best model fitting, between linear or quadratic model, was chosen based on their respective AIC criterion. The explanatory power of the fit were measured to adjusted r-square values.

Finally, 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. The PCA analysis lowered the weight of correlations among traits as the axes are combinations of the most decoupled traits. The two main PCA axis respectively hold 26% and 19% of the trait dataset variance. For each species, the traits probability density (TPD) were computed from the mapping of individuals through two-dimension kernel density estimators. We used



the `kde2d` function of the `MASS` package (Venables & Ripley, 2002) that is a gaussian density estimator for a 2-dimensional space. Second, for each community, the TPD weighted by species abundance were summed across 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

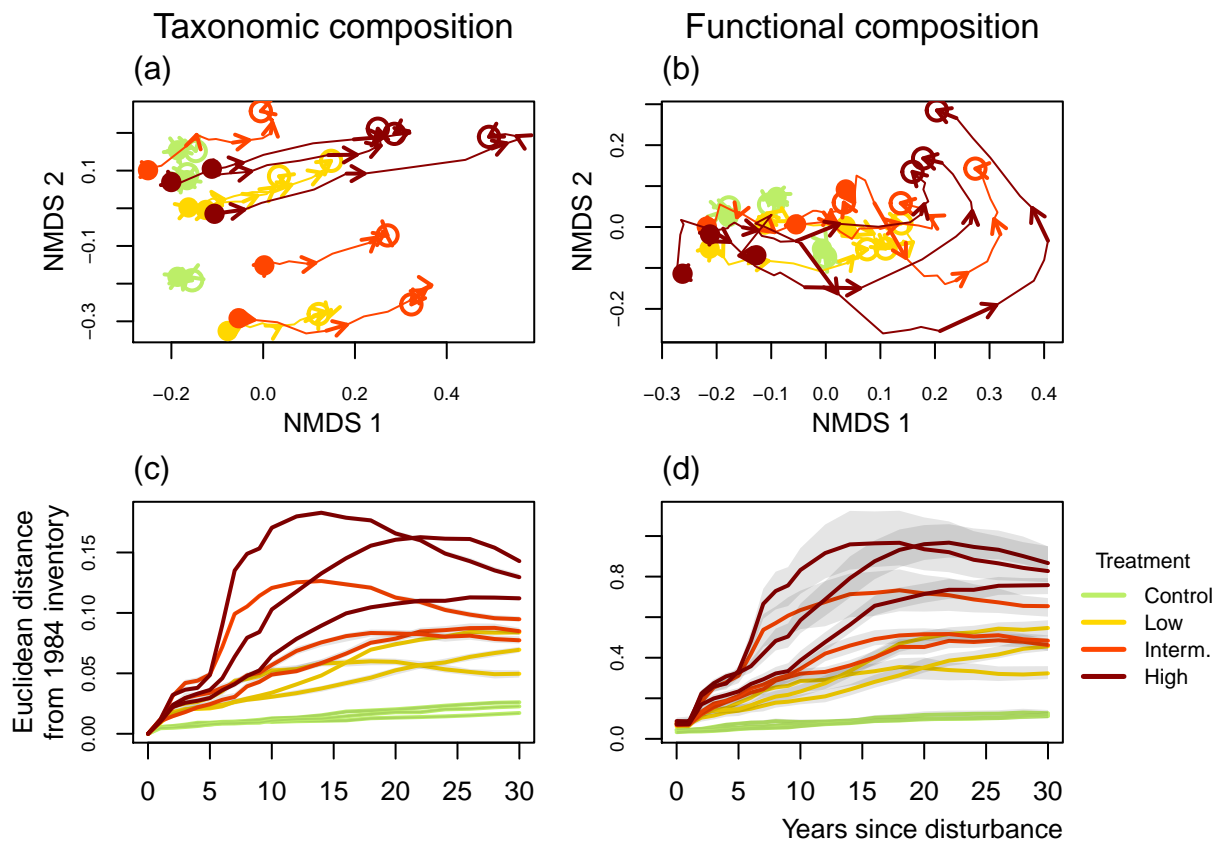
### 3.1 Community Composition

From 1984, the first pre-disturbance inventory, to 2015, 28 years after disturbance, 828 388 individual trees and 591 botanical species spanning 223 genera and 64 families were recorded.

In undisturbed plots, both taxonomic and functional composition remained stable (Fig. 1). In disturbed plots, both trajectories followed marked and consistent trajectories over time.

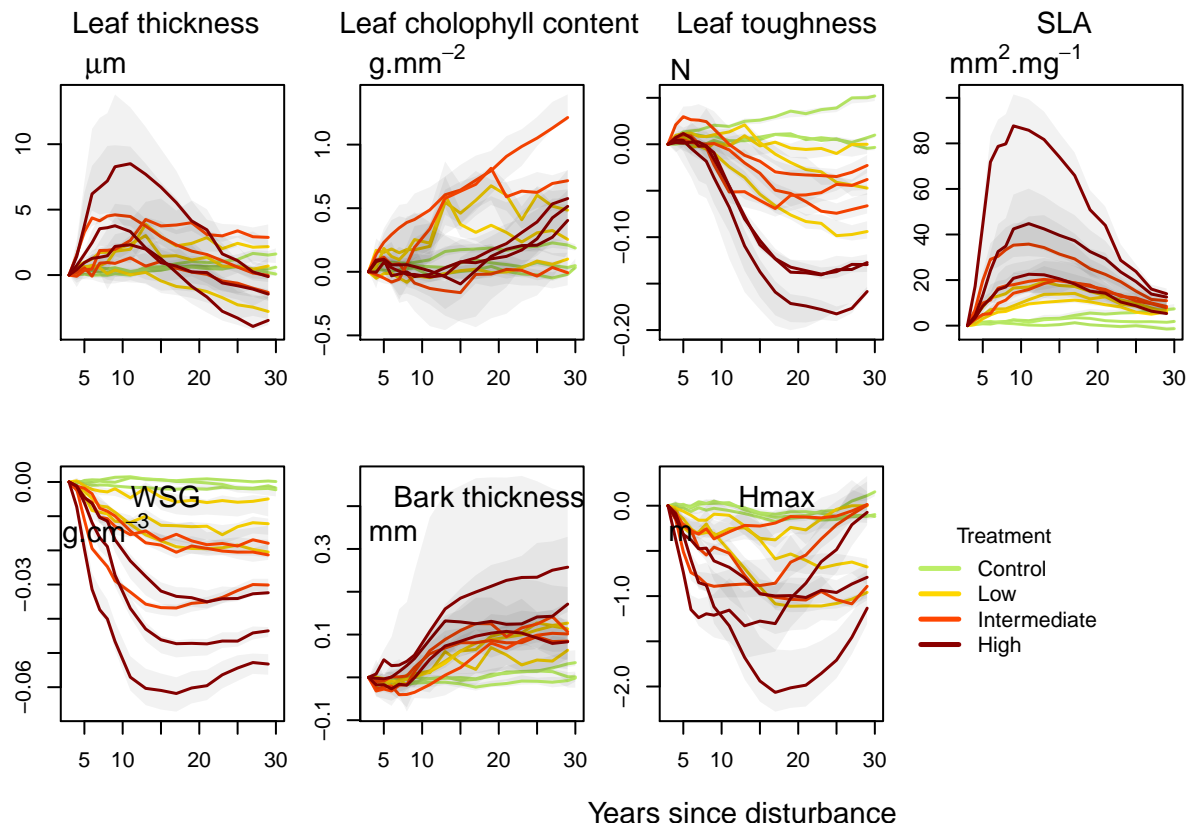
The functional composition trajectory resembled, in disturbed communities, to cyclic compositional changes with an incomplete recovery of the initial composition (Fig.1). The maximum dissimilarity with the initial state was positively correlated with the disturbance intensity for both taxonomic and functional composition ( $\rho_{Spearman}^{Taxonomic} = 0.94$  and  $\rho_{Spearman}^{Functional} = 0.90$ , respectively. Fig. 6). The maximum dissimilarity with the initial state was reached for taxonomic composition between 15 to 25 years, and between 20 to 25 years for functional composition.

In control plots, Community Weighted Means (CWM) of functional traits remained stable in time. In disturbed plots, they mostly followed unimodal trajectories, either stabilizing or returning towards their initial values, to the exception of leaf chlorophyll content, which continued to increase 30 years after disturbance for 4 out of 6 highly disturbed plots. Main tendencies for disturbed plots were a decrease followed by a slight increase of maximum height at adult stage (*Hmax*), leaf toughness, and wood specific gravity (*WSG*), but trait values remained significantly lower than their initial value (Fig. 2). Bark thickness and specific leaf area (*SLA*) both increased along time. Bark thickness remained substantially high after 30 years, and *SLA* had almost recovered to its initial value. Whatever the functional traits, the maximum difference to initial value was highly correlated to the disturbance intensity. Positive correlations were observed for leaf thickness, chlorophyll content, *SLA* and bark thickness ( $\rho_{Spearman}^{Leafthickness} = 0.79$ ,  $\rho_{Spearman}^{Chlorophyllcontent} = 0.61$ ,  $\rho_{Spearman}^{SLA} = 0.99$ ,  $\rho_{Spearman}^{Barkthickness} = 0.68$ ). Maxima were observed between 5 and 15 years following disturbance for leaf thickness and *SLA* while chlorophyll content and bark thickness kept increasing after 30 years for leaf chlorophyll content and bark thickness. Negative correlation was observed for leaf toughness, *WSG*, and *Hmax* ( $\rho_{Spearman}^{Leaftoughness} = -0.47$ ,  $\rho_{Spearman}^{WSG} = -0.80$ ,  $\rho_{Spearman}^{Hmax} = -0.28$ ). Minima were observed between 5 and 15 years following disturbance for *Hmax*,



**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.

## Community Weighted Means



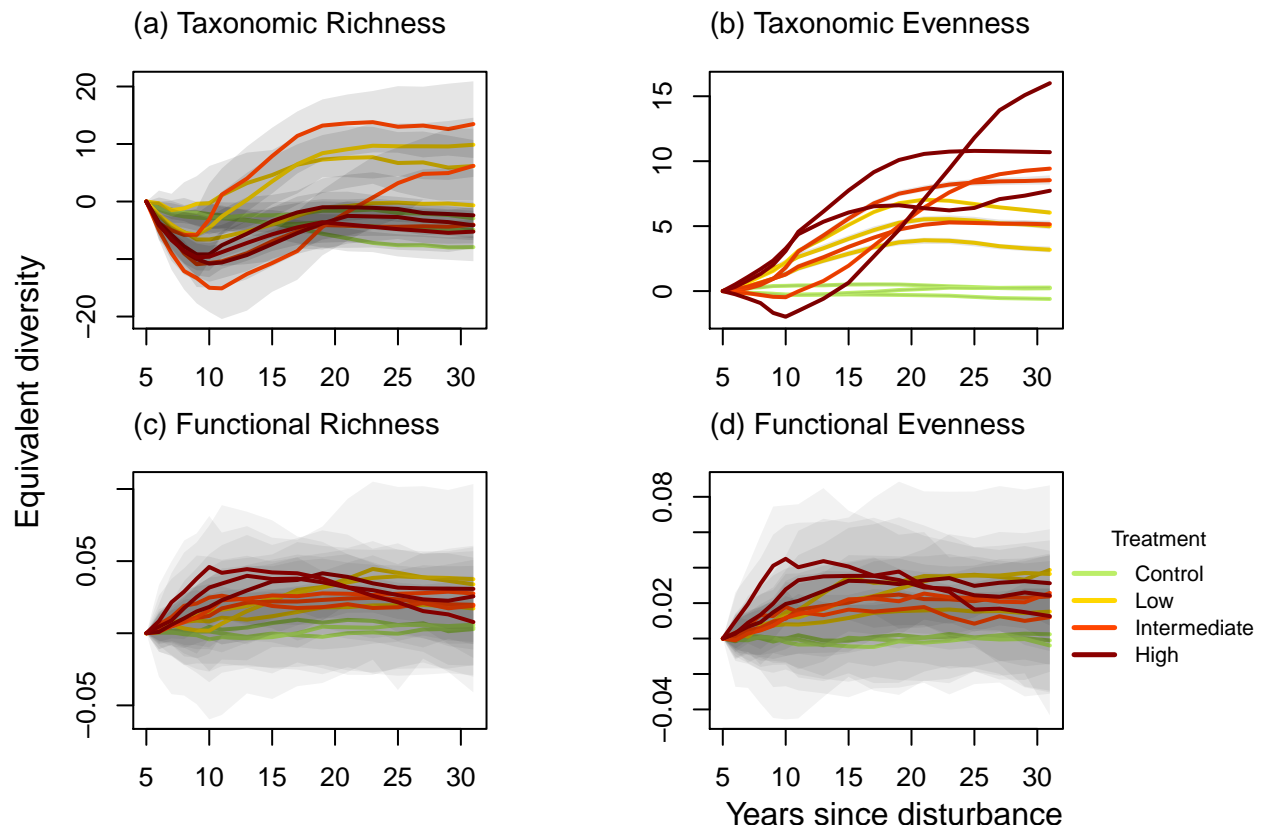
**Figure 2.** Trajectories of community weighted means over 30 years after disturbance of four leaf traits (leaf thickness, chlorophyll content, toughness, and specific area), two stem traits (wood specific gravity and bark thickness), and one life history trait (species maximum height at adult stage).

10 and 20 years for WSG, and between 15 and 25 years following disturbance for leaf toughness. 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. S3).

### 3.2 Community taxonomic and functional diversity

Taxonomic richness and evenness remained stable in control plots 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. 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 rate of change compared to initial richness was positively correlated with the disturbance intensity ( $\rho_{Spearman}^{Richness} = 0.73$ ).

In all disturbed plots, to the exception of plots 5 (T2) and 12 (T3) that showed a small initial drop, the evenness first increased until a maximum reached after around 20 years. This maximum was positively correlated with the disturbance intensity ( $\rho_{Spearman}^{Evenness} = 0.82$ , Fig. 6). The evenness then stabilized except for two intensively-disturbed plots (number 8 and

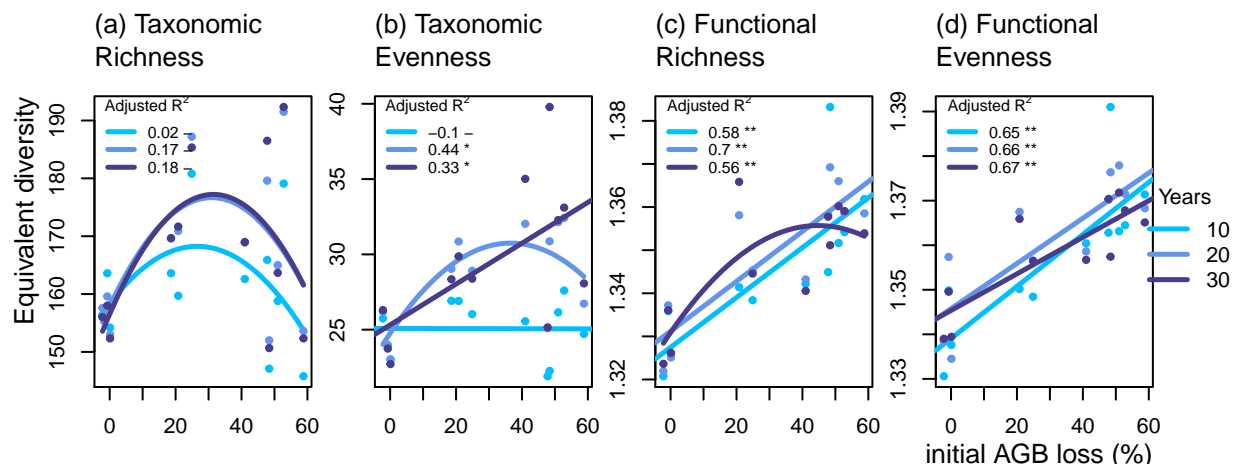


**Figure 3.** Trajectories of community taxonomic richness (a), taxonomic evenness, (b), functional richness (c), and functional evenness (d). Values correspond to the difference over 30 years of community diversity with the values of 1989 inventories of reference, 5 years after disturbance. Shaded areas are the credibility intervals

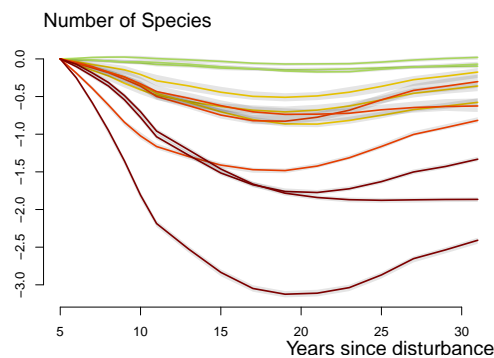
12) for which it kept increasing (Fig. 3).

Functional richness and evenness remained stable in control plots over the 30 years of monitoring. In disturbed communities, both functional richness and evenness trajectories increased following disturbance, with maxima positively correlated to %AGB loss  $\rho_{Spearman}^{Richness} = 0.76$  and  $\rho_{Spearman}^{Evenness} = 0.60$  (Fig. 6). For low and intermediate disturbance intensity, functional richness and evenness displayed a low but long-lasting increase up to a maximum reached after 20-25 years. For high disturbance intensity, they generally 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) the taxonomic and functional diversity showed various shapes depending on the diversity indices and on the time since disturbance (Fig. 4). Regarding taxonomic diversity, the taxonomic richness showed a humped-shaped trajectory with the disturbance intensity, and peaked at 20% of initial AGB loss. The relationship between disturbance intensity and taxonomic evenness, however, was humped-shaped only 20 years after disturbance and linear for 10 and 30 years after disturbance times. Regarding functional



**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.

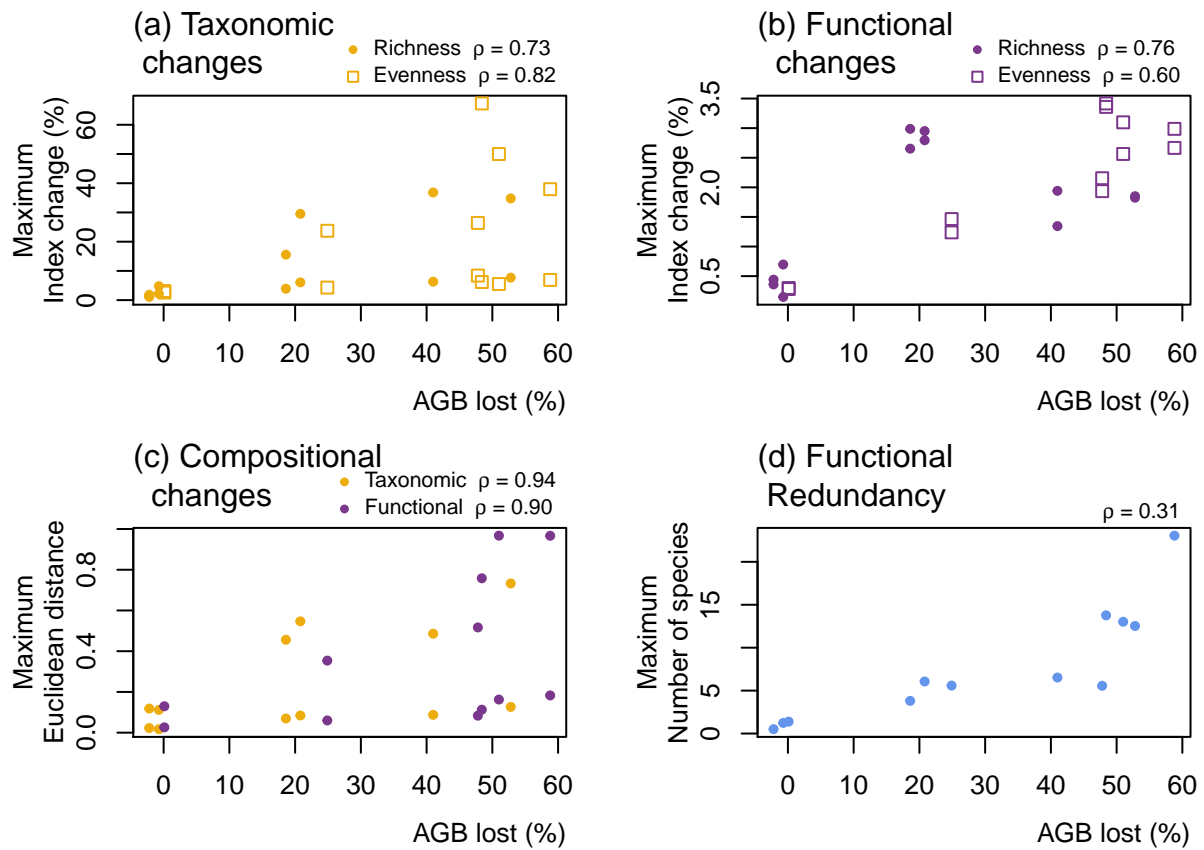


**Figure 5.** Trajectories of the functional redundancy within the initial functional space over 30 years after disturbance. The redundancy is measured in a two-dimensional plan summarizing 45% of species variance in the functional space of the 7 leaf, stem, and life history traits. Redundancy value represent the average number of species in the community that share the same trait values. Shaded areas are the credibility intervals.

diversity, the relationship was linear for both taxonomic richness and evenness, except for the functional diversity after 30 years.

### 3.3 Functional redundancy

Control plots displayed stable functional redundancy over time. All disturbed plots had lower functional redundancy than control plots and followed similar humped-shaped trajectories (Fig. 5). The maximum redundancy loss was positively correlated with the disturbance intensity ( $\rho_{Spearman} = 0.31$ , (Fig. 6)) and the recovery trajectory had not attained initial values for any disturbed communities after 30 years.



**Figure 6.** Maximum changes in taxonomic and functional diversity and composition against disturbance intensity, expressed as percentage of initial disturbance. Upper panels display taxonomic richness and evenness (a), and functional richness and evenness (b) expressed in percentage of change compared to initial value. Lower panels display taxonomic and functional euclidean distance from pre-disturbance inventory, respectively in the spaces of species and functional traits (c), and functional redundancy expressed as number of redundant species in the community (d).

## 4. Discussion

Our analysis revealed that community post-disturbance trajectories in taxonomic and functional diversity and composition were decoupled. The taxonomic composition specificities between communities before disturbance were maintained following disturbance, while their functional composition converged in the functional space. In terms of diversity, only the taxonomic trajectories validated the IDH that explained humped-shaped post-disturbance trajectories with an amplitude depending on the disturbance intensity. The decoupling between taxonomic and functional response could be explained by variations in community functional redundancy. The loss of species or the changes in their abundance would impact the taxonomic but not the functional diversity and composition, as redundant species with the same functional characteristics remain in the community. The trajectory of the functional redundancy hence appeared determinant for community recovery.

### 4.1 Decoupled taxonomic and functional trajectories

From pre-disturbance to 30 years after disturbance, communities showed different location along NMDS axis 2 that hardly changed along time. Specificities in community taxonomic composition, materialized by the distinct location on the NMDS axis 2, existed before disturbance. The disturbance led a displacement on the NMDS axis 1 only. Taxonomic post-disturbance changes in composition were similar among plots and may correspond to the recruitment of a group of pioneers, like *Cecropia spp.* or *Miconia spp.*, common to all plots, whatever their initial taxonomic specificities and the intensity of the disturbance (Denslow & Guzman, 2000; Bongers *et al.*, 2009). Taxonomic trajectories initiated a recovery towards the initial composition. This recovery, although far from being achieved after 30 years, suggested the resilience of community taxonomic composition. Although the composition dramatically changed following disturbance, community specificities were maintained (Folke, 2006). This maintenance suggested that the recruitment came from (i) a common set of pioneer and light-demanding species in all plots that shape the similar trajectories on NMDS axis 1 and (ii) a very local set of late-successional species that signs (and maintains in time) the initial position of each plot on NMDS axis 2. This can be related to species dispersal limitation that is common among tropical species (Svenning & Wright, 2005).

Community functional composition trajectories, in contrast, were similar in the functional space. Such functional convergence contrasting with community taxonomic divergence was already observed in plant communities (Fukami *et al.*, 2005). The amplitude of the compositional changes depended on the disturbance intensity. Functional trajectories were probably driven by the recruitment of species infrequent or absent before disturbance, and belonging to a pool of species common to all plots. This common pool was composed of pioneers with “resource-acquisitive” strategies displaying low leaf toughness, wood specific gravity, maximum height, and high specific leaf area. The recruitment of these pioneers drove a displacement to the right along the first NMDS axis (Westoby, 1998; Wright *et al.*, 2004; Reich, 2014). This recruitment

went along with an increase of the mean SLA, and a decrease in the mean WSG in disturbed communities (2). These fast and significant changes in mean functional traits closely linked to species light acquisition (Wright *et al.*, 2004; Chave *et al.*, 2009) suggested major changes in the light environment following disturbance that shape species assemblage in tropical forests (Peña-Claros *et al.*, 2008; Carreño-Rocabado *et al.*, 2012). Thereafter, the first recruited pioneers were progressively excluded by long-lived, more competitive, and shade-tolerant species. The recruitment of these late-successional species marked the recovery of the initial functional composition with more “resource-conservative” strategies, corresponding to a fast decrease in community mean SLA and a stabilisation of community WSG, suggesting the progressive closing of forest canopy. This recovery translated in the functional plane by a displacement left along the first axis and upward along the second axis (Fig. 1).

The decoupling between taxonomic and functional trajectories suggested that simultaneous operation of trait-based assembly rules and species-level priority effects shaped tree community assembly in Paracou forest. Tree community assembly would then be both deterministic in the functional space, and historically contingent in the taxonomic space.

We must temper these results with the low number of plots (3) for each treatment. However, the size of each plot is 6.25ha that has been regularly censused over 25 years so that the trajectories have been drawn using 75ha of permanent plot information, a spatial hold very rarely achieved in such studies. Given the relative homogeneity of environmental characteristics of terra firme forests over the Guiana Shield and even the amazonian basin, it seems reasonable that similar trajectories would apply to neighboring areas (Guitet *et al.*, 2015, 2018).

## 4.2 The scope of the intermediate disturbance hypothesis

Trajectories of taxonomic richness and evenness differed markedly below and above an intensity threshold (Fig. 3). For low and intermediate disturbance, both taxonomic richness and evenness increased according to the disturbance intensity (Martin *et al.*, 2015; Chaudhary *et al.*, 2016). This suggested that the recruitment of pioneers, previously infrequent or absent, increased the taxonomic richness, and that trees surviving after disturbance remained numerous enough to maintain the richness of the pre-disturbance community (Bongers *et al.*, 2009). The pioneers thus recruited became abundant, which balanced the usual hyper-dominance of tropical forests and increased the taxonomic evenness (Baraloto *et al.*, 2012). Above the intensity threshold, like for treatment 3 (high intensity), the taxonomic richness did not exceed the initial value in the first years following disturbance. No increase of the taxonomic richness suggested that the richness of surviving trees was lower than this of the pre-disturbance community, and that this difference was not offset by the recruitment of pioneers. In the Guiana shield, the pool of **hard** pioneers specifically recruited after disturbance is restricted to a few common genera (e.g. *Cecropia* spp., *Miconia* spp., *Tapirira* spp.) (Guitet *et al.*, 2018). The disturbance intensity showed a humped-shaped relationship with the post-disturbance increase in taxonomic richness at all the different times after disturbance, and with



the increase in taxonomic evenness 10 years after disturbance (Fig. 4). Taxonomic richness, and to some extent taxonomic evenness, were maximized at an intermediate intensity, around 20-25% of AGB lost.

#### 4.3 The functional redundancy explaining the taxonomic-functional decoupling

Regarding community functional trajectories (Fig. 4), there was no intensity threshold above which the diversity-disturbance relationship changed. The functional diversity kept increasing along with the disturbance intensity, hence the IDH would not apply. Surprisingly, although some species were lost after disturbance, the functional diversity did not decrease in the first place. On the contrary, functional diversity increased, probably following the rapid recruitment of pioneers that were functionally highly different from the pre-disturbance community (Denslow, 1980; Molino & Sabatier, 2001).

The loss of species following disturbance, however, decreased the functional redundancy, all the more so that disturbance was intense. All in all, because functional diversity was not lowered by disturbance while functional redundancy was, this means that the species that were lost in disturbance are, on the whole, functionally equivalent to the species that survive the disturbance. This makes functional redundancy a key to understand community dynamics at a functional level. In other words, the high redundancy of tropical forest mean that several species occupy the same functional space, so changes in taxonomic diversity or composition do not necessarily result in changes in community functional characteristics because species are commutable. The loss of a redundant species doesn't change anything for the community functional characteristics, so functional trajectories do not necessarily track taxonomic ones. This commutability explains the taxonomic-functional decoupling and the fact that the taxonomic diversity-disturbance relationship supports the IDH while it functional diversity do not.

Following disturbance, the redundancy was progressively restored through the replacement of "resource-acquisitive" species by more late-successional "resource-conservative" species functionally closer to the pre-disturbance community. The time for the functional redundancy to recover would hence be important to assess community recovery.

## 5. Conclusion

Post-disturbance trajectories of tree community composition and diversity would be driven by the recruitment of a determined pool of pioneers, identical among local communities, and independent of the disturbance intensity. The taxonomic composition trajectories maintained the initial differences among communities, while the functional trajectories were similar, and converged in the functional space towards the recovery of the initial composition. The diversity trajectories were contrasted as well. While the functional trajectories displayed the same tendency with a linear increase following all disturbance intensity, taxonomic trajectories were markedly different after a threshold of 20-25% AGB lost that maximized the taxonomic richness. The Intermediate Disturbance Hypothesis would apply well to taxonomic diversity, but not

to functional diversity. The decoupling between taxonomic and functional trajectories was mediated by the variations in functional redundancy, as the loss of a species does not necessarily entails the loss of its functional characteristics. 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. Given the long-term impacts of disturbance observed, we suggest that 30 years is not enough time for tropical communities to recover, even after relatively low intensity disturbance. Much of community response to disturbance rely on the processes of species recruitment. A more refined understanding of the post-disturbance trajectories would be gained by a closer analysis of the recruitment process.

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## 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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