Post-Disturbance Tree Community Trajectories 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 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, remaining similar and convergent. The taxonomic diversity followed humped-shaped trajectories depending on the disturbance intensity, which validated the IDH (Intermediate Disturbance Hypothesis). The functional diversity trajectories,however, were homogeneous among all 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, and questioned 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 local and regional climates, as well as carbon, water and nutrient cycles. However, the growing demand in forests products together with current global changes increase the pressure on remaining undisturbed forests (Morales-Hidalgo *et al.*, 2015). These threats affect the natural disturbance regime that defines 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, it is urgent to understand tree community response to disturbance, and the underlying ecological processes. The forest cover is generally maintained 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, however, observations of the IDH often diverge from theoretical expectations (Randall Hughes *et al.*, 2007; Sheil & Burslem, 2003; Norden *et al.*, 2017), and the underlying processes might be complicated by the diversity of tropical tree communities (Lindenmayer *et al.*, 2012; Garcia Florez *et al.*, 2017). In this context, the IDH is controversial in tropical forests and remains to be tested (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.

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^{-1} (30-y period). The climate comprises 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). 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 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 commercially exploited species (Gourlet-Fleury *et al.*, 2004). Treatment T2 additionally comprised

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 $trees.ha^{-1}$	-	-	$[12 - 33]$
T2, intermediate	DBH $\geq$ 50 cm, commercially exploited species, $\approx$ 10 $trees.ha^{-1}$	DBH $\geq$ 40 cm, non-commercially exploited species, $\approx$ 30 $trees.ha^{-1}$	-	$[33 - 56]$
T3, high	DBH $\geq$ 50 cm, commercially exploited species, $\approx$ 10 $trees.ha^{-1}$	DBH $\geq$ 50 cm, non-commercially exploited species, $\approx$ 15 $trees.ha^{-1}$	40 cm $\leq$ DBH $\leq$ 50 cm, non-commercially exploited species, $\approx$ 15 $trees.ha^{-1}$	$[35 - 56]$

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). 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*, *Chrysobal-anaceae*, *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 commmon 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 years to identify all trees at the species level. In 2015, however, identification levels still varied among plots and campaigns.

This variability of protocols in time raised methodological issues as vernacular names usually correspond to various

botanical species. This resulted in significant taxonomic uncertainty that had to be accounted for in the measure of composition and diversity metrics. Uncertainty propagation was implented withing a Bayesian framework using vernacular/botanical names associations to reconstitute complete inventories at genus level from real incomplete ones. 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. A.1 and Aubry-Kientz *et al.* (2013) for the detailed methodology.

Six functional traits representing the leaf economics (*i.e.* leaf thickness, toughness, total chlorophyll content, and specific leaf area), and the stem economics (*i.e.* wood specific gravity and bark thickness) were obtained 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 belonging to 157 genera. Whenever a species was in the dataset but missed some trait values (10% of the species), missing values were filled using multivariate imputation by chained equation (van Buuren & Groothuis-Oudshoorn, 2011). To account for the phylogenetic signal in the filling process, imputations were based on samples of species from the same genus or from the same family. 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). Two life-history traits, maximum specific height and seed mass, came from the Mariwenn database [2]. The database compiles information from a vast literature on the flora of French Guiana (Ollivier *et al.*, 2007) and comprises 362 species belonging to 188 genera. As seed mass information was classified into classes, no data filling process was applied and analyses were restricted to the 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 variable precision of botanical identification efforts, we had to conduct the taxonomic composition and diversity analysis at the genus level. Taxonomic and functional trajectories of community composition were drawn in a two-dimensional NMDS 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 HCDT or generalized entropy corresponding, respectively, to the 0 and 2 order of diversity (q). The functional diversity was reported using the functional richness and functional evenness,

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

[2] https://www.ecofog.gf/mariwenn/

166 through the Rao index of quadratic entropy. The Rao index combines species abundance distribution, and the average

167 pairwise functional dissimilarity between species computed by the Gower distance.

168 The impacts of the initial disturbance levels on the maximum gain or loss in richness and evenness were tested with the

169 Spearman rank correlation tests. Richness and evenness trajectories were besides analyzed through polynomial regression

170 between (i) taxonomic and functional richness and evenness, and (ii) the initial %AGB loss at 10, 20, and 30 years after

171 disturbance.

172 Finally, functional redundancy was measured as the overlap among species in community functional space (Carmona

173 *et al.*, 2016). First, the individuals of the trait database were mapped in the plane of the first two axes from a PCA analysis.

174 The PCA analysis lowered the weight of correlations among traits as the axes are combinations of the most decoupled

175 traits. For each species, the traits probability density (TPD) were computed from the mapping of individuals through

176 two-dimension kernel density estimators. Second, for each community, the TPD weigthed by species abundance were

177 summed accross the functional space. Third, the functional space was divided into a 100 x 100 grid, and the number of

178 species with a positive TPD was counted in each cell. The average count across cells minus 1 returned the Community

179 Functional Redundancy, which was the average number of species in the community that share the same trait values.

3. Results

3.1 Community Composition

182 From 1984, the first pre-disturbance inventory, to 2015, 28 years after disturbance, 828 388 individual trees and 591

183 botanical species spanning 223 genera and 64 families were recorded.

184 In undisturbed plots, both taxonomic and functional composition remained stable (Fig. 1). In disturbed plots, both

185 trajectories followed marked and consistent trajectories over time.

186 The functional composition trajectory resembled, in disturbed communities, to cyclic compositional changes with an

187 incomplete recovery of the initial composition (Fig.1). The maximum dissimilarity with the initial state was positively

188 correlated with the disturbance intensity for both taxonomic and functional composition ($\rho_{Spearman}^{Taxonomic} = 0.87$ and $\rho_{Spearman}^{Functional} = $

189 0.90, respectively). The maximum dissimilarity with the initial state was reached for taxonomic composition between 15 to

190 25 years, and between 20 to 25 years for functional composition.

191 In control plots, Community Weighted Means (CWM) of functional traits remained stable in time.

192 In disturbed plots, they mostly followed unimodal trajectories, either stabilizing or returning towards their initial values,

193 to the exception of leaf chlorophyll content, which continued to increase 30 years after disturbance for 4 out of 6 highly

194 disturbed plots. Maximum height at adult stage (*Hmax*), leaf toughness, and wood specific gravity (*WSG*) decreased in

195 time and then slightly increased, but remained significantly lower than their initial value (Fig. 2). Bark thickness and

196 specific leaf area (*SLA*) both increased along time. Bark thickness remained substantially high after 30 years, and *SLA* had

197 almost recovered to its initial value. Whatever the functional traits, the maximum difference to initial value was highly

198 correlated to the disturbance intensity. Positive correlations were observed for leaf thickness, chlorophyll content, SLA and

199 bark thickness ($\rho_{Spearman}^{Leaf thickness} = 0.76$, $\rho_{Spearman}^{Chlorophyll content} = 0.60$, $\rho_{Spearman}^{SLA} = 0.93$, $\rho_{Spearman}^{Bark thickness} = 0.71$). Negative correlation

200 was observed for leaf toughness, WSG, and Hmax ($\rho_{Spearman}^{Leaf toughness} = -0.53$, $\rho_{Spearman}^{WSG} = -0.75$, $\rho_{Spearman}^{Hmax} = -0.40$) The

201 proportions of the three lightest seed mass classes increased in all disturbed plots. After 30 years the proportion of lightest

202 seed mass class decreased while it stabilized for the two other lightest seed mass classes (Supp. Mat. - Fig. A.2).
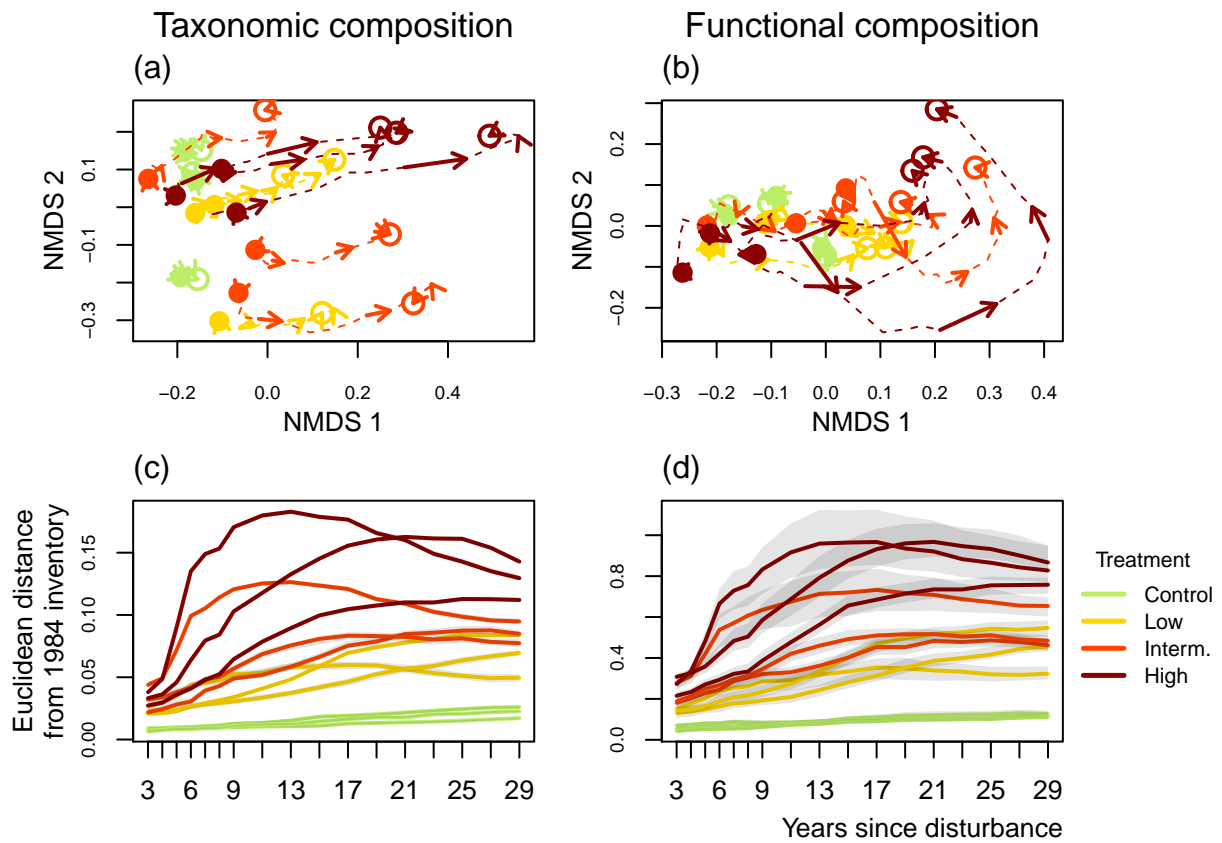
Figure 1. Plot trajectories in terms of taxonomic composition ((**a**) and (**c**)), and functional composition ((**b**) and (**d**)) in a two-dimensional NMDS plane. Lower panels ((**c**) and (**d**)) represent the Euclidean distance to initial condition along the 30 sampled years. Shaded areas are the credibility intervals.
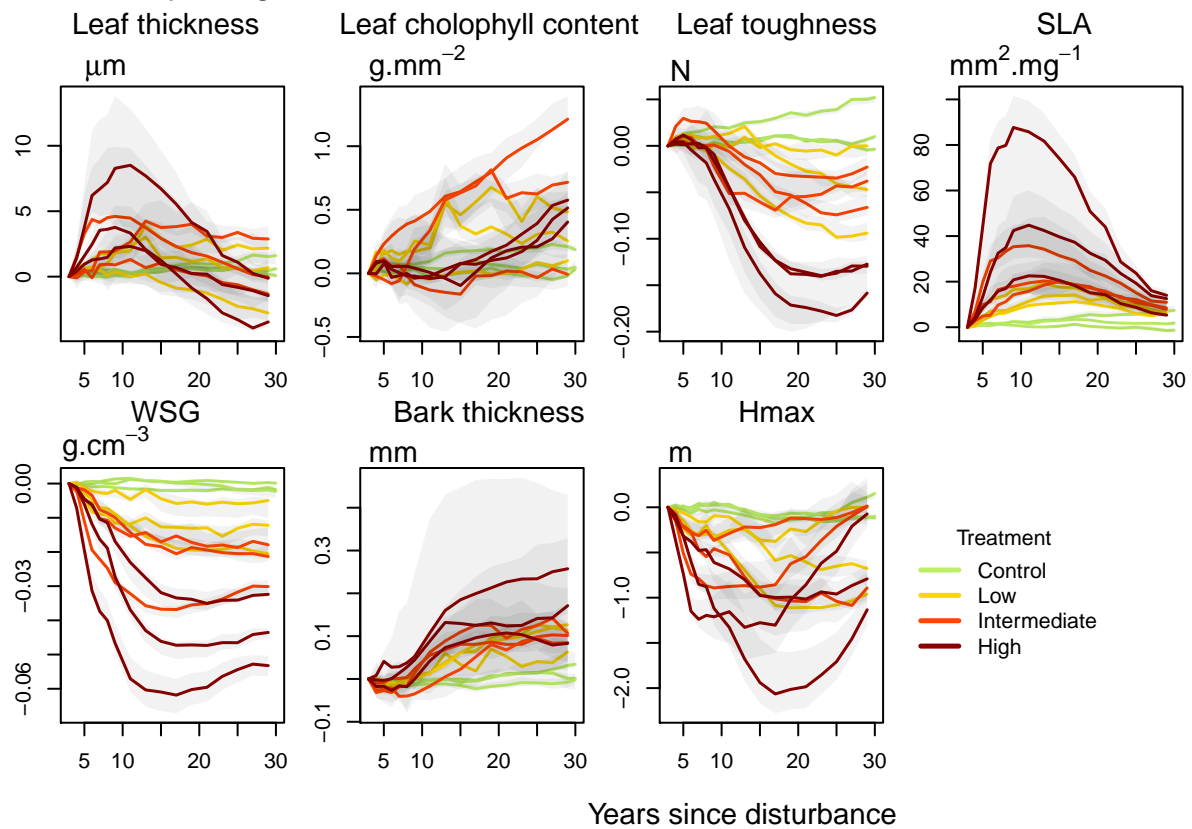
Community Weighted Means

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).
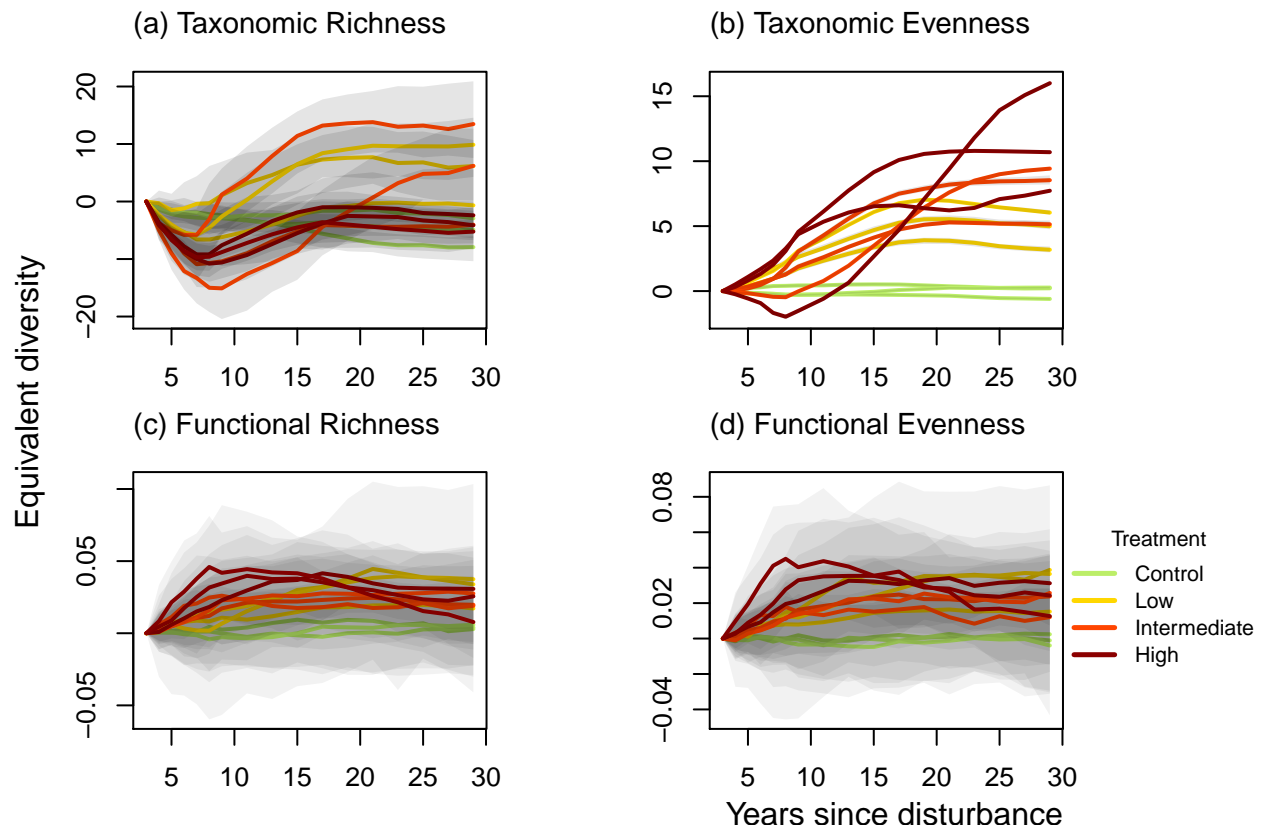
Figure 3. Trajectories of community taxonomic richness **(a)**, Simpson diversity **(b)**, functional richness **(c)**, and Rao diversity **(d)**. Values correspond to the difference over 30 years of community diversity with the values of 1984 pre-disturbance inventories of reference. Shaded areas are the credibility intervals

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 richness loss or gain after disturbance was positively correlated with the disturbance intensity ($\rho_{Spearman}^{Richness} = 0.50$).

In all disturbed plots the evenness first increased until a maximum reached after around 20 years. This maximum was positively correlated with the disturbance intensity ($\rho_{Spearman}^{Simpson} = 0.77$). The evenness then stabilized except for two intensively-disturbed plots (number 8 and 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 trajectories depended on the disturbance intensity, with their maximum values in time being positively correlated to %AGB loss $\rho_{Spearman}^{Richness} = 0.76$ and $\rho_{Spearman}^{Rao} = 0.60$. For low 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
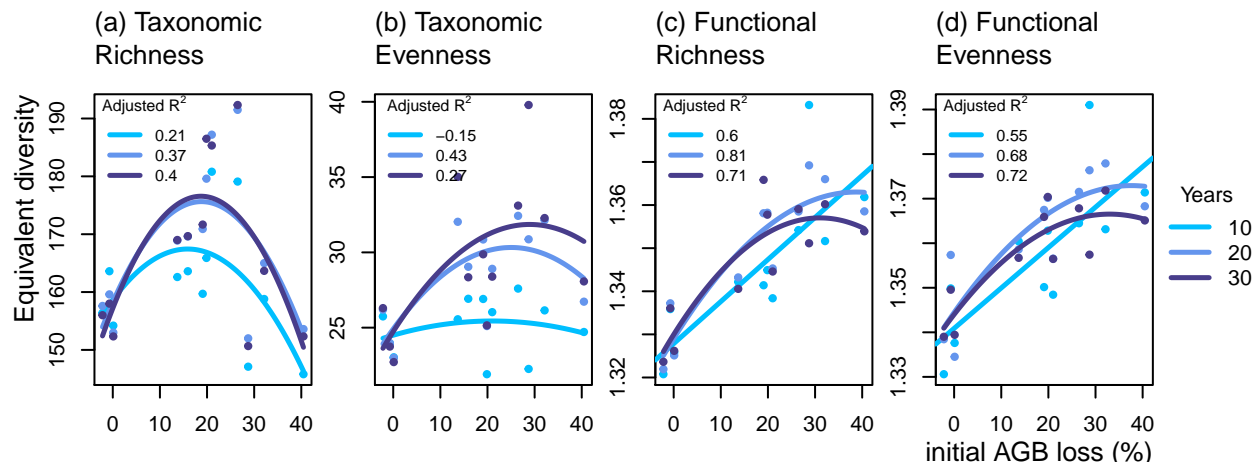
Figure 4. Relationship between the initial %AGB loss and community taxonomic richness **(a)**, taxonomic evenness **(b)**, functional richness **(c)**, and functional evenness **(d)** at 10, 20, and 30 years after disturbance.

taxonomic diversity, the relationship between disturbance intensity and diversity was more markedly hump-shaped for richness than for evenness, and peaked at 20% of initial AGB loss. Regarding functional diversity, the relationship was almost linear, and was similar between richness and evenness. All the relationships between disturbance intensity and diversity were stronger 20 or 30 years after disturbance than they were 10 years after disturbance.

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

4. Discussion

Our analysis revealed the decoupling between functional and taxonomic trajectories. While the initial differences in taxonomic composition among plots were maintained, the functional composition trajectories converged in the functional space. In terms of diversity, only the taxonomic trajectories validated the IDH that explained humped-shaped post-disturbance trajectories whith an amplitude depending on the disturbance intensity. The decoupling between taxonomic and functional response was explained by variations of community functional redundancy that mitigated the functional impact of disturbance, and appeared as a determinant of community recovery.

4.1 Decoupled taxonomic and functional trajectories

Community taxonomic composition substantially differed before disturbance, as materialized by their distinct location on the NMDS axis 2. These initial differences were maintained along the 30 years following disturbance, with the disturbance leading a displacement on the NMDS axis 1 only. Taxonomic composition changes 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 differences and the intensity of 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 and the maintenance of initial composition
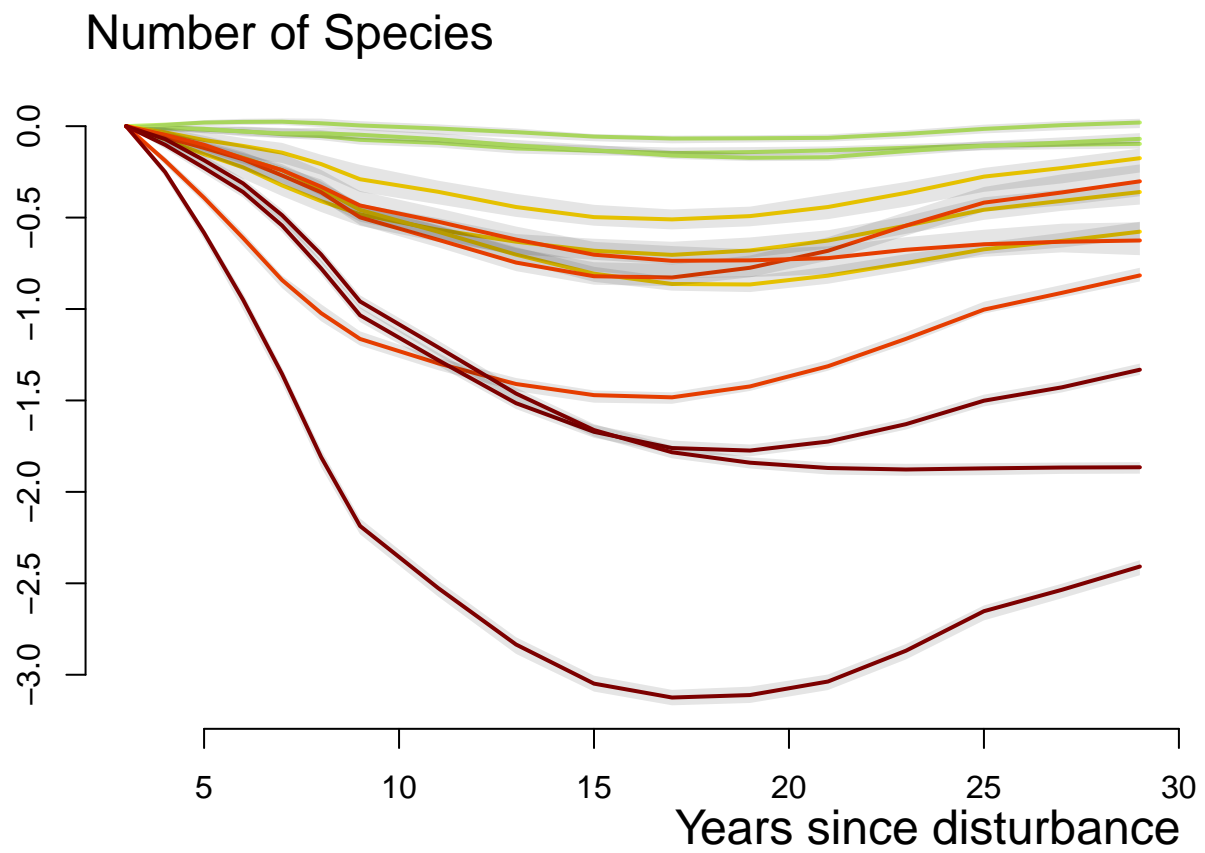
Figure 5. Trajectories of the functional redundancy within the initial functional space over 30 years after disturbance. Shaded areas are the credibility intervals.

differences (Folke, 2006). Such resilience suggested that species not belonging to the pre-disturbance community were rarely recruited in the long-term, probably because of species dispersal limitation that is common among tropical species (Svenning & Wright, 2005).

Community functional composition trajectories, in contrast, were similar in the functional space (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). Thereafter, the first recruited pioneers were progressively excluded by long-lived, more competitive, and shade-tolerant species. The recruitment of these late-successionals marked the recovery of the initial functional composition with more "resource-conservative"" strategies . 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.

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 (Martin *et al.*, 2015; Chaudhary *et al.*, 2016), 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 true pioneers specifically recruited after disturbance is restricted to a few common genera (e.g. *Cecropia spp.*, *Miconia spp.*, *Tapirira spp.*) (Guitet *et al.*, 2018). Considering the different times after disturbance, there was always a humped-shaped pattern linking the disturbance intensity with the post-disturbance increase in taxonomic richness and evenness (Fig. 4). Both taxonomic richness and evenness were maximized at an intermediate intensity, around 20-25% of AGB lost.

Regarding community functional trajectories, however, no marked differences were observed among post-disturbance trajectories (Fig. 3). Whenever the disturbance intensity, there was first an increase of both functional richness and evenness. Such increase suggested the recruitment of pioneers that were functionally highly different from the pre-disturbance community (Denslow, 1980; Molino & Sabatier, 2001). The recruitment of pioneers hampered the recruitment of other species in the first place. After 15 to 20 years, the first pioneer recruits declined and were replaced by species functionally more similar to the pre-disturbance community, which decreased the functional richness and evenness (Walker & del Moral, 2009).

4.3 The functional redundancy, key of community resilience

The loss of species following disturbance decreased community functional redundancy during the first 15 years. Progressively though, the functional redundancy was restored through the replacement of the species with "resource-acquisitive"" strategies by more late-successional species, functionally closer to the pre-disturbance community. The replacement of pioneers by late-successionals followed the lottery recruitment rules. This rules mean an easy recruitment of the first species that becomes increasingly difficult, as the following species are hampered by the emergence of interspecific competition (Busing & Brokaw, 2002). The increasing competition among species explained why the recovery trajectory slowed down 20 years after disturbance. 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). This suggested a low resilience of the functional redundancy with the random recovery of infrequent species increasing the risks of losing keystone species, with unexpected ecological consequences (Jones *et al.*, 1994; Chazdon, 2003; Díaz *et al.*, 2005). Infrequent species might indeed have unique functional characteristics in the ecosystem, apart from the ones considered here, in the ecosystem or be a key resource for some of the fauna (Schleuning *et al.*, 2016).

5. Conclusion

Post-disturbance trajectories of tree community composition and diversity were 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 remained similar whatever the disturbance intensity, taxonomic trajectories were markedly different from a threshold of 20-25% AGB lost that maximized the taxonomic richness. The Intermediate Disturbance Hypothesis applied 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.

6. Acknowledgement

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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