Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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.

# 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, Oswalt, and Somanathan 2015). These threats affect the natural disturbance regime that defines and maintains the structure, composition, and functioning of tree communities (Schnitzer and 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 and Piponiot 2018). Community diversity and composition trajectories, however, have not been as thoroughly understood (Guitet et al. 2018; J. F. Molino and Sabatier 2001), and manifold biodiversity trajectories might emerge given the variety of species response to disturbance and the diversity of tropical forests (Lindenmayer, Burton, and Franklin 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, Roxburgh, and Rauschert 2004; Pulsford, Lindenmayer, and Driscoll 2016). In tropical forests, however, observations of the IDH often diverge from theoretical expectations (Randall Hughes et al. 2007; Sheil and Burslem 2003; Norden et al. 2017), and the underlying processes might be complicated by the diversity of tropical tree communities (Lindenmayer, Burton, and Franklin 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 and Burslem 2013).

Analysing community response to disturbance and grasp all aspects of community changes requires a wide array of metrics (Sheil and Burslem 2003; Shea, Roxburgh, and Rauschert 2004; Mayfield and 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 (S. Lavorel and 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 (I. J. Wright et al. 2004; Steege et al. 2006; Westoby and 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.

# Material and Methods

## 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, Guehl, and Laroussinie 2004).

The experiment is a network of twelve 6.25 ha plots (Table ??) that underwent three disturbance treatments in 1987 according to a randomized plot design (Gourlet-Fleury, Guehl, and Laroussinie 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, Guehl, and Laroussinie 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). The three treatments were then transformed into a continuous disturbance intensity gradient with increasing above-ground biomass (AGB) loss.

## 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 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 observed across all inventories between each vernacular name *v* and all species :

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]](#footnote-25) 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 and 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]](#footnote-27) The database compiles information from a vast literature on the flora of French Guiana (Ollivier, Baraloto, and Marcon 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.

## 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 and 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, through the Rao index of quadratic entropy. The Rao index combines species abundance distribution, and the average pairwise functional dissimilarity between species computed by the Gower distance.

The impacts of 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 between (i) taxonomic and functional richness and evenness, and (ii) the initial %AGB loss at 10, 20, and 30 years after disturbance.

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. For each species, the traits probability density (TPD) were computed from the mapping of individuals through two-dimension kernel density estimators. Second, for each community, the TPD weigthed by species abundance were summed accross the functional space. Third, the functional space was divided into a 100 x 100 grid, and the number of species with a positive TPD was counted in each cell. The average count across cells minus 1 returned the Community Functional Redundancy, which was the average number of species in the community that share the same trait values.

# Results

## 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.). The maximum dissimilarity with the initial state was positively correlated with the disturbance intensity for both taxonomic and functional composition ( and , respectively). 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.

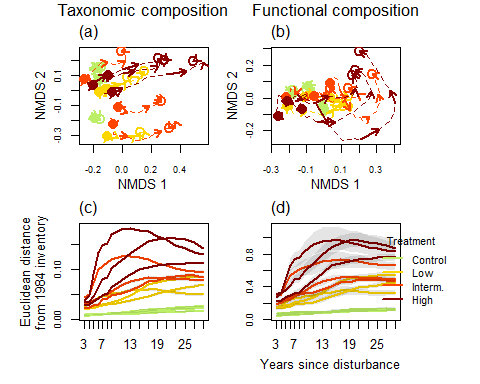


Figure 1 Plot trajectories in terms of taxonomic composition (**(a)** and **(c)**), and functional composition (**(b)** and **(d)**) in a two-dimensional NMDS plane. Lower panels (**(c)** and **(d)**) represent the Euclidean distance to initial condition along the 30 sampled years. Shaded areas are the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

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. Maximum height at adult stage (*Hmax*), leaf toughness, and wood specific gravity (*WSG*) decreased in time and then slightly increased, but remained significantly lower than their initial value (Fig. ). 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 (, , , ). Negative correlation was observed for leaf toughness, WSG, and Hmax (, , ) 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. A.2).

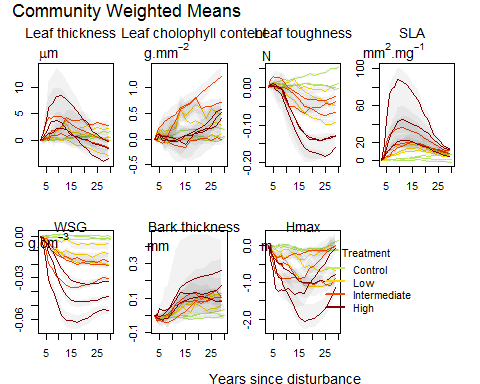


Figure 2 Trajectories of community weighted means over 30 years after disturbance of four leaf traits (leaf thickness, chlorophyll content, toughness, and specific area), two stem traits (wood specific gravity and bark thickness), and one life history trait (species maximum height at adult stage).

## 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 ().

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 (). The evenness then stabilized except for two intensively-disturbed plots (number 8 and 12) for which it kept increasing (Fig. 3).

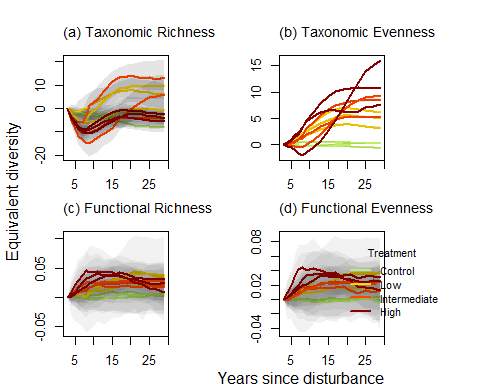


Figure 3 Trajectories of community taxonomic richness **(a)**, Simpson diversity **(b)**, functional richness **(c)**, and Rao diversity **(d)**. Values correspond to the difference over 30 years of community diversity with the values of 1984 pre-disturbance inventories of reference. Shaded areas are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

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 and  
. 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. ). Regarding 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.

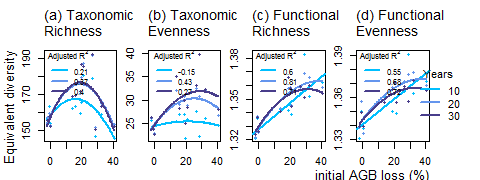


Figure 4 Relationship between the initial %AGB loss and community taxonomic richness **(a)**, taxonomic evenness **(b)**, functional richness **(c)**, and functional evenness **(d)** at 10, 20, and 30 years after disturbance.

## 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. ). The maximum redundancy loss was positively correlated with the disturbance intensity () and the recovery trajectory had not attained initial values for any disturbed communities after 30 years.

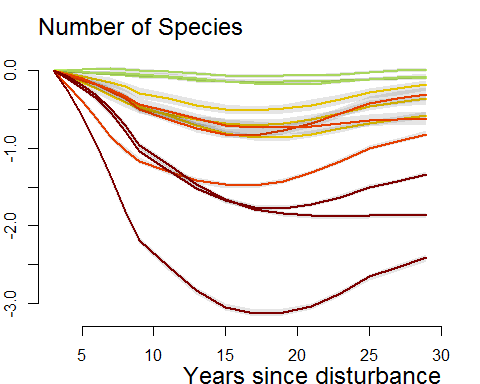


Figure 5 Trajectories of the functional redundancy within the initial functional space over 30 years after disturbance. Shaded areas are the credibility intervals.

# 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.

## 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 (Julie S Denslow and 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 differences (C. 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 and 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; I. J. 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. ).

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.

## The scope of the intermediate disturbance hypothesis

Trajectories of taxonomic richness and evenness differed markedly below and above an intensity threshold (Fig. ). 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. ). 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. ). 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 (Julie Sloan Denslow 1980; J. F. Molino and 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 (L. R. Walker and Moral 2009).

## 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 and 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, Lawton, and Shachak 1994; R. L. 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).

# 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.

# Acknowledgement

We are in debt with all Paracou station technicians and colleagues who helped setting up the plots and collecting data over years. Without their precious work, this study would have not been possible and they may be warmly thanked here. Our work benefited from an “Investissement d’Avenir” grant managed by the Agence Nationale de la Recherche (LABEX CEBA, ref ANR-10-LBX-25). We thank Niklas Tysklind for the usefull help with english proofing.

# 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.

# 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>).

Anderson-Teixeira, Kristina J., Adam D. Miller, Jacqueline E. Mohan, Tara W. Hudiburg, Benjamin D. Duval, and Evan H. DeLucia. 2013. “Altered dynamics of forest recovery under a changing climate.” *Global Change Biology* 19 (7): 2001–21. doi:[10.1111/gcb.12194](https://doi.org/10.1111/gcb.12194).

Aubry-Kientz, Mélaine, Bruno Hérault, Charles Ayotte-Trépanier, Christopher Baraloto, and Vivien Rossi. 2013. “Toward Trait-Based Mortality Models for Tropical Forests.” *PLoS ONE* 8 (5). doi:[10.1371/journal.pone.0063678](https://doi.org/10.1371/journal.pone.0063678).

Baraloto, Christopher, Bruno Hérault, C. E. Timothy Paine, Hélène Massot, Lilian Blanc, Damien Bonal, Jean-François François Molino, Eric a. Nicolini, and Daniel Sabatier. 2012. “Contrasting taxonomic and functional responses of a tropical tree community to selective logging.” *Journal of Applied Ecology* 49 (4): 861–70. doi:[10.1111/j.1365-2664.2012.02164.x](https://doi.org/10.1111/j.1365-2664.2012.02164.x).

Bellwood, David R., P.C Wainwright, C.J Fulton, and A.S Hoey. 2006. “Functional versatility supports coral reef biodiversity.” *Proceedings of the Royal Society B: Biological Sciences* 273 (1582): 101–7. doi:[10.1098/rspb.2005.3276](https://doi.org/10.1098/rspb.2005.3276).

Bongers, Frans, Lourens Poorter, William D. Hawthorne, and Douglas Sheil. 2009. “The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity.” *Ecology Letters* 12 (8): 798–805. doi:[10.1111/j.1461-0248.2009.01329.x](https://doi.org/10.1111/j.1461-0248.2009.01329.x).

Busing, Richard T, and Nicholas Brokaw. 2002. “Tree Species Diversity in Temperate and Tropical Forest Gaps: The Role of Lottery Recruitment.” *Folia Geobotanica* 37 (1). Springer: 33–43.

Carmona, Carlos P., Francesco de Bello, Norman W.H. Mason, and Jan Lepš. 2016. “Traits Without Borders: Integrating Functional Diversity Across Scales.” *Trends in Ecology and Evolution* 31 (5): 382–94. doi:[10.1016/j.tree.2016.02.003](https://doi.org/10.1016/j.tree.2016.02.003).

Chaudhary, Abhishek, Zuzana Burivalova, Lian Pin Koh, and Stefanie Hellweg. 2016. “Impact of Forest Management on Species Richness: Global Meta-Analysis and Economic Trade-Offs.” *Scientific Reports* 6. Nature Publishing Group: 1–10. doi:[10.1038/srep23954](https://doi.org/10.1038/srep23954).

Chave, Jérôme, David Coomes, Steven Jansen, Simon L. Lewis, Nathan G. Swenson, and Amy E. Zanne. 2009. “Towards a worldwide wood economics spectrum.” *Ecology Letters* 12: 351–66. doi:[10.1111/j.1461-0248.2009.01285.x](https://doi.org/10.1111/j.1461-0248.2009.01285.x).

Chazdon, Robin L. 2003. “Tropical forest recovery: legacies of human impact and natural disturbances.” *Perspectives in Plant Ecology, Evolution and Systematics* 6 (1-2): 51–71. doi:[10.1078/1433-8319-00042](https://doi.org/10.1078/1433-8319-00042).

Connell, Joseph H. 1978. “Diversity in Tropical Rain Forests and Coral Reefs.” *Science* 199 (4335). American Association for the Advancement of Science: 1302–10.

Denslow, Julie S, and G Sandra Guzman. 2000. “Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama.” *Journal of Vegetation Science* 11 (2): 201–212. doi:[10.2307/3236800](https://doi.org/10.2307/3236800).

Denslow, Julie Sloan. 1980. “Gap Partitioning among Tropical Rainforest Trees.” *Biotropica* 12 (2): 47–55. doi:[10.2307/2388156](https://doi.org/10.2307/2388156).

Díaz, Sandra, Sandra Lavorel, Francesco de Bello, Fabien Quétier, Karl Grigulis, and T Matthew Robson. 2007. “Incorporating Plant Functional Diversity Effects in Ecosystem Service Assessments.” *Proceedings of the National Academy of Sciences* 104 (52). National Acad Sciences: 20684–9. doi:[10.1073/pnas.0704716104](https://doi.org/10.1073/pnas.0704716104).

Díaz, Sandra, D Tilman, J Fargione, F. Stuart Chapin III, Rodolfo Dirzo, T Kitzberger, B Gemmill, et al. 2005. “Biodiversity Regulation of Ecosystem Services.” *Trends and Conditions*, 297–329.

Elmqvist, T, C Folke, M Nystrom, G Peterson, J Bengtsson, B Walker, and J Norberg. 2003. “Response diversity, ecosystem change, and resilience.” *Frontiers in Ecology and the Environment* 1 (9): 488–94. doi:[10.2307/3868116](https://doi.org/10.2307/3868116).

Folke, Carl. 2006. “Resilience: The Emergence of a Perspective for Social–ecological Systems Analyses.” *Global Environmental Change* 16 (3). Elsevier: 253–67.

Fox, Jeremy W. 2013. “The Intermediate Disturbance Hypothesis Should Be Abandoned.” *Trends in Ecology & Evolution* 28 (2). Elsevier: 86–92.

Fukami, Tadashi, T. Martijn Bezemer, Simon R. Mortimer, and Wim H. Van Der Putten. 2005. “Species divergence and trait convergence in experimental plant community assembly.” *Ecology Letters* 8 (12): 1283–90. doi:[10.1111/j.1461-0248.2005.00829.x](https://doi.org/10.1111/j.1461-0248.2005.00829.x).

Garcia Florez, Lina, Jerome K Vanclay, Kevin Glencross, and J Doland Nichols. 2017. “Understanding 48 Years of Changes in Tree Diversity, Dynamics and Species Responses Since Logging Disturbance in a Subtropical Rainforest.” *Forest Ecology and Management* 393. Elsevier: 29–39.

Goulamoussène, Youven, Caroline Bedeau, Laurent Descroix, Laurent Linguet, and Bruno Hérault. 2017. “Environmental control of natural gap size distribution in tropical forests.” *Biogeosciences* 14 (2): 353–64. doi:[10.5194/bg-14-353-2017](https://doi.org/10.5194/bg-14-353-2017).

Gourlet-Fleury, Sylvie, Jean Marc Guehl, and OIivier Laroussinie. 2004. “Ecology & management of a neotropical rainforest. Lessons drawn from Paracou, a long-term experimental research site in French Guiana.” Paris: Elsevier.

Guitet, Stéphane, Daniel Sabatier, Olivier Brunaux, Pierre Couteron, Thomas Denis, Vincent Freycon, Sophie Gonzalez, et al. 2018. “Disturbance regimes drive the diversity of regional floristic pools across Guianan rainsforest landscapes.” *Scientific Reports* 8 (1): 3872. doi:[10.1038/s41598-018-22209-9](https://doi.org/10.1038/s41598-018-22209-9).

Hérault, Bruno, and Camille Piponiot. 2018. “Key drivers of ecosystem recovery after disturbance in a neotropical forest.” *Forest Ecosystems* 5 (1). Forest Ecosystems: 2. doi:[10.1186/s40663-017-0126-7](https://doi.org/10.1186/s40663-017-0126-7).

Hérault, Bruno, Bénédicte Bachelot, Lourens Poorter, Vivien Rossi, Frans Bongers, Jérôme Chave, C. E Timothy Paine, Fabien Wagner, and Christopher Baraloto. 2011. “Functional traits shape ontogenetic growth trajectories of rain forest tree species.” *Journal of Ecology* 99: 1431–40. doi:[10.1111/j.1365-2745.2011.01883.x](https://doi.org/10.1111/j.1365-2745.2011.01883.x).

Hill, M. O. 1973. “Diversity and Evenness : A Unifying Notation and Its Consequences.” *Ecological Society of America* 54 (2): 427–32. doi:[10.2307/1934352](https://doi.org/10.2307/1934352).

Hubbell, Stephen P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

Jones, Clive G, John H Lawton, and Moshe Shachak. 1994. “Organisms as Ecosystem Engineers.” In *Ecosystem Management*, 130–47. Springer.

Lavorel, S, and Éric Garnier. 2002. “Predicting changes in community composition and ecosystem functioning from plant traits:” *Functional Ecology* 16 (5): 545–56.

Lindenmayer, David B, Philip J Burton, and Jerry F Franklin. 2012. *Salvage Logging and Its Ecological Consequences*. Island Press.

Marcon, Eric, and Bruno Hérault. 2015. “Entropart: An R Package to Measure and Partition Diversity.” *Journal of Statistical Software* 67 (1): 1–26.

Martin, Philip A., Adrian C. Newton, Marion Pfeifer, MinSheng Khoo, and James M. Bullock. 2015. “Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis.” *Forest Ecology and Management* 356. Elsevier B.V.: 224–33.

Mayfield, Margaret M., and Jonathan M. Levine. 2010. “Opposing effects of competitive exclusion on the phylogenetic structure of communities.” *Ecology Letters* 13 (9): 1085–93. doi:[10.1111/j.1461-0248.2010.01509.x](https://doi.org/10.1111/j.1461-0248.2010.01509.x).

Molino, J F, and Daniel Sabatier. 2001. “Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis.” *Science* 294 (5547): 1702–4. doi:[10.1126/science.1060284](https://doi.org/10.1126/science.1060284).

Morales-Hidalgo, David, Sonja N. Oswalt, and E. Somanathan. 2015. “Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015.” *Forest Ecology and Management* 352. Elsevier B.V.: 68–77. doi:[10.1016/j.foreco.2015.06.011](https://doi.org/10.1016/j.foreco.2015.06.011).

Norden, Natalia, Vanessa Boukili, Anne Chao, KH Ma, Susan G Letcher, and Robin L Chazdon. 2017. “Opposing Mechanisms Affect Taxonomic Convergence Between Tree Assemblages During Tropical Forest Succession.” *Ecology Letters* 20 (11). Wiley Online Library: 1448–58.

Ollivier, Mariwenn, Christopher Baraloto, and Eric Marcon. 2007. “A Trait Database for Guianan Rain Forest Trees Permits Intra-and Inter-Specific Contrasts.” *Annals of Forest Science* 64 (7). EDP Sciences: 781–86.

Piponiot, Camille, Plinio Sist, Lucas Mazzei, Marielos Peña-Claros, Francis E. Putz, Ervan Rutishauser, Alexander Shenkin, et al. 2016. “Carbon recovery dynamics following disturbance by selective logging in amazonian forests.” *ELife* 5: e21394. doi:[10.7554/eLife.21394](https://doi.org/10.7554/eLife.21394).

Pulsford, Stephanie A, David B Lindenmayer, and Don A Driscoll. 2016. “A Succession of Theories: Purging Redundancy from Disturbance Theory.” *Biological Reviews* 91 (1). Wiley Online Library: 148–67.

Randall Hughes, A, Jarrett E Byrnes, David L Kimbro, and John J Stachowicz. 2007. “Reciprocal Relationships and Potential Feedbacks Between Biodiversity and Disturbance.” *Ecology Letters* 10 (9). Wiley Online Library: 849–64.

Rees, Mark, Rick Condit, Mick Crawley, Steve Pacala, and Dave Tilman. 2001. “Long-Term Studies of Vegetation Dynamics.” *Science* 293 (5530). American Association for the Advancement of Science: 650–55.

Reich, Peter B. 2014. “The world-wide ’fast-slow’ plant economics spectrum: A traits manifesto.” *Journal of Ecology* 102: 275–301. doi:[10.1111/1365-2745.12211](https://doi.org/10.1111/1365-2745.12211).

Réjou-Méchain, Maxime, Ariane Tanguy, Camille Piponiot, Jérôme Chave, and Bruno Hérault. 2017. “Biomass: An R Package for Estimating Above-Ground Biomass and Its Uncertainty in Tropical Forests.” *Methods in Ecology and Evolution* 8 (9). Wiley Online Library: 1163–7.

Rutishauser, Ervan, Bruno Hérault, Pascal Petronelli, and Plinio Sist. 2016. “Tree Height Reduction After Selective Logging in a Tropical Forest.” *Biotropica* 48 (3): 285–89. doi:[10.1111/btp.12326](https://doi.org/10.1111/btp.12326).

Schleuning, Matthias, Jochen Fruend, Oliver Schweiger, Erik Welk, Joerg Albrecht, Matthias Albrecht, Marion Beil, et al. 2016. “Ecological Networks Are More Sensitive to Plant Than to Animal Extinction Under Climate Change.” *Nature Communications* 7: 13965.

Schnitzer, Stefan A, and Walter P Carson. 2001. “Treefall Gaps and the Maintenance of Species Diversity in a Tropical Forest.” *Ecology* 82 (4): 913–19.

Shea, Katriona, Stephen H Roxburgh, and Emily SJ Rauschert. 2004. “Moving from Pattern to Process: Coexistence Mechanisms Under Intermediate Disturbance Regimes.” *Ecology Letters* 7 (6). Wiley Online Library: 491–508.

Sheil, Douglas, and D. F R P Burslem. 2003. “Disturbing hypotheses in tropical forests.” *Trends in Ecology and Evolution* 18 (1): 18–26. doi:[10.1016/S0169-5347(02)00005-8](https://doi.org/10.1016/S0169-5347(02)00005-8).

Sheil, Douglas, and David FRP Burslem. 2013. “Defining and Defending Connell’s Intermediate Disturbance Hypothesis: A Response to Fox.” *Trends in Ecology & Evolution* 28 (10). Elsevier: 571–72.

Sist, Plinio, Pablo Pacheco, Robert Nasi, and Jürgen Blaser. 2015. “Management of natural tropical forests for the future.” Vol. 32. IUFRO WFSE.

Steege, Hans ter, Nigel C A Pitman, Oliver L Phillips, Jérôme Chave, Daniel Sabatier, Alvaro Duque, Jean-François Molino, et al. 2006. “Continental-scale patterns of canopy tree composition and function across Amazonia.” *Nature* 443 (7110): 0–2. doi:[10.1038/nature05134](https://doi.org/10.1038/nature05134).

Svenning, J.C., and S.J. Wright. 2005. “Seed Limitation in a Panamian Forest.” *Journal of Ecology* 93 (5): 853–562. doi:[10.1111/j.1365-2745.2005.01016.x](https://doi.org/10.1111/j.1365-2745.2005.01016.x).

van Buuren, Stef, and Karin Groothuis-Oudshoorn. 2011. “mice: Multivariate Imputation by Chained Equations in R.” *Journal of Statistical Software* 45 (3): 1–67. doi:[10.1177/0962280206074463](https://doi.org/10.1177/0962280206074463).

Violle, Cyrille, Marie-Laure Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène Hummel, and Eric Garnier. 2007. “Let the concept of trait be functional!” *Oikos* 116 (5): 882–92. doi:[10.1111/j.2007.0030-1299.15559.x](https://doi.org/10.1111/j.2007.0030-1299.15559.x).

Wagner, Fabien, Bruno Hérault, Clément Stahl, Damien Bonal, and Vivien Rossi. 2011. “Modeling water availability for trees in tropical forests.” *Agricultural and Forest Meteorology* 151 (9). Elsevier B.V.: 1202–13. doi:[10.1016/j.agrformet.2011.04.012](https://doi.org/10.1016/j.agrformet.2011.04.012).

Walker, Lawrence R, and Roger del Moral. 2009. “Transition Dynamics in Succession: Implications for Rates, Trajectories and Restoration.” *New Models for Ecosystem Dynamics and Restoration*. Island Press Washington, DC, US, 33–49.

Westoby, Mark. 1998. “A leaf-height-seed (LHS) plant ecology strategy scheme.” *Plant and Soil* 199: 213–27. doi:[10.1023/A:1004327224729](https://doi.org/10.1023/A:1004327224729).

Westoby, Mark, and Ian J. Wright. 2006. “Land-plant ecology on the basis of functional traits.” *Trends in Ecology and Evolution* 21 (5): 261–68. doi:[10.1016/j.tree.2006.02.004](https://doi.org/10.1016/j.tree.2006.02.004).

Wright, Ian J., Peter B. Reich, Mark Westoby, David D. Ackerly, Zdravko Baruch, Frans Bongers, Jeannine Cavender-Bares, et al. 2004. “The worldwide leaf economics spectrum.” *Nature* 428 (6985): 821–27. doi:[10.1038/nature02403](https://doi.org/10.1038/nature02403).

1. <http://www.ecofog.gf/Bridge/> [↑](#footnote-ref-25)
2. <https://www.ecofog.gf/mariwenn/> [↑](#footnote-ref-27)