

# 30 Years of Post-disturbance Recruitment in a Neotropical Forest

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## Abstract

The role of tree diversity for tropical forests functioning and services makes it crucial tree diversity and composition fate in the global changing context. Community long-term response to disturbance rely on tree recruitment, long seen as following deterministic successional pathways. These pathways however might be altered in the hyper-diverse tropical forests and of slight but recurrent disturbances induced by global changes. Post-disturbance recruitment trajectories would (i) disentangle the determinants of tree recruitment between stochastic and deterministic processes that enhance a restricted pool of species, and (ii) elucidate tropical forests taxonomic and functional resilience. We examined the trajectories over 30 years of recruited trees taxonomic and functional diversity in 12 plots of 6.25 ha of forest following a disturbance gradient. We analyzed taxonomic richness, evenness, and turnover, and functional diversity and composition (regarding 7 leaf, stem and life-history functional traits). We highlighted a three-phased successional pathway defined by the interplay of stochastic and deterministic recruitment processes. The succession translated into (i) saplings growth mirroring pre-disturbance communities, (ii) light-demanding species enhanced recruitment entailing, above a disturbance intensity threshold, the dominance of pioneers and (iii) the recovery of pre-disturbance taxonomic and functional characteristics and of stochastic recruitment processes. Although tangible, community taxonomic and functional resilience was decades-long. Post-disturbance recruitment relied on deterministic competition processes for light balancing the stochastic processes ruling undisturbed communities. Although resilient, recruitment taxonomic and functional characteristics remained altered in the long-term, calling caution for forest management.

## Keywords

Disturbance Dynamics, Neotropical Forests, Recruitment, Resilience, Taxonomic and Functional Diversity, Tree Community

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## Contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
<b>2</b>	<b>Material and Methods</b>	<b>2</b>
2.1	Study Site . . . . .	2
2.2	Inventories Protocol and Dataset Collection . . . . .	2
2.3	Recruitment trajectories . . . . .	3
<b>3</b>	<b>Results</b>	<b>4</b>
3.1	Taxonomic richness and evenness and functional diversity	4
3.2	Functional composition . . . . .	4
3.3	Recruitment Turnover . . . . .	4
<b>4</b>	<b>Discussion</b>	<b>4</b>
4.1	A three-phased deterministic successional pathway	4
4.2	Community recovery . . . . .	6
<b>5</b>	<b>Conclusion</b>	<b>6</b>
<b>6</b>	<b>Acknowledgement</b>	<b>7</b>
<b>7</b>	<b>Data availability</b>	<b>7</b>

## 1. Introduction

Determining the response of tropical forests to disturbance is key to predict their fate in the global changing context. In the last decades, tropical forests experienced a wide range of disturbance, from radical land-use changes for agriculture or mining (Dezécache *et al.*, 2017a,b) to more insidious changes following climatic changes or anthropogenic activities like selective logging (Baraloto *et al.*, 2012; Aubry-Kientz *et al.*, 2015). In that respect a vast literature successfully modeled community response to disturbance in terms of tree growth, tree height and fluxes of carbon, water and nutrients (Gourlet-Fleury & Houllier, 2000; Putz *et al.*, 2012; Piponiot *et al.*, 2016; Rutishauser *et al.*, 2016). Regarding tree community diversity and composition, the ecological theory of succession assumes that disturbance initiates a suit of deterministic recruitment processes. The different processes depend on the variability of species resource use and competitive abilities (Clements, 1916; Meiners *et al.*, 2015), and their succession shape predictable trajectories corresponding to a gradual recovery of the pre-disturbance communities (Chesson, 2000; Rees *et al.*, 2001; Adler *et al.*, 2007). Specifically in forest ecosys-

tem, the successional framework comprises first the recruitment of saplings benefiting from the available resources and the low competition. Then, stand maturation implies the progressive exclusion of low-competitive species until the senescence of early-successional species and the emergence of late-successional, which restore the pre-disturbance state (Denslow & Guzman, 2000). Empirical evidence, however, show that post-disturbance trajectories often deviate from the predicted successional pattern and result from an interplay of deterministic processes with stochastic ones. Post-disturbance trajectories would also depend on random processes, like dispersal limitations, and different equilibrium state may be restored after disturbance (Hubbell, 2001; Chave, 2004; Norden *et al.*, 2015). The issue to tackle is determining the balance between deterministic and stochastic processes. This balance remains specifically debated in the highly diverse tropical forests, where several studies highlighted predictable and homogeneous successional patterns restoring pre-disturbance communities (Norden *et al.*, 2009; Letcher *et al.*, 2015), while other showed diverging trajectories following disturbance and different equilibrium state (Longworth *et al.*, 2014; Norden *et al.*, 2015).

Recruitment processes impact both community taxonomic characteristics (that refer to neutral species assemblages) and functional characteristics (that account for species ecology and functioning) (MacArthur & Levins, 1967; Violle *et al.*, 2007; Kunstler *et al.*, 2016). A joint analysis of community taxonomic and functional characteristics would then highlight the successive processes underlying post-disturbance trajectories (Fukami *et al.*, 2005; Chalmandrier *et al.*, 2015; Cequinel *et al.*, 2018). Stochastic processes would correspond to a random recruitment of species independent of their functional characteristics, and would result in diverging trajectories among communities. Deterministic processes to the contrary would translate into predictable recruitment trajectories driven by a succession of processes based on species competitive ability (Rees *et al.*, 2001; Perronne *et al.*, 2017). As light is the limiting resource in tropical forests, deterministic trajectories would correspond to a functional gradient from fast-growing species with “acquisitive” resource use to slow-growing, long-lived species with “conservative” resource use (Denslow, 1980; Molino & Sabatier, 2001; Bongers *et al.*, 2009).

Key leaf, wood and life-history functional traits assessing species resources acquisition strategy and ecology would then grasp the competition processes at stake (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011). Post-disturbance recruitment processes besides determine community recovery and the restoration of pre-disturbance community (Clements, 1916; Diamond, 1975).

In this paper we followed recruitment trajectories over 30 years of 75 ha of Neotropical forest plots set up on a gradient of disturbance intensity, from 10 to 60% of forest biomass removed. We examined the recruited trees (i) taxonomic composition, richness and evenness, (ii) taxonomic turnover compared to pre-disturbance community, and (iii) functional composition and diversity based on seven major leaf, stem and life-history traits. We compared the re-

cruitment trajectories to neutral models corresponding to a stochastic recruitment and a randomization of species functional traits. Specifically, we (i) elucidated the successional pathway shaping community response to disturbance and the underlying ecological processes and (ii) clarified the extent of community taxonomic and functional resilience, in the sense of pre-disturbance characteristics recovery, and its consequences for tropical forest management.

## 2. Material and Methods

### 2.1 Study Site

The Paracou station is located in a lowland tropical rain-forest in French Guiana (518°N and 5253°W). Climate is tropical wet with mean annual precipitation averaging 2980 mm.yr<sup>-1</sup> (30-yr period) and a 3-months dry season (< 100 mm.mo<sup>-1</sup>) from mid-August to mid-November, and a one-month dry season in March (Wagner *et al.*, 2011). The mean annual temperature is 26°C. Elevation ranges from 5 to 50 m. Across all plots the topography mainly corresponds to hilltops or hillsides, while bottomlands cover less than 1 % of the area. Plots are shallow 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 (Table 1) that underwent three disturbance treatments in 1987 according to a randomized plot design (Hérault & Piponiot, 2018).

The experiment comprised three replicates of three silvicultural treatments (hereafter plots T1, T2 and T3) and three control plots (T0). All treatments T1, T2 and T3 comprised the logging of 10 trees/ha with 50 cm minimum DBH that belonged to a set of 58 commercial species (Gourlet-Fleury *et al.*, 2004). Treatment T2 additionally comprised a thinning treatment by poison-girdling of non-commercial, randomly selected species with an average 30 trees/ha with 40 cm minimum DBH. Treatment T3 additionally comprised the logging of 15 trees/ha with 40 cm minimum DBH and the poison-girdling of 20 trees/ha with a 50 cm minimum DBH, all belonging to non-commercial species. Considering the silvicultural treatments and the following damage, disturbance intensity was measured as the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984 and five years after disturbance (Piponiot *et al.*, 2016) estimated with the BIOMASS R package (?). The three treatments constituted a disturbance intensity gradient with increasing of above-ground biomass (AGB) lost and surface disturbed.

### 2.2 Inventories Protocol and Dataset Collection

Dominant families in the study site are Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae. All trees above 10 cm DBH were 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. Botanical campaigns have been carried out every five to six

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

Treatment	Timber	Thinning	Fuelwood	%AGB lost
Control	-	-	-	0
T1	DBH $\geq$ 50 cm, commercial species, $\approx 10 \text{ trees.ha}^{-1}$	-	-	[12 – 33]
T2	DBH $\geq$ 50 cm, commercial species, $\approx 10 \text{ trees.ha}^{-1}$	DBH $\geq$ 40 cm, non-valuable species, $\approx 30 \text{ trees.ha}^{-1}$	-	[33 – 56]
T3	DBH $\geq$ 50 cm, commercial species, $\approx 10 \text{ trees.ha}^{-1}$	DBH $\geq$ 50 cm, non-valuable species, $\approx 15 \text{ trees.ha}^{-1}$	40 cm $\leq$ DBH $\leq$ 50 cm, non-valuable species, $\approx 15$ $\text{trees.ha}^{-1}$	[35 – 56]

years from 2003 onwards but identification levels varied between campaigns.

This variability of protocols in time raised methodological issues as vernacular names usually correspond to different botanical species. It resulted in significant taxonomic uncertainties that had to be propagated to composition and diversity metrics. The uncertainty propagation was done through a Bayesian framework reconstituting complete inventories at genus level from real incomplete ones on the basis of vernacular/botanical names association. Vernacular names were replaced through multinomial trials based on the association probability  $[\alpha_1, \alpha_2, \dots, \alpha_N]$  observed across all inventories between each vernacular name  $v$  and the species  $[s_1, s_2, \dots, s_N]$ :

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

See appendix 1 and Aubry-Kientz *et al.* (2013) for the detailed methodology.

To minimize the remaining identification uncertainties, the simulated botanical inventories were reported at genus level.

Six functional traits representing leaf economics (leaf thickness, toughness, total chlorophyll content and specific leaf area) and stem economics (wood specific gravity and bark thickness) were considered. These traits came from the BRIDGE project <sup>1</sup>, which proved to reliably assess species functional traits and community functional diversity (Paine *et al.*, 2015). Trait values were assessed from a selection of individuals located in nine permanent plots in French Guiana, including two in Paracou, and comprised 294 species pertaining to 157 genera. Whenever a species was in the dataset was missing 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 based on samples 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 <sup>2</sup>. The database compiles information from a vast literature on the flora of French Guiana (Olivier *et al.*, 2007) and comprises 362 species pertaining 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 Recruitment trajectories

Communities were split into surviving trees of pre-disturbance communities and trees recruited afterward. Trajectories of recruitment diversity (hereafter  $H'_{q\_obs}$ ) and turnover started from the first year after disturbance and then considered the trees recruited by 2-years intervals (*i.e.* for the date Y, the trees that were under 10 cm DBH at Y-1 but above 10 cm DBH at Y).

Trajectories of taxonomic diversity were assessed through species richness and evenness (the Hill number translation of the Simpson index) (Chao & Jost, 2015; Marcon & Hérault, 2015).

The two diversities belong to the set of Tsallis or generalized entropy, respectively corresponding to the zero and two order of diversity ( $q$ ) that emphasizes common species. These two metrics grasps community richness and evenness, that assesses the structure of dominance in the community. Both metric are complementary to detect the changes in community structure (Magurran, 2004).

Functional diversity trajectories were assessed through the Rao index of quadratic entropy, which combines species abundance distribution and average pairwise dissimilarity based on all functional traits. Functional composition trajectories were assessed through the functional traits community weighted means (CWM), representing the average trait value in a community weighted by species relative abundance based on the number of stem (Díaz *et al.*, 2007). Seed

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

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

mass trajectories were reported by the stems proportion of each class recorded in the inventories.

The taxonomic similarity between recruited trees and pre-disturbance forest was measured with the relativized abundance replacement measuring species turnover between communities (Podani *et al.*, 2013)

$$T_{ab} = \frac{\sum_{i=1}^n |x_i^a - x_i^b| - \left| \sum_{i=1}^n x_i^a - \sum_{i=1}^n x_i^b \right|}{\sum_{i=1}^n \max(x_i^a, x_i^b)} \quad (1)$$

. With  $T_{ab}$  the turnover between communities  $a$  and  $b$ ,  $n$  the total number of species in the two communities and  $x_{ij}$  the abundance of species  $i$  in community  $j$ .

The observed recruitment trajectories were compared to null trajectories obtained from taxonomic and functional null models. A taxonomic null model was independently built for each plot and for each year. Taxonomic null trajectories were simulated by randomly sampling the recruited trees in the current living community, according to the observed number of recruits. Functional null trajectories were simulated by randomly reassigning the combinations of functional trait values among species. The functional null models allowed maintaining the community abundance distribution but randomizing the relative abundance of trait values (Mason *et al.*, 2013). Trajectories of null diversity (hereafter  $H^*_{[null]}$ ) were similarly obtained after 50 iterations of the random sampling models.

### 3. Results

#### 3.1 Taxonomic richness and evenness and functional diversity

The average number of recruited trees per plot and per year along the whole time survey increased with the increasing disturbance intensity. For a 2-year laps, the number of recruits per plot was around 74 in plots T0, 142 in plots T1, 211 in plots T2 and 273 in plots T3. In total, during the 30 years, 602 species were recruited across the 12 plots. Among those, 26% occurred in one plot only and 7% occurred in all plots.

In undisturbed communities the taxonomic richness and evenness of recruited trees remained stable over the 30 years, with values equivalent to those of the taxonomic null model (Figure (1)).

In disturbed communities the taxonomic richness followed hump-shaped trajectories first increasing until a maximum reached after around 15 years and positively correlated to the disturbance intensity ( $\rho_{\text{richness spearman}}^{\text{Richness}} = 0.93$ ). Afterward the taxonomic richness decreased and recovered the pre-disturbance values after 30 years. The observed taxonomic richness was lower than this of null model and this difference increased for 15 years. The difference then started to shrink but the observed richness remained negative remained negative until after 30 years. The taxonomic evenness decreased independently of the disturbance intensity over the 30 years ( $\rho_{\text{evenness spearman}}^{\text{Simpson}} = -0.35$ ). The observed taxonomic evenness was lower than this of the null model and for some of the plots T1 and T2 this difference kept increasing until 25 years after disturbance.

The functional diversity in the undisturbed plots remained stable and equivalent to this of the functional null model over the 30 years. In the lowest disturbance plots the functional diversity remained stable or slightly increasing, and was higher than this of the null model for two of the T1 plots. In the disturbed plots of higher disturbance intensity (T2 and T3) the functional diversity decreased until 15 years after disturbance, when it started to recover towards initial values. The observed functional diversity remained lower than this of the null model over the 30 years.

#### 3.2 Functional composition

In undisturbed plots functional traits values remained stable over the 30 years while it followed hump-shaped trajectories in all disturbed plots, to the exception of the leaf chlorophyll content. Trajectories of SLA and bark thickness first increased before decreasing towards initial values. Conversely, trajectories of leaf thickness, leaf toughness, wood specific gravity, and maximum height first decreased and then started returning towards initial values but their recovery remained unachieved after 30 years (Figure 2).

#### 3.3 Recruitment Turnover

Over the 30 years in control plots the turnover of recruited species compared to initial community remained low (Figure 3). In disturbed plots the recruited species turnover followed a marked hump-shaped trajectory, with a maximum reached around 15 years after disturbance. The maximum turnover was positively correlated to the disturbance intensity ( $\rho_{\text{turnover spearman}} = 0.93$ ). Thirty years after disturbance the turnover had returned to low values.

### 4. Discussion

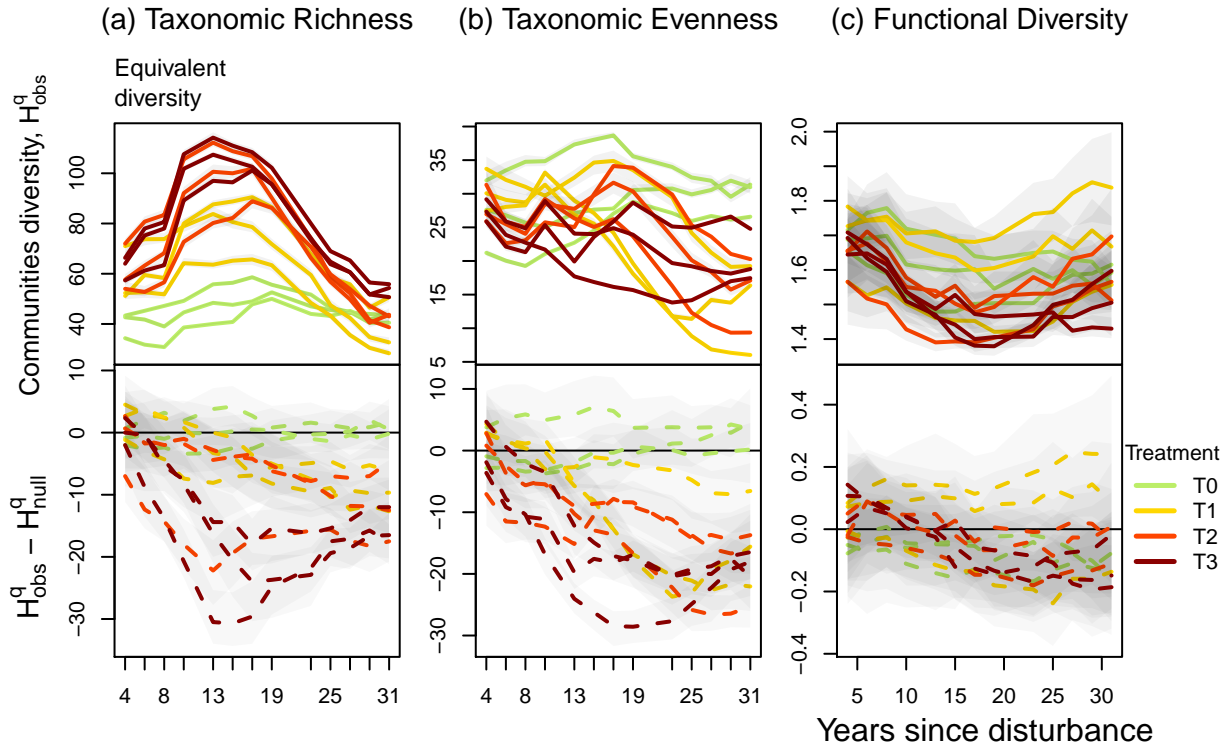
Our analysis of the taxonomic and functional response of tree recruitment over 30 years following a disturbance gradient highlighted a three-phased successional pathway shaped by an interplay between stochastic recruitment and deterministic processes. Although the recruitment trajectories suggested community taxonomic and functional recovery, this remained unachieved after 30 years.

#### 4.1 A three-phased deterministic successional pathway

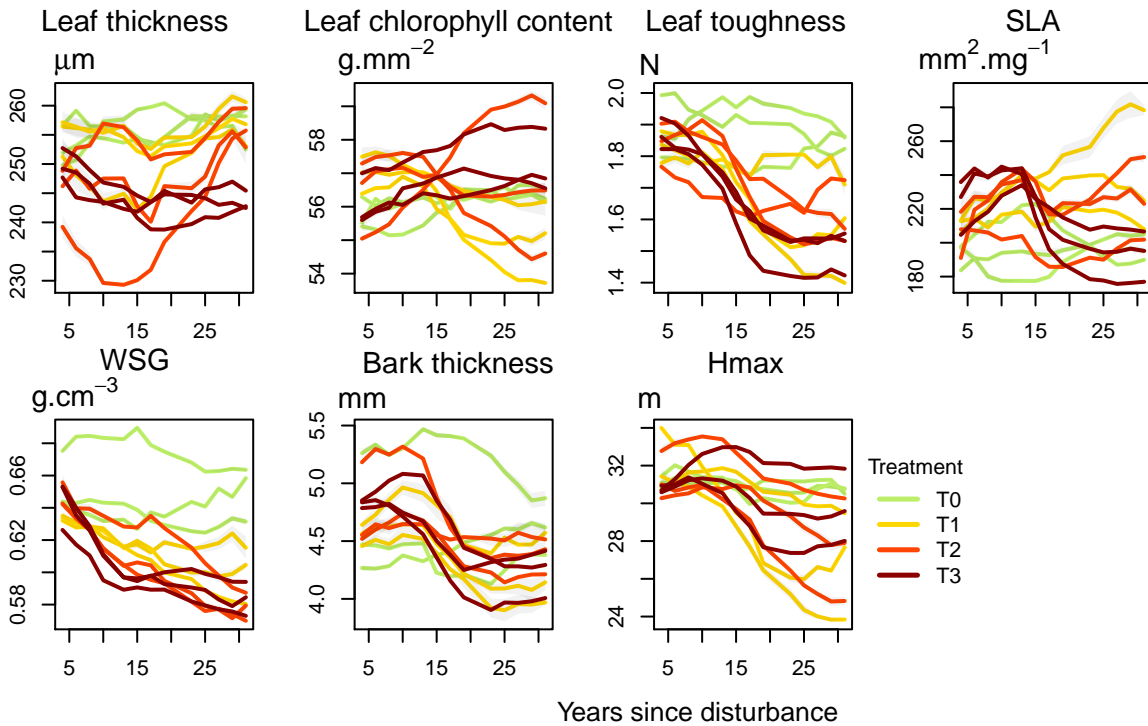
Post-disturbance recruitment trajectories followed a three-phased successional pathway defined by the emergence of deterministic competition processes for light, which gradually balanced the stochastic recruitment observed in the undisturbed communities.

A first phase (0-8 years) was defined by a very low taxonomic turnover between recruited trees and initial communities, suggesting the maintenance of the recruitment processes involved in the pre-disturbance communities (Figure 3). During this phase, the recruitment taxonomic and functional trajectories matched those of the null model, suggesting the predominance of stochastic processes (Figure (1)). The first phase might then correspond to the recruitment of pre-disturbance surviving saplings (DBH < 10 cm), grown and almost settled before disturbance and that were the first to benefit from the increased light availability and

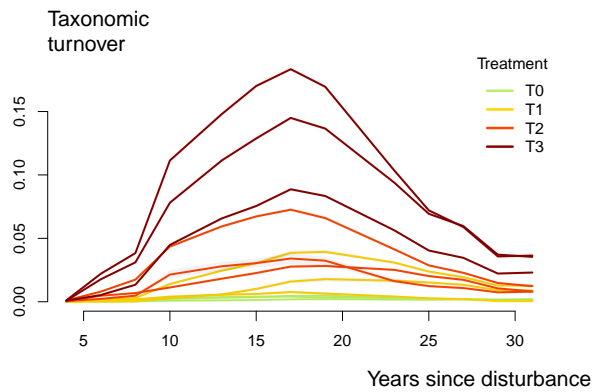




**Figure 1.** Upper panels, trajectories over 30 years of taxonomic richness (a), taxonomic evenness (b) and functional diversity (c) of observed 2-years laps recruitment  $H_{obs}^q$ . Lower panels, diversity differences to null models  $H_{obs}^q - H_{null}^q$ . Shaded areas are the credibility intervals.



**Figure 2.** Community weighted means (CWM) of the 7 functional traits considered: leaf thickness, leaf chlorophyll content, leaf toughness, specific leaf area (SLA), wood specific gravity (WSG), bark thickness and maximum height at adult stage (Hmax). Shaded areas are the credibility intervals.



**Figure 3.** Trajectories over 30 years of the abundance-based turnover between 2-years laps recruited trees pre-disturbance communities.

alleviated competition induced by disturbance (Denslow & Guzman, 2000; Herault *et al.*, 2010).

A second phase (8-15 years) was marked by an increase of the taxonomic turnover between recruited trees and initial communities, a decrease of recruits richness and evenness compared to the null model, and a shift in the functional composition of recruits towards more “resource-acquisitive” strategies. Given the time past since disturbance, this second phase might correspond to the recruitment of “true recruits”, *i.e.* trees germinating from the seeds bank that represent the main part of the post-disturbance recruitment (Lawton & Putz, 1988). The recruitment was dominated by a restricted pool of short-lived, fast growing pioneers with large exchange surface and low density tissues, *i.e.* high SLA and low maximum height, leaf toughness and wood specific gravity (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011). This second phase was marked by the emergence of trait-based deterministic processes favoring species with efficient light acquisition (high SLA and leaf chlorophyll content) and inexpensive, short-lived tissues (low leaf thickness and toughness, small Hmax and low wood specific gravity and bark thickness), as already demonstrated in temperate and tropical forests (Peña-Claros *et al.*, 2008; Carreño-Rocabado *et al.*, 2012; Kunstler *et al.*, 2016; Both *et al.*, 2019). The balance between these trait-based deterministic processes and the stochastic processes first observed depended on the disturbance intensity. Following low intensity disturbance (T1 plots), deterministic and stochastic processes were balanced and recruited communities included more long-lived pioneers and light-demanding species but still mirrored the pre-disturbance taxonomic composition (Bongers *et al.*, 2009). Following intense disturbance (T2 and T3 plots), deterministic processes prevailed and the composition of recruited communities rapidly differed from this of the pre-disturbance community with a high dominance of hard pioneers like *Cecropia spp.* or *Vismia spp.*

A third recruitment phase (15-30 years) delineated by trajectories’ return towards pre-disturbance state corresponded to the recovery of community diversity and composition. Al-

though recruited species remained mainly light-demanding, the functional diversity of recruited communities increased and their taxonomic composition increasingly resembled pre-disturbance communities (Fortunel *et al.*, 2014). Deterministic recruitment processes then gradually left room to stochastic recruitment processes specific to undisturbed forest (Lawton & Putz, 1988; Chave, 2004).

## 4.2 Community recovery

Following disturbance, there was a recovery of community taxonomic and functional composition and of the stochastic recruitment processes observed for undisturbed communities. This confirmed previous results from the Paracou experiment, conducted 10 years (Molino & Sabatier, 2001) and 20 years (Baraloto *et al.*, 2012) after disturbance, where the early signs of the resilience of pre-disturbance taxonomic and functional composition recovery had been detected.

Thirty years after disturbance, recruited community taxonomic richness and evenness returned towards pre-disturbance values and their taxonomic composition returned towards this of pre-disturbance states. This maintained community initial diversity and composition and meant a low recruitment of species absent in the pre-disturbance community, confirming the importance of dispersal limitation among tropical tree species (Svenning & Wright, 2005). Functional composition and diversity trajectories returned as well towards pre-disturbance values, which confirmed the functional convergence among tropical tree communities (Fukami *et al.*, 2005; Fortunel *et al.*, 2014).

Although community taxonomic and functional recovery was ongoing, recruits diversity and composition remained altered 30 years after disturbance. Specifically, the higher the disturbance intensity, the more persistent the dominance of light-demanding species. This long-term impact on community composition likely alters community functioning (Díaz *et al.*, 2005), which raises questions for tropical forests management. Most valuable species indeed are late-successional species and their exploitation would require cutting cycles of more than 30 years (Putz *et al.*, 2012).

## 5. Conclusion

Post-disturbance recruitment trajectories highlighted a three-phased deterministic successional pathway driven by the emergence of trait-based deterministic processes balancing pre-disturbance stochastic processes and enhancing light-acquisitive species. A first phase would correspond to the recruitment of pre-disturbance surviving saplings mirroring the taxonomic and functional diversity and composition of pre-disturbance communities. A second phase corresponded to the recruitment of true recruits from the seeds bank belonging to a restricted pool of pioneers favored by the emergence of competitive exclusion for light. Above a disturbance intensity threshold, this second recruitment phase saw the dominance of short-lived hard pioneers that drastically changed community composition, diversity, and likely functioning. A third phase eventually corresponded to the recovery of stochastic recruitment processes and to the return towards pre-disturbance taxonomic and func-

tional characteristics. Although resilient, recruits diversity and composition remained altered 30 years after disturbance, all the more so that disturbance was intense. This emphasises the importance of evaluating forest management sustainability in modelling forest dynamics from observed trajectories and successional pathways.

## 6. Acknowledgement

We are in debt with all technicians and colleagues who helped setting up the plots and collecting data over years. Without their precious work, this study would have not been possible and they may be warmly thanked here.

## 7. 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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