

30 Years of Post-disturbance Recruitment in Tropical Forest

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Abstract

Trees biodiversity is central for tropical forests functioning and services. In the current climatic and land-use changing context it is urgent to clarify the response of communities diversity and composition to disturbance. Succession patterns shaped by deterministic recruitment processes are recognized to shape communities trajectories after disturbance but those need be tested for highly biodiverse tropical forests and for cases where the initial communities are partly maintained like selective logging and climatic changes. Recruitment trajectories would allow (i) disentangling neutral, stochastic and deterministic, selective processes shaping post-disturbance succession, and (ii) clarify the taxonomic and functional facets of forests resilience. We examined the trajectories over 30 years of recruitment diversity and composition in 75 ha of a neotropical forest following a gradient of logging and thinning disturbance (from 15 to 60% of AGB removed). Specifically we analysed and compared to neutral models the recruitment trajectories in taxonomic richness, evenness, and compositional turnover compared to initial communities, and in Rao functional diversity integrating species ecology through 7 key functional traits. We evidenced three recruitment phases shaped by the gradual balance between stochastic and deterministic processes. First, trajectories relied upon the growth of saplings randomly recruited among the pre-disturbance community. Second, trajectories relied on *true recruits* germinated from the seeds bank and selected through competitive exclusion for light favoring acquisitive, light-demanding species. Eventually an inversed balance progressively restored the stochastic recruitment observed in undisturbed forests. Recruitment trajectories ensured both functional and taxonomic recovery, thus maintaining communities initial differences. Communities disturbance response was driven by the emergence of deterministic competition processes for light that balanced stochastic processes observed in undisturbed forests. Communities taxonomic and functional characteristics were consistently restored and initial differences among communities were maintained. Still, the recovery was decades-long and called cautions regarding the time prescribed for forest recovery.

Keywords

Taxonomic and Functional Diversity, Recruitment, Resilience, Tropical Forests, Disturbance Dynamics

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Contents

1	Introduction	1
2	Material and Methods	2
2.1	Study Site	2
2.2	Inventories Protocol and Dataset Collection	3
2.3	Recruitment trajectories	3
3	Results	3
3.1	Recruitment Diversity	3
	Taxonomic Diversity • Functional Diversity and Composition	
3.2	Recruitment Turnover	5
4	Discussion	5
4.1	A three-phased succession shaped by deterministic processes	5
4.2	The achievement of communities recovery	6
5	Conclusion	7

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 of communities structure, diversity and functioning following climatic changes (Aubry-Kientz *et al.*, 2015) or anthropogenic activities like selective logging (Baraloto *et al.*, 2012; Hérault & Gourlet-Fleury, 2016). In that respect a vast literature successfully modeled communities response to disturbance in terms of tree growth (Gourlet-Fleury & Houllier, 2000), tree height (Rutishauser *et al.*, 2016), carbon, water and nutrient fluxes (Putz *et al.*, 2012; Martin *et al.*, 2015; Piponiot *et al.*, 2016). However, similar approaches regarding forest diversity remain hindered by the scarcity of long-term monitoring and by the huge biological diversity imposing to focus on common or commercial species (Sebbenn *et al.*, 2008; Rozendaal *et al.*, 2010; Vin-

son *et al.*, 2015). Trees diversity is a major determinant of forests functioning and productivity, so it is urgent to elucidate its response to disturbance and the underlying mechanisms. The diversity response would assess communities resilience and recovery time, and eventually help adjusting exploitation and conservation guidelines (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017).

Communities response to intense disturbance have been recognized to follow succession models based on changes in resources availability and interactions among species. First, the succession patterns involves already grown saplings that establish under conditions of high light, high nutrient availability and low competition. A second phase sees the tree growth increasing the competition for the space and resources until excluding species with respect to their functional strategy and competitive ability. Eventually a third phase corresponds to the senescence of the first established seedlings and to the emergence of understory species restoring the composition and diversity of pre-disturbance communities. This succession model proved relevant in temperate forests but might be blurred in tropical rainforests by their biodiversity and by tree species rapid vegetative growth (?). Besides the succession model predicts forests trajectories after very intense disturbance or clear cutting, but it might not be as robust in cases of climatic changes or selective logging where the pre-disturbance communities and their steady-state dynamics still remain. In those cases communities trajectories would depend on both on the dynamics of surviving trees from before disturbance, and on the recruitment of new trees (Héroult & Piponiot, 2018). The recruitment in tropical forests either rely upon stochastic processes driven only by recruitment and dispersal limitations (Hurtt & Pacala, 1995; Hubbell, 2001), or upon deterministic processes driven by niche-based competition and biotic interactions (Adler *et al.*, 2007). Stochastic processes, translating Hubbell's neutral theory, build communities as random samples of the larger regional-scale forest (Hubbell, 2001; Chave, 2004). In contrast deterministic processes select species with respect to their ecology and competitive ability. The involvement of stochastic and deterministic processes remains debated and post-disturbance trajectories probably result from a gradual balance between them.

Communities are defined by their taxonomic characteristics, that refer to a neutral species assemblages, and by their functional characteristics, that account for species ecology and ecosystem functioning (Violle *et al.*, 2007; Kunstler *et al.*, 2016). The ecological processes shaping recruitment trajectories may differently affect communities taxonomic and functional characteristics, and two communities may be very different in terms of taxonomy but very similar in terms of functioning (Villéger *et al.*, 2012). The correlations, or not, between taxonomic and functional [??? system] trajectories are therefore insightful of the ecological rules involved in the recruitment processes, specifically to explicit the deterministic processes at stake (Mayfield & Levine, 2010; Fukami *et al.*, 2005). Competitive interactions among species indeed depend on their functional differences, specifically regarding the use of the limited

shared resources, that determine their competitive ability and ecological niche (Webb *et al.*, 2002; Perronne *et al.*, 2017). In tropical forests where the light is limiting, communities response to disturbance translate in a shift from slow-growing, long-lived species with “conservative” resource use to fast growing, resource “acquisitive” species (Denslow, 1980; Molino & Sabatier, 2001; Bongers *et al.*, 2009).

The competition processes at stake would be grasped by shifts in key leaf, wood and life-history functional traits assessing species resources acquisition strategy and ecology (Wright *et al.*, 2004; Chave *et al.*, 2009; Héroult *et al.*, 2011; Gerhold *et al.*, 2015).

Beyond the mere understanding of response mechanisms, disentangle deterministic from stochastic processes elucidates the resilience of communities. Controversies remain about whether resilience is either deterministic, entailing the convergence of communities towards stable taxonomic and functional characteristics likely defined by the environment (Clements, 1916), or stochastic, entailing species stochastic recruitment and communities random divergence (Diamond, 1975). These contrasting views were reconciled under the hypothesis that communities might diverge in the taxonomic space while they converge in the functional space. Under this hypothesis communities have a determined diversity and composition in functional niches, but this hypothesis remains to be tested in tropical forests.

In this paper we followed the fate of recruited tree diversity and composition (60 121 individuals) over 30 years after a large disturbance gradient, with 10 to 60% of forest biomass removed. We assessed the taxonomic dissimilarity between recruited trees and initial communities, the taxonomic and functional diversity of recruited trees and the corresponding trajectories of functional traits, using a large functional trait database covering the leaf, wood and life-history spectra. We compared the observed trajectories to neutral processes corresponding to the stochastic recruitment of individuals and to the randomization of species functional traits. These trajectories aimed to highlight the recruitment processes underlying forests response to disturbance, specifically assessing (i) the succession pattern and the underlying ecological processes and (ii) clarify the taxonomic and functional facets of forests resilience and their consequences for 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.y⁻¹ (30-y period) and a 3-months dry season (< 100 mm.months⁻¹) from mid-August to mid-November, and a one-month dry season in March (Wagner *et al.*, 2011). Elevation ranges from 5 to 50 m and mean annual temperature is 26 C. Soils are thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains. The disturbance experiment spread over a network of twelve 6.25ha plots (Table 1) that underwent three disturbance treatments in

1986-1987 (Hérault & Piponiot, 2018). Dominant families are Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae.

2.2 Inventories Protocol and Dataset Collection

All trees above 10 cm DBH were mapped and measured annually since 1984. During inventories, trees were first identified with a vernacular name assigned by the field team, and afterward with a scientific name assigned by a botanist during regular botanical campaigns. Botanical campaigns have been carried out every 5 to 6 years from 2003 onwards. These changes in identification protocol raised methodological issues as vernacular names usually correspond to different botanical species, resulting in significant taxonomic uncertainties that had to be propagated to composition and diversity metrics. Vernacular names were replaced through multinomial trials $M_v([s_1, s_2, \dots, s_N], [\alpha_1, \alpha_2, \dots, \alpha_3])$ based on the observed association probability $[\alpha_1, \alpha_2, \dots, \alpha_3]$ between each vernacular name v and the species $[s_1, s_2, \dots, s_N]$ recorded in the inventory. See appendix 1 and Aubry-Kientz *et al.* (2013) for the detailed methodology. To avoid remaining identification caveats, the simulated botanical inventories were reported at genus level.

Eight functional traits representing the leaf economic (leaves thickness, toughness, total chlorophyll content and specific leaf area) and wood economic spectra (wood specific gravity and bark thickness), and life history traits (maximum specific height and seed mass) were considered. Traits were extracted from the BRIDGE project¹ where trait values were measured on nine forest plots in French Guiana, including two in Paracou. Missing trait values of the trait database (10%) were filled by multivariate imputation by chained equation using the Mice R package (van Buuren & Groothuis-Oudshoorn, 2011). F-tests demonstrated that traits variance were essentially lower within genera and families compared to the whole inventory: we accounted for the phylogenetic signal of the functional traits by restricting the gap filling processes to samples pertaining to the next higher taxonomic level. As seed mass information corresponded to a classification into discrete mass classes, no data filling process was applied and analysis were performed only considering the 414 botanical species of the seed mass dataset.

2.3 Recruitment trajectories

To tease apart recruitment trajectories communities were split into per-disturbance surviving trees and recruited trees afterward. Recruited communities were examined either considering the “punctual recruitment”, *i.e.* recruited trees by 2-year intervals, or all recruits since disturbance as the “accumulated recruits”. Eventually, in disturbed plots the recruited communities were examined distinguishing the undisturbed and logging gap areas to test the validity of recruitment processes for the whole plot scale (see Annexe I).

The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973; Chao & Jost, 2015; Marcon, 2015).

The three diversities belong to the set of HCDT or generalized entropy, respectively corresponding to the 0, 1 and 2 order of diversity (q), which grasps the balance between richness and evenness in the community through the value of q that emphasizes common species. Functional trajectories were estimated with the Rao quadratic entropy, summarizing the functional richness and evenness (Clark *et al.*, 2012) through the measure of communities functional divergence using Gower distance as recommended by Pavoine *et al.* (2009). Functional diversity was completed by the trajectories of traits community weighted means (CWM), representing the average trait value in a community weighted by relative abundance of the species carrying each value (Díaz *et al.*, 2007; Garnier *et al.*, 2004; Mason *et al.*, 2013). Seed mass trajectories were reported by the proportion of each class recorded in the inventories. The similarity between recruited trees and pre-disturbance forest was measured with the turnover metrics detailed in Podani *et al.* (2013). To estimate the importance of stochastic processes the recruitment was compared to the trajectories of a stochastic model of random samplings. For the taxonomic trajectories the stochastic model was a random sampling of individuals among surviving trees according to their observed abundance that preserved species abundance and tree density. For the functional diversity the stochastic model was a random reassignment of functional trait values among species that randomizes abundances across species but within communities (Mason *et al.*, 2013).

All composition and diversity metrics corresponded to the median and 90% percentile obtained after 50 iterations of the taxonomy uncertainty propagation and gap filling frameworks. The stochastic trajectories were similarly obtained after 50 iterations of the random sampling.

3. Results

3.1 Recruitment Diversity

All the trajectories were identical in disturbed and undisturbed areas, confirming that recruitment processes applied to whole communities and not restricted to logging gaps.

3.1.1 Taxonomic Diversity

The diversity trajectories of punctual recruitment followed a consistent trajectory after disturbance, first with an increase of the richness and a decrease of the evenness (Figure 1). For all disturbed plots both richness and evenness tended to return towards initial values but none had recovered 30 years after disturbance. The accumulated recruits displayed sharp increasing richness (order 0) and decreasing evenness (order 2) after intense disturbance (T3 and some T2, Appendix I, fig. S1).

Compared to stochastic trajectories, observed richness (order 0) and evenness (order 2) of punctual recruitment remained equivalent or higher than for a random sampling in control plots while both were lower in disturbed plots. Disturbed plots followed humped shaped trajectories heading towards a recovery of the initial state (Figure 1). Accumulated recruitment richness and evenness were higher or equivalent to those of a random sampling after low disturbance intensity (plots T1 and some plots T2) but lower after

¹<http://www.ecofog.gf/Bridge/>

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 trees/ha			[12% – 33%]
T2	DBH \geq 50 cm, commercial species, \approx 10 trees/ha	DBH \geq 40 cm, non-valuable species, \approx 30 trees/ha		[33% – 56%]
T3	DBH \geq 50 cm, commercial species, \approx 10 trees/ha	DBH \geq 50 cm, non-valuable species, \approx 15 trees/ha	40 cm \leq DBH \leq 50 cm, non-valuable species, \approx 15 trees/ha	[35% – 56%]

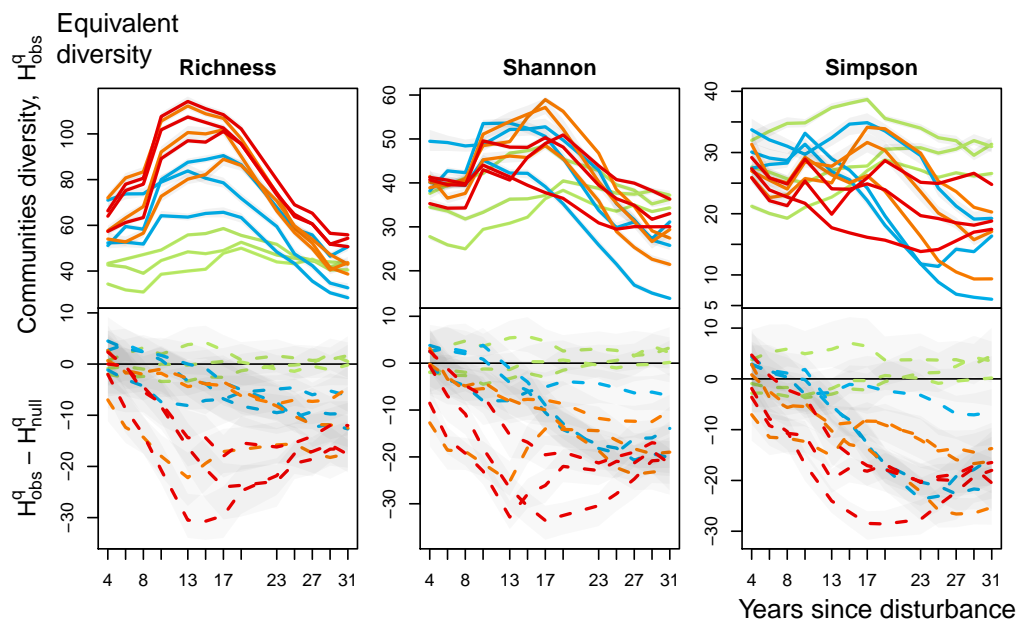


Figure 1. Trajectories over 30 years of Richness, Shannon and Simpson diversities of punctual recruitment (2-years laps, upper panels) and divergence to null model (lower panels). Values reported correspond to plot-level 0.025 and 0.975 percentiles (grey envelopes) and median (solid or dotted lines) obtained after 50 repetitions of the taxonomic uncertainty propagation and the functional database gap-filling frameworks. Colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3, see Table 1 for details).

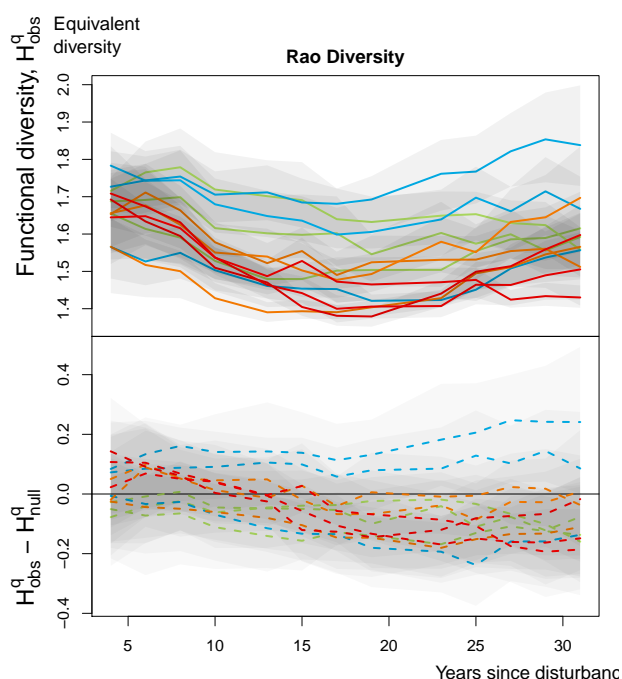


Figure 2. Functional diversity of punctual recruited trees (2-years laps) from the 7 functional traits (upper panel) and divergence to null model (lower panel). Values reported correspond to plot-level 0.025 and 0.975 percentiles (grey envelopes) and median (solid lines) obtained after 50 run of the null model and 50 repetitions of the taxonomic uncertainty propagation and the functional database gap-filling frameworks. Colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3, see Table 1 for details).

intense disturbance (plots T3 and a plot T2, Appendix I fig. S1).

3.1.2 Functional Diversity and Composition

In disturbed plots (T2 and T3), the functional diversity decreased until 15 years after disturbance (Figure 2) before recovering towards initial values. If the recovery was not achieved for the most disturbed plots, it was faster after the low disturbance intensity and for some T1 plots exceeded the initial values 30 years after disturbance. For both disturbed and undisturbed plots, the observed functional diversity was lower than this of the random model, to the exception of two plots T1.

Trajectories of the functional traits showed a switch in disturbed plots towards species with large exchange surface area, light tissues (high SLA, low leaf toughness and thickness and low wood specific gravity) and with smaller maximum height (Figure 3). Functional traits either followed humped shaped trajectories with an ongoing recovery or an achieved return to the initial state (for SLA, Bark thickness and leaf thickness and Hmax to a certain extent).

3.2 Recruitment Turnover

In control plots species turnover remained highly stable for the 30 sampled years (Figure 4), reflecting a strong similarity between the initial plots composition and the punctual re-

cruits. In disturbed plots, the taxonomic turnover followed a marked humped shaped trajectory, with a maximum reached around 15 years after disturbance and a value positively correlated to the disturbance intensity ($\rho_{\text{spearman}} = 0.93$). Thirty years after disturbance the turnover of all disturbed plots had returned to low values close to zero.

4. Discussion

4.1 A three-phased succession shaped by deterministic processes

Recruitment trajectories followed a three-phased succession pattern shaped the emergence of deterministic competition processes for light that balanced the steady-state stochastic processes of undisturbed communities.

In a first phase (0-8 years), recruited trees mirrored the pre-disturbance communities in terms of taxonomic and functional characteristics and the recruitment trajectories resembled those of a stochastic recruitment. This first recruitment phase, likely involved already grown saplings (DBH < 10cm) immediately benefitting from the increased enlightenment and the alleviated competition induced by disturbance (Hérault *et al.*, 2010).

A second phase (8-15 years) corresponded to a functional shift, marked by changes of trajectory for several functional traits, and to a decrease in recruitment evenness and functional diversity. At that time recruits likely corresponded to true recruits, *i.e.* trees germinated from the seeds bank, that are the main part of the whole post-disturbance recruitment (Lawton & Putz, 1988). The recruitment was then dominated by short-lived, fast growing hard pioneer species with competitive and efficient light acquisition (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011; Reich, 2014). Hence, exclusive competition processes based on species light acquisition strategy restricted the pool of recruited species, as already demonstrated in temperate forests (Chave, 2004; Mayfield & Levine, 2010; Kunstler *et al.*, 2012). The emergence of deterministic processes then offset the stochastic recruitment observed in the first place, and the balance was determined by the initial disturbance intensity. After light disturbance (T1 plots), recruited species included more pioneers and light demanders, with strategies of efficient resource acquisition (high SLA and leaf chlorophyll content) and inexpensive, short-lived tissues (low leaf thickness and toughness, small Hmax and low wood density and bark thickness) (Hubbell *et al.*, 1999; Schnitzer & Carson, 2001; Sheil & Burslem, 2003; Bongers *et al.*, 2009). At these low disturbance intensity the pool of recruited species was restricted to more light-demanding species but still mirrored the pre-disturbance communities. The recruitment was not overwhelmed by hard pioneers, probably because of the dispersal limitations due to the short dispersal distances observed for tropical trees (Leclerc *et al.*, 2015; Scotti *et al.*, 2015). After intense disturbance in contrast (T2 and T3 plots), the recruitment rapidly differed from the pre-disturbance composition and corresponded to a sharp increase of the SLA and bark thickness. These drastic changes of trajectory reflected an overwhelming recruitment of hard pioneers, such as *Cecropia* spp. likely entailing significant changes in communities functioning

Punctual recruits CWM

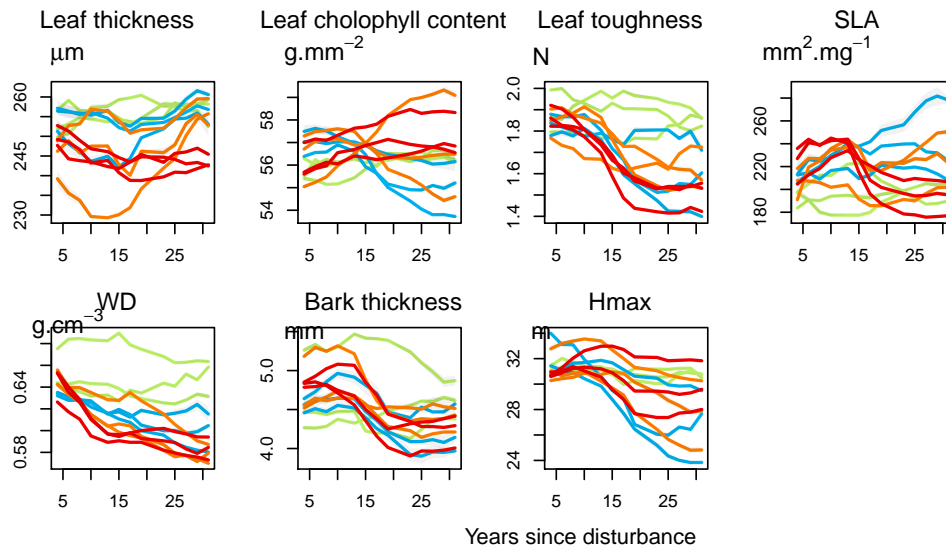


Figure 3. Community weighted means (CWM) of the four leaf traits, the two stem traits and the specific maximum height. Values reported correspond to plot-level 0.025 and 0.975 percentiles (grey envelopes) and median (solid lines) obtained after 50 repetitions of the taxonomic uncertainty propagation and the functional database gap-filling frameworks. Colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3, see Table 1 for details).

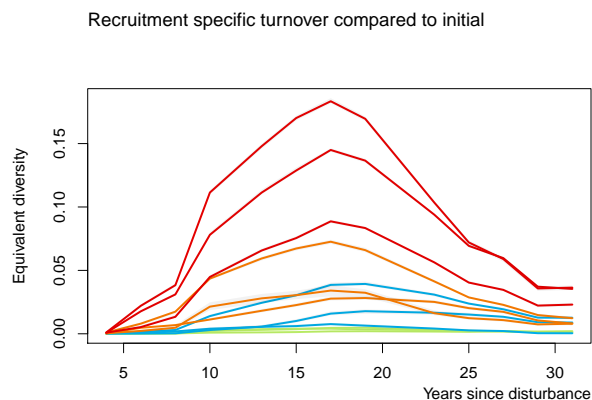


Figure 4. Trajectories over 30 years of the abundance-based turnover between recruited trees (2-years laps) and initial communities before disturbance. Values reported correspond to plot-level 0.025 and 0.975 percentiles (grey envelopes) and median (solid lines) obtained after 50 repetitions of the taxonomic uncertainty propagation framework. Colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3, see Table 1 for details).

(Díaz *et al.*, 2005).

A third recruitment phase entailed a return towards initial taxonomic and functional diversities: although the recruited species remained mainly light-demanding and submitted to competitive exclusion, they displayed increasing functional diversity and similarity with pre-disturbance communities. Initial stochastic recruitment eventually recovered, restoring the steady-state equilibrium between neutral and deterministic processes (Lawton & Putz, 1988; Chave, 2004; Mayfield & Levine, 2010).

4.2 The achievement of communities recovery

After disturbance the stochastic recruitment of undisturbed communities progressively recovered, shaping taxonomic and functional trajectories that converged towards the characteristic of pre-disturbance communities.

The taxonomic diversity and composition of recruited trees recovered after disturbance, meaning the long-term maintenance of initial taxonomic differences highlighted among the studied communities. >> Here I should argue that initial there were actual differences among communities, otherwise it doesn't make sense-> cite the other article?

Initial communities restored after disturbance would correspond to multiple stable equilibria, that are assumed to shape the highly diverse and productive ecosystems (Chase, 2003). The taxonomic trajectory after disturbance were determined by the composition of the initial communities which defined the pool grown saplings and the local seeds bank and directed the trajectories towards its recovery (Dalling & Hubbell, 2002; Anderson, 2007).

The functional diversity and some traits trajectories were similar among treatments and recovered quickly, translating the convergence of communities in the functional space and the recovery of similar functioning despite their

taxonomic differences (Fukami *et al.*, 2005). 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 taxonomic and functional composition had been detected.

Communities recovery was consistent but lasted for decades, specifically communities taxonomic diversity and composition and the average value of several functional traits remained altered for more than 30 years.

5. Conclusion

The hindsight of 30 years monitored in Paracou highlighted a three-phased succession pattern after disturbance defined by the emergence of deterministic competition for light balancing the stochastic recruitment of undisturbed communities. Recruitment trajectories were first driven by the growth of pre-disturbance saplings mirroring initial communities. Then recruitment trajectories were shaped by true recruits from the seeds bank selected through the emergence of competitive exclusion for light. After intense disturbance the second recruitment phase was dominated by short-lived hard pioneers that drastically changed communities diversity and functioning. A third phase eventually restored communities taxonomic and functional characteristics through the recovery of stochastic recruitment progressively offsetting competitive exclusion. The recruitment succession revealed communities taxonomic and functional recovery and the maintenance of their initial composition and functioning. Although consistent, the recovery of recruitment processes and hence of the whole communities proved decades long. Besides, post disturbance trajectories involved the seeds bank and probably altered the composition and diversity of the seeds stock (Norden *et al.*, 2009). The diversity and composition of recruitable species and hence the resilience of the communities might then be altered, entailing great caution regarding forests management guidelines aiming to a complete recovery of ecosystems.

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