

30 Years of Post-disturbance Recruitment in Tropical Forest

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Abstract

Résumé de l'article.

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

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1. Introduction

Determining the response of tropical forests to disturbance is a key to predict their fate in a global change context where disturbance are expected to become more and more frequent. Tropical forests indeed currently experience a wide range of disturbance, from radical land-use changes for agriculture or mining (Dezecache *et al.*, 2017; Dezecache *et al.*, 2017) to insidious changes in communities structure and functioning following changes in the precipitation regime or after selective logging (Baraloto *et al.*, 2012; Hérault & Gourlet-Fleury, 2016). In that respect a vast literature successfully modeled the response of tropical forests structure, carbon stocks and fluxes to anthropogenic and natural disturbances (Gourlet-Fleury & Houllier, 2000; Putz *et al.*, 2012; Martin *et al.*, 2015; Piponiot *et al.*, 2016). Regarding diversity, however, similar attempts have been hindered by both the huge biological diversity and the scarcity of long-term monitoring. If the response to disturbance has been identified for common species assemblages, it usually remained confined

to few commercial and valuable species (Sebbenn *et al.*, 2008; Rozendaal *et al.*, 2010; Vinson *et al.*, 2015). Forests communities functioning and dynamics, though, result from the constantly evolving interactions and feedbacks among trees and their environment and they would only be assessed through the study of entire communities (de Avila *et al.*, 2016; Liang *et al.*, 2016). Forests response to disturbance is build on the the population of disturbance survivors and the recruitment of new individuals. The latter proved to mirror the composition of pre-disturbance forest (Hérault & Piponiot, 2018) so the response of the whole community will be driven by the diversity and composition of the recruitment. Recruitment trajectories, directly determining the community to be, are then key to elucidate the future of tropical forest in the changing global environment.

Recruitment diversity and composition trajectories elucidate the resilience of hyperdiverse tropical forest ecosystems and highlight the determinants of their response after disturbance. To our opinion taxonomic and functional trajectories would depend on the composition and diversity of initial community, partly conditioning the pool of recruited species. Thereafter, the communities composition will in turn influence the assembly rules governing further recruitment and result in a self-perpetuated trajectory along time (Kunstler *et al.*, 2016). Similar reasoning apply to both taxonomic and functional trajectories, although given the possible decoupling between taxonomic and functional characteristics in a community their respective trajectories might differ (Fukami *et al.*, 2005). The dependency of communities trajectories upon their initial state besides brings the question of its resilience, meaning the convergence of communities towards pre-disturbance conditions and the maintenance of the initial differences among communities (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017). In addition to those intrinsic communities parameters, the recruitment results from the interplay of external processes either stochastic, like random dispersal, recruit-

ment and death (Hubbell, 2001), or deterministic like niche-based competition processes (Adler *et al.*, 2007). While stochastic processes would build communities as random samples of larger, regional ones, deterministic processes rely on the abiotic environment and filter-out recruited species according to their ecology. Specifically, species would be selected through their tolerance to stress or competition for resources. Based on the Intermediate Disturbance Hypothesis (IDH) these deterministic processes and the patchy variability of environmental conditions in space and time maintain a large ecological range in the community via the species selected under past environmental conditions (Guitet *et al.*, 2018). In tropical forests deterministic processes depend on the strategy of resource use, specifically light, and therefore result in shifts from fast growing, resources-acquisitive but stress-intolerant species favored in disturbance gaps, to slow-growing, stress-tolerant and resource-conservative species dominating in mature forests (Denslow, 1980; Molino & Sabatier, 2001; Bongers *et al.*, 2009). Communities functional diversity would then be driven either by selective pressures filtering-out some functional strategies or by the competitive exclusion for resources limiting the functional similarity among species (Ackerly, 2003; McGill *et al.*, 2006). It would be translated by either the overdispersion or the restriction of leaf and stem functional traits (leaf thickness, toughness, chlorophyll content and specific area; wood specific gravity and bark thickness) and life-history traits (maximum height at adult stage and class of seed mass) (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011).

Empirical tests of those mechanisms, the validation of the IDH in tropical rainforests, and the resilience of communities proved hard to succeed and yielded controversial results (Hubbell *et al.*, 1999; Molino & Sabatier, 2001; Sheil & Burslem, 2003). In this paper we follow the fate of a recruited tree communities (60121 individuals) over 30 years on a disturbance gradient, with 10 to 60% of forest biomass removed. We assessed the taxonomic as well as functional diversity of recruited trees, using a large functional trait database covering the leaf, wood and life-history spectra. We compared the observed trajectories to null models representing random trees recruitment and randomized functional traits. We aimed to (i) assess the role of deterministic processes compared to stochastic recruitment after disturbance, (ii) assess the taxonomic and functional convergence of forest communities and the maintenance of taxonomic composition in the long term, and (iii) determine the resilience of the ecosystem.

2. Material and Methods

2.1 Study Site

The Paracou station is located in a lowland tropical rain forest in French Guiana (5°18'N and 52°53'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. This raised methodological issues as vernacular names usually correspond to different botanical species, resulting in significant taxonomic uncertainties that were 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.

Six functional traits, representing leaf economics (leaves thickness, toughness, total chlorophyll content and specific leaf area, the leaf area per unit dry mass), wood economics (wood specific gravity and bark thickness) and life history traits (maximum specific height and seed mass), come from the BRIDGE project¹ where trait values were measured on nine french guianan forest plots, including two in Paracou. Missing trait values (10%) were filled using multivariate imputation by chained equation (mice). As traits variability was lower within species and within genus, we accounted for the phylogenetic signal of the functional traits in restricting the gap filling processes to samples pertaining to the next higher taxonomic level (refs MICE). As seed mass information corresponds to a classification into mass classes, no data filling process was applied so analysis were performed only considering the 414 botanical species of the seed mass dataset.

Functional trajectories were estimated with the Rao quadratic entropy using community weighted means (CWM) (Díaz *et al.*, 2007; Garnier *et al.*, 2004). Seed mass trajectories were reported by the proportion of each class recorded in the inventories. All composition and diversity metrics are the average obtained after 50 iterations of taxonomy and trait values uncertainty propagation.

2.3 Recruitment trajectories

We split the forest community in ‘survivors’, that are the trees surviving since disturbance, and the trees recruited after disturbance. Two recruitment metrics were examined: on the one hand the “punctual recruitment” by 2-year intervals after disturbance, on the other hand all recruited

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%]

trees since disturbance, hereafter “accumulated recruits”. Eventually it was to determine whether plot scale trajectories either reflected to overall recruitment processes or were driven by processes restricted to disturbance gaps while the recruitment of undisturbed zones remained unchanged.

The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973; Chao & Jost, 2015; Marcon, 2015). These three indices 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, with common species weighting more than rare ones when q increases. The similarity between the recruited trees and the pre-disturbance forest was measured with the turnover metrics detailed in Podani *et al.* (2013). To determine whether recruitment trajectories ensued from a random process, observed trajectories were compared to those generated by 50 repetitions of a random null model shuffling individuals among plots while preserving species abundance and plots’ tree density.

To draw plots trajectories we applied a moving average with a one step (3 years) window to mitigate the heterogeneity of inventory protocols between years.

3. Results

3.1 Recruitment Diversity

3.1.1 Taxonomic Diversity

Punctual recruits’ diversity followed a consistent trajectory among disturbance treatments with first higher richness and lower evenness than in control plots and then equivalent richness and lower evenness (Figure (1)). For recruits accumulated since disturbance, the richness (order 0) in highly disturbed plots (T3 and some T2) was higher than in control plots, consistently with the increase of recruited trees after disturbance, and the evenness (order 2) was lower, specifically for the most disturbed plots (Appendix I, fig. S1).

Punctual and accumulated recruitment diversity of orders 0, 1 and 2 were then compared to a null random recruitment model. In control plots the richness (order 0) and

evenness (order 2) of punctual recruits remained equivalent or higher than for the null random model. For all disturbed plots in contrast both richness and evenness were lower than these of a random null model but displayed a significant but unachieved humped-shaped trajectory for all plots (Figure 1). Accumulated recruitment richness and evenness were higher or equivalent to those of the null model for plots T1 and some plots T2 but lower for plots T3 and a plot T2 (AppendixI, fig. S1).

The trajectories obtained

3.1.2 Functional Diversity and Composition

The functional diversity (Rao diversity) of punctual recruitment was measured and compared to a null model of random traits shuffling. In most disturbed plots (plots T2 and T3) the functional diversity was decreasing and lower to this of control plots until 15 years after disturbance (Figure 3). It then increased to values equivalent or higher to those observed in control plots. For all disturbed and control plots the observed functional diversity was lower than for the null model of random traits shuffle, except for two T1 plots.

Trajectories of recruited trees in the functional spaces showed the dominance after disturbance of species displaying large exchange surface area and light tissues (high SLA, low leaf toughness and thickness and low wood specific gravity) (Figure 3). All traits trajectories displayed univariate CWM trajectories with leaf toughness, wood specific gravity and bark thickness decreasing before stabilizing at low values around 15 after disturbance, except SLA and leaf thickness that displayed a unimodal trajectory with a maximum reach around 15 years after disturbance.

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 recruits. In disturbed plots, turnover displayed a unimodal response to disturbance, with maximum reached around 15 years and with a value positively correlated to the disturbance intensity ($\rho_{\text{spearman}} = 0.93$). The turnover trajectory returned close to zero for all plots 30 years after

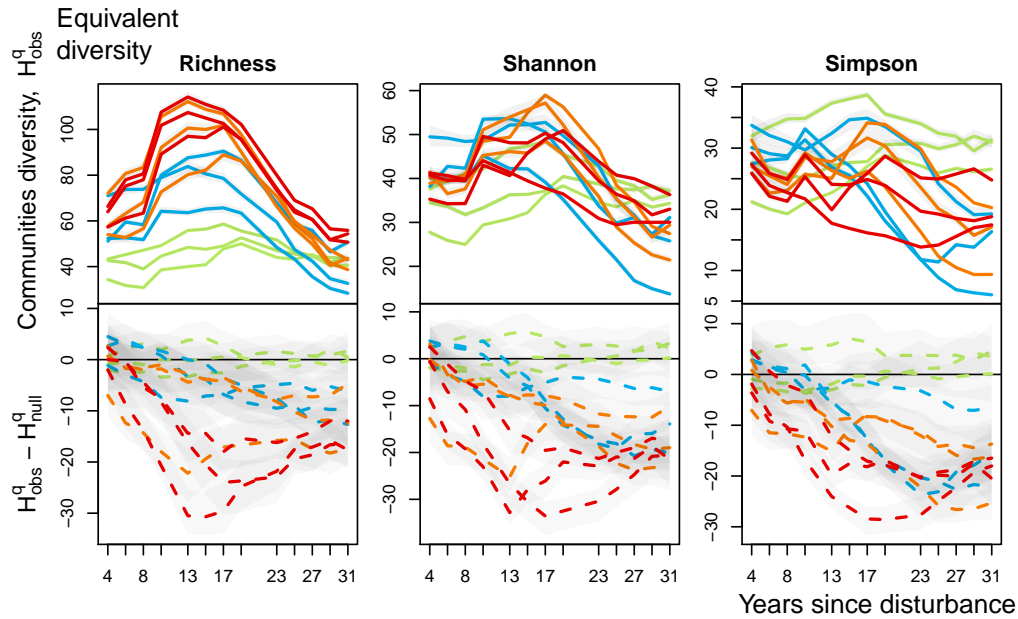


Figure 1. Trajectories of Richness, Shannon and Simpson diversity for 2-years laps punctual recruitment (upper panels) and divergence to null model (lower panels). Lines colors refer to the perturbation regime: green for control, blue for T1, orange for T2 and red for T3 disturbance treatments. Plain lines correspond to the median observed after uncertainty propagation and are given along with the 95% confidence interval (grey envelope).

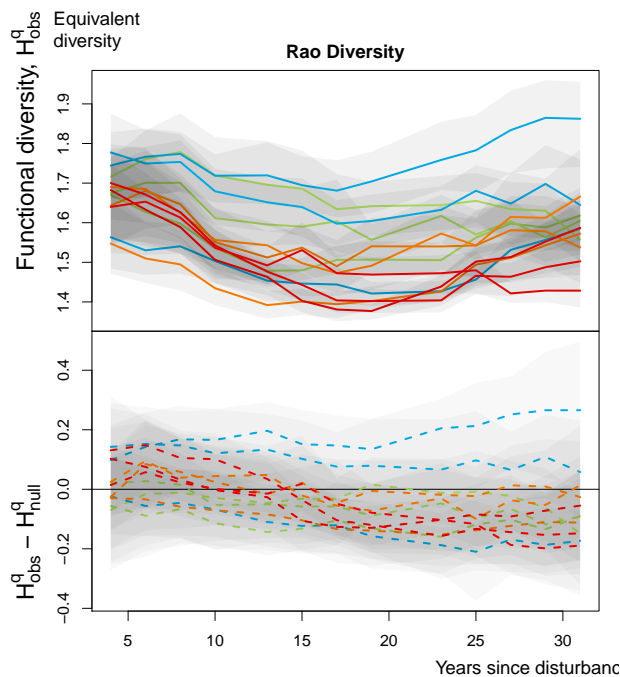


Figure 2. Functional diversity of punctual recruited trees from the considered functional traits and divergence to null model. Values reported correspond to the plot-level median and the 95% confidence interval obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling processes and 50 run of the null model. Lines colors correspond to the logging treatment initially applied (green for control, blue for T1, orange for T2 and red for T3).

disturbance.

4. Discussion

We analyzed the trajectories followed by the composition, diversity, and functional characteristics of trees recruited after disturbance to highlight the response of tropical forests and determine their resilience and help future conservation strategies. The 30 years-long monitoring analysed allowed to identify the different steps of forests recovery and the corresponding assembly rules. We identified two distinct phases, the first corresponding to the recruitment of pre-disturbance saplings that reflected the diversity and composition of the stand in place, and the second driven by “true recruits” germinated from the seed bank after disturbance. The second phase involved environmental selection and progressive competition among species according to the disturbance intensity, which build recruited communities divergent from the initial stand persisting in the long term.

4.1 On the underlyings of the hump-shaped trajectories

The trajectories of punctual recruitment richness, of some key functional traits (SLA and bark thickness) and of species turn-over exhibited hump-shaped, unimodal trajectories.

The recruitment for 10-15 first years after disturbance did not substantially differ from this of control plots. Recruitment trajectories were driven by the growth of pre-disturbance saplings benefiting from the environmental changes and alleviated competition following disturbance (Hérault *et al.*, 2010). The functional diversity of the recruitment remained stable after low disturbance intensity, equating these of control plots and matching stochastic recruitment processes. After intense disturbance, this phase

Punctual recruits CWM

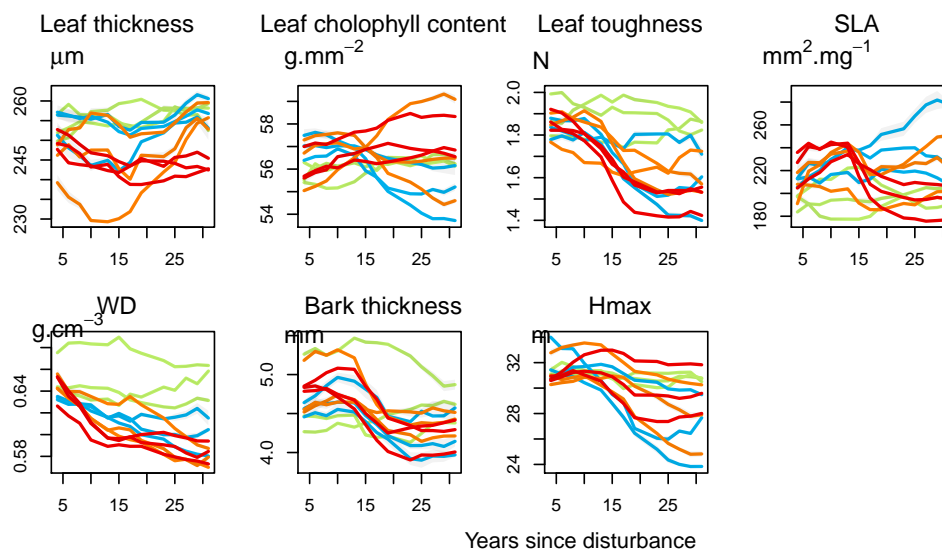


Figure 3. Community weighted means (CWM) of the four disturbance treatment for the four leaf traits, the two stem traits and the specific Hmax. Values reported correspond to the plot-level median obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling processes. Lines colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3).

brought sharp increases in the SLA, wood density and leaf thickness trajectories. This tendencies revealed prominent recruitment, above an intensity threshold, of short-lived, fast growing *hard pioneers* species with competitive and efficient light acquisition (Figure 4) (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011; Reich, 2014).

Following this first phase, the recruitment progressively incorporated true recruits, *i.e.* trees germinated from the seed bank, resulting in a decrease of recruited trees evenness and functional diversity. A restriction in the pool of species was then recruited, following an interplay between deterministic processes excluding less competitive and stress-tolerant species, and stochastic recruitment as in mature forests that progressively emerged again. The balance between both processes was determined by the intensity of the initial disturbance. After low disturbance intensity (T1 plots), the taxonomic composition of the recruitment resembled the pre-disturbance communities but pool of recruited species was restricted by selective pressures on the strategy of resource use. Favored species were 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). Correspondingly the functional diversity increased, equating or exceeding this of control plots, which revealed an overdispersion of the functional traits that was probably driven by the limitation of functional similarity among species. Despite some competitive exclusion then, recruited species still browsed a large functional range with no high dominance of hard pioneers (Hubbell *et al.*, 1999; Sheil & Burslem, 2003; Bongers *et al.*, 2009). This might due to recruitment and dispersal limitation due to the short dispersal distance observed for tropical trees, specifically in Paracou with the

Recruitment specific turnover compared to initial

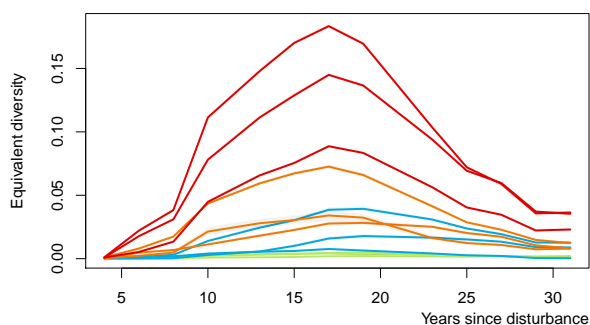


Figure 4. Trajectories over the 30 sampled years of the abundance-based turnover between recruited trees and initial communities before disturbance. Grey envelopes correspond to the 0.025 and 0.975 percentiles of the uncertainty propagation procedure and lines to the median in green for control, blue for T1, orange for T2 and red for T3).

genetic clumping of some pioneers (Leclerc *et al.*, 2015; Scotti *et al.*, 2015). After intense disturbance however, the first species recruited were hard pioneers, which taxonomic composition highly differed from the initial community and that generated a sharp increase for the SLA and bark thickness weighted values. This was observed for 15 years after disturbance, which corresponds to the life expectancy of hard pioneers, before the functional diversity increased again, acquisitive functional still dominating, and the recruited trees progressively resembled the initial composition and diversity. Communities trajectories then involved the interplay between stochastic recruitment and deterministic processes and advocated the role of disturbance to maintain forests diversity, in line with the Intermediate Disturbance Hypothesis (Molino & Sabatier, 2001; Sheil & Burslem, 2003).

4.2 On the resilience of the recruitment process

Both recruitment richness and functional diversity had recovered thirty years after all disturbance intensity, reaching equivalent levels as those of undisturbed forests. At that time though the recruitment remain more important in disturbed plots and did not match the richness and evenness of stochastic recruitment. However the divergence from stochasticity progressively shrunked, arguing for a consistent but long-term recovery of the recruitment process. These processes eventually made the recruitment converging towards the initial state, with the recruited species durably mirroring the pre-disturbance community. More than commonly thought, the taxonomic trajectories therefore depended on the pre-disturbance ecosystem characteristics and leads to maintain the initial differences among communities (Anderson, 2007; Hérault & Pioniot, 2018). In contrast the trajectories of traits and functional diversity were essentially similar among treatments, arguing for the confluence of communities in the functional space despite their divergence in taxonomic composition (Fukami *et al.*, 2005).

The taxonomic and functional characteristics of tropical forests were both resilient, even if the settlement of long lived pioneers after intense disturbance make a long term process of their recovery and still impact communities functioning and diversity 30 years after disturbance. This confirms previous results from the Paracou experiment, conducted 10 years (Molino & Sabatier, 2001) and 20 years (Baraloto *et al.*, 2012) after disturbance, which suggested the resilience of taxonomic and functional composition.

The time length of the recovery processes entails great caution regarding the forest conservation and exploitation guidelines which should allow a complete recovery of pre-disturbance conditions. To that was added the involvement of the seed bank in the recovery processes which own resilience remains unknown. Any storage effect, altering the pool of recruitable species, would modify the resilience of the community itself and impact the response to further disturbance events (Norden *et al.*, 2009). In such case, the competitive exclusion among dormant life-stage (seeds or even seedlings) would be harsher and likely bring more radical changes in the recruitment composition and functional profile of the community.

5. Conclusion

The 30 years monitoring of the Paracou plots highlighted the tropical forests' response to disturbance composed of two recruitment phase modulated by the disturbance intensity. In the short-term forests response was driven by the enhanced growth of grown saplings benefiting from the alleviated competition and the environmental changes. Above an intensity threshold the recruitment was besides dominated by hard-pioneers radically changing the recruitment composition, diversity and, likely, functioning. In the long-term response was driven by recruits from the seed bank which underwent dselection towards light demanding species and similarity limitation enhancing the functional diversity. These deterministic processes followed a gradual balance with the stochastic recruitment of mature forests which eventually restored communities diversity and composition, maintaining their initial differences. Although forests proved resilient to intense disturbance this appeared to be a long-term processes likely only valid for single disturbance events.

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