

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 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 (Dezecache *et al.*, 2017; Dezecache *et al.*, 2017) to more insidious changes of communities structure, diversity and functioning following anthropogenic activities like selective logging (Baraloto *et al.*, 2012; Hérault & Gourlet-Fleury, 2016) or climate change (Aubry-Kientz *et al.*, 2015). In that respect a vast literature successfully modeled communities response to disturbance in terms of tree growth (Gourlet-Fleury & Houllier, 2000), tree height (?), carbon stocks and fluxes (Putz *et al.*, 2012; Martin *et al.*, 2015; Piponiot *et al.*, 2016). Similar approaches regarding forest composition and diversity, however, have been hindered by the huge biological diversity, often focusing on common or mainly commercial species, and the scarcity

of long-term monitoring (Sebbenn *et al.*, 2008; Rozendaal *et al.*, 2010; Vinson *et al.*, 2015).

Communities trajectories after disturbance, defined here as the evolution of communities diversity along time, depend on the trees surviving from before disturbance and on the new trees recruited afterward (Hérault & Piponiot, 2018). Surviving trees proved to mirror the composition of pre-disturbance forest so communities' diversity response is driven by the diversity and composition of recruited trees, which build the future community and determine the resilience of pre-disturbance state. Recruitment trajectories depend first on the composition and diversity of initial community that partly condition the available pool of recruited species (Hérault & Piponiot, 2018). Then trajectories depend on recruitment processes either stochastic, like random dispersal, recruitment and death (Hubbell, 2001), or deterministic like niche-based competition processes (Adler *et al.*, 2007) While stochastic processes would build communities similar to random samples of larger regional meta-communities, deterministic processes rely on the abiotic environment and filter-out recruited species according to their ecology. Understand communities response to disturbance comes back first to estimate the balance between these determinants, the initial composition and the different recruitment processes, and then to elucidate communities resilience and the maintenance of the initial differences among local communities (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017).

The processes shaping communities response will differently affect the functional diversity (Kunstler *et al.*, 2016), that considers species functioning and ecology (?), and the taxonomic diversity, which consider all species equal. The coupling between functional and taxonomic trajectories will then be insightful for the identification of ecological processes at stake, and communities resilience should be addressed considering both functional and taxonomics characteristics (Fukami *et al.*, 2005). Functional trajectories of

recruited trees are shaped by the deterministic processes that are oriented towards the use of limiting resources. Recruitment processes will then either filter-out the less efficient functional strategies and restrict the functional diversity, or exclude the less competitive ones and increase the functional diversity through the competition among species and limitation of their functional similarity (Ackerly, 2003; McGill *et al.*, 2006). The disturbance response of tropical forests where the light is limiting would then be a shift from slow-growing, long-living species with “conservative” resource use to fast growing, resource “acquisitive” species (Denslow, 1980; Molino & Sabatier, 2001; Bongers *et al.*, 2009). To detect these processes the large functional trait-based literature identified key leaf, wood and life-history functional traits assessing species ecology and resources acquisition strategy (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011).

In this paper we follow the fate of a recruited tree communities (60121 individuals) over 30 years on a large disturbance gradient, with 10 to 60% of forest biomass removed. We assess the taxonomic and functional diversity of recruited trees, using a large functional trait database covering the leaf, wood and life-history spectra. We compare the observed trajectories to null models representing random trees recruitment and randomized functional traits. We aimed (i) to 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 degree of 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. These changes in identification protocol raised methodological issues as vernacular names usually correspond to dif-

ferent 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.

Eight functional traits were considered, representing leaf economics (leaves thickness, toughness, total chlorophyll content and specific leaf area), wood economics (wood specific gravity and bark thickness) and life history traits (maximum specific height and seed mass). 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). As traits variability was lower within genus and families, 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 so analysis were performed only considering the 414 botanical species of the seed mass dataset.

2.3 Recruitment trajectories

To disentangle the recruitment processes from overall dynamics, communities were split into per-disturbance surviving trees and those recruited since disturbance. 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 area.

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 and 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). Seed mass trajectories were reported by the proportion of each class recorded in the inventories. The similarity between the recruited trees and the pre-disturbance forest was measured with the turnover metrics detailed in Podani *et al.* (2013). To estimate the importance of stochastic processes

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%]

the recruitment was compared to the trajectories of a random sampling. For the taxonomic trajectories the random sampling was a shuffle of trees among plots that preserved species abundance and tree density, and for the functional diversity it was a shuffling of functional trait values among species.

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

3. Results

3.1 Recruitment Diversity

3.1.1 Taxonomic Diversity

The diversity trajectories of punctual recruitment followed a consistent trajectory after disturbance with first 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).

Punctual and accumulated recruitment diversities were then compared to the stochastic trajectories of a random sampling. Richness (order 0) and evenness (order 2) of punctual recruits remained equivalent or higher than for a random sampling in control plots while both were lower in disturbed plots. Disturbed plots however 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 the random sampling after low disturbance intensity (plots T1 and some plots T2) but lower after intense disturbance (plots T3 and a plot T2, Appendix I fig. S1).

3.1.2 Functional Diversity and Composition

Communities functional diversity was measured with the Rao diversity and compared to the stochastic trajectories of

a random traits shuffling. In disturbed plots (T2 and T3), the functional diversity decreased until 15 years after disturbance (Figure 2) before recovering towards the initial values. While the recovery was not achieved for the most disturbed plots, the functional diversity of lighter disturbance plots recovered faster and for some T1 plots exceeded the initial values. For all plots, disturbed or not, 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) with smaller maximum height (Figure 3). Functional traits either followed hump-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 recruits. In disturbed plots, the taxonomic turnover followed a marked hump-backed trajectory, with a maximum value reached around 15 years after disturbance and a maximum positively correlated to the disturbance intensity ($\rho_{\text{Spearman}} = 0.93$). Thirty years after disturbance the turnover of all disturbed plots had return to low values close to zero.

4. Discussion

The composition, diversity, and functional trajectories in post-disturbance times were analysed in the Paracou station to determine the determinants of forests response to disturbance and their resilience. The 30 years-long monitoring identified two distinct recruitment phases, first defined by the stochastic recruitment of already grown saplings and then driven by ecological rules restricting the pool of recruited species on the basis of their functional strategy. The second phase changed the functioning and diversity

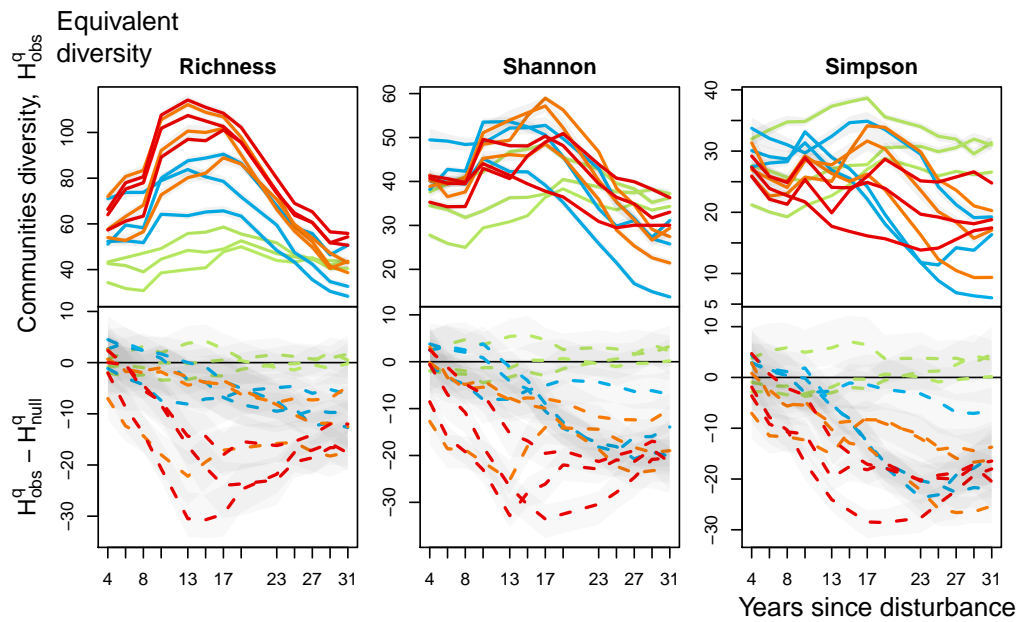


Figure 1. Trajectories of Richness, Shannon and Simpson diversity for 2-years laps punctual recruitment (upper panels) and divergence to null model (lower panels). Lines colors refer to the perturbation regime: green for control, blue for T1, orange for T2 and red for T3 disturbance treatments. Plain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

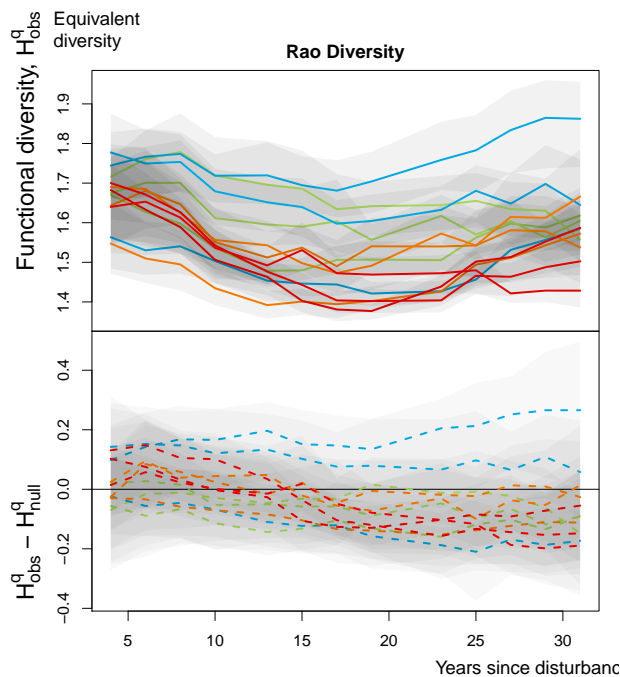


Figure 2. Functional diversity of punctual recruited trees from the considered functional traits and divergence to null model. Values reported correspond to the plot-level median and the 95% confidence interval obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database 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).

of communities for more than 30 years after disturbance, disclaiming communities functioning.

4.1 On the underlyings of the hump-shaped trajectories

The trajectories of recruitment richness, key functional traits (SLA and bark thickness) and the species turnover exhibited clear hump-shaped, unimodal trajectories.

Trees recruited in the first place (0-8 years) resembled the pre-disturbance communities and their functional diversity matched this of a stochastic recruitment process. This first recruitment phase likely involved already grown saplings (DBH <10cm) that germinated before disturbance and immediately benefitted from the increased enlightenment and the alleviated competition following disturbance (Héroult *et al.*, 2010).

Then during a second phase the evenness and the functional diversity of recruited trees decreased, translating a more restricted pool of recruited species based on their functional strategy. Following intense disturbance, sharp changes in the SLA, wood density and leaf thickness trajectories then revealed the prominent recruitment of short-lived, fast growing hard pioneers species with competitive and efficient light acquisition (Figure 2 (fig:Turnover)) (Wright *et al.*, 2004; Chave *et al.*, 2009; Héroult *et al.*, 2011; Reich, 2014).

The second phase therefore likely incorporated true recruits, *i.e.* trees germinated from the seed bank, submitted to deterministic recruitment processes excluding the least competitive species. Along time diversity trajectories returned towards the initial state and matched the values of stochastic recruitment, reflecting a decreasing importance of the deterministic recruitment processes. The balance between deterministic and stochastic processes was determined by the ini-

Punctual recruits CWM

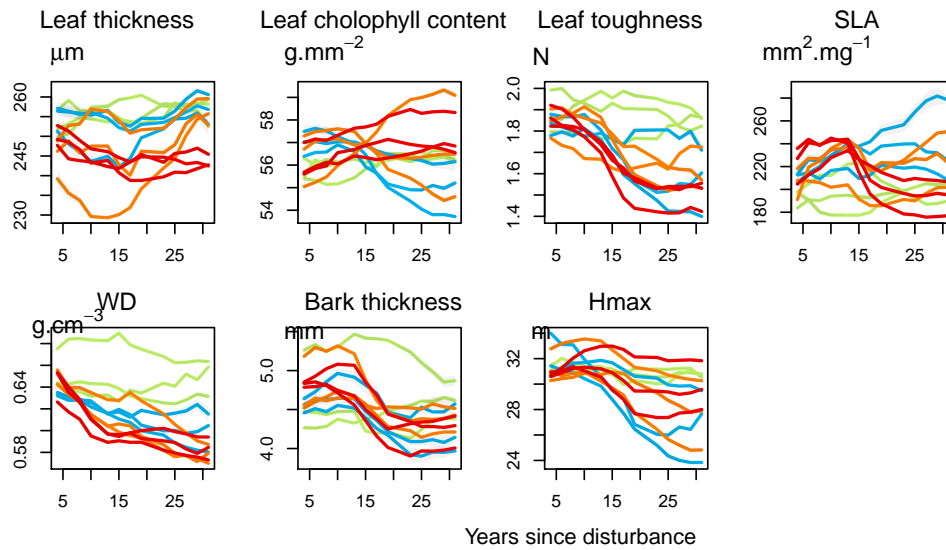


Figure 3. Community weighted means (CWM) of the four disturbance treatment for the four leaf traits, the two stem traits and the specific Hmax. Values reported correspond to the plot-level median obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling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

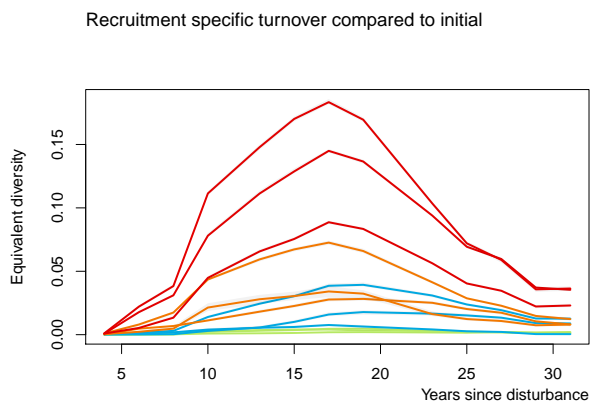


Figure 4. Trajectories over the 30 sampled years of the abundance-based turnover between recruited trees and initial communities before disturbance. Grey envelopes correspond to the 0.025 and 0.975 percentiles of the uncertainty propagation procedure and lines to the median in green for control, blue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

tial disturbance intensity. After light disturbance (T1 plots), the recruitment matched the composition of the initial communities but the pool of recruited species was restricted by the competitive exclusion for resources. dominant 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). Although competitive exclusion decreased the functional diversity of recruited trees, their evenness remained high, so there was no high dominance of hard pioneers (Hubbell *et al.*, 1999; Sheil & Burslem, 2003; Bongers *et al.*, 2009). This might be due to recruitment and dispersal limitation due to the short dispersal distance observed for tropical trees, specifically in Paracou with the genetic clumping of some pioneers (Leclerc *et al.*, 2015; Scotti *et al.*, 2015). After intense disturbance however, the recruitment composition rapidly differed from the pre-disturbance state and corresponded to a sharp increase for the SLA and bark thickness CWM, likely reflecting the overwhelming recruitment of hard pioneers. This recruitment lasted for 15 years after disturbance, that is the life expectancy of hard pioneers, and was followed by a progressive increase of the functional diversity. The recruitment remained dominated by acquisitive functional strategies but the initial composition and diversity progressively recovered. Communities trajectories involved an interplay between stochastic and deterministic recruitment, advocating that disturbance effectively maintains forest diversity (Molino & Sabatier, 2001; Sheil & Burslem, 2003).

4.2 On the resilience of the recruitment process

After 30 years, although taxonomic and functional diversity had recovered initial values, the recruitment rates remained

higher and the processes did not match the stochastic recruitment observed in undisturbed plots. Recruitment processes might then be consistently resilient, despite the settlement of long-lived pioneers after intense disturbance, but slow to recover.

The recovery of recruitment processes involves the convergence of communities towards the initial state. More than commonly thought, the ecosystem trajectories in the taxonomic space would depend on the pre-disturbance ecosystem characteristics and this concur to maintain the initial taxonomic differences among local communities (?). 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). This confirms 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. The time length, i.e. several decades, of the recovery processes entails great caution regarding the forest conservation and exploitation guidelines if the pursued objectives are a complete recovery of pre-disturbance ecosystem properties.

????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 selection 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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