

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. In that respect a vast literature has successfully modeled the response of tropical forest dynamics, carbon stocks and fluxes to anthropogenic and natural disturbances (Gourlet-Fleury & Houllier, 2000; Putz *et al.*, 2012; Martin *et al.*, 2015; Pioniot *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). Forest dynamics, though, result from the constantly evolving interactions and feedbacks among trees and their environment and requires to encompass complete communities (de Avila *et al.*, 2016). Forests response to disturbance is build on

the recruitment of new individuals and on the mortality of disturbance survivors. As disturbance survivors proved to mirror the pre-disturbance forest composition (Hérault & Pioniot, 2018), the recruitment composition and dynamics is the key to elucidate the future of tropical forest in a changing global environment. This would give insights into the resilience of hyperdiverse tropical forest ecosystems, elucidate the determinism of tropical forests trajectories and their convergence towards initial states and eventually help future adaptative conservation strategies (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017).

Recruitment result from the interplay of stochastic processes like random dispersal, recruitment and death (?) and niche-based deterministic processes (?). The latter, relying on communities abiotic environment, exclude species according to their tolerance to stress or to the competition for resources that limits functional similarity (Ackerly, 2003; McGill *et al.*, 2006). These deterministic processes along with the patchy variability of environmental conditions in space and time would then explain the maintenance of tropical forests biodiversity according to the Intermediate Disturbance Hypothesis (IDH) (Guitet *et al.*, 2018). Disturbance would maintain large ecological range of species in the community, 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). Specifically, in tropical wet forests changes in light availability after disturbance enhance the recruitment of pioneers and light-demanding species to the contrary of mature forests dominated by more competitive shade bearers. Empirical tests of the IDH in tropical rainforests, though, proved hard to succeed and yielded controversial results (Hubbell *et al.*, 1999; Molino & Sabatier, 2001; Sheil & Burslem, 2003).

The recruitment processes would be identified through the divergence of trait diversity patterns within communi-

ties to random species and traits samples. An selection of species based in their ecology and stress-tolerance would reduce the communities trait diversity while an overdispersion of functional traits translates the exclusion of species using shared resources and a limitation of similarity. The subsequent shift from resource-acquisitive to resource-conservative ecological strategies may be detected in leaves (leaf thickness, toughness, chlorophyll content and specific area) and stem (wood specific gravity and bark thickness) functional traits and in 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).

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, i.e. trees that survived the disturbance, and post-disturbance recruited trees. Two recruitment metrics were examined: on the one hand the ‘punctual recruitment’ by 2-year intervals after disturbance, on the other hand all recruited trees since disturbance, hereafter ‘accumulated recruits’. 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 pure 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 window allowing to mitigate the heterogeneity of inventory protocols between years.

3. Results

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%]

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 (Appendix I, fig. S1).

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 disturbance.

4. Discussion

4.1 On the underlyings of the hump-shaped trajectories

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

The 10-15 first years of these trajectories seemed driven by the growth of pre-disturbance saplings benefiting from the environmental changes and alleviated competition that follow disturbance (Héroult *et al.*, 2010). After low disturbance intensity this translated into a stable functional diversity of the recruited community, equivalent to these of control plots shaped by stochastic recruitment processes. After intense disturbance, this phase 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; Héroult *et al.*, 2011; Reich, 2014).

Following this first phase, the recruitment progressively incorporated true recruits, *i.e.* trees germinated from the seed bank after disturbance. The resulting trajectories were shaped by the interplay between deterministic processes,

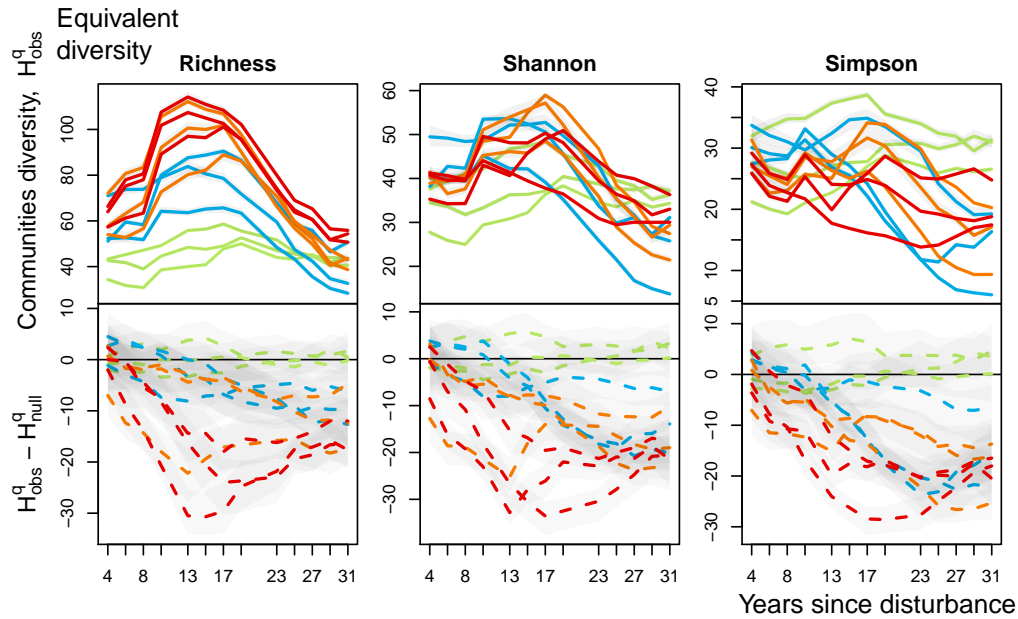


Figure 1. Trajectories of Richness, Shannon and Simpson diversity for 2-years laps punctual recruitment (upper panels) and divergence to null model (lower panels). Lines colors refer to the perturbation regime: green for control, blue for T1, orange for T2 and red for T3 disturbance treatments. Plain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

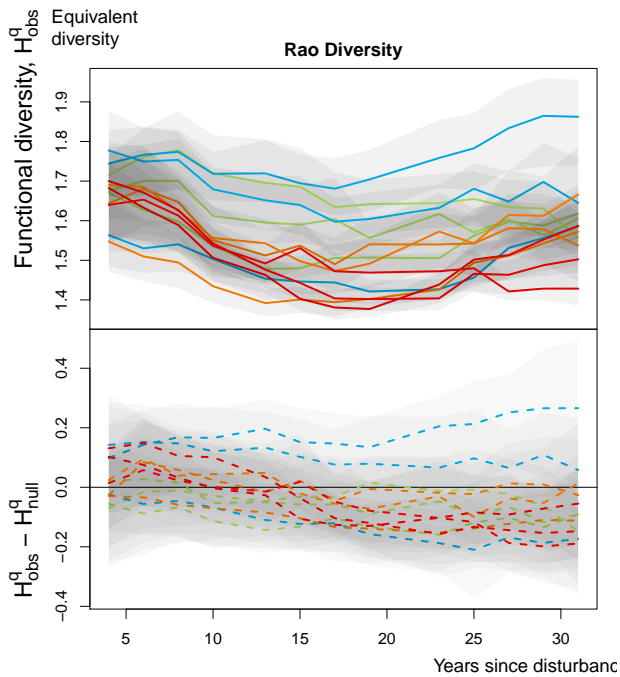


Figure 2. Functional diversity of punctual recruited trees from the considered functional traits and divergence to null model. Values reported correspond to the plot-level median and the 95% confidence interval obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database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

excluding stress-intolerant and uncompetitive species, and mature forests-like stochastic recruitment that progressively emerged again. The balance between both processes resulted in different trajectories according to the disturbance intensity.

After low disturbance intensity (T1 plots), although the taxonomic composition of the recruitment resembled the pre-disturbance composition the pool of recruited species was more restricted and evenly distributed. These restrictions revealed selective pressures favouring pioneers and light demanding species with efficient resource acquisition (high SLA and leaf chlorophyll content) and inexpensive, short-lived tissues (low leaf thickness and toughness, small H_{max} and low wood density and bark thickness). In parallel the recruitment's functional diversity increased, equating or exceeding this of control plots, revealing an overdispersion of functional traits driven by the limitation of similarity. At this disturbance intensity, recruitment seemed preserved from the competitive exclusion of hard pioneers which would have prevented the maintenance of inferior competitors in the community and have lowered the functional diversity (Hubbell *et al.*, 1999; Sheil & Burslem, 2003; Bongers *et al.*, 2009). The low dominance of hard pioneers might result from 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). The consistent interplay between stochastic recruitment and deterministic processes advocated the role of low intensity disturbance to maintain forests diversity, in line with the Intermediate Disturbance Hypothesis (Molino & Sabatier, 2001; Sheil & Burslem, 2003).

The trajectories after intense disturbance, first driven by the settlement of hard pioneers, matched afterward the same

Punctual recruits CWM

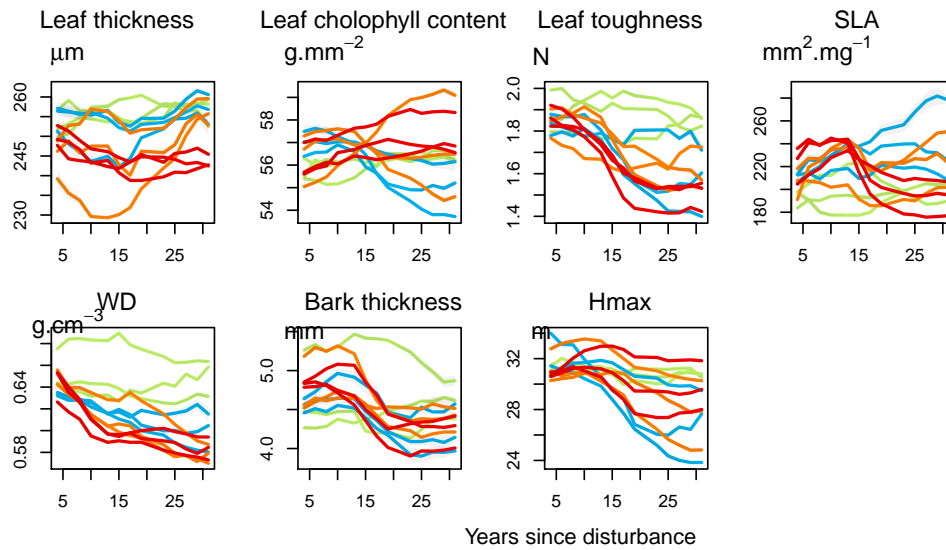


Figure 3. Community weighted means (CWM) of the four disturbance treatment for the four leaf traits, the two stem traits and the specific Hmax. Values reported correspond to the plot-level median obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling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

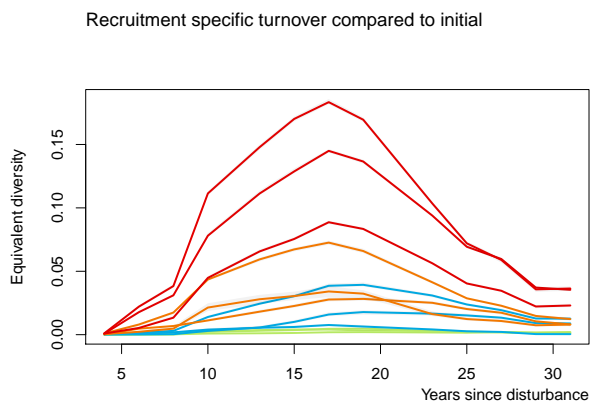


Figure 4. Trajectories over the 30 sampled years of the abundance-based turnover between recruited trees and initial communities before disturbance. Grey envelopes correspond to the 0.025 and 0.975 percentiles of the uncertainty propagation procedure and lines to the median in green for control, blue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

progressive balance between deterministic and stochastic processes. This translated by a progressive decrease of recruitment taxonomic turnover and an increase of functional diversity. Although acquisitive strategies remained dominant (high leaf chlorophyll content and low wood density and leaf toughness), the weighted values of other traits stabilized and the SLA and bark thickness decreased again (then following a unimodal trajectory with a peak after the first recruitment phase). The 15 years laps of the unimodal turnover and traits trajectories corresponding to the first recruitment phase matched the life expectancy of hard pioneers and of their competitive pressure. The recruitment would progressively shift towards long-lived pioneers, that participate to forest recovery as they might have been part of pre-disturbance communities, but still hold dominant more acquisitive functional strategies.

4.2 On the resilience of the recruitment process

For all plots the richness and functional diversity of recruitment had recovered thirty years after disturbance to levels equivalent as those observed short after disturbance and in control plots. In contrast the species distribution evenness and functional diversity of recruited trees remained lower than initial and control values, revealing similar but unachieved trajectories as those of other plots.

Still, for all treatments recruitment processes were restored, matching the stochastic recruitment of mature forests. Besides, whatever the disturbance intensity, the recruitment turnover between recruited and pre-disturbance communities ended up close to zero. More than commonly, then, the taxonomic recovery trajectories would depend on the pre-disturbance ecosystem characteristics and maintain the initial taxonomic differences among communities (Anderson, 2007; Hérault & Piponiot, 2018). In contrast the functional

diversity and traits trajectories essentially followed a common trajectory among treatments, supporting communities convergence in the functional space despite their divergence in taxonomic composition (Fukami *et al.*, 2005).

This makes these communities both functionally and taxonomically resilient despite the settlement of long lived pioneers, which make a long term process of recovery for high disturbance intensity as evidenced by the persistent impact on traits and diversity trajectories. Our results extend previous ones from the Paracou experiment, 10 years (Molino & Sabatier, 2001) and 20 years (Baraloto *et al.*, 2012) after disturbance which already suggested the resilience of taxonomic and functional composition.

These conclusions however only hold for a single disturbance event, given the involvement of the seed bank triggering a storage effect likely to modify the resilience of the community (Norden *et al.*, 2009). In this hypothetical 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 Paracou plots highlighted contrasting recruitment trajectories determined 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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