

30 Years of Recruitment in Tropical Forest After Selective Logging

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Abstract

Résumé de l'article.

Mots-clés

mot-clés, séparés par des virgules

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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. A vast literature has successfully modeled the response of tropical forest dynamics, carbon stocks and fluxes to anthropogenic and natural disturbances (Gourlet-Fleury & Houl-
lier, 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 as-
semblages, 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 could therefore only
be assessed through a complete community-scale approach
(de Avila *et al.*, 2016).

Key to understand communities response to disturbance
is to identify the processes shaping the composition and
diversity of recruited trees. Forests dynamics stem from the
suit of recruitment process from seed production, dispersion
and germination to seedlings' and saplings' growth until
the adult stage. Recruitment mechanisms result from the
interplay of deterministic environmental processes, like the
exclusion of stress-intolerant species or the limitation of sim-
ilarity through resource competition (Ackerly, 2003; McGill
et al., 2006), and stochastic processes like random disper-
sal, recruitment and death (?). The deterministic processes
are inherently linked to disturbance regime which locally
changes ecosystem's biotic and abiotic conditions and main-
tains species able of efficient acquisition of resource but
living shortly and poorly resistant to hazards and diseases
(Denslow, 1980). They rely on the Intermediate Distur-
bance Hypothesis (IDH) that explains the maintenance of
tropical forests biodiversity by the patchy variability of envi-
ronmental conditions in space and time (Guitet *et al.*, 2018).
Specifically, in tropical wet forests changes light availability
has a central role enhancing the recruitment of pioneers and
light-demanding species after disturbance compared to ma-
ture stands where more competitive shade bearers dominate.
Disturbance then enlarges the ecological range of species in
the community (Molino & Sabatier, 2001; Bongers *et al.*,
2009) and shapes their taxonomic diversity, vegetative struc-
ture, physiology as well as carbon, nutrients, and water
cycles (Anderson-Teixeira *et al.*, 2013). >>(on parle plus
vraiment de IDH maintenant) 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).

During post-disturbance times, the shift from resource-
acquisitive to resource-conservative ecological strategies
may be detected in leaves (leaf thickness, toughness, chloro-
phyll content and specific area) and stem (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). The relative importance of recruitment of new individuals and of mortality of disturbance survivors will shape the new forest and its functioning. Given that disturbance survivors largely mirror the pre-disturbance forest composition (?), predicting the recruitment composition and diversity trajectories would be a major step towards the prediction of the future of tropical forest in a changing global environment where disturbance are expected to become more and more frequent. This would give insights into the resilience of this hyperdiverse ecosystems, elucidate the determinism, or not, of tropical forests trajectories, test the convergence after disturbance of taxonomic and functional communities towards initial state and also help future adaptative conservation strategies (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017).

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 aimed to (i) assess the role of environmental filtering selecting the recruited trees according to their competitiveness for resource acquisition, (ii) resolve the convergence of communities and the maintenance of taxonomic composition in the long term, and (iii) determine the global 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 (X%) were filled using multivariate imputation by chained equation (mice) restricted to samples pertaining to the next higher taxonomic level, in order to account for the phylogenetic signal of the functional traits (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; *et al.* Garnier, 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 uncertainty propagation (taxonomy and trait values).

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. While in control plots the richness and evenness of punctual recruits remained equivalent or higher than for the null random model (Figure 1), it was significantly lower for all disturbed plots all along the monitoring period. Accumulated recruitment richness (order 0) and evenness (order 2) 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

From the 30 years of forest dynamics survey in the Paracou station, we highlighted contrasting recruitment patterns depending on disturbance intensity. Disturbance increased the recruitment rate and thus also the richness of recruited trees but in contrast impaired the recruitment evenness, all the more so that disturbance intensity was high. Post disturbance recruitment underwent significant selective pressure in favour of acquisitive functional strategies, which steered the diversity trajectories away from random processes and restricted the pool of recruited trees that did not reflect the initial stand composition, unlike the recruitment of control plots. The most intense disturbance induced strong species selection that changed the recruitment rules and marked plots composition and diversity for more than 30 years while less disturbed plots displayed a faster recovery.

4.1 On the underlyings of the hump-shaped trajectories

The punctual recruitment richness, some key functional traits (SLA and bark thickness) and the species turn-over trajectories exhibited hump-shaped, unimodal trajectories. The 10-15 first years of these trajectories seemed driven by the growth of pre-disturbance saplings benefitting from the environmental changes and alleviated competition following disturbance (Herault *et al.*, 2010). This translated first by

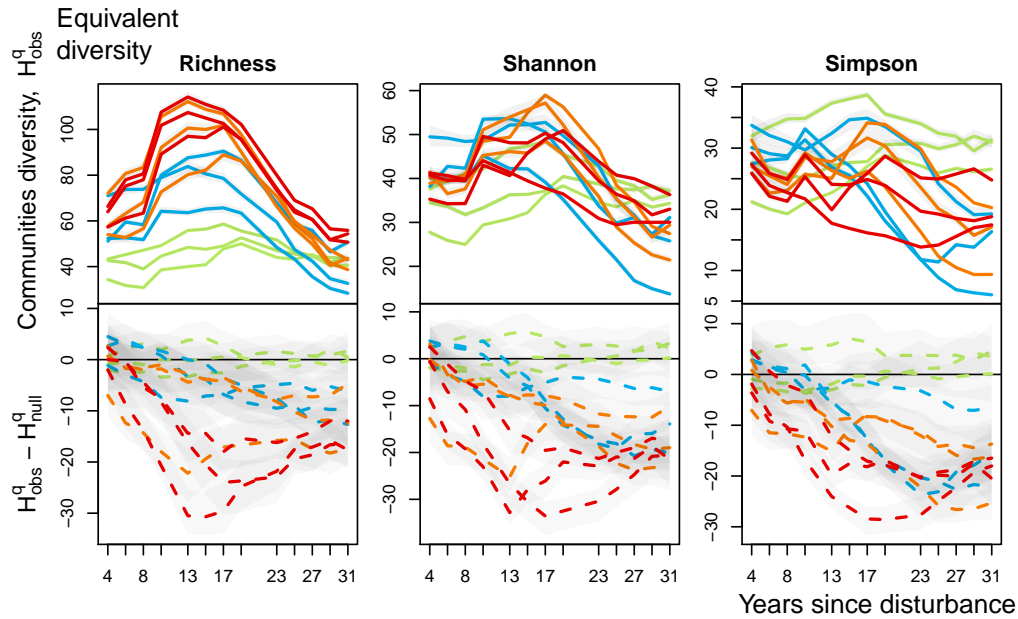


Figure 1. Trajectories of Richness, Shannon and Simpson diversity for 2-years laps punctual recruitment (upper panels) and divergence to null model (lower panels). Lines colors refer to the perturbation regime: green for control, blue for T1, orange for T2 and red for T3 disturbance treatments. Plain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

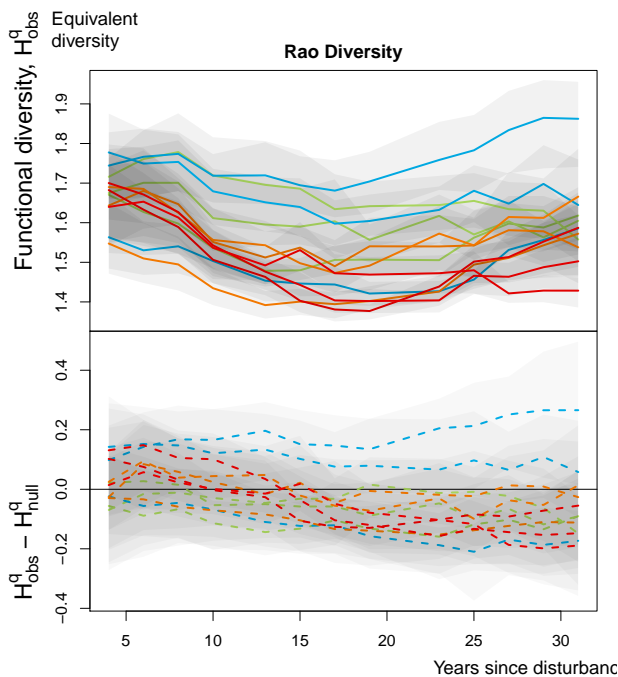


Figure 2. Functional diversity of punctual recruited trees from the considered functional traits and divergence to null model. Values reported correspond to the plot-level median and the 95% confidence interval obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database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

a stable functional diversity of the recruitment, equivalent as this of control plots, and low difference to random null model, specifically for low disturbance intensities. After the most intense disturbance this translated by a sharp increase of SLA and bark thickness values reflecting the dominance of short-lived pioneers capable of effective light acquisition and fast growth (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.* individual trees that had germinated after the disturbance, which underwent competition for light resources. Different trajectories were then observed according to the disturbance intensity. In the case of low disturbance intensity (T1 plots), although the recruitment resembled the pre-disturbance species composition, it displayed decreasing evenness compared to control plots and random models. This revealed selective pressures and competition for resources leading to an increase in functional diversity, equating or exceeding this of control plots, and an overdispersion of functional traits compared to a null random model. This competition benefited pioneers and light demanding species preserved from the overwhelming settlement of hard pioneers by recruitment limitation (Hubbell *et al.*, 1999; Sheil & Burslem, 2003; Bongers *et al.*, 2009). Recruitment limitation of hard pioneers that mitigated competitive exclusion and maintained inferior competitors in the community, would be consistent with 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).

In the case of high disturbance intensity, the species turnover remains very high after the initial 10 year phase and the functional diversity decreased sharply towards a restricted range of acquisitive functional strategies.

Punctual recruits CWM

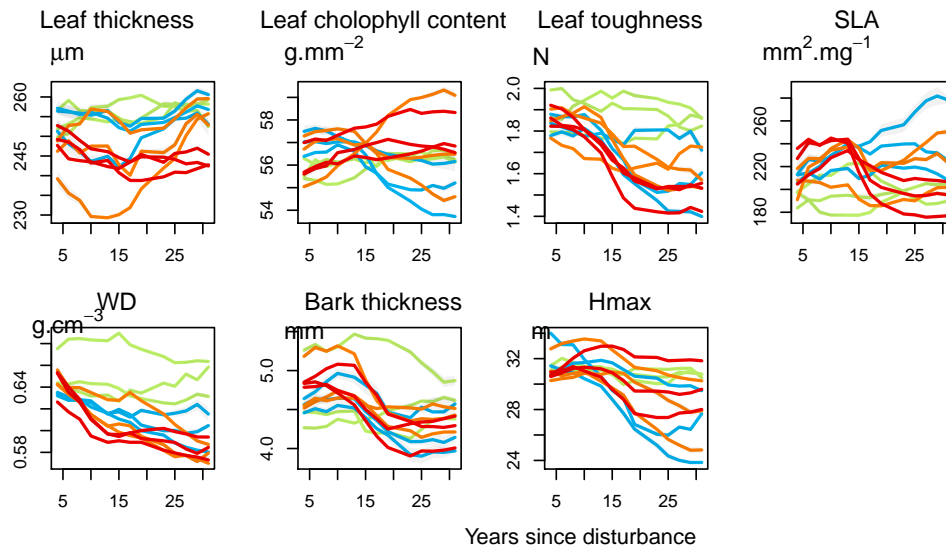


Figure 3. Community weighted means (CWM) of the four disturbance treatment for the four leaf traits, the two stem traits and the specific Hmax. Values reported correspond to the plot-level median obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling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

This translated by a decrease in leaf toughness, Wood Specific Gravity and Hmax from the incorporation of long-lived pioneers.

4.2 On the resilience of the recruitment process

Thirty years after disturbance, recruitment functional diversity and richness had recovered equivalent levels as those observed for the plots short after after disturbance and equivalent to those of control plots. The functional and taxonomic composition of the recruitment and the evenness of recruited species distribution, though, remained lower for all disturbed plots, along with and weighted means of all functional traits was remained altered thirty years after disturbance. Would this mean that ecosystem functioning recover faster than taxonomic composition? The link between functional traits and ecosystem functioning is not trivial but our results may highlight the key role of functional redundancy in ecological systems and also suggest. >> that the recovery trajectory may be, more than commonly thought, upon dependence of the pre-disturbance functional ecosystem signature (Héroult & Pioniot, 2018). -> What makes us say that?

Whatever the disturbance intensity, the recruitment turnover compared to initial stand ended up close to zero. This argued for the high dependence of the composition recovery trajectory on the pre-disturbance ecosystem characteristics (Anderson, 2007). In other words, initial compositional variation caused tree communities to remain divergent in taxonomic composition, even though these same tree communities strongly converged in functional space (Fukami *et al.*, 2005). This makes these communities both functionally and taxonomically resilient despite the settlement of long lived pioneers which make it a long term process for high disturbance intensity. >> Not that much because the

Recruitment specific turnover compared to initial

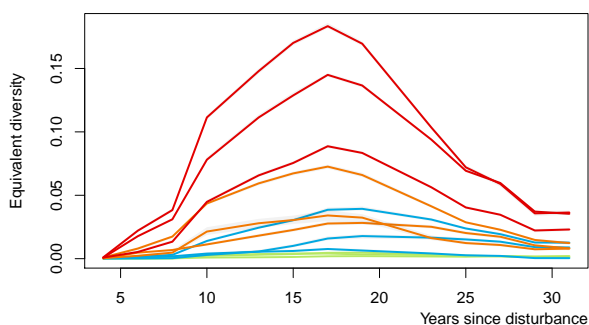


Figure 4. Trajectories over the 30 sampled years of the abundance-based turnover between recruited trees and initial communities before disturbance. Grey envelopes correspond to the 0.025 and 0.975 percentiles of the uncertainty propagation procedure and lines to the median in green for control, blue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

long lived pioneers probably remain long after disturbance, it would be in the long term.

Our results extend previous ones from the Paracou experiment, 10 years (Molino & Sabatier, 2001) and 20 years (Baraloto *et al.*, 2012) after disturbance that suggested the recovery towards pre-disturbance taxonomic and functional composition. This is however only valid for a single disturbance event, given that second recruitment phase assumed to rely on the seed bank triggers a storage effect likely to modify the recruitment trajectories in case of a new disturbance event. In this hypothetical case, the competitive exclusion among dormant life-stage (seeds or even seedlings) would be harsher and would bring more radical changes in the recruitment composition and functional profile.

5. Conclusion

Our long-term study of diversity trajectories after disturbance disentangled the mechanisms underlying the forest trajectory in the diversity space. While, in undisturbed forests, mechanisms like negative density dependence enhanced species diversity, disturbance induced new mechanisms depending on its intensity. In the short-term communities response was always driven by the enhanced growth of grown saplings benefitting from alleviated competition and low selective pressure resulting in increased communities taxonomic and functional evenness. In the long-term communities trajectory strongly depended on the disturbance intensity. At low intensity competition resumed to shape a functionally diversified and even community preserved from the over-whelming hard pioneers by recruitment limitation. For high intensity, strong environmental filters maintained high species turnover and a recruitment restricted to long lived pioneers. Communities composition and functioning proved consistently resilient to single disturbance events but the functional redundancy and the diversified seed bank of mature forests proved altered and consequently communities resilience themselves.

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