# 30 Years of Post-disturbance Recruitment in Tropical Forest

Ariane MIRABEL[1][*]
Eric MARCON[1]
Bruno HERAULT[2]

**Abstract**
Trees biodiversity is central for tropical forests functioning and services. In the current climatic and land-use changing context it is urgent to clarify the response of communities diversity and composition to disturbance. In that regard, recruitment processes as major driver of communities trajectories are suited to highlight their response to disturbance and the underlying processes. Recruitment trajectories would allow (i) disentangling neutral, stochastic and deterministic, selective processes they rely on, and (ii) specifying the competition rules involved in species selection, and finally (iii) resolving the duration and the completeness of recruitment processes. We examined the trajectories over 30 years of recruitment diversity and composition in 75 ha of a neotropical forest following a gradient of logging and thinning disturbance (from 15 to 60% of AGB removed). Specifically we analysed and compared to neutral models the recruitment trajectories in taxonomic richness, evennes, and compositional turnover compared to initial communities, and in Rao functional diversity integrating species ecology through 7 key functional traits. We evidenced three recruitment phases shaped by the gradual balance between stochastic and deterministic underlying processes. First, trajectories relied on the growth of saplings randomly recruited among the pre-disturbance community. Second, trajectories relied on *true recruits* germinated from the seed bank and depending on competitive exclusion processes favoring acquisitive, light-demandings species. Eventually an inversed balance progressively restored the stochastic recruitment observed in mature forests and drove a recovery of initial functioning and taxonomic structure. While the functional recovery of the recruitment was fast, the taxonomic recovery lasted for decades and prevented a complete resilience. Communities disturbance response combined stochastic processes, predominant before disturbance and progressively restored along time, and deterministic competition processes favoring light-demanding species. Although the taoxnomic and functional structure proved resilient, the taxonmic recovery was decades-long and called cautions regarding the time required for forest recovery and the completeness of communities resilience.

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

[1]UMR EcoFoG, AgroParistech, CNRS, Cirad, INRA, Université des Antilles, Université de Guyane.
   Campus Agronomique, 97310 Kourou, France.
[2]INPHB (Institut National Ploytechnique Félix Houphoüet Boigny)
   Yamoussoukro, Ivory Coast
[*]**Corresponding author**: ariane.mirabel@ecofog.gf, http://www.ecofog.gf/spip.php?article47

## Contents

## 1. Introduction

Determining the response of tropical forests to disturbance is key to predict their fate in the global changing context. In the last decades, tropical forests experienced a wide range of disturbance, from radical land-use changes for agriculture or mining (Dezécache *et al.*, 2017a,b) to more insidious changes of communities structure, diversity and functioning following climatic changes (Aubry-Kientz *et al.*, 2015) or anthropogenic activities like selective logging (Baraloto *et al.*, 2012; Hérault & Gourlet-Fleury, 2016). In that respect a vast literature successfully modeled communities response to disturbance in terms of tree growth (Gourlet-Fleury & Houllier, 2000), tree height (Rutishauser *et al.*, 2016), carbon stocks and water and nutrient fluxes (Putz *et al.*, 2012; Martin *et al.*, 2015; Piponiot *et al.*, 2016). However, similar approaches regarding forest diversity remain hindered by the scarcity of long-term monitoring and by the huge biological diversity constraining the analysis to focus on common or commercial species (Sebbenn *et al.*, 2008;

Rozendaal *et al.*, 2010; Vinson *et al.*, 2015).

Major insights on the response of forests diversity to disturbance and the underlying ecological processes would be given by the trajectories of tree communities along time. The structuring effects of determinant ecological processes might be confounded at the community scale (Chave, 2004) and would be clarified by decomposing the communities according to underlying demographic processes. Communities comprise on the one hand the trees surviving from before disturbance and on the other hand those recruited afterward (Hérault & Piponiot, 2018). Surviving trees obviously mirror the diversity and composition of pre-disturbance communities, so the dynamics and the resilience of communities would depend on the diversity of recruited trees. First, recruitment trajectories depend on the composition and diversity of the initial, pre-disturbance community as this conditions the pool of recruitable species via the existing saplings and seeds bank (Hérault & Piponiot, 2018). Trajectories besides depend on recruitment processes, either stochastic and driven only by recruitment and dispersal limitations (Hurtt & Pacala, 1995; Hubbell, 2001), or deterministic and driven by niche-based competition and biotic interaction (Adler *et al.*, 2007). Stochastic processes, translating Hubbell's neutral theory, build communities as random samples of the larger regional-scale forest (Hubbell, 2001; Chave, 2004). Deterministic processes in turn rely at the spatial scale on the species interactions with abiotic environment that filter-out recruited species. Consequently, understanding the ecological mechanisms underlying communities trajectories first meant estimating the importance of the initial taxonomic composition and second to explicit the balance between stochastic and deterministic processes. Focusing on the recruitment processes would thus shed light on the resilience of communities and on the time needed to recover the pre-disturbance ecosystem properties, and eventually help adjusting exploitation and conservation guidelines (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017).

Communities are defined by their taxonomic structure, that refers to a neutral assemblage of species composition and diversity, and by their functional structure, that accounts for species ecology and ecosystem functioning (Violle *et al.*, 2007; Kunstler *et al.*, 2016). The ecological processes shaping recruitment trajectories may differently affect their taxonomic and their functional structure, and two communities may be very different in terms of taxonomic diversity but very similar in terms of diversity and composition of functional traits (Villéger *et al.*, 2012). The correlations, or not, between taxonomic and functional system trajectories are therefore insightful of the ecological rules involved in the recruitment processes, specifically to explicit the deterministic processes at stake (Mayfield & Levine, 2010; Fukami *et al.*, 2005). Competitive interactions among species are indeed determined by their differences in competitive ability and ecological niche and therefore depend their functional differences, specifically regarding the use of the limited shared resources (Webb *et al.*, 2002; Perronne *et al.*, 2017). In tropical forests where the light is limiting, communities response to disturbance translate in a shift from slow-growing,

long-lived species with "conservative" resource use to fast growing, resource "acquisitive" species (Denslow, 1980; Molino & Sabatier, 2001; Bongers *et al.*, 2009).
The competition processes at stake would be grasped by shifts in key leaf, wood and life-history functional traits assessing species resources acquisition strategy and ecology (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011; Gerhold *et al.*, 2015). (Chesson, 2000) defines two types of competitive processes interplaying in communities maintenance, either *equalizing* and decreasing the differences in species fitness or *stabilizing* favoring species coexistence in limiting the amount of shared resources. Equalizing mechanisms drive the most competitive species to dominance and the least competitive to exclusion and decrease the functional diversity of the community. Stabilizing competiton would mitigate the species competitive exclsion in decreasing the functional overlap among species, limit the species abundance through intraspecific competition and increase the functional diversity of the community (Ackerly, 2003; McGill *et al.*, 2006; Kunstler *et al.*, 2012).

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

In this paper we followed the fate of recruited tree diversity and composition (60 121 individuals) over 30 years after a large disturbance gradient, with 10 to 60% of forest biomass removed. We assessed the taxonomic dissimilarity between recruited trees and initial communities, the taxonomic and functional diversity of recruited trees and the corresponding trajectories of functional traits, using a large functional trait database covering the leaf, wood and life-history spectra. We compared the observed trajectories to neutral processes corresponding to the stochastic recruitment of individuals and to the randomization of species functional traits. These trajectories aimed to highlight the recruitment processes underlying forests response to disturbance, specifically assessing (i) the role of deterministic compared to stochastic processes, (ii) determine the competition processes involved, and eventually (iii) clarify the taxonomic and functional facets of forests resilience and their consequences for forest management.

## 2. Material and Methods

### 2.1 Study Site
The Paracou station is located in a lowland tropical rain forest in French Guiana (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 different botanical species, resulting in significant taxonomic uncertainties that had to be propagated to composition and diversity metrics. Vernacular names were replaced through multinomial trials $M_v\Big([s_1, s_2, \ldots, s_N], [\alpha_1, \alpha_2, \ldots, \alpha_3]\Big)$ based on the observed association probability $[\alpha_1, \alpha_2, \ldots, \alpha_3]$ between each vernacular name $v$ and the species $[s_1, s_2, \ldots, s_N]$ recorded in the inventory. See appendix 1 and Aubry-Kientz *et al.* (2013) for the detailed methodology. To avoid remaining identification caveats, the simulated botanical inventories were reported at genus level.

Eight functional traits representing the leaf economic (leaves thickness, toughness, total chlorophyll content and specific leaf area) and wood economic spectra (wood specific gravity and bark thickness), and life history traits (maximum specific height and seed mass) were considered. Traits were extracted from the BRIDGE project [1] where trait values were measured on nine forest plots in french guianan, including two in Paracou. Missing trait values of the trait database (10%) were filled by multivariate imputation by chained equation using the Mice R package (van Buuren & Groothuis-Oudshoorn, 2011). F-tests demonstrated that traits variance were essentially lower within genera and families compared to the whole inventory: we accounted for the phylogenetic signal of the functional traits by restricting the gap filling processes to samples pertaining to the next higher taxonomic level. As seed mass information corresponded to a classification into discrete mass classes, no data filling process was applied and analysis were performed only considering the 414 botanical species of the seed mass dataset.

## 2.3 Recruitment trajectories

To tease apart recruitment trajectories communities were split into per-disturbance surviving trees and recruited trees afterward. Recruited communities were examined either considering the "punctual recruitment", *i.e.* recruited trees by 2-year intervals, or all recruits since disturbance as the

[1]http://www.ecofog.gf/Bridge/

"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.t whole plot scale

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, summerizing the functional richness and evenness (Clark *et al.*, 2012) through the measure of communities functional divergence using Gower distance as recommended by Pavoine *et al.* (2009). Functional diversity was completed by the trajectories of traits community weighted means (CWM), representing the average trait value in a community weighted by relative abundance of the species carrying each value (Díaz *et al.*, 2007; Garnier *et al.*, 2004; Mason *et al.*, 2013). Seed mass trajectories were reported by the proportion of each class recorded in the inventories. The similarity between recruited trees and pre-disturbance forest was measured with the turnover metrics detailed in Podani *et al.* (2013). To estimate the importance of stochastic processes the recruitment was compared to the trajectories of a stochastic model of random samplings. For the taxonomic trajectories the stochastic model was a random sampling of individual trees according to their observed abundance that preserved species abundance and tree density. For the functional diversity the stochastic model was a shuffle of functional trait values among species that randomizes abundances across species but within coomunities (Mason *et al.*, 2013).

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

# 3. Results

## 3.1 Recruitment Diversity

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

### 3.1.1 Taxonomic Diversity

The diversity trajectories of punctual recruitment followed a consistent trajectory after disturbance, 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 compared to the stochastic trajectories of a random sampling. Richness (order 0) and evenness (order 2) of punctual

**Table 1.** Intervention table, summary of the disturbance intensity for the 4 plot treatments in Paracou.

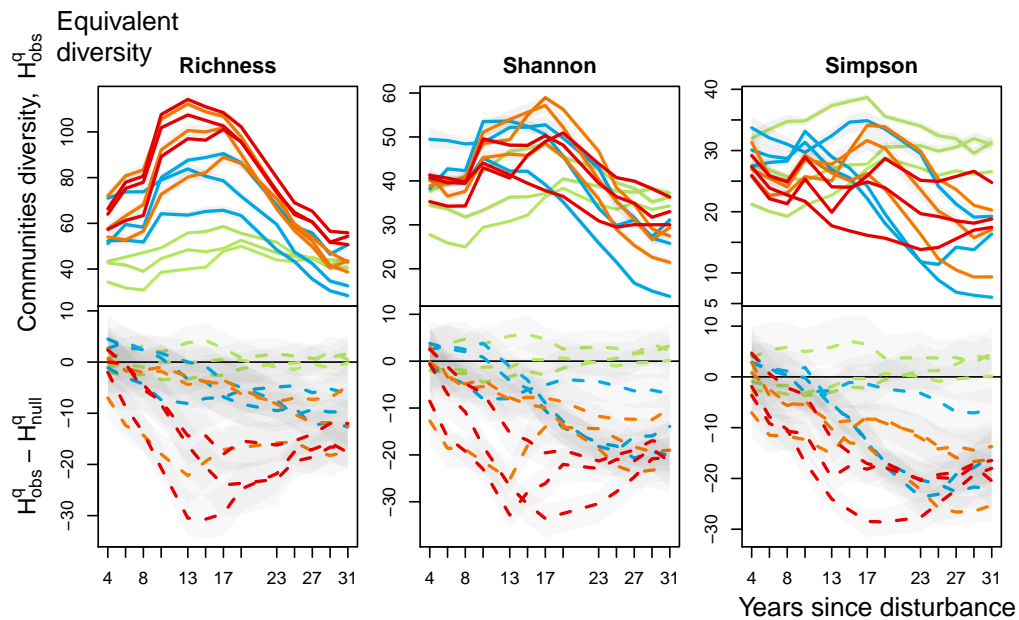| Treatment | Timber | Thinning | Fuelwood | %AGB lost |
|---|---|---|---|---|
| Control | | | | 0 |
| T1 | DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha | | | $[12\% - 33\%]$ |
| T2 | DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha | DBH $\geq$ 40 cm, non-valuable species, $\approx$ 30 trees/ha | | $[33\% - 56\%]$ |
| T3 | DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha | DBH $\geq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha | 40 cm $\leq$ DBH $\leq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha | $[35\% - 56\%]$ |



**Figure 1.** Trajectories over 30 years of Richness, Shannon and Simpson diversities of punctual recruitment (2-years laps, upper panels) and divergence to null model (lower panels). Values reported correspond to plot-level 0.025 and 0.975 percentiles (grey envelopes) and median (solid or dotted lines) obtained after 50 repetitions of the taxonomic uncertainty propagation and the functional database gap-filling frameworks. Colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3, see Table 1 for details).
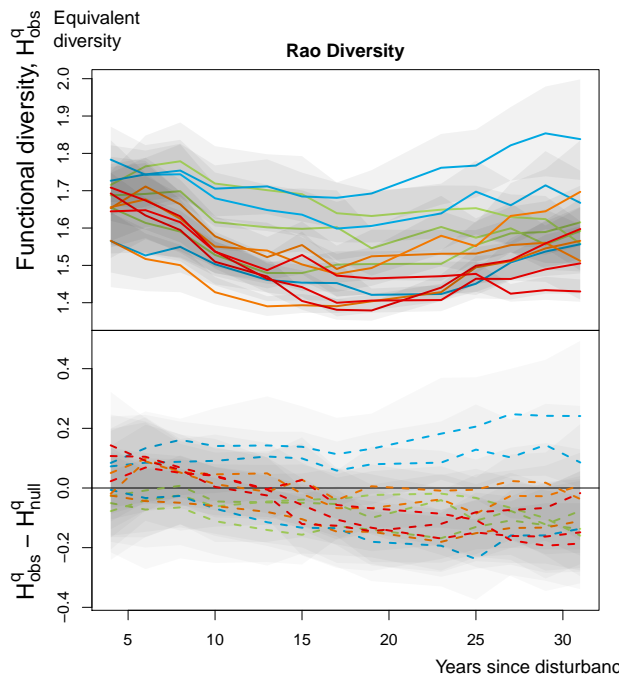
**Figure 2.** Functional diversity of punctual recruited trees (2-years laps) from the 7 functional traits (upper panel) and divergence to null model (lower panel). Values reported correspond to plot-level 0.025 and 0.975 percentiles (grey envelopes) and median (solid lines) obtained after 50 run of the null model and 50 repetitions of the taxonomic uncertainty propagation and the functional database gap-filling frameworks. Colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3, see Table 1 for details).

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 a 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 initial values. While the recovery was not achieved for the most disturbed plots, it was faster after the low disturbance intensity and for some T1 plots exceeded the initial values. For both disturbed and undisturbed plots, the observed functional diversity was lower than this of the random model, to the exception of two plots T1.

Trajectories of the functional traits showed a switch in disturbed plots towards species with large exchange surface area, light tissues (high SLA, low leaf toughness and thickness and low wood specific gravity) and with smaller

maximum height (Figure 3). Functional traits either followed humped shaped trajectories with an ongoing recovery or an achieved return to the initial state (for SLA, Bark thickness and leaf thickness and Hmax to a certain extent).

### 3.2 Recruitment Turnover

In control plots species turnover remained highly stable for the 30 sampled years (Figure 4), reflecting a strong similarity between the initial plots composition and the punctual recruits. In disturbed plots, the taxonomic turnover followed a marked humped shaped trajectory, with a maximum reached around 15 years after disturbance and a value positively correlated to the disturbance intensity ($\rho_{spearman} = 0.93$). Thirty years after disturbance the turnover of all disturbed plots had returned to low values close to zero.

## 4. Discussion

### 4.1 Three-phased trajectories shaped by deterministic processes

Along the 30 years, the recruitment richness and species turnover compared to the initial composition, and the trajectories of key functional traits (SLA and bark thickness) exhibited clear humped shaped trajectories, which revealed three distinct recruitment phases. The three phases corresponded to combinations of deterministic processes through species competitive exclusion for resources, and stochastic and neutral recruitment specific to undisturbed communities.

As a first phase (0-8 years), recruited trees showed low turnover compared to the initial composition and matched the functional diversity of a stochastic recruitment process. This first recruitment phase, mirroring the old-growth pre-disturbance communities, likely involved already grown saplings (DBH < 10cm) immediately benefitting from the increased enlightment and the alleviated competition induced by disturbance (Hérault *et al.*, 2010).

A second phase (8-15 years) then fell into place, corresponding to marked changes in several functional traits trajectories and to a decrease in recruitment evenness and functional diversity. This second phase likely incorporated true recruits, *i.e.* trees germinated from the seed bank that constitute the main part of the recruitment (Lawton & Putz, 1988). The pool of species recruited then was restricted, following deterministic processes based on species resource acquisition strategy, and balanced the stochastic and neutral recruitment observed in the first place (Chave, 2004). Indeed, sharp changes in the SLA, wood density and leaf thickness trajectories occured after intense disturbance and revealed the prominent recruitment of short-lived, fast growing hard pioneer species with competitive and efficient light acquisition (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011; Reich, 2014).

The recruitment was shaped by exclusive competition among species based on their differences in competitive ability for light acquisition (Mayfield & Levine, 2010), as already demonstrated in temperate forests (Kunstler *et al.*, 2012). The balance between deterministic and stochastic processes shaping the second phase was determined by the initial disturbance intensity. After light disturbance (T1 plots),
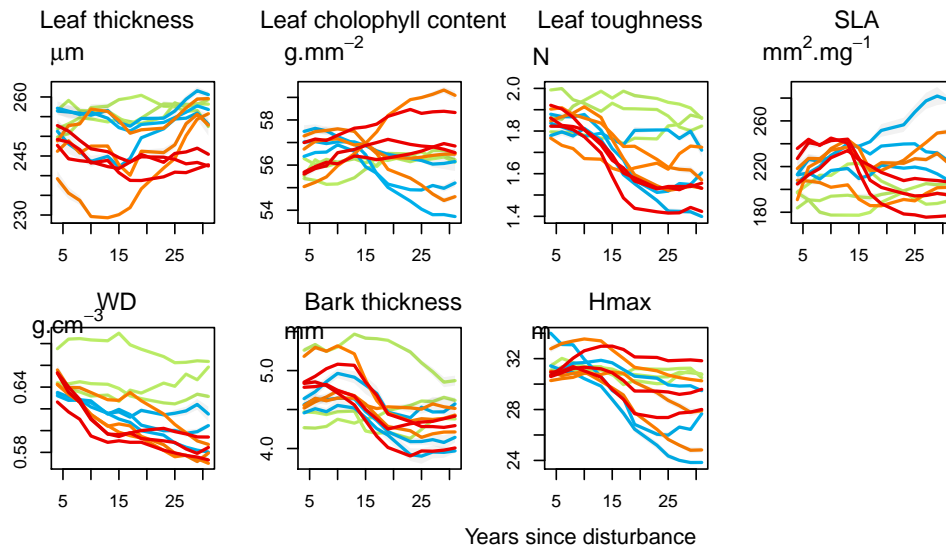
**Punctual recruits CWM**



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



**Figure 4.** Trajectories over 30 years of the abundance-based turnover between recruited trees (2-years laps) and initial communities before disturbance. Values reported correspond to plot-level 0.025 and 0.975 percentiles (grey envelopes) and median (solid lines) obtained after 50 repetitions of the taxonomic uncertainty propagation framework. Colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3, see Table 1 for details).
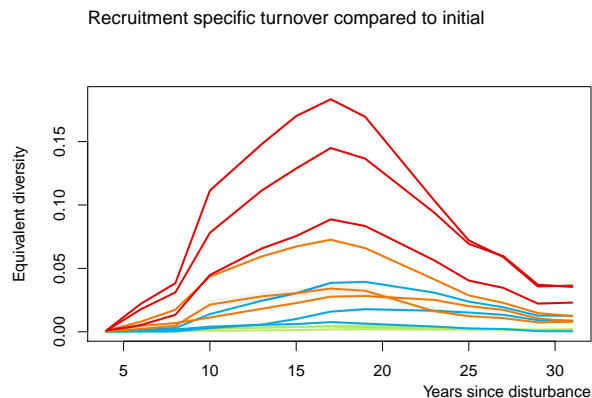
despite a restricted pool of recruited species, the species turnover compared to initial state remained low. Recruited trees still mirrored the pre-disturbance communities but recruited species were more pioneers and light demanders, with strategies of efficient resource acquisition (high SLA and leaf chlorophyll content) and inexpensive, short-lived tissues (low leaf thickness and thoughness, small Hmax and low wood density and bark thickness) (Hubbell *et al.*, 1999; Schnitzer & Carson, 2001; Sheil & Burslem, 2003; Bongers *et al.*, 2009). At these low disturbance intensity the recruitment evenness and functional diversity remained high so despite the selection of more light-demanding species the recruitment was not overwhelmed by hard pioneers. This might be explained by the recruitment and dispersal limitations due to the short dispersal distances observed for tropical trees, specifically in Paracou (Leclerc *et al.*, 2015; Scotti *et al.*, 2015). After intense disturbance in contrast (T2 and T3 plots), the recruitment rapidly differed from the pre-disturbance composition and corresponded to a sharp increase of the SLA and bark thickness. These drastic trajectories changes reflected an overhelming recruitment of hard pioneers likely entailing significant changes in communities functioning (Díaz *et al.*, 2005).

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

Recruitment trajectories of disturbed and undisturbed areas were identical, supporting a recruitment success and

an enlightenment homogeneous in undisturbed communities (Dalling & Hubbell, 2002) and evenly increasing in disturbed communities through large gaps edge effects (Rüger *et al.*, 2009).

## 4.2 The questioned completeness of communities resilience

After 30 years, although taxonomic and functional diversity had recovered initial values the recruitment processes remained constrained by the deterministic selection of recruited species, contrasting with the stochastic recruitment of undisturbed forests. The stochastic recruitment proved eventually resilient and ensured communities taxonomic convergence towards different stable equilibria, but lasted for several decades.

The recovery of both recruitment processes and initial composition and diversity meant the maintenance of the taxonomic differences between communities. Multiple stable equilibria, corresponding to the initial commmunities restored after disturbance, were maintained as predicted for highly diverse and productive ecosystems (Chase, 2003). These different equilibria besides oriented communities trajectories towards their initial composition, as suggested with the involvement of pre-disturbance grown saplings and local seed bank and as already observed consistently with other case study (Dalling & Hubbell, 2002; Anderson, 2007).

In contrast, recruitment functional diversity and some traits trajectories were similar among treatments and recovered quickly, translating communities convergence in the functional space and their fast functioning recovery despite their divergence in the taxonomic space (Fukami *et al.*, 2005). This confirmed previous results from the Paracou experiment, conducted 10 years (Molino & Sabatier, 2001) and 20 years (Baralot *et al.*, 2012) after disturbance, where the early signs of the resilience of taxonomic and functional composition had been detected.

Communities recovery was then consistent but slow, specifically for taxonomic diversity and several functional traits that remained altered 30 years after disturbance. Besides, the recovery invovled and probably altered the seed bank stock, hence changing the diversity of the recruitable species and the resilience of the communities (Norden *et al.*, 2009).

## 5. Conclusion

The hindsight of the 30 years of forest monitoring highlighted a three-phased disturbance response, defined by the balance between stochastic neutral processes and determinisitic recruitment based on species strategy of light acquisition. Communities trajectories were first driven by the stochastic recruitment of already-grown saplings mirroring pre-disturbance communities before it was shaped by true recruits from the seed bank slected through the competitive exclusion for light. After intense disturbance the second recruitment phase was dominated by short-lived hard pioneers that drastically changed communities diversity and functioning. A third phase eventually carried out the recovery towards the initial communities with the recovery of stochastic recruitment progressively balancing competi-

tive exclusion. Recruitment trajectories demonstrated a fast functional recovery driving communities convergence in the functional space, and a decades long taxonomic recovery that maintained the initial composition differences. Even though the accurate impact on the seed bank remains to be clarified, communities recovery was tangible but slow and entailed great caution regarding forests management guidelines aiming to a complete recovery of ecosystems.

---

## References

Ackerly, D.D. (2003) Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments. *International Journal of Plant Sciences*, **164**, 165–184.

Adler, P.B., HilleRislambers, J. & Levine, J.M. (2007) A niche for neutrality. *Ecology Letters*, **10**, 95–104.

Anderson, K.J. (2007) Temporal patterns in rates of community change during succession. *The American naturalist*, **169**, 780–93.

Aubry-Kientz, M., Rossi, V., Wagner, F. & Hérault, B. (2015) Identifying climatic drivers of tropical forest dynamics. *Biogeosciences*, **12**, 5583–5596.

Aubry-Kientz, M., Hérault, B., Ayotte-Trépanier, C., Baraloto, C. & Rossi, V. (2013) Toward Trait-Based Mortality Models for Tropical Forests. *PLoS ONE*, **8**.

Baraloto, C., Hérault, B., Paine, C.E.T., Massot, H., Blanc, L., Bonal, D., Molino, J.F.F., Nicolini, E.a. & Sabatier, D. (2012) Contrasting taxonomic and functional responses of a tropical tree community to selective logging. *Journal of Applied Ecology*, **49**, 861–870.

Bongers, F., Poorter, L., Hawthorne, W.D. & Sheil, D. (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecology Letters*, **12**, 798–805.

Chao, A. & Jost, L. (2015) Estimating diversity and entropy profiles via discovery rates of new species. *Methods in Ecology and Evolution*, **6**, 873–882.

Chase, J.M. (2003) Community assembly: When should history matter? *Oecologia*, **136**, 489–498.

Chave, J. (2004) Neutral theory and community ecology. *Ecology letters*, **7**, 241–253.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, **31**, 343–366.

Clark, C.M., Flynn, D.F., Butterfield, B.J. & Reich, P.B. (2012) Testing the Link between Functional Diversity and Ecosystem Functioning in a Minnesota Grassland Experiment. *PLoS ONE*, **7**.

Clements, F.E. (1916) *Plant succession: an analysis of the development of vegetation.* 242. Carnegie Institution of Washington.

Dalling, J.W. & Hubbell, S.P. (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology*, **90**, 557–568.

Denslow, J.S. (1980) Gap Partitioning among Tropical Rainforest Trees. *Biotropica*, **12**, 47–55.

Dezécache, C., Faure, E., Gond, V., Salles, J.M., Vieilledent, G. & Hérault, B. (2017a) Gold-rush in a forested el dorado: deforestation leakages and the need for regional cooperation. *Environmental Research Letters*, **12**, 034013.

Dezécache, C., Salles, J.M., Vieilledent, G. & Hérault, B. (2017b) Moving forward socio-economically focused models of deforestation. *Global Change Biology*, **23**, 3484–3500.

Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities*, pp. 342–444.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684–20689.

Díaz, S., Tilman, D., Fargione, J., Chapin III, F.S., Dirzo, R., Kitzberger, T., Gemmill, B., Zobel, M., Vilà, M., Mitchell, C., Wilby, A., Daily, G.C., Galetti, M., Laurance, W.F., Pretty, J., Naylor, R., Power, A., Harvell, A., Potts, S., Kremen, C., Griswold, T. & Eardley, C. (2005) Biodiversity Regulation of Ecosystem Services. *Trends and conditions*, pp. 297–329.

Fukami, T., Bezemer, T.M., Mortimer, S.R. & Van Der Putten, W.H. (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, **8**, 1283–1290.

Gardner, T.A., Barlow, J., Parry, L.W. & Peres, C.A. (2007) Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica*, **39**, 25–30.

Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, B.P. (2004) Plant functional markers capture ecosystem properties during secondary successsion. *Ecology*, **85**, 2630–2637.

Gerhold, P., Cahill, J.F., Winter, M., Bartish, I.V. & Prinzing, A. (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, **29**, 600–614.

Gourlet-Fleury, S. & Houllier, F. (2000) Modelling diameter increment in a lowland evergreen rain forest in French Guiana. *Forest Ecology and Management*, **131**, 269–289.

Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C.E.T., Wagner, F. & Baraloto, C. (2011) Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology*, **99**, 1431–1440.

Hérault, B. & Gourlet-Fleury, S. (2016) Will tropical rainforests survive climate change? *Climate Change and Agriculture Worldwide*, pp. 183–196. Springer.

Hérault, B., Ouallet, J., Blanc, L., Wagner, F. & Baraloto, C. (2010) Growth responses of neotropical trees to logging gaps. *Journal of Applied Ecology*, **47**, 821–831.

Hérault, B. & Piponiot, C. (2018) Key drivers of ecosystem recovery after disturbance in a neotropical forest. *Forest Ecosystems*, **5**, 2.

Hill, M.O. (1973) Diversity and Evenness : A Unifying Notation and Its Consequences. *Ecological Society of America*, **54**, 427–432.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & De Lao, S.L. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton University Press.

Hurtt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of theoretical biology*, **176**, 1–12.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E. & Westoby, M. (2016) Plant functional traits have globally consistent effects on competition. *Nature*, **529**, 204–207.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E., Kattge, J. & Coomes, D.A. (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. *Ecology Letters*, **15**, 831–840.

Lawton, R.O. & Putz, F.E. (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology*, **69**, 764–777.

Leclerc, T., Vimal, R., Troispoux, V., Périgon, S. & Scotti, I. (2015) Life after disturbance (I): changes in the spatial genetic structure of Jacaranda copaia (Aubl.) D. Don (Bignonianceae) after logging in an intensively studied plot in French Guiana. *Annals of Forest Science*, **72**, 509–516.

Marcon, E. (2015) Practical Estimation of Diversity from Abundance Data. *HAL archives-ouvertes*, p. 9.

Martin, P.A., Newton, A.C., Pfeifer, M., Khoo, M. & Bullock, J.M. (2015) Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis. *Forest Ecology and Management*, **356**, 224–233.

Mason, N.W.H., De Bello, F., Mouillot, D., Pavoine, S. & Dray, S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, **24**, 794–806.

Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.

Molino, J.F. & Sabatier, D. (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science*, **294**, 1702–1704.

Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.H. & Vílchez-Alvarado, B. (2009) Resilience of tropical rain forests: Tree community reassembly in secondary forests. *Ecology Letters*, **12**, 385–394.

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S. & Daniel, H. (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos*, **118**, 391–402.

Perronne, R., Munoz, F., Borgy, B., Reboud, X. & Gaba, S. (2017) How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. *Perspectives in Plant Ecology, Evolution and Systematics*, **25**, 29–44.

Piponiot, C., Sist, P., Mazzei, L., Peña-Claros, M., Putz, F.E., Rutishauser, E., Shenkin, A., Ascarrunz, N., de Azevedo, C.P., Baraloto, C., França, M., Guedes, M., Coronado, E.N., D'Oliveira, M.V., Ruschel, A.R., da Silva, K.E., Sotta, E.D., de Souza, C.R., Vidal, E., West, T.A. & Hérault, B. (2016) Carbon recovery dynamics following disturbance by selective logging in amazonian forests. *eLife*, **5**.

Podani, J., Ricotta, C. & Schmera, D. (2013) A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. *Ecological Complexity*, **15**, 52–61.

Putz, F.E., Zuidema, P.A., Synnott, T., Peña-Claros, M., Pinard, M.A., Sheil, D., Vanclay, J.K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J. & Zagt, R. (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters*, **5**, 296–303.

Reich, P.B. (2014) The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, **102**, 275–301.

Rozendaal, D.M.A., Soliz-Gamboa, C.C. & Zuidema, P.A. (2010) Timber yield projections for tropical tree species: The influence of fast juvenile growth on timber volume recovery. *Forest Ecology and Management*, **259**, 2292–2300.

Rüger, N., Huth, A., Hubbell, S.P. & Condit, R. (2009) Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology*, **97**, 1360–1368.

Rutishauser, E., Hérault, B., Petronelli, P. & Sist, P. (2016) Tree Height Reduction After Selective Logging in a Tropical Forest. *Biotropica*, **48**, 285–289.

Schnitzer, S.A. & Carson, W.P. (2001) Treefall Gaps and the Maintenance of Species Diversity in a Tropical Forest. *Ecology*, **82**, 913–919.

Schwartz, G., Falkowski, V. & Peña-Claros, M. (2017) Natural regeneration of tree species in the Eastern Amazon: Short-term responses after reduced-impact logging. *Forest Ecology and Management*, **385**, 97–103.

Scotti, I., Montaigne, W., Cseke, K. & Traissac, S. (2015) Life after disturbance (II): the intermediate disturbance hypothesis explains genetic variation in forest gaps dominated by Virola michelii Heckel (Myristicaceae). *Annals of Forest Science*, **72**, 1035–1042.

Sebbenn, A.M., Degen, B., Azevedo, V.C., Silva, M.B., de Lacerda, A.E., Ciampi, A.Y., Kanashiro, M., Carneiro, F.d.S., Thompson, I. & Loveless, M.D. (2008) Modelling the long-term impacts of selective logging on genetic diversity and demographic structure of four tropical tree species in the Amazon forest. *Forest Ecology and Management*, **254**, 335–349.

Sheil, D. & Burslem, D.F.R.P. (2003) Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution*, **18**, 18–26.

van Buuren, S. & Groothuis-Oudshoorn, K. (2011) mice: Multivariate imputation by chained equations in r. *Journal of Statistical Software*, **45**, 1–67.

Villéger, S., Miranda, J.R., Hernandez, D.F. & Mouillot, D. (2012) Low functional Beta-diversity despite high taxonomic Beta-diversity among tropical estuarine fish communities. *PLoS ONE*, **7**.

Vinson, C.C., Kanashiro, M., Harris, S.A. & Boshier, D.H. (2015) Impacts of selective logging on inbreeding and gene flow in two Amazonian timber species with contrasting ecological and reproductive characteristics. *Molecular Ecology*, **24**, 38–53.

Violle, C., Navas, M.L.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, É. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Wagner, F., Hérault, B., Stahl, C., Bonal, D. & Rossi, V. (2011) Modeling water availability for trees in tropical forests. *Agricultural and Forest Meteorology*, **151**, 1202–1213.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and Community Ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, &., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.