30 Years of Post-disturbance Recruitment in Tropical Forest

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

Abstract
To clarify the fate of tropical forests in the current global changing context we examined the taxonomic and functional response of tree recruitment processes after a gradient of disturbance.

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

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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 (Dezecache *et al.*, 2017; Dezécache *et al.*, 2017) 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 huge biological diversity constraining

studies to focus on common or commercial species, and by the scarcity of long-term monitoring (Sebbenn *et al.*, 2008; Rozendaal *et al.*, 2010; Vinson *et al.*, 2015).

Major insights on forests diversity response to disturbance would be given by communities trajectories along time. 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 already proved mirroring the diversity of pre-disturbance communities, so communities trajectories and resilience would depend on the diversity of recruited trees that build the future community. First, recruitment trajectories depend on the composition and diversity of the initial, pre-disturbance community that conditions the pool of recruitable species via the existing saplings and seed bank (Hérault & Piponiot, 2018). Then, trajectories depend either on stochastic recruitment determined by recruitment and dispersal limitations (Hurtt & Pacala, 1995; Hubbell, 2001), or deterministic processes like niche-based competition or biotic interaction (Adler *et al.*, 2007). Stochastic processes build communities as random samples of the larger regional-scale forest. Deterministic processes in turn rely at this spatial scale on the interactions among species and with abiotic environment that filter-out recruited species following their ecology. Understand the mechanisms of communities trajectories primarily requires to estimate the importance of the initial community composition and then balance between stochastic and deterministic processes. These mechanisms would then shed light on communities resilience and on the time to recover pre-disturbance ecosystem properties, eventually to adjust exploitation and conservation guidelines (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017).

The ecological processes shaping the trajectories differently affect communities taxonomic characteristics, that consider all species equal, and functional characteristics,

which accounts for species ecology and functioning (Violle *et al.*, 2007; Kunstler *et al.*, 2016). Two communities may indeed be very different in terms of species diversity but very similar in terms of morphological traits and functioning (Villéger *et al.*, 2012). The differences between taxonomic and functional trajectories are insightful of recruitment rules, specifically regarding the deterministic processes and their strengh (Mayfield & Levine, 2010; Fukami *et al.*, 2005). At this local spatial scale, deterministic processes rely on competitive interactions among trees determined by their functional differences in the use of limited shared resources (Webb *et al.*, 2002; Perronne *et al.*, 2017). Determinisitic processes ruling the assemblages of species are a balance between the differences in species competitive ability and ecological niche. Differences in competitive ability will drive the most competitive species to dominance and the least competitive to elimination, thus decreasing the functional diversity. Niche differences in turn favor low densities and low similarity among species, thus increasing the functional diversity (Ackerly, 2003; McGill *et al.*, 2006; Kunstler *et al.*, 2012). In tropical forests where the light is limiting, communities response to disturbance proved 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 therefore be grasp by 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; Gerhold *et al.*, 2015).

Beyond the mere understanding of response mechanisms, disentangle deterministic from stochastic processes insights the underlyings of communities resilience. Controversies remained about resilience determinism, entailing the convergence of communities towards a given structure likely defined by the environment (Clements, 1916), opposed to a stochastic point of view entailing commnuities divergence through species random recruitment (Diamond, 1975). Recently both points of view were reconciled under the hypothesis the communities diverge in the taxonomic space while they converge in the functional space with determined diversity and composition in functional niches. This hypothesis however remains to be tested for in tropical forest, despite their importance in guiding ecosystems management and conservation policies.

In this paper we followed the fate of recruited tree communities (60121 individuals) over 30 years on a large disturbance gradient, with 1 to 60% of forest biomass removed. We assessed the taxonomic and functional diversity of recruited trees and associated traits trajectories, using a large functional trait database covering the leaf, wood and life-history spectra. We besides followed the dissimilarity in composition of recruited trees compared to the initial communities. Eventually we compared the observed trajectories to a stochastic recruitment entailing the recruits random sampling and the randomization of their functional traits. These trajectories aimed to asses the recruitment mechanisms underlying forests response to disturbance, specif-

ically assessing (i) the role of deterministic compared to stochastic processes and (ii) the competition deterministic processes invovled. Recruitment trajectories eventually (iii) enlightened the taxonomic and functional facets of forests resilience and its consequences on forests future.

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 were 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 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 exctracted from the BRIDGE project [1] where trait values were measured on nine forest plots infrench 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). 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

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[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	$[35\% - 56\%]$

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, a useful summary variable assess both functional richness and evenness (Clark *et al.*, 2012), measuring the functional divergence within communities using Gower distance as recommended by Pavoine *et al.* (2009). Functoinal 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 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 the recruitment was compared to the trajectories of a stochastic model corresponding to 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 for the functional diversity the stochastic model was a shuffling of functional trait values among species that randomizes abundances across species but within coomunities (Mason *et al.*, 2013).

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 similarily 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 the recruitment processes applied to whole communities and were not restricted to logging gaps.

3.1.1 Taxonomic Diversity

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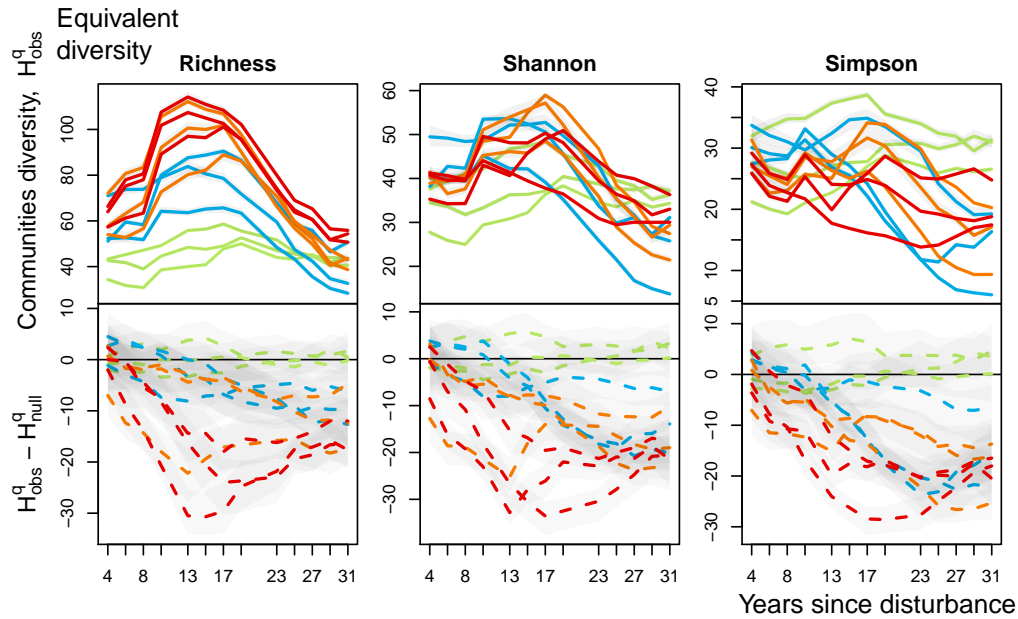
Figure 1. Trajectories of Richness, Shannon and Simpson diversity for 2-years laps punctual recruitment (upper panels) and divergence to null model (lower panels). Lines colors refer to the perturbation regime: green for control, blue for T1, orange for T2 and red for T3 disturbance treatments. Plain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

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 ($\rho_{spearman} = 0.93$). Thirty years after disturbance the turnover of all disturbed plots had return to low values close to zero.
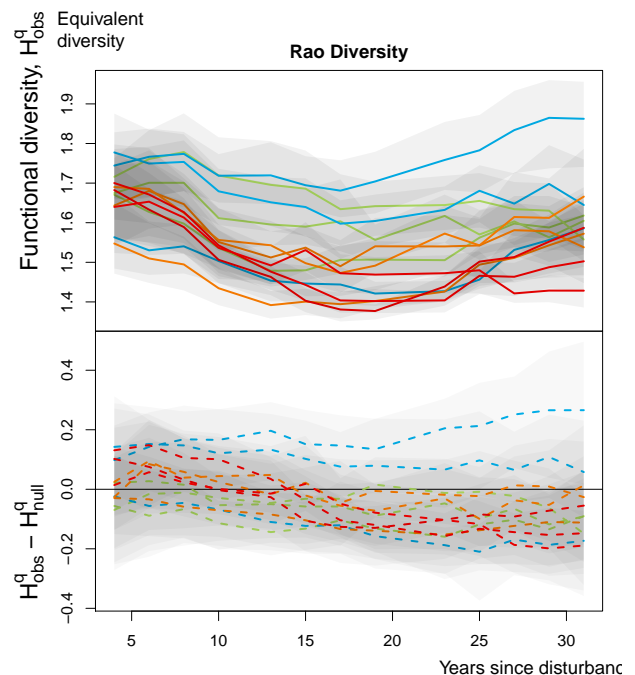

Figure 2. Functional diversity of punctual recruited trees from the considered functional traits and divergence to null model. Values reported correspond to the plot-level median and the 95% confidence interval obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database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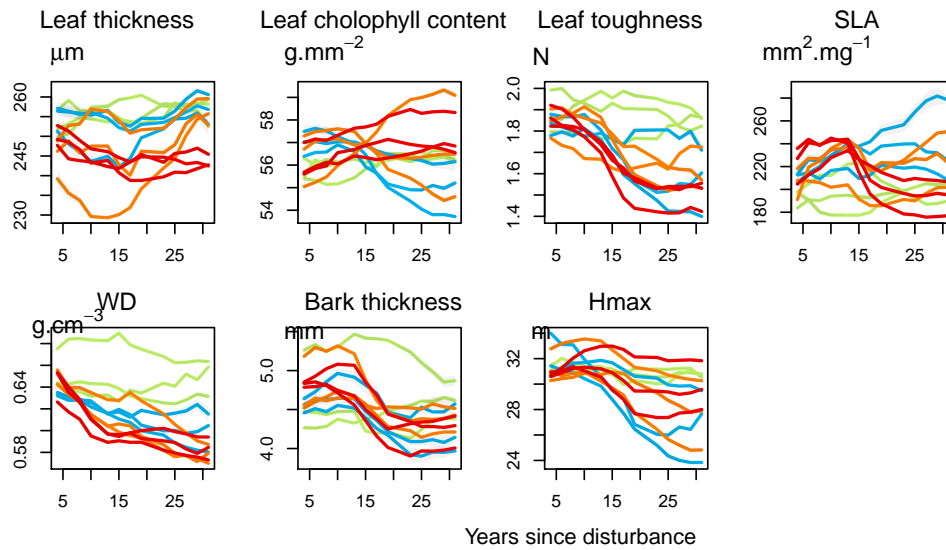
Punctual recruits CWM

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 intial communities before disturbance. Grey envelopes correspond to the 0.025 and 0.975 percentiles of the uncertainty propagation procedue and lines to the median in green for control, blue for T1, orange for T2 and red for T3).

4. Discussion

4.1 The three phases of recruitment trajectories

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 hump-shaped trajectories, revealing three distinct recruitment phases. Communities trajectories involved an interplay between stochastic and deterministic recruitment, first involving species competitive exclusion and then niche partitioning, before recovering initial recruitment processes.

As a first step (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 predisturbance community then likely involved already grown saplings (DBH <10cm) immediatly benefitting from the increased enlightment and the alleviated competition induced by disturbance (Hérault *et al.*, 2010).

A second phase (8-15 years) then fall 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 according to their resource acquisition strategy and revealed the deterministic processes that balanced the stochastic recruitment observed in the first place. 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 pionneer species with competitive and efficient light acquisition (Wright *et al.*,
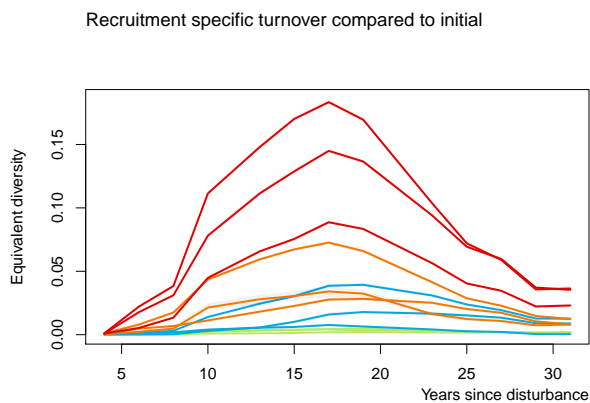
2004; Chave *et al.*, 2009; Hérault *et al.*, 2011; Reich, 2014). The recruitment was therefore shaped by exclusive competition among species based on their competitive ability differences for light acquisition (Mayfield & Levine, 2010), as already demonstrated in for tree species in temperate forests (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), despite the pool of recruited species was restricted, the species turnover compared to initial state remained low. Recruited trees then 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 this 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 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 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 eventually entailed a return towards initial taxonomic and functional diversities. Recruited species remained mainly light-demanding and still submitted to competitive exclusion, but their functional diversity and their compositional similarity with initial communities progressively increased which revealed the recovery of stochastic recruitment processes dominating in mature forests (Lawton & Putz, 1988; Mayfield & Levine, 2010).

The recruitment trajectories proved identical in disturbed versus untouched areas with plots, suggesting community scale processes. In undisturbed forests the light availability proved quite homogeneous and unrelated to trees recruitment success (Dalling & Hubbell, 2002) while disturbance gaps and associated edge effect significantly increasing the global enlightment enhancing trees recruitment success (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 recruitment processes proved then consistently resilient but over long time period.

The recovery of both recruitment processes and initial composition and diversity meant the maintenance of pre-disturbance differences in communities taxonomy. This entailed the existence of multiple stable equilibrium among communities, corresponded to the initial commmunities restored after disturbance, consistently with the assumptions made for highly diverse and productive ecosystems (Chase, 2003). Besides it meant the dependence of communities response on their initial composition that oriented their trajectories, consistently with previous observation and with the involvement of pre-disturbance grown saplings and local seed bank (Dalling & Hubbell, 2002; Anderson, 2007).

In contrast the trajectories of some traits and of functional diversity were essentially similar among treatments and recovered quickly. This translated the confluence of communities in the functional space quickly resotring communities functioning, 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 (Baraloto *et al.*, 2012) after disturbance, where the early signs of the resilience of taxonomic and functional composition had been detected.

Although consistent communities recovery proved slow, specifically for taxonomic diversity and several functional traits that remained altered 30 years after disturbance. The disturbance response besides impacted the seed bank, that is the stock of recruitable species and that determines communities recoveryresilience. Its involvment might therefore alter the resilience and future trajectories of communities (Norden *et al.*, 2009).

5. Conclusion

The hindsight of the 30 years of forest monitoring highlighted a three-phase disturbance response, defined by the balance between stochastic and determinisitic recruitment processes. Communities trajectories were first driven by the stochastic recruitment of already-grown saplings mirroring the pre-disturbance state before it was shaped by the true recruits from the seed bank that underwent competitive exclusion based on species light acquisition strategy. After intense disturbance the second recruitment phase was dominated by short-lived hard pioneers that drastically changed the diversity and the functioning of communities. A third phase eventually carried out the recovery towards the initial communities with the resurgence of stochastic recruitment progressively balancing the competitive exclusion for resources. The recruitment response to disturbance demonstrated communities quick functional resilience in a common functional space while it highlighted the long-term taxonomic resilience, *i.e.* several decades, that maintained initial composition differences. Even though the accurate impact on the seed bank remains to be clarified, communities recovery was tangible but its length entailed great caution regarding forests management guidelines that aim to a complete recovery of ecosystems.

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