

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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Contents

1	Introduction	1
2	Material and Methods	2
2.1	Study Site	2
2.2	Inventories Protocol and Dataset Collection	2
2.3	Recruitment trajectories	2
3	Results	3
3.1	Recruitment Diversity	3
	Taxonomic Diversity • Functional Diversity and Composition	
3.2	Recruitment Turnover	3
4	Discussion	3
4.1	On the underlyings of the hump-shaped trajectories	4
4.2	On the resilience of the recruitment process	6
5	Conclusion	6

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 assemblages, it usually remained confined to few commercial and valuable species (Sebbenn *et al.*, 2008; Rozendaal *et al.*, 2010; Vinson *et al.*, 2015). Forest dynamics, though, result from the constantly evolving interactions and feedbacks among trees and their environment and 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 similarity through resource competition (Ackerly, 2003; McGill *et al.*, 2006), and stochastic processes like random dispersal, recruitment and death (?). The deterministic processes are inherently linked to disturbance regime which locally changes ecosystem's biotic and abiotic conditions and maintains species able of efficient acquisition of resource but living shortly and poorly resistant to hazards and diseases (Denslow, 1980). They rely on the Intermediate Disturbance Hypothesis (IDH) that explains the maintenance of tropical forests biodiversity by the patchy variability of environmental 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 mature 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 structure, 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, chlorophyll 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 project ¹ where trait values were measured on nine french guianan forest plots, including two in Paracou. Missing trait values (10%) were filled using multivariate imputation by chained equation (mice). As traits variability was lower within species and within genus, we accounted for the phylogenetic signal of the functional traits in restricting the gap filling processes to samples pertaining to the next higher taxonomic level (refs MICE). As seed mass information corresponds to a classification into mass classes, no data filling process was applied so analysis were performed only considering the 414 botanical species of the seed mass dataset.

Functional trajectories were estimated with the Rao quadratic entropy using community weighted means (CWM) (Díaz *et al.*, 2007; Garnier *et al.*, 2004). Seed mass trajectories were reported by the proportion of each class recorded in the inventories. All composition and diversity metrics are the average obtained after 50 iterations of taxonomy and trait values uncertainty propagation.

2.3 Recruitment trajectories

We split the forest community in ‘survivors, i.e. trees that survived the disturbance, and post-disturbance recruited trees. Two recruitment metrics were examined: on the one hand the ‘punctual recruitment’ by 2-year intervals after disturbance, on the other hand all recruited trees since disturbance, hereafter ‘accumulated recruits’. The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973; Chao & Jost, 2015; Marcon, 2015). These three indices belong to the set of HCDT or generalized entropy, respectively corresponding to the 0, 1 and 2 order of diversity (q), which grasps the balance between richness and evenness in the community, with common species weighting more than rare ones when q increases. The similarity between the recruited trees and the pre-disturbance forest was measured with the turnover metrics detailed in Podani *et al.* (2013). To determine whether recruitment trajectories ensued from a pure random process, observed trajectories were compared to those generated by 50 repetitions of a random null model shuffling individuals among plots while preserving species abundance and plots’ tree density.

To draw plots trajectories we applied a moving average with a one step window allowing to mitigate the heterogeneity of inventory protocols between years.

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. Results

3.1 Recruitment Diversity

3.1.1 Taxonomic Diversity

Punctual recruits' diversity followed a consistent trajectory among disturbance treatments with first higher richness and lower evenness than in control plots and then equivalent richness and lower evenness (Figure 1). For recruits accumulated since disturbance, the richness (order 0) in highly disturbed plots (T3 and some T2) was higher than in control plots, consistently with the increase of recruited trees after disturbance, and the evenness (order 2) was lower, specifically for the most disturbed plots (Appendix I, fig. S1).

Punctual and accumulated recruitment diversity of orders 0, 1 and 2 were then compared to a null random recruitment model. In control plots the richness (order 0) and evenness (order 2) of punctual recruits remained equivalent or higher than for the null random model. For all disturbed plots in contrast both richness and evenness were lower than these of a random null model but displayed a significant but unachieved humped-shaped trajectory for all plots (Figure 1). Accumulated recruitment richness and evenness were higher or equivalent to those of the null model for plots T1 and some plots T2 but lower for plots T3 and a plot T2 (Appendix I, fig. S1).

3.1.2 Functional Diversity and Composition

The functional diversity (Rao diversity) of punctual recruitment was measured and compared to a null model of random traits shuffling. In most disturbed plots (plots T2 and T3) the functional diversity was decreasing and lower to this of control plots until 15 years after disturbance (Figure 3). It then increased to values equivalent or higher to those observed in control plots. For all disturbed and control plots the observed functional diversity was lower than for the null model of random traits shuffle, except for two T1 plots.

Trajectories of recruited trees in the functional spaces showed the dominance after disturbance of species displaying large exchange surface area and light tissues (high SLA, low leaf toughness and thickness and low wood specific

gravity) (Figure 3). All traits trajectories displayed univariate CWM trajectories with leaf toughness, wood specific gravity and bark thickness decreasing before stabilizing at low values around 15 after disturbance, except SLA and leaf thickness that displayed a unimodal trajectory with a maximum reach around 15 years after disturbance.

3.2 Recruitment Turnover

In control plots species turnover remained highly stable for the 30 sampled years (Figure 4), reflecting a strong similarity between the initial plots composition and the punctual recruits. In disturbed plots, turnover displayed a unimodal response to disturbance, with maximum reached around 15 years and with a value positively correlated to the disturbance intensity ($\rho_{\text{Spearman}} = 0.93$). The turnover trajectory returned close to zero for all plots 30 years after disturbance.

4. Discussion

From the 30 years monitoring in Paracou forest, we highlighted contrasting recruitment trajectories determined by the disturbance intensity. Disturbance increased the number of recruits and hence their taxonomic richness, but the recruitment was dominated by a pool of species all the more restricted that disturbance intensity was high. Recruitment trajectories after disturbance were thus governed by a gradual balance between deterministic processes, the selection towards light acquisitive functional strategies and the similarity limitation, and stochastic processes defining the demography of mature forests. For the highest disturbance intensity, though, this was preceded by an additional phase where the exclusive competition of newly settled hard pioneers decreased the diversity and changed the composition of recruited trees. Communities then followed longer-term but similar trajectories. Pre-disturbance composition, diversity and functioning, then consistently recovered and initial differences among communities were maintained. Still, trajectories involved the soil seed bank which likely altered communities resilience, which questions the consistency of those trajectories after additional disturbance.

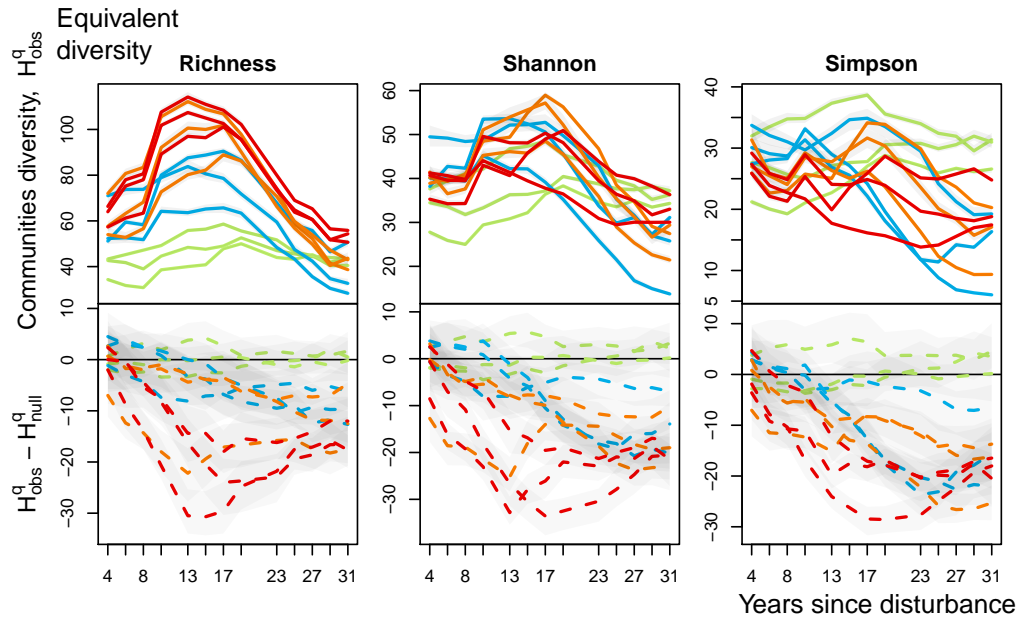


Figure 1. Trajectories of Richness, Shannon and Simpson diversity for 2-years laps punctual recruitment (upper panels) and divergence to null model (lower panels). Lines colors refer to the perturbation regime: green for control, blue for T1, orange for T2 and red for T3 disturbance treatments. Plain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

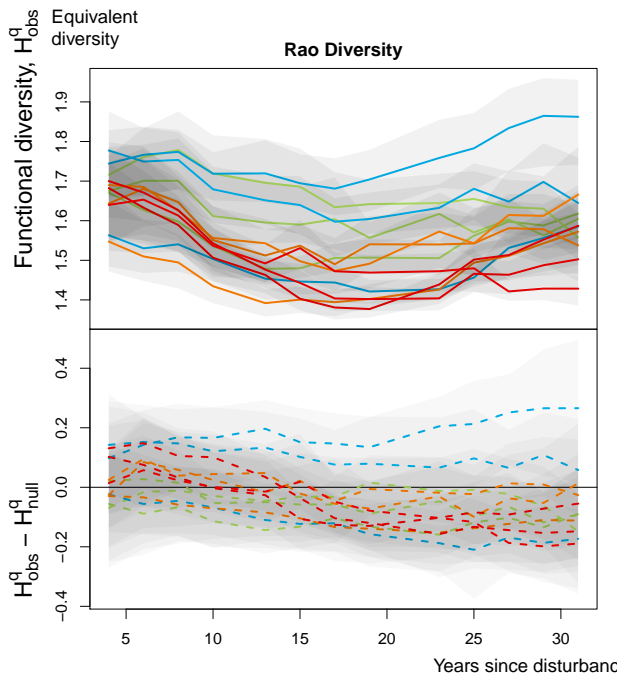


Figure 2. Functional diversity of punctual recruited trees from the considered functional traits and divergence to null model. Values reported correspond to the plot-level median and the 95% confidence interval obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database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

4.1 On the underlyings of the hump-shaped trajectories

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

The 10-15 first years of these trajectories seemed driven by the growth of pre-disturbance saplings benefiting from the environmental changes and alleviated competition that follow disturbance (Hérault *et al.*, 2010). After low disturbance intensity this translated into a stable functional diversity of the recruited community, equivalent to this of control plots that is governed by stochastic recruitment processes. After intense disturbance, this phase corresponded to sharp increase of SLA and bark thickness and decrease of wood density weighted means, revealing prominent recruitment of species with efficient light acquisition, short-lived tissues and fast growth (Figure 4) (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011; Reich, 2014). The first recruitment phase then in addition involved short-lived and competitive species, *i.e.* hard pioneers, that rapidly dominated the recruited population and reduced its functional diversity.

Following this first phase, the recruitment progressively incorporated true recruits, *i.e.* individual trees that had germinated after disturbance. Disturbance trajectories corresponded to the interplay of random demographic processes of mature forests that progressively replaced deterministic processes involving selection and similarity limitation. The balance between both processes resulted in different trajectories according to the disturbance intensity.

After low disturbance intensity (T1 plots) the recruitment trajectories were determined by selective pressures towards light demanding species that underwent similarity limitation enhancing their functional diversity. Although

Punctual recruits CWM

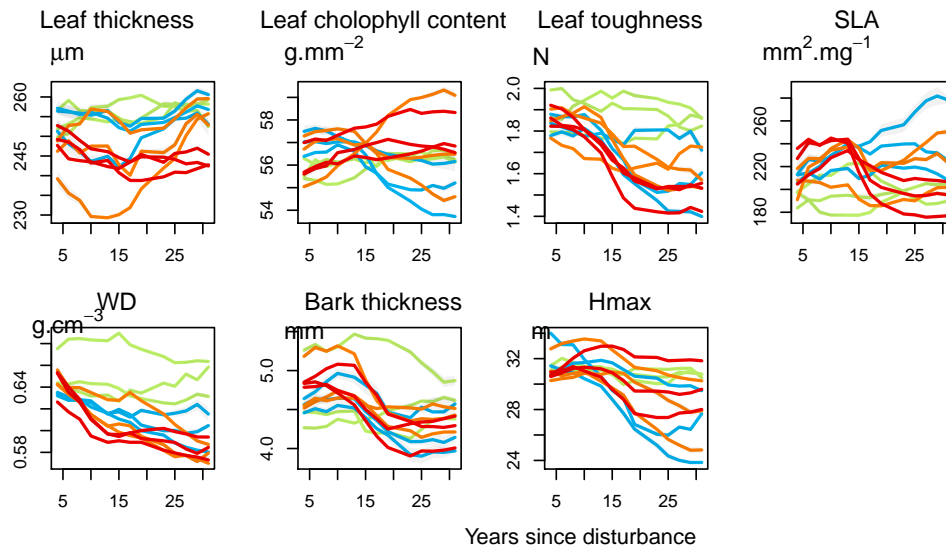


Figure 3. Community weighted means (CWM) of the four disturbance treatment for the four leaf traits, the two stem traits and the specific Hmax. Values reported correspond to the plot-level median obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling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

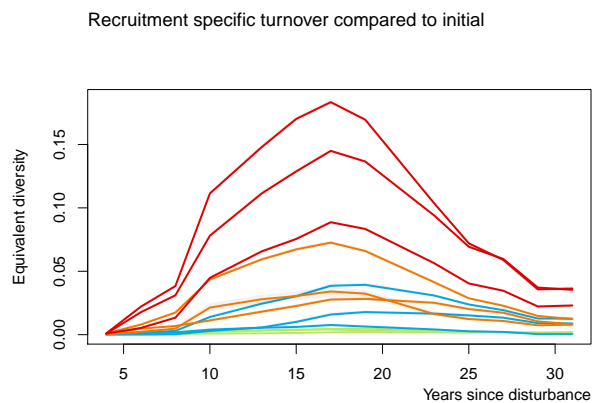


Figure 4. Trajectories over the 30 sampled years of the abundance-based turnover between recruited trees and initial communities before disturbance. Grey envelopes correspond to the 0.025 and 0.975 percentiles of the uncertainty propagation procedure and lines to the median in green for control, blue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

the taxonomic composition of the recruitment resembled the pre-disturbance composition the pool of recruited species was more restricted and evenly distributed. These restrictions revealed selective pressures favouring pioneers and light demanding species with efficient resource acquisition (high SLA and leaf chlorophyll content) and inexpensive, short-lived tissues (low leaf thickness and toughness, small Hmax and low wood density and bark thickness). In parallel the recruitment's functional diversity increased, equating or exceeding this of control plots, revealing an overdispersion of functional traits driven by the limitation of similarity. At this disturbance intensity, recruitment seemed preserved from the competitive exclusion of hard pioneers which would have prevented the maintenance of inferior competitors in the community and would thus have lowered the functional diversity (Hubbell *et al.*, 1999; Sheil & Burslem, 2003; Bongers *et al.*, 2009). The low dominance of hard pioneers might result from recruitment and dispersal limitation due to the short dispersal distance observed for tropical trees, specifically in Paracou with the genetic clumping of some pioneers (Leclerc *et al.*, 2015; Scotti *et al.*, 2015).

The trajectories after intense disturbance, first driven by the settlement of hard pioneers, progressively matched the same progressive balance between deterministic and stochastic processes. This translated by a progressive decrease of recruitment taxonomic turnover and an increase of functional diversity. Although acquisitive strategies remained dominant (high leaf chlorophyll content and low wood density and leaf toughness), the weighted values of other traits stabilized and the SLA and bark thickness decreased again (then following a unimodal trajectory with a peak after the first recruitment phase). The 15 years laps of the unimodal turnover and traits trajectories corresponding

to the first recruitment phase matched the life expectancy of hard pioneers and of their competitive pressure. The recruitment would progressively shift towards long-lived pioneers which participate to forest recovery as they might have been part of pre-disturbance communities, but still hold dominant more acquisitive functional strategies.

4.2 On the resilience of the recruitment process

Thirty years after disturbance, for all treatments the recruitment richness and functional diversity had recovered levels equivalent as those observed short after disturbance and in control plots. In contrast the species distribution evenness and functional diversity had not recovered for the most disturbed plots, displaying similar but unachieved trajectories as those of other plots. Still, the recruitment processes were restored for all treatments, the recruited species showed very low turnover compared to initial stands and the difference with random processes equated those of control plots. 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. Our results extend previous ones from the Paracou experiment, 10 years (Molino & Sabatier, 2001) and 20 years (Baraloto *et al.*, 2012) after disturbance which suggested the recovery towards pre-disturbance taxonomic and functional composition.

The trajectories of functional traits proved very different among plots and treatments, sometimes showing opposed tendencies (like for the Leaf Chlorophyll Content, SLA or Hmax), which suggested that the recovery may be, more than commonly thought, upon dependence of the pre-disturbance functional ecosystem signature (Héroult & Piponiot, 2018). For all traits the difference with control plots and initial conditions remained marked 30 years after disturbance, although the corresponding functional diversity had recovered. This supported the role of similarity limitation increasing maintaining high functional diversity whenever the dominant strategies.

These conclusions however are only valid for a single disturbance event, given that the second recruitment phase involves the seed bank and therefore triggers a storage effect likely to modify the recruitment trajectories after another disturbance event. In this hypothetical case, the competitive exclusion among dormant life-stage (seeds or even seedlings) would be harsher and likely bring more radical changes in the recruitment composition and functional profile.

5. Conclusion

The long-term study of recruitment diversity trajectories disentangle the mechanisms ruling recruitment dynamics after disturbance. While in undisturbed forests mechanisms like negative density dependence enhanced species diversity, dis-

turbance induced new mechanisms depending on its intensity. In the short-term communities response was driven by the enhanced growth of grown saplings benefiting from the alleviated competition and the environmental changes following disturbance. This resulted in increased communities taxonomic and functional evenness and a selection of more acquisitive functional strategies compared to mature forests. 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, rapidly recovering the pre-disturbance composition and recruitment processes. At high intensity, the recruitment incorporated long-lived pioneers which maintained high species turnover in the long term. Still, communities composition and functioning proved resilient to single disturbance events, maintaining the pre-disturbance difference among plots. The recruitment processes however relied on the diversified seed bank of mature forests that was altered by disturbance and therefore impacted communities resilience itself.

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