Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract
Résumé de l'article.

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Contents

1. Introduction

The large areas covered with tropical forests worldwide hold crucial economic, social and cultural value. They provide wood and multiple non-timber forest products, shelter for a diversified fauna, regulate the local climate, support the carbon, water and nutrient cycles, and ensure cultural and human well-being. The simultaneous increase of forests products demand and substantial climatic changes heightened the pressure on the remaining forests (Gibson *et al.*, 2011; Morales-Hidalgo *et al.*, 2015) and threatened the maintenance of communities structure, composition and functioning and their underlying dynamics (Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015).

In tropical forests communities are shaped by a constant range of disturbance that changes the abiotic environment, as the light, heat and water fluxes, and the biotic interaction and competitive pressure. The cornerstone of tropical forests ecology is then to understand their response to disturbance and its mechanisms (White & Jentsch, 2001; Chazdon, 2003). Forests response to disturbance has been largely studied through structural parameters rapid and convenient to measure, as aboveground biomass, tree height or stem density. These structural parameters have then been sucessfully modeled and assessed the maintenance of ecosystems processes and services (Denslow & Guzman, 2000; Blanc *et al.*, 2009; Rutishauser *et al.*, 2016). However the response of tree species diversity although it is determinant of ecosystems productivity, stability and functioning (Tilman *et al.*, 2014) and it would be most probably impacted by the biotic and abiotic changes after disturbance (Cazzolla Gatti *et al.*, 2014).

In the short-term diversity dynamics demonstrated negligible or even positive impacts of disturbance on communities diversity, which have been formalized by the intermediate disturbance hypothesis (IDH) stating a maximized species diversity at intermediate disturbance intensity (Molino & Sabatier, 2001; Kariuki *et al.*, 2006; Berry *et al.*, 2008). However, validations of the IDH in the long term remain scarce and mainly rely on the analysis of species richness that gives limited or misleading information on forests recovery and functioning (Martin *et al.*, 2015; Chaudhary *et al.*, 2016). More releveant monitoring would encompass communities composition, that are crucial for conservation issues, and evenness, that revealing ecological rules underlying communities' structure (Magurran, 1988; Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Furthermore, the functional approach accounting for species biological attributes would be insightful as it reveals species fitness and

ecosystems functioning (Violle *et al.*, 2007; Moretti *et al.*, 2009; Baraloto *et al.*, 2012; Scheiter *et al.*, 2013). In that respect major functional traits related to species ecology and performance were largely adopted through a relevant framework (Díaz *et al.*, 2005; Villéger *et al.*, 2008). The functonial trait-based approach, for example, highlighted in tropical rainforests the environmental filters fostering disturbance resistant species with rapid growth and efficient resources acquisition (Molino & Sabatier, 2001; Haddad *et al.*, 2008). This translated by shifts from "conservative" slow-growing species dealing with scarce resources, to "acquisitive" fast-growing species with rapid and efficient use of abundant resources (TerSteege & Hammond, 2001; Reich, 2014; Hérault *et al.*, 2011). It was mirrored by shifts in key functional traits related to resource acquisition (leaf area, density and chlorophyll content, and stem specific gravity and bark thickness), tree growth and reproduction life history traits (seed mass and maximum height) (Wright *et al.*, 2004; Westoby & Wright, 2006; Chave *et al.*, 2009). A proper monitoring of communities response should therefore encompass taxonomic and functional diversity and composition measures to test the validity of the IDH in the long term for tropical forests, and clarify the resilience of communities evenness, composition,and also functioning. The trajectories followed by all these facets would highlight the role of deterministic processes, like competitive exclusion or abiotic selection, and the communities' convergence maintaining intrinsinc differences in diversity and composition,which is as much insgights for future adaptive conservation strategies (Adler *et al.*, 2007).

Here we investigated over 30 years the response of 75 ha of forests plots set up on a gradient of disturbance intensity, from 10 to 60% of ecosystem biomass removed. We made use of a large functional traits database browsing major leaf, stem and seed traits and species maximum height to draw the trajectories over time of communities taxonomic and functional composition and diversity. Specifically, we (i) tested the validity of the IDH in the long term for tropical hiperdiverse forest and highlighted the ecological rules shaping their response to disturbance, (ii) clarified the different facets of communities resilience in terms of communities composition, diversity and functioning (iii) questioned the completeness of communities recovery given the altered functional redundancy. >>revoir la fin

2. Material and Methods

2.1 Study site
Paracou station in French Guiana (5°18'N and 52°53'W) is located in a lowland tropical rain forest corresponding to a tropical wet climate with mean annual precipitation averaging 2980 mm.y^{-1} (30-y period) with 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 between 5 and 50 m and mean annual temperature is 26°C. Soils correspond to thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains. The experiment corresponds to a network of twelve 6.25ha plots that have undergone a gradient of three logging, thinning and fuel-

wood treatments (Table 1). Disturbance treatments were attributed according to a randomized plot design with three replicate blocks of four plots. The disturbance corresponds to averages of 10 trees removed per hectare with a diameter at 1.3 m height (DBH) above 50 cm for treatment 1 (T1), 32 trees/ha above 40 cm DBH for treatment 2 (T2) and 40 trees above 40 cm DBH for treatment 3 (T3). Treatments T2 and T3 besides included the thinning of trees by poison girdling (Blanc *et al.*, 2009).

2.2 Inventories protocol and dataset collection
The study site corresponds to a tropical rainforest with a dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae botanical families. In the twelve experimental plots of the experiment, 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. In 1984, specific vernacular names were given to 62 commercial or common species whereas other less common species were identified under two identifiers only separating trees and palm trees. The botanical campaigns carried every 5 to 6 years to identify all trees at the species level only started in 2003 and identification practices varied among plots and successive campaigns. This 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 throught a Bayesian framework. The uncertainty propagation was done by the replenishment of inventories completed at genus level from real incomplete ones on the basisof vernacular/botanical names association.

Vernacular names were replaced through multinomial trials $M_v\left([s_1, s_2, \ldots, s_N], [\alpha_1, \alpha_2, \ldots, \alpha_3]\right)$ 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.

To avoid remaining identification caveats and consider complete inventories, the simulated inventories were then reported at genus. See appendix 1 and Aubry-Kientz *et al.* (2013) for the detailed methodology.

The functional diversity metrics used a dataset for 6 functional traits representing leaf economics (leaves thickness, toughness, total chlorophyll content and specific leaf area, the leaf area per unit dry mass) and wood economics (wood specific gravity and bark thickness), and life history traits (maximum specific height and seed mass).

The trait database came from the BRIDGE project [^1] where traits values were assessed from a selection of individuals located in nine permanent plots in French Guiana, including two in Paracou. Missing trait values were filled using multivariate imputation by chained equation (mice) restricted to samples pertaining to the next higher taxonomic level, in order to account for the phylogenetic signal of the functional traits. The dataset comprised 294 botanical species pertaining to 157 botanical genera.

Whenever a species inventoried was not in the dataset, it was attributed a set of traits values randomly sampled

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	$[35\% - 56\%]$

among species of the same next higher taxonomic level. As seed mass information corresponds to a classification into mass classes, no data filling process was applied so analysis were performed considering the 414 botanical species of the seed mass dataset. All composition and diversity metrics corresponded to the average obtained after 50 iterations of the taxonomic uncertainty propagation framework and of the filling process of missing trait values.

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

2.3 Composition and diversity metrics

To counter the remaining taxonomic uncertainty plots taxonomic composition and diversity were analysed at the genus level, *i.e.* referring to the genus of observed or trialed botanical names. Variations in plots taxonomic and functional composition after disturbance was visualized by their trajectories in a two-dimensional ordination space over 30 years. Two NMDS were conducted, either from taxonomic flora inventories or from plots functional composition based on the 8 leaf, stem and life history traits. Plots trajectories along time was reported comparatively to the inventories in 1989, 5 years after disturbance, which corresponded to first inventory with a sufficient degree of uncertainty (<30% of undetermined trees). The inventories dissimilarity compared to the reference 1989 inventory was reported using occurrence-based (Jaccard) and abundance-based (Bray-Curtis) similarity measures. The trajectory of inventories along time was visualized with the euclidean distance in the two-dimensional ordination space to the 1989 inventory. The trajectories of the leaf and stem and life traits were also visualized with the 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; et al. Garnier, 2004). To compensate the intrinsinc difference among plots the trajectories corresponded to the differences along time with the reference inventory in 1984 (5 year after disturbance). Species seed mass corresponded to 5 classes of increasing mass, seed mass trajectories were therefore reported as the proportion of each class in the inventories.

The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973).

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 proved well suited for diversity studies (Patil & C., 1982; Tothmeresz & Tóthmérész, 1995). The functional diversity was reported using the Rao index of quadratic entropy which combines species abundance distribution and average pairwise dissimilarity based on all functional and life traits.

3. Results

3.1 Disturbance impacts on communities composition and average functional traits values

3.1.1 Composition trajectories

Over time, 828388 trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. Taxonomic and functional plots trajectories were examined through the ordination in a two dimensional ordiantion space of successive inventories from 1989 (5 years after disturbance) to 2015 (31 years after disturbance). Classifications were performed using either abundance-based Bray-Curtis (Figure 1) or incidence-based Jaccard dissimilarity, this last having given similar results (data not shown).

Both taxonomic and functional composition of disturbed plots followed consistent trajectories over time, translating compositional changes while control plots remained stable. The addition of functional traits in the two dimensional space revealed a shift of plots composition towards more acquisitive functional strategies (disturbed plots changed from high average WD to high average SLA and chlorophyll content). The dissimilarity of the successive inventories for disturbed plots compared to their respective reference inventory in 1989 followed unimodal trajectories (AppendixI, Figure A2). The maximum dissimilarity of plot strajectories was positively correlated to the disturbance intensity for taxonomic ($\rho_{spearman}^{taxonomic} = 0.91$) as well as functional composition ($\rho_{spearman}^{taxonomic} = 0.96$). The time at maximum dissimilarity for taxonomic composition was reached around 26 years after disturbance while it was 22 years for functional
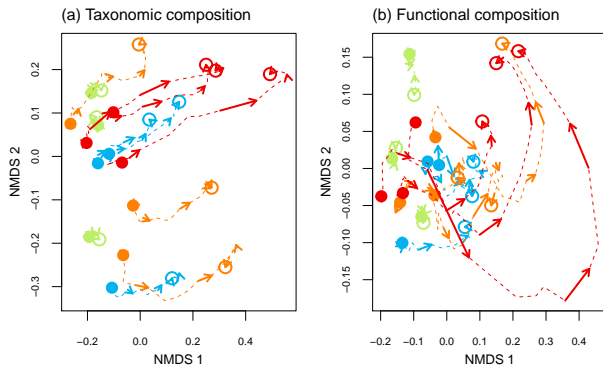
Figure 1. Trajectories of the plots in terms of **(a)** flora composition and **(b)** functional composition regarding the 6 leaf and stem functional traits,the maximum allometric height and seed mass class in the two-dimensional space from the NMDS performed for the 30 years after disturbance. Distance matrix for NMDS were computed from the Bray-curtis dissimilarity between successive inventories. Line colors represent the disturbance treatment (green for control, blue for T1,orange for T2 and red for T3).

composition. All trajectories returned towards the initial composition and translated cyclic compositional changes as visualized in figure (Figure 1).

3.1.2 Traits community weighted means
The changes observed in plots functional composition went hand to hand with consistent trajectories of the 8 functional and life history traits (Leaf thickness, chlorophyll content, toughness and specific area,wood specific gravity and barck thickness and seed mass and maximum adult height) visaualized with plots community weighted means (CWM) (Figure 2).

Except for leaf cholorphyll content, which continued to increase for some T3 and T2 plots 30 years after disturbance, all traits and seed mass proportions displayed a unimodal trajectories. The weighted means of communities specific maximum height at adult stage ($Hmax$), leaf toughness ($L\_toughness$) and wood specific gravity (WD) remained significantly lower than their initial value and than these of the control plots (Figure 2). The weighted means of bark thickness ($Bark\_thick$) similarly remained substantilly higher than initially for all disturbed plots while the specfic leaf area (SLA) had almost recovered its initial value and this of the undisturbed plots at the end of the experiment. Once again the maximum difference to initial state was correlated to the disturbance intensity ($\rho_{spearman}^{L_t hickness} = 0.67$, $\rho_{spearman}^{L_c hloro} = 0.45$, $\rho_{spearman}^{L_t oughness} = -0.43$, $\rho_{spearman}^{SLA} = 0.93$, $\rho_{spearman}^{WD} = -0.78$, $\rho_{spearman}^{Bark-thickness} = 0.88$, $\rho_{spearman}^{Hmax} = -0.48$).

3.2 Trajectories of communities diversity after disturbance

3.2.1 Taxonomic diversity
Trajectories of Richness, Shannon and Simpson taxonomic diversity were examined at genus level in relation to the 1989 inventories (5 years after disturbance) (Figure 3).

For undisturbed plots the Richness, Shannon and Simpson diversity remained stable over the 30 monitored years. After disturbance the richness increased when the disturbance intensity was low, with a maximum increase of 14 botanical genuses (plot 3 from treatment 2). When the disturbance was intense however, plot staxonomic richness followed a unimodal decrease with a return to initial values after intense disturbance. The taxonomic evenness (Shannon and Simpson diversities) significantly increased whenever the disturbance intensity. The evenness followed a unimodal trajectory with a just beginning return towards initial values and a maximum reached around 20 years and positively correlated to the disturbance intensity ($\rho_{spearman}^{Shannon} = 0.86$, and $\rho_{spearman}^{Simpson} = 0.89$). Only two T3 plots, plots 8 and 12, remained increasing 30 years after disturbance 3), suggesting a similar be much delayed unimodal trajectory.

3.2.2 Functional diversity
The functional diversity trajectories of plots based on the 8 leaf, stem and life history traits was examined through the Rao diversity. For all undisturbed plots the functional diversity remained comparable to the reference values 5 years after disturbance (1989 inventories). For all disturbed plots the functional trajectories followed a unimodal trajectory with a maximum positively correlated to disturbance intensity ($\rho_{spearman} = 0.73$) (Figure 4). The plot 7 from treatment 1 that displayed a constantly outlying diversity was removed from the graphical representation for better readability, see appendix for full graph. Thirty years after disturbance all plots, whenever the initial disturbance intensity, regained diversity values similar to their initial avule and to those of control plots.

4. Discussion

4.1 A validation of the intermediate disturbance hypothesis
The monitoring of disturbed forest communities confirmed a limited negative impact of disturbance on species richness, as observed on several post logging surveys (Cannon, 1998; Baraloto *et al.*, 2012). Thirty years after disturbance, the genus richness was restored to initial plot values after high disturbance intensity while it substantially increased after low disturbance intensity, reaching a gain of almost 12 genuses for some plots.

Both richness and evenness after disturbance followed asymptotic trajectories, sharply increasing for 15 years before stabilizing at higher values than those of control plots. An increase of communities evenness stems from a higher homogeneity of species distribution. After disturbance, communities are made of the old, pre-disturbance survivors and the newly recruited trees: changes in composition and abundance distribution are to be found in the recruitment processes and in the pre-disturbance survivors mortality. The composition of old survivors proved to mirror the initial community (Hérault & Piponiot, 2018), which leads to support a species turnover among recruited trees with enhanced growth and survival of previously infrequent species. Indeed, the increase in taxonomic diversity was accompanied by an increase of taxonomic dissimilarity with plots ini-
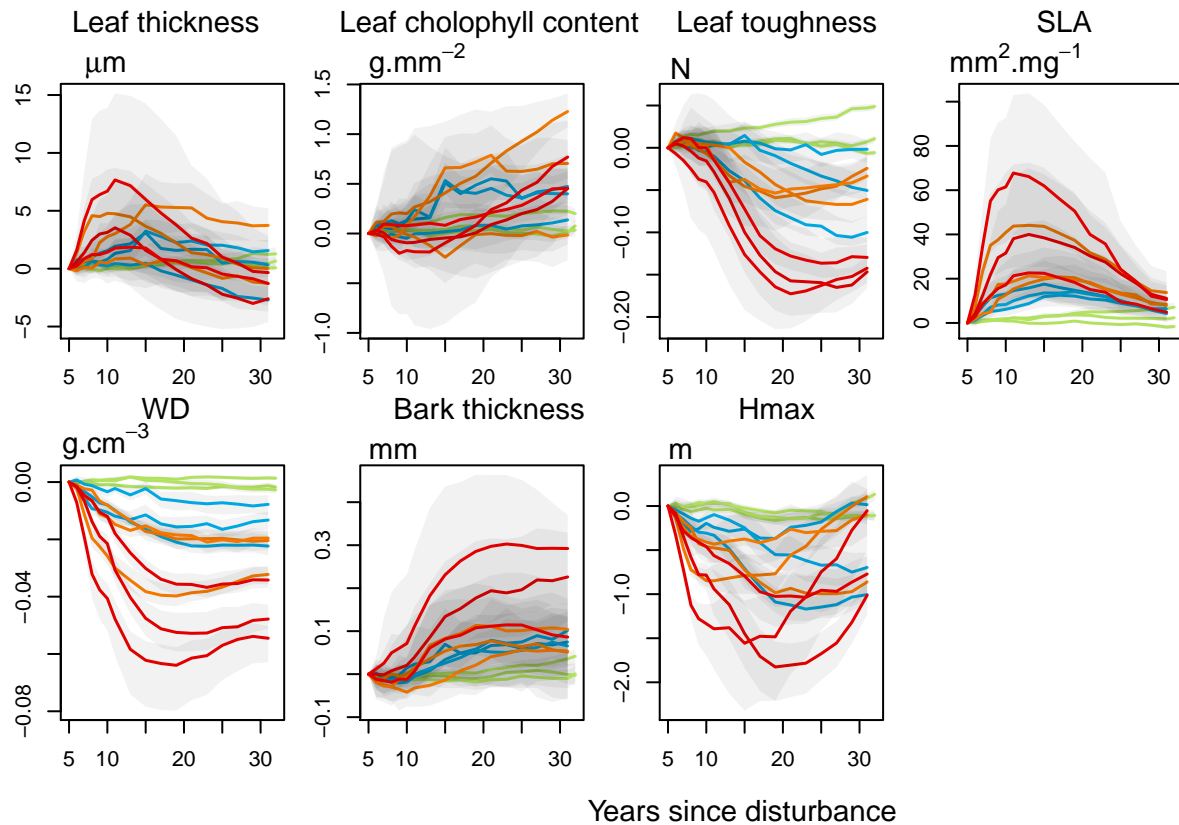
Community Weighted Means

Figure 2. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, *L_thickness*, chlorophyll content, *L_chloro*, toughness, *L_toughness* and specific area, *SLA*), 2 stem traits (wood specific gravity, *WD*, and bark thickness, *Bark-thick*) and one life trait (Specific maximum height at adult stage, *Hmax*). Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colorswith green for control, blue for T1,orange for T2 and red for T3.
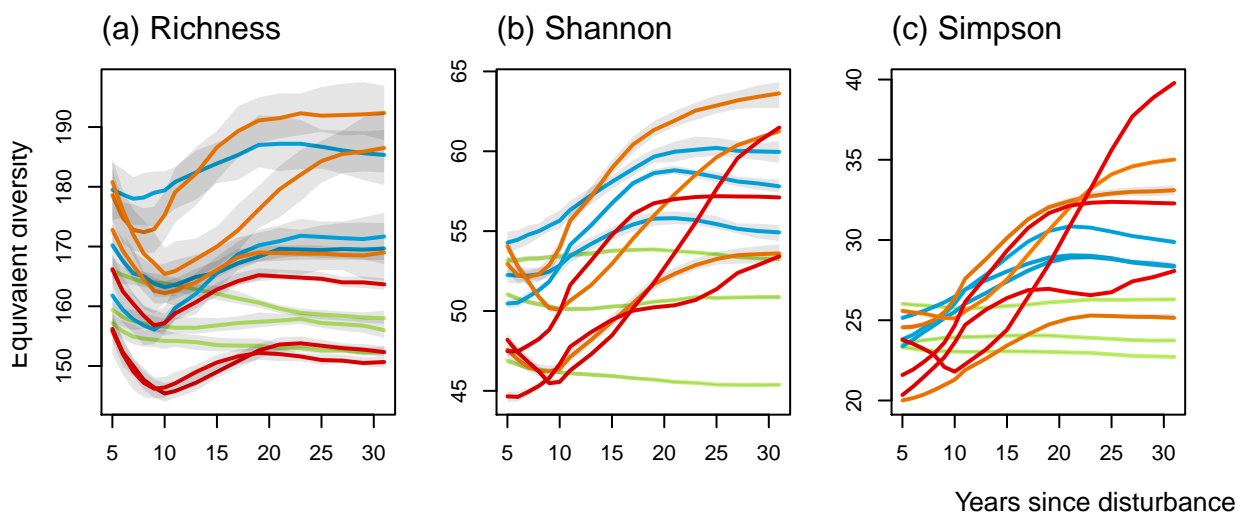

Figure 3. Trajectories of the difference to the 1989 inventories (5 years after disturbance) over 30 years after disturbance of plots communities **(a)** Richness, **(b)** Shannon and **(c)** Simpson diversities. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation. Initial treatments are represented by solid lines colors with green for control, blue for T1,orange for T2 and red for T3.

Rao diversity

Figure 4. Trajectories of the Rao functional diversity over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation. Initial treatments are represented by solid lines colorswith green for control, blue for T1,orange for T2 and red for T3.and the missing trait value filling processes.
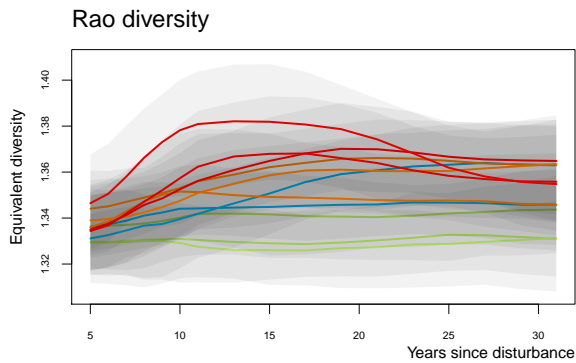
tial state and a functional shift towards resource-acquisitive strategies (sharp increase in the SLA, leaf thickness and bark thickness and decrease in wood density, leaf toughness and maximum height) (Westoby, 1998; Wright *et al.*, 2004; Reich, 2014). Disturbance then causes a reorganization of the typical high dominance structure of hyperdiverse mature forests after disturbance, benefiting to pioneers and light demanding species. Likely, the changes in abiotic environment and competitive pressure favored pioneers which outcompete others in non limiting resources but are excluded in mature forests by long-lived, more resistant and shade tolerant species.

As stated by the IDH, communities dynamics after disturbance then rely on species functional strategy and corresponding ability to fill the environmental niches made available by disturbance. Recruited species then mix with pre-disturbance ones from which they differ and constitue a community all the more diversified that the disturbance is intense (Molino & Sabatier, 2001).

4.2 On the recovery of disturbed communities

The trajectories of almost all leaf and stem functional traits, life history traits,and functional diversity followed a hump-back trajectory which maximum were positively correlated to the disturbance intensity, and were recovering towards initial values after 30 years that trajectory. Functoinal traits and communities functional diversity are the most direct link between biodiversity and ecosystem functioning (Díaz *et al.*, 2005): these trajectories reflected a consistent recovery in the long term of ecosystem processes (Guariguata & Ostertag, 2001).

Same hump-back trajectories were followed by the composition of plots species and functoinal composition. This similarly meant a recovery of the pre-disturbance state and the maintenance of the initial differences among plots which supports the idea of a convergence of communities compo-

sition (Hubbell *et al.*, 1999; Molino & Sabatier, 2001; Baraloto *et al.*, 2012). Although plots followed homogeneous trends these initial differences in compositon difference, and probably also some abiotic parameters, strongly determined the maximum and time path of the trajectories (Anderson, 2007)•.

4.3 Functional redundancy of disturbed ecosystems

Despite the consistent recovery of initial diversity and composition there was a time lag between the trajectories followed by taxonomic and functional characteristics. Taxonomic composition had longer time path and while communities had recovered their functional characteristics, their taxonomic composition and evenness remained altered by disturbance. This delay between functional and taxonomic dynamics was already observed for grasslands (Tilman, 1997; Mouillot *et al.*, 2011) and more recently for tropical forests (Lohbeck *et al.*, 2015; Guariguata & Ostertag, 2001). The functional diversity of communities rely on the functional strategy of dominant species, according to the "vegetation quantity effect" (Grime, 1998). The functional trajectories of communities are then driven first by the increase of diversity and evenness of dominant species and then by the recruitment of species resembling the old pre-disturbance community which reduced the overall diversity. Although dominant species restoredthe functional pre-disturbance characteristics, communities composition remained altered and the infrequent species of initial communities remain missing to achieve plots recovery. According to the funcitonal traits trajectories, those infrequent species would match the dominant functional type and would participate to the functional redundancy. The functional redundancy, thas is the functional overlap between species that is typical of the huge biodiversity of tropical forests (Bellwood *et al.*, 2006), therefore was not restored 30 years after disturbance and this is majr to consider as it defines forests' resilience (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

Besides the long-term alteration of functional redundancy, the persistent compositional changes which might have favored disturbance resistant species (Haddad *et al.*, 2008), lianas or epiphytes (Martin *et al.*, 2013) and would probably have come along with environmental change, like in the soils nutrient cycling and compaction (Olander *et al.*, 2005). These presistent changes highly question forest's resilience(Chazdon, 2003). New conditions would not only be longer lasting but self-maintained as tied to disturbance regime (Burslem *et al.*, 2000). Specificaly, this would impair species contingent to undisturbed forests, threatening their maintenance, and run the risk to loose cornerstone species and trigger unexpected ecological consequences (Jones *et al.*, 1994; Díaz *et al.*, 2005; Gardner *et al.*, 2007).

5. Conclusions

Our study showed the significant impact of disturbance on tropical forests communities. It validated the consistency of the IDH in the long term and revealed the contrasting response of taxonomic and functional characteristics with

the decoupling between communities taxonomic evenness and their functional diversity and th dominant functional strategies. Communities recovery remained unachieved but consistent recovery of communities assembly for the lowest disturbance intensity but questioned it after higher disturbance.

References

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**, 780–793.

Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D. & DeLucia, E.H. (2013) Altered dynamics of forest recovery under a changing climate. *Global Change Biology*, **19**, 2001–2021.

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.

Bellwood, D., Wainwright, P., Fulton, C. & Hoey, A. (2006) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 101–107.

Berry, N.J., Phillips, O.L., Ong, R.C. & Hamer, K.C. (2008) Impacts of selective logging on tree diversity across a rainforest landscape: The importance of spatial scale. *Landscape Ecology*, **23**, 915–929.

Blanc, L., Echard, M., Herault, B., Bonal, D., Marcon, E., Baraloto, C. & Chave, J. (2009) carbon stocks Dynamics of aboveground in a selectively logged tropical forest. *Ecological Applications*, **19**, 1397–1404.

Burslem, D.F.R.P., Whitmore, T.C. & Brown, G.C. (2000) Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology*, **88**, 1063–1078.

Cannon, C.H. (1998) Tree Species Diversity in Commercially Logged Bornean Rainforest. *Science*, **281**, 1366–1368.

Cazzolla Gatti, R., Castaldi, S., Lindsell, J.A., Coomes, D.A., Marchetti, M., Maesano, M., Di Paola, A., Paparella, F. & Valentini, R. (2014) The impact of selective logging and clearcutting on forest structure, tree diversity and above-ground biomass of African tropical forests. *Ecological Research*, **30**, 119–132.

Chaudhary, A., Burivalova, Z., Koh, L.P. & Hellweg, S. (2016) Impact of Forest Management on Species Richness: Global Meta-Analysis and Economic Trade-Offs. *Scientific Reports*, **6**, 1–10.

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.

Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 51–71.

Denslow, J.S. & Guzman, G.S. (2000) Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science*, **11**, 201–212.

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. *Ecosystems and human well-being: Current state and trends*, pp. 297–329 ST – Biodiversity Regulation of Ecosystem.

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.

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488–494.

et al. Garnier, E. (2004) Pant functional markers capture ecosystem properties during secondary successsion. *Ecology*, **85**, 2630–2637.

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.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, **478**, 378–381.

Grime, J. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Guariguata, M.R. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, **148**, 185–206.

Haddad, N.M., Holyoak, M., Mata, T.M., Davies, K.F., Melbourne, B.A. & Preston, K. (2008) Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters*, **11**, 348–356.

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. & 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 (Washington D C)*, **283**, 554–557.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Ecosystem management*, pp. 130–147. Springer.

Kariuki, M., Kooyman, R.M., Smith, R.G.B., Wardell-Johnson, G. & Vanclay, J.K. (2006) Regeneration changes in tree species abundance, diversity and structure in logged and unlogged subtropical rainforest over a 36-year period. *Forest Ecology and Management*, **236**, 162–176.

Lavorel, S. & Garnier, É. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. *Functional ecology*, **16**, 545–556.

Lohbeck, M., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Poorter, L. & Bongers, F. (2015) Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. *PLoS ONE*, **10**, 1–15.

Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton, nj, prince edition.

Martin, P.A., Newton, A.C. & Bullock, J.M. (2013) Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20132236–20132236.

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.

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

Morales-Hidalgo, D., Oswalt, S.N. & Somanathan, E. (2015) Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. *Forest Ecology and Management*, **352**, 68–77.

Moretti, M., De Bello, F., Roberts, S.P. & Potts, S.G. (2009) Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology*, **78**, 98–108.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason, N.W. (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, **6**.

Olander, L.P., Bustamante, M.M. & Asner, G.P. (2005) Surface Soil Changes Following Selective Logging in an Eastern Amazon Forest. *Earth Interaction*, **9**.

Patil, G. & C., T. (1982) Diversity as a concept and its measuremente: Rejoinder.

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

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

Scheiter, S., Langan, L. & Higgins, S.I. (2013) Next-generation dynamic global vegetation models: learning from community ecology. *The New phytologist*, **198**, 957–69.

Sist, P., Pacheco, P., Nasi, R. & Blaser, J. (2015) Management of natural tropical forests for the future. Technical report, IUFRO WFSE.

TerSteege, H. & Hammond, D.S. (2001) Character Convergence , Diversity , and Disturbance in Tropical Rain Forest in Guyana. *Ecology*, **82**, 3197–3212.

Tilman, D. (1997) The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science*, **277**, 1300–1302.

Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 471–493.

Tothmeresz, B. & Tóthmérész, B. (1995) Comparison of different methods for diversity ordering. *Journal of Vegetation Science*, **6**, 283–290.

Trenbath, B.R. (1999) Multispecies cropping systems in India - Predictions of their productivity, stability, resilience and ecological sustainability. *Agroforestry Systems*, **45**, 81–107.

Villéger, Mason & Mouillot (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. *Ecology*, **89**, 2290–2301.

Violle, C., Navas, M.L.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (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.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.

Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.

White, P.S. & Jentsch, A. (2001) The Search for Generality in Studies of Disturbance and Ecosystem Dynamics. *Progress in Botany*, volume 62, pp. 399–450. Springer.

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.