

Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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Abstract

Résumé de l'article.

Keywords

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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	Composition and diversity metrics	3
3	Results	3
3.1	Communities Diversity	3
3.2	Communities composition	4
	Taxonomic and functional trajectories • Traits community weighted means (CWM) • Functional redundancy	
4	Discussion	8
4.1	Decoupled recovery of communities taxonomic and functional characteristics	8
4.2	A validation of the intermediate disturbance hypothesis	8
4.3	Functional redundancy of disturbed ecosystems . . .	8
5	Conclusions	9

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 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 currently heighten the pressure on the remaining forests (Gibson *et al.*, 2011; Morales-Hidalgo *et al.*, 2015). It threatens the maintenance of communities structure, composition and functioning and the underlying dynamics in space and time (Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015).

In tropical forest, ecological communities are constantly re-shaped by the natural disturbance events that changes the abiotic environment, through the fluxes of light, heat and water, and the biotic interaction and competitive pressure (Goulamoussène *et al.*, 2017). The cornerstone of tropical forests ecology is then to understand the underlyings of ecosystem response to disturbance, its mechanisms and drivers (White & Jentsch, 2001; Chazdon, 2003). For now, this has been largely studied through structural parameters, rapid and convenient to measure, as above-ground biomass, tree height or stem density (Piponirot *et al.*, 2016; Rutishauser *et al.*, 2016). These structural parameters have then been successfully modeled and allowed to assess the maintenance of ecosystems processes and services (Denslow & Guzman, 2000; Blanc *et al.*, 2009). However the response of tree species diversity remains unclear, also it is determinant of ecosystems productivity, stability and functioning (Tilman *et al.*, 2014; Liang *et al.* (2016)) and would be most probably impacted by post-disturbance environmental changes (Baraloto *et al.*, 2012).

In the short-term disturbance demonstrated negligible or even positive impacts 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). Validations of the IDH in the long term, however, remain scarce and mainly rely on the analysis of the rough species richness that gives limited or misleading information on forests recovery and functioning (Martin *et al.*, 2015; Chaudhary *et al.*, 2016). More relevant monitoring would encompass communities composition, that is crucial for conservation issues, and diversity profiles, that reveals ecological rules underlying communities' structure (Magurran, 1988; Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Furthermore,

the functional approach accounting for differences species biological attributes would be insightful as it reveals the species role in the post-disturbance trajectory of 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 an integrative framework (Díaz *et al.*, 2005; Villéger *et al.*, 2008). The functional 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). In disturbed tropical rainforests, this framework translates into the fostering of disturbance resistant species with rapid growth and efficient resources acquisition (Molino & Sabatier, 2001; Haddad *et al.*, 2008). It results in a shift from “conservative” slow-growing species dealing with scarce resources that dominate before disturbance, 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 intrinsic differences in diversity and composition, which is as much insights 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 hyperdiverse 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.

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-month dry season (< 100 mm.month⁻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). The disturbance intensity was measured as the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984 and five years after disturbance (ref to be found). Biomass measurements were performed with the BIOMASS package R package (REJOU-MECHAIN *et al.*, 2018).

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 through a Bayesian framework. The uncertainty propagation was done by the replenishment of inventories completed at genus level from real incomplete ones on the basis of vernacular/botanical names association.

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.

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

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% – 66%]

where trait 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 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.

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 over 30 years in a two-dimensional ordination space. Two NMDS were conducted, either from taxonomic flora inventories or from plots functional composition based on the 7 leaf, stem and life history traits (without seed mass classes). In both cases the NMDS were performed using occurrence-based (Jaccard) as well as abundance-based (Bray-Curtis) dissimilarity measures. Trajectories along time were reported through the euclidean distance of successive inventories to the reference inventories in 1989, 5 years after disturbance, when the uncertainty degree did not exceed 30% of undetermined trees. 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 intrinsic

difference among plots the trajectories corresponded to the differences along time with the reference inventory in 1989. 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; Tothmérés, 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.

The functional redundancy was measured as the overlap among species in communities' functional space (Carmona *et al.*, 2016). The samples of the trait database were first located with a PCA analysis in a two-dimensional functional space summarizing the 8 functional traits considered. We choose to summarize species functional space through a PCA because functional traits considered were already somehow redundant and allows not to overweight the role of one trait. Then, multivariate kernel density estimator associated with individual trees were summed to give the distribution of traits probabilities of each species. For each community the trait probability distributions of corresponding species were combined and weighted by species abundance. Eventually communities functional redundancy was measured as the sum of overlap between species weighted functional density. Communities functional redundancy is expressed as the average number of species that could be removed from the community without reducing the functional space.

3. Results

3.1 Communities Diversity

Communities taxonomic diversity trajectories were examined through the Richness, Shannon and Simpson diversities at genus level, in relation to the 1989 inventories (5 years

after disturbance) (See annexe I). For undisturbed plots the Richness, Shannon and Simpson diversities remained stable over the 30 years monitored. After low disturbance intensity the richness increased, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2). After intense disturbance, plots taxonomic richness followed unimodal trajectories first decrease for around ten years and then increasing to return to pre-disturbance values. For all disturbed plots the taxonomic evenness (Shannon and Simpson diversities) increased, following unimodal trajectories with a just beginning return towards initial values after 30 years. The maximum evenness, reached after around 20 years, was positively correlated to the disturbance intensity ($\rho_{\text{spearman}}^{\text{Shannon}} = 0.86$, and $\rho_{\text{spearman}}^{\text{Simpson}} = 0.89$). Only two T3 plots (plots 8 and 12) were still increasing 30 years after disturbance 1, suggesting similar but delayed trajectories.

Communities functional diversity trajectories were examined through the Rao diversity based on the 7 leaf, stem and life history traits (the seed mass was excluded as a qualitative variable). The plot 7 from treatment 1 displayed a constantly outlying diversity and was removed from the graphical representation for better readability (see appendix for full graphs). The functional diversity of all undisturbed communities remained stable along the 30 years. For all disturbed communities the functional diversity followed unimodal trajectories with a return towards the initial state, comparable to the control plots.

The impact of disturbance was examined specifically through the linear correlation between the disturbance intensity (initial %AGB removed) and the Simpson and Rao diversities (diversities of order 2) at three focus times after disturbance (10, 20 and 30 years) 1. The Simpson diversity was weakly related to the disturbance intensity ($R^2 < 0.25$) and only from 20 years after disturbance. The Rao diversity was more strongly correlated to the disturbance intensity ($0.55 < R^2 < 0.75$) for the three times studied. The impact of disturbance, translated by the slope of the linear correlation, was the highest 20 years after disturbance.

3.2 Communities composition

3.2.1 Taxonomic and functional trajectories

In the inventories from 1989 (5 years after disturbance) to 2015 (31 years after disturbance), 828388 trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. The trajectories of taxonomic and functional composition were visualized in a two dimensional ordination space mapping the successive inventories according to their flora and the corresponding traits. Classifications were performed using either abundance-based Bray-Curtis (Figure 2) or incidence-based Jaccard dissimilarity. Both metrics gave similar results, so only analysis using Bray-Curtis dissimilarity will be discussed here.

While both taxonomic and functional composition remained stable in undisturbed communities, after disturbed they followed consistent trajectories over time that revealed significant compositional changes. Considering the mapping of functional traits in the same dimensional space, the post-disturbance trajectories corresponded to shifts towards more acquisitive functional strategies: disturbed communities changed from high average WD to high average SLA

and chlorophyll content. For disturbed communities the distance of successive inventories to the reference inventory in 1989 followed unimodal trajectories (AppendixI, Figure A2). The maximum of communities dissimilarity to their initial state was positively correlated to the disturbance intensity for both taxonomic and functional composition ($\rho_{\text{spearman}}^{\text{taxonomic}} = 0.91$ and $\rho_{\text{spearman}}^{\text{functional}} = 0.96$ respectively). The time at maximum dissimilarity was reached around 26 years after disturbance for taxonomic composition and 22 years for functional composition. All trajectories followed cyclic composition changes with a return towards the initial composition (Figure 2).

3.2.2 Traits community weighted means (CWM)

The changes observed in plots functional composition went hand to hand with consistent trajectories of the 8 functional and life history traits visualized through plots community weighted means (CWM) (Figure 3) of the leaves thickness, chlorophyll content, toughness and specific area, wood specific gravity, bark thickness, seed mass and maximum adult height.

Except for leaf chlorophyll content, which continued to increase for some T3 and T2 plots, all traits and seed mass proportions followed a unimodal trajectories and either stabilized or returned towards their initial values 30 years after disturbance. At that time the weighted means of communities specific maximum height at adult stage (H_{max}), leaf toughness ($L_{\text{toughness}}$) and wood specific gravity (WD) remained significantly lower than their initial value and than these of the control plots (Figure 3). The weighted means of bark thickness (B_{thick}) similarly remained substantially higher than initially for all disturbed plots while the specific leaf area (SLA) had almost recovered its initial value, similar as those of undisturbed plots. For all traits the maximum difference to initial state was correlated to the disturbance intensity ($\rho_{\text{spearman}}^{L_{\text{thickness}}} = 0.67$, $\rho_{\text{spearman}}^{L_{\text{chloro}}} = 0.45$, $\rho_{\text{spearman}}^{L_{\text{toughness}}} = -0.43$, $\rho_{\text{spearman}}^{SLA} = 0.93$, $\rho_{\text{spearman}}^{WD} = -0.78$, $\rho_{\text{spearman}}^{B_{\text{thick}}} = 0.88$, $\rho_{\text{spearman}}^{H_{\text{max}}} = -0.48$).

3.2.3 Functional redundancy

Communities functional redundancy was measured as the sum of weighted overlap among species in communities' functional space. Functional spaces were defined in the main two-dimensional space of a PCA analysis summarizing the 7 leaf, stem, and maximum height traits (see appendix I for PCA details). Communities functional redundancy remained stable in control plots but after disturbance the redundancy trajectories were quite variable (See appendix I). Globally after most intense disturbance (plots T2 and T3) communities redundancy decreased at first place before increasing to edge, recover or exceed the initial value.

Considering the functional redundancy restricted to the functional space of the initial inventory, all disturbed plots followed similar decreasing humped-shaped trajectories (@ref(fig:RedFun_rest)). The maximum redundancy loss observed was positively correlated with the disturbance intensity (XX spearman to be measured) and none of the disturbed plots had recovered the functional redundancy within the initial functional space.

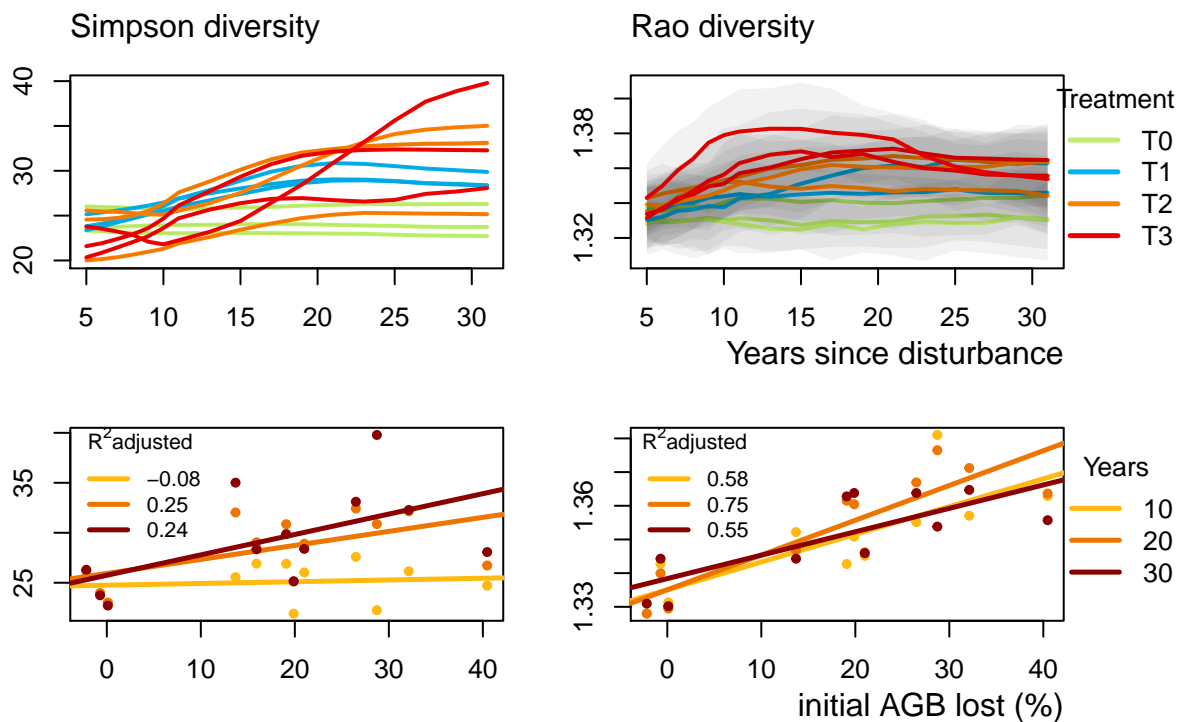


Figure 1. Upper panels, Trajectories of the Simpson taxonomic diversity (a) and Rao functional diversity (b) over 30 years after disturbance, corresponding to the median and 0.025 and 0.975 percentile observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1, orange for T2 and red for T3. Lower panels, Relationship between the initial %AGB removed and the median values of Simpson (c) and Rao (d) diversities at three times after disturbance. Solid lines colors represent the time, 10 years (yellow), 20 years (orange) and 30 years (brown) after disturbance.

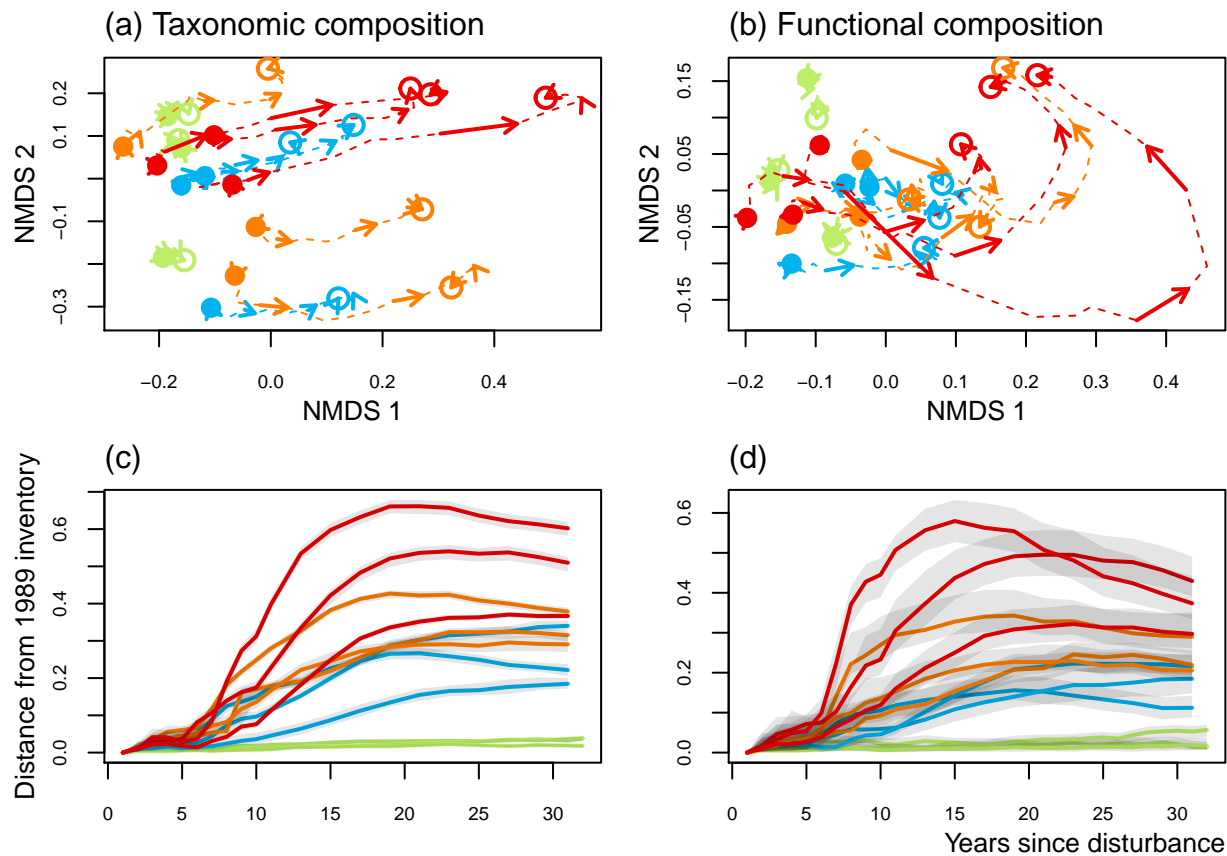


Figure 2. Trajectories of the plots in terms of flora composition (left panels (a) and (c)) and functional composition (right panels (b) and (d)) regarding the 6 leaf and stem functional traits, the maximum allometric height and seed mass class. Plots trajectories are first represented in the two-dimensional space from the NMDS performed for the 30 years after disturbance based on Bray-Curtis dissimilarity measures between successive inventories (Upper panels (a) and (b)). Then the lower panels ((c) and (d)) represent the euclidean distance to initial condition along the 30 sampled years. Line colors represent the disturbance treatment (green for control, blue for T1, orange for T2 and red for T3). The 0.025 and 0.975 percentile correspond to the variance observed for 50 iteration of the taxonomic uncertainty propagation and functional trait filling processes.

Community Weighted Means

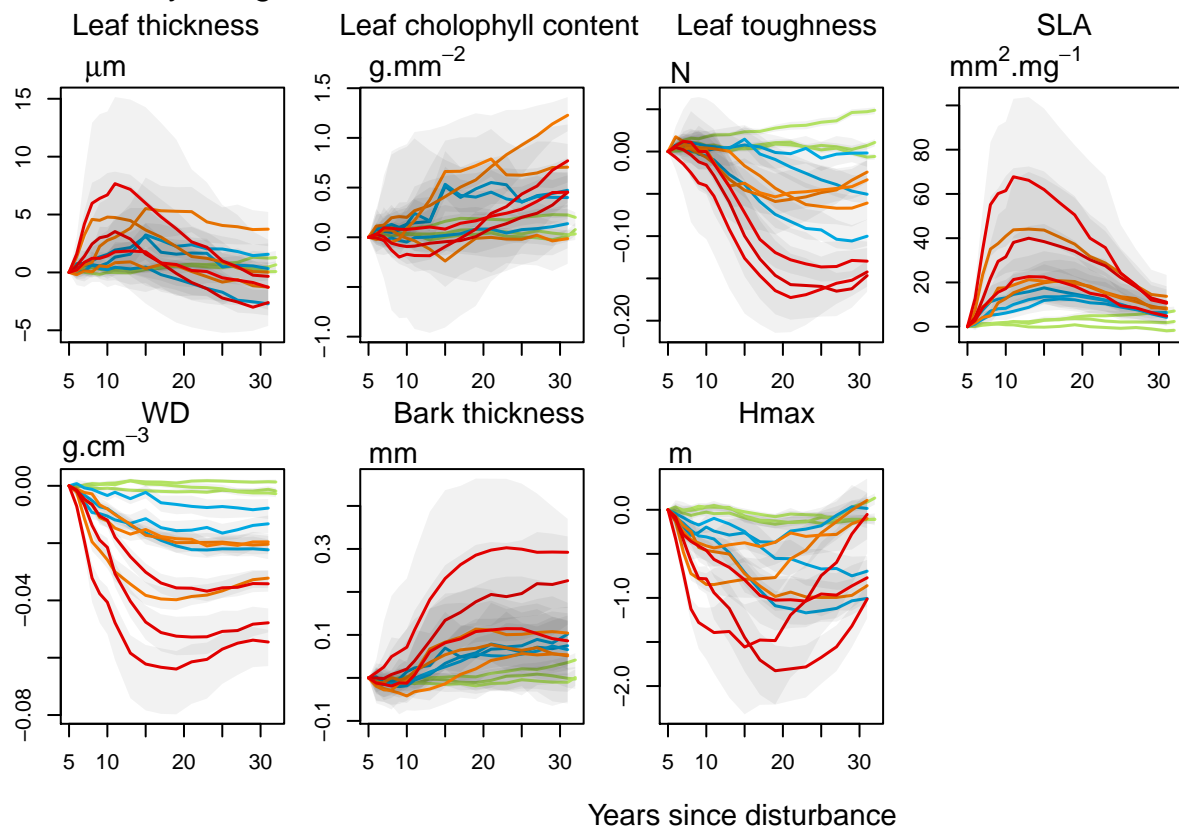


Figure 3. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, $L_thickness$, chlorophyll content, L_chloro , toughness, $L_toughness$ and specific area, SLA), 2 stem traits (wood specific gravity, WD , and bark thickness, $Bark-thick$) 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 colors with green for control, blue for T1, orange for T2 and red for T3.

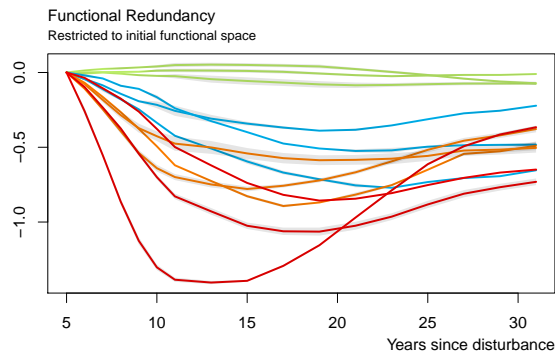


Figure 4. Trajectories of the functional redundancy within the initial communities functional space over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling processes. Initial treatments are represented by solid lines colors with green for control, blue for T1, orange for T2 and red for T3. (#fig:RedFun_rest)

4. Discussion

4.1 Decoupled recovery of communities taxonomic and functional characteristics

Both communities taxonomic and functional diversity and composition proved resilient, following similar humped-back trajectories with a return towards initial values. The resilience of communities functional characteristics, the most direct link between biodiversity and ecosystem functioning (Díaz *et al.*, 2005), meant a consistent recovery of ecosystem processes in the long term (Guariguata & Ostertag, 2001). The resilience of communities taxonomic characteristics, in turn, meant the maintenance of their initial differences in composition and structure. It suggested that communities response to disturbance were somehow constraint to converge towards determined compositions (Hubbell *et al.*, 1999; Molino & Sabatier, 2001; Anderson, 2007; Baraloto *et al.*, 2012).

Although both communities taxonomic and functional characteristics proved resilient and followed similar humped-back trajectories, the taxonomic recovery systematically lagged behind the corresponding functional dynamics. Such delay between functional and taxonomic dynamics has already been observed for grasslands (Tilman, 1997; Mouillot *et al.*, 2011) and more recently for tropical forests (Lohbeck *et al.*, 2015; Guariguata & Ostertag, 2001). According to the “vegetation quantity effect” (Grime, 1998), functional trajectories rely on the pool of dominant species which diversity and evenness were enhanced after disturbance and which rapidly restored the functional diversity and composition. However, infrequent species that would further lower the functional diversity and communities evenness still missed to the recovery of taxonomic characteristics. Taxonomic recovery then mechanically lagged behind, all the more so that unrecovered species are functionally redundant and

would probably undergo competitive pressures.

4.2 A validation of the intermediate disturbance hypothesis

The monitoring of disturbed forest communities confirmed a limited or negative impact of intense disturbance on species richness, as observed on several post logging surveys (Cannon, 1998; Baraloto *et al.*, 2012), while . 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 genera for some plots.

Both richness and evenness followed asymptotic trajectories after disturbance, 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. Because the composition of old survivors proved to mirror the initial community (Héroult & Pioniot, 2018), a specific turnover was expected 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 initial 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 relied on species functional strategy and corresponding ability to fill the environmental niches made available by disturbance. Recruited species then mixed with pre-disturbance ones, from which they differed, and constituted a community all the more diversified that the disturbance was intense (Molino & Sabatier, 2001).

4.3 Functional redundancy of disturbed ecosystems

The functional redundancy, the functional overlap between species that is typical of the huge biodiversity of tropical forests (Bellwood *et al.*, 2006), was then not restored 30 years after disturbance and this is major 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, there was probably persistent compositional changes favoring disturbance resistant species (Haddad *et al.*, 2008), lianas or epiphytes (Martin *et al.*, 2013) and environmental changes, like in the soils nutrient cycling and compaction

(Olander *et al.*, 2005). These persistent 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). Specifically, 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 and validated the consistency of the IDH in the long term. It revealed the contrasting response of communities taxonomic and functional characteristics, with persisting impacts on the species abundance distribution while the functional diversity and dominant functional strategies were restored. Communities recovery therefore remained unachieved but consistent for the range of disturbance studied here. The length of the recovery, however, severely questioned the sustainability of intense selective logging and advocated felling cycle much longer than 30 years (Gourlet-Fleury *et al.*, 2005).

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., Hérault, 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.
- Carmona, C.P., de Bello, F., Mason, N.W. & Lepš, J. (2016) Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology and Evolution*, **31**, 382–394.
- 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) Plant functional markers capture ecosystem properties during secondary succession. *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.

- Goulamoussène, Y., Bedeau, C., Descroix, L., Linguet, L. & Hérault, B. (2017) Environmental control of natural gap size distribution in tropical forests. *Biogeosciences*, **14**, 353–364.
- Gourlet-Fleury, S., Cornu, G., Jérel, S., Dessard, H., Jourget, J.G., Blanc, L. & Picard, N. (2005) Using models to predict recovery and assess tree species vulnerability in logged tropical forests: A case study from French Guiana. *Forest Ecology and Management*, **209**, 69–85.
- 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.
- Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y., Lei, X., Schelhaas, M.J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavan, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawila-Niedzwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M. & Reich, P.B. (2016) Positive biodiversity–productivity relationship predominant in global forests. *Science*, **354**, aaf8957.
- 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 measurement: Rejoinder.
- Piponiot, C., Sist, P., Mazzei, L., Peña-Claros, M., Putz, F.E., Rutishauser, E., Shenkin, A., Ascarrunz, N., de Azevedo, C.P., Baraloto, C., França, M., Guedes, M.C., Coronado, E.N., D'Oliveira, M.V., Ruschel, A.R., da Silva, K.E., Sotta, E.D., de Souza, C.R., Vidal, E., West, T.A. & Hérault, B. (2016) Carbon recovery dynamics following disturbance by selective logging in amazonian forests. *eLife*, **5**.
- Reich, P.B. (2014) The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, **102**, 275–301.
- REJOU-MECHAIN, M., TANGUY, A., PIPONIOT, C., CHAVE, J. & HERAULT, B. (2018) *BIOMASS: Estimating Aboveground Biomass and Its Uncertainty in Tropical Forests*. R package version 1.2.
- 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, M. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework 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, U., 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.