

Post-Disturbance Tree Community Trajectories in a Neotropical Forest

Ariane MIRABEL^{1*}

Eric Marcon¹

Bruno Hérault^{2 3}

Abstract

Understand the maintenance of forests biodiversity structure, functioning and dynamics is urgent to anticipate their fate in the global changing context. Communities diversity structure is assumed to rely on a constant regime of disturbance and peak at intermediate intensity. For tropical forests this intermediate disturbance hypothesis (IDH) remain debated as well as the completeness of forests resilience in all taxonomic and functional facets.

Keywords

Taxonomic and Functional Biodiversity, Neotropical Forests, Disturbance Trajectories, Intermediate Disturbance Hypothesis, Long-term Resilience

¹UMR EcoFoG, AgroParistech, CNRS, Cirad, INRA, Université des Antilles, Université de Guyane.
Campus Agronomique, 97310 Kourou, France.

²Cirad, Univ montpellier, UR Forests & Societies.
Montpellier, France.

³INPHB, Institut National Polytechnique Félix Houphouët-Boigny
Yamoussoukro, Ivory Coast.

*Corresponding author: ariane.mirabel@ecofog.gf, <http://www.ecofog.gf/spip.php?article47>

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	4
3.1	Communities Diversity	4
3.2	Communities composition	4
	Taxonomic and functional trajectories • Traits community weighted means (CWM) • Functional redundancy	
4	Discussion	8
4.1	Decoupled taxonomic and functional trajectories . . .	8
4.2	A validation of the intermediate disturbance hypothesis	8
4.3	The functional redundancy, key of communities resilience	9
5	Conclusions	9

1. Introduction

The large areas covered with tropical forests worldwide hold crucial environmental, economic and social values. 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 increased demand in forests products and the substantial climatic changes currently heighten the pressure on remaining forests (Gibson *et al.*, 2011; Morales-Hidalgo *et al.*, 2015), threatening

the maintenance of communities structure, composition and functioning and their dynamics in space and time (Anderson-Teixeira *et al.*, 2013; Sist *et al.*, 2015).

In tropical forest, ecological communities are constantly re-shaped by natural disturbance events that change both abiotic environment, through the fluxes of light, heat and water (Goulamoussène *et al.*, 2017), and biotic interactions like competition among species (Hérault & Piponiot, 2018). The cornerstone of tropical forests ecology is to understand the mechanisms and the determinants of ecosystems response to disturbance (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 (Piponiot *et al.*, 2016; Rutishauser *et al.*, 2016). These structural parameters were thereafter successfully modeled, giving important insights into the maintenance of ecosystems processes and services (Denslow & Guzman, 2000; Blanc *et al.*, 2009). However the response of forests diversity in tree species remains unclear, albeit it determines the productivity, stability and functioning of ecosystems (Tilman *et al.*, 2014; Liang *et al.* (2016)) and would be most probably impacted by the changes following disturbance (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). Still, validations of the IDH remain scarce in the long term and mainly rely on species richness analyses that give limited or misleading information on forests recovery and functioning (Martin *et al.*, 2015;

Chaudhary *et al.*, 2016). More relevant monitoring would encompass communities composition, crucial for conservation issues, and complete diversity profiles integrating both species richness and evenness, to reveal the ecological rules structuring communities (Magurran, 1988; Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Furthermore, the functional approach that accounts for species biological attributes and role in the ecosystem would be essential to understand the correlations between ecosystems biodiversity, functioning and environmental constraints (Violle *et al.*, 2007; Moretti *et al.*, 2009; Baraloto *et al.*, 2012; Scheiter *et al.*, 2013). The functional trait-based approach focused on major traits related to species ecology and performance was successfully adopted (Díaz *et al.*, 2005; Villéger *et al.*, 2008), for example in highlighting deterministic processes in tropical rainforests that foster fast growing species with efficient resources acquisition after disturbance (Molino & Sabatier, 2001; Haddad *et al.*, 2008; Rüger *et al.*, 2009). Communities then shifted from a dominance of “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). This shift translated into consistent trajectories for key functional traits related to resource acquisition (leaf area, density and chlorophyll content, and stem specific gravity and bark thickness), tree growth and reproduction and life history traits (seed mass and maximum height) (Wright *et al.*, 2004; Westoby & Wright, 2006; Chave *et al.*, 2009).

A combination of taxonomic and functional approaches are essential to fully assess communities response to disturbance and differences in their respective trajectories are insightful of underlying mechanisms (Lohbeck *et al.*, 2015; Guariguata & Ostertag, 2001). Although taxonomic and functional diversity are complementary and sometimes decouples, they are combined in the measure of communities functional redundancy that quantifies the amount of shared trait values among species (Carmona *et al.*, 2016). Functional redundancy is determinant of communities resilience as high redundancy, like in highly diverse tropical forests (Bellwood *et al.*, 2006), mitigates the impacts of species removal on ecosystem functioning (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

Grasp all facets of communities response to disturbance comes to examine the taxonomic and functional trajectories in diversity and composition. These trajectories would highlight the ecological rules constraining or not communities dynamics towards the recovery of initial composition, diversity and functioning. They would therefore clarify the tenants in the long term of the debated Intermediate Disturbance Hypothesis for tropical forests, a crucial point for future adaptive conservation strategies (Adler *et al.*, 2007). Here we monitored 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 functional traits and species maximum height to draw the trajectories over time of communities taxonomic and functional composition and diversity. Specif-

ically, we (i) questioned the coupling between taxonomic and functional response to disturbance and identified the underlying assembly processes, which allowed to (ii) clarify the validity of the IDH in the long term for tropical forest and (iii) question the completeness of communities recovery regarding their 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 in a tropical wet climate with mean annual temperature of 26°C, mean annual precipitation averaging 2980 mm.y⁻¹ (30-y period) and 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 soils correspond to thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains.

The experiment is a network of twelve 6.25ha plots that underwent a gradient of three logging, thinning and fuelwood cutting 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/ha above 40 cm DBH for treatment 3 (T3). Treatments T2 and T3 besides included the thinning of trees by poison girdling (Schmitt & Bariteau, 1989; 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) measured with the BIOMASS R package (Réjou-Méchain *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 are mapped and measured annually since 1984. Trees are first identified during inventories 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 are given to 62 commercial or common species whereas more infrequent ones were identified under general identifiers only distinguishing trees and palm trees. From 2003 botanical campaigns were conducted every 5 to 6 years to identify all trees at the species level but identification practices still varied among plots and campaigns.

This variability of protocols raised methodological issues as vernacular names usually correspond to different botanical species. It resulted in significant taxonomic uncertainties that had to be propagated to composition and diversity metrics. The uncertainty propagation was done through a Bayesian framework reconstituting complete inventories at genus level from real incomplete ones on the basis of

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%]

vernacular/botanical names association. Vernacular names were replaced through multinomial trials $M_v([s_1, s_2, \dots, s_N], [\alpha_1, \alpha_2, \dots, \alpha_N])$ based on the association probability $[\alpha_1, \alpha_2, \dots, \alpha_N]$ observed across all inventories between each vernacular name v and the species $[s_1, s_2, \dots, s_N]$. See appendix 1 and Aubry-Kientz *et al.* (2013) for the detailed methodology.

The functional approach used a dataset of 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 project¹ where trait values were assessed from a selection of individuals located in nine permanent plots in French Guiana, including two in Paracou, and comprised 294 botanical species pertaining to 157 botanical genera. Missing trait values were filled using multivariate imputation by chained equation (mice) from the mice R package (van Buuren & Groothuis-Oudshoorn, 2011). Imputations were restricted within genus, or family when samples were too scarce, in order to account for the phylogenetic signal of the functional traits. 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 (same genus or family). As seed mass information corresponds to a classification into mass classes, no data filling process was applied and analysis were restricted to the 414 botanical species recorded.

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 taxonomic uncertainties due to the variability of botanical identification protocols (see [#protocols]), the taxonomic composition and diversity analysis were conducted at the genus level, *i.e.* referring to the genus of observed or trialed botanical names. Trajectories of communities

taxonomic and functional variations in composition after disturbance were followed in a two-dimensional ordination space the 30 years monitored. Two NMDS were conducted to map either taxonomic flora inventories or communities 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) and abundance-based (Bray-Curtis) dissimilarity measures. Trajectories along time in the plan 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), recommended 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.

The impacts of initial disturbance were first tested with the spearman rank correlation between the extremum of taxonomic and functional metrics reached over the 30 years and the initial %AGB removed. Then they were analysed through the linear correlations between Simpson and Rao diversities and the initial %AGB removed at 10, 20 and 30 years after disturbance.

The functional redundancy was measured as the overlap

¹<http://www.ecofog.gf/bridge/>

among species in communities' functional space (Carmona *et al.*, 2016). The samples of the trait database were first mapped in a 2-dimensional plan from a PCA analysis. Then, multivariate kernel density estimator associated with individual trees returned species traits probability distribution (TDP). Species TDP weighted by species abundance were eventually summed for each community: the functional redundancy was the sum of TDPs overlap, expressed as the average number of species that could be removed from without reducing the functional space (see appendix I for a more comprehensive scheme).

3. Results

3.1 Communities Diversity

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. 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. In disturbed communities the taxonomic richness increased after low disturbance intensity, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2) while it followed unimodal trajectories after intense disturbance, decreasing for ten years before recovering pre-disturbance values. In all disturbed plots the taxonomic evenness (Shannon and Simpson diversities) increased, following unimodal trajectories with a maximum, reached after around 20 years, positively correlated to the disturbance treatment ($\rho_{Spearman}^{Shannon} = 0.86$, and $\rho_{Spearman}^{Simpson} = 0.89$). Return towards initial evenness values was beginning after 30 years except for two T3 plots (plots 8 and 12) which evenness still increased, suggesting similar but delayed trajectories 1.

Trajectories of communities functional diversity were examined through the Rao diversity based on the 7 leaf, stem and life history traits (to the exception of seed mass). 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). In undisturbed plots the functional diversity remained stable along the 30 years while in disturbed plots it followed unimodal trajectories with a return towards initial values that started around 20 years after disturbance.

The impact of disturbance was examined specifically through the linear correlation between the initial %AGB removed and the Simpson and Rao diversities (diversities of order 2) after 10, 20 and 30 years 1. The correlation with disturbance intensity was weak for the Simpson diversity ($R^2 < 0.25$) and only valid from 20 years after disturbance but it was much stronger for the Rao diversity ($0.60 < R^2 < 0.75$) for all the time studied. Slope of linear correlations, reflecting the impact of disturbance, was the highest 20 years after disturbance.

3.2 Communities composition

3.2.1 Taxonomic and functional trajectories

The trajectories of taxonomic and functional composition were visualized in a two dimensional ordination space mapping the successive inventories according to their flora and corresponding traits. Classifications were performed using either abundance-based Bray-Curtis (Figure 2) or incidence-based Jaccard dissimilarity, both giving similar results only analysis using Bray-Curtis dissimilarity are discussed.

While both taxonomic and functional composition remained stable in undisturbed communities, they followed consistent trajectories over time after disturbance which revealed significant compositional changes. According to the mapping of functional traits (see appendix I) these compositional changes corresponded to shifts towards species with more acquisitive functional strategies, from communities with high average WD to high average SLA and chlorophyll content. For disturbed communities the distance of successive inventories to the 1989 reference inventory followed unimodal trajectories translating cyclic compositional changes with a recovery of the initial composition (Figure 2). The maximum dissimilarity with the initial state was positively correlated to the disturbance treatment for both taxonomic and functional composition ($\rho_{Spearman}^{taxonomic} = 0.91$ and $\rho_{Spearman}^{functional} = 0.96$ respectively) and the time at maximum was reached around 26 years after disturbance for taxonomic composition and 22 years for functional composition.

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 with the trajectories of community weighted means (CWM) of leaves economics (leaves thickness, chlorophyll content, toughness and specific area), wood economics (wood specific gravity, bark thickness), and life history traits (seed mass and maximum adult height) (Figure 3).

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

3.2.3 Functional redundancy

Communities functional redundancy was measured as the sum within communities the species weighted functional overlap based on the 7 leaf, stem, and maximum height

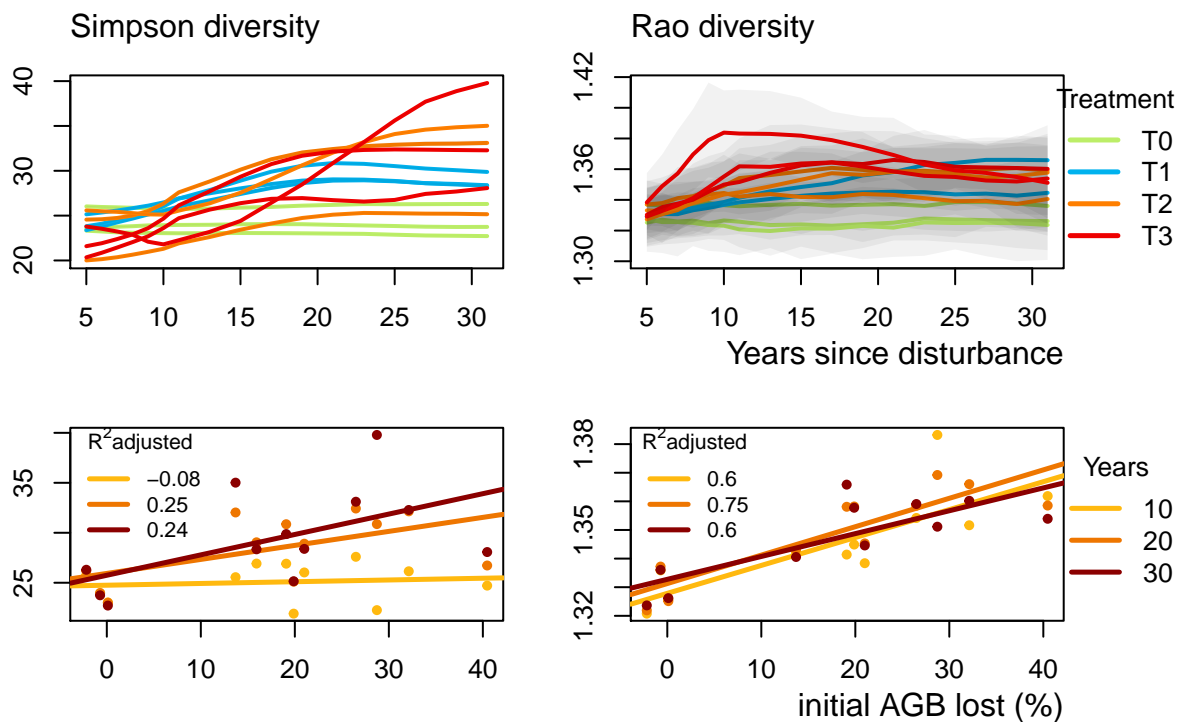


Figure 1. Upper panels, Trajectories of the Simpson taxonomic diversity (a) and Rao functional diversity (b) over 30 years after disturbance, corresponding to the median and 0.025 and 0.975 percentile observed after 50 iteration of the taxonomic uncertainty propagation and the missing trait value filling 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.

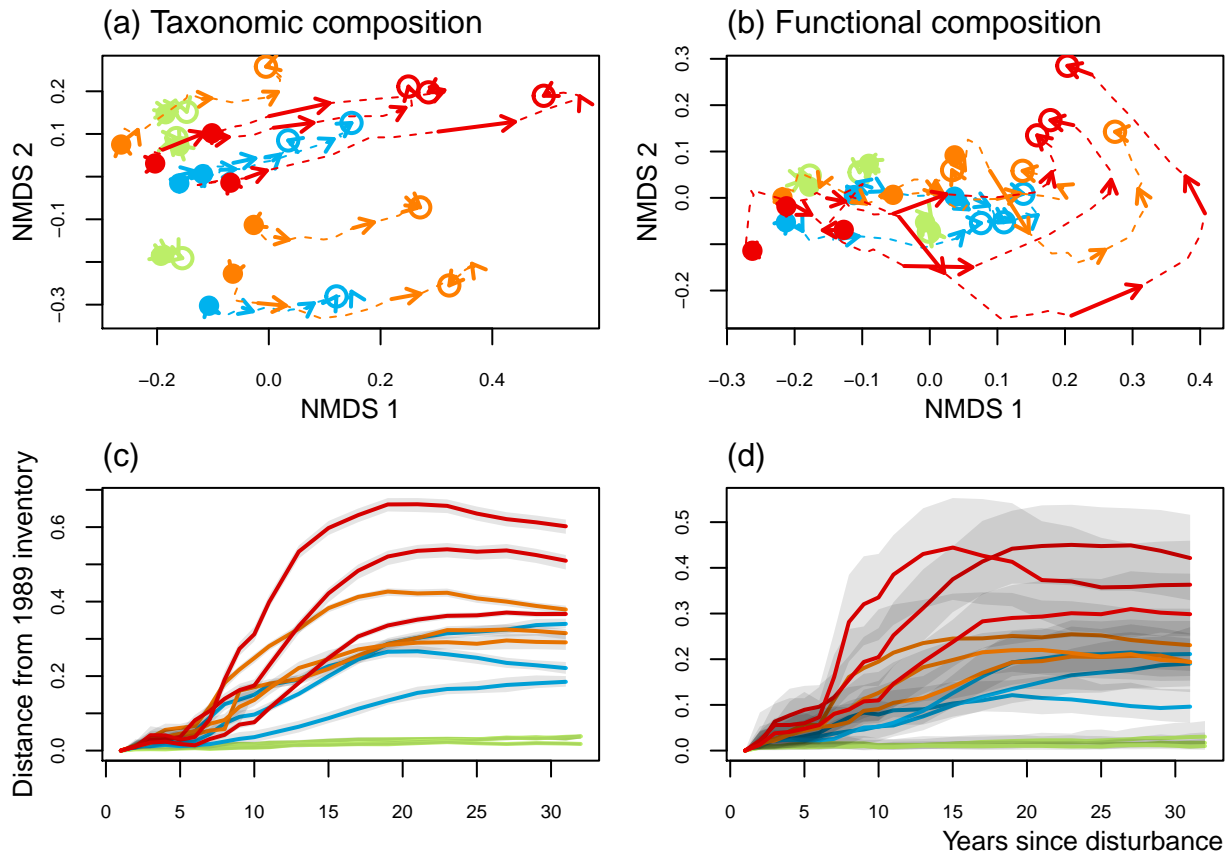


Figure 2. Trajectories of the plots in terms of flora composition (left panels (a) and (c)) and functional composition (right panels (b) and (d)) regarding the 6 leaf and stem functional traits, the maximum allometric height and seed mass class. Plots trajectories are first represented in the two-dimensional 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

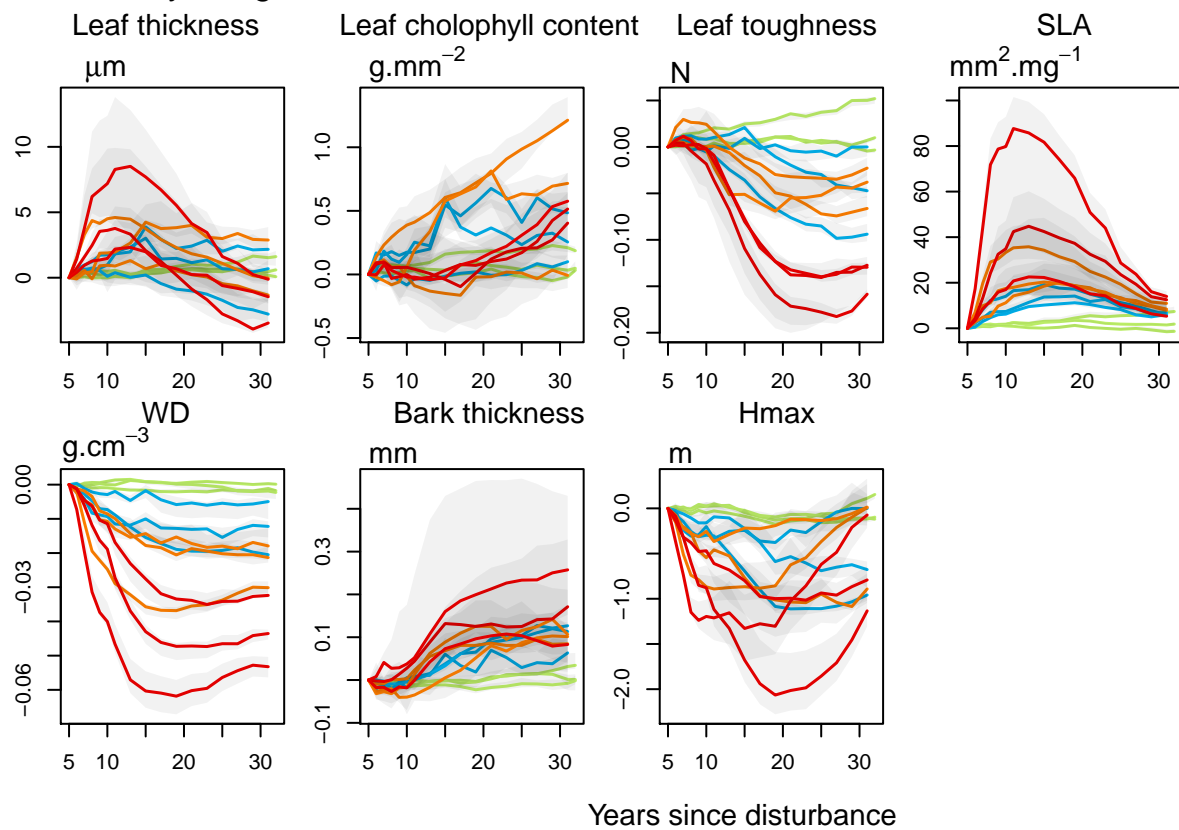


Figure 3. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, $L_thickness$, chlorophyll content, L_chloro , toughness, $L_toughness$ and specific area, SLA), 2 stem traits (wood specific gravity, WD , and bark thickness, $Bark-thick$) 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.

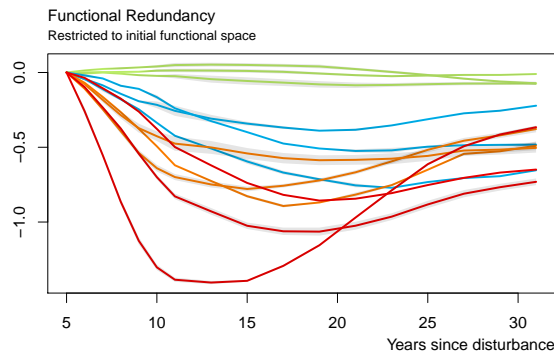


Figure 4. Trajectories of the functional redundancy within the initial communities functional space over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation and 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)

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) and apparently independently of the initial disturbance. 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 was positively correlated with the disturbance intensity (XX spearman to be measured) and the initial value had not recovered for any disturbed communities.

4. Discussion

4.1 Decoupled taxonomic and functional trajectories

Both communities taxonomic and functional diversity and composition proved resilient, following similar humped shaped trajectories returning towards initial values. The resilience of communities functional structure, that is 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 taxonomy meant the maintenance of their initial differences in composition and diversity, suggesting the existence of multiple stable equilibria as assumed for highly diverse and productive ecosystems (Chase, 2003). It besides suggested that recovery trajectories depend on the initial composition eventually restored that would be the asymptot of the humped shaped dynamics (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 shaped trajectories, the taxonomic recovery systematically lagged behind the functional one. The decoupling 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 recovered their initial functional structure. However, communities evenness remained high so infrequent species still missed to the taxonomic recovery that proved all the more longer to recover that unrecovered species would be functionally redundant and probably underwent competition processes.

4.2 A validation of the intermediate disturbance hypothesis

Validating the IDH, communities trajectories confirmed the diversity increase after disturbance through an enhanced growth of otherwise less favored species. This was strong regarding the functional diversity but more blurry regarding their taxonomic structure.

The taxonomic richness was weakly or negatively impacted by intense disturbance, as observed on several post logging surveys (Cannon, 1998; Baraloto *et al.*, 2012), while it substantially increased after low intensity disturbance. Disturbance also enhanced taxonomic evenness, but the disturbance intensity was only weakly and lately correlated to communities evenness (*i.e.* Simpson diversity). Contrastingly, disturbance intensity consistently predicted the significant increase of communities functional diversity for 30 years. Disturbance entailed specific turnover within communities, either among pre-disturbance survivors or among newly recruited trees. As the composition of old-growth survivors proved to mirror initial communities (Héroult & Pioniot, 2018), disturbance likely impacted trees recruitment through the enhanced growth and survival of previously infrequent species and functional types. Consistently, disturbance resulted in increasing taxonomic dissimilarity compared to pre-disturbance communities and significant functional shifts 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 caused 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 other species in non limiting resources but are excluded in mature forests through the competition with long-lived, more resistant and shade bearers. Therefore, consistently with the IDH the trajectories after disturbance relied on the environmental niches made available by disturbance filled by species from a restricted functional range. Recruited species therefore differed from pre-disturbance

ones, constituting a community all the more diversified that the disturbance was intense (Molino & Sabatier, 2001).

4.3 The functional redundancy, key of communities resilience

Both the lag between taxonomic and functional recovery and the middling consistency of the IDH regarding communities taxonomic diversity made central the role of functional redundancy. Functional redundancy, determinant of communities resilience (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005), seemed not to have recovered 30 years after disturbance.

Communities with high functional redundancy are expected to be able to lose species with a limited impact on their functional structure (Carmona *et al.*, 2016). Functional redundancy therefore mitigates the impacts of disturbance, but we expect the redundancy itself to be reduced or re-organized within the functional space. Although the overall functional redundancy did not follow consistent trajectories after disturbance, the redundancy restricted to the functional space of the initial community clearly followed humped shaped trajectories. This restricted redundancy decreased according to the disturbance intensity before returning towards the initial value but had not recovered for any disturbed community after 30 years. The recovery of the redundancy within the initial functional space explained the hampered recovery of infrequent species specific to old-growth forests that would be functionally redundant and therefore underwent competitive pressures limiting species functional similarity (Mayfield & Levine, 2010). The unachieved humped shaped redundancy trajectory meant a decrease of the resilience of pre-disturbance communities and an increase in the resilience of disturbance-specific communities (corresponding to lower richness and higher dominance of pioneer species). After disturbance the chances were higher to have long lasting or self-maintained compositional changes in favor of disturbance resistant species, lianas or epiphytes (Haddad *et al.*, 2008; Burslem *et al.*, 2000; Martin *et al.*, 2013), which highly questioned the completeness of the resilience (Chazdon, 2003). Specifically, species contingent to undisturbed forests might be impaired, threatening their maintenance, the risk to loose cornerstone species and trigger unexpected ecological consequences would be higher (Jones *et al.*, 1994; Díaz *et al.*, 2005; Gardner *et al.*, 2007).

5. Conclusions

our study defined the decoupled functional and taxonomic trajectories of tropical rainforests after disturbance. These trajectories shed light on their rapid functional recovery but slower and more variable taxonomic dynamics. Consistently with the IDH, functional trajectories were constrained by determined processes favoring pioneers and light-demanding species after disturbance. The taxonomic dynamics however proved more stochastic due to the recovery of infrequent, functionally redundant species hampered by limiting similarity processes. Although communities functioning rapidly recovered, their taxonomic structure and functional redundancy remained altered for several decades. The tra-

jectories therefore demonstrated a decades-long resilience of tropical forests in the face of quite intense disturbance (Gourlet-Fleury *et al.*, 2005). Within the mechanisms of this resilience the recruitment processes proved central, in accordance with the IDH, and would deserved closer focus to clarify their determinisms and ecological rules. The disturbance range however stayed within the spectrum of selective logging, with a forest cover remaining all along the experiment, and the response mechanisms would probably be much different after harder disturbance.

References

- Adler, P.B., HilleRisIambers, 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.

- Chase, J.M. (2003) Community assembly: When should history matter? *Oecologia*, **136**, 489–498.
- 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., Jéssel, 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. & Vancley, 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., Brulheide, 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., Bus-sotti, 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.
- Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.
- 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**.
- 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.
- Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J. & Hérault, B. (2018) *BIOMASS: Estimating Aboveground Biomass and Its Uncertainty in Tropical Forests*. R package version 1.2.
- Rüger, N., Huth, A., Hubbell, S.P. & Condit, R. (2009) Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology*, **97**, 1360–1368.
- Rutishauser, E., Hérault, B., Petronelli, P. & Sist, P. (2016) Tree Height Reduction After Selective Logging in a Tropical Forest. *Biotropica*, **48**, 285–289.
- Scheiter, S., Langan, L. & Higgins, S.I. (2013) Next-generation dynamic global vegetation models: learning from community ecology. *The New phytologist*, **198**, 957–69.
- Schmitt, L. & Bariteau, M. (1989) Gestion de l'écosystème forestier guyannais. étude de la croissance et de la régénération naturelle. dispositif de paracou. *BOIS & FORETS DES TROPIQUES*, **220**, 3–24.
- 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.
- van Buuren, S. & Groothuis-Oudshoorn, K. (2011) mice: Multivariate imputation by chained equations in r. *Journal of Statistical Software*, **45**, 1–67.
- Villéger, Mason & Mouillot (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, &, 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.