

Post-Disturbance Tree Community Trajectories in a Neotropical Forest

Ariane MIRABEL^{1*}

Eric Marcon¹

Bruno Hérault^{2 3}

Abstract

Understanding the ecological rules underlying the maintenance of tropical forests biodiversity, structure, functioning and dynamics is urgent to anticipate their fate in the global changing context. The huge diversity of tropical forests is often assumed to be shaped by constant regime of disturbance yielding a diversity peak at intermediate intensity, but for tropical forests this intermediate disturbance hypothesis (IDH) remains debated, and this controversy also questions the extent of communities resilience regarding their functional and taxonomic facets is also to be clarified. To disentangle the ecological processes driving communities response to disturbance we analysed the taxonomic and functional diversity trajectories following a logging and thinning disturbance gradient. Specifically we examined over 30 years the trajectories of communities taxonomic richness and evenness and functional composition, diversity and redundancy based on 7 leaf, stem and life history traits. Trajectories highlighted communities taxonomic resilience, maintaining their initial differences in composition, and functional resilience through fast functional trajectory common to all communities in the functional space. The IDH consistently predicted communities functional trajectories according to the disturbance intensity, but poorly represented their taxonomic trajectories, blurred by the alteration of the functional redundancy and the recruitment of infrequent, shade tolerant species slowed by competitive exclusion processes. Although communities functioning had recovered after 30 years their taxonomic diversity and composition in infrequent species and their functional redundancy remained altered. these results acknowledged the need of decades-long recovery cycles to ensure communities complete resilience, and questioned communities maintenance after repeated disturbance.

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	3
3.1	Communities Diversity	3
3.2	Communities Composition	5
	Taxonomic and functional trajectories • Traits community weighted means (CWM) • Functional redundancy	
4	Discussion	5
4.1	Decoupled taxonomic and functional trajectories . . .	5
4.2	The extent of the intermediate disturbance hypothesis	5
4.3	The functional redundancy, key of communities resilience	8
5	Conclusions	8

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, and the carbon, water and nutrient cycles, and ensure cultural and human well-being. The growing demand in forests products together with current climatic changes increases the pressure on remaining forests (??) and threatens the maintenance and dynamics in space and time of communities structure, composition and functioning (??).

In tropical forest, ecological communities are constantly re-shaped by natural disturbance events that change both the abiotic environment, through the fluxes of light, heat and water (?), and the biotic interactions like competition among species (??). One of the cornerstone of tropical forest ecology is to understand the processes and drivers of ecosystems response to disturbance (??). For now, this has been largely studied through forest structural parameters, rapid and convenient to measure, as aboveground

biomass, tree height or stem density (??). These structural parameters were thereafter successfully modeled, giving important insights into the recovery of ecosystems processes and services (?). However the response of forests diversity is still unclear, albeit it determines the productivity, stability and functioning of ecosystems (?, ?) and would be most probably impacted by the changes induced by disturbance (?).

In the short-term, moderate disturbance may lead to positive impacts on communities diversity, which have been formalized by the intermediate disturbance hypothesis (IDH) stating a maximized species diversity at intermediate disturbance intensity (???). Still, validations of the IDH remain scarce in the long term and mainly rely on the analysis of species richness that gives limited or misleading information on forests recovery and functioning (??). More complete analysis would besides encompass communities composition that is crucial for conservation issues, and abundance distribution to reveal the ecological rules structuring communities (???). Furthermore, a functional approach accounting for species biological attributes and role in the ecosystem directly links ecosystems biodiversity, functioning and environmental constraints (????). The functional trait-based approach focused on major traits related to species ecology and performance was successfully adopted (??), for example to reveal in tropical rainforests the deterministic processes that foster after disturbance the fast growing species with efficient resources acquisition (???). This basic deterministic process entails a functional shift 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 (???). This shift is translated into consistent trajectories of 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) (????). Besides communities functional composition and diversity, a last key aspect of communities response to disturbance is the changes in functional redundancy that quantifies the amount of shared trait values among species (?). High functional redundancy, as in the very diverse tropical forests (?), mitigates the impacts of species removal on ecosystem functioning and determines communities resilience (???). High functional redundancy also increases the functional overlap among species and would foster neutral stochastic processes (?).

To grasp all facets of communities response to disturbance we examined here the taxonomic and functional trajectories in diversity and composition (??). These trajectories would highlight the recovery of communities initial composition, diversity and functioning and the underlying ecological processes. They would clarify the tenants in the long term of the Intermediate Disturbance Hypothesis debated in tropical forests, and provide indications for future adaptive conservation strategies (?). We monitored over 30 years the response of 75 ha of neotropical forest 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. Specifically, we (i) questioned the coupling between taxonomic and functional response to disturbance and identified the underlying assembly processes, (ii) clarified the validity of the IDH in the long term for tropical forest and (iii) questioned the completeness of communities recovery regarding communities 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 (?). 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 ??) 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 (?). The disturbance intensity was measured as the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984 and five years after disturbance (?) estimated with the BIOMASS R package (?).

2.2 Inventories protocol and dataset collection

The study site corresponds to a tropical rainforest typical of the Guiana Shield 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 have been mapped and measured annually since 1984. Trees are first identified during inventories with a vernacular name assigned by the forest worker team, and afterward with a scientific name assigned by botanists 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 have been conducted every 5 to 6 years to identify all trees at the species level but identification levels 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 vernacular/botanical names association. Vernacular names were replaced through multinomial trials based on the association probability $[\alpha_1, \alpha_2, \dots, \alpha_3]$ observed across all inventories between each vernacular name v and the species $[s_1, s_2, \dots, s_N]$:

$$M_v([s_1, s_2, \dots, s_N], [\alpha_1, \alpha_2, \dots, \alpha_3])$$

See appendix 1 and ? for the detailed methodology.

Six 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) came from the BRIDGE project ¹. Traits 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 (?). 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 were 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 levels (in space) and protocols (in time), 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 NMDS ordination space of 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 abundance-based (Bray-Curtis) dissimilarity measures. Trajectories along time were reported through the distance between successive inventories and the reference inventories in 1989, *i.e.* 2-3 years after disturbance, when the uncertainty degree did not exceed 30% of undetermined trees. Taxonomic trajectories were measured through the euclidean distance between inventories in the multivariate space of all inventories species. Functional trajectories were measured through

the sum of euclidean distances among traits density distributions between inventories. To compensate the intrinsic difference among plots, the trajectories corresponded to the euclidean differences along time with the reference inventory in 1989. Univariate trajectories of the leaf, stem and life-history traits were also visualized with the community weighted means (CWM) (??). 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 (?). 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 (???). 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 among species in community functional space (?). 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

From 1989 (2-3 years after disturbance) to 2015 (28-29 years after disturbance), 828388 individual trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. For undisturbed plots Richness and taxonomic evenness (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 to 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 ($\rho_{\text{Spearman}}^{\text{Shannon}} = 0.86$, and $\rho_{\text{Spearman}}^{\text{Simpson}} = 0.89$). Return towards initial evenness values was beginning after 30 years except for two T3 plots (plots

¹<http://www.ecofog.gf/Bridge/>

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 strated 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

While both taxonomic and functional composition remained stable in undisturbed communities (Figure 2), 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)

Changes in functional composition trajectories went hand to hand with consistent trajectories of the 8 functional traits (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 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. > restrict to initial functional space

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 ($\rho_{spearman} = 0.50$) 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 diversities and composition proved resilient, following similar humped-shaped trajectories starting to return towards initial values 30 years after disturbance. Communities functional signature is the most direct link between biodiversity and ecosystem functioning (?) and its resilience meant the recovery of ecosystem processes in the long term (?). The resilience of communities taxonomy, despite the multiple NMDS starting points, suggest the long term maintenance of the initial differences in species composition and diversity. This maintenance in turn suggest the existence of multiple stable equilibria as assumed for highly diverse and productive ecosystems (?) and the dependency of recovery trajectories on the initial composition to be recovered (????).

Although communities taxonomic and functional trajectories were similar the taxonomic recovery lagged behind the functional one, confirming a decoupling between functional and taxonomic dynamics already observed for grasslands (??) and tropical forests (??). According to the “vegetation quantity effect” (?) the functional trajectories rely on the pool of dominant species, which diversity and evenness increased and rapidly recovered after disturbance. At the same time communities taxonomic evenness remained high, revealing the unachieved recovery of infrequent species.

4.2 The extent of the intermediate disturbance hypothesis

Disturbance intensity poorly predicted the taxonomic richness regardless of the period studied, as already observed in the Guiana Shield (?) and in Bornean tropical forests (?). Contrastingly, the disturbance intensity consistently predicted the increase in functional diversity after disturbance along the 30 years. The functional diversity increase paralleled the significant functional shifts towards resource-acquisitive strategies (sharp increase in the SLA, leaf thick-

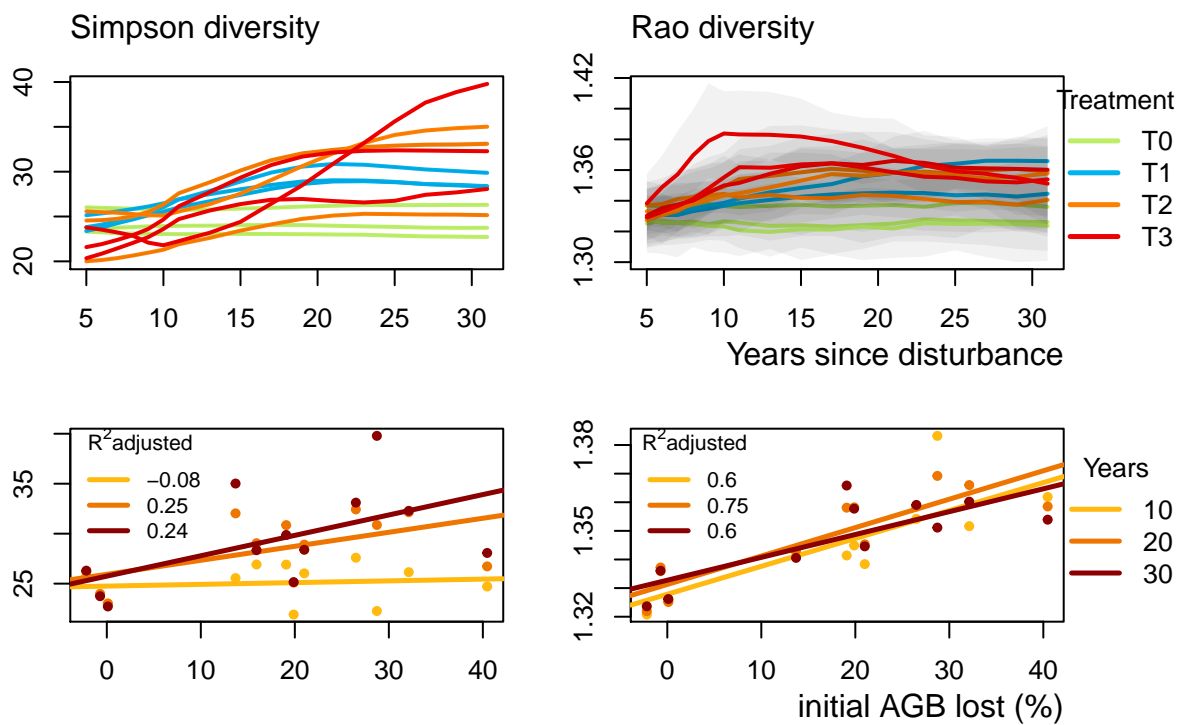


Figure 1. Upper panels, Trajectories of the Simpson taxonomic diversity (a) and Rao functional diversity (b) over 30 years after disturbance. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals. Lower panels, Relationship between the initial %AGB removed and Simpson (c) and Rao (d) diversities 10, 20 and 30 years after disturbance.

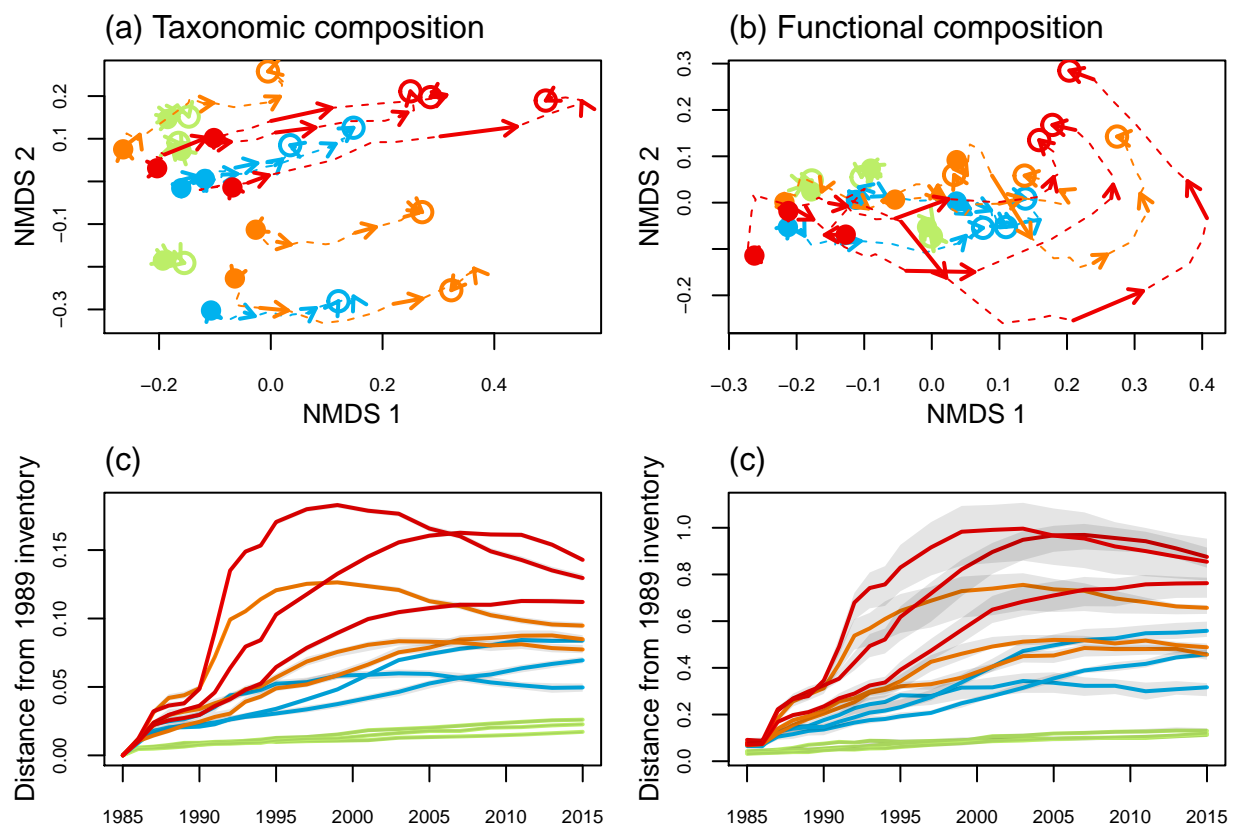


Figure 2. Plot trajectories in terms of flora composition (left panels (a) and (c)) and functional composition (right panels (b) and (d)) in a two-dimensional NMDS space. Lower panels ((c) and (d)) represent the euclidean distance to initial condition along the 30 sampled years. Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals

Community Weighted Means

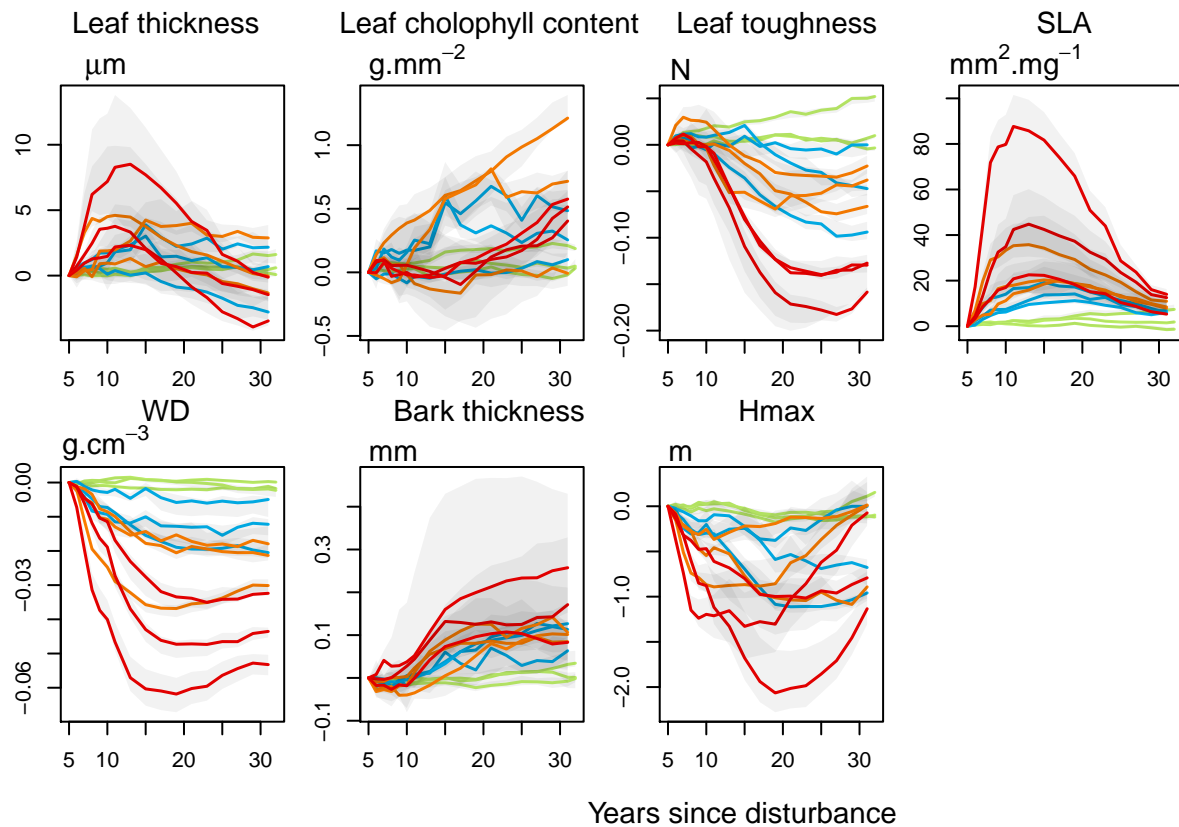


Figure 3. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, $L_{thickness}$, chlorophyll content, L_{chloro} , toughness, $L_{toughness}$ and specific area, SLA), 2 stem traits (wood specific gravity, WD , and bark thickness, $Bark-thick$) and one life history trait (Specific maximum height at adult stage, $Hmax$). Colors are treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals.

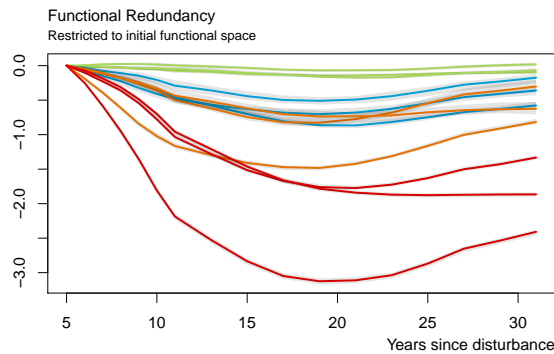


Figure 4. Trajectories of functional redundancy within the initial functional space over 30 years after disturbance. Colors are disturbance treatments: green (control), blue (T1), orange (T2), red (T3) with shaded areas the credibility intervals.
(#fig:RedFun_rest)

ness and bark thickness and decrease in wood density, leaf toughness and maximum height) (???). As the old-growth, pre-disturbance survivor trees proved mirroring the initial communities (?) the functional trajectories and taxonomic turnover rather relied upon the pool of newly recruited trees driven by the enhanced growth and survival of previously infrequent species and functional types. Disturbance entailed a reorganization, benefiting to pioneers and light demanding species, of the typical high dominance structure of hyperdiverse mature forests. The changes in abiotic environment and competitive pressure favored pioneers which outcompeted other species in non limiting light resources but were excluded in mature forests by long-lived, more resistant and shade tolerant species.

Not clear Disturbance trajectories therefore relied upon the environmental niches made available and filled by species from a restricted functional range that became dominant and structured the functional characteristics of the community (?). The intermediate disturbance hypothesis was suitable to predict communities functional diversity and pool of dominant species (?), but it poorly represented the whole taxonomic structure that was hampered by the slow recovery of rare species (??).

4.3 The functional redundancy, key of communities resilience

The functional and taxonomic decoupling as well as the rebuttal of the IDH for communities taxonomic structure were explained by a reorganization of the functional redundancy within the functional traits space that implied the >> incomplete resilience of communities (???).

The functional redundancy restricted to the functional

space of the initial community clearly followed humped shaped trajectories. After disturbance communities differently occupied the functional space, following the observed shifts in traits trajectories and functional composition, and the redundancy in the initial functional space decreased according to the disturbance intensity. After 30 years the recovery of the initial redundancy structure was consistent but remained unachieved. >> unclear It depended on infrequent species specific to old-growth forests that were functionally and therefore underwent competitive exclusion limiting functional similarity (??).

unclear The persistent alteration of functional redundancy meant a lower resilience of pre-disturbance communities and an higher resilience disturbance-specific communities (corresponding to lower richness and higher dominance of pioneer species) so chances to observe self-maintained compositional changes in favor of disturbance resistant species, lianas or epiphytes were increased after disturbance (??).

not so long Communities resilience depended on the functional redundancy structure that proved long to recover.

unclear (cornerstone?) This decades-long recovery specifically increased the risks of losing cornerstone species, with unexpected ecological consequences (????).

5. Conclusions

Our study defined the decoupled functional and taxonomic trajectories of tropical rainforests after disturbance demonstrating a rapid functional recovery but a slower and more variable taxonomic one. Consistently with the IDH, functional trajectories were driven after disturbance by enrichment of the system with pioneers and light-demanding species.

unclear The following functional shifts entailed a re-organization of communities functional redundancy that proved long to recover and explained the more variable and longer taxonomic trajectories as shade tolerant species of old-growth forests faced functional redundancy and limiting similarity processes.

The resilience of tropical forests then proved long in the face of quite intense disturbance and did not preclude the settling of a persistent disturbance-specific community (?). As the trajectories highlighted the recruitment processes proved central for communities response to disturbance

and closer focus on demographical drivers of communities response would clarify the fate of the future forests.

unclear 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., 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.
- 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. (2004) Neutral theory and community ecology. *Ecology Letters*, **7**, 241–253.
- 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.
- 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.
- 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. *Trends and conditions*, pp. 297–329.
- 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.
- 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.
- Garnier, É., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, B.P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- 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.

- Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006) Reconciling niche and neutrality: The continuum hypothesis. *Ecology Letters*, **9**, 399–409.
- 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.
- Héroult, 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.
- Héroult, 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*, **283**, 554–557.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.
- 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., Héroult, 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., Tchekakova, 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., Bruehlheide, H., Coomes, D.A., Piotta, 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*. Springer, 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*, **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**, e17476.
- Patil, G. & Taillie, C. (1982) Diversity as a concept and its measurement. *Journal of the American statistical Association*, **77**, 548–561.

- 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) Management of the guianese forest ecosystem : study of growth and natural regeneration (Paracou program). *Bois et Forêts des Tropiques*.
- Sist, P., Pacheco, P., Nasi, R. & Blaser, J. (2015) Management of natural tropical forests for the future. Technical report, IUFRO WFSE.
- ter Steege, H., Pitman, N.C.a., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.F., Prévost, M.F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vásquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 0–2.
- 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.