Post-Disturbance Tree Community Trajectories in a Neotropical Forest

Ariane MIRABEL[1*]

Eric Marcon[1]

Bruno Hérault[2 3]

Abstract
Résumé de l'article.

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[1]UMR EcoFoG, AgroParistech, CNRS, Cirad, INRA, Université des Antilles, Université de Guyane.
   Campus Agronomique, 97310 Kourou, France.
[2]Cirad, Univ montpellier, UR Forests & Societies.
   Montpellier, France.
[3]INPHB, Institut National Polytechnique Félix Houphouet-Boigny
   Yamoussoukro, Ivory Coast.
***Corresponding author**: ariane.mirabel@ecofog.gf, http://www.ecofog.gf/spip.php?article47

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1. Introduction

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

In tropical forests, a constant range of disturbance determines the ecological rules shaping the communities through the reallocation of resources (as light, heat and water fluxes), changes in interspecific relations, etc. The response of communities to disturbance is then the cornerstone of tropical forests ecology, modelling and management (White & Jentsch, 2001; Chazdon, 2003). Disturbance recovery have been largely studied through structural parameters as aboveground biomass, tree height or stem density, which all reflect rapid and measurable changes of ecosystems functioning asses crucial issues about the maintenance of ecosystems processes and services (Denslow & Guzman, 2000; Blanc *et al.*, 2009; Rutishauser *et al.*, 2016). In this perspective tree species diversity is inevitable as it determines ecosystems productivity, stability and functioning through the interspecific complementarity that enhances resources use, nutrients storing, and hazards mitigation (Tilman *et al.*, 2014). Revealing diversity dynamics is besides all the more important that disturbance modifies the environment and interspecific relations and surely impacts trees composition and diversity (Cazzolla Gatti *et al.*, 2014).

Until now, although, short-term dynamics demonstrated negligible or even positive impacts on communities diversity in accordance with the intermediate disturbance hypothesis (IDH) (Molino & Sabatier, 2001; Kariuki *et al.*, 2006; Berry *et al.*, 2008). The long-term response of communities composition and diversity to disturbance remains unclear. The IDH predicting a maximized species diversity at intermediate level of disturbance has besides mainly been tested through species richness, which gives limited or misleading information on forests recovery and functioning (Martin *et al.*, 2015; Chaudhary *et al.*, 2016). Studies of communities response to disturbance should encompass taxonomic composition and evenness, which only can assess some conservation issues and the ecological rules that determine communities abundance distribution (Magurran, 1988; Lavorel & Garnier, 2002; Bellwood *et al.*, 2006). Beyond

taxonomic metrics, communities recovery should also encompass functional diversity metrics (Moretti *et al.*, 2009; Baraloto *et al.*, 2012) through functional traits, that are species biological attributes relating to individuals fitness and ecosystem properties (Violle *et al.*, 2007; Scheiter *et al.*, 2013). Functional traits were largely adopted and integrated within a workable framework to assess forests dynamics and functioning (Díaz *et al.*, 2005; Villéger *et al.*, 2008) and a vast litterature revealed some major functional traits determinant for species ecology and performance. These major traits proved relevant to assess the ecological rules shaping species assembly: post-disturbance trajectories in tropical rainforests, for example, are assumed to be driven by environmental filters fostering disturbance resistant species with rapid growth and efficient resources acquisition (Molino & Sabatier, 2001; Haddad *et al.*, 2008). Communities dynamics would then be reflected by a shift from "conservative" species displaying long-lived, dense tissues growing slowly but with scarce resources, to "acquisitive" species with fast-growing, light tissues allowing fast resources acquisition (TerSteege & Hammond, 2001; Reich, 2014; Hérault *et al.*, 2011). In this perspective a combination of resource acquisition traits (leaf area, density and chlorophyll content and stem specific gravity and bark thickness) and life history traits of growth and reproduction (seed mass and maximum height) already proved relevant (Wright *et al.*, 2004; Westoby & Wright, 2006; Chave *et al.*, 2009).

Here we investigated over 30 years the response of 75 ha of forests plots set up on a gradient of disturbance intensity, from 10 to 60% of ecosystem biomass removed. We made use of a large functional traits database browsing major leaf, stem and seed traits and species maximum height to draw communities taxonomic and functional composition and diversity trajectories after disturbance. Specifically, we (i) tested the validity of the IDH arguing for enhanced diversity after moderate disturbance and (ii) confirmed the changes in ecological rules shaping communities, from competitive exclusion between "conservative", slow-growing tree species to environmental filtering of "acquisitive", fasting-growing ones. Eventually we examined the different trajectories to (iii) resolve the resilience of tropical forests and question their future dynamics regarding their state 30 years after disturbance.

2. Material and Methods

2.1 Study site
Paracou station in French Guiana (5°18'N and 52°53'W) is located in a lowland tropical rain forest corresponding to a tropical wet climate with mean annual precipitation averaging 2980 mm.y^{-1} (30-y period) with a 3-months dry season (< 100 mm.months^{-1}) from mid-August to mid-November, and a one-month dry season in March (Wagner *et al.*, 2011). Elevation ranges between 5 and 50 m and mean annual temperature is 26°C. Soils correspond to thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains. The experiment corresponds to a network of twelve 6.25ha plots that have undergone a gradient of three logging, thinning and fuel-wood treatments (Table 1). Disturbance treatments were

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

2.2 Inventories protocol and dataset collection
The study site corresponds to a tropical rainforest with a dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae botanical families. In the twelve experimental plots of the experiment, all trees above 10 cm DBH were mapped and measured annually since 1984. During inventories, trees were first identified with a vernacular name assigned by the field team, and afterward with a scientific name assigned by a botanist during regular botanical campaigns. In 1984, specific vernacular names were given to 62 commercial or common species whereas other less common species were identified under two identifiers only separating trees and palm trees. The botanical campaigns carried every 5 to 6 years to identify all trees at the species level only started in 2003 and identification practices varied among plots and successive campaigns. This raised methodological issues as vernacular names usually correspond to different botanical species, resulting in significant taxonomic uncertainties that had to be propagated to composition and diversity metrics throught a Bayesian framework. The uncertainty propagation was done by the replenishment of inventories completed at genus level from real incomplete ones on the basisof vernacular/botanical names association.

Vernacular names were replaced through multinomial trials $M_v\left([s_1, s_2, \ldots, s_N], [\alpha_1, \alpha_2, \ldots, \alpha_3]\right)$ based on the observed association probability $[\alpha_1, \alpha_2, \ldots, \alpha_3]$ between each vernacular name v and the species $[s_1, s_2, \ldots, s_N]$ recorded in the inventory.

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

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

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

Whenever a species inventoried was not in the dataset, it was attributed a set of traits values randomly sampled among species of the same next higher taxonomic level. As

Table 1. Intervention table, summary of the disturbance intensity for the 4 plot treatments in Paracou.

Treatment	Timber	Thinning	Fuelwood	%AGB lost
Control				0
T1	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha			$[12\% - 33\%]$
T2	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha	DBH $\geq$ 40 cm, non-valuable species, $\approx$ 30 trees/ha		$[33\% - 56\%]$
T3	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha	DBH $\geq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha	40 cm $\leq$ DBH $\leq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha	$[35\% - 56\%]$

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

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

2.3 Composition and diversity metrics

To counter the remaining taxonomic uncertainty plots taxonomic composition and diversity were analysed at the genus level, *i.e.* referring to the genus of observed or trialed botanical names. The analysis of taxonomic and functional composition of plots along time was visualized in a two-dimensional ordination space based on non-metric dimensional scaling of succesive floristic or functional inventories. Plots trajectories along time was reported comparatively to the inventories in 1989, 5 years after disturbance, which corresponded to first inventory with a sufficient degree of uncertainty (<30% of undetermined trees). The inventories dissimilarity compared to the reference 1989 inventory was reported using occurrence-based (Jaccard) and abundance-based (Bray-Curtis) similarity measures. The trajectory of inventories along time was visualized with the euclidean distance in the two-dimensional ordination space to the 1989 inventory. The functional 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). Species seed mass correspond to 5 classes of increasing mass, the seed mass trajectories were reported by the proportion of each class recorded in the inventories. To determine whether communities' assembly deviated from the expectation of a random process we compared the observed similarity patterns to those generated by 50 repetitions of stochastic null models. The null model for taxonomic composition randomly shuffled individuals among plots while preserving the overall species abundance and plots' tree density. The null model for functional composition pro-

duced random traits assemblages by permuting the set of functional traits values among species.

The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973). To tackle the unequal number of recruited trees among treatments the indices bias corrected estimator were used, following (Chao & Jost, 2015; Marcon, 2015). These three indices belong to the set of HCDT or generalized entropy, respectively corresponding to the 0, 1 and 2 order of diversity (q), which proved well suited for diversity studies (Patil & C., 1982; Tothmeresz & Tóthmérész, 1995). The functional diversity was reported using the Rao index of quadratic entropy which combines species abundance distribution and average pairwise dissimilarity based on all functional and life traits.

3. Results

3.1 Taxonomic and functional composition

3.1.1 Composition trajectories

Over time, 828388 trees and 591 botanical species pertaining to 223 genus and 64 botanical families were recorded. Trajectories of taxonomic and functional composition after disturbance were examined through the ordination of successive inventories from 1989 (5 years after disturbance) in the two-dimensional space from NMDS analysis based on flora inventories and the corresponding functional composition. Classifications were performed using either abundance-based Bray-Curtis (Figure 1) or incidence-based Jaccard dissimilarity (data not shown).

Both taxonomic and functional composition were substantially affected by disturbance, and the maximum dissimilarity to 1984 reference inventory composition was positively correlated with the disturbance intensity. Until 30 years after disturbance, all disturbed plots taxonomic composition remained significantly dissimilar to that of the 1989 reference inventory composition (Figure 1). All plots, though, displayed a unimodal trajectory with a the return toward the taxonomic and functional composition of the 1989 reference inventory suggesting a shift towards a cyclic regime (Figure 2). For taxonomic composition, the maxi-

mum dissimilarity to 1984 inventory composition was reach around 20 years after disturbance for the T2 and T3 plots and for one T1 plot while control and other T1 plots continued to increase (Figure 2.a). For functional composition, the maximum dissimilarity to 1984 inventory composition was reach from 15 to 20 years after disturbance for the T2 and T3 plots while T1 and control plots continued to increase (Figure 2.b). The functional composition distancing from the reference inventory was also positively correlated with disturbance intensity and similarly stabilized or reduced (for 5 of T1, T2 and T3 plots) from 20 years after disturbance (Figure 2).

The coordinates of the functional traits were measured in the two-dimensional ordination space that mapped plots evolution along time (graphs not showed) revealed a trajectory of disturbed plots toward acquisitive functional strategies (from high WD to high SLA and chlorophyll content).

3.1.2 Traits community weighted means
For all plots the trajectories of the community weighted means (CWM) were drawn for the 8 functional and life history traits (Leaf thickness, chlorophyll content, toughness and specific area,wood specific gravity and barck thickness and seed mass and maximum adult height) (Figure 3).

> To compensate the intrinsinc difference among plots the trajectories drawn correspond to the difference in value between the reference inventory in >1984 (5 year after disturbance) and the successive years inventoried.

Except for leaf cholorphyll content, which displayed higher difference between plots than among treatments which may be due to the completeness of dataset, all CWM trajectories corresponded to significant changes after disturbance. All functional traits and seed mass proportions displayed a unimodal trajectories but with different times at maximum and different values 30 years after disturbance. The weighted means of communities specific maximum height at adult stage (*Hmax*), leaf toughness (*L_toughness*) and wood specific gravity (*WD*) remained significantly lower than their initial value and than these of the control plots (Figure 3). The weighted means of bark thickness (*Bark_thick*) similarly remained substantilly higher than initially for all disturbed plots while the specfic leaf area (*SLA*) had almost recovered its initial value and this of the undisturbed plots at the end of the experiment.

3.2 Disturbance impact on diversity
3.2.1 Taxonomic diversity
Trajectories of Richness, Shannon and Simpson taxonomic diversity were examined in relation to the 1989 inventories (5 years after disturbance) (Figure 5). *For the three indices the OLS regression confirmed the time-dependency of the diversity variations (P<0.01) and a covariance analysis confirmed the significant effect of the disturbance treatment (P<0.01).*

While for undisturbed plots the Richness, Shannon and Simpson diversity remained comparable to the values in 1989, the trajectories of all disturbed plots showed significant increase positively correlated with the disturbance intensity (Figure 5). The Richness was less affected by the initial disturbance except for the higher intensity (T3 plots) (Figure 5). The Shannon and Simpson diversities however first significantly increased, illustrating an increasing evenness, before reaching a maximum around 15 years after disturbance for all plots except one from T1 treatment and one from T2 treatment (Figure 5).

3.2.2 Functional diversity
For all undisturbed plots the Rao diversity remained comparable to the values in 1989, the trajectories of all disturbed plots showed significant increase positively correlated with the disturbance intensity (Figure 6). Although a first increase of plots functional diversity that was all the more important than initial disturbance was intense, 30 after disturbance the diversity was similar among disturbed plots and significantly higher than this of control plots. *The OLS regression confirmed the time-dependency of the diversity variations (P<0.01) and the covariance analysis confirmed the significant effect of the disturbance treatment (P<0.01).*

4. Discussion

Our study showed the significant impact of disturbance on tropical forests communities. The subsequent diversity trajectories confirmed the intermediate disturbance hypothesis debated for tropical forests through their correlation with disturbance intensity. Besides it revealed the contrasting response of taxonomic and functional characteristics, specifically the decoupling between communities taxonomic evenness and their functional diversity and dominant functional traits values. The long-term disturbance trajectories observed highlighted the unachieved but consistent recovery of communities assembly for the lowest disturbance intensity but questioned it after higher disturbance.

4.1 Validation of the IDH
The enhanced communities evenness and functional richness after disturbance confirmed the IDH for all treatment intensity. The divergence from the initial state however was very variable among plots, specifically after intense disturbance, which meant a strong dependency of plots recovery to initial composition or to abiotic conditions. All plots, though, followed the same unimodal trajectory which confirmed both the resilience of forests taxonomic and functional composition and the convergence of communities towards initial states (Hubbell *et al.*, 1999; Molino & Sabatier, 2001; Baraloto *et al.*, 2012). Functional traits are the most direct link between biodiversity and ecosystem functioning (Díaz *et al.*, 2005) the recovery of communities functional characteristics would go along the recovery of ecosystems processes although taxonomic composition remain altered (Guariguata & Ostertag, 2001). Disturbance proved to favor species with acquisitive strategies, displaying efficient resource acquisition (high SLA) but short-lived tissues (low wood density, leaf toughness and thickness) and with a dispresive strategy (low seed mass) (Westoby, 1998; Wright *et al.*, 2004; Reich, 2014). #The comparison of observed trajectories to a null model with random traits set shuffling showed an oriented functional shift after disturbance which
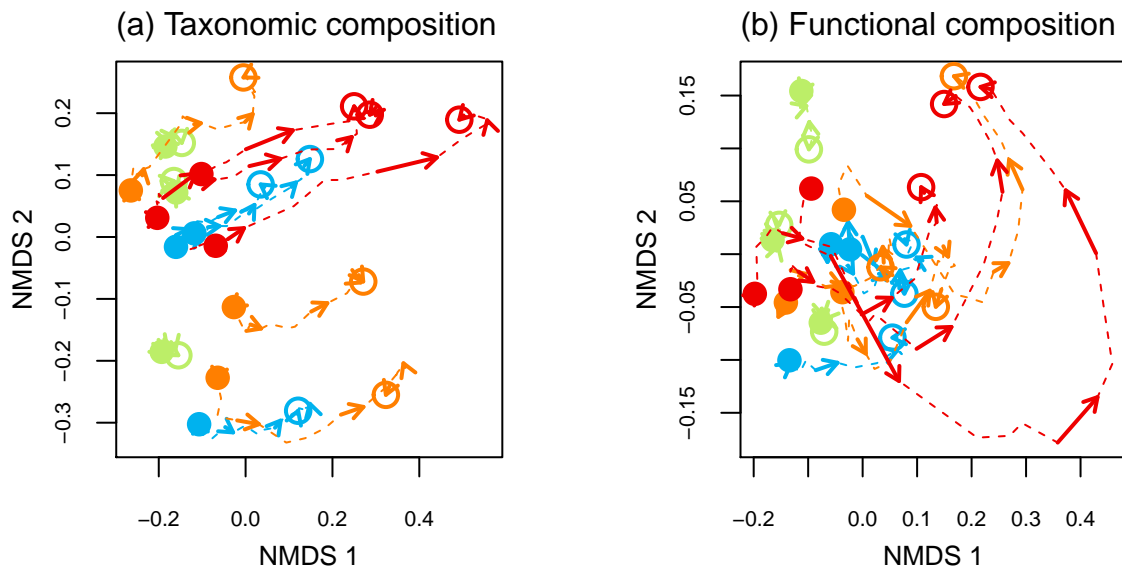
Figure 1. Trajectories of the plots in terms of **(a)** flora composition and **(b)** functional composition regarding the 6 leaf and stem functional traits,the maximum allometric height and seed mass class in the two-dimensional space from the NMDS performed for the 30 years after disturbance. Distance matrix for NMDS were computed from the Bray-curtis dissimilarity between successive inventories. Line colors represent the disturbance treatment (green for control, blue for T1,orange for T2 and red for T3).
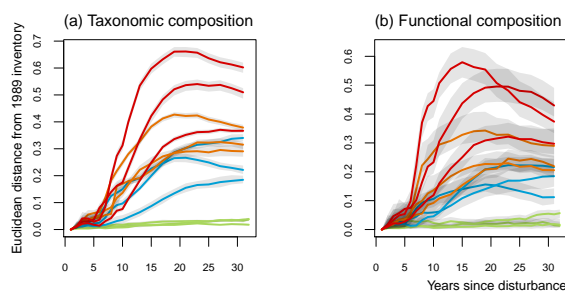

Figure 2. Trajectories of the distance to initial condition of the 30 sampled years in the two-dimensional space from the NMDS of **(a)** taxonomic composition at genus level and **(b)** functional composition. Distance are abundance-based Bary-Curtis metric. Line colors represent the disturbance treatment (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.

suggest additional biotic and abiotic filters for the 10 to 15 years after disturbance. #This means a shift from exclusive competition favoring competitive species before disturbance to environmental filtering selecting acquisitive and disturbance resistant species. In particular, the evolution seed mass classes proportions revealed a clear increase in small seeded, therefore large dispersive, species (TerSteege & Hammond, 2001; Flores *et al.*, 2006; Haddad *et al.*, 2008).

4.2 Functional redundancy of disturbed ecosystems

After disturbance, communities functional characteristics followed a similar but delayed trajectory as this of taxonomic characteristics which difference to initial state remained higher after 30 years. This confirms conclusions drawn for grasslands (Tilman, 1997; Mouillot *et al.*, 2011) and more recently for tropical forests (Lohbeck *et al.*, 2015; Guariguata & Ostertag, 2001). Assuming the "vegetation quantity effect", suggesting that communities functional characteristics are defined by dominant species rather that subtle changes in biodiversity (Grime, 1998), this delay between functional and taxonomic diversities meant the rapid recovery of dominant species while this of rare ones would be much longer. Besides, it meant that species missing to plots taxonomic recovery would be functionally redundant with those already in place. The functional overlap between species, typical of the huge biodiversity of tropical forests (Bellwood *et al.*, 2006), is then not trivially recovered after disturbance and as a determinant of forests resilience this
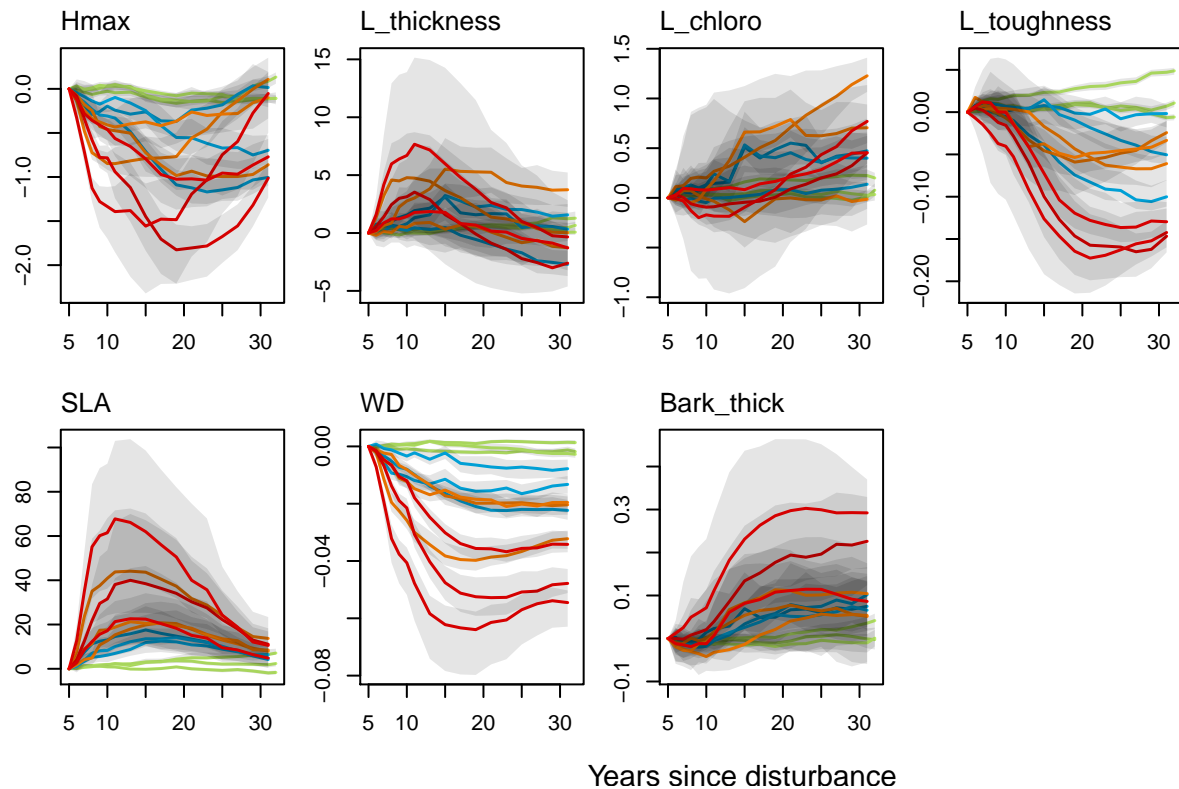
Community Weighted Means

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 colorswith green for control, blue for T1,orange for T2 and red for T3.
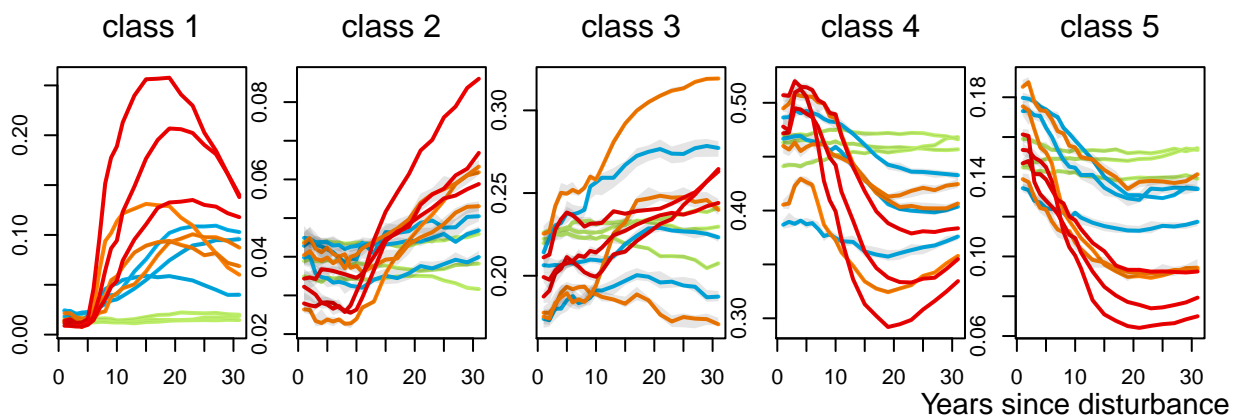
Proportion of seed mass classes

Figure 4. Trajectories of seed mass classes proportions over 30 years after disturbance, corresponding to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation. No gap filling process was applied in this case. Initial treatments are represented by solid lines colors with green for control, blue for T1,orange for T2 and red for T3.
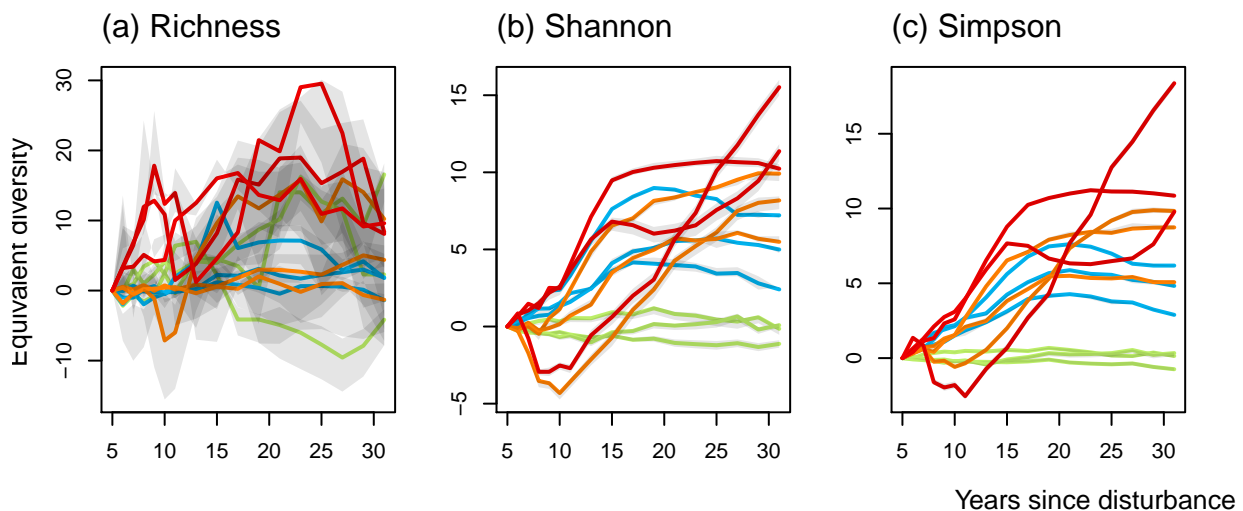
Figure 5. Trajectories of the difference to reference inventory over 30 years after disturbance of plots communities **(a)** Richness, **(b)** Shannon and **(c)** Simpson diversities. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation. Initial treatments are represented by solid lines colorswith green for control, blue for T1,orange for T2 and red for T3.

Figure 6. Trajectories of the Rao functional diversity over 30 years after disturbance. Trajectories correspond to the median (solid line) and 0.025 and 0.975 percentile (gray envelope) observed after 50 iteration of the taxonomic uncertainty propagation. Initial treatments are represented by solid lines colorswith green for control, blue for T1,orange for T2 and red for T3.and the missing trait value filling processes.
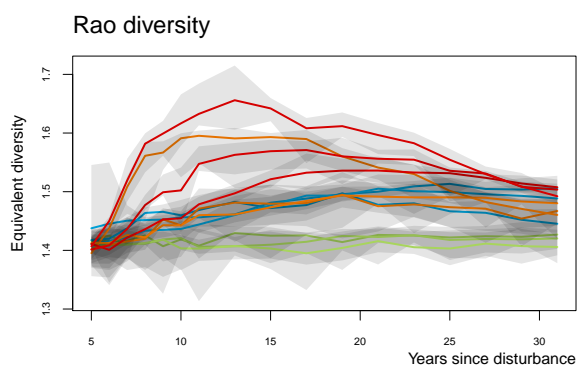
questions forests resilience to multiple disturbance (Trenbath, 1999; Elmqvist *et al.*, 2003; Díaz *et al.*, 2005).

Besides such impact on functional redundancy along with persitant compositional changes regarding disturbance resistant species (Haddad *et al.*, 2008) and probably lianas or epiphytes (Martin *et al.*, 2013), and the modification of environmental conditions like soils nutrient cycling and compaction (Olander *et al.*, 2005) forest resilience remains under question (Chazdon, 2003). New conditions would not only be longer lasting but self-maintained as tied to disturbance regime (Burslem *et al.*, 2000). Specificaly, this would impair species contingent to undisturbed forests, threatening their maintenance, and run the risk to loose cornerstone species and trigger unexpected ecological consequences (Jones *et al.*, 1994; Díaz *et al.*, 2005; Gardner *et al.*, 2007).

To confirm this long-term communities changes and highlight the ecological rules shaping communities assembly, we suggest a focus on recruitment dynamics, that would follow the diversity and functional characteristic of recruited communities and, by extension, of the forest to be.

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