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Post-Disturbance Tree Community Trajectories in a Neotropical Forest

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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 change context. The huge diversity of tropical forests is often assumed to be regularly reshaped by natural disturbance yielding a diversity peak at intermediate intensity. This intermediate disturbance hypothesis (IDH), though, remains debated and the controversy questions the extent of communities' resilience regarding their taxonomic and functional facets. To disentangle the ecological processes driving community response to disturbance, we analysed the tree community trajectories over 30 years following a disturbance gradient in a Neotropical forest. Specifically, we examined community functional and taxonomic trajectories with regards to diversity, composition and redundancy. Functional trajectories were drawn based on 7 leaf, stem and life-history traits. We highlighted the cyclic recovery of community taxonomic and functional composition. While pre-disturbance taxonomic differences were maintained over time, functional composition trajectories were quite similar among communities. The IDH did predict communities taxonomic diversity response while functional diversity was enhanced whatever the disturbance intensity. Although consistent, the recovery of community composition, diversity and redundancy remained unachieved after 30 years. This acknowledged the need of decades-long cycles with no disturbance to ensure a complete recovery, and questioned tropical forest community resilience after repeated disturbances.

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

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Contents

Species TDP weighted by species abundance were eventually summed for each community. Community 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 (Supp. Mat. - Figure S1 for a more comprehensive sheme).

1. Results

1.1 Communities Composition

From 1989 (2 years after disturbance) to 2015 (28 years after disturbance), 828 388 individual trees and 591 botanical species pertaining to 223 genus and 64 families were recorded.

While both taxonomic and functional composition remained stable in undisturbed communities (Figure 1), they followed marked and consistent trajectories over post-disturbance time. In disturbed communities, these compositional changes corresponded to shifts towards species with more acquisitive functional strategies, from communities with high average WSG to high average SLA and chlorophyll content (see appendix I). For functional composition, this translated into cyclic compositional changes with an unachieved recovery of the initial composition (Figure 1). The maximum dissimilarity with the initial state was positively correlated to the disturbance intensity for both taxonomic and functional composition ($\rho^{taxonomic}_{spearman} = 0.87$ and $\rho^{functional}_{spearman} = 0.90$ respectively). The maximum value was reached around 26 years after disturbance for taxonomic composition and 22 years for functional composition.

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.

Maximum height at adult stage (*Hmax*), leaf toughness (*L_toughness*) and wood specific gravity (*WSG*) first decreased and then slightly increased but remained significantly lower than their initial value (Figure 2). On the

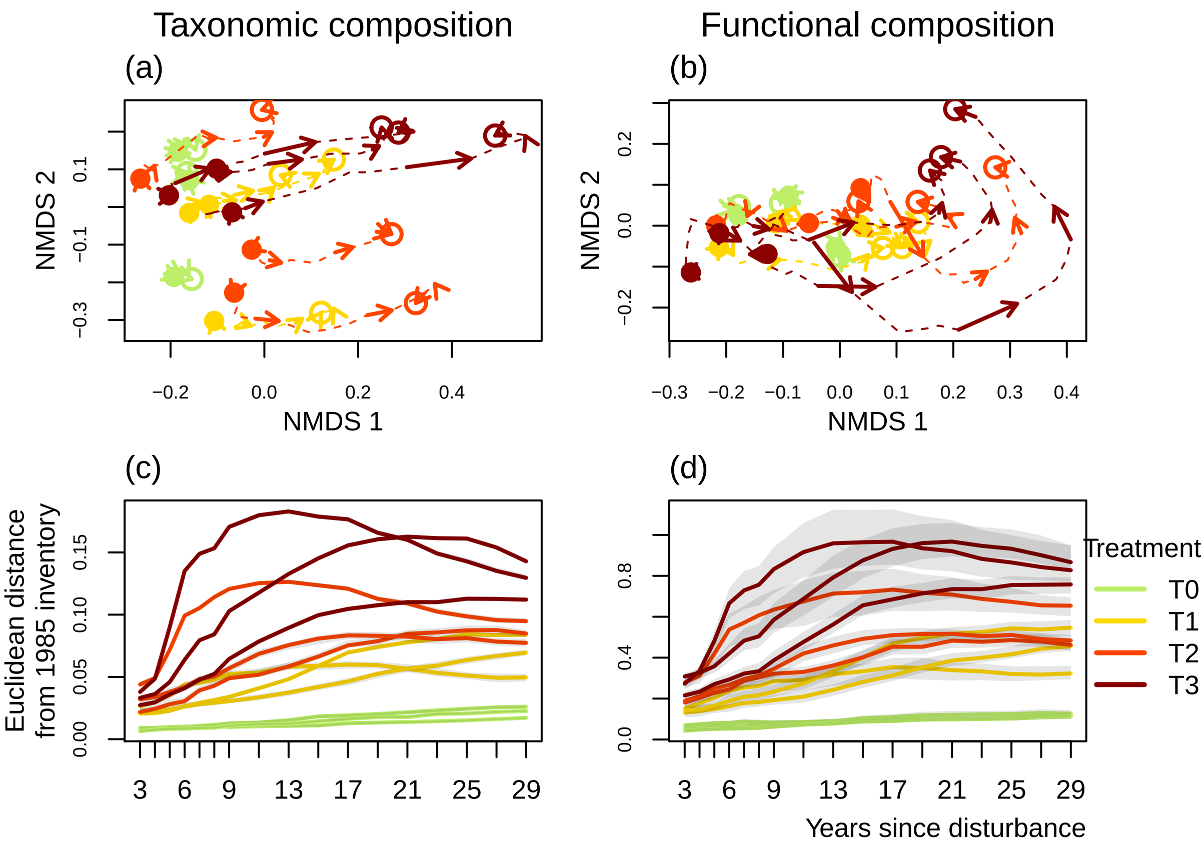

Figure 1. Plot trajectories in terms of flora composition (left panels **(a)** and **(c)**) and functional composition (right panels **(b)** and **(d)**) in a two-dimensional NMDS space. Lower panels (**(c)** and **(d)**) represent the euclidean distance to initial condition along the 30 sampled years. Colors are treatments: green (control), yellow (T1), orange (T2), red (T3) with shaded areas the credibility intervals.

other side, Bark thickness (*Bark_thick*) and specific leaf area (*SLA*) increased and while *Bark_thick* remained substantially high after 30 years, *SLA* had almost recovered its initial value. For all traits, the maximum difference to initial value was correlated to the disturbance intensity ($\rho^{L_{thickness}}_{spearman} = 0.76$, $\rho^{L_{chloro}}_{spearman} = 0.60$, $\rho^{L_{toughness}}_{spearman} = -0.53$, $\rho^{SLA}_{spearman} = 0.93$, $\rho^{WSG}_{spearman} = -0.75$, $\rho^{Bark-thickness}_{spearman} = 0.71$, $\rho^{Hmax}_{spearman} = -0.40$). The proportions of the three lightest seed mass classes increased in all disturbed plots, and decreased after 30 years for the lightest class while it stabilized for the two other (Supp. Mat. - Figure S2).

1.2 Communities richness and evenness

For undisturbed plots, taxonomic Richness and Evenness remained stable over the 30 years monitored. In disturbed communities, after low disturbance intensity the taxonomic richness increased, reaching a maximum gain of 14 botanical genera (plot 3 from treatment 2). After intense disturbance the taxonomic richness followed a more complex trajectory, decreasing for ten years after disturbance before recovering to pre-disturbance values. The maximum richness loss or gain after disturbance was positively correlated to the disturbance intensity ($\rho^{Richness}_{spearman} = 0.50$). In all disturbed plots the taxonomic evenness first increased until a maximum reached after around 20 years. This maximum was positively correlated to the disturbance intensity ($\rho^{Evenness}_{spearman} = 0.77$). The evenness then stabilized except for two T3 plots (plots 8 and 12) for which evenness kept increasing.

The plot 7 from treatment 1 displayed constantly outlying functional richness and evenness and was removed from the graphical representation for better readability. In undisturbed plots both functional richness and evenness remained stable along the 30 years. In disturbed plots, functional richness and evenness trajectories depended on the disturbance intensity with their maximum positively correlated to %AGB loss $\rho^{Richness}_{spearman} = 0.76$ and $\rho^{Evenness}_{spearman} = 0.60$. Functional richness and evenness displayed for low disturbance intensity a low but long-lasting increase up to a maximum reached after 20-25 years, and for high intensity, a fast but short increase followed after 10 years by a slow decrease towards the inital values.

The second-degree polynomial regressions between (i) the %AGB loss and (ii) taxonomic and functional richness and evenness after 10, 20 and 30 years best predicted the hump-shaped curve of the disturbance impact along the disturbance intensity gradient 4. The relationship between the disturbance impact and its intensity was more markedly hump-shaped for the taxonomic richness than for the taxonomic evenness. For both functional richness and evenness the relationship was almost linear. The regression model better predicted the functional richness and evenness ($0.55 < R^2_{FunctionalRichness} < 0.72$, and $0.60 < R^2_{FunctionalEvenness} < 0.81$) than the taxonomic richness and evenness ($0.21 < R^2_{TaxonomicRichness} < 0.4$, and $-0.15 < R^2_{TaxonomicEvenness} < 0.43$ respectively)

1.3 Functional redundancy

All disturbed plots had lower functional redundancy than control plots and followed similar hump-shaped trajectories (5). The maximum redundancy loss was positively correlated with the disturbance intensity ($\rho_{spearman} = 0.47$) and the initial value had not recovered for any disturbed communities after 30 years.

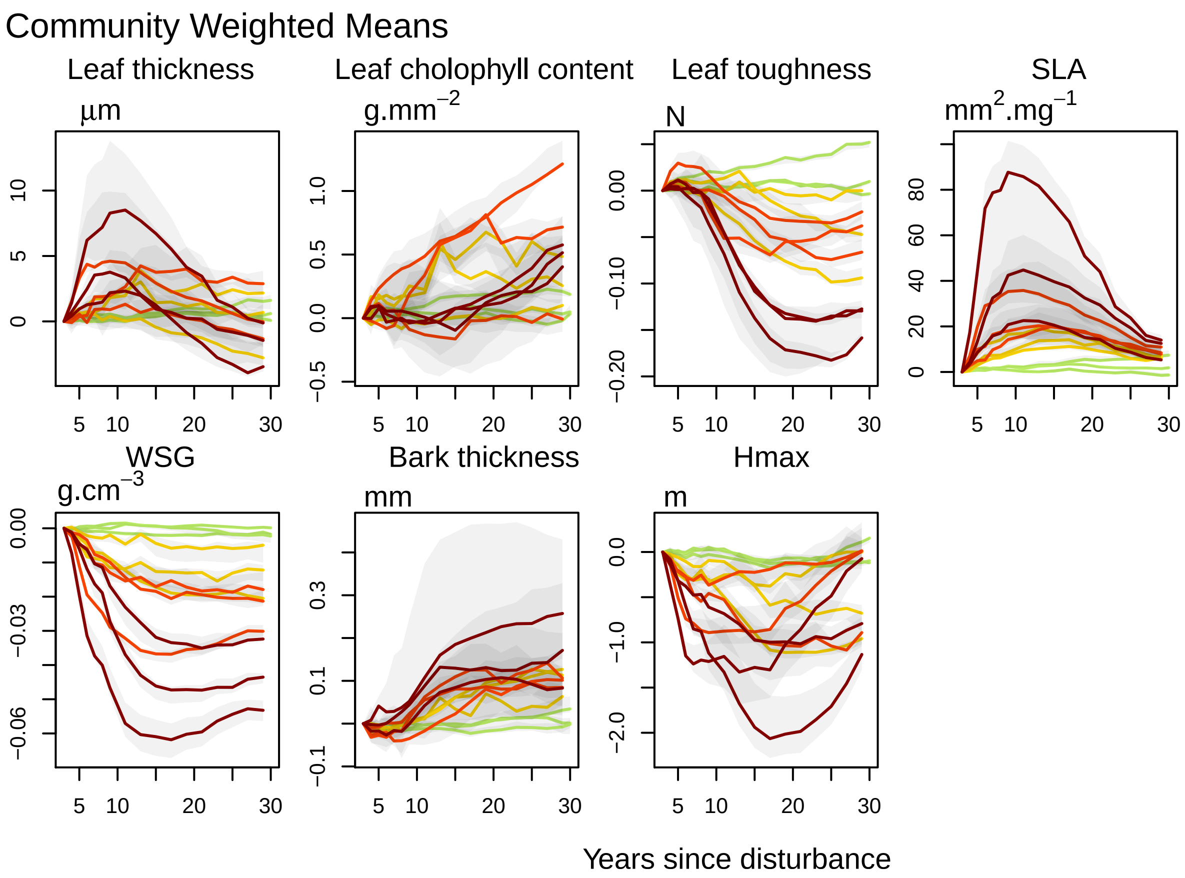

Figure 2. Trajectories of the communities weighted means (CWM) over 30 years after disturbance of 4 leaf traits (Leaf thickness, *L_thickness*, chlorophyll content, *L_chloro*, toughness, *L_toughness* and specific area, *SLA*), 2 stem traits (wood specific gravity, *WSG*, and bark thickness, *Bark-thick*)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

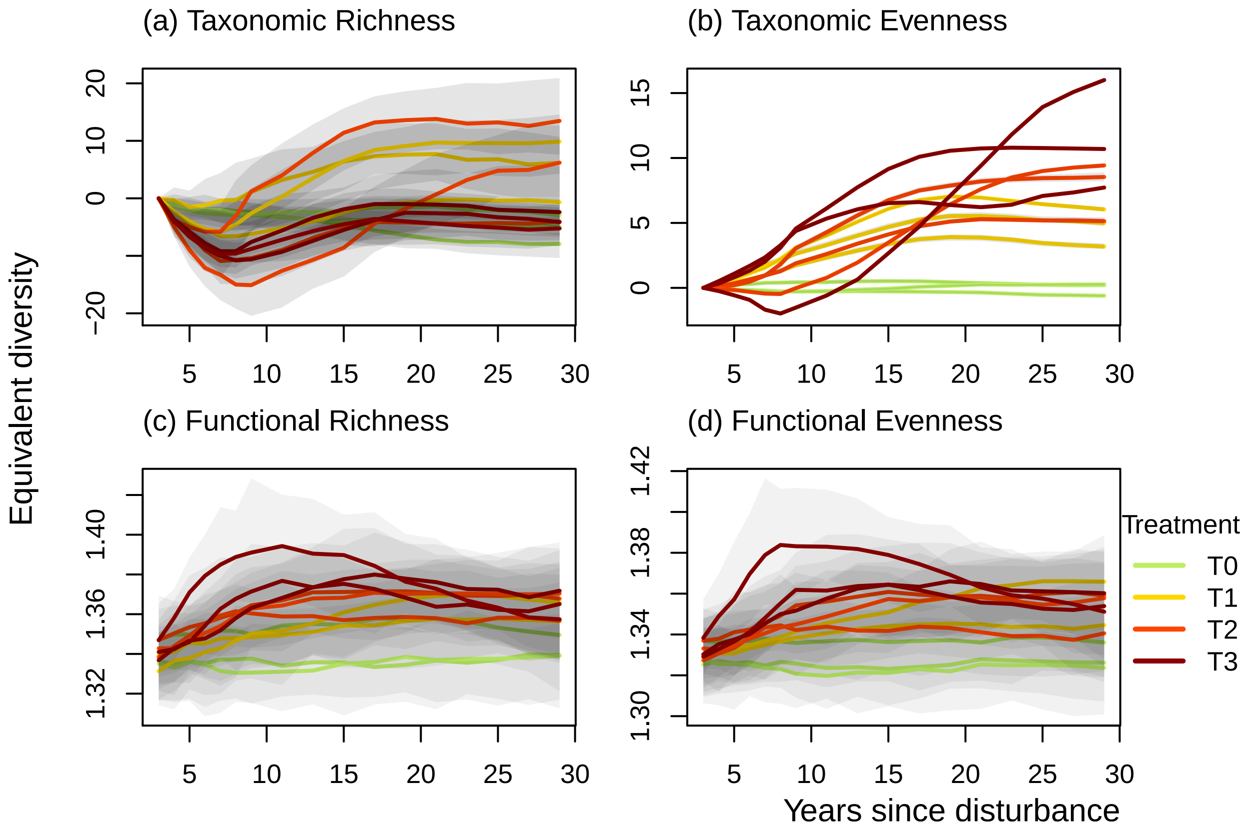

Figure 3. Trajectories over 30 years of the difference with the 1989 inventory (2 years after disturbance) of community taxonomic **(a)** richness, **(b)**, taxonomic evenness, **(c)** functional richness, and **(d)** functional evenness. Colors are treatments: green (control), yellow (T1), orange (T2), red (T3) with shaded areas the credibility intervals

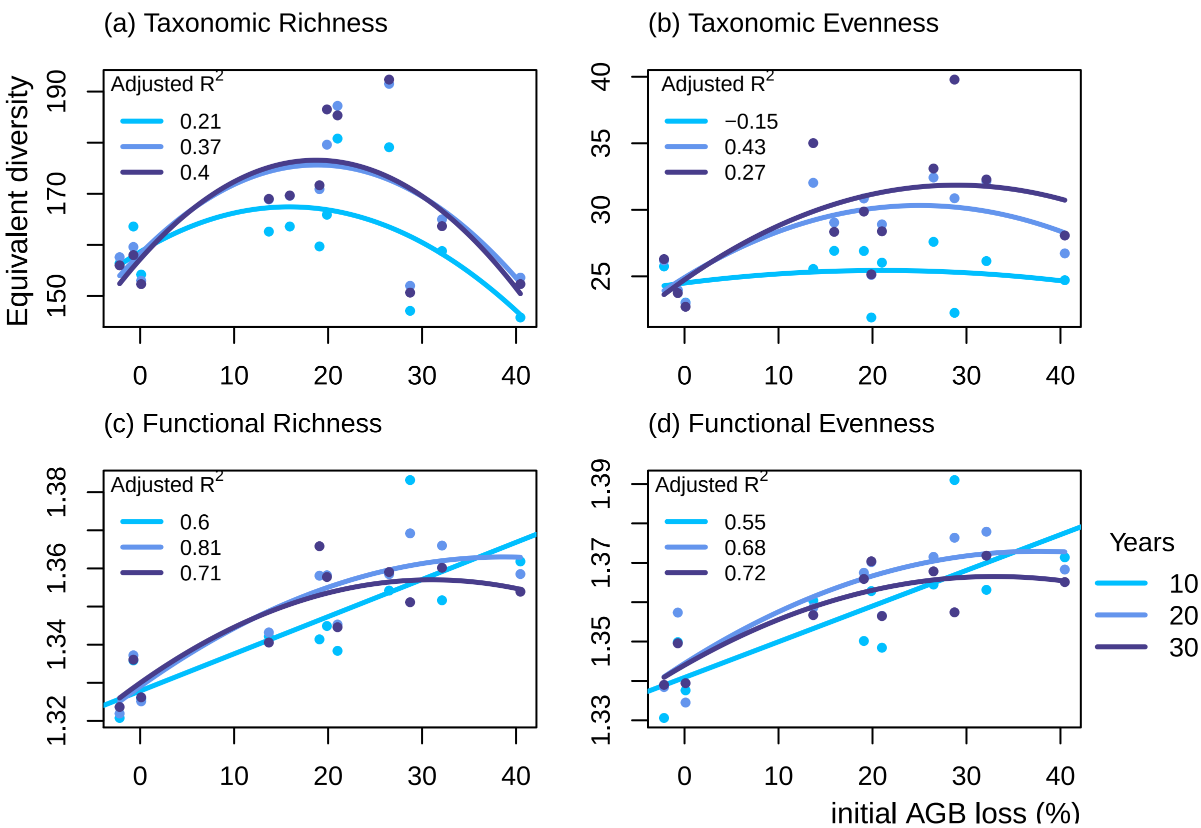

Figure 4. Relationship between the initial %AGB loss and community taxonmic richness **(a)**, taxonomic evenness **(b)**, functional richness **(c)**,and functional evenness **(d)** at 10, 20 and 30 years after disturbance

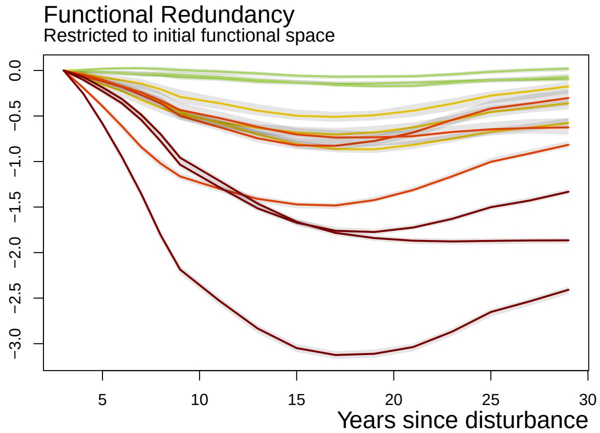

Figure 5. Trajectories of the functional redundancy within the initial functional space over 30 years after disturbance. Colors are disturbance treatments: green (control), yellow (T1), orange (T2), red (T3) with shaded areas the credibility intervals.