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1 **Diverging taxonomic and functional trajectories following**
2 **disturbance in a Neotropical forest**

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12 **ABSTRACT**

13 In the current global change context, it is urgent to anticipate the fate of tropical forests.
14 This means understanding tree community response to disturbance and the underlying
15 processes. In that respect, we aim here to clarify taxonomic and functional post-disturbance
16 trajectories, and determine the scope of the Intermediate Disturbance Hypothesis (IDH) that
17 remains debated in tropical forests. We analyzed community trajectories following a
18 disturbance gradient from 10 to 60% of above-ground biomass loss in a Neotropical forest
19 over 30 years. We considered trajectories along time of community taxonomic and functional
20 trajectories in terms of richness, evenness, composition, and redundancy. We based on the
21 annual botanical inventories of 75 ha of a Neotropical forest and on large trait datasets
22 comprising seven leaf, stem, and life-history traits. We identified a decoupling between
23 taxonomic composition, differing among communities, and functional composition, similar
24 among communities and convergent in the functional space. The taxonomic diversity
25 followed humped-shaped trajectories along time after disturbance depending on the initial
26 disturbance intensity, which validated the IDH (Intermediate Disturbance Hypothesis). The
27 functional diversity trajectories, however, were homogeneous among plots and dismissed
28 the IDH. We explained this decoupling by the variations in community functional
29 redundancy that mitigated the functional impact of disturbance. Although consistent, the
30 recovery of community composition, diversity, and redundancy remained divergent from
31 the initial state after 30 years. These results acknowledged the need of decades-long cycles
32 without disturbance to ensure community complete recovery.

33 **KEY WORDS** Community Ecology, Disturbance Trajectories, Intermediate Disturbance
34 Hypothesis, Mid-term Resilience, Neotropical Forests, Taxonomic and Functional
35 Biodiversity

36 **1. INTRODUCTION**

37 The large areas covered with tropical forests worldwide hold crucial environmental,
38 economic, and social values. They provide wood and multiple non-timber forest products,
39 shelter a diversified fauna, and ensure cultural and human well-being. They regulate local
40 and regional climates, as well as carbon, water and nutrient cycles. However, the growing
41 demand in forests products together with current global changes increase the pressure on
42 remaining undisturbed forests (Morales-Hidalgo, Oswalt, and Somanathan 2015). These
43 threats may change the frequency and magnitude of the natural disturbance regime that
44 defines and maintains the structure, composition, and functioning of tree communities
45 (Schnitzer and Carson 2001; Anderson-Teixeira et al. 2013; Sist et al. 2015). To anticipate
46 the fate of tropical forests, it is urgent to understand tree community response to
47 disturbance, and the underlying ecological processes. The forest cover is generally
48 maintained following disturbance, but modifications in the fluxes of light, heat, and water
49 (Goulamoussène et al. 2017) change community abiotic and biotic environments. These
50 changes translate into post-disturbance community trajectories that have been largely
51 studied through trajectories of forest structural parameters such as aboveground biomass,
52 tree height or stem density (Piponiot et al. 2016; Rutishauser et al. 2016). Some of the
53 determinants of post-disturbance biomass trajectories are already identified, like the
54 structure and composition of the pre-disturbance community, or the post-disturbance

55 environmental parameters (Hérault and Piponiot 2018). Community diversity and
56 composition trajectories, however, have not been as thoroughly understood (Guitet et al.
57 2018; J. F. Molino and Sabatier 2001), and manifold biodiversity trajectories might emerge
58 given the variety of species response to disturbance and the diversity of tropical forests
59 (Lindenmayer, Burton, and Franklin 2012; Garcia Florez et al. 2017).

60 An early conceptual basis of the linkage between biodiversity and disturbance is the
61 Intermediate Disturbance Hypothesis (IDH). The IDH states a relationship between the
62 community diversity and the intensity and frequency of disturbance events, and postulates
63 a diversity peak at intermediate level of disturbance (Connell 1978). This is based on the
64 fluctuations of community environment following disturbance that foster both competitively
65 superior species and fast colonizers, and prevents competitive exclusion (Shea, Roxburgh,
66 and Rauschert 2004; Pulsford, Lindenmayer, and Driscoll 2016). In tropical forests, some
67 studies advocate community deterministic response to disturbance, as for example in the
68 dry and wet forests in Ghana (F. Bongers et al. 2009) or in the guianese rainforests (J. F.
69 Molino and Sabatier 2001), where intermediate disturbance proved to increase the
70 community richness by increasing the proportion of pioneers or heliophilous species in the
71 community while maintaining the richness in old-growth forest species. In other cases,
72 however, observations of the IDH diverge from theoretical expectations (Randall Hughes et
73 al. 2007; Sheil and Burslem 2003; Norden et al. 2017). Some studies refute the role of
74 disturbance intensity, as observed in forest gaps in Panama where no difference in species
75 richness was found between forest gaps and undisturbed areas (Hubbell 2001), or in costa-
76 rican forests where forests that did not follow deterministic convergence display stochastic
77 trajectories (Norden et al. 2015).

78 The high diversity of tropical forests may foster the emergence of numerous facilitation,
79 adaptation, and inter- and intra-specific competition following disturbance (Garcia Florez et
80 al. 2017; F. Bongers et al. 2009). These interactions can result in a variety of responses to
81 disturbance (Lindenmayer, Burton, and Franklin 2012), which question the validity of the
82 IDH in tropical forests (Hubbell 2001; Fox 2013; Sheil and Burslem 2013).

83 Analyzing community response to disturbance and grasp all aspects of community changes
84 requires a wide array of metrics (Sheil and Burslem 2003; Shea, Roxburgh, and Rauschert
85 2004; Mayfield and Levine 2010). The analysis should first consider community
86 composition, which is crucial for conservation issues and reveals the pool of species fostered
87 or hampered by disturbance (S. Lavorel and Garnier 2002; Bellwood et al. 2006). This should
88 be completed with diversity metrics encompassing both community richness and evenness
89 to assess the changes in community abundance distribution. Besides, functional approaches
90 have been shown to usefully complement pure taxonomic approaches as they shed light on
91 the species biological attributes directly linking community diversity, composition, and
92 redundancy to ecosystem functioning (Violle et al. 2007; Baraloto et al. 2012). In that respect,
93 a vast literature allowed recognizing major traits representing species ecological strategy
94 and determining how they respond to changing conditions (Díaz et al. 2005). Specifically, in
95 tropical forests, the functional approach revealed the emergence of deterministic processes
96 following disturbance. Such deterministic processes entailed a shift from a dominance of
97 “conservative” slow-growing species dealing with scarce resources, to a dominance of
98 “acquisitive” fast-growing species with rapid and efficient use of abundant resources (Rees
99 et al. 2001; Reich 2014; Hérault et al. 2011). This shift is translated into the trajectories of
100 average community value of key functional traits related to resource acquisition, as leaf and

101 stem traits, and life-history strategy, as seed mass and maximum size (Wright et al. 2004;
102 Steege et al. 2006; Westoby and Wright 2006; Chave et al. 2009).

103 The functional approach also encompasses the analysis of functional redundancy, which
104 quantifies the amount of shared trait values among species (Carmona et al. 2016). The typical
105 high functional redundancy of hyper-diverse tropical forests (Bellwood et al. 2006) mitigates
106 the impacts of species removal on ecosystem functioning, and determines community
107 resilience after disturbance (Elmqvist et al. 2003; Díaz et al. 2005).

108 Here, we monitored over 30 years the response of 75 ha of Neotropical forest plots set up
109 on a gradient of disturbance intensity, from 10 to 60% of above-ground biomass (AGB) loss.
110 We made use of a large functional traits database encompassing major leaf, stem, and life-
111 history traits in order to draw the taxonomic and functional trajectories in terms of richness,
112 evenness, composition, and redundancy. Specifically, (i) we drew taxonomic and functional
113 post-disturbance trajectories and examined the underlying ecological processes, (ii) we
114 discussed the scope of the IDH regarding taxonomic and functional facets of community
115 diversity, and (iii) we analyzed community resilience and time to recovery. We hypothesized
116 that community functional and taxonomic trajectories might not track each other, given the
117 high functional redundancy in tropical forests. While functional diversity would be enhanced
118 by the environmental changes following disturbance, specifically the increase in light
119 availability, taxonomic diversity would only increase until a disturbance intensity threshold,
120 as pioneers recruited following disturbance are not as diverse as late-successional species.
121 Community taxonomic and functional trajectories would hence follow different rates of
122 recovery.

123 2. MATERIAL AND METHODS

124 2.1. STUDY SITE

125 Paracou station in French Guiana (5° 18'N and 52° 53'W) is located in a lowland tropical
126 rain forest in a tropical wet climate with mean annual temperature of 26° C, and mean annual
127 precipitation averaging 2980 mm.y⁻¹ (30-y period). The climate comprises a 3-month dry
128 season (< 100 mm.month⁻¹) from mid-August to mid-November, and a one-month dry season
129 in March (Wagner et al. 2011). Across all plots, elevation ranges from 5 to 50 m, and the
130 topography mainly corresponds to hilltops or hillsides, while bottomlands cover less than 1
131 % of the area. Plots are shallow ferralitic acrisols over a layer of transformed saprolite with
132 low permeability and lateral drainage. Soil conditions are homogeneous, to the exception of
133 the highest hilltops where the thick surface allows a free vertical drainage (Gourlet-Fleury,
134 Guehl, and Laroussinie 2004).

135 The experiment is a network of twelve 6.25 ha plots, distributed over a 400ha area (Table
136 1, Supp. Mat. Fig. S1), that undergone three disturbance treatments in 1987 according to a
137 randomized plot design (Gourlet-Fleury, Guehl, and Laroussinie 2004).

138 The experiment intended to simulate logging intensities and distinguished the treatments
139 for non-commercial and commercial species, logged at 40cm DBH to simulate thinning
140 operations. The experiment comprised three replicates of three silvicultural treatments
141 (hereafter plots T1, T2, and T3), and three control plots (T0). Control plots are set in mature
142 forest stand that did not undergone any logging nor intense anthropic activities for the last
143 500 years. All treatments T1, T2, and T3 comprised the logging of 10 trees/ha with 50 cm
144 minimum DBH that belonged to a set of 58 commercially exploited species (Gourlet-Fleury,

145 Guehl, and Laroussinie 2004). Treatment T2 additionally comprised a thinning treatment by
 146 poison-girdling of non-commercially exploited species randomly selected with an average of
 147 30 trees/ha with 40 cm minimum DBH. Treatment T3 additionally comprised the logging of
 148 15 trees/ha with 40 cm minimum DBH, and the poison-girdling of 20 trees/ha with a 50 cm
 149 minimum DBH, all belonging to non-commercially exploited species. Considering the
 150 silvicultural treatments and the following damage, disturbance intensity was measured as
 151 the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984
 152 and five years after disturbance (Piponiot et al. 2016) estimated with the BIOMASS R
 153 package (Réjou-Méchain et al. 2017). Tree diameter were provided in the experimental
 154 dataset, wood density was extracted from global wood density (GWD) database (A. E. Zanne
 155 et al. 2009), and tree height was retrieved from a generic H-D model based on a single
 156 bioclimatic predictor (eqn 6a in (Chave et al. 2014)). The AGB was measured from the
 157 generalized allometric model eqn 4 of (Chave et al. 2014). The three treatments were then
 158 transformed into a continuous disturbance intensity gradient with increasing above-ground
 159 biomass (AGB) loss.

160 **Table1.** *Intervention table, summary of the disturbance intensity for the 4 plot treatments in*
 161 *Paracou. Treatment intensities are defined by the minimum logging DBH (Diameter at Breast*
 162 *Height), the type of logged species (commercially exploited or not), the density of logged trees,*
 163 *and the increasing percentage loss of above-ground biomass (AGB) after treatment.*

Treatment	Timber	Thinning	Fuelwood	%AGB Lost
Control	-	-	-	0

T1	50 cm ≤ DBH , Commercial species, ≈ 10 trees.ha-1	-	-	[12-33]
T2	50 cm ≤ DBH , Commercial species, ≈ 10 trees.ha-1	40 cm ≤ DBH , non-valuable species, ≈ 30 trees.ha-1	-	[33-56]
T3	50 cm ≤ DBH , Commercial species, ≈ 10 trees.ha-1	50 cm ≤ DBH , non-valuable species, ≈ 15 trees.ha-1	40 cm ≤ DBH ≤ 50 cm, non-valuable species, ≈ 15 trees.ha-1	[35-56]

164

165 2.2. INVENTORIES PROTOCOL AND DATASET COLLECTION

166 The study site corresponds to a tropical rainforest typical of the Guiana Shield with a
167 dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae, and Sapotaceae. In the 12
168 experimental plots, all trees above 10 cm DBH have been mapped and measured annually
169 since 1984. Trees are first identified with a vernacular name assigned by the forest worker
170 team, and afterward with a scientific name assigned by botanists during regular botanical
171 campaigns. In 1984, specific vernacular names were given to 62 common or commercially
172 exploited species. More infrequent species were identified under general identifiers only
173 distinguishing trees and palms. From 2003, botanical campaigns have been conducted every
174 5 to 6 years to identify all trees at the species level. In 2015, however, identification levels
175 still varied among plots and campaigns.

176 This variability of protocols in time raised methodological issues as vernacular names
177 usually correspond to various botanical species. This resulted in significant taxonomic
178 uncertainty that had to be accounted for in the measure of composition and diversity metrics.
179 Uncertainty propagation was implemented within a Bayesian framework using
180 vernacular/botanical names associations to reconstitute complete inventories at genus level

181 from real incomplete ones. Vernacular names were replaced through multinomial trials
182 based on the association probability $[\alpha_1, \alpha_2, \dots, \alpha_V]$ observed across all inventories between
183 each vernacular name v and all species $[s_1, s_2, \dots, s_N]$:

$$184 \quad M_v([s_1, s_2, \dots, s_N], [\alpha_1, \alpha_2, \dots, \alpha_V])$$

185 See Supplementary Materials -Fig. S2 and Aubry-Kientz et al. (2013) for the detailed
186 methodology.

187 Six functional traits representing the leaf economics (*i.e.* leaf thickness, toughness, total
188 chlorophyll content, and specific leaf area), and the stem economics (*i.e.* wood specific
189 gravity and bark thickness) were obtained from the BRIDGE project.¹ Trait values were
190 assessed from a selection of individuals located in nine permanent plots in French Guiana,
191 including two in Paracou, and comprised 294 species belonging to 157 genera. Whenever a
192 species was in the dataset but missed some trait values (10% of the species), missing values
193 were filled using multivariate imputation by chained equation (van Buuren and Groothuis-
194 Oudshoorn 2011). To account for the phylogenetic signal in the imputation process,
195 imputations were based on samples of species from the same genus or from the same family.
196 Whenever a species was not in the dataset, it was attributed a set of trait values randomly
197 sampled among species of the next higher taxonomic level (same genus or family). Two life-
198 history traits, maximum specific height and seed mass, came from the Mariwenn database.²
199 The database compiles information from a vast literature on the flora of French Guiana

¹ <http://www.ecofog.gf/Bridge/>

² <https://www.ecofog.gf/mariwenn/>

200 (Ollivier, Baraloto, and Marcon 2007) and comprises 362 species belonging to 188 genera.
201 As seed mass information was classified into classes, no data filling process was applied and
202 analyses were restricted to the botanical species recorded.

203 Confidence intervals of the composition and diversity metrics were computed after 50
204 iterations of the uncertainty propagation framework.

205 2.3. COMPOSITION AND DIVERSITY METRICS

206 Because of the variable precision of botanical identification efforts, we had to conduct the
207 taxonomic composition and diversity analysis at the genus level. Functional composition,
208 diversity, and redundancy measures were conducted at species level. Taxonomic and
209 functional trajectories of community composition were drawn in a two-dimensional NMDS
210 ordination plane. Two NMDS using abundance-based (*i.e.* Bray-Curtis) dissimilarity
211 measures were conducted to map either taxonomic or functional composition, the latter
212 based on the seven leaf, stem, and life history traits (without seed mass classes). Trajectories
213 along time were reported through the Euclidean distance between the target inventories and
214 the 1984 pre-disturbance inventories of reference. Univariate trajectories of the leaf, stem,
215 and life-history traits were also visualized with the community weighted means (CWM)
216 (Díaz et al. 2007). Species seed mass were given in 5 mass classes, and seed mass trajectories
217 were reported as the proportion of each class in the inventories (Supplementary materials).

218 The taxonomic and functional diversity trajectories were analyzed from the 1989 pre-
219 disturbance inventories of reference. The taxonomic diversity was reported through species
220 richness and the Hill number translation of the Simpson index (Hill 1973). The comparison
221 between these two metrics assesses community taxonomic richness and evenness:

222 thereafter, results will be discussed directly in terms of taxonomic richness and evenness.
223 Both indices are recommended for diversity studies (Marcon and Hérault 2015), and belong
224 to the set of Tsallis or generalized entropy corresponding, respectively, to the 0 and 2 order
225 of diversity (q). Diversity metrics were measured using the Hqz function from the entropart
226 package (Marcon and Hérault 2015). The functional diversity was reported using the
227 functional richness and functional evenness. Both functional richness and evenness were
228 measured through a distance-based dissimilarity matrix built with the daisy function of the
229 cluster R package (Maechler et al. 2019), using the Gower distance between species, similar
230 to Hérault and Honnay (2007), Hérault (2007). The functional diversity was measured
231 through the Rao index of quadratic entropy. The Rao index combines the community
232 abundance distribution, from species relative abundance, and the average pairwise
233 functional dissimilarity between species computed by the Gower distance. The comparison
234 between these two metrics assesses community functional richness and evenness:
235 thereafter, results will be discussed directly in terms of functional richness and evenness.

236 The impacts of the initial disturbance levels on the maximum gain or loss in richness and
237 evenness were tested with the Spearman rank correlation tests. Richness and evenness
238 trajectories were besides analyzed through polynomial regression or simple linear models
239 between (i) taxonomic and functional richness and evenness, and (ii) the initial %AGB loss
240 at 10, 20, and 30 years after disturbance. The best model fitting, between linear or quadratic
241 model, was chosen based on their respective AIC criterion. The explanatory power of the fit
242 were measured to adjusted r-square values. Models' significance was assessed with the p-
243 value of the regression coefficient.

244 Finally, functional redundancy was measured as the overlap among species in community
245 functional space (Carmona et al. 2016). First, the individuals of the trait database were
246 mapped in the plane of the first two axes from a PCA analysis. The PCA analysis lowered the
247 weight of correlations among traits as the axes are combinations of the most decoupled
248 traits. The two main PCA axis respectively hold 26% and 19% of the trait dataset variance.
249 For each species, the traits probability density (TPD) were computed from the mapping of
250 individuals through two-dimension kernel density estimators. We used the kde2d function
251 of the MASS package (Venables and Ripley 2002) that is a gaussian density estimator for a 2-
252 dimensional space. Second, for each community, the TPD weighed by species abundance
253 were summed across the functional space. Third, the functional space was divided into a 100
254 x 100 grid, and the number of species with a positive TPD was counted in each cell. The
255 average count across cells minus 1 returned the Community Functional Redundancy, which
256 was the average number of species in the community that share the same trait values.

257 **3. RESULTS**

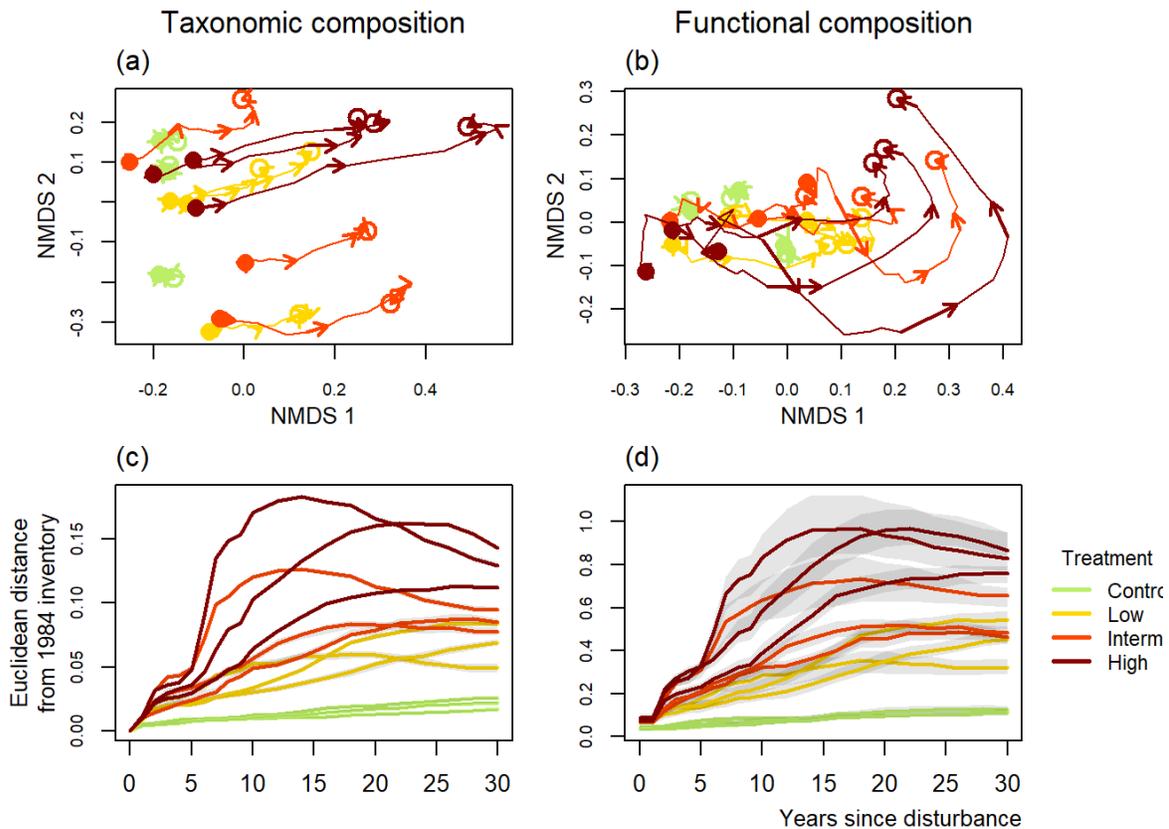
258 3.1. COMMUNITY COMPOSITION

259 From 1984, the first pre-disturbance inventory, to 2015, 28 years after disturbance, 828
260 388 individual trees and 591 botanical species spanning 223 genera and 64 families were
261 recorded.

262 In undisturbed plots, both taxonomic and functional composition remained stable (Fig. 1).
263 In disturbed plots, both trajectories followed marked and consistent trajectories over time.

264 The functional composition trajectory resembled, in disturbed communities, to cyclic
265 compositional changes with an incomplete recovery of the initial composition (Fig. 1). The

266 maximum dissimilarity with the initial state was positively correlated with the disturbance
 267 intensity for both taxonomic and functional composition ($\rho_{Spearman}^{Taxonomic} = 0.94$ and
 268 $\rho_{Spearman}^{Functional} = 0.90$, respectively). The maximum dissimilarity with the initial state was
 269 reached for taxonomic composition between 15 to 25 years, and between 20 to 25 years for
 270 functional composition.

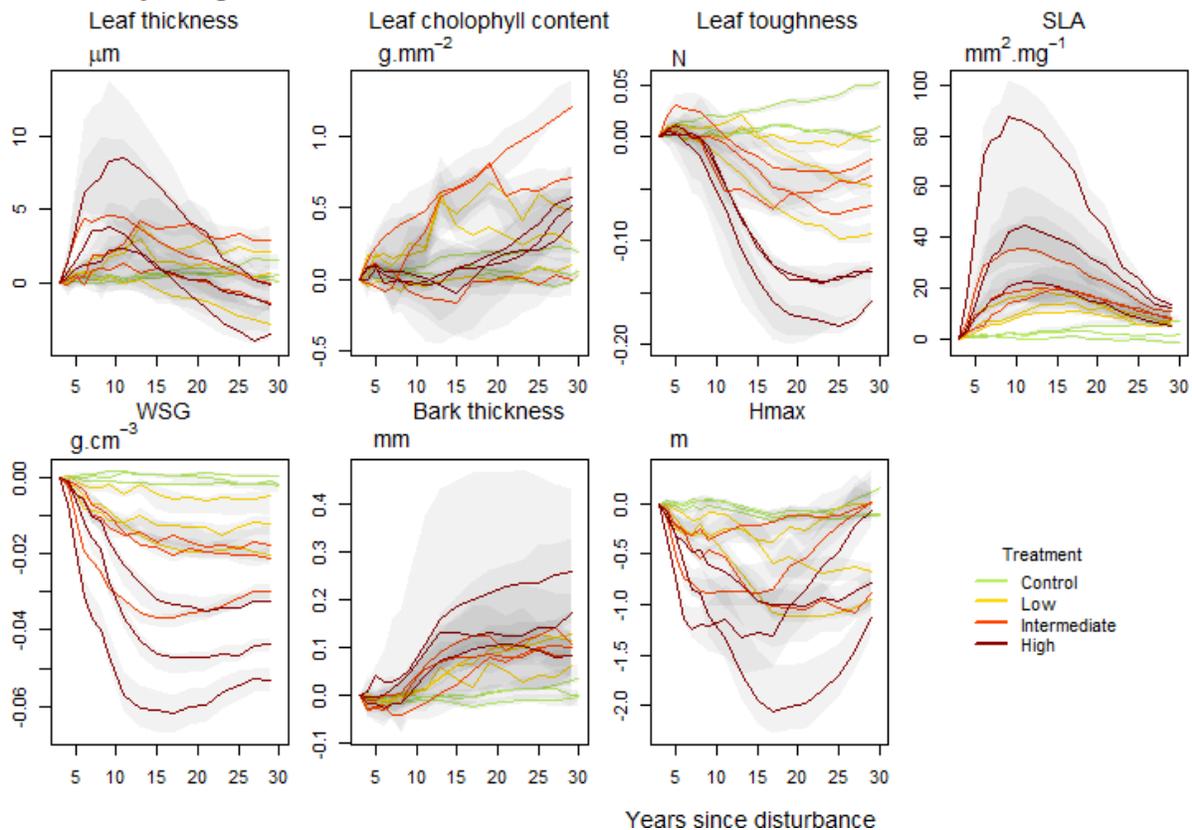


271

272 **Figure 1:** Plot trajectories in terms of taxonomic composition ((a) and (c)), and functional
 273 composition ((b) and (d)) in a two-dimensional NMDS plane. Lower panels ((c) and (d))
 274 represent the Euclidean distance to initial condition along the 30 sampled years. Shaded areas
 275 are the credibility intervals.

276 In control plots, Community Weighted Means (CWM) of functional traits remained stable
277 in time. In disturbed plots, they mostly followed unimodal trajectories, either stabilizing or
278 returning towards their initial values, to the exception of leaf chlorophyll content, which
279 continued to increase 30 years after disturbance for 4 out of 6 highly disturbed plots. Main
280 tendencies for disturbed plots were a decrease followed by a slight increase of maximum
281 height at adult stage (Hmax), leaf toughness, and wood specific gravity (WSG), but trait
282 values remained significantly lower than their initial value (Fig. 2). Bark thickness and
283 specific leaf area (SLA) both increased along time. Bark thickness remained substantially
284 high after 30 years, and SLA had almost recovered to its initial value. Whatever the functional
285 traits, the maximum difference to initial value was highly correlated to the disturbance
286 intensity. Positive correlations were observed for leaf thickness, chlorophyll content, SLA
287 and bark thickness ($\rho_{Spearman}^{Leafthickness} = 0.79$, $\rho_{Spearman}^{Chlorophyllcontent} = 0.61$, $\rho_{Spearman}^{SLA} = 0.99$,
288 $\rho_{Spearman}^{Barkthickness} = 0.68$). Maxima were observed between 5 and 15 years following disturbance
289 for leaf thickness and SLA while chlorophyll content and bark thickness kept increasing after
290 30 years for leaf chlorophyll content and bark thickness. Negative correlation was observed
291 for leaf toughness, WSG, and Hmax ($\rho_{Spearman}^{Leaftoughness} = -0.47$, $\rho_{Spearman}^{WSG} = -0.80$, $\rho_{Spearman}^{Hmax} =$
292 -0.28). Minima were observed between 5 and 15 years following disturbance for Hmax, 10
293 and 20 years for WSG, and between 15 and 25 years following disturbance for leaf toughness.
294 The proportions of the three lightest seed mass classes increased in all disturbed plots. After
295 30 years the proportion of lightest seed mass class decreased while it stabilized for the two
296 other lightest seed mass classes (Supp. Mat. - Fig. S3).

Community Weighted Means



297

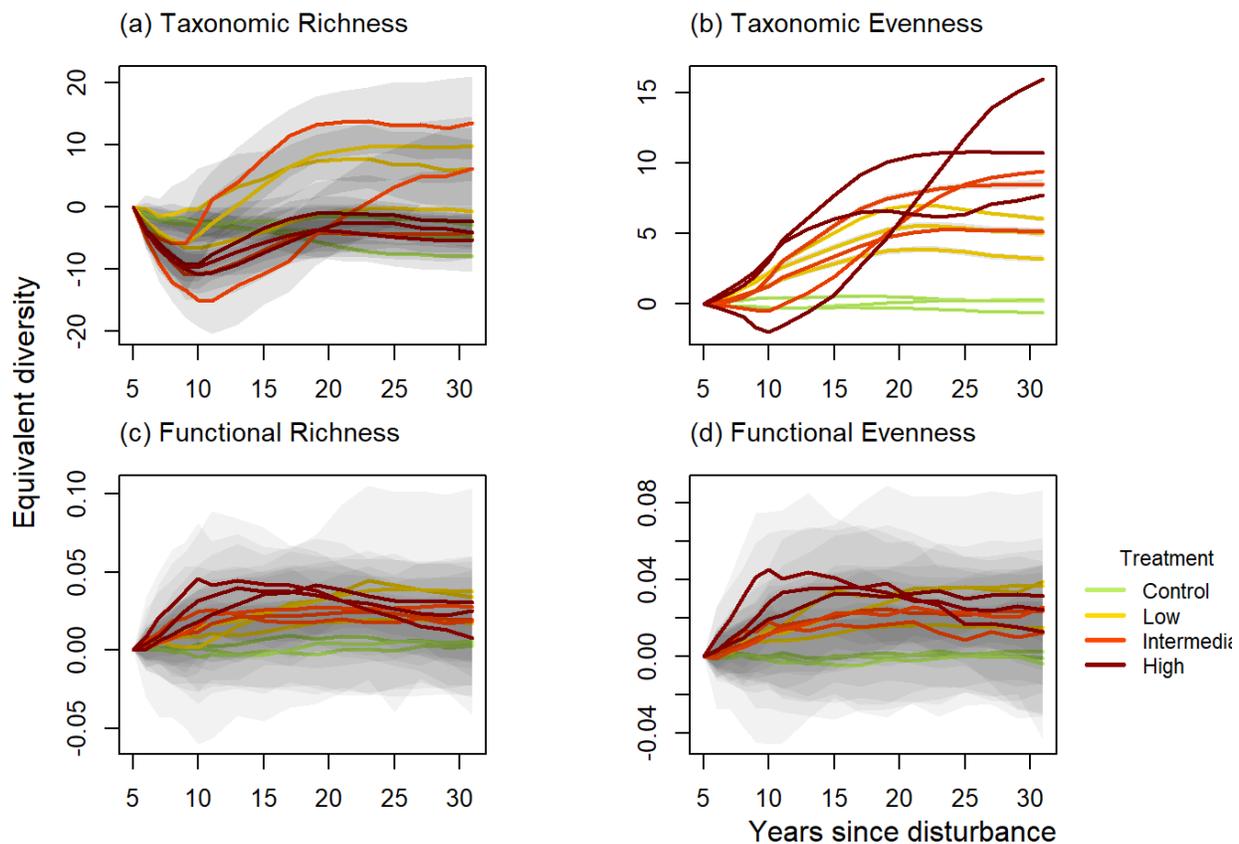
298 **Figure 2:** Trajectories of community weighted means over 30 years after disturbance of four
299 leaf traits (leaf thickness, chlorophyll content, toughness, and specific area), two stem traits
300 (wood specific gravity and bark thickness), and one life history trait (species maximum height
301 at adult stage).

302 3.2. COMMUNITY TAXONOMIC AND FUNCTIONAL DIVERSITY

303 Taxonomic richness and evenness remained stable in control plots over the 30 years of
304 monitoring. In disturbed communities, after low disturbance intensity the taxonomic
305 richness increased, reaching a maximum gain of 14 botanical genera. After intense
306 disturbance the taxonomic richness followed a more complex trajectory, decreasing for ten
307 years after disturbance before recovering to pre-disturbance values. The maximum rate of

308 change compared to initial richness was positively correlated with the disturbance intensity
309 ($\rho_{Spearman}^{Richness} = 0.73$).

310 In all disturbed plots, to the exception of plots 5 (T2) and 12 (T3) that showed a small initial
311 drop, the evenness first increased until a maximum reached after around 20 years. This
312 maximum was positively correlated with the disturbance intensity ($\rho_{Spearman}^{Evenness} = 0.82$, Fig.
313 6). The evenness then stabilized except for two intensively-disturbed plots (number 8 and
314 12) for which it kept increasing (Fig. 3).

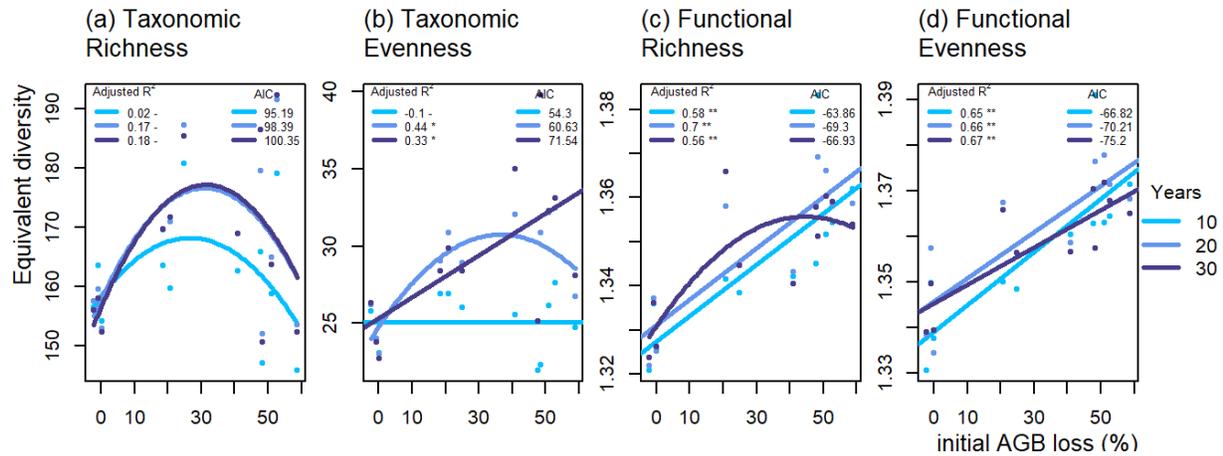


315
316 **Figure 3:** Trajectories of community taxonomic richness **(a)**, taxonomic evenness, **(b)**,
317 functional richness **(c)**, and functional evenness **(d)**. Values correspond to the difference over

318 30 years of community diversity with the values of 1989 inventories of reference, 5 years after
319 disturbance. Shaded areas are the credibility intervals

320 Functional richness and evenness remained stable in control plots over the 30 years of
321 monitoring. In disturbed communities, both functional richness and evenness trajectories
322 increased following disturbance, with maxima positively correlated to %AGB loss
323 $\rho_{Spearman}^{Richness} = 0.76$ and $\rho_{Spearman}^{Evenness} = 0.60$ (Fig. 6). For low and intermediate disturbance
324 intensity, functional richness and evenness displayed a low but long-lasting increase up to a
325 maximum reached after 20-25 years. For high disturbance intensity, they generally
326 displayed a fast but short increase followed, after 10 years, by a slow decrease towards the
327 initial values.

328 The second-degree polynomial regressions between (i) the percentage AGB loss, and (ii)
329 the taxonomic and functional diversity showed various shapes depending on the diversity
330 indices and on the time since disturbance (Fig. 4). Regarding taxonomic diversity, the
331 taxonomic richness showed a humped-shaped trajectory with the disturbance intensity, and
332 peaked at 20% of initial AGB loss. The relationship between disturbance intensity and
333 taxonomic evenness, however, was humped-shaped only 20 years after disturbance and
334 linear for 10 and 30 years after disturbance times. Regarding functional diversity, the
335 relationship was linear for both taxonomic richness and evenness, except for the functional
336 diversity after 30 years.

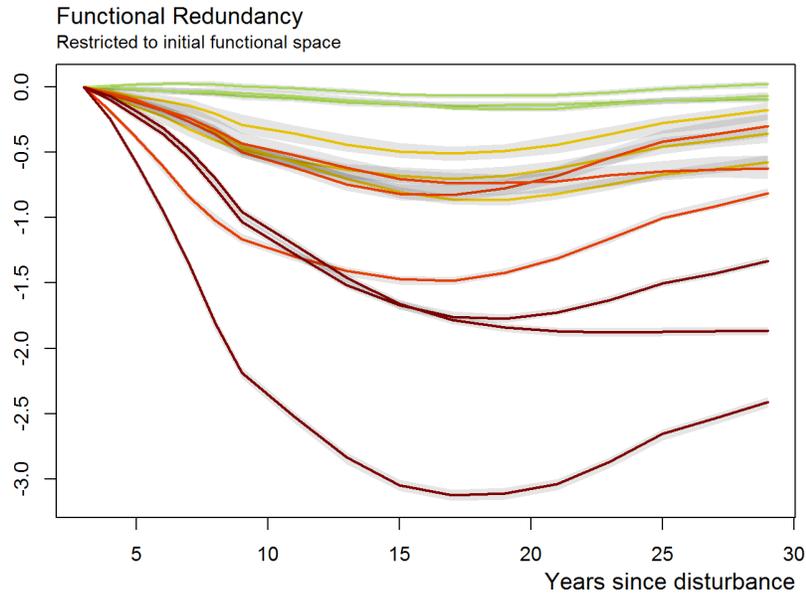


337

338 **Figure 4:** Relationship between the initial %AGB loss and community taxonomic richness (a),
 339 taxonomic evenness (b), functional richness (c), and functional evenness (d) at 10, 20, and 30
 340 years after disturbance. Models R-squared and AIC values are provided, along with models'
 341 significance with - indicating a non-significant model, * a p-value under 0.05, and ** a p-value
 342 under 0.01.

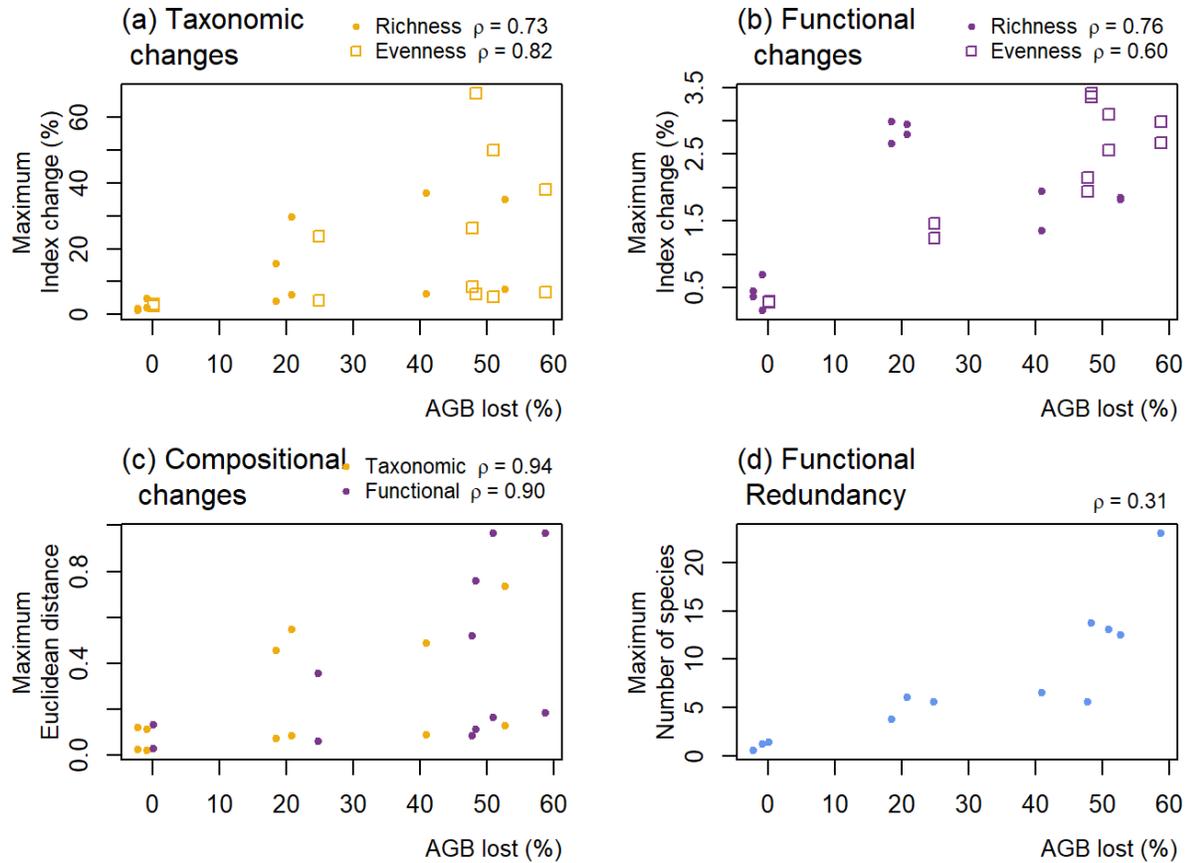
343 3.3. FUNCTIONAL REDUNDANCY

344 Control plots displayed stable functional redundancy over time. All disturbed plots had
 345 lower functional redundancy than control plots and followed similar humped-shaped
 346 trajectories (Fig. 5). The maximum redundancy loss was positively correlated with the
 347 disturbance intensity ($\rho_{Spearman} = 0.31$, (Fig. 6)) and the recovery trajectory had not
 348 attained initial values for any disturbed communities after 30 years.



349

350 **Figure 5:** Trajectories of the functional redundancy within the initial functional space over 30
 351 years after disturbance. The redundancy is measured in a two-dimensional plan summarizing
 352 45% of species variance in the functional space of the 7 leaf, stem, and life history traits.
 353 Redundancy value represent the average number of species in the community that share the
 354 same trait values. Shaded areas are the credibility intervals.



355

356 **Figure 6:** Maximum changes in taxonomic and functional diversity and composition against
 357 disturbance intensity, expressed as percentage of initial disturbance. Upper panels display
 358 taxonomic richness and evenness **(a)**, and functional richness and evenness **(b)** expressed in
 359 percentage of change compared to initial value. Lower panels display taxonomic and functional
 360 Euclidean distance from pre-disturbance inventory, respectively in the spaces of species and
 361 functional traits **(c)**, and functional redundancy expressed as number of redundant species in
 362 the community **(d)**. In each case, the value of the Spearman correlation coefficient (ρ) between
 363 the maximum change considered and the percentage of AGB lost after disturbance is reminded.

364 4. DISCUSSION

365 Our analysis revealed that community post-disturbance trajectories in taxonomic and
366 functional diversity and composition were partly decoupled. Communities' specificity in
367 taxonomic composition before disturbance, *i.e.* the singular tree species composition that
368 differentiate them from one another, were maintained following disturbance, while their
369 functional composition converged in the functional space. In terms of diversity, only the
370 taxonomic trajectories validated the IDH that explained humped-shaped post-disturbance
371 trajectories with an amplitude depending on the disturbance intensity. The decoupling
372 between taxonomic and functional response could be explained by variations in community
373 functional redundancy. The loss of species or the changes in their abundance would impact
374 the taxonomic but not **necessarily** the functional diversity and composition, as redundant
375 species with the same functional characteristics remain in the community. The trajectory of
376 the functional redundancy hence appeared determinant for community recovery.

377 4.1. DECOUPLED TAXONOMIC AND FUNCTIONAL TRAJECTORIES

378 From pre-disturbance to 30 years after disturbance, communities showed different
379 location along NMDS axis 2 that hardly changed along time. Specificities in community
380 taxonomic composition, materialized by the distinct location on the NMDS axis 2, existed
381 before disturbance. The disturbance led a displacement on the NMDS axis 1 only. Taxonomic
382 post-disturbance changes in composition were similar among plots and may correspond to
383 the recruitment of a group of pioneers, like *Cecropia spp.* or *Miconia spp.*, common to all plots,
384 whatever their initial taxonomic specificities and the intensity of the disturbance (Julie S
385 Denslow and Guzman 2000; F. Bongers et al. 2009). Taxonomic trajectories initiated a

386 recovery towards the initial composition. This recovery, although far from being achieved
387 after 30 years, suggested the resilience of community taxonomic composition. Although the
388 composition dramatically changed following disturbance, community specificities were
389 maintained (C. Folke 2006). This maintenance suggested that the recruitment came from (i)
390 a common set of pioneer and light-demanding species in all plots that shape the similar
391 trajectories on NMDS axis 1 and (ii) a very local set of late-successional species that signs
392 (and maintains in time) the initial position of each plot on NMDS axis 2. This can be related
393 to species dispersal limitation that is common among tropical species (Svenning and Wright
394 2005).

395 Community functional composition trajectories, in contrast, were similar in the functional
396 space. Such functional convergence contrasting with community taxonomic divergence was
397 already observed in plant communities (Fukami et al. 2005). The amplitude of the
398 compositional changes depended on the disturbance intensity. Functional trajectories were
399 probably driven by the recruitment of species infrequent or absent before disturbance, and
400 belonging to a pool of species common to all plots. This common pool was composed of
401 pioneers with "resource-acquisitive" strategies displaying low leaf toughness, wood specific
402 gravity, maximum height, and high specific leaf area. The recruitment of these pioneers
403 drove a displacement to the right along the first NMDS axis (Westoby 1998; I. J. Wright et al.
404 2004; Reich 2014). This recruitment went along with an increase of the mean SLA, and a
405 decrease in the mean WSG in disturbed communities (Fig. 2). These fast and significant
406 changes in mean functional traits closely linked to species light acquisition (I. J. Wright et al.
407 2004; Chave et al. 2009) suggested major changes in the light environment following
408 disturbance that shape species assemblage in tropical forests (M. Peña-Claros et al. 2008;

409 Carreño-Rocabado et al. 2012). Thereafter, the first recruited pioneers were progressively
410 excluded by long-lived, more competitive, and shade-tolerant species. The recruitment of
411 these late-successional species marked the recovery of the initial functional composition
412 with more “resource-conservative” strategies, corresponding to a fast decrease in
413 community mean SLA and a stabilisation of community WSG, suggesting the progressive
414 closing of forest canopy. This recovery translated in the functional plane by a displacement
415 left along the first axis and upward along the second axis (Fig. 1).

416 The decoupling between taxonomic and functional trajectories suggested that
417 simultaneous operation of trait-based assembly rules and species-level priority effects
418 shaped tree community assembly in Paracou forest. Tree community assembly would then
419 be both deterministic in the functional space, and historically contingent in the taxonomic
420 space.

421 We must temper these results with the low number of plots (3) for each treatment.
422 However, the size of each plot is 6.25ha that has been regularly censused over 25 years so
423 that the trajectories have been drawn using 75ha of permanent plot information, a spatial
424 hold very rarely achieved in such studies. Given the relative homogeneity of environmental
425 characteristics of terra firme forests over the Guiana Shield and even the amazonian basin,
426 it seems reasonable that similar trajectories would apply to neighboring areas (Guitet et al.
427 2015; Guitet et al. 2018).

428 4.2. THE SCOPE OF THE INTERMEDIATE DISTURBANCE HYPOTHESIS

429 Trajectories of taxonomic richness and evenness differed markedly below and above an
430 intensity threshold (Fig. 3). For low and intermediate disturbance, both taxonomic richness

431 and evenness increased according to the disturbance intensity (Martin et al. 2015;
432 Chaudhary et al. 2016). This suggested that the recruitment of pioneers, previously
433 infrequent or absent, increased the taxonomic richness, and that trees surviving after
434 disturbance remained numerous enough to maintain the richness of the pre-disturbance
435 community (F. Bongers et al. 2009). The pioneers thus recruited became abundant, which
436 balanced the usual hyper-dominance of tropical forests and increased the taxonomic
437 evenness (Baraloto et al. 2012). Above the intensity threshold, like for treatment 3 (high
438 intensity), the taxonomic richness did not exceed the initial value in the first years following
439 disturbance. No increase of the taxonomic richness suggested that the richness of surviving
440 trees was lower than this of the pre-disturbance community, and that this difference was not
441 offset by the recruitment of pioneers. In the Guiana shield, the pool of hard pioneers
442 specifically recruited after disturbance is restricted to a few common genera (e.g. *Cecropia*
443 *spp.*, *Miconia spp.*, *Tapirira spp.*) (Guitet et al. 2018). The disturbance intensity showed a
444 humped-shaped relationship with the post-disturbance increase in taxonomic richness at all
445 the different times after disturbance, and with the increase in taxonomic evenness 10 years
446 after disturbance (Fig. 4). Taxonomic richness, and to some extent taxonomic evenness,
447 were maximized at an intermediate intensity, around 20-25% of AGB lost.

448 4.3. THE FUNCTIONAL REDUNDANCY EXPLAINING THE TAXONOMIC-FUNCTIONAL 449 DECOUPLING

450 Regarding community functional trajectories (Fig. 3), there was no intensity threshold
451 above which the diversity-disturbance relationship changed. The functional diversity kept
452 increasing along with the disturbance intensity, hence the IDH would not apply. Surprisingly,

453 although some species were lost after disturbance, the functional diversity did not decrease
454 in the first place. On the contrary, functional diversity increased, probably following the
455 rapid recruitment of pioneers that were functionally highly different from the pre-
456 disturbance community (Julie Sloan Denslow 1980; J. F. Molino and Sabatier 2001).

457 The loss of species following disturbance, however, decreased the functional redundancy,
458 all the more so that disturbance was intense. All in all, because functional diversity was not
459 lowered by disturbance while functional redundancy was, this means that the species that
460 were lost in disturbance are, on the whole, functionally equivalent to the species that survive
461 the disturbance. This makes functional redundancy a key to understand community
462 dynamics at a functional level. In other words, the high redundancy of tropical forest mean
463 that several species occupy the same functional space, so changes in taxonomic diversity or
464 composition do not necessarily result in changes in community functional characteristics
465 because species are commutable. The loss of a redundant species doesn't change anything
466 for the community functional characteristics, so functional trajectories do not necessarily
467 track taxonomic ones. This commutability explains the taxonomic-functional decoupling and
468 the fact that the taxonomic diversity-disturbance relationship supports the IDH while it
469 functional diversity do not.

470 Following disturbance, the redundancy was progressively restored through the
471 replacement of "resource-acquisitive" species by more late-successional "resource-
472 conservative" species functionally closer to the pre-disturbance community. The time for the
473 functional redundancy to recover would hence be important to assess community recovery.

474 **5. CONCLUSION**

475 Post-disturbance trajectories of tree community composition and diversity would be
476 driven by the recruitment of a determined pool of pioneers, identical among local
477 communities, and independent of the disturbance intensity. The taxonomic composition
478 trajectories maintained the initial differences among communities, while the functional
479 trajectories were similar, and converged in the functional space towards the recovery of the
480 initial composition. The diversity trajectories were contrasted as well. While the functional
481 trajectories displayed the same tendency with a linear increase following all disturbance
482 intensity, taxonomic trajectories were markedly different after a threshold of 20-25% AGB
483 lost that maximized the taxonomic richness. The Intermediate Disturbance Hypothesis
484 would apply well to taxonomic diversity, but not to functional diversity. The decoupling
485 between taxonomic and functional trajectories was mediated by the variations in functional
486 redundancy, as the loss of a species does not necessarily entails the loss of its functional
487 characteristics. Community resilience, in terms of recovery of the pre-disturbance state, was
488 tangible but required several decades, and relied upon the random lottery recruitment of
489 rare species. Given the long-term impacts of disturbance observed, we suggest that 30 years
490 is not enough time for tropical communities to recover, even after relatively low intensity
491 disturbance. Much of community response to disturbance rely on the processes of species
492 recruitment. A more refined understanding of the post-disturbance trajectories would be
493 gained by a closer analysis of the recruitment process.

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501 **7. AUTHOR’S CONTRIBUTIONS**

502 AM, EM & BH designed the study, developed the analysis framework, and interpreted the
503 results. AM wrote the manuscript with contributions by EM & BH. All authors gave final
504 approval for publication.

505 **8. DATA AVAILABILITY**

506 This article is based upon the dataset of the Paracou station, which is part of the Guyafor
507 permanent plot network in French Guiana (Cirad-CNRS-ONF). The dataset is available upon
508 request to the scientific director (<https://paracou.cirad.fr>).

509

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