



**HAL**  
open science

## Diverging taxonomic and functional trajectories following disturbance in a Neotropical forest

A. Mirabel, Bruno Héroult, Eric Marcon

► **To cite this version:**

A. Mirabel, Bruno Héroult, Eric Marcon. Diverging taxonomic and functional trajectories following disturbance in a Neotropical forest. *Science of the Total Environment*, 2020, 720, pp.137397. 10.1016/j.scitotenv.2020.137397 . hal-03016102

**HAL Id: hal-03016102**

**<https://hal.science/hal-03016102v1>**

Submitted on 26 Nov 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 Mirabel A.1\*, Hérault B.2, Marcon E.1

4 1 UMR EcoFoG, AgroParisTech, CNRS, Cirad, INRA, Université des Antilles, Université de  
5 Guyane.

6 2 INPHB (Institut National Polytechnique Félix Houphouët Boigny), Yamoussoukro, Ivory  
7 Coast

8

9 \*Corresponding author: ariane.mirabel@gmail.com, <https://github.com/ArianeMirabel>

10 Permanent address: UMR EcoFoG, Campus Agronomique, avenue de France, 97310  
11 Kourou, FRANCE

## 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<sup>-1</sup> (30-y period). The climate comprises a 3-month dry  
128        season (< 100 mm.month<sup>-1</sup>) 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.<sup>1</sup> 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.<sup>2</sup>  
199 The database compiles information from a vast literature on the flora of French Guiana

---

<sup>1</sup> <http://www.ecofog.gf/Bridge/>

<sup>2</sup> <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**

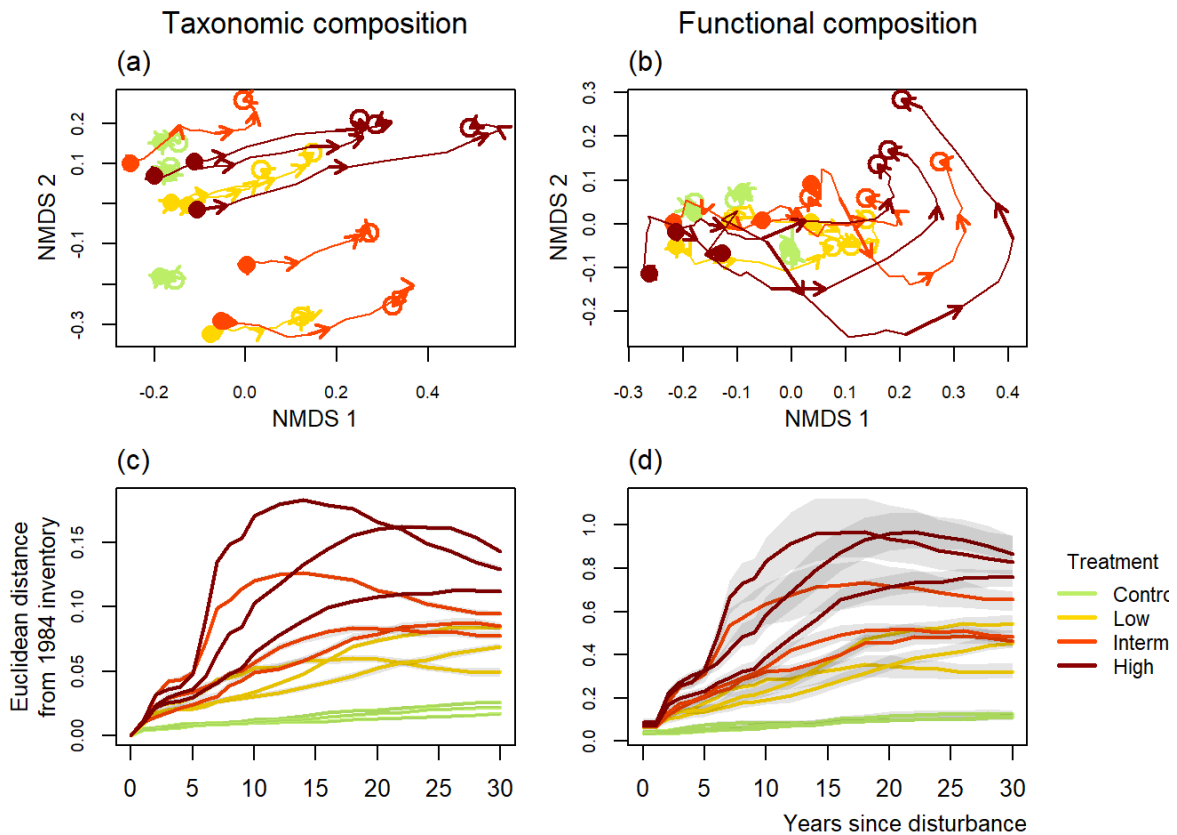
#### 258 3.1. COMMUNITY COMPOSITION

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.



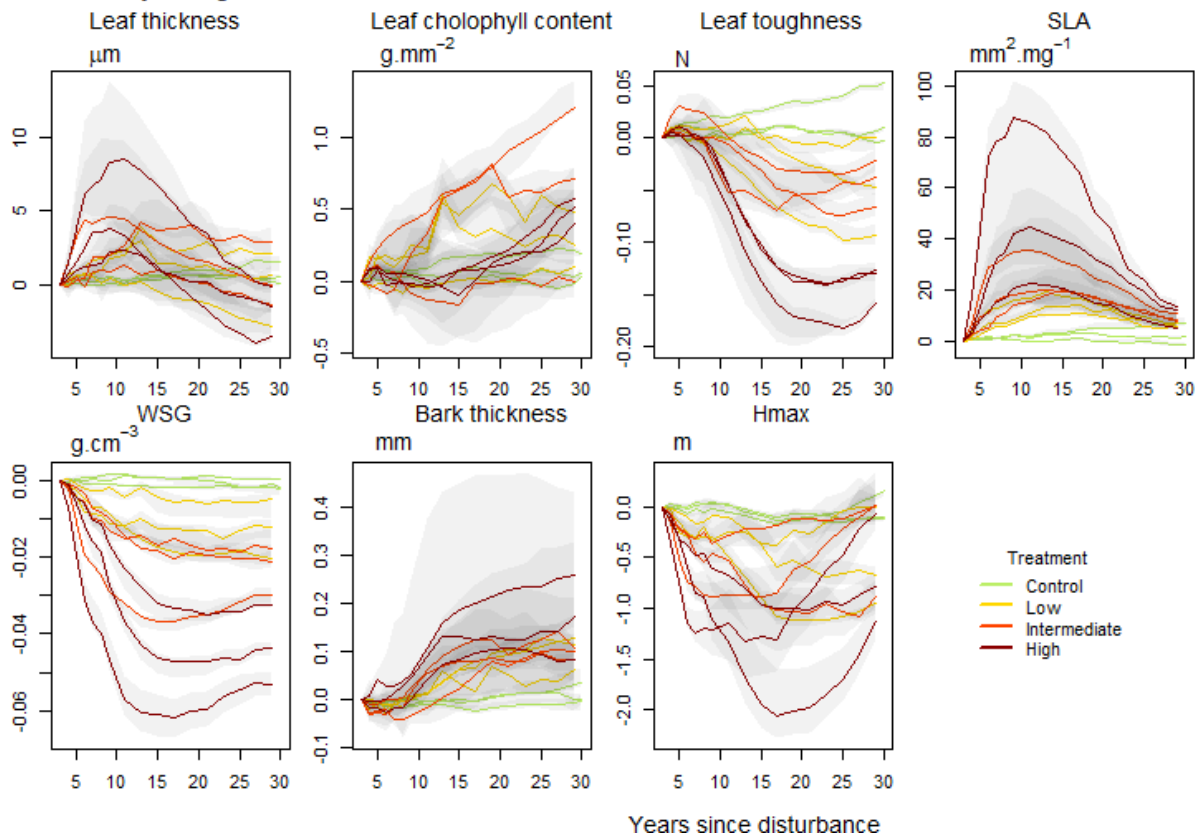
271

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

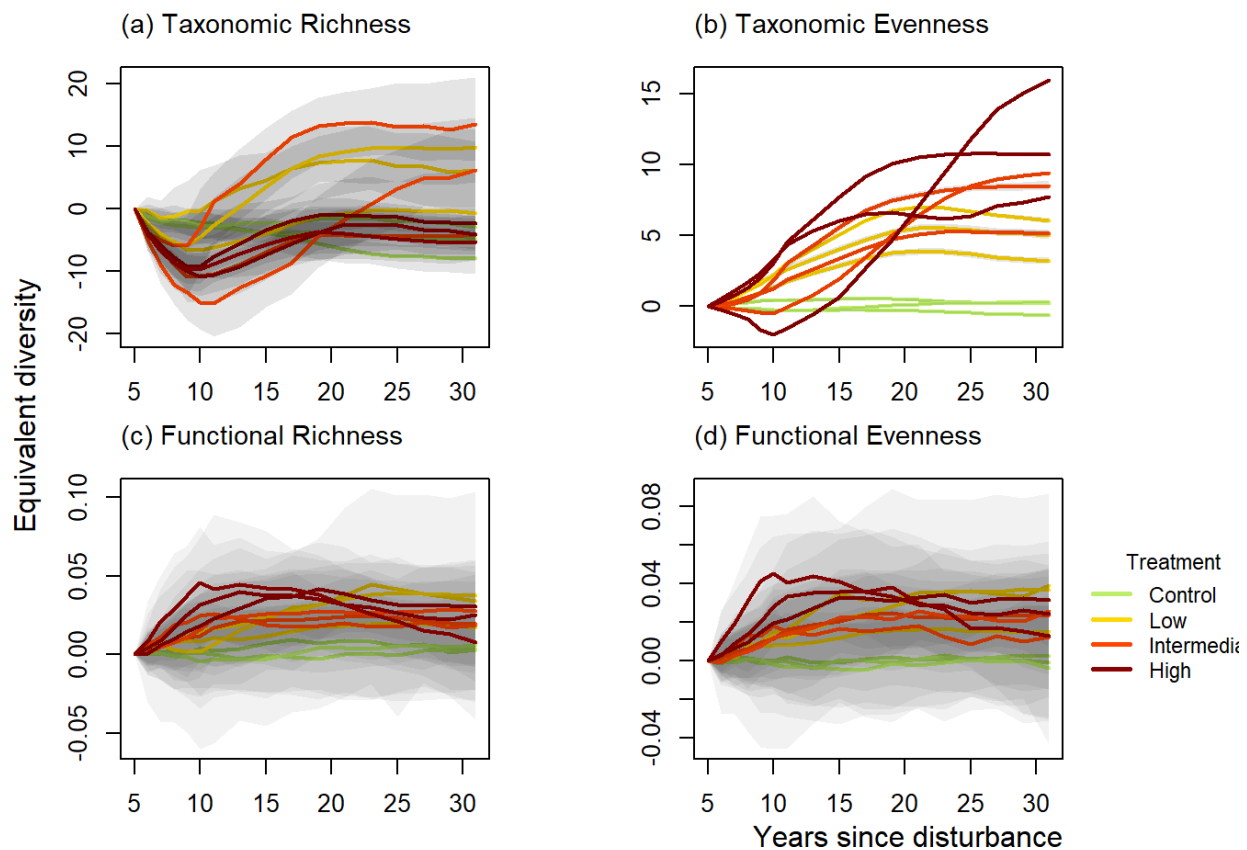
298 **Figure 2:** Trajectories of community weighted means over 30 years after disturbance of four  
299 leaf traits (leaf thickness, chlorophyll content, toughness, and specific area), two stem traits  
300 (wood specific gravity and bark thickness), and one life history trait (species maximum height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

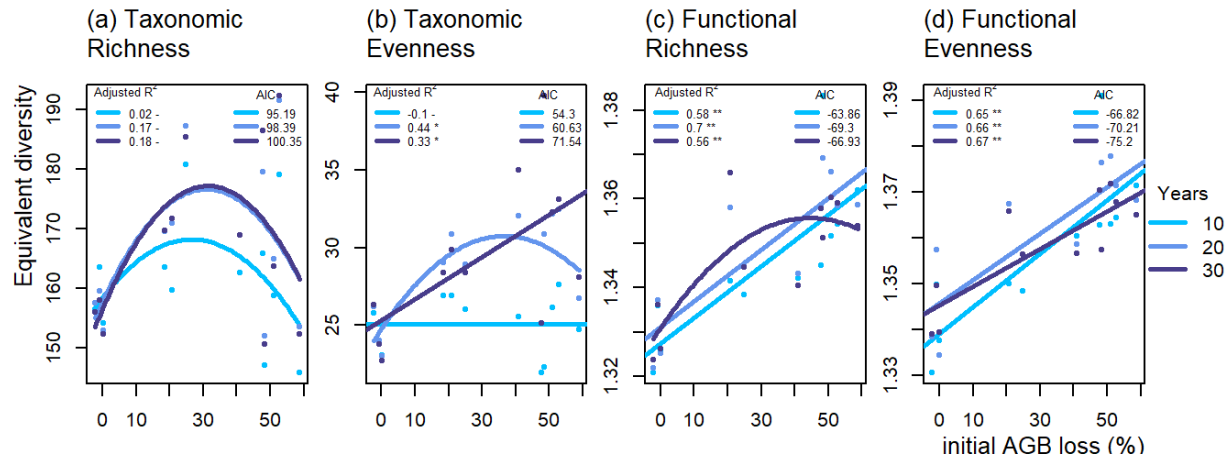


315  
316 **Figure 3:** Trajectories of community taxonomic richness **(a)**, taxonomic evenness, **(b)**,  
317 functional richness **(c)**, and functional evenness **(d)**. Values correspond to the difference over

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.

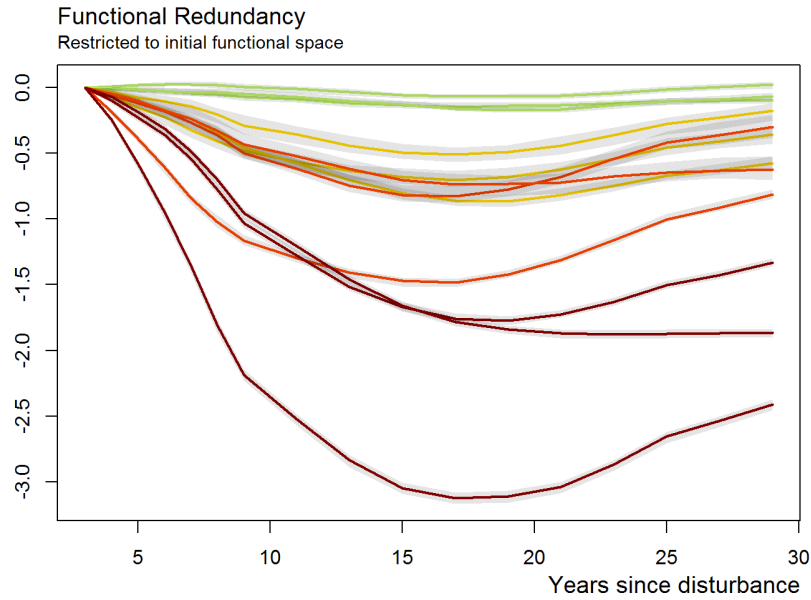


337

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.

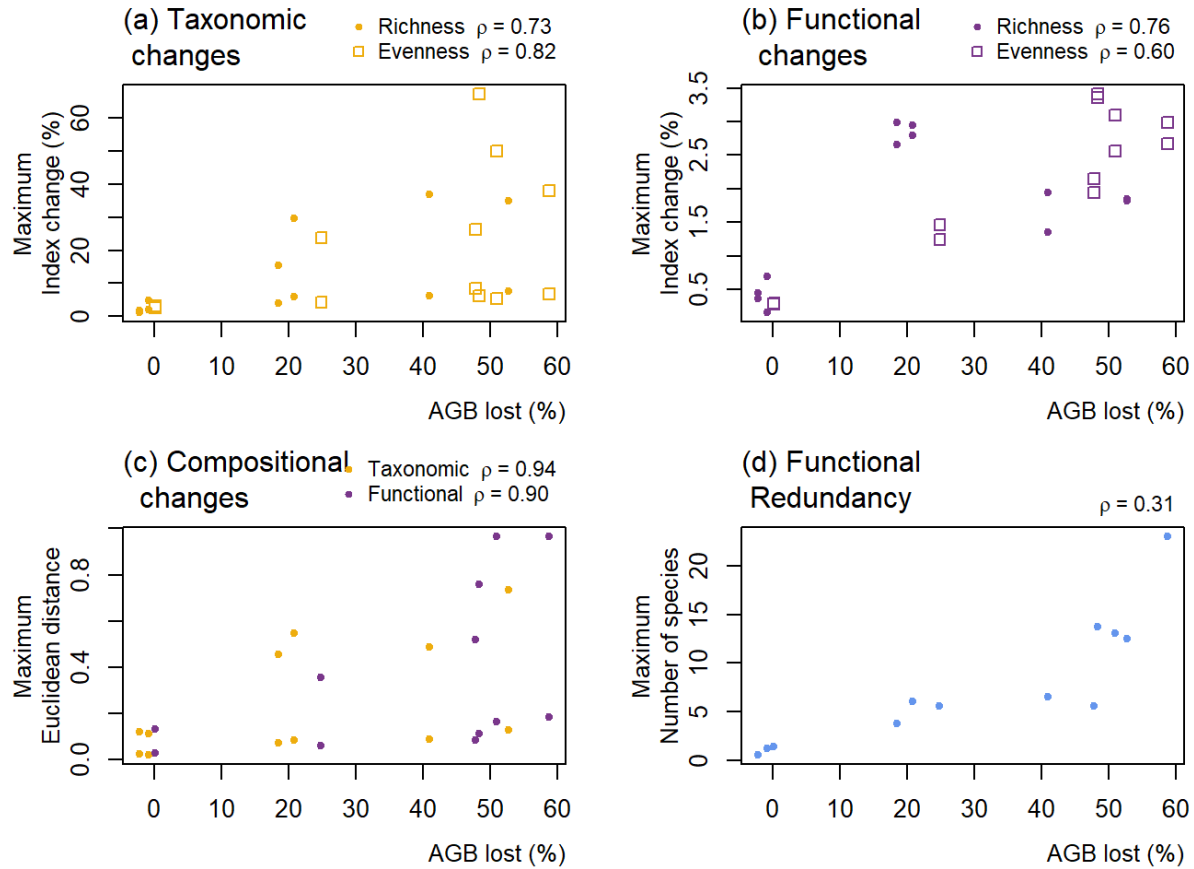
343 3.3. FUNCTIONAL REDUNDANCY

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 ( $\rho$ ) 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.

## 494 **6. ACKNOWLEDGEMENT**

495 We are in debt with all Paracou station technicians and colleagues who helped setting up the  
496 plots and collecting data over years. Without their precious work, this study would have not

497 been possible and they may be warmly thanked here. Our work benefited from an  
498 “Investissement d’Avenir” grant managed by the Agence Nationale de la Recherche (LABEX  
499 CEBA, ref ANR-10-LBX-25). We thank Niklas Tysklind for the usefull help with english  
500 proofing.

## 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

## 510 **9. REFERENCES**

511 Anderson-Teixeira, Kristina J., Adam D. Miller, Jacqueline E. Mohan, Tara W. Hudiburg,  
512 Benjamin D. Duval, and Evan H. DeLucia. 2013. “Altered dynamics of forest recovery under a  
513 changing climate.” *Global Change Biology* 19 (7): 2001–21. doi:10.1111/gcb.12194.

514 Aubry-Kientz, Méline, Bruno Hérault, Charles Ayotte-Trépanier, Christopher Baraloto, and  
515 Vivien Rossi. 2013. “Toward Trait-Based Mortality Models for Tropical Forests.” *PLoS ONE* 8  
516 (5). doi:10.1371/journal.pone.0063678.

517 Baraloto, Christopher, Bruno Hérault, C. E. Timothy Paine, Hélène Massot, Lilian Blanc,  
518 Damien Bonal, Jean-François François Molino, Eric a. Nicolini, and Daniel Sabatier. 2012.  
519 “Contrasting taxonomic and functional responses of a tropical tree community to selective  
520 logging.” *Journal of Applied Ecology* 49 (4): 861–70. doi:10.1111/j.1365-2664.2012.02164.x.

521 Bellwood, David R., P.C Wainwright, C.J Fulton, and A.S Hoey. 2006. “Functional versatility  
522 supports coral reef biodiversity.” *Proceedings of the Royal Society B: Biological Sciences* 273  
523 (1582): 101–7. doi:10.1098/rspb.2005.3276.

524 Bongers, Frans, Lourens Poorter, William D. Hawthorne, and Douglas Sheil. 2009. “The  
525 intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes  
526 little to tree diversity.” *Ecology Letters* 12 (8): 798–805. doi:10.1111/j.1461-  
527 0248.2009.01329.x.

528 Carmona, Carlos P., Francesco de Bello, Norman W.H. Mason, and Jan Lepš. 2016. “Traits  
529 Without Borders: Integrating Functional Diversity Across Scales.” *Trends in Ecology and*  
530 *Evolution* 31 (5): 382–94. doi:10.1016/j.tree.2016.02.003.

531 Carreño-Rocabado, Geovana, Marielos Peña-Claros, Frans Bongers, Alfredo Alarcón, Juan  
532 Carlos Licona, and Lourens Poorter. 2012. “Effects of disturbance intensity on species and  
533 functional diversity in a tropical forest.” *Journal of Ecology* 100 (6): 1453–63.  
534 doi:10.1111/j.1365-2745.2012.02015.x.

535 Chaudhary, Abhishek, Zuzana Burivalova, Lian Pin Koh, and Stefanie Hellweg. 2016. “Impact  
536 of Forest Management on Species Richness: Global Meta-Analysis and Economic Trade-Offs.”  
537 *Scientific Reports* 6. Nature Publishing Group: 1–10. doi:10.1038/srep23954.

538 Chave, Jérôme, David Coomes, Steven Jansen, Simon L. Lewis, Nathan G. Swenson, and Amy  
539 E. Zanne. 2009. "Towards a worldwide wood economics spectrum." *Ecology Letters* 12: 351–  
540 66. doi:10.1111/j.1461-0248.2009.01285.x.

541 Chave, Jérôme, Maxime Réjou-Méchain, Alberto Búrquez, Emmanuel Chidumayo, Matthew S  
542 Colgan, Wellington BC Delitti, Alvaro Duque, et al. 2014. "Improved Allometric Models to  
543 Estimate the Aboveground Biomass of Tropical Trees." *Global Change Biology* 20 (10). Wiley  
544 Online Library: 3177–90.

545 Connell, Joseph H. 1978. "Diversity in Tropical Rain Forests and Coral Reefs." *Science* 199  
546 (4335). American Association for the Advancement of Science: 1302–10.

547 Denslow, Julie S, and G Sandra Guzman. 2000. "Variation in stand structure, light and seedling  
548 abundance across a tropical moist forest chronosequence, Panama." *Journal of Vegetation*  
549 *Science* 11 (2): 201–212. doi:10.2307/3236800.

550 Denslow, Julie Sloan. 1980. "Gap Partitioning among Tropical Rainforest Trees." *Biotropica*  
551 12 (2): 47–55. doi:10.2307/2388156.

552 Díaz, Sandra, Sandra Lavorel, Francesco de Bello, Fabien Quétier, Karl Grigulis, and T  
553 Matthew Robson. 2007. "Incorporating Plant Functional Diversity Effects in Ecosystem  
554 Service Assessments." *Proceedings of the National Academy of Sciences* 104 (52). National  
555 Acad Sciences: 20684–9. doi:10.1073/pnas.0704716104.

556 Díaz, Sandra, D Tilman, J Fargione, F. Stuart Chapin III, Rodolfo Dirzo, T Kitzberger, B  
557 Gemmill, et al. 2005. "Biodiversity Regulation of Ecosystem Services." *Trends and Conditions*,  
558 297–329.

559 Elmqvist, T, C Folke, M Nystrom, G Peterson, J Bengtsson, B Walker, and J Norberg. 2003.  
560 “Response diversity, ecosystem change, and resilience.” *Frontiers in Ecology and the*  
561 *Environment* 1 (9): 488–94. doi:10.2307/3868116.

562 Folke, Carl. 2006. “Resilience: The Emergence of a Perspective for Social–ecological Systems  
563 Analyses.” *Global Environmental Change* 16 (3). Elsevier: 253–67.

564 Fox, Jeremy W. 2013. “The Intermediate Disturbance Hypothesis Should Be Abandoned.”  
565 *Trends in Ecology & Evolution* 28 (2). Elsevier: 86–92.

566 Fukami, Tadashi, T. Martijn Bezemer, Simon R. Mortimer, and Wim H. Van Der Putten. 2005.  
567 “Species divergence and trait convergence in experimental plant community assembly.”  
568 *Ecology Letters* 8 (12): 1283–90. doi:10.1111/j.1461-0248.2005.00829.x.

569 Garcia Florez, Lina, Jerome K Vanclay, Kevin Glencross, and J Doland Nichols. 2017.  
570 “Understanding 48 Years of Changes in Tree Diversity, Dynamics and Species Responses  
571 Since Logging Disturbance in a Subtropical Rainforest.” *Forest Ecology and Management* 393.  
572 Elsevier: 29–39.

573 Goulamoussène, Youven, Caroline Bedeau, Laurent Descroix, Laurent Linguet, and Bruno  
574 Hérault. 2017. “Environmental control of natural gap size distribution in tropical forests.”  
575 *Biogeosciences* 14 (2): 353–64. doi:10.5194/bg-14-353-2017.

576 Gourlet-Fleury, Sylvie, Jean Marc Guehl, and Olivier Laroussinie. 2004. “Ecology &  
577 management of a neotropical rainforest. Lessons drawn from Paracou, a long-term  
578 experimental research site in French Guiana.” Paris: Elsevier.



579 Guitet, Stéphane, Raphaël Pélissier, Olivier Brunaux, Gaëlle Jaouen, and Daniel Sabatier.  
580 2015. "Geomorphological Landscape Features Explain Floristic Patterns in French Guiana  
581 Rainforest." *Biodiversity and Conservation* 24 (5). Springer: 1215–37.

582 Guitet, Stéphane, Daniel Sabatier, Olivier Brunaux, Pierre Couteron, Thomas Denis, Vincent  
583 Freycon, Sophie Gonzalez, et al. 2018. "Disturbance regimes drive the diversity of regional  
584 floristic pools across Guianan rainsforest landscapes." *Scientific Reports* 8 (1): 3872.  
585 doi:10.1038/s41598-018-22209-9.

586 Hérault, Bruno. 2007. "Reconciling Niche and Neutrality Through the Emergent Group  
587 Approach." *Perspectives in Plant Ecology, Evolution and Systematics* 9 (2). Elsevier: 71–78.

588 Hérault, Bruno, and Olivier Honnay. 2007. "Using Life-History Traits to Achieve a Functional  
589 Classification of Habitats." *Applied Vegetation Science* 10 (1). Wiley Online Library: 73–80.

590 Hérault, Bruno, and Camille Piponiot. 2018. "Key drivers of ecosystem recovery after  
591 disturbance in a neotropical forest." *Forest Ecosystems* 5 (1). Forest Ecosystems: 2.  
592 doi:10.1186/s40663-017-0126-7.

593 Hérault, Bruno, Bénédicte Bachelot, Lourens Poorter, Vivien Rossi, Frans Bongers, Jérôme  
594 Chave, C. E Timothy Paine, Fabien Wagner, and Christopher Baraloto. 2011. "Functional  
595 traits shape ontogenetic growth trajectories of rain forest tree species." *Journal of Ecology*  
596 99: 1431–40. doi:10.1111/j.1365-2745.2011.01883.x.

597 Hill, M. O. 1973. "Diversity and Evenness : A Unifying Notation and Its Consequences."  
598 *Ecological Society of America* 54 (2): 427–32. doi:10.2307/1934352.

599 Hubbell, Stephen P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*.  
600 Princeton University Press.

601 Lavorel, S, and Éric Garnier. 2002. "Predicting changes in community composition and  
602 ecosystem functioning from plant traits:" *Functional Ecology* 16 (5): 545–56.

603 Lindenmayer, David B, Philip J Burton, and Jerry F Franklin. 2012. *Salvage Logging and Its*  
604 *Ecological Consequences*. Island Press.

605 Maechler, Martin, Peter Rousseeuw, Anja Struyf, Mia Hubert, and Kurt Hornik. 2019. *Cluster:*  
606 *Cluster Analysis Basics and Extensions*.

607 Marcon, Eric, and Bruno Hérault. 2015. "Entropart: An R Package to Measure and Partition  
608 Diversity." *Journal of Statistical Software* 67 (1): 1–26.

609 Martin, Philip A., Adrian C. Newton, Marion Pfeifer, MinSheng Khoo, and James M. Bullock.  
610 2015. "Impacts of tropical selective logging on carbon storage and tree species richness: A  
611 meta-analysis." *Forest Ecology and Management* 356. Elsevier B.V.: 224–33.

612 Mayfield, Margaret M., and Jonathan M. Levine. 2010. "Opposing effects of competitive  
613 exclusion on the phylogenetic structure of communities." *Ecology Letters* 13 (9): 1085–93.  
614 doi:10.1111/j.1461-0248.2010.01509.x.

615 Molino, J F, and Daniel Sabatier. 2001. "Tree diversity in tropical rain forests: a validation of  
616 the intermediate disturbance hypothesis." *Science* 294 (5547): 1702–4.  
617 doi:10.1126/science.1060284.

618 Morales-Hidalgo, David, Sonja N. Oswalt, and E. Somanathan. 2015. "Status and trends in  
619 global primary forest, protected areas, and areas designated for conservation of biodiversity  
620 from the Global Forest Resources Assessment 2015." *Forest Ecology and Management* 352.  
621 Elsevier B.V.: 68–77. doi:10.1016/j.foreco.2015.06.011.

622 Norden, Natalia, Héctor A. Angarita, Frans Bongers, Miguel Martínez-Ramos, Iñigo Granzow-  
623 de la Cerda, Michiel van Breugel, Edwin Lebrija-Trejos, et al. 2015. "Successional dynamics  
624 in Neotropical forests are as uncertain as they are predictable." *Proceedings of the National*  
625 *Academy of Sciences* 112 (26): 8013–8. doi:10.1073/pnas.1500403112.

626 Norden, Natalia, Vanessa Boukili, Anne Chao, KH Ma, Susan G Letcher, and Robin L Chazdon.  
627 2017. "Opposing Mechanisms Affect Taxonomic Convergence Between Tree Assemblages  
628 During Tropical Forest Succession." *Ecology Letters* 20 (11). Wiley Online Library: 1448–58.

629 Ollivier, Mariwenn, Christopher Baraloto, and Eric Marcon. 2007. "A Trait Database for  
630 Guianan Rain Forest Trees Permits Intra-and Inter-Specific Contrasts." *Annals of Forest*  
631 *Science* 64 (7). EDP Sciences: 781–86.

632 Peña-Claros, M, EM Peters, MJ Justiniano, FJMM Bongers, Greg M Blate, TS Fredericksen, and  
633 FE Putz. 2008. "Regeneration of Commercial Tree Species Following Silvicultural Treatments  
634 in a Moist Tropical Forest." *Forest Ecology and Management* 255 (3-4). Elsevier: 1283–93.

635 Piponiot, Camille, Plinio Sist, Lucas Mazzei, Marielos Peña-Claros, Francis E. Putz, Ervan  
636 Rutishauser, Alexander Shenkin, et al. 2016. "Carbon recovery dynamics following  
637 disturbance by selective logging in amazonian forests." *ELife* 5: e21394.  
638 doi:10.7554/eLife.21394.

639 Pulsford, Stephanie A, David B Lindenmayer, and Don A Driscoll. 2016. "A Succession of  
640 Theories: Purging Redundancy from Disturbance Theory." *Biological Reviews* 91 (1). Wiley  
641 Online Library: 148–67.

642 Randall Hughes, A, Jarrett E Byrnes, David L Kimbro, and John J Stachowicz. 2007.  
643 "Reciprocal Relationships and Potential Feedbacks Between Biodiversity and Disturbance."  
644 *Ecology Letters* 10 (9). Wiley Online Library: 849–64.

645 Rees, Mark, Rick Condit, Mick Crawley, Steve Pacala, and Dave Tilman. 2001. "Long-Term  
646 Studies of Vegetation Dynamics." *Science* 293 (5530). American Association for the  
647 Advancement of Science: 650–55.

648 Reich, Peter B. 2014. "The world-wide 'fast-slow' plant economics spectrum: A traits  
649 manifesto." *Journal of Ecology* 102: 275–301. doi:10.1111/1365-2745.12211.

650 Réjou-Méchain, Maxime, Ariane Tanguy, Camille Piponiot, Jérôme Chave, and Bruno Hérault.  
651 2017. "Biomass: An R Package for Estimating Above-Ground Biomass and Its Uncertainty in  
652 Tropical Forests." *Methods in Ecology and Evolution* 8 (9). Wiley Online Library: 1163–7.

653 Rutishauser, Ervan, Bruno Hérault, Pascal Petronelli, and Plinio Sist. 2016. "Tree Height  
654 Reduction After Selective Logging in a Tropical Forest." *Biotropica* 48 (3): 285–89.  
655 doi:10.1111/btp.12326.

656 Schnitzer, Stefan A, and Walter P Carson. 2001. "Treefall Gaps and the Maintenance of Species  
657 Diversity in a Tropical Forest." *Ecology* 82 (4): 913–19.

658 Shea, Katriona, Stephen H Roxburgh, and Emily SJ Rauschert. 2004. "Moving from Pattern to  
659 Process: Coexistence Mechanisms Under Intermediate Disturbance Regimes." *Ecology*  
660 *Letters* 7 (6). Wiley Online Library: 491–508.

661 Sheil, Douglas, and D. F R P Burslem. 2003. "Disturbing hypotheses in tropical forests." *Trends*  
662 *in Ecology and Evolution* 18 (1): 18–26. doi:10.1016/S0169-5347(02)00005-8.

663 Sheil, Douglas, and David FRP Burslem. 2013. "Defining and Defending Connell's  
664 Intermediate Disturbance Hypothesis: A Response to Fox." *Trends in Ecology & Evolution* 28  
665 (10). Elsevier: 571–72.

666 Sist, Plinio, Pablo Pacheco, Robert Nasi, and Jürgen Blaser. 2015. "Management of natural  
667 tropical forests for the future." Vol. 32. IUFRO WFSE.

668 Steege, Hans ter, Nigel C A Pitman, Oliver L Phillips, Jérôme Chave, Daniel Sabatier, Alvaro  
669 Duque, Jean-François Molino, et al. 2006. "Continental-scale patterns of canopy tree  
670 composition and function across Amazonia." *Nature* 443 (7110): 0–2.  
671 doi:10.1038/nature05134.

672 Svenning, J.C., and S.J. Wright. 2005. "Seed Limitation in a Panamian Forest." *Journal of*  
673 *Ecology* 93 (5): 853–562. doi:10.1111/j.1365-2745.2005.01016.x.

674 van Buuren, Stef, and Karin Groothuis-Oudshoorn. 2011. "mice: Multivariate Imputation by  
675 Chained Equations in R." *Journal of Statistical Software* 45 (3): 1–67.  
676 doi:10.1177/0962280206074463.

677 Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics with S*. Fourth. New York:  
678 Springer. <http://www.stats.ox.ac.uk/pub/MASS4>.

679 Violle, Cyrille, Marie-Laure Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène  
680 Hummel, and Eric Garnier. 2007. "Let the concept of trait be functional!" *Oikos* 116 (5): 882–  
681 92. doi:10.1111/j.2007.0030-1299.15559.x.

682 Wagner, Fabien, Bruno Hérault, Clément Stahl, Damien Bonal, and Vivien Rossi. 2011.  
683 "Modeling water availability for trees in tropical forests." *Agricultural and Forest*  
684 *Meteorology* 151 (9). Elsevier B.V.: 1202–13. doi:10.1016/j.agrformet.2011.04.012.

685 Westoby, Mark. 1998. "A leaf-height-seed (LHS) plant ecology strategy scheme." *Plant and*  
686 *Soil* 199: 213–27. doi:10.1023/A:1004327224729.

687 Westoby, Mark, and Ian J. Wright. 2006. "Land-plant ecology on the basis of functional traits."  
688 *Trends in Ecology and Evolution* 21 (5): 261–68. doi:10.1016/j.tree.2006.02.004.

689 Wright, Ian J., Peter B. Reich, Mark Westoby, David D. Ackerly, Zdravko Baruch, Frans  
690 Bongers, Jeannine Cavender-Bares, et al. 2004. "The worldwide leaf economics spectrum."  
691 *Nature* 428 (6985): 821–27. doi:10.1038/nature02403.

692 Zanne, Amy E, G Lopez-Gonzalez, David A Coomes, Jugo Ilic, Steven Jansen, Simon L Lewis,  
693 Regis B Miller, Nathan G Swenson, Michael C Wiemann, and Jerome Chave. 2009. "Global  
694 Wood Density Database."