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11                                              Abstract

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16        **Introduction**

17        The large areas covered with tropical forests worldwide hold crucial environmental,

18   economic and social values. They provide wood and multiple non-timber forest products,

19   shelter a diversified fauna, regulate the local and regional climates, the carbon, water and

20   nutrient cycles, and ensure cultural and human well-being. The growing demand in forests

21   products together with current global changes increases the pressure on remaining natural

22   forests (**???**) and threatens the maintenance and dynamics in space and time of communities

23   structure, composition and functioning (**???**).

24        In tropical forests, ecological communities are regularly re-shaped by natural

25   disturbance events changing both the abiotic environment, through the fluxes of light, heat

26   and water (**???**), and the biotic interactions such as competition among species (**???**). One

27   of the cornerstone of tropical forest ecology is to understand the processes and drivers of

28   ecosystems response to disturbance (**???**). For now, this has been largely studied through

29   forest structural parameters such as aboveground biomass, tree height or stem density (**???**,

30   **???**) that are rapid and convenient to measure. These structural parameters have been

31   sucessfully modeled, giving important insights into the recovery of ecosystem processes and

32   services (**???**). However the response of forests diversity and composition remains unclear,

33   albeit it determines the productivity, stability and functioning of ecosystems (**???**, **???**). In

34   the short-term, moderate disturbance may lead to positive impacts on communities diversity,

35   an idea formalized by the intermediate disturbance hypothesis (IDH) stating a maximized

36   species diversity when disturbance intensity is not too high (**???**, **???**).

37        Validations of the IDH though remain scarce in the long-term and mainly rely on the

38   analysis of taxonomic richness (**???**). Taxonomic richness alone, however, gives limited or

39   misleading information on forests recovery and functioning (**???**). More

40   ecological-meaningful analysis would couple richness with (i) evenness, that would reveal the

41   changes in the species abundance distribution and thus the underlying ecological processes,

42 and (ii) composition that is crucial for conservation issues (**???**, **???**). Furthermore, a

43 functional approach accounting for species biological attributes would directly link

44 communities diversity, composition and redundancy to ecosystem functioning and to its

45 environmental constraints (**???**, **???**). In that respect, the functional trait-based approach

46 that focus on major traits related to species ecology and mediate species performance in a

47 given environment was sucessfully adopted (**???**). For instance, the functional approach

48 revealed in tropical rainforests the deterministic processes entailing, after disturbance, a

49 functional shift from a dominance of "conservative" slow-growing species dealing with scarce

50 resources to "acquisitive" fast-growing species with rapid and efficient use of abundant

51 resources (**???**, **???**). This shift is translated into the trajectories of key functional traits

52 related to resource acquisition (leaf and stem traits) and life-history traits (seed mass,

53 maximum size) (**???**, **???**, **???**, **???**). Eventually a complete overview of communities

54 response to disturbance would encompass the changes in functional redundancy, that

55 quantifies the amount of shared trait values among species (**???**). The high functional

56 redundancy of hyperdiverse tropical forests (**???**) mitigates the impacts of species removal

57 on ecosystem functioning and determines the resilience of communities after disturbance

58 (**???**, **???**).

59      In this study, we monitored over 30 years the response of 75 ha of neotropical forest

60 plots set up on a gradient of disturbance intensity, from 10 to 60% of ecosystem above-ground

61 biomass (AGB) loss. We made use of a large functional traits database encompassing major

62 leaf, stem and life-history traits in order to draw the taxonomic and functional trajectories in

63 terms of richness, evenness, composition and redundancy. Specifically, we (i) elucidated

64 community taxonomic and functional recovery and the underlying ecological processes, (ii)

65 clarified the validity of the IDH in the long term for tropical forest and its translation into

66 different trajectories in time, and (iii) questioned community recovery time.

## Material and Methods

### Study site

Paracou station in French Guiana (5°18'N and 52°53'W) is located in a lowland tropical rain forest in a tropical wet climate with mean annual temperature of 26°C, mean annual precipitation averaging 2980 mm.y$^{-1}$ (30-y period) and a 3-month dry season ($< 100$ mm.month$^{-1}$) from mid-August to mid-November, and a one-month dry season in March (**???**). Elevation ranges between 5 and 50 m and soils correspond to thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains.

The experiment is a network of twelve 6.25ha plots that underwent a disturbance gradient of three logging, thinning and fuelwood cutting treatments (Table **??**) according to a randomized plot design with three replicate blocks of four plots. The disturbance corresponds to averages of 10 trees removed per hectare with a diameter at 1.3 m height (DBH) above 50 cm for treatment 1 (T1), 32 trees/ha above 40 cm DBH for treatment 2 (T2) and 40 trees/ha above 40 cm DBH for treatment 3 (T3). Treatments T2 and T3 besides included the thinning of trees by poison girdling (**???**). The disturbance intensity was measured as the percentage of aboveground biomass (%AGB) lost between the first inventory in 1984 and five years after disturbance (**???**) estimated with the BIOMASS R package (**???**).

### Inventories protocol and dataset collection

The study site corresponds to a tropical rainforest typical of the Guiana Shield with a dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae. In the twelve experimental plots, all trees above 10 cm DBH have been mapped and measured annually since 1984. Trees are first identified with a vernacular name assigned by the forest worker team, and afterward with a scientific name assigned by botanists during regular botanical campaigns. In 1984, specific vernacular names were given to 62 commercial or common species whereas more infrequent ones were identified under general identifiers only

<sup>93</sup> distinguishing trees and palm trees. From 2003, botanical campaigns have been conducted

<sup>94</sup> every 5 to 6 years to identify all trees at the species level but identification levels still varied

<sup>95</sup> among plots and campaigns.

<sup>96</sup>      This variability of protocols in time raised methodological issues as vernacular names

<sup>97</sup> usually correspond to different botanical species. It resulted in significant taxonomic

<sup>98</sup> uncertainties that had to be propagated to composition and diversity metrics. The

<sup>99</sup> uncertainty propagation was done through a Bayesian framework reconstituting complete

<sup>100</sup> inventories at genus level from real incomplete ones on the basis of vernacular/botanical

<sup>101</sup> names association. Vernacular names were replaced through multinomial trials based on the

<sup>102</sup> association probability $\left[\alpha_1, \alpha_2, ..., \alpha_V\right]$ observed across all inventories between each

<sup>103</sup> vernacular name $v$ and all species $\left[s_1, s_2, ..., s_N\right]$:

$$M_v\Big(\left[s_1, s_2, ..., s_N\right], \left[\alpha_1, \alpha_2, ..., \alpha_V\right]\Big)$$

<sup>104</sup>      See Supplementary Materials -Figure S1 and (**???**) for the detailed methodology.

<sup>105</sup>      Six functional traits representing leaf economics (leaves thickness, toughness, total

<sup>106</sup> chlorophyll content and specific leaf area) and stem economics (wood specific gravity and

<sup>107</sup> bark thickness), and life-history traits (maximum specific height and seed mass) came from

<sup>108</sup> the BRIDGE project.[1] Trait values were assessed from a selection of individuals located in

<sup>109</sup> nine permanent plots in French Guiana, including two in Paracou, and comprised 294 species

<sup>110</sup> pertaining to 157 genera. Missing trait values (10%) were filled using multivariate

<sup>111</sup> imputation by chained equation (**???**). Imputations were restricted within genus or family

<sup>112</sup> when samples were too scarce, in order to account for the phylogenetic signal. Whenever a

<sup>113</sup> species was not in the dataset, it was attributed a set of trait values randomly sampled

<sup>114</sup> among species of the next higher taxonomic level (same genus or family). As seed mass

<sup>115</sup> information was classified into classes, no data filling process was applied and analyses were

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

116 restricted to the 414 botanical species recorded.

117 All composition and diversity metrics were obtained after 50 iterations of the

118 uncertainty propagation framework.

## Composition and diversity metrics

120 To counter taxonomic uncertainties due to the variability of botanical identification

121 levels (in space) and protocols (in time), the taxonomic composition and diversity analysis

122 were conducted at the genus level. Taxonomic and functional trajectories of community

123 composition were followed in a two-dimensional NMDS ordination space. Two NMDS using

124 abundance-based (Bray-Curtis) dissimilarity measures were conducted to map either

125 taxonomic or functional composition, the later based on the 7 leaf, stem and life history

126 traits (without seed mass classes). Trajectories along time were reported through the

127 euclidean distance between the target inventories and the reference inventories in 1989, *i.e.* 2

128 years after disturbance. Univariate trajectories of the leaf, stem and life-history traits were

129 also visualized with the community weighted means (CWM) (**???**). Species seed mass

130 corresponded to 5 classes of increasing mass, seed mass trajectories were therefore reported

131 as the proportion of each class in the inventories (Supplementary materials).

132 The taxonomic diversity was reported through species richness and evenness, *i.e* the

133 Hill number translation of the Simpson index (**???**). These indices belong to the set of

134 HCDT or generalized entropy, respectively corresponding to the 0 and 2 order of diversity

135 (q), recomended for diversity studies (**???**). The functional diversity was reported using the

136 functional richness and functional evenness, *i.e* Rao index of quadratic entropy which

137 combines species abundance distribution and average pairwise dissimilarity based on species

138 functional traits.

139 The impacts of initial disturbance were tested with the spearman rank correlation

140 between the extrema of taxonomic and functional metrics reached over the 30 years and the

141 initial %AGB loss. They were besides analysed through polynomial regression between (i)

142  taxonomic and functional richness and evenness and (ii) the initial %AGB loss at 10, 20 and

143  30 years after disturbance.

144      The functional redundancy was measured as the overlap among species in community

145  functional space (**???**). The samples of the trait database were first mapped in a

146  2-dimensional plan with a PCA analysis. Then, multivariate kernel density estimator

147  associated with individual trees returned species traits probability distribution (TDP).

148  Species TDP weighted by species abundance were eventually summed for each community.

149  Community functional redundancy was the sum of TDPs overlap, expressed as the average

150  number of species that could be removed from without reducing the functional space (Supp.

151  Mat. - Figure S1 for a more comprehensive sheme).

## Results

### Communities Composition

154      From 1989 (2 years after disturbance) to 2015 (28 years after disturbance), 828 388

155  individual trees and 591 botanical species pertaining to 223 genus and 64 families were

156  recorded.

157      While both taxonomic and functional composition remained stable in undisturbed

158  communities (Figure **??**), they followed marked and consistent trajectories over post-

159  disturbance time. In disturbed communities, these compositional changes corresponded to

160  shifts towards species with more acquisitive functional strategies, from communities with

161  high average WSG to high average SLA and chlorophyll content (see appendix I). For

162  functional composition, this translated into cyclic compositional changes with an unachieved

163  recovery of the initial composition (Figure **??**). The maximum dissimilarity with the initial

164  state was positively correlated to the disturbance intensity for both taxonomic and

165  functional composition ($\rho_{spearman}^{taxonomic} = 0.87$ and $\rho_{spearman}^{functional} = 0.90$ respectively). The maximum

166  value was reached around 26 years after disturbance for taxonomic composition and 22 years

167  for functional composition.

168    Except for leaf chlorophyll content, which continued to increase for some T3 and T2

169 plots 30 years after disturbance, all traits and seed mass proportions followed unimodal

170 trajectories either stabilizing or returning towards their initial values.

171    Maximum height at adult stage (*Hmax*), leaf toughness (*L_toughness*) and wood

172 specific gravity (*WSG*) first decreased and then slightly increased but remained significantly

173 lower than their initial value (Figure **??**). On the other side, Bark thickness (*Bark_thick*)

174 and specific leaf area (*SLA*) increased and while *Bark_thick* remained substantially high

175 after 30 years, *SLA* had almost recovered its initial value. For all traits, the maximum

176 difference to initial value was correlated to the disturbance intensity ($\rho_{spearman}^{L_{thickness}} = 0.76$,

177 $\rho_{spearman}^{L_{chloro}} = 0.60$, $\rho_{spearman}^{L_{toughness}} = -0.53$, $\rho_{spearman}^{SLA} = 0.93$, $\rho_{spearman}^{WSG} = -0.75$,

178 $\rho_{spearman}^{Bark-thickness} = 0.71$, $\rho_{spearman}^{Hmax} = -0.40$). The proportions of the three lightest seed mass

179 classes increased in all disturbed plots, and decreased after 30 years for the lightest class

180 while it stabilized for the two other (Supp. Mat. - Figure S2).

## Communities richness and evenness

182    For undisturbed plots, taxonomic Richness and Evenness remained stable over the 30

183 years monitored. In disturbed communities, after low disturbance intensity the taxonomic

184 richness increased, reaching a maximum gain of 14 botanical genera (plot 3 from treatment

185 2). After intense disturbance the taxonomic richness followed a more complex trajectory,

186 decreasing for ten years after disturbance before recovering to pre-disturbance values. The

187 maximum richness loss or gain after disturbance was positively correlated to the disturbance

188 intensity ($\rho_{spearman}^{Richness} = 0.50$). In all disturbed plots the taxonomic evenness first increased

189 until a maximum reached after around 20 years. This maximum was positively correlated to

190 the disturbance intensity ($\rho_{spearman}^{Evenness} = 0.77$). The evenness then stabilized except for two T3

191 plots (plots 8 and 12) for which evenness kept increasing.

192    The plot 7 from treatment 1 displayed constantly outlying functional richness and

193 evenness and was removed from the graphical representation for better readability. In

194  undisturbed plots both functional richness and evenness remained stable along the 30 years.

195  In disturbed plots, functional richness and evenness trajectories depended on the disturbance

196  intensity with their maximum positively correlated to %AGB loss $\rho_{spearman}^{Richness} = 0.76$ and

197  $\rho_{spearman}^{Evenness} = 0.60$. Functional richness and evenness displayed for low disturbance intensity a

198  low but long-lasting increase up to a maximum reached after 20-25 years, and for high

199  intensity, a fast but short increase followed after 10 years by a slow decrease towards the

200  inital values.

201      The second-degree polynomial regressions between (i) the %AGB loss and (ii)

202  taxonomic and functional richness and evenness after 10, 20 and 30 years best predicted the

203  hump-shaped curve of the disturbance impact along the disturbance intensity gradient **??**.

204  The relationship between the disturbance impact and its intensity was more markedly

205  hump-shaped for the taxonomic richness than for the taxonomic evenness. For both

206  functional richness and evenness the relationship was almost linear. The regression model

207  better predicted the functional richness and evenness $(0.55 < R_{FunctionalRichness}^2 < 0.72$, and

208  $0.60 < R_{FunctionalEvenness}^2 < 0.81)$ than the taxonomic richness and evenness

209  $(0.21 < R_{TaxonomicRichness}^2 < 0.4$, and $-0.15 < R_{TaxonomicEvenness}^2 < 0.43$ respectively)

**Functional redundancy**

211      All disturbed plots had lower functional redundancy than control plots and followed

212  similar hump-shaped trajectories (**??**). The maximum redundancy loss was positively

213  correlated with the disturbance intensity $(\rho_{spearman} = 0.47)$ and the initial value had not

214  recovered for any disturbed communities after 30 years.

## Discussion

**A cyclic recovery of community composition**

217      Communities taxonomic and functional composition appeared resilient, following

218  similar hump-shaped trajectories starting to return towards pre-disturbance composition

after 30 years.

The taxonomic differences among local communities, marked before disturbance by the distinct starting points on the NMDS axis 2, were maintained throughout recovery trajectories. More than commonly thought, post-disturbance trajectories depended on community initial composition, that partly determined the pool of recruited species and constrained the trajectories towards the initial composition. The high resilience of communities taxonomy revealed that species not belonging to the pre-disturbance community were hardly recruited because of the commonness of dispersal limitation among tropical tree species (**???**).

Conversely, disturbed communities followed functional trajectories that are highly similar in terms of functional composition. As pre-disturbance surviving trees mirror the initial community (**???**), changes in functional composition relied upon the recruitment of species or functional types that were infrequent or absent before disturbance. Competitive pioneers became dominant in filling the environmental niches of high availability of light, space and nutrients vacated by the disturbance. The recruitment of pioneers changed community functional composition in the same way for all disturbance intensity towards more resource-acquisitive strategies, moving community functional composition right along the first axis in Figure **??** (**???, ???, ???**). Thereafter long-lived, more resistant and shade-tolerant species excluded the first established pioneers and started the recovery of pre-disturbance functional composition, moving similarly community functional composition left along the first axis and upward along the second axis in Figure **??**.

These trajectories provided empirical support to the hypothesis that community assembly is both deterministic and historically convergent at different levels of community organization. Deterministic, trait-based processes drove community convergence in functional composition, while at the same time dispersal limitation maintained their divergence in taxonomic composition (**???**).

**Another perspective on the intermediate disturbance hypothesis**

The IDH well predicted well the disturbance impact on community taxonomic richness, enhanced until an intensity threshold (20-25% AGB loss), and to some extent on taxonomic evenness, somewhat decoupled from the disturbance intensity as already observed in the Guiana Shield (**???**) and in Bornean tropical forests (**???**). The disturbance intensity determined the balance in the community between pre-disturbance surviving trees and those recruited afterward. The pool of true pioneer species specifically recruited after disturbance is restricted in the Guiana Shield to a few common genera (e.g. Cecropia spp., Vismia spp.) (**???**). Below the intensity threshold the size of the surviving community maintained the pre-disturbance high taxonomic richness while the recruitment of pioneers, infrequent or absent before disturbance, increased both community taxonomic richness and evenness. Beyond the intensity threshold, the disturbance decreased the taxonomic richness of surviving trees which was not offset by the enrichment of pioneers, so that the overall community taxonomic richness decreased according to the disturbance intensity (**???**). For community taxonomic evenness the disturbance impact was similar but slighter, as the evenness is less sensitive to the loss of rare species. Taxonomic evenness rather represented the increasing dominance of pionneers that balanced the usual hyper-dominance of a few species in tropical forests below the intensity threshold, thus increasing community overall evenness up to the intensity threshold beyond which pioneers became in turn highly dominant and decreased the overall evenness (**???**).

Conversely the IDH was disproved regarding the disturbance impact on community functional richness and evenness. Irrespective of the disturbance intensity the recruitment of pionneers, functionally highly different from the composition of pre-disturbance community, increased both community functional richness and eveness.

Along time, taxonomic richness trajectories of all disturbed communities first dropped similarly, following the species loss due to disturbance, and then displayed a species gain depending on the disturbance intensity. Up to an intensity threshold, the species gain was all

the more significant that the disturbance intensity increased, with the establishment of
long-lived pioneers enhancing community taxonomic richness and evenness in the long term.
These long-lived pioneers, functionally quite different from the functional composition,
entailed as well a progressive and long-lasting increase of the functional richness and
evenness (**???**, **???**). Beyond an intensity threshold, though, a few short-lived pioneers
occupied the vacated environmental space and prevented the establishment of other species.
These short-lived pioneers were functionally very different from the pre-disturbance
community and entailed a rapid and significant increase of functional richness en evenness.
Already after 10 years, though, short-lived pioneers started to decline and the functional
richness and evenness decreased. Likely this decrease will be followed by the establishment of
long-lasting pioneers, and by the time they recruit we expect the taxonomic and functional
trajectories to catch up with those observed after intermediate disturbance (**???**).

**The functional redundancy, key of community resilience**

For 15 years the species loss during disturbance, determined by the disturbance
intensity, commensurately decreased the functional redundancy within the pre-disturbance
functional space. The redundancy decrease was not compensated in the first place as the
first recruited pioneers were functionally different from the pre-disturbance functional
composition. Progressively though, first established species were replaced by more
competitive long-lived pioneers or late-successional species resembling more the
pre-disturbance functional composition and restoring the functional redundancy. This
replacement was stochastic and followed the lottery recruitment rules, implying a recruitment
eased for the first recruited species but then increasingly hampered by the emergence of
interspecific competition (**???**). Along time the recovery of infrequent species was
increasingly slow, so that the time for the full recovery of the functional redundancy, in some
communities just initiated after 30 years, was extremely difficult to estimate (**???**, **???**).

The long-term impact of disturbance on community functional redundancy meant a

lower resilience of the pre-disturbance communities, with higher chances to see the

persistence of disturbance-specific species at the expense of late-successional ones (**???**).

Besides, the long-term recovery of infrequent species increases the risks to loose cornerstone

species, with unexpected ecological consequences (**???, ???, ???**). Apart from the functional

characteristics considered here, infrequent species might indeed have unique functions in the

ecosystem or be a key for some fauna (**???**).

## Conclusions

Our study revealed community recovery through the combination of deterministic

processes driving their convergence in functional composition, and dispersal limitation

maintaining their divergence in taxonomic composition. The IDH was validated for

community taxonomic richness and, to some extent, taxonomic evenness but disproved

regarding community functional richness and evennes that were enhanced for any

disturbance intensity by the high functional differences of pioneers compared to

late-successional functoinal composition. The IDH was translated in time by the recruitment,

beyond an intensity threshold, of short-lived pionneers that prevented in the first times the

establishment of more diverse long-lived pionneers, recruited otherwise below the intensity

threshold. The resilience of tropical forests proved consistent although several decades-long.

Still, the disturbance impact on communities redundancy cautioned against the risks of

infrequent species loss and the persistence of disturbance-specific communities (**???**).

317 # References