Research article

Don't miss the forest for the trees! Evidence for vertical differences in the response of plant diversity to disturbance in a tropical rain forest

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ABSTRACT

Ecological studies in tropical rain forests traditionally focus on trees above a threshold diameter at breast height (dbh), since ignoring plant species of the other structural compartments is believed to be an acceptable tradeoff between exhaustiveness and effectiveness. However, the consequences of missing species below a threshold dbh value have been largely neglected so far. We evaluated whether the response of species diversity of $\geq$10-cm dbh trees was similar to the response of other structural ensembles (namely treelets, saplings, and terricolous herbs) in a lowland tropical rain forest, to three disturbance regimes: natural gap dynamics (control), and selective logging with and without additional thinning. We studied forest vegetation composition and diversity in a 20-yr replicated field experiment comprising nine 1 ha permanent plots established in a semi-deciduous rain forest of the Congo Basin and equally distributed among the three treatments. Once corrected by stem density, species richness was similar between logged (20 years since logging) and untouched old-growth forest stands with respect of trees, but higher with respect of treelets. As disturbance intensity increased, species richness increased within sapling layers but decreased within herb layers, while species spatial turnover (beta diversity) increased in both cases. Regarding the parameters of the partitioned rarefaction curves and relative abundance distribution curves, no correlation was found between trees and any of the other structural compartments. Whilst tree and treelet species composition was similar among treatments, the understories still reflected past disturbance intensity, with a strong response of the sapling and herb layers. These results show that ecological studies based solely on tree layers (dbh $\geq$ 10 cm) are misleading because their response to disturbance cannot be used as a surrogate for the response of other structural ensembles. Long-lasting effects of anthropogenic disturbance on the sapling bank and the herb layer may durably influence the long-term forest dynamics. Since overstory but not understory plant communities have recovered from human disturbances 20 years after silvicultural operations, African tropical rain forest ecosystems may not be as resilient to selective logging as previously thought.

Introduction

Tropical rain forests are the world's most species-rich ecosystems but the causes of this exceptional biodiversity are not fully elucidated (Primack and Corlett, 2005). Among other drivers, disturbance is widely acknowledged as a major cause of variations in species diversity, as illustrated by the popularity of the intermediate disturbance hypothesis (IDH; Connell, 1978; Noss, 1996). Biodiversity maintenance of these forests has been primarily attributed to small-scale gap phase dynamics (Huston, 1994; Schnitzer and Carson, 2001; Sheil and Burslem, 2003). Tree death and gap creation occur at all forest succession stages and provide opportunities for the regeneration of light-demanding species, a turnover sufficient to counteract local competitive exclusion and allow the coexistence of species with contrasted light requirements (Sheil and Burslem, 2003).

Although it remains highly controversial (e.g. Mackey and Currie, 2001; Sheil and Burslem, 2003), the IDH largely

permeates forest management guidelines (e.g. Hartshorn, 1995). Selective logging is the most widespread silviculture mode in these forests, which, at low intensity, is thought to mimic closely natural disturbances (Hartshorn, 1995). According to the IDH, species richness is expected to rise to a maximum level after a human-induced disturbance pulse, and then to slowly return to its initial stage. Hence, it is expected that tropical forests recover rapidly after selective logging, the strongest changes in species composition being detected in the first few years after logging (Toledo et al., 2011; Carreño-Rocabado et al., 2012; Gourlet-Fleury et al., 2013). However, selective logging often results in much more severe disturbances than gap phase dynamics do. Logging gaps are usually larger than natural ones and log extraction is done by heavy vehicles that compact the soils. The effect of logging on tree species diversity in tropical forests is still a subject of speculation. Recent meta-analyses did evidence an overall negative impact of logging on tree species richness (Clark and Covey, 2012; Gibson et al., 2011; Putz et al., 2012) but this impact resulted from a high variety of logging situations (in terms of logging regime – frequency and intensity, initial state of forests, interaction with other types of disturbance) and hid a variety of results. Some studies have indeed suggested that moderate anthropogenic disturbances can maintain (Molino and Sabatier, 2001; Hall et al., 2003; van Gemerden et al., 2003; Kassi and Decocq, 2008; Carreño-Rocabado et al., 2012; Gourlet-Fleury et al., 2013) or even increase (Bobo et al., 2006; Swaine and Agyeman, 2008; van Andel, 2001; see also Sahu et al., 2008) species diversity in tropical rain forests. A serious drawback of the available studies is that they are often restricted to tree species above a threshold diameter at breast height (dbh) value (usually ≥ 10 cm; e.g. Connell, 1978; Hall et al., 2003; Carreño-Rocabado et al., 2012; Gourlet-Fleury et al., 2013). It is increasingly realized however that this traditional approach of biodiversity is misleading as non-tree species account for an important part of species richness (Gentry and Dodson, 1987; Tchouto et al., 2006; Cicuzza et al., 2013) and include many species of high conservation value (Cable and Cheek, 1998), though the relative contribution of canopy trees, lianas, epiphytes, understory herbs and shrubs varies considerably with ecological conditions and the forest type (Cicuzza et al., 2013). Understories also host overstory tree species' seedlings and saplings, which represent the regeneration potential of the forest and affects the future course of succession and canopy composition. The impact of disturbance on these particular components has been rarely studied (e.g. epiphytes: Barthlott et al., 2001; terricolous herbs: Costa and Magnusson, 2002; lianas: Addo-Fordjour et al., 2009), and to our knowledge the response to disturbance of the different vegetation layers has been rarely considered simultaneously and never in the African rain forest biome.

Many environmental gradients influence vertical vegetation patterns both at a micro- and macro-scale, and plants may detect these gradients more or less sharply (Baker, 1989; Rosenzweig, 1995; Stohlgren et al., 1997). For instance in temperate forests, it has been evidenced by virtue of the differences in their usual sizes that trees, shrubs and herbs react differently to environmental conditions (Carlile et al., 1989; Decocq, 2002). The abundance and diversity of the smaller plants should reflect more readily small-scale variations in environmental conditions than bigger do. As in tropical forests too contrasted disturbance regimes are likely to create different patterns of environmental heterogeneity, we expect diversity trends in distinct structural compartments to differ due to a contrasted sensitivity of vegetation layers, but to our knowledge this still has to be evaluated.

There is thus an urgent need for increasing knowledge on how tropical forest composition and diversity respond to different levels of human disturbances, as (1) more insight is needed about disturbance–diversity relationships among the different structural compartments of the forest, and (2) it is a prerequisite to the implementation of effective sustainable management of tropical forests and biodiversity conservation. In this study we took advantage of the permanent plots of the long-term experimental research station of Mbaïki, Central African Republic, to examine how species diversity and composition in a tropical rain forest respond to logging disturbance, and especially how structural components of vegetation do so. More specifically, we tested the following hypotheses: by virtue of the differences in the sizes of their standing components, the different structural compartments differ in their response to disturbance with respect to species diversity and composition, and time for post-disturbance recovery.

Study site and methods

Study site

The study was conducted at the M'Baïki experimental station (3°90′N, 17°93′E; 500 to 600 m a.s.l.), which is located in the near-primary forest of the Lobaye province, 110 km south-west to Bangui, Central African Republic (CAR). The climate is humid tropical with a 3 to 4-months dry season (November/December–February, with less than 50 mm precipitation over this period). The average annual rainfall is 1738 mm (1982–2007 period), and the mean annual temperature is 24.9 °C (coolest month: 19.6 °C – warmest month: 30.2 °C). The plots are located within a 10 km radius on a large plateau, where deep, locally gravelly, red ferralitic soils (acrisols according to the WRB soil classification; IUSS Working Group WRB, 2014) have developed on the Precambrian substrate. The vegetation is a semi-deciduous rainforest of the Guineo–Congolian type (White, 1983), whose canopy is dominated by trees of the Meliaceae, Myristicaeae, Cannabaceae, Malvaceae, Ulmaceae, Sapotaceae, and Fabaceae families.

Nine permanent plots of the station were used in this study, which were equally distributed among three sites: Boukoko1 (B1), Boukoko2 (B2) and La Lolé (LL). Each plot consists of a 4-ha central square divided in four 1-ha smaller squares, and surrounded by a 50 m wide buffer zone. Of the 10 plots established in 1982, 7 were selectively logged in 1984–1985 (2 to 7 $\geq$ 80 cm dbh tree ha^{-1} harvested, from 16 timber species) while 3 were kept untouched (controls). Four logged plots were additionally thinned in 1986–1987, by poison girdling all trees from non-timber species with a dbh $\geq$ 50 cm (16–26 stems ha^{-1}) and removing all lianas. One of latter has been severely damaged by a fire in 1992 and was thus excluded from the study. The three treatments (control, logging, logging + thinning; one plot per site) thus led to a strong gradient of disturbance intensity, ranging from 0 to 15.8 m^2 ha^{-1} in terms of basal area loss (hereafter δG, measured at the 1-ha square level).

Sampling design

For the purpose of this study, we distinguished the following structural compartments of the forest after the "structural ensembles" of Oldeman (1990), which are not taxonomically exclusive but functionally linked:

- trees (A): all standing stems (i.e. trees and lianas) with a dbh $\geq$ 10 cm, corresponding to the individuals of the present (sensu Oldeman) forming the overstories;
- juveniles (J): non-mature trees (treelets) and lianas (i.e. the structural ensemble of the future sensu Oldeman), as well as typically understory shrubs, palms and lianas, with a 0.5 $\leq$ dbh < 10 cm;
- saplings (R): all woody standing stems with a dbh < 0.5 cm but a height $\geq$ 20 cm, (i.e. the regeneration zone sensu Oldeman);

- small lianas and terricolous herbs (*LH*): lianas with a dbh < 0.5 cm (partly taxonomically shared with compartments *R* and *J*), forbs, and grasses, taxonomically exclusive compared to the former compartments.

In each of the nine plots, one of the four 1-ha squares was randomly chosen for subsequent field measurements. Trees and lianas of compartment *A* were recorded over the entire 1-ha square. Stems of compartments *J* and *R* were recorded in a smaller 40 m × 40 m (1600 m²) quadrat, which was randomly placed into the 1-ha square. This quadrat was further divided into 256 2.5 m × 2.5 m (6.25 m²) squares, to survey species of compartment *LH*; only occurrence data were compiled for each of the 256 squares.

All stems were counted (except for compartment *LH*) and botanically identified to the species level, directly in the field or later at the herbarium from voucher specimen collected in the field. Thirty-four species remained unidentified and were further considered as 'morphospecies'. Nomenclature follows Lebrun and Stork (1991–1997).

Data analyses

All analyses were performed on abundance (*A, J, R*) or occurrence (*LH*) data for each compartment separately.

Community structure

To investigate the relationship between disturbance intensity and species diversity, we used additive partitioning of rarefaction curves (Crist and Veech, 2006; Clarke et al., 2011). Rarefaction curves allow calculation of the expected species richness of an area at any level up to the maximum sampling effort in that area; they are commonly used to control for variation in sampling effort, hence to examine variation in species diversity independently from stem density. Comparison of species rarefaction curves in highly diverse tropical forests has been previously shown to be important for fully understanding ecological response of these communities to disturbance (Gotelli and Colwell, 2001), and the scale at which disturbance impacts diversity (Dumbrell et al., 2008). Changes in the slope could occur if habitat disturbance has different effects on local diversity at sampling points (*α* diversity) compared with species turnover between sampling points (*β* diversity) (Condit et al., 2002). The shape of the species abundance distribution curve is also expected to change in response to disturbance as a consequence of the shifts on both composition and relative abundance among species within the community (Spellerberg, 1993).

First, we generated rarefaction curves for each plot by random permutations of the sampling stems (*A, J, R*) or squares (*LH*) without replacement. Statistical significance was tested using the approximate 95% confidence interval (CI) for the rarefaction curves: two curves were considered as significantly different whenever their CI, calculated as ±1.96 standard deviations around expected values, did not overlap.

Second, we fitted these curves to 8 different functions suggested by various authors, especially Dengler (2009) and Dengler and Oldeland (2010): Arrhenius (power law), Michaelis–Menten, logistic, Gleason (semi-log), Lomolino, Gompertz, power quadratic, and Weibull. We selected the best models based on the corrected Akaike information criterion (AICc) and Bayesian information criterion (BIC) and assessed their goodness-of-fit using the adjusted R^2 (R_a^2) and mean square error (MSE). As we were primarily interested in comparing the treatment effect on the different vegetation compartments, we chose the same model across all compartments, namely the one that most often had the lowest AICc and BIC

values and gave the best goodness-of-fit ($R_a^2 \geq 0.999$ and lowest MSE; see Appendix S1), namely the four-parameter Weibull function:

$$S = a\left[1 - e^{-(b(N-c)^d)}\right] \tag{1}$$

where *S* is species richness; *N* the number of stems (sampled unit); *a, b, c* and *d* four parameters representing the total number of species in the community (asymptote), the rate of species accumulation, the scaling factor determining the *x*-axis intercept, and the shape parameter, respectively.

Third, we extracted *α*-, *β*- and *γ*-diversity from the survey data through the additive partitioning of rarefaction curves (Crist and Veech, 2006; Clarke et al., 2011). Moreover, to get independent measures of species richness and turnover, we used the formulation of additive partitioning introduced by Ricotta (2008):

$$\bar{\beta} = 1 - \frac{\bar{\alpha}}{\gamma} \tag{2}$$

The *α*-diversity equated the estimated number of species per 100 stems (*A, J, R*) or per 2.5 m × 2.5 m square (*LH*); the *γ*-diversity was given by the last point of the curve, which corresponded to the total number of species recorded; and the *β*-diversity determined the shape of the curve after the first point.

Fourth, we constructed species abundance distribution curves (SADs; McGill et al., 2007), by ranking species from the most to the least frequent within each quadrat. To compare treatments and explore the underlying processes, we determined which one of the seven following distribution models fitted our SAD curves the best: linear, logistic, log series (broken stick), log-normal, geometric (niche pre-emption), Zipf and Zipf–Mandelbrodt; we retained the model with the lowest deviance and Bayesian Information Criterion (BIC).

All parameters of the partitioned rarefaction curves (*a, b, c, d, α, β* and *γ*) and SAD curves were regressed against disturbance intensity (δ*G*) using linear models. Furthermore, to test whether the parameters obtained for compartment *A* were good predictors of the corresponding parameters found for the other compartments, we computed Spearman rank correlations (*P* < 0.05).

Species composition

To explore the relationship between species composition and disturbance intensity, we used multivariate analyses. We first performed a non-metric multidimensional scaling (NMS) of each of the vegetation data matrices, after having excluded rare species (i.e. species occurring once). We then computed Spearman rank correlations between disturbance intensity and species composition represented by the NMS quadrat scores on each significant axis.

To test whether species composition significantly differed among the three treatments, we ran a permutational multivariate analysis of variance (NPMANOVA; McArdle and Anderson, 2001). *F*-ratios were estimated from variance estimates that are provided by non-parametric multivariate analysis of variance. When significant, species composition difference between the three treatments was subsequently described using indicator species analysis for each quadrat (ISA; Dufrêne and Legendre, 1997). Monte Carlo test of significance was based on 1000 randomizations (*P* < 0.05).

All statistical analyses were performed using the "vegan" (Oksanen et al., 2010), and "labdsv" (Roberts, 2010) libraries of R v. 2.12.0 software (R Development Core Team, 2009).

Results

Community structure

We found a total of 630 species; 252, 389, 476 and 157 were recorded in compartment *A*, *J*, *R* and *LH*, respectively, of which 36, 14, 85 and 77 were exclusive of the corresponding compartment.

All rarefaction curves (Fig. 1; see also Appendix S1 for curve fitting and Appendix S2 for confidence intervals) were very well described by the fitted Weibull function ($R_a^2 \geq 0.999$), except for the *LH* compartment of one control plot (B1) for which the model did not converge. The α-, β- and γ-diversity values derived from the rarefaction curves are presented in Table 1. For compartments *A*, *J* and *R*, SAD curves were best fitted by a Zipf–Mandelbrot model in all cases except for one logged + thinned plot (*J*) and one control plot (*R*), for which a log-normal model gave the best fit. In contrast, SAD curves accounting for compartment *LH* were best fitted by a Niche pre-emption model, except for two plots (one logged and another logged + thinned) for which a Zipf–Mandelbrot model gave the best fit.

The rarefaction curves revealed very consistent patterns across the three sites, irrespective to the compartment considered, with no significant difference between sites (except for *LH*, see below).

Species richness did not differ among treatments within compartment *A* (Fig. 1a), whilst in compartment *J* control plots exhibited significantly lower rarefaction indices than disturbed plots (Fig. 1b). Regarding compartment *J*, the curves describing the three control plots were diverging as the number of sampled stems increased, whilst the six curves accounting for disturbed plots largely overlapped, indicating reduction of between-sites differences in species richness. No significant relationship was found between disturbance intensity and any of the parameters of the partitioned rarefaction curves for either compartments. SAD curves were similar among treatments for the two compartments, and their parameters did not correlate with disturbance intensity (Table 1).

In contrast, species richness of compartment *R* significantly increased with increasing disturbance intensity (Fig. 1c). Rarefaction curves exhibited very contrasting patterns among the three treatments, with the most disturbed plots accumulating species significantly faster than the least disturbed ones. This was well reflected by the increased values for α diversity ($R_a^2 = 0.413$, $F = 6.64$, $df = 7$, $P = 0.037$), γ diversity ($R_a^2 = 0.638$, $F = 15.13$, $df = 7$, $P = 0.006$), and Weibull parameter a ($R_a^2 = 0.521$, $F = 9.706$, $df = 7$, $P = 0.017$) with disturbance intensity. Species turnover also increased with disturbance intensity (β diversity; $R_a^2 = 0.608$, $F = 13.41$, $df = 7$, $P = 0.008$). SAD curves exhibited
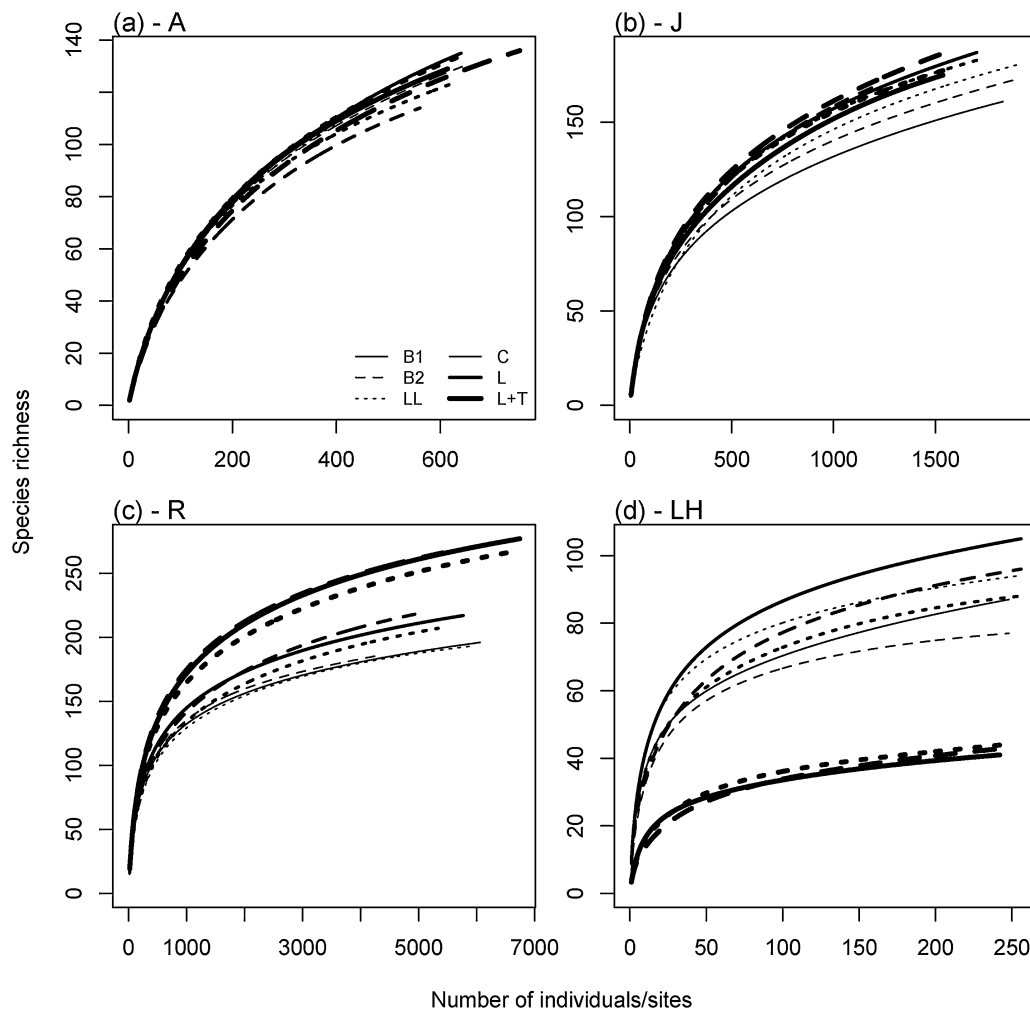
Fig. 1. Rarefaction curves for each plot. (a) compartment *A*: dbh ≥ 10-cm trees and lianas; (b) compartment *J*: 0.5 ≤ dbh < 10-cm treelets, shrubs, palms and lianas; (c) compartment *R*: dbh < 0.5 cm, ≥ 20-cm saplings; (d) compartment *LH*: lianas with a dbh < 0.5 cm, forbs, and grasses). Plots: B1, Boukoko 1; B2, Boukoko 2; LL: La Lolé; C: control; L: logged; L + T: logged + thinned. See Appendix S2 for color figures with 95% confidence intervals.

Table 1
Parameters of the partitioned rarefaction curves and relative abundance distribution curves describing species richness among plots and compartments.

	SRC Parameters				Additive partitioning			SAD parameters		
	a	b	c	d	α	β	γ	C (a)	g	b
Compartment A										
Bl–L	213.05	217.75	−4.24	0.66	51.8	0.62	135	0.781	−1.296	4.796
Bl–LT	173.77	178.17	−4.16	0.7	52.8	0.59	129	0.380	−1.117	2.695
Bl–C	161.46	164.61	−4.29	0.74	53.1	0.58	127	0.236	−1.000	1.339
B2–L	161.25	163.49	−4.27	0.71	47.8	0.58	114	0.988	−1.370	4.627
B2–LT	187.72	191.63	−4.27	0.69	49.6	0.63	136	0.326	−1.118	1.485
B2–C	182.91	187.22	−4.18	0.68	51.4	0.61	131	0.730	−1.282	4.461
LL–L	169.23	175.58	−3.88	0.65	52.3	0.57	123	0.501	−1.173	3.766
LL–LT	206.71	213.17	−4.03	0.63	53.5	0.60	135	2.704	−1.544	10.759
LL–C	207.03	212.44	−4.13	0.64	51.7	0.58	124	0.754	−1.278	4.818
∼δG	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Compartment J										
Bl–L	291.65	313.93	−3.4	0.47	56.5	0.70	187	Inf	−231.700	7823.62
Bl–LT	301.28	318.54	−3.58	0.48	53.7	0.69	175	804.000	−2.684	37.21
Bl–C	344.22	372.79	−3.17	0.38	50.1	0.69	161	114.000	−2.379	23.03
B2–L	268.48	279.98	−3.86	0.55	53.4	0.69	170	10.996	−1.859	16.11
B2–LT	293.01	313.01	−3.53	0.49	56.5	0.70	188	15.780	−1.911	19.43
B2–C	298.91	323.87	−3.26	0.42	51.8	0.70	173	16.353	−1.973	15.94
LL–L	241.44	257.32	−3.6	0.54	54.9	0.70	183	6.262	−1.742	13.90
LL–LT	249.03	267.11	−3.49	0.51	55.8	0.69	178	1.670	−1.458	8.48
LL–C	233.7 2	44.45	−4.07	0.59	45.8	0.75	181	0.209	−1.085	0.000
∼δG	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Compartment R										
Bl–L	318.17	407.74	−2.09	0.28	57.7	0.73	217	1409,176	−3.983	78.83
Bl–LT	373.03	440.27	−2.66	0.35	62.8	0.77	277	Inf	Inf	Inf
Bl–C	328.24	458.91	−1.62	0.21	55.8	0.71	196	Inf	−5.980	131.52
B2–L	376.4 4	32.88	−2.65	0.31	55.1	0.75	218	99,231	−3.567	60.20
B2–LT	359.15	429.37	−2.61	0.35	63.7	0.76	268	1697,266	−3.885	98.63
B2–C	231.26	283.16	−2.38	0.36	55.3	0.70	186	369,267,700	−4.954	102.70
LL–L	332.49	389.31	−2.53	0.31	52.8	0.74	207	2369	−2.938	38.06
LL–LT	445.54	543.52	−2.33	0.28	61.7	0.77	266	493,902	−3.729	83.27
LL–C	261.42	330.59	−2.21	0.31	50.7	0.74	193	0.542	−1.280	2.34
∼δG	∕*	ns	ns	ns	∕*	∕**	∕**	ns	ns	ns
Compartment LH										
Bl–L	142.88	178.22	−1.27	0.31	9.82	0.91	105	0.055	–	–
Bl–LT	111.64	154.03	−1.07	0.15	3.46	0.92	41	0.125	–	–
Bl–C	NA	NA	NA	NA	8.71	0.90	87	0.065	–	–
B2–L	122.05	131.26	−1.91	0.43	8.93	0.91	96	0.070	–	–
B2–LT	59.06	63.81	−2.05	0.43	3.33	0.92	43	0.152	–	–
B2–C	86.26	105.82	−1.31	0.4	6.93	0.91	77	0.066	–	–
LL–L	124.83	151.17	−1.34	0.3	8.90	0.90	88	0.065	–	–
LL–LT	53.64	60.93	−1.71	0.42	3.36	0.92	44	0.129	–	–
LL–C	122.89	190.01	−0.71	0.24	9.14	0.90	94	0.051	–	–
∼δG	ns	∖*	∖*	ns	∖*	∕*	∖*	∕*		

Plots: B1, Boukoko 1; B2, Boukoko 2; LL, La Lolé; L: logged; LT: logged + thinned; C: control. *Compartments*: A = dbh $\geq$ 10 cm-trees and lianas, J = 0.5 $\leq$ dbh <10 cm-treelets, R = dbh < 0.5 cm, $\geq$ 20 cm-woody saplings, LH = lianas with a dbh < 0.5 cm, forbs, and grasses. SRC, species rarefaction curve: a, b, c and d are respectively, the asymptote, the species accumulation rate, the scaling factor, and the shape parameter of the Weibull function, $S = a \left[1 - e^{-(b(N-c)^d)} \right]$. *Additive partitioning*: α = estimated species richness for 100 stems (A, J, R) or one 6.25 m^2 square (LH), $\beta = 1 - (\alpha/\gamma)$, $\gamma = -$ total species richness. SAD, species abundance distribution: c, g and b are the parameters of the Zipf–Mandelbrot model (compartments A, J and R), which gives the frequency of a species at rank i as $F(i) = c(i+b)^{-g}$; Inf means that the parameter could not be estimated; a is the parameter of the Niche pre-emption model (compartment LH), which gives the frequency of a species at rank i as $F(i) = a(1-a)^{(i-1)}$. ∼δG gives the result of the regression of the parameter against the disturbance intensity (basal area removed in m^2 ha^{-1}). ns = non significant. Inf = infinite value. NA = not applicable.

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.
∕ Monotonic positive.
∖ Monotonic negative.

similar shapes among treatments, none of the parameters of Zipf–Mandelbrot-modeled curves correlating with disturbance intensity (Table 1).

The species accumulation rate in compartment LH decreased with disturbance intensity (negative linear relationship between δG and b: $R_a^2 = 0.489$, $F = 7.709$, $df = 6$, $P = 0.032$), but this was mainly due to the strong difference between logged + thinned plots and the other plots, as revealed by the shape of the rarefaction curves (Fig. 1d). A strong site effect appeared for one set of plots (La Lolé), corresponding to shallower soils compared to the others (Boukoko): while there was almost no difference in species

richness between logged and control plots for the former, logged plots were significantly more species-rich than their paired control plots for the latter. As disturbance intensity increased, total species richness per plot decreased (γ diversity; $R_a^2 = 0.508$, $F = 9.26$, $df = 7$, $P = 0.019$), and the same trend was observed for the asymptote of the fitted curve (Weibull parameter a; $R_a^2 = 0.376$, $F = 5.217$, $df = 6$, $P = 0.062$). Local species density also decreased with disturbance intensity, as reflected by the negative relationship between δG and both mean species richness per area unit (α diversity; $R_a^2 = 0.518$, $F = 9.59$, $df = 7$, $P = 0.017$) and the scaling factor (Weibull parameter c; $R_a^2 = 0.453$, $F = 6.788$, $df = 6$, $P = 0.040$) (Table 1). Conversely,

Table 2
Analysis of species composition among compartments.

Compartment A	
Total number of species[§]	252 (211)
Number of significant NMS axes	3
Correlation with δG	none
NPMANOVA	$F = 0.911$, $R^2 = 0.233$; $P = 0.68$
ISA C/L/LT	–

Compartment J	
Total number of species[§]	389 (316)
Number of significant NMS axes	4
Correlation with δG	none
NPMANOVA	$F = 1.121$, $R^2 = 0.272$; $P = 0.21$
ISA C/L/LT	1/2/5

Compartment R	
Total number of species[§]	476 (414)
Number of significant NMS axes	3
Correlation with δG	NMS axis 1 ($\rho = -0.75$; $P = 0.025$)
NPMANOVA	$F = 1.651$, $R^2 = 0.355$; $P = 0.03$
ISA C/L/LT	1/1/37

Compartment LH	
Total number of species[§]	157 (140)
Number of significant NMS axes	2
Correlation with δG	NMS axis 1 ($\rho = 0.92$; $P = 0.0013$)
NPMANOVA	$F = 5.666$, $R^2 = 0.654$; $P = 0.003$
ISA C/L/LT	2/9/0

[§] In brackets: number of species used for analyses, once rare species excluded. Compartments: $A = $ dbh ≥ 10 cm-trees and lianas, $J = 0.5 \leq$ dbh < 10 cm-treelets, $R = $ dbh < 0.5 cm, ≥ 20 cm-woody saplings, $LH = $ lianas with a dbh < 0.5 cm, forbs, and grasses. NMS: non-metric multidimensional scaling. δG: disturbance intensity (basal area removal in $m^2\,ha^{-1}$). ρ is the Spearman rank correlation. NPMANOVA: non-parametric multivariate analysis of variance. ISA: number of indicator species provided by the indicator species analysis for control (C), logged (L), and logged + thinned (LT) plots; see Appendix S3 for the complete list of indicator species.

species turnover increased as disturbance intensity increased (β diversity; $R_a^2 = 0.486$, $F = 8.56$, $df = 7$, $P = 0.022$). SAD curves also strongly differed between the logged + thinned plots and the other treatments: the single parameter of the Niche pre-emption-modelled curves showed a positive linear relationship with δG: as disturbance intensity increased, the decay rate of abundance per rank also increased.

No significant correlation was found between the diversity of dbh ≥ 10-cm trees and the diversity of the three other compartments, irrespective to the parameter of the partitioned rarefaction curves and SAD curves considered. Hence, the response of tree diversity to disturbance could not be used to predict the response of the other compartments.

Species composition

NMS analyses of the plots × species matrices gave a three and four dimensional solution for compartment A and J, respectively, but none of the axes correlated with disturbance intensity, indicating that variability in species composition was not explained by past anthropogenic disturbance (Table 2). The NPMANOVA was not significant, indicating no different species composition between the three treatments for these two compartments.

In contrast, for compartment R, the NMS gave a three dimensional solution and plot scores along the first axis strongly correlated with δG ($\rho = -0.75$, $P = 0.025$). The NPMANOVA confirmed the significant differences in species composition among the three treatments ($R^2 = 0.355$, $F = 1.651$, $P = 0.03$); this was mainly due to logged + thinned plots, which presented 37 indicator species

(among which 36 with an indicator value of 100; see Appendix S3), while control and logged plots had only one each. Remarkably, 36 of the 37 indicator species of logged + thinned plots were lianas (e.g. *Landolphia landolphoides*, *Neuropeltis acuminata*, *Piper guineensis*, *Rourea obliquifoliata*, *Strophantus gratus*), while the two indicator species associated to control and logged plots were mesophanerophytes (*Coelocaryon preussii* and *Funtumia elastica*, respectively).

For compartment LH, the NMS analysis returned two significant axes, with the first one strongly correlated with disturbance intensity ($\rho = 0.92$, $P = 0.0013$). Species composition significantly differed among treatments (NPMANOVA: $R^2 = 0.654$, $F = 5.666$, $P = 0.003$), with 2, 9 and 0 indicator species for control, logged and logged + thinned plots, respectively. Indicator species of logged stands were all lianas except *Leptaspis zeylanica* (therophyte) and *Geophila obvalata* (chamaephyte). Interestingly several species associated to compartment LH of logged (*Triclisia dictyophylla*, *Salacia nitida*, *Motandra guineensis*) or control (*Iodes pierlotii*) plots were indicators of compartment R in logged + thinned plots.

Discussion

In this study, we were interested in disturbance–diversity relationships across different structural compartments of an African tropical rain forest, and the resilience of the forest as a whole to logging and thinning operations. Partitioned species rarefaction curves graphically suggested that experimentally controlled disturbances, even more than 20 years later, left a characteristic signature on the structure and composition of the plant community. While the tree layers seem to have fully recovered their species richness and composition, understories still bore the imprints of past anthropogenic disturbances, revealing vertical differences in the response of vegetation to disturbance. Hereafter, we first discuss the contrasted patterns among the structural compartments of the forest, as well as the different rates of recovery within a given compartment as a function of past disturbance intensity. Then, we discuss the potential processes behind these patterns and highlight the necessity to take into account all plant compartments when assessing tropical forest resilience.

Overstories have recovered from past artificial disturbance

Our results show that the canopy trees (compartment A or structural ensemble of the present sensu Oldeman, 1990) have fully recovered from disturbance two decades after logging and thinning with respect of both their structure and composition. This confirms and extends the results of Ouédraogo et al. (2011) and Gourlet-Fleury et al. (2013). This lack of long-term effect of logging on tree diversity is consistent with many previous studies using similar logging intensity and threshold dbh (Hall et al., 2003; van Gemerden et al., 2003; Verburg and van Eijk-Bos, 2003; Carreño-Rocabado et al., 2012). This result indicates that the initial logging-induced decrease in canopy tree species has been compensated by a recruitment from the juveniles (compartment J), which was not biased toward the same suite of light-demanding species. A negative response of pioneer trees to disturbance has already been reported in this type of forest, due to the massive recruitment of the early-successional, fast-growing *Musanga cecropioides*, which rapidly invades gaps, preempts space and resources (Gourlet-Fleury et al., 2013). This is also consistent with the hypothesis of non-random processes of diversity maintenance, according to which rare species have a higher survival rate than more common species, resulting in enrichment for rare species and increasing diversity with age and size class in tropical forests (Wills et al., 2006). These processes would enable forests that have lost part

of their species following a disturbance to recover their former diversity levels rapidly. Hence no significant relationship between disturbance intensity and diversity can be evidenced. This high resilience can also be attributed to the history of African rainforests, which have experienced stronger and more long-lasting anthropogenic and/or climatic disturbances than their counterparts of the rest of the world (Corlett and Primack, 2006). In our study forest, the dominance of the canopy by emergent light-demanding trees such as *Triplochiton scleroxylon*, *Terminalia superba* or *Entandrophragma* spp., which all require large gaps to regenerate and/or grow up to the canopy and hardly regenerate, clearly reflects past disturbances and can be related to the severe drought and fire episodes that accompanied regional rainfall fluctuations during the last 500 years (Brncic et al., 2009). Hence it is not surprising that the small-scale disturbance we added 20 years ago have no significant effects on the diversity of these light-demanding species-dominated canopies.

Species richness of juveniles was still increased in past-disturbed stands

Within compartment *J*, which contains the future trees of compartment *A* (potential trees sensu Oldeman, 1990), as well as tall shrubs, palms and some lianas, species richness corrected for stem density was higher in artificially disturbed plots than in control plots. However, none of the parameters of the partitioned rarefaction curves showed a significant relationship with disturbance intensity, suggesting that within-plot patterns of species distribution were similar among treatments, irrespective of disturbance intensity. The lack of difference between logged and logged + thinned plots regarding species richness and SAD suggests that this structural ensemble may be saturated in both treatments. We indeed observed a very dense layer of small trees in disturbed plots with very few empty spaces left to other individuals. The observed increased species richness in compartment *J* 20 years after logging and thinning operations suggests that the possible initial decrease in species richness following these artificial disturbances has been overcompensated by a massive recruitment from the sapling bank (compartment *R*), the soil seed bank and the seed rain (Brokaw, 1985), and possibly by active resprouting from the remaining stumps, roots and damaged stems. Consistent with our results, Cannon et al. (1998) suggested that the reduction in abundance of commercial species following selective logging permitted an increased number of species among the individuals of treelets, thus mitigating effects of reduced density on species-area relationships. In most cases, SAD curves were best fitted by a Zipf–Mandelbrot model, under which the entry of a species into the community is dependent on prior changes in the environment and resources, as in the facilitation model of succession (Frontier, 1985). This model predicts a few very abundant species with many minor species of comparable abundance (long tail of minor species), with parameter *b* representing the degree of niche diversification.

Remarkably, a site effect appeared only for control plots, as revealed by the divergence of rarefaction curves, indicating that past anthropogenic disturbances have homogenized community structure in the other plots, an effect already known from temperate forests (Decocq, 2000), where overstories were artificially homogenized by silviculture, thus "masked" the diversity of the entire forest plant community.

Post-disturbance positive effect on the sapling bank diversity is intensity-dependent

The sapling bank (compartment *R*) strongly responded to artificial disturbances. Species richness monotonically increased with disturbance intensity at both α and γ scales, being the greatest in the logged + thinned plots, as well as within-plot species turnover (β diversity). The greater number of stems in the most disturbed plots (as revealed by the greater length of the rarefaction curves) without significant alteration of SAD patterns suggest that past anthropogenic disturbance has promoted the recruitment of previously missing species, slightly increasing stem density. The removal of lianas in the logged + thinned plots likely contributed to the greater species richness among saplings since liana infestation has been shown to negatively impact tree growth and survival (Ingwell et al., 2010). Another recent study showed that removing lianas increased tree growth, recruitment and richness, and suggested that competition between growth forms constrains diversity in species-rich tropical forests (Schnitzer and Carson, 2010). It should be noted however that logged + thinned plots differed from control and logged plots mostly by the presence/abundance of lianas (36 of the 37 indicator species; 97.3%) that have regenerated over the last 20 years. The massive light arrival at the forest floor caused by logging and thinning operations likely promoted the germination of seeds from the seed bank and/or the seed rain (Brokaw, 1985), an effect which was first beneficial to lianas, because they invade gaps with large numbers and then grow rapidly in high-resource environments (Schnitzer and Bongers, 2002). Most of these lianas were light-demanding species with a pioneer (e.g. *Manotes griffoniana*, *P. guineensis*, *Rourea* spp., *Triclisia* spp., *Clerodendron splendens*) or mid-succesional (e.g. *Hippocratea* spp., *Iodes* spp., *Neuropeltis* spp., *Salacia* spp., *Strychnos* spp.) status (Steentoft, 1988). With canopy closure, it is likely the most shade-tolerant species (e.g. *L. landolphoides*, *M. guineensis*, *Synclisia scabrida*) will persist as suppressed saplings, whilst light-demanding species will be progressively shaded out; ultimately the species richness is expected to decrease down to pre-disturbance levels. The absence of these indicator species in compartment *R* of control and logged plots may be due to the fact that these plots already experienced canopy closure, since gaps were smaller and/or scarcer. This hypothesis is confirmed by the fact that some of the indicator species mentioned above were also indicators of the compartment *LH* in control (*I. pierlotii*) and logged (*T. dictyophylla*, *S. nitida*, *M. guineensis*) plots.

Strong disturbance has long-lasting negative effects on the ground flora diversity

The compartment *LH*, which includes herbs and climbers, was also still significantly altered by past disturbances. Species richness corrected for sample area was the lowest in logged + thinned plots, irrespective of the site considered, thus contrasting with the response of compartment *R*. Conversely, two of the three logged plots were more species-rich than their paired controls, indicating that moderate disturbance may increase local species richness, a pattern which appeared here site-dependent. Overall, as past disturbance intensity increased, the species accumulation rate decreased, whilst minimal species density decreased. Local (α diversity) and total (γ diversity) species richness both decreased linearly as disturbance intensity increased, whilst within-plot species turnover (β diversity) increased. This indicates that in the most heavily disturbed plots, anthropogenic disturbance not only decreased species richness but also made the herb layer more patchy, as a plausible combined effect of habitat heterogeneity, dispersal limitation, and chance (Condit et al., 2002). The observed decreased species richness may be an effect of competition. The higher density of the sapling bank (compartment *R*) in logged + thinned plots compared to logged and control plots, may pre-empt more space and resources and thus negatively affect smaller, herbaceous plants. This is well reflected by the SAD curves, which were better fitted by a Niche pre-emption model,

whilst a Zipf–Mandelbrot gave better results for the other compartments. The Niche pre-emption model can be seen as each species taking a constant fraction of the remaining resources, in order of their competitive dominance. It has been suggested to fit especially in stressful environments (Whittaker, 1972). The pre-emption parameter increased with disturbance intensity, indicating a decreased species equitability, especially in the most intensively disturbed plots, with a restricted number of abundant species, mostly grasses, and very few rare species compared to control and logged plots. Understorey herbs are often unevenly distributed on the tropical forest ground, and species with rhizomes or stolons are frequent. Many clonal species of the Poaceae (e.g. *L. zeylanica*) and Rubiaceae (e.g. *G. obvalata*) families form dense patches of several square meters over compacted soil areas and gaps, especially along skid trails of logged plots (Costa and Magnusson, 2002).

Are tropical rain forests resilient to anthropogenic disturbances?

Despite the low number of disturbance treatments and relatively low number of plots per treatment, our study uncovered important differences in the way a tropical rain forest regenerates. The contrasted patterns of vegetation diversity among treatments may be related to changes in habitat structure following disturbance. Changes in habitat heterogeneity were associated with changes in α and β diversity (R and LH), consistent with the observed increase of the slope of the species–sampling relationship following disturbance, which in turn results in a scale-dependent response of diversity to disturbance (Dumbrell et al., 2008). For example, control plots exhibit a mosaic of successional patches representing innovation, aggradation, biostasic, and degradation phases of the forest (sensu Oldeman, 1990). Hence they have greater heterogeneity in canopy cover and tree size, which in turn likely affect the amount of light penetrating the forest, and thus the distribution of plant species throughout the forest. In contrast, logged and logged + thinned plots were more homogeneous since the degradation phase and subsequent innovation phase were missing. Moreover, following selective logging, spatial heterogeneity in soil compaction and canopy removal is high, resulting in more gaps and small clearings, hence in more light reaching the forest floor compared to untouched stands. Anthropogenic land use history has been shown to have long-lasting effects (40–60 years) in other tropical forests as well (Thompson et al., 2002; Brown and Gurevitch, 2004).

A major implication of our study is that when assessing plant diversity in tropical forests, the usual approach restricting investigation to trees above a certain dbh may be misleading, not only because it misses an important proportion of species (Tchouto et al., 2006), but because their response to disturbance cannot be used as a surrogate for the response of other structural ensembles as shown by the lack of correlation between compartments with respect of SRC and SAD parameters. Ecological studies based solely on tree layers (dbh ≥ 10 cm) may thus lead to false conclusions. This might be attributed to the "power of resolution" of plants, which likely increases as the size of individuals decreases because smaller plants like herbs are more prone to detect fine scale variations in spatial abiotic heterogeneity (e.g. microtopography, soil compaction or humus properties) than bigger plants like trees (Carlile et al., 1989; Decocq, 2000). Our results thus qualify the widely accepted idea that selective logging does not significantly impact plant species diversity in tropical forests (Molino and Sabatier, 2001; Hall et al., 2003; van Gemerden et al., 2003; Kassi and Decocq, 2008; Sahu et al., 2008; Carreño-Rocabado et al., 2012; Gourlet-Fleury et al., 2013; but see Ding et al., 2012). Instead, we evidenced long-lasting effects of anthropogenic disturbance on the sapling bank and the herb layer that are likely to durably influence the long-term dynamics of the entire forest. Indeed, the initial steps of forest succession and regeneration take place within these two compartments. In selectively logged plots, logging gaps that exceed natural ones in size and support trampled soils may be invaded by clonal herbs, which have been found to persist on the long term (Costa and Magnusson, 2002) and inhibit seed germination of trees and suppress young seedlings (Bazzaz and Pickett, 1980). In logged + thinned plots, larger and denser gaps promote liana infestation despite their initial removal, which is known to impair tree recruitment, growth and survival (Ingwell et al., 2010; Schnitzer and Carson, 2010). We thus conclude that even after a single anthropogenic disturbance pulse, tropical rain forests may not fully recover their initial diversity and composition, at least over the first decades following disturbance. As upper layers (tree and treelets in our study) may not be replenished from lower layers (saplings) over this time frame, changes in plant composition and diversity are even likely to accumulate over time with repeated felling operations (every 30 years in this type of forest; Gourlet-Fleury et al., 2013).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2014.09.001.

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