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## 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 tercolous 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.

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## 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

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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  $\geq 10$  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 (Carliile 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 ( $3^{\circ}90'N$ ,  $17^{\circ}93'E$ ; 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  $24.9^{\circ}C$  (coolest month:  $19.6^{\circ}C$  – warmest month:  $30.2^{\circ}C$ ). 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*, *Myristicaceae*, *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  $\delta G$ , 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);

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