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1 **Testing a general approach to assess the degree of disturbance in**
2 **tropical forests**

3

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36 **Abstract**

37 **Questions:** Is there any theoretical model enabling predictions of the optimal tree-size
38 distribution in tropical communities? Can we use such a theoretical framework for
39 quantifying the degree of disturbance?

40 **Location:** Reserve of Yangambi, north-eastern region of the Democratic Republic of
41 Congo.

42 **Methods:** We applied an allometric model based on the assumption that a virtually
43 undisturbed forest uses all available resources. In this condition, the forest structure
44 (e.g. the tree-size distribution) is theoretically predictable from the scaling of the tree
45 crown with tree height at an individual level. The degree of disturbance can be
46 assessed by comparing the slopes of the tree-size distribution curves in the observed
47 and predicted conditions. We tested this tool in forest stands subjected to different
48 degrees of disturbance. We inventoried trees >1.3 m in height by measuring the DBH
49 in three plots of 1 ha each and we measured tree height, crown radius and crown
50 length in a sub-sample of trees.

51 **Results:** All tree species, independently of the site, shared the same exponents of
52 allometric relationships: tree height vs. tree diameter, crown radius vs. tree height,
53 crown length vs. tree height and consequently crown volume vs. tree height,
54 suggesting that similar trajectories of biomass allocation have evolved irrespective of
55 species. The observed tree-size distributions appeared to be power laws (excluding
56 the finite-size effect) and, as predicted, the slope was steeper in the less disturbed
57 forest (-2.34) compared to the most disturbed (-1.99). The difference in the slope
58 compared to the theoretical fully functional forest (-2.65) represents the metric for
59 assessing the degree of disturbance.

Conclusions: We developed a simple tool for operationalizing the concept of “disturbance” in tropical forests. This approach is species-independent, needs minimal theoretical assumptions, the measurement of only few structural traits and requires a low investment in equipment, time and computer skills. Its simple implementation opens new perspectives for effectively addressing initiatives of forest protection and/or restoration.

Keywords: crown volume; allometric relationships; finite-size scaling; operationalization; restoration strategies; tree-size distribution; tropical ecology.

Running head: How to operationalize the term “disturbance”

Abbreviations:

B = tree metabolic rate;

CDF= Cumulative Distribution Function;

DBH = tree diameter at breast height;

EDG = Plot within an old-growth forest subject to edge effect;

h = Tree height;

H = scaling exponent of crown radius vs. crown length;

JEU = Plot within a relatively young regrowth forest;

l_{cro} = Crown length;

MIX = Plot within an old-growth mixed forest;

r = tree diameter at the stem base;

r_{cro} = Crown radius;

V_{cro} = Crown volume.

Introduction

Tropical forests are a key biome in controlling planetary carbon stocks and fluxes, water cycles, biodiversity and global climate patterns whilst also providing ecological, economic and social services (Lewis 2006; Lewis *et al.* 2009; Slik *et al.* 2015). However, they are under severe threat and major discussions are underway to determine the exact rates of forest loss and degradation (Hansen *et al.* 2013; Achard *et al.* 2014; Kim *et al.* 2015). Forest losses are essentially driven by human population growth that requires more cultivated lands and pastures to improve food security and by numerous economic interests such as palm oil plantations and timber extraction (Sayer *et al.* 2012; Wilcove *et al.* 2013; West *et al.* 2014; Carrasco, Larrosa & Edwards 2014; Lewis *et al.* 2015). This trend will continue as long as conservation strategies remain less appealing than what private companies can offer to forest-dwelling communities (Novotny 2010).

Assessments of whole forest functionality and the degree of disturbance are essential for defining strategies for specific forest management and restoration activities. The UN Framework Convention on Climate Change, UN Food and Agriculture Organization (FAO), UN Convention on Biological Diversity (CBD) and International Tropical Timber Organization (ITTO) have different definitions of “disturbance”. This is generally defined as a discrete event in space and time that affects forest functionality, structure, species composition, canopy cover and carbon stocks. Assessing variations in forest structure or canopy cover rely on a combination of remote sensing technology and field studies. However, forests can undergo subtle changes that remote sensing is unable to detect, such as non-mechanized and small scale logging and cryptic effects of climate change (Peres *et al.* 2006; Goldstein 2014). Field studies require a lot of time and human resources, and still need a set of

110 recognized metrics providing specific information about disturbances (Nagendra
111 2012; Ghazoul *et al.* 2015). Consequently, the assessment of “disturbance” is
112 nowadays ruled by uncertainty, especially in the tropics.

113 Our aim is to partially fill this gap by applying a species-independent allometric tool
114 that, differently from other more sophisticated and complex models (e.g. forest gap
115 models; Bugmann, 2001), can easily predict the slope of the tree-size distribution
116 relative to a “fully functional” forest (i.e. a forest which uses all available resources).
117 Thus any deviation from this predicted distribution can be interpreted as metric of
118 disturbance.

119 A similar allometric approach was already proposed by Kerkhoff, & Enquist (2007),
120 who demonstrated that systematic departures for the (universal) expected allometric
121 relationships might be used as an indication of perturbation processes both in forest
122 ecosystems and in human settlements size. We further developed this idea by using
123 the “*H-model*” (Simini *et al.* 2010; Anfodillo *et al.* 2013) that, contrary to the
124 approach of Kerkhoff & Enquist (2007), is characterized by different allometric
125 relationships (i.e. the scaling exponent of the DBH distribution can assume values
126 different from -2). The expected exponent characterizing the tree-size distribution is
127 estimated by the scaling of the tree crown with tree height at an individual level. We
128 believe this scaling to be independent of specific and episodic disturbance (i.e.
129 harvesting, wind, fire) because natural selection favoured only a limited set of scaling
130 relationships, determining plant structure.

131 We already tested this tool successfully in temperate forests (Anfodillo *et al.* 2013)
132 and in a virtually undisturbed tropical forest (Simini *et al.* 2010). Here, we further test
133 the capacity to assess the degrees of disturbance in tropical communities in the Congo
134 basin by selecting three different forests in which the disturbance regime was

135 relatively well known (i.e. an old-growth mixed forest, a young regrowth forest and
136 old growth forest undergoing edge effects).

137 In summary, we tested the following hypotheses: i) allometric relationships at the tree
138 level are species-independent and unrelated to the degree of forest disturbance and; ii)
139 disturbances lead to systematic deviations from allometrically predicted tree-size
140 distributions with a shallower slope in the most disturbed forests and a steeper slope
141 in the less disturbed forests. This deviation represents the metric of forest disturbance.

142

Material and Methods

Study area

The study plots are situated in the UNESCO Man and Biosphere reserve of Yangambi in the north-eastern region of the Democratic Republic of Congo between 0° and 1° N latitude. The area has an Af-type tropical rain forest climate (Peel *et al.* 2007) with mean annual precipitation of $1,762 \pm 295$ mm (1961-2010) (Kearsley *et al.* 2013). It has a dry season from January to February with a minimum precipitation of about 100 mm per month (Hijmans *et al.* 2005). The highest and lowest temperatures are in March (25.5 ± 0.6 °C) and July (24.2 ± 0.4 °C) respectively. The soil is a Ferralsol with aeolian sediments, mainly composed of quartz sand, kaolinite and hydrated iron oxides (Van Ranst *et al.* 2010; Gilson *et al.* 1956).

The COBIMFO project established the plots in 2012 (Kearsley *et al.* 2013). Each plot was 1 ha of a square (100x100 m with subplots of 20x20 m) or rectangular shape (50x200 m with subplots of 25x25 m). COBIMFO researchers tagged, identified to species and measured at breast height (*DBH*) each tree ≥ 10 cm in diameter. In terms of forest disturbance, the main difference among the plots was due to human activity. The local communities practice slash-and-burn agriculture, including clearing after burning and cultivation until the soil loses fertility; the fields are then left uncultivated for up to 20 years to allow soil regeneration (De Wasseige *et al.* 2012).

In total we sampled three hectares of forest that were divided in three plots: one plot of old growth mixed forest (MIX plot), one of relatively young regrowth forest (JEU plot) and one of old growth forest subject to edge effects (EDG plot). The old-growth forest contains more than 70 species per ha (Table 1) with dominance of para-climax, long-living, light-demanding species such as *Prioria oxyphylla* [(Harms) Breteler] or *Pericopsis elata* [(Harms) Meeuwen] (Gilson *et al.* 1956) and shade tolerant species

such as *Scorodophloeus zenkeri* (Harms). The old-growth forest (MIX) could be defined as “virtually undisturbed” according to the work of Lebrun & Gilbert (1954), Gilson *et al.* (1956) and the field knowledge of guides and local communities but the presence of *Pericopsis elata* (a light-demanding species) might suggest that the MIX plot has been slightly disturbed many decades ago (see below for comments). The regrowth forest (JEU) was about 10 years old, but with some bigger trees that had survived the slash-and-burn practice. This forest is characterized by fast-growing and light-demanding species (e.g. *Musanga cecropioides* R. Br. ex Tedliee, *Macaranga spinosa* Muell.Arg.). The understory was tightly filled with herbaceous species and trees were more dispersed than in the old growth plot. The old growth plot undergoing edge effects (EDG) was of rectangular shape; its shorter side was along the forest boundary, adjacent to cultivated fields. The harvesting outside the plot had been done about 5 years before the sampling.

Dendrometric data

In addition to the measurements already done by the COBIMFO Project, we measured tree height (i.e. top leaves), crown radius and crown height on approximately 100 individuals >10 cm DBH per plot. We tried to record the widest possible range of heights. These data were used to estimate the value of the H exponent (see below), which drives all other allometric relationships used. We also measured total height, crown radius (r_{cro}), tree height (and, consequently, crown length, l_{cro}) and DBH of all living trees above 1.3 m and <10 cm in diameter in two randomly selected 20x20 m subplots within each plot. We measured DBH with calipers (mean of two perpendicular measurements), tree height (h) with a Tru-Pulse 200B laser rangefinder (Laser Technology Inc., Centennial, CO, USA) or with a measuring tape for young

individuals and r_{cro} with a measuring tape. We measured a total of about 1500 small individuals across all six 20x20m subplots.

Model structure and implementation

The *H-model* allowed us to determine the slope of the tree-size distribution curve of the “fully functional” forest (i.e. a forest able to use at maximum the available resources) from the scaling of crown volume with tree height at an individual tree level. Details on the structure of the model and the main assumptions are given in Anfodillo *et al.* (2013) and Simini *et al.* (2010): here we summarize the three necessary steps for basically understanding and applying the model.

i) *Metabolic rate in individual trees*: as in other allometric approaches (e.g. West *et al.* 2009) the metabolic rate of an individual tree (B) is assumed to be linearly related to leaf area and, therefore, to crown volume (V_{cro}) (assuming constant crown density with ontogenesis; see discussion for comments). The use of resources (i.e. productivity) of a single tree depends on its V_{cro} . V_{cro} is assumed to scale as $l_{cro} * r_{cro}^2$, where l_{cro} is the crown length and r_{cro} is the crown radius. The formula simplicity does not affect the scaling exponent, as we are interested in the relative change in crown volume with respect to height. Thus, the same scaling exponent is obtained even when considering more convoluted formulas to describe crown volume. This approach ensures a good estimation of scaling of B with respect to tree height (h), as we are interested in the relative change of V_{cro} with h and not its absolute variation.

Assuming that 1) the $r_{cro} \propto l_{cro}^H$ and 2) the $l_{cro} \propto h^a$ (a is a newly introduced parameter that allows for the possibility that l_{cro} might scale with h with an exponent larger than 1, see discussion), the relationship linking V_{cro} with h is therefore $V_{cro} \propto l_{cro}^{1+2H} \propto h^{a(1+2H)} \propto B$.

When $a=1$ and $H=1$ then $V_{cro} \propto h^3$ as in the West *et al.* (2009) model. Note that, due to geometrical constraints, the *maximum* value of H is assumed to be equal to 1 but lower values are possible (see discussion). The case of exponent $H=1$ and $a>1$ (i.e. $a=1.11$) was found in trees growing in the Yangambi forest yielding $V_{cro} \propto h^{3.33}$.

ii) *Finite size scaling*: the tree-size distribution curve is not a pure power law (Maritan *et al.* 1996), as shown, for example, in Fig. 2 (grey dots). The behaviour of the log-log tree-size distribution curve is linear (black dots) until a certain threshold. Naturally, physiological constraints and lack of resources limit the maximum height of trees in an ecological community. The scaling theory takes into account the finite range of tree sizes by introducing an upper cut-off to the pure power law behaviour. The upper cut-off identifies the so-called characteristic height (h_c) or diameter (r_c) and it sets the maximum value for correctly fitting any tree-size distribution curve (Stanley 1999). There is also a lower cut-off. While the upper boundary to power law behaviour is due to resource limitations the lower one is experimentally biased because it is impossible to measure all very small plants (seedlings) in a given area (some may be hidden, others might have died just after emergence). The two cut-offs are estimated by selecting the range of values that maximizes the r^2 of the linear regression.

iii) *Community use of resources*: the model assumes that a virtually undisturbed forest is able to use all the available resources in a given site. Therefore, the metabolic rate of the community (i.e. the gross primary productivity) is *proportional* to the amount of leaves filling the volume, that is $A \cdot h_c$, where A is the area of the forest and h_c the characteristic tree height (i.e. the upper limit of the power law regime). It derives that

243 the productivity is clearly higher in sites where resources are greater because h_c is also
 244 greater. In this condition we can easily demonstrate (Simini *et al.* 2010; Anfodillo *et*
 245 *al.* 2013) that the probability, $P(h_i)$, of finding a tree of a given size h_i scales inversely
 246 with the metabolic rate (B_i) of that particular size or, analytically, that
 247 $-dP^>(h|h_c)/dh \propto 1/h^{a(1+2H)}$ corresponding to $-dP^>(h|h_c)/dh \propto B^{-1}$
 248 Thus, when h is used as metric for tree-size distribution it follows exactly the Energy
 249 Equivalence Rule proposed in animals (Damuth 1981), which states that density (N
 250 per unit of area) of individuals of a given species scales inversely with the average
 251 metabolic rate of the species (i.e. $N \propto M^{0.75}$ or $N \propto B^{-1}$). Importantly it follows that
 252 the scaling of metabolic rate at tree level drives the structure of the whole community
 253 or, equivalently, that the tree architecture sets the structure of the whole forest. If tree
 254 height is used as metric for describing the tree-size distribution curve then the
 255 relationships come directly as mentioned above (e.g. $N_{max,hc} \propto h^{-a(1+2H)}$) and, in the
 256 specific case, when $a=1.11$ and $H=1$ then $N_{max,hc} \propto h^{-3.33}$, where $N_{max,hc}$ is the number
 257 of trees of height h in the domain between the two cut-offs under the condition of full
 258 resources use. However, in dense forests it is very difficult to measure the height of
 259 all trees. The *DBH* (or the diameter at stem base, r) can be used as an alternative but a
 260 variable transformation becomes necessary. In this specific case, the full resource use
 261 condition will predict a tree-size distribution scaling as $N_{max,rc} \propto r^{-2.65}$ (see the
 262 Appendix for the use of *DBH* or r in the tree-size distribution curve). The condition of
 263 full resource use would represent a state of maximum leaf area and biomass of the
 264 community. If this condition is met, then the slope of the size distribution curve is
 265 easily derivable ($N_{max,hc} \propto h^{-a(1+2H)}$). Thus any deviation of the size distribution curve
 266 in the real forest (observed) allows us to quantify the degree of forest disturbance.
 267 Indeed, if the community is somehow disturbed (i.e. it behaves as a “non-saturated

community”) the competition among the individuals is less severe and the size distribution curve is less steep.

Operationally, we used the Cumulative Distribution Function (CDF) for assessing the tree-size distribution of the communities (Newman 2005). Generally, forestry studies bin the diameters in size-classes, but it is necessary to choose the bin size (e.g. 2 or 5 cm) “a priori” and this subjective binning can affect the diameter distributions, the regression and its exponent. We circumvented this hindrance by building a Cumulative diameter-Distribution Function (CDF). The CDF describes the probability of finding a diameter larger than each diameter considered. This probability is calculated, after sorting all the diameters in ascending order, with the following formula: $F_d = N_r / N_{tot}$, where N_{tot} is the total number of individuals measured in a given plot and N_r is the rank of diameter r , i.e. the number of trees with a larger diameter than any number of the sorted series. Notably, for mathematical reasons, the scaling exponent of the CDF is equal to the predicted exponent for the Probability Distribution Function (PDF) +1 (see Newman 2005). We then estimated the distribution exponent with a linear regression of log CDF on log r ,

Our <10 cm DBH tree dataset was representative for 800 m² of forest in each 1 ha plot, so we multiplied the number of trees by 12.5. We thus obtained a dataset representative for one ha of <10cm trees and merged it with the >10 cm DBH census done by COBIMFO.

We conducted all analyses with the R-project software package.

Results

Forest inventories

The full inventories revealed a marked difference between the old-growth (MIX) and regrowth-forest plots (JEU). Although the number of individuals greater than 10 cm

DBH was similar in all plots, there was a notable difference in the distribution of small trees (*DBH* <10 cm) with the MIX plot hosting almost twice as many small trees as the JEU plot (Table 1); the EDG plot had a similar number of small trees to the MIX plot. Trees were markedly shorter in the most disturbed plot (JEU): the tallest measured tree was 36 m in height compared to 55 to 60 m in the other two plots (Table 1).

Allometric scaling at individual level

The scaling of V_{cro} with h did not differ among the three plots (Table 2) even though the number of woody species was different (78 species in the MIX and 30 in the JEU). The MIX plot showed an exponent of 3.36 (95%CI ± 0.10), the EDG plot 3.30 (95%CI ± 0.09) and JEU 3.38 (95%CI ± 0.12). Since $H=1$, $V_{cro} \propto h^{3a}$ implies $a=1.12$, 1.10 and 1.13 respectively. The most general exponent was obtained merging all the available data leading V_{cro} to scale with h with an exponent of 3.34 (95%CI ± 0.06), corresponding to $a = 1.11$ (Fig. 1a).

We also tested whether other scaling relationships were species independent and/or influenced by disturbances. The r_{cro} vs. h scaling returned similar exponents that did not differ from 1.11 as also occurred in the scaling of l_{cro} with h (Table 2; Fig. 1b and 1c). This means that the scaling of the lateral expansion of the crown (r_{cro}) with crown length (l_{cro}) is strictly isometric (i.e. $H=1$) in all species and plots.

The scaling between h vs. r showed a very small (but significant looking at the confidence intervals) variation among plots with exponents of 0.74, 0.69 and 0.68 in MIX, EDG and JEU plots respectively (Table 2 and Fig. 1d). When all data were pooled, h scaled with r with a power of 0.71.

Forest disturbance assessment

The slope of the observed self-thinning line was estimated *only* considering the black dots (i.e. within the cutoffs identified by the *H-model*), thus excluding 18% of trees in the old-growth plot and 14 % of trees in the other two plots. The steepest self-thinning line was measured in the MIX plot (-1.34) with the smallest difference compared to the prediction (-1.65 dashed line) although this was significant (i.e. 95% CIs did not include -1.65, Fig. 2a). The slope in the EDG plot was slightly less steep than the MIX plot (-1.25) whereas that in the JEU plot (-0.99) was the least steep.

Discussion

Disturbance assessment is a fundamental requirement for implementing forest protection policies and prioritizing restoration activities. Furthermore, numerous ecological theories consider forest disturbance, which still has no standard assessment approach (Asner 2013). Our results show that the slopes of tree-size distributions in tropical forests of the Congo change with the degree of disturbance in agreement with model expectations. Thus, by means of a minimum-effort inventory, a diagnostic tool assessing forest disturbance can be implemented by simply comparing the slope of the actual tree-size distribution with the potential slope predicted by the *H-model*. This difference then represents a metric of forest disturbance related to functional processes within the whole forest.

Tree-level scaling relationships

The V_{cro} vs. h scaling returns almost identical exponents in the three forests in spite of structural and composition differences showing that the allocation trajectories are genetically determined and are therefore site (i.e. plot) and disturbance independent.

Moreover, our study provides further evidence that the scaling of V_{cro} vs. h is nearly species independent (Anfodillo et al. 2013) in forests growing at about the same latitude. Indeed, comparing MIX and JEU, the composition changes are significant. For instance, fully 69% of MIX species are not found in the JEU forest, and 24% of JEU species are found only in the regrowth forest.

An additional in-depth analysis allows us also to include the possibility of a hyper-allometric (i.e. >1) relationship among r_{cro} vs. h and also l_{cro} vs. h (Table 2). We are thus able to further generalize the assumptions of the *H-model* by introducing a new parameter “ a ”, which was not proposed in the model of Simini et al. (2010). The parameter “ a ” could account for a scaling of V_{cro} with h larger than 3 (that would be a geometrical limit) as in the Yangambi forest (e.g. 3.34). When r_{cro} and l_{cro} scale with h with an exponent >1 , crown radius and length increase slightly faster than height with tree size, thus big trees will have a proportionally larger crown than small ones.

The slope of the “potential” tree-size distribution and its variations.

The *H-model* predicts the slope of tree-size distributions under maximum resource use: however in the less-disturbed plot (MIX) the difference between the predicted and the empirical distribution was relatively large (Fig. 2a). There are two explanations for this result. The most plausible is that forests are continuously subjected to temporal and spatial disturbances (Wright 2005; Muller-Landau 2009; Chambers et al. 2013), making the community seldom able to achieve a state for maximally using the available resources. Indeed, the MIX forest is relatively close (<2 km) to very disturbed or deforested areas so it is plausible that some harvesting had been done as suggested by the presence of *Pericopsis elata*, a light-demanding species

that regenerates in abandoned fields. Moreover, even natural processes might lead towards “non-saturated conditions”: for example, when a large tree falls and dies younger plants might replace the whole leaf area lost (i.e. the amount of resources used), but this process will need several years to be accomplished. Thus, there might be a sort of “minimum background disturbance” that probably occurs because growing processes in trees are relatively slow (years) compared to biomass losses caused by disturbances (days) (Connell, 1978).

The second possible explanation is that the assumption of constant leaf density with ontogenesis (i.e. B is proportional to V_{cro}) might be partially incorrect. Indeed, if the self-shading of the leaves increases with tree size (Duursma et al. 2010), then B of a single tree would increase less than V_{cro} and the scaling of V_{cro} would over-estimate the slope of the tree-size distribution (i.e. *H-model* would predict a steeper fully functional exponent than the real one). Since the total leaf area of a tree is very difficult to precisely measure, especially in large trees, the isometry between B and V_{cro} is an assumption to be further tested.

In summary, it may be possible to predict the potential tree-size distribution in forests anywhere on the earth, regardless of species composition and disturbance just by measuring how V_{cro} scales with h in some individuals of the area (e.g. even 100-150 trees with the widest possible span of tree heights). Our approach could hence leap over the “shifting baseline syndrome” (Vera, 2010; Ghazoul *et al.* 2015) without needing any historical data or records of past disturbances and it might provide a universal practical metric for addressing forest restoration and sustainable management.

Operationalizing forest disturbance.

Forest disturbances include different events with different frequency, degree of severity and rates of recovery, which all can differ in relation to ecosystem type. Thus, it is challenging to find a simple tool for operationalizing (i.e. to measure) the general term “disturbance”. However, our framework allows us to predict the slope of the potential tree-size distribution and, consequently, provides a metric for quantifying the degree of disturbance. Indeed, the steepest tree-size distribution curve (i.e. most similar to the potential one) (Fig. 2a) was observed in the virtually undisturbed forest, but the distribution diverged markedly in the JEU plot (Fig. 2c). In the EDG plot, the slope was slightly less steep than the potential condition (Fig. 2b). The variation between MIX and JEU plots in terms of degree of disturbance (the slope difference is 0.35) depicts an overall difference of 2441 individuals ha^{-1} , with the most notable 44% density reduction in small trees (<8.9 cm in diameter). However, we point out that slope variations are only related to the proportion of individuals in the different size-classes, and not to absolute stem density *per se*. For instance, we randomly removed 2438 individuals from the inventory of the MIX plot, thus obtaining the same stem density as in the JEU plot, and we fitted the new data. In spite of the “artificial” exclusion of more than 1/3 of the individuals, the slope of the diameter distribution did not change and we obtained the same slope as the original MIX dataset (i.e. -1.34).

The EDG and MIX slopes differed slightly (difference of 0.09). Laurance et al. (2006) showed artificial boundaries induced a reduction in stem density among larger cohorts (>60 cm *DBH*) only 20 years after forest fragmentation in Amazonia. The smaller cohorts should instead follow a “pulsating recruitment pattern” immediately after the boundary establishment (Laurance et al. 1998; Laurance et al. 2011). Our edge plot boundary was created about five years before sampling, so the EDG forest is

very likely in the pulsating phase reported by Laurance et al. (1998). The disturbance might have increased the availability of resources (i.e. radiation) leading to less severe competition among trees.

Awareness of finite-size scaling forces us to correctly estimate the slope of the distribution only within the upper and lower cut-off (Fig 2). We suppose this might have important consequences on the “stability” of the predictions. Indeed, other authors assessed the degree of disturbance mainly by comparing biomass and structure in subsequent inventories (e.g. Chave *et al.* 2008). However, episodic mortality of large trees, which include a significant part of total biomass (Chambers *et al.* 2013), might affect the results. For example, in the MIX plot, we estimate that the 5 largest trees account for more than 20% of the total biomass and the largest 100 trees (out of 6138) amount to about 75% of total biomass and 40% of total leaf area. This dominance would explain why episodic disturbances to 8-10 trees, often the biggest, could cause detectable variation in total biomass and create a sawtooth pattern of biomass gain punctuated by occasional losses (Chambers *et al.* 2013). Our approach behaves differently: the biggest trees are not *directly* used for estimating the use of resources by the community because they are above the upper cut-off. For example, in the MIX plot the upper cut-off is about 33 cm thus excluding about 130 of the biggest trees. Undoubtedly, the presence of the large trees impacts on the number of trees in the smaller cohorts because some resources are exploited, but we can speculate that competition among all of them (which produces the tree-size distribution) might, on average, be much less affected by the episodic losses of some large trees.

As highlighted by Coomes et al. (2003) and Coomes & Allen (2007), disturbances alter the expected tree-size distribution. Our data, and theory, suggest

that the slope of the tree-size distribution becomes flatter with more disturbance (as in the JEU plot; Fig. 7). This is because when a disturbance causes tree mortality and losses, resources become available for the remaining trees to exploit. Thus, competition is generally lower in a sparse community leading to a flatter slope and the size frequency distribution (within a diachronic approach) will be parallel to the X axis (i.e. slope 0). Hence in our framework, after a disturbance event, the forest approaches the slope of the “virtual steady state” coming from “above” (i.e. from -1.9 to -2.3) as reported also by Coomes *et al.* (2003) who found flatter slopes when the finite size effect was excluded (trees <18 cm *DBH*) and Kerkhoff & Enquist (2007).

Relevance for planning restoration activities

We show that it is possible to predict “base-line” forest structure by measuring simple traits, such as r_{cro} , l_{cro} and h . The independence of these variables from species and disturbances might allow us to calculate the potential slope for all forests across the globe, thus adding a quantitative tool for monitoring old-growth forest dynamics also in temperate regions (Paillet et al. 2015). Furthermore, we show that the comparison between the potential and observed slope provides a simple functional metric depicting the degree of disturbance. This would allow us to prioritize restoration activities simply by ranking all studied forests from the most to the least disturbed. This ranking will be based on functional processes and not on subjective biomass thresholds, which can vary among ecosystems.

The effectiveness of our minimum effort inventory (1-2 ha in tropical forests) can be partially tested by comparing the results with other published data (even if the finite size effect was, unfortunately, never considered in previous reports). Indeed, if we consider the Yangambi MIX slope built with *DBH* values, without the finite-size

effect, we obtain a diameter distribution exponent of -1.06. This slope is relatively similar to the slopes reported by Muller-Landau *et al.* (2006) in Ituri-Edoro, about 450 km away and sharing many species with Yangambi, which ranged from -2.04 to -2.07 (so their CDF ranged from -1.04 to -1.07). Thus, Ituri trees' scaling of V_{cro} vs. h might be very similar to Yangambi trees'. This could mean that our medium-effort inventory may have a similar capacity in defining the forest structure as the 20 ha inventory used for Ituri-Edoro. It thus appears that it is possible to achieve a realistic representation of the forest structure with two 20x20m plots per ha for trees <10cm and a total inventory of trees >10cm *DBH* in 1 ha. Further tests will be necessary to fully demonstrate that our approach might overcome the necessity for measuring all trees in an area of at least 10 ha to detect forest disturbances in tropical forests (Chambers *et al.* 2013).

Conclusions

We propose a framework for predicting the structure (i.e. the slope of the tree-size distribution curve) of a virtually undisturbed forest built on metabolic scaling at the individual-level. This slope represents the general "baseline" for assessing the degree of disturbance in all forests. The application of our approach in three forests with different degree of disturbance shows how simple and effective the implementation of this metric can be. Thus, the *H-model* appears particularly suitable for implementation within the routine forest assessments. We emphasize that the importance of this tool for prioritizing forest protection and/or restoration activities in the tropics will be sorely needed in the coming years.

492

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Tables and Figures.

Table 1. Main structural parameters of the three sampled one hectare plots (all trees >1.3 m in height) in the Yangambi region, Congo.

Plot	Maximum Tree height (m)	Maximum <i>DBH</i> (cm)	Number of Individuals >10 cm (ha ⁻¹)	Number of individuals < 10 cm (ha ⁻¹)	Number of species (ha ⁻¹)
MIX	55	127.7	323	5815	78
EDG	60	157.0	456	5162	77
JEU	36	62.5	322	3250	30

667 Table 2. Results of the regression analyses of V_{cro} , r_{cro} , l_{cro} vs. h and h vs. tree base
668 diameter (r) considering three plots in the Yangambi Region, Congo, under various
669 disturbance regimes separately (MIX, EDG and JEU).

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	Site	Intercept	Exponent	r^2	CI 95%	
$V_{cro} \sim h^{[a(1+2H)]}$					Intercept	Exponent
	MIX	0.0011	3.36	0.888	± 0.0006	± 0.10
	EDG	0.0018	3.30	0.896	± 0.0011	± 0.09
	JEU	0.0016	3.38	0.897	± 0.0013	± 0.12
$r_{cro} \sim h^{(aH)}$						
	MIX	0.092	1.11	0.844	± 0.022	± 0.04
	EDG	0.121	1.07	0.845	± 0.03	± 0.04
	JEU	0.083	1.14	0.866	± 0.024	± 0.05
$l_{cro} \sim h^a$						
	MIX	0.127	1.14	0.833	± 0.033	± 0.04
	EDG	0.12	1.16	0.825	± 0.034	± 0.04
	JEU	0.235	1.09	0.812	± 0.08	± 0.05
$h \sim r^{[2/(a(1+2H))]}$						
	MIX	160.8	0.74	0.924	± 4.11	± 0.02
	EDG	159.2	0.69	0.872	± 4.98	± 0.03
	JEU	167.3	0.68	0.902	± 5.29	± 0.03

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Fig. 1. Scaling of (a) V_{cro} vs. h ; (b) of r_{cro} vs. h ; (c) l_{cro} vs. h ; (d) h vs. r in three plots of variously disturbed forest in Yangambi, The Congo (all data pooled together). In parenthesis the $\pm 95\%$ CI of the parameters

679 *Fig. 2. Cumulative Distribution Function (CDF) of base diameters (r). Grey dots*
680 *represent the upper and lower cut-off in the (a) MIX, (b) EDG, (c) JEU plot at*
681 *Yangambi, The Congo. The dashed line is the slope representing the “fully functional*
682 *forest”. In parenthesis the $\pm 95\%$ CI of the intercepts and slopes.*

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