





# Testing a general approach to assess the degree of disturbance in tropical forests

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## Keywords

Allometric relationships; Crown volume; Finite size scaling; Operationalization; Restoration strategies; Tree size distribution; Tropical ecology

## Abbreviations

$B$  = tree metabolic rate; CDF = Cumulative Distribution Function; EDG = Plot within an old-growth forest subject to edge effect;  $H$  = scaling exponent of crown radius vs crown length;  $h$  = Tree height; JEU = Plot within a relatively young regrowth forest;  $l_{cro}$  = Crown length; MIX = Plot within an old-growth mixed forest;  $r_{cro}$  = Crown radius;  $r$  = tree diameter at the stem base;  $V_{cro}$  = Crown volume.

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## Abstract

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

**Location:** Reserve of Yangambi, northeast region of the Democratic Republic of Congo.

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

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

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## 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 land and pasture 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 et al. 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 recognized metrics providing specific information about disturbances (Nagendra 2012; Ghazoul et al. 2015). Consequently, the assessment of 'disturbance' is nowadays ruled by uncertainty, especially in the tropics.

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

A similar allometric approach was already proposed by Kerkhoff & Enquist (2007), who demonstrated that systematic departures for the (universal) expected allometric relationships might be used as an indication of perturbation processes both in forest ecosystems and in human

settlements size. We further developed this idea by using the '*H*-model' (Simini et al. 2010; Anfodillo et al. 2013) that, contrary to the approach of Kerkhoff & Enquist (2007), is characterized by different allometric relationships (i.e. the scaling exponent of the DBH distribution can assume values different from  $-2$ ). The expected exponent characterizing the tree size distribution is estimated by the scaling of the tree crown with tree height at an individual level. We believe this scaling to be independent of specific and episodic disturbance (i.e. harvesting, wind, fire) because natural selection favours only a limited set of scaling relationships, determining plant structure.

We already tested this tool successfully in temperate forests (Anfodillo et al. 2013) and in a virtually undisturbed tropical forest (Simini et al. 2010). Here, we further test the capacity to assess the degrees of disturbance in tropical communities in the Congo Basin by selecting three different forests in which the disturbance regime was relatively well known (i.e. an old-growth mixed forest, a young regrowth forest and old-growth forest undergoing edge effects).

In summary, we tested the following hypotheses: (1) allometric relationships at the tree level are species-independent and unrelated to the degree of forest disturbance and; (2) disturbances lead to systematic deviations from allometrically predicted tree size distributions, with a shallower slope in the most disturbed forests and a steeper slope in the less disturbed forests. This deviation represents the metric of forest disturbance.

## Methods

### Study area

The study plots are situated in the UNESCO Man and Biosphere reserve of Yangambi in the northeast region of the Democratic Republic of Congo, between  $0^\circ$  and  $1^\circ\text{N}$ . 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 Jan to Feb, with minimum precipitation of about 100 mm per month (Hijmans et al. 2005). The highest and lowest temperatures are in Mar ( $25.5 \pm 0.6$  °C) and Jul ( $24.2 \pm 0.4$  °C), respectively. The soil is a Ferralsol with aeolian sediments, mainly composed of quartz sand, kaolinite and hydrated iron oxides (Gilson et al. 1956; Van Ranst et al. 2010).

The COBIMFO project established the plots in 2012 (Kearsley et al. 2013). Each plot was 1 ha of a square ( $100\text{ m} \times 100\text{ m}$  with subplots of  $20\text{ m} \times 20\text{ m}$ ) or rectangular shape ( $50\text{ m} \times 200\text{ m}$  with subplots of  $25\text{ m} \times 25\text{ m}$ ). COBIMFO researchers tagged, identified to species and measured DBH of each tree  $\geq 10$  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 yr to allow soil regeneration (De Wasseige et al. 2012).

In total we sampled 3 ha of forest that was 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-ha<sup>-1</sup> (Table 1) with dominance of para-climax, long-lived, 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 field knowledge of guides and local communities, but the presence of *P. elata* (a light-demanding species) might suggest that the MIX plot was slightly disturbed many decades ago (see below for comments). The regrowth forest (JEU) was about 10 yr 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 understorey 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 for about 5 yr 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

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

Plot	Maximum Tree Height (m)	Maximum DBH (cm)	Number of Trees DBH > 10 cm (ha <sup>-1</sup> )	Number of Trees DBH < 10 cm (ha <sup>-1</sup> )	Number of Species (ha <sup>-1</sup> )
MIX	55	127.7	323	5815	78
EDG	60	157.0	456	5162	77
JEU	36	62.5	322	3250	30

measured total height, crown radius ( $r_{\text{cro}}$ ), tree height (and, consequently, crown length,  $l_{\text{cro}}$ ) and DBH of all living trees above 1.3 m and <10 cm DBH in two randomly selected 20 m × 20 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, Centennial, CO, US) or with a measuring tape for young individuals and  $r_{\text{cro}}$  with a measuring tape. We measured a total of about 1500 small individuals across all six 20 m × 20 m 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.

1 *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 ( $V_{\text{cro}}$ ; assuming constant crown density with ontogenesis; see Discussion for comments). The use of resources (i.e. productivity) of a single tree depends on its  $V_{\text{cro}}$ .  $V_{\text{cro}}$  is assumed to scale as  $l_{\text{cro}} \times r_{\text{cro}}^2$ , where  $l_{\text{cro}}$  is the crown length and  $r_{\text{cro}}$  is the crown radius. The simplicity of the formula 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  $V_{\text{cro}}$  with  $h$  and not its absolute variation. Assuming that (1) the  $r_{\text{cro}} \propto l_{\text{cro}}^H$  and 2) the  $l_{\text{cro}} \propto h^a$  ( $a$  is a newly introduced parameter that allows for the possibility that  $l_{\text{cro}}$  might scale with  $h$  with an exponent > 1, see Discussion), the relationship linking  $V_{\text{cro}}$  with  $h$  is therefore  $V_{\text{cro}} \propto l_{\text{cro}}^{1+2H} \propto h^{a(1+2H)} \propto B$ . When  $a = 1$  and  $H = 1$  then  $V_{\text{cro}} \propto h^3$  as in the West et al. (2009) model. Note that, due to geometric 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  $V_{\text{cro}} \propto h^{3.33}$ .

2 *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.

**3 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  $A \times h_c$ , 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 can be derived that the productivity is clearly higher in sites where resources are higher because  $h_c$  is also higher. In this condition we can easily demonstrate (Simini et al. 2010; Anfodillo et al. 2013) that the probability,  $P(h_i)$ , of finding a tree of a given size  $h_i$  scales inversely with the metabolic rate ( $B_i$ ) of that particular size or, analytically, that  $-dP>(h|h_c)/dh \propto 1/h^{a(1+2H)}$  corresponding to  $-dP>(h|h_c)/dh \propto B^{-1}$

Thus, when  $h$  is used as metric for tree size distribution it follows exactly the Energy Equivalence Rule proposed for animals (Damuth 1981), which states that density ( $N$  per unit of area) of individuals of a given species scales inversely with the average metabolic rate of the species (i.e.  $N \propto M^{-0.75}$  or  $N \propto B^{-1}$ ). Importantly, it follows that the scaling of metabolic rate at tree level drives the structure of the whole community or, equivalently, that the tree architecture sets the structure of the whole forest. If tree height is used as metric for describing the tree size distribution curve then the relationships come directly as mentioned above (e.g.  $N_{\max,hc} \propto h^{-a(1+2H)}$ ) and, in the specific case, when  $a = 1.11$  and  $H = 1$  then  $N_{\max,hc} \propto h^{-3.33}$ , where  $N_{\max,hc}$  is the number of trees of height  $h$  in the domain between the two cut-offs under the condition of full resource use. However, in dense forests it is very difficult to measure the height of all trees. The DBH (or diameter at stem base,  $r$ ) can be used as an alternative, but a variable transformation becomes necessary. In this specific case, the full resource use condition will predict a tree size distribution scaling as  $N_{\max,rc} \propto r^{-2.65}$  (see Appendix S1 for use of DBH or  $r$  in the tree size distribution curve). The condition of full resource use would represent a state of

maximum leaf area and biomass of the community. If this condition is met, then the slope of the size distribution curve is easily derivable ( $N_{\max,hc} \propto h^{-a(1+2H)}$ ). Thus any deviation of the size distribution curve in the real forest (observed) allows us to quantify the degree of forest disturbance. 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:  $F_d = N_r / N_{\text{tot}}$ , where  $N_{\text{tot}}$  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 data set was representative of 800 m<sup>2</sup> of forest in each 1-ha plot, so we multiplied the number of trees by 12.5. We thus obtained a data set representative for 1 ha of <10 cm trees and merged it with the >10 cm DBH census done by COBIMFO.

We conducted all analyses with the R-project software package (R Foundation for Statistical Computing, Vienna, AT).

## 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 >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 55–60 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  $\pm 0.10$ ), the EDG plot 3.30 (95% CI  $\pm 0.09$ ) and JEU 3.38 (95% CI  $\pm 0.12$ ); 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  $\pm 0.06$ ), 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, c). 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 of  $h$  vs  $r$  showed a very small (but significant, when looking at the CI) variation among plots, with exponents of 0.74, 0.69 and 0.68 in MIX, EDG and JEU plots, respectively (Table 2, 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 power law domain), 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% CI did not include  $-1.65$ ; Fig. 2a). The slope in the EDG

plot was slightly less steep than the MIX plot ( $-1.25$ ) while that in the JEU plot ( $-0.99$ ) was the least steep.

### Discussion

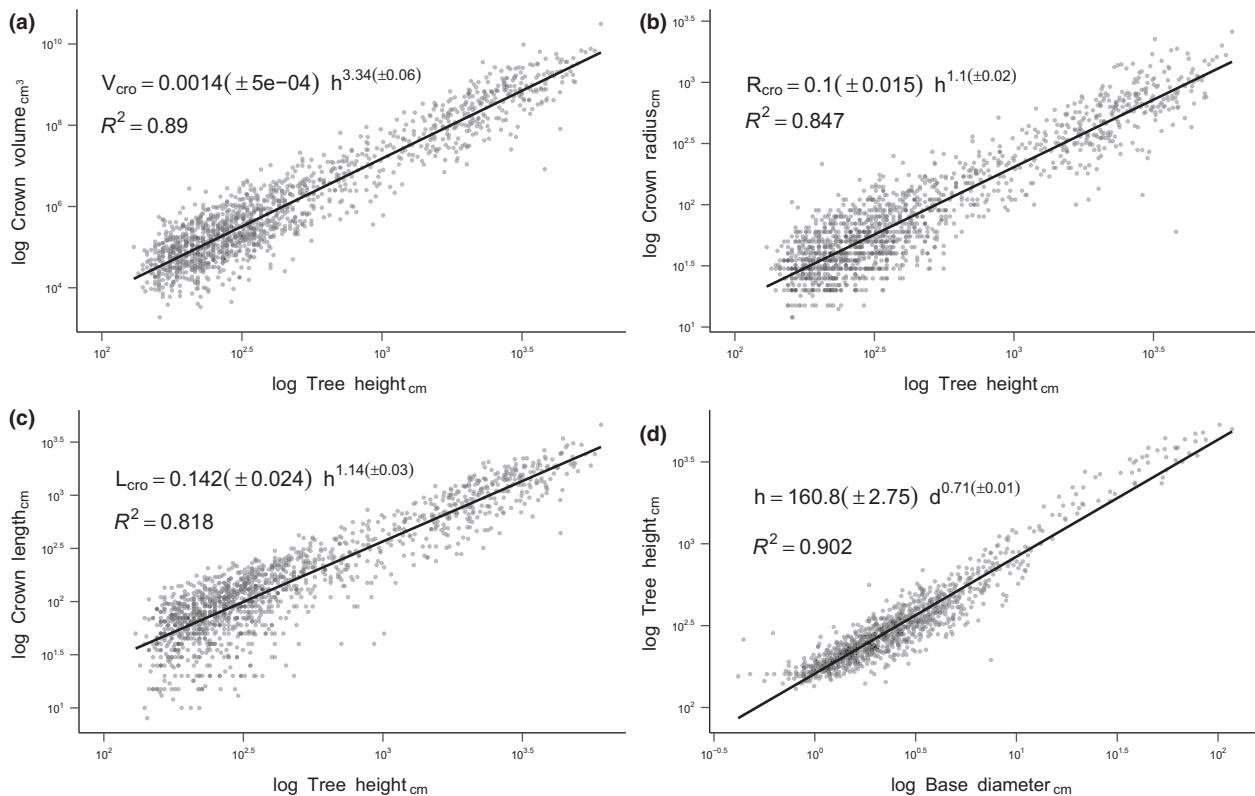
Disturbance assessment is a fundamental requirement for implementing forest protection policies and prioritizing restoration activities. Furthermore, numerous ecological theories consider forest disturbance, which still has no standard assessment approach (Asner 2013). Our results show that the slopes 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.

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

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



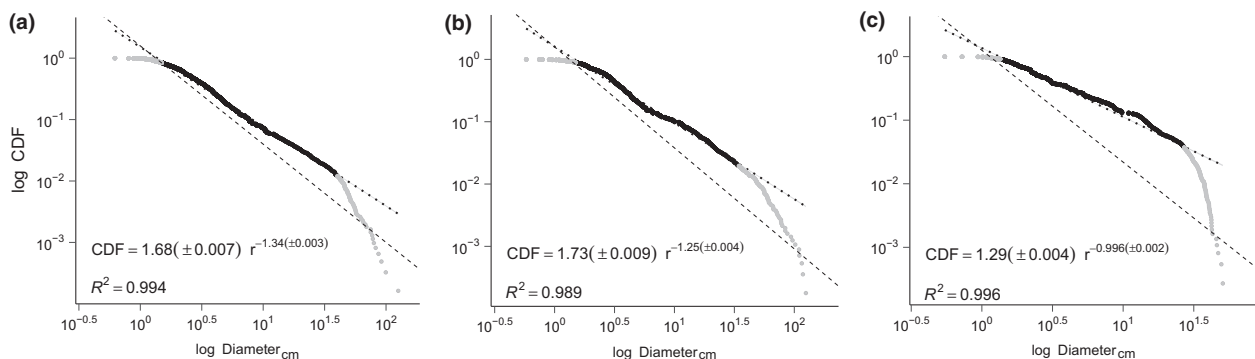
**Fig. 1.** Scaling of (a)  $V_{cro}$  vs  $h$ ; (b) of  $r_{cro}$  vs  $h$ ; (c)  $l_{cro}$  vs  $h$ ; (d)  $h$  vs  $r$  in three plots of variously disturbed forest in Yangambi, Congo (all data pooled together). In parenthesis  $\pm$  95% CI of the parameters.

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  $h > 3$  (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. 2.** Cumulative Distribution Function (CDF) of base diameters ( $r$ ). Grey dots represent the upper and lower cut-off in the (a) MIX, (b) EDG, (c) JEU plot at Yangambi, Congo. The dashed line is the slope representing the 'fully functional forest'. In parenthesis  $\pm$  95% CI of the intercepts and slopes.

(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 maximum use of 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 *P. 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 overestimate 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 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 can all 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<sup>-1</sup>, 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 data set (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 yr after forest fragmentation in Amazonia. The smaller cohorts should instead follow a 'pulsating recruitment pattern' immediately after the boundary establishment (Laurance et al. 1998, 2011). Our edge plot boundary was created about 5 yr 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 for 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 five 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 eight to ten 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 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 disturbances (as in the JEU plot; Fig. 2). 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 'baseline' 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 tree 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  $20\text{ m} \times 20\text{ m}$  plots per ha for trees  $<10$  cm and a total inventory of trees  $>10$  cm DBH in 1 ha. Further tests will be necessary to fully demonstrate that our approach might overcome the necessity of measuring all trees in an area of at least 10 ha to detect forest disturbances in tropical forests (Chambers et al. 2013).

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### References

- Achard, F., Beuchle, R., Mayaux, P., Stibig, H.-J., Bodart, C., Brink, A., Carboni, S., Desclee, B., Donnay, F., (...) & Simonetti, D. 2014. Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology* 20: 2540–2554.
- Anfodillo, T., Carrer, M., Simini, F., Popa, I., Banavar, J.R. & Maritan, A. 2013. An allometry-based approach for understanding forest structure, predicting tree-size distribution and assessing the degree of disturbance. *Proceedings of the Royal Society of London, Series B* 280: 20122375.
- Asner, G.P. 2013. Geography of forest disturbance. *Proceedings of the National Academy of Sciences of the United States of America* 110: 3711–3712.
- Bugmann, H. 2001. A review of forest gap models. *Climatic Change* 51: 259–305.
- Carrasco, B.L.R., Larrosa, C. & Edwards, D.P. 2014. A double-edged sword for tropical forests. *Science* 346: 38–41.



- Chambers, J.Q., Negron-Juarez, R.I., Marra, D.M., Vittorio, A.D.I., Tews, J., Roberts, D., Ribeiro, G.H.P.M., Trumbore, S.E. & Higuchi, N. 2013. The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proceedings of the National Academy of Sciences of the United States of America* 110: 3949–3954.
- Chave, J., Condit, R., Muller-Landau, H.C., Thomas, S.C., Ashton, P.S., Bunyavejchewin, S., Co, L.L., Dattaraja, H.S., Davies, S.J., (...) & Losos, E.C. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biology* 6: 455–462.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302–1310.
- Coomes, D.A. & Allen, R.B. 2007. Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology* 95: 27–40.
- Coomes, D.A., Duncan, R.B., Allen, R.B. & Truscott, J. 2003. Disturbances prevent stem size–density distributions in natural forests from following scaling relationships. *Ecology Letters* 6: 980–989.
- Damuth, J. 1981. Population density and body size in mammals. *Nature* 290: 699–700.
- De Wasseige, C., de Marcken, P., Bayol, N., Hiol, F., Mayaux, P., Desclée, B., Nasi, R., Billand, A., Defourny, P. & Eba'a Atyi, R. (eds.) (2012) *The forests of the Congo Basin-State of the forest 2010*. Publications Office of the European Union, Luxembourg City.
- Duursma, R.A., Mäkelä, A., Reid, D.E.B., Jokela, E.J., Annabel, J. & Roberts, S.D. 2010. Self-shading affects allometric scaling in trees. *Functional Ecology* 24: 723–730.
- Ghazoul, J., Burivalova, Z., Garcia-Ulloa, J. & King, L.A. 2015. Review conceptualizing forest degradation. *Trends in Ecology & Evolution* 30: 622–632.
- Gilson, P., VanWambeke, A. & Gutzweiler, R. (1956) *Notice explicative de la carte des sols et de la végétation*, N° 6. Yangambi, planchette 2, Yangambi, CG.
- Goldstein, J.E. 2014. The afterlives of degraded tropical forests. *Environment and Society: Advances in Research* 5: 124–140.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., (...) & Townshend, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342: 850–853.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- Kearsley, E., de Haulleville, T., Hufkens, K., Kidimbu, A., Toirambe, B., Baert, G., Huygens, D., Kebede, Y., Defourny, P., (...) & Verbeeck, H. 2013. Conventional tree height–diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. *Nature Communications* 4: 1–8.
- Kerkhoff, A.J. & Enquist, B.J. 2007. The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *BioScience* 57: 489–500.
- Kim, D., Sexton, J.O. & Townshend, J.R. 2015. Accelerated deforestation in the humid tropics from the 1990s to the 2000s. *Geophysical Research Letters* 42: 1–7.
- Laurance, W.F., Ferreira, L.V., Merona, J.M.R., Laurance, S.G., Hutchings, R.W. & Lovejoy, T.E. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12: 460–464.
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Giraldo, J.P., Lovejoy, T.E., Condit, R., Chave, J. & Harms, K.E. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* 103: 19010–19014.
- Laurance, W.F., Camargo, J.L., Luizao, R.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Williamson, G.B., Benitez-Malvido, J., (...) & Lovejoy, T.E. 2011. The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation* 144: 56–67.
- Lebrun, J. & Gilbert, G. 1954. Une Classification Ecologique des Forêts du Congo. *Série Scientifiques INEAC* 63: 1–88.
- Lewis, S.L. 2006. Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society of London, Series B* 361: 195–210.
- Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A. & Laurance, W.F. 2009. Changing ecology of tropical forests: evidence and drivers. *Annual Review of Ecology and Systematics* 40: 529–549.
- Lewis, S.L., Edwards, D. & Galbraith, D. 2015. Increasing human dominance of tropical forests. *Science* 349: 827–832.
- Maritan, A., Rinaldo, A., Rigon, R., Giacometti, A. & Rodriguez-Iturbe, I. 1996. Scaling laws for river networks. *Physical Review E* 53: 1510–1515.
- Muller-Landau, H.C. 2009. Sink in the African jungle. *Nature* 457: 969–970.
- Muller-Landau, H.C., Condit, R.S., Harms, K.E., Marks, C.O., Thomas, S.C., Bunyavejchewin, S., Chuyong, G., Co, L., Davies, S., (...) & Ashton, P. 2006. Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. *Ecology Letters* 9: 589–602.
- Nagendra, H. 2012. Assessing relatedness and redundancy of forest monitoring and change indicators. *Journal of Environmental Management* 95: 108–113.
- Newman, M.E. 2005. Power laws, Pareto distributions and Zipf's law. *Contemporary Physics* 46: 323–351.
- Novotny, V. 2010. Rain forest conservation in a tribal world: why forest dwellers prefer loggers to conservationists. *Biotropica* 42: 546–549.
- Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O. & Gosselin, F. 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. *Forest Ecology and Management* 346: 51–64.

- Peel, M.C., Finlayson, B.L. & McMahon, T.A. 2007. Updated world map of the Koppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11: 1633–1644.
- Peres, C.A., Barlow, J. & Laurance, W.F. 2006. Detecting anthropogenic disturbance in tropical forests. *Trends in Ecology & Evolution* 21: 227–229.
- Sayer, J., Ghazoul, J., Nelson, P. & Boedihartono, A.K. 2012. Oil palm expansion transforms tropical landscapes and livelihoods. *Global Food Security*, 1: 114–119.
- Simini, F., Anfodillo, T., Carrer, M., Banavar, J.R. & Maritan, A. 2010. Self-similarity and scaling in forest communities. *Proceedings of the National Academy of Sciences of the United States of America* 112: 7472–7477.
- Slik, J.W.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L., Bellingham, P.J., (...) & Venticinque, E.M. 2015. An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America* 107: 7658–7662.
- Stanley, H. 1999. Scaling, universality and renormalization: three pillars of modern critical phenomena. *Reviews of Modern Physics* 71: 358–366.
- Van Ranst, E., Baert, G., Ngongo, M. & Mafuka, P. (2010) *Carte Pedologique de Yangambi*, planchette 2: Yangambi, échelle 1:50.000. Ugent, Hogent, UNILU, UNIKIN.
- Vera, F. 2010. The shifting baseline syndrome in restoration ecology. In: Hall, M. (ed.) *Restoration and history: the search for a usable past*, pp. 98–110. Routledge, New York, NY, US.
- West, G., Enquist, B.J. & Brown, J.H. 2009. A general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences of the United States of America* 106: 7040–7045.
- West, P.C., Gerber, J.S., Engstrom, P.M., Mueller, N.D., Brauman, K.A., Carlson, K.M., Cassidy, E.S., Johnston, M., MacDonald, G.K., Ray, D.K. & Siebert, S. 2014. Leverage points for improving global food security and the environment. *Science* 325: 325–328.
- Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B. & Koh, L.P. 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution* 28: 531–540.
- Wright, S.J. 2005. Tropical forests in a changing environment. *Trends in Ecology & Evolution* 20: 553–560.

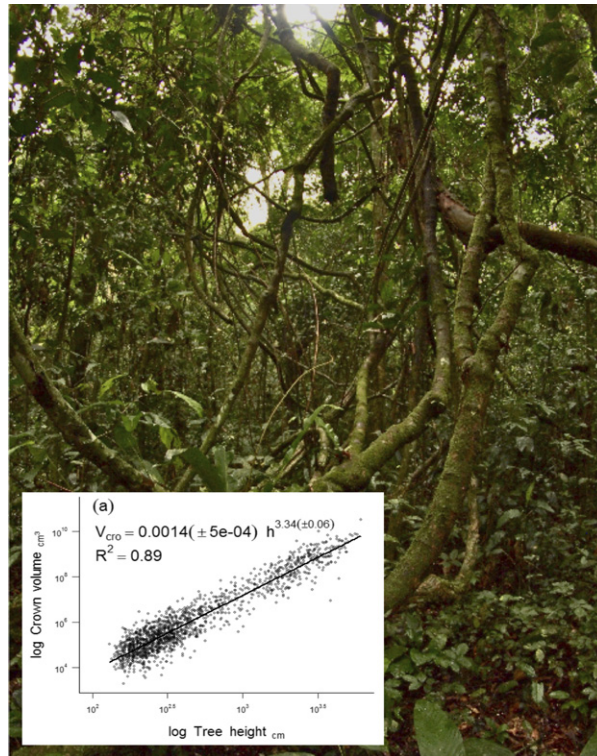
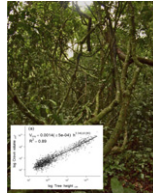
### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Transformations needed for using DBH as metric in frequency distributions.

# Graphical Abstract

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We proposed an allometric approach for quantifying the degree of disturbance in forest ecosystems. We assume that the tree-size distribution in a fully functional forest is predictable from the scaling of the tree crown with tree height at an individual level. The degree of disturbance can be quantified by comparing the predicted vs observed tree-size distribution curves.