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# Improving methods in gap ecology: revisiting size and shape distributions using a model selection approach

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**Nomenclature**
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## Abstract

**Questions:** We assess gap size and shape distributions, two important descriptors of the forest disturbance regime, by asking: which statistical model best describes gap size distribution; can simple geometric forms adequately describe gap shape; does gap size or shape vary with forest type, gap age or the method used for gap delimitation; and how similar are the studied forests and other tropical and temperate forests?

**Location:** Southeastern Atlantic Forest, Brazil.

**Methods:** Analysing over 150 gaps in two distinct forest types (seasonal and rain forests), a model selection framework was used to select appropriate probability distributions and functions to describe gap size and gap shape. The first was described using univariate probability distributions, whereas the latter was assessed based on the gap area–perimeter relationship. Comparisons of gap size and shape between sites, as well as size and age classes were then made based on the likelihood of models having different assumptions for the values of their parameters.

**Results:** The log-normal distribution was the best descriptor of gap size distribution, independently of the forest type or gap delimitation method. Because gaps became more irregular as they increased in size, all geometric forms (triangle, rectangle and ellipse) were poor descriptors of gap shape. Only when small and large gaps (> 100 or 400 $m^2$ depending on the delimitation method) were treated separately did the rectangle and isosceles triangle become accurate predictors of gap shape. Ellipsoidal shapes were poor descriptors. At both sites, gaps were at least 50% longer than they were wide, a finding with important implications for gap microclimate (e.g. light entrance regime) and, consequently, for gap regeneration.

**Conclusions:** In addition to more appropriate descriptions of gap size and shape, the model selection framework used here efficiently provided a means by which to compare the patterns of two different types of forest. With this framework we were able to recommend the log-normal parameters $\mu$ and $\sigma$ for future comparisons of gap size distribution, and to propose possible mechanisms related to random rates of gap expansion and closure. We also showed that gap shape varied highly and that no single geometric form was able to predict the shape of all gaps, the ellipse in particular should no longer be used as a standard gap shape.

## Introduction

The opening of gaps in the canopy has profound effects on the structure and dynamics of most temperate and tropical forests. Thus, the description of gap patterns is critical to forest ecology (Clark 1990; Runkle 1992), and is used to compare forest sites and to infer on important ecological processes (Connell 1978; Denslow 1980, 1987; Sheil & Burslem 2003). Among several metrics used to describe such disturbance patterns, gap frequency, size, and shape are the most important (Brokaw 1985; Clark 1990; Gagnon et al. 2004; Schliemann & Bockheim 2011). Gap

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frequency reflects the periodicity of disturbances and determines the proportion of gaps at each successional stage (sensu Whitmore 1975). Gap size reflects the magnitude of the disturbance (i.e. the type, number and size of falls – Ogden et al. 1991; Midgley et al. 1995; van der Meer & Bongers 1996a; Lima et al. 2008), which has a direct influence on gap microclimate and understorey damage levels. Gap shape also substantially influences gap microclimate and may reflect the direction and architecture of the falling tree (Brown 1993; Eysenrode et al. 1998). Therefore, although some forest species do not depend on gaps to regenerate (Hunter & Barbour 2001; Cowell et al. 2010), gap frequency, size and shape have a direct influence on the recruitment, growth and spatial distribution of many species (Popma et al. 1988; Howe 1990; Fujita et al. 2003).

Despite the importance of gaps to forest ecology, patterns associated with their frequency, size and shape remain open after more than three decades of gap research. For example, there continues to be uncertainty with regard to which statistical distribution best describes gap sizes (Foster & Reiners 1986; Lertzman & Krebs 1991; Yamamoto et al. 2011) or whether gap opening is a random or clumped process in space and time (Brokaw 1985; van der Meer & Bongers 1996a; Nuske et al. 2009). Assessments of gap shape, which has a direct influence on gap microclimate and species colonization (Howe 1990; Brown 1993; van Dam 2001), are also scarce (Lertzman & Krebs 1991; Battles et al. 1996; Eysenrode et al. 1998). Furthermore, descriptions using a large number of gaps are rare (e.g. Runkle 1982; Cuevas 2003; Kathke & Bruelheide 2010). The use of varying methods has also prevented straightforward comparisons (Clark 1990; Lima 2005), making general synthesis difficult to achieve (Schliemann & Bockheim 2011). The most common example of this methodological variation is the use of different gap delimitation methods (e.g. Brokaw 1982; Runkle 1982), which generate very different results (Popma et al. 1988; Ogden et al. 1991; van der Meer et al. 1994; Fujita et al. 2003). This lack of standardization makes it difficult to tell apart differences generated by methodological procedures and by ecological factors.

The use of appropriate statistical description is also critical to the assessment of gap patterns, as for other types of ecological data (Johnson & Omland 2004; Canham & Uriarte 2006). Today, the accessibility of modern statistical and computational tools makes it easier to avoid poor data representations that can lead to misinterpretations (Limpert et al. 2001). For instance, the use of broad class limits in frequency histograms of gap size distribution can lead to the conclusion of an exponential distribution even when the data has a mode clearly different than zero. It is difficult to assess whether these previous approaches have led to incorrect conclusions, but the use of more appropriate and standardized techniques to describe gap patterns will improve our ability to assess the variability of these patterns and the processes to which they are related (Limpert et al. 2001; Canham & Uriarte 2006). In addition, more precise gap descriptions will be useful to test predictions in forest models (Chave 1999; Dubé et al. 2001; Robert 2003), as well as the design of silvicultural systems that aim to mimic natural gap disturbance regimes (Lundquist & Beatty 2002; Schliemann & Bockheim 2011).

The main goal of the present study was to assess unresolved issues regarding forest gaps using a model selection framework (Hilborn & Mangel 1997; Johnson & Omland 2004). This approach is not entirely new but has only recently been applied in ecology (Canham & Uriarte 2006), and it is especially recommended for the analysis of data produced by non-replicable phenomena in environments that are difficult to control (Burnham & Anderson 2002), such as gap openings in forest ecosystems. We apply this framework using data from two forest types (i.e. seasonal and rain forests) within the Atlantic Forest, one of the hottest biodiversity hotspots in the world. We use a fairly large number of gaps within two permanent plots to assess gap size and shape distributions, which were obtained using the two most common methods for gap delimitations (Runkle 1992). We provide general descriptions and comparisons of the disturbance regime between the two forest plots, and compare them to the existing literature to generalize about the mechanisms controlling gap size and shape. Specifically, we investigate the following questions: (i) which statistical model best describes the gap size distribution; (ii) is there a geometric form that can serve as an effective approximation of gap shape; (iii) is there any difference in shape associated with gap delimitation methods or different types of forest; and (iv) how similar are the patterns found for the studied forests to other tropical and temperate forests?

## Methods

### Study sites

Data were collected in two 10.24-ha (320 m × 320 m) permanent plots established in 2002 in different Atlantic Forest types in the State of São Paulo, southeast Brazil. One plot is within the seasonal forest of the Estação Ecológica de Caetetus (EEC–area: 2178 ha), Gália County (22° 24′40″ S, 49°42′04″ W). The other plot is within the rain forest of Carlos Botelho State Park (PECB–area: 37 644 ha), Sete Barras County (24º10′52″ S, 47º55′29″ W). Both permanent plots are sub-divided into 256 20 m × 20 m subplots and have no recent record of large-scale human disturbances, although illegal palm-heart harvesting at PECB has been common.

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The EEC plot has a flat terrain with elevation ranging from 570 to 610 m a.s.l. The local climate is humid subtropical with dry winters (Cwa, according to the Köppen climate classification). The mean annual rainfall and temperature are 1300 mm and 21 °C, respectively. The dry season lasts from April to September, when monthly rainfall is typically < 50 mm. Frost events can also occur. The predominant plot soil types are red-yellow Acrisols (Ultisols) and red-yellow Ferrasols (Oxisols). The forest is an old-growth seasonal forest with a canopy height of 20–30 m, mean tree density of 1176 trees $ha^{-1}$ and mean basal area of 25.8 $m^2{\cdot}ha^{-1}$ (2005 plot census). The most species-rich families include Fabaceae, Myrtaceae, Meliaceae, Rutaceae and Euphorbiaceae, and the most abundant tree species are *Metrodorea nigra*, *Ocotea indecora*, *Trichilia clausenii*, *Aspidosperma polyneuron* and *Trichilia catigua*. The topography of the PECB plot is characterized by steep slopes and altitudes of 350–450 m. The local climate is classified as humid subtropical with no dry season (Cfa). Mean annual rainfall and temperature are approximately 1600 mm and 21 °C, respectively. Although there is no dry season, monthly rainfall can drop below 50 mm during El-Niño years, from May to August. Frost events are rare. The soils in this plot are Haplic Cambisols (Inceptisols) and Fluvic Neosols, and the vegetation is an old-growth tropical rain forest with a canopy height of 20–30 m (tree density and basal area: 1048 trees $ha^{-1}$ and 28.6 $m^2{\cdot}ha^{-1}$, respectively). Species composition is markedly different from that of the EEC plot (with only 34 species in common out of a total of 326 species). The most species-rich families in the PECB plot include Myrtaceae, Fabaceae, Rubiaceae, Lauraceae and Sapotaceae, and the most abundant species are *Euterpe edulis*, *Guapira opposita*, *Garcinia gardneriana*, *Bathysa australis* and *Tetrastylidium grandifolium*.

### Canopy gap census and mapping

In September 2005 (EEC) and January 2006 (PECB), the two permanent plots were surveyed for gaps in the canopy. In the EEC plot, where gap density was higher (see Results section), gaps were surveyed until a total of 8.96 ha (280 m × 320 m) had been surveyed. Gaps were defined as the death or absence from the canopy of at least a large part of a canopy tree (Runkle 1992), referred to here as *'regular gaps'*. In addition, we measured *'canopy openings'*, i.e. openings in the canopy without any evidence of dead trees or branch falls. Gaps formed by distinct episodes of tree mortality (Runkle 1992) were considered as a special type of gap, hereafter referred to as *'complex gaps'*. Regular gaps, canopy openings and complex gaps were delimited using the two most commonly used methods: (1) the vertical projection of the 'hole in the forest extending through all levels down to an average height of 2 m above ground' (i.e. 'canopy gap'(CG), Brokaw 1982); and (2) 'the ground area under a canopy opening extending to the bases of canopy trees surrounding the canopy opening' (i.e. 'expanded gap'(EG), Runkle 1982). Because these methods assess both direct and indirect effects of light entrance related to gap creation, their combination provides a characterization of both the canopy dynamics and vegetation response to gaps (Popma et al. 1988; Runkle 1992). We established a minimum diameter of 20 cm to define gap makers (i.e. trees or part of trees whose fall or death creates a gap) and canopy trees surrounding the EG limits. Methods were always applied by the same observers.

Once gap limits were set, the gap area and perimeter were estimated using the triangles method proposed by Lima (2005). For each gap, we set an arbitrary centre within the CG limits, from which CG and EG measures were taken using an ultrasonic measuring instrument (DME 201; Haglöf Sweden AB, Långsele, Sweden) attached to a 360° adaptor. Very large gaps or gaps exceeding plot limits (six at EEC and eight at PECB) were not directly measured. In these cases, EG size was determined based on the coordinates of the surrounding canopy trees using a graphic editor (ArcView GIS; ESRI Inc., Redlands, CA, US), and CG size was then estimated based on the relationship between the delimitation methods (see details below). Thus, there is no information on the perimeter or shape of these gaps. In addition, the assessment of gap reactivation events was not carried out in the very large, bamboo-dominated gaps at PECB, because the origin of these gaps is unknown (Lima et al. 2012). For all other gaps, *ArcView* was used to produce drawings of CG and EG, which are easily obtained when using the triangles method (Lima 2005).

Gap age class was estimated based on the presence/absence of identification tags on gap makers. Because the tags were placed in 2002, we divided gaps into recent (gaps younger than 3 yr old) and older gaps. When there was no complete superposition of the two disturbance events, complex gaps were subdivided into two contiguous gap fractions, each with its own age class and area. During gap age analysis, partially overlapped complex gaps were excluded, except for the estimates of turnover rate, i.e. the mean time between openings of successive gaps in the same location (Poore 1968). Turnover rate estimation was based on the mean gap disturbance rate (i.e. new gaps $ha^{-1}{\cdot}yr^{-1}$), which was obtained by dividing the total area of recent gaps by the period since plot establishment (EEC: 3.2 yr, PECB: 3.7 yr). Thus, the rate was expressed indirectly as the number of years necessary to cover the entire plot area with gaps (Hartshorn 1978). Large bamboo-dominated gaps within the PECB plot were not treated as complex gaps because their origin and dynamics are markedly different from those of regular gaps.

### Gap size and shape analysis

Model fit and selection by maximum likelihood (Hilborn & Mangel 1997; Bolker 2008) were used for the analyses of gap size and shape variables, which followed the same general framework. First, candidate models were chosen based on the existing theory and nature of the variables assessed. To describe gap size distribution, we selected the log-normal and exponential distributions, two continuous univariate distributions that are commonly used to describe gap size. We also added as candidate models the gamma and the Weibull distributions, which can also be right-skewed. The four distributions were truncated at the minimum gap size observed (CG and EG: 10 and 54 $m^2$, respectively).

Gap size distributions were compared between plots (EEC and PECB), among gap types (canopy openings, regular gaps and complex gaps) and between age classes (recent and old) to see whether the parameters of the distributions are the same or different (Bolker 2008). For each comparison, four log-normal distribution models were fitted to the data, each of which represented one of the following assumptions about the log-normal parameters: (1) $\mu$ (log-mean) and $\sigma$ (log-standard deviation) are equal in the groups being compared, (2) $\mu$ is equal but $\sigma$ is different, (3) $\mu$ is different but $\sigma$ is equal, and (4) $\mu$ and $\sigma$ are different. Comparisons among gap types and between age classes were done separately for the EEC and PECB plot, respectively. In addition, because the difference between EG and CG sizes decreases as gap size increases, a simple power-law function was used to describe the relation between the two gap delimitation methods. Thus, gap size was modelled as a log-normal variable in which the expected EG value is a power-law function of CG area ($E[EG] = aCG^k$; see Appendix S1 for mathematical details).

Gap shape assessment was based on the gap perimeter–area relationship. The observed perimeter–area relationship was compared to theoretical relationships predicted by three geometric forms, often cited as effective descriptors of gap shape (Runkle 1982; Brokaw 1985; Eysenrode et al. 1998): rectangular, triangular and ellipsoidal. Because the relationships predicted by these forms vary according to the ratio between sides or radii, the ratio between the major axis of the gap and axis perpendicular to it (i.e. the length–width ratio) was obtained from the drawings made for each gap, as described above. Therefore, the expected perimeter was modelled as a function of the gap area and length–width ratio (E[Perimeter] = $f$(Area, Ratio); Appendix S1), where ratios equal to 1 correspond to squares or circles, and ratios equal to 1.15 correspond to equilateral triangles. Because all geometric forms have a perimeter–area relationship with a fixed scaling exponent of 0.5, this parameter was not estimated. A power-law function with a free exponent was included as a candidate model to account for the fractal dimension of the gap perimeter–area relationship. The gap perimeter was also log-normally distributed; thus, the log-normal distribution was used to generate all the negative log-likelihood functions. As described above, we assessed whether models assuming different model parameters with regard to forest type, gap age and size class generated better fits to the observed perimeter values. To complement gap shape assessment, we also calculated the fractal dimension of each gap ($FD = 2 \ln(0.25\ \text{perimeter})/\ln(\text{area})$). All these procedures were performed for CG and EG.

Candidate distributions or perimeter–area functions were fitted to the data through the numerical optimization of negative log-likelihood functions (Bolker 2008); that is, optimization was used to determine the combination of parameter values that maximizes the log-likelihood function, the maximum likelihood estimates (MLE). Candidate models were compared according to their Akaike's information criteria (AIC), which is a function of the model maximum likelihood and the number of parameters of the model ($AIC = -2 \log L + 2K$, where $L$ and $K$ are the model maximum log-likelihood and number of parameters, respectively; Akaike 1973). Differences in AIC values (i.e. $\Delta$AIC) above *log*(8) were regarded as indicators of difference between two model fits (Burnham & Anderson 2002). All analyses were performed with R (v. 2.14, R Foundation for Statistical Computing, Vienna, AT) using the package *bbmle* (v. 0.9.3, Ben Bolker, http://CRAN.R-project.org/package=bbmle, 2009). The codes are given in Appendix S2 in the Supporting Information.

## Results

### Description of the disturbance regime

There were 163 gaps and canopy openings totally or partially inside the two plots, which were markedly different in gap density and total gap area. Although the EEC plot (seasonal forest) had a higher gap density, the total gap area was roughly twice as high in PECB (rain forest; Table 1). This finding was due to two major gaps dominated by woody bamboos, which together accounted for ~60% of the gap area in PECB. Canopy openings were rare (EEC and PECB: 0.8 and 0.5 openings $ha^{-1}$, respectively) and complex gaps were more abundant in EEC than in PECB (2.4 and 0.7 gaps $ha^{-1}$, respectively). Differences in CG and EG size among canopy openings, regular gaps and complex gaps were found only for the EEC plot (Appendix S3). The model assuming that old gaps are larger than recent gaps was more plausible only at EEC (differences in AIC from the second best model were $\Delta AIC = 2.5$ and 4.4 for CG and EG, respectively; complex gaps and canopy openings were excluded from this analysis). In addition,

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**Table 1.** Descriptive statistics of the 163 canopy gaps found totally or partially inside two permanent plots of seasonal forest (EEC plot) and rain forest (PECB plot). Although there was no difference in the model fit between EEC and PECB, the maximum likelihood estimates are presented separately. The results in parentheses include the large clearings dominated by woody bamboo, which were present only in PECB. The $^{x}$/is the log-normal equivalent of ± of the normal distribution. All estimates of forest turnover rate include the influence of gap reactivation events.

| Parameters | EEC | | PECB | |
|---|---|---|---|---|
| | CG | EG | CG | EG |
| $\mu$ $^{x}$/$\sigma$ (log-Normal) | 4.26 $^{x}$/0.89 | 5.49 $^{x}$/0.68 | 4.36 $^{x}$/1.01 | 5.36 $^{x}$/0.81 |
| Median ($m^2$) | 89 | 302 | 99 | 279 |
| Mode ($m^2$) | 43 | 198 | 39 | 164 |
| Range ($m^2$) | 10–1004 | 62–1619 | 17–885 (9657) | 54–1496 (16 955) |
| Total Gap area* | 13.2% | 35.6% | 7.4 (25.7%) | 16.6 (48.8%) |
| Gap Density ($ha^{-1}$) | 11.2 | | 6.2 | |
| Gap Rate ($ha^{-1}\cdot yr^{-1}$) | 1.1 | | 0.5 | |
| Turnover Rate (yr) | 79.5 | 28.3 | 151.7 (184.5) | 62.3 (90.7) |

*Values corrected by subtracting the portions of gaps that exceeded the limits of the plots.

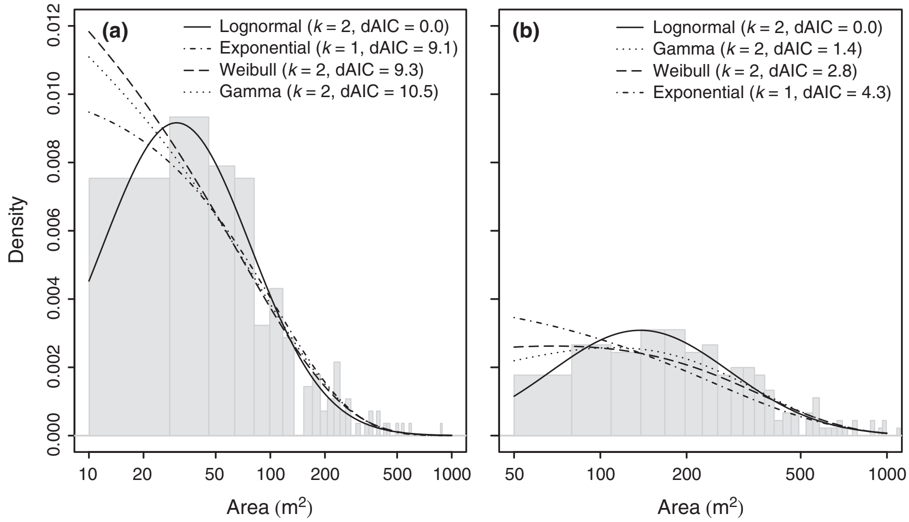

**Fig. 1.** Gap size distributions and results of model selection by maximum likelihood for (**a**) canopy gaps and (**b**) expanded gaps. The MLEs of the log-normal parameters for canopy and expanded gaps were 4.30 ± 0.94 and 5.45 ± 0.72, respectively (data from both sites together). Legend: $k$ = number of parameters of the distribution; dAIC = difference in Akaike information criterion from the minimum – AIC model (see Methods section for details). The *x*-axis is presented in log scale to aid visual inspection of the model fit.

the gap disturbance rate (i.e. number of gaps opened $ha^{-1}\cdot yr^{-1}$) in EEC was twice as high as in PECB, leading to a much faster canopy turnover rate. Because we did not consider possible gap reactivation events inside the very large gaps at PECB, the turnover rate in this plot was also estimated excluding these gaps (Table 1).

## Gap size and shape

Among the probability distributions chosen to describe canopy gap size distribution, the log-normal distribution provided the best fit for both gap delimitation methods (Fig. 1). The gamma distribution fitted poorly CG size compared to the log-normal ($\Delta AIC = 10.5$) but was a plausible model for EG ($\Delta AIC = 1.4$). This result held when the two forest plots were considered separately or when very large, indirectly measured gaps were included in the analysis (results not shown). Models assuming different gap size distributions between plots did not provide better fits (CG and EG: $\Delta AIC = 1.6$ and 1.8, respectively; Appendix S3), as shown by the overlap in the plausibility ellipses of their MLEs (Fig. 2). Thus, based on the log-normal MLEs of gap size distribution of both plots together, we can estimate that 77% of CG in both forest types is smaller than 150 $m^2$, whereas only 3% is larger than 400 $m^2$. EG smaller than 400 $m^2$ comprise the same

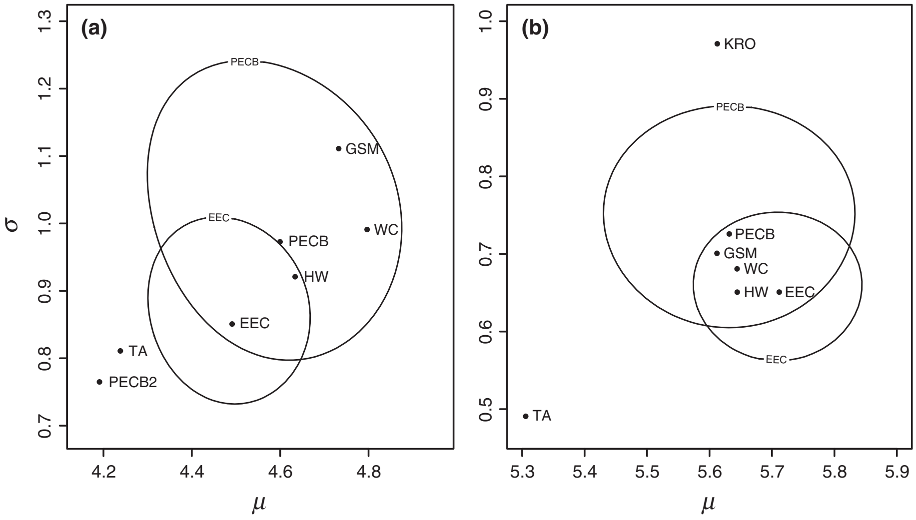

**Fig. 2.** Plausibility ellipses of the maximum likelihood estimates (MLE) of the log-normal parameters μ and σ for (**a**) canopy gaps and (**b**) expanded gaps. Points PECB and EEC are the log-normal MLEs, and ellipses around them delimit the combinations of μ and σ that provide equally plausible log-normal models for gap size distribution (i.e. $\Delta \text{AIC} \leq \mathit{log}(8)$) to describe the gap size distribution at each plot. Although there was no difference in model fit between EEC and PECB plots, their plausibility ellipses are presented separately. Gap size data were corrected by the formulas provided in Lima (2005) to allow for the parameter comparison with other studies that used the ellipse formula to obtain gap area; therefore, the MLEs presented here are different from those provided in Table 1, which were obtained using the triangles method. Other points correspond to the μ and σ estimates compiled from the following studies: GSM, WC, HW and TA = sites studied by Runkle (1982); PECB2 = log-normal fit of Lima's (2005) data; KRO = Zeibig et al. (2005).

77% of gaps (this size was equivalent to the 150 $m^2$ for the CG), whereas EG larger than 1000 $m^2$ represent only 2%.

The model assuming different log-normal parameters for CG and EG size was more plausible than the constant parameter model ($|\Delta\text{AIC}| = 128.7$), a result which is well documented and has been extensively discussed elsewhere (Popma et al. 1988; van der Meer et al. 1994). The relevant remark is that the two gap delimitation methods differ not only with respect to the location parameter μ, but also with respect to the shape parameter σ, that is, EG have larger values for μ and σ parameters ($|\Delta\text{AIC}| = 9.3$). According to the power-law model, the relationship between the two methods was $E[EG] = 15.5\, CG^{0.643}$ with log-normal parameter $\sigma = 0.359$. The model assuming different power-law parameters between plots was more plausible ($|\Delta\text{AIC}| = 4.3$), suggesting that this relationship may vary across forest types (Appendix S4).

For the perimeter–area relationship, all models based on geometric forms (triangle, rectangle and ellipse) fitted poorly to the overall data (Fig. 3), probably because geometric forms have a perimeter–area relationship based on a function with a fixed exponent of 0.5. These models were only plausible descriptors of gap shape when small and large gaps (i.e. CG > 100 $m^2$ or EG > 400 $m^2$) were treated separately. In this case, the best description for small canopy gaps was the rectangle and for large canopy and expanded gaps was the isosceles triangle (Fig. 3). Models based on the ellipse perimeter–area relationship always resulted in poor fits. The power-law model with a free exponent provided better fits when all gap sizes were pooled together, suggesting that the gaps have a fractal dimension (i.e. gaps became more irregular in shape as gap size increased). Indeed, models assuming a larger μ for the observed fractal dimension of large gaps provided a better fit for both CG ($|\Delta\text{AIC}| = 5.3$) and EG ($|\Delta\text{AIC}| = 2.1$). The maximum likelihood fits of the power-law model for the perimeter–area relationship were $E[\text{Perimeter}] = 3.373\text{Area}^{0.571}$ ($\sigma = 0.116$), and $E[\text{Perimeter}] = 3.476\text{Area}^{0.546}$ ($\sigma = 0.104$) for CG and EG, respectively. Differences in the function parameters between plots were also found for EG (Appendix S5).

For the length–width ratio distribution, the most plausible models were those assuming different log-normal parameters for each plot (CG and EG: $|\Delta\text{AIC}| = 2.6$ and 10.2, respectively), with narrower gaps in PECB than in EEC. Nevertheless, the probability of having gaps with a length–width ratio of 1 (i.e. circles or squares) was very low in both plots, at 0.035 and 0.028 for the CG and EG ratios, respectively. The probability of having gaps with a ratio of 1.15 (i.e. equilateral triangles) was slightly higher but also considerably low (0.085 and 0.088 for CG and

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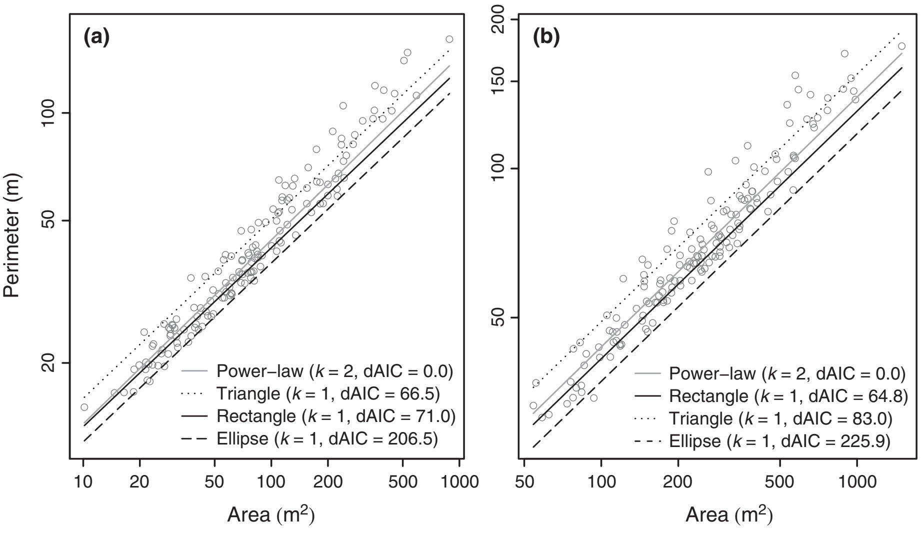

**Fig. 3.** The perimeter–area relationship in log scale for (**a**) canopy gaps and (**b**) expanded gaps. Lines represent the relationship predicted by a power-law function with a free exponent (grey line) and predicted by simple geometric forms: ellipse, triangle and rectangle (black lines; exponent fixed at 0.5). Legend: *k* = number of model free parameters; dAIC = difference in Akaike information criterion from the minimum – AIC model.

EG, respectively). In addition, CG ($\mu = 0.574$) were narrower than EG ($\mu = 0.477$; $|\Delta AIC| = 12.0$). We found no evidence of the length–width ratio being linked to gap size or age (i.e. $|\Delta AIC| < log(8)$).

## Discussion

### Inferences regarding the disturbance regime

Our findings indicate that the two forests studied here have markedly different disturbance regimes. The higher gap density in the EEC plot (seasonal forest) and the occurrence of large bamboo-dominated gaps in the PECB plot (rain forest) were the main features of their canopy disturbance patterns. Although defining the causes of differences between the two disturbance regimes is beyond our scope, we propose that these causes are related to the processes generating higher disturbance frequency at EEC and higher disturbance intensity at PECB. The higher frequency of liana tangles and strong winds in the EEC plot (R.A.F. Lima, pers. obs.) may provide explanations for the higher disturbance and repeated disturbance rates there. In the PECB plot, soils are shallower and steeper, favouring tree uprooting and, consequently, the opening of larger gaps (Lima & Moura 2008). Past landslides are possible explanations for the presence of the large bamboo-dominated gaps (Lima et al. 2012). General comparisons using data from several other sites will be needed to test these suggestions, and the analytical framework used here may provide a useful starting point for these future analyses.

### Gap size

We reported that the log-normal is an appropriate statistical distribution to model both CG and EG size distribution, for both studied sites. This statement is not new (Runkle 1982; Arriaga 1988); however, since we compared distributions simultaneously using a fairly large number of gaps (ca. 150), we can now affirm that the log-normal outperforms the exponential, gamma and Weibull distributions. For EG size, the gamma distribution was also a plausible model. Although very flexible, the gamma is generally outperformed by the log-normal when there are many large values in the data set (i.e. the log-normal has a heavier tail), a situation that may occur when sampling gaps at larger scales. Because the log-normal also describes a reasonable mechanism for gap size distribution (see discussion below), we also recommend it for EG description. The exponential distribution poorly fitted the data because gap size distribution based on field measurements typically has a mode between 50 and 80 m$^2$, which is higher than the minimum gap size (e.g. Brokaw 1982; Abe et al. 1995; Lima 2005). This mode likely results from the fact that trees large enough to reach the canopy will generally open gaps larger than the minimum gap openings or will knock down other trees.

There are theoretical reasons to suppose that the log-normal distribution of gap areas may express a general process of tropical and temperate forests. Runkle (1982) once suggested gaps as the result of random process with multiplicative effects, but he did not explicitly propose what these effects would be. Building on his suggestion, we hypothesize the following. If we assume that gap area $A_{t+1}$ is proportional to a previous gap area $A_t$ (gains and losses in gap area are proportional to $A_t$) then gap area can be given by:

$$A_{t+1} = A_t + eA_t - gA_t = (1 + e - g)A_t = \lambda A_t \qquad (1)$$

where $\lambda$ is the gap decay rate, given by the net result between the rates of gap expansion $e$ and gap closure $g$. Gaps expand by the fall of trees at a gap border or by the delayed death of injured trees inside gaps, whereas they close by lateral and vertical growth of trees around or inside gaps. Since all gaps eventually close, $g > e$ results in mean values of $\lambda < 1$. If these assumptions are valid, then the iteration of Eq. 1 over time will lead to the general model:

$$A_t = A_0 \lambda^t \qquad (2)$$

where $A_0$ is the initial gap area. It is reasonable to assume that $\lambda$ varies in time, since gap gains and losses are not constants over time (van der Meer & Bongers 1996b; Runkle 1998). Thus, the area of a single gap at any given time is the result of the multiplication of many random $\lambda$ values, which leads to a log-normal distribution when all gaps in the forest are taken together (Limpert et al. 2001). This argument is valid if $\lambda$ is close enough to 1 (i.e. small differences between $g$ and $e$) to allow enough time steps for single gap areas to vary over time. Preliminary simulations using Eq. 2, which predicts a geometrical decay in gap area over time, suggest that a minimum of 15–25 yr may be enough to generate log-normal distributions for mean $\lambda$ between 0.96 and 0.99. This is in accordance with gap closure time observed in natural forests by Ogden et al. (1991), van der Meer & Bongers (1996b) and Fujita et al. (2003). Moreover, if there are enough random $\lambda$ values to be multiplied (i.e. enough time steps) gap sizes will tend to a log-normal distribution independently of the distribution of $A_0$ and independently of the occurrence of large-scale disturbances.

Equation 2 is analogous to other natural processes, which also lead to log-normal distributions of sizes. The size of a wound, for example, also depends on the wound area at a previous stage and on a random tissue growth rate (Graham et al. 2003), and similarly to gaps, wounds close in a geometrical decay process. Similar examples can be found for fire expansion process (He & Mladenoff 1999). Further refinements can be added to Eq. 2. For instance, because gaps expand by the fall of trees at gap edges, expansion of gap area could be modelled as a function of the number of trees at a gap border (which is a function of gap area) and the forest background mortality rate (cf. van der Meer & Bongers 1996a). Thus, the larger the gap is, the higher its chance of expanding in area. We still need field data to properly estimate the distributions of $e$, $g$ and $A_0$. Nevertheless, Eq. 2 certainly provides a promising framework to build forest models to assess the effects of $e$, $g$ and $A_0$ on gap size distribution and consequently on the forest dynamics.

Given its fit to gap data and its reasonable explanation of gap processes, we suggest that future comparisons of gap size be made based on the $\mu$ and $\sigma$ parameters of the log-normal distribution. In the present study, although plots had markedly different disturbance regimes (i.e. gap frequency and density), there was no difference in their gap size distributions. In addition, the parameter estimates found here were not different from those of temperate mesic deciduous forests (except for one secondary site – see Fig. 2 for a comparison of $\mu$ and $\sigma$ between these forests). As shown in this figure, the similarity in the log-normal parameters was more pronounced for EG. This finding suggests that EG may depend more on canopy tree spacing, which may be more similar than other parameters between different forest types, and less on the size of the dead crown, tree mode of death or lateral in-growth of bordering trees (Runkle 1982; Lertzman & Krebs 1991). However, the contrasting results found for montane forests (Arriaga 1988; Lima 2005; Zeibig et al. 2005) indicate that montane forests may have different gap size distributions. This suggestion is supported by Cuevas (2003), who reported a smaller mean gap size at higher altitudes, and by Ogden et al. (1991), who reported a much smaller median canopy gap size in a montane forest (38.5 $m^2$). Higher altitude acts indirectly by reducing the mean size of trees (Cuevas 2003). Nevertheless, higher altitude is not the only reason some forests have smaller gap sizes. For example, forests with disproportioned contributions of gaps created by single tree-falls, dead standing trees and branch-falls may also have smaller mean gap sizes (Lertzman & Krebs 1991; Jans et al. 1993; Midgley et al. 1995; Kathke & Bruelheide 2010).

Unfortunately, very few studies present fits of the log-normal distribution to gap size distribution. Nevertheless, the gap size class distributions of several studies (Brokaw 1982; Lertzman & Krebs 1991; Qinghong & Hytteborn 1991; Abe et al. 1995; Midgley et al. 1995; Yavitt et al. 1995; Green 1996; Kathke & Bruelheide 2010; Yamamoto et al. 2011) confirm what seems to be a general pattern in forest ecology: canopy gaps smaller than 150 $m^2$ are very abundant (>75%) whereas gaps larger than 400 $m^2$ are rare (<5%). The exceptionally high proportion of large gaps found by Sanford et al. (1986) is probably an artefact of the large minimum gap area used (40 $m^2$). This general pattern is quite robust because markedly different types of forest with different disturbance regimes, as found in the present study, can have the same gap size distribution. Several scientific disciplines have found patterns that are

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typically log-normal and have benefitted from this distribution to adequately describe variability and its components (Limpert et al. 2001), and gap ecology appears to represent an example. There probably is (or will be) a better statistical distribution to describe gap size, especially to more closely fit the excess of larger gaps (Fig. 1). To date, however, the log-normal distribution appears to be a simple and effective description that can be made with only two relatively easy to interpret parameters.

### Gap shape

Gap shape is probably one of the least-studied gap metrics (but see Lertzman & Krebs 1991; Eysenrode et al. 1998), despite its importance to gap microclimate (Brokaw 1985; Brown 1993; van Dam 2001) and species colonization (Howe 1990). Shapes often ascribed to gaps include the ellipse (Runkle 1982), the circle (Howe 1990) and the isosceles triangle (Eysenrode et al. 1998; Robert 2003). Our results confirmed the isosceles triangle as a good descriptor of gap shape, but only for large gaps (CG > 100 $m^2$ and EG > 400 $m^2$). For small gaps, the rectangle was an effective descriptor. One possible explanation for these findings is that only large gap makers (capable of generating large gaps) would be able to create the triangular 'footprint' described by Eysenrode et al. (1998): the falling crown drags down more trees than the stem, leaving a wider gap area near the crown (triangle base) than at the base of the initiating gap maker (the tip of the triangle). Conversely, in smaller gaps formed by single tree-falls or dead-standing trees, the base and crown areas would be more proportional, leading to more rectangular shapes. In addition to differences in shape, the difference between small and large gaps can result from the more pronounced fractal dimension of larger gaps, suggesting that the gap perimeter–area relationship would be more precisely described using fractal objects. This difference imposes limitations to the use of line transects to estimate gap size distributions (Battles et al. 1996). Irregularities in gap shape probably arise from multiple gap makers falling in different directions or from gap makers with irregular crowns. However, our results have demonstrated that circular or ellipsoidal shapes are not likely (Lertzman & Krebs 1991; Battles et al. 1996; Gagnon et al. 2004) and should therefore not be used as the standard gap shape (e.g. Howe 1990).

Another main finding was that gaps with length–width ratios close to 1 were quite rare (the lengths of gaps were at least 50% larger than their widths), as found by Battles et al. (1996). This finding is important because two gaps with similar sizes but different ratios have different microclimates and soil properties (van Dam 2001), especially when the gap orientation of the larger axis is also different. Because gaps with length–width ratio close to 1 have higher light entrance than narrower gaps (ratio $\gg 1$), more rapid vertical growth and higher rate of recruitment of pioneers can be expected in gaps with length–width ratios closer to 1. Thus, gap size should not be considered alone to assess the level of influence of gaps in forest composition and regeneration (Howe 1990). Narrower gap shapes can be explained by the fact that tree height is generally higher than crown width and that the falling crowns damage other trees, creating openings not immediately above the bole of initiating gap makers (i.e. domino-wise falls; van der Meer & Bongers 1996a Eysenrode et al. 1998). It is important to stress, however, that the perimeter–area relationship of gaps varied between plots and size classes (Appendix S5). In addition, the differences in the relationship between plots found only for EG suggest a possible association between the delimitation method and the type of forest. Thus, the definition of a general gap shape should be interpreted with caution. Each gap should have its shape determined individually according to the number and type of falls and the particular architecture of the fallen trees (Brokaw 1985; Lundquist & Beatty 2002).

## Concluding remarks

Based on large samples of gaps from two types of forest we show that gap size distributions are well fitted by the log-normal distribution. This finding was true for the two most commonly used gap delimitation methods (canopy and expanded gaps). Thus, we recommend that future comparison between forests should be made based on the log-normal parameters $\mu$ and $\sigma$, which will help to make explicit predictions of changes in gap size distribution across different types of forest. Moreover, we build on the existing gap literature to propose that gap area is given by the interaction over time of random rates of gap expansion and closure, fulfilling the requirements of the multiplicative random effects of the log-normal distribution. This proposal explains the generation of skewed size distributions in the absence of large-scale disturbances and can be used to implement forest gap models.

We also show that no single geometric form can describe gap shape, which means that gaps are, in fact, fractals, and that appropriate gap size measurement methods should account for fractality of the gap perimeter. Rectangles were effective descriptors of the shape of small gaps, whereas isosceles triangles were effective descriptors of the shape of large gaps (>150 $m^2$) The frequently used ellipsoidal shape had a particularly poor performance for both size classes. We propose that these findings are due to differences in tree architecture and understorey damage patterns between large and small gap makers. In addition, we found that for both sites gaps were much longer than wide.

Because gaps of the same areas but different length–width ratios have different light entrance levels, and thus different microclimates, the mean gap area should not be considered alone to assess the influence of gaps on forest dynamics and composition.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Maximum likelihood methods used during the gap size and shape analyses.

**Appendix S2.** Basic R codes and functions used during the gap size and shape analyses.

**Appendix S3.** Overall results of the gap size comparison between plots (Table S1), gap type (Table S2) and gap age (Table S3).

**Appendix S4.** Power-law function describing the relationship between CG and EG sizes.

**Appendix S5.** Results of CG and EG shape comparison between plots, and between classes of gap size and age.

**Appendix S6.** Data set used to run the R codes given in Appendix S2.

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