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TECHNICAL COMMENT

Are the dynamics of tropical forests dominated by large and rare disturbance events?

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Abstract

A recent *Ecology Letters* paper of Fisher *et al.* (2008) utilized a modelling framework to investigate disturbance effects on forest biomass dynamics. But it contains serious methodological and conceptual errors. Associated conclusions are unlikely to be correct.

Keywords
Tropical forests, disturbance, mortality, carbon.

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Fisher *et al.* (2008) modelled the effects of the size-frequency distribution of forest disturbance events on rates of biomass accumulation, ΔAGB, in permanent sample plots. They suggested a well-documented increase in Amazonian forest biomass (Baker *et al.* 2004) to be inflated because forest dynamics are dominated by large and rare disturbance events. Although the attempt by Fisher *et al.* (2008) to place their 'disturbance hypothesis' on strict quantitative grounds is applauded, the underlying parameterisation is flawed and the conclusions almost certainty also so.

Fisher *et al.* (2008) assumed that gap-size and frequency relationships follow a power-law distribution and, in their Fig. 1, analysed already published data using ordinary least squares (OLS) regression. They obtained a scaling exponent (α) for gap frequency vs. gap area of −1.6 to −1.1 and based much of their subsequent discussion on the assumption that disturbance regimes with $\alpha > -1.6$ are realistic.

Unfortunately, this constitutes a false premise. This is because Fisher *et al.* (2008) excluded bins in original data presentations for which no gaps had been observed; treating them as missing observations rather than zero-frequency observations. As shown in Fig. 1, the more appropriate approach of pooling bin classes and thus including zero observations (Dunn 2004) leads to a more accurate and lower average probability for the occurrence of rare yet larger gaps. The Fisher *et al.*'s (2008) approach ignoring zero-frequency observations yields $\alpha \approx -1.6$. The more correct value using OLS is $\alpha \approx -2.1$. Fisher *et al.* (2008) thus seriously overestimated the frequency of occurrence of large and rare disturbance events. This in turn gave rise to an inflated view of the importance of such events in influencing forest dynamics.

Moreover, OLS methods underestimate power-law exponents, with maximum likelihood estimation (MLE) providing a more robust alternative (Goldstein *et al.* 2004). Applying the continuous power-law expression algorithm of Clauset *et al.* (2007) to the original data of Jans *et al.* (1993), we found α varying from −2.7 to −1.9 with an exponent of −3.1 obtained for the Nelson *et al.*'s (1994) blowdown data. Using MLE, Kellner *et al.* (2009) estimated α to vary between −2.7 and −2.2 for the La Selva tropical forest in Costa Rica.

Such correctly calculated values contrast with the Fisher *et al.*'s (2008) estimates of −1.6 to −1.1. These differences are critical, as Fisher *et al.* (2008) showed that effects of disturbance clustering on forest dynamics decreases dramatically between $\alpha = -1.5$ and $\alpha = -2.0$. As is evidenced in their Fig. 5, for $\alpha < -2.0$, a documented increase in Amazonian forest biomass (Baker *et al.* 2004) cannot be a simple consequence of under-sampling.

Also of concern, Fisher *et al.* (2008) represented any sampling bias as the departure of the median from the mean rather than (correctly) as the difference between the mean and the true value. This has led to a lack of transparency as to the validity of their conclusions. For example, in their Fig. 5(j–h), more than half the modelled ΔAGB were always above the median but this tells us nothing about any true sampling error. This is because for the simulations, the maximum positive ΔAGB in any 1 year can only be 1 unit, but the maximum decline in simulated ΔAGB can potentially

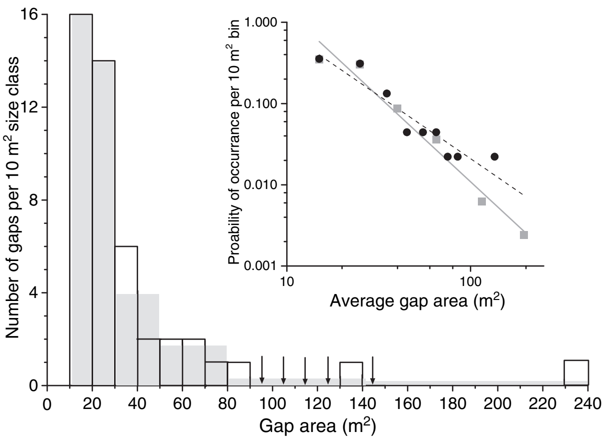

Figure 1 Statistical distribution of gap occurrence for the Para forest in Ivory Coast. This provides an extreme but clear example of the effects of ignoring bins of zero frequency when fitting a power function. Black open histogram: uniform 10-m bin widths as originally presented by Jans *et al.* (1993). Grey (revised) histogram: increasing bin width as the population frequency decreases (Dunn 2004). The latter circumvents the problem that some of the original 10-m gap classes as given by Jans *et al.* (1993) had zero observations (shown by black arrows). The inset shows the same data on a log–log sale showing the ordinary least squares (OLS) regression of Fisher *et al.* (2008) as black circles and broken line and an OLS regression where the zero observations are accounted for (grey symbols and line). Including the zero observations gives rise to a steeper negative slope and thus a much lower modelled frequency for the occurrence of larger gaps. In the original graph, only gaps < 150 m^2 were included but our analysis also includes one gap of 231 m^2 not included in Fisher *et al.* (2008).

be substantially more. Indeed, for the Fisher *et al.*'s (2008) model, the entire biomass of a 1 ha plot (*c.* 50 units) can be lost in a single year when a large-scale but infrequent disturbance occurs. Medians can never be the appropriate test metric for an analysis of sampling bias.

In any case, gap distributions as analysed by Fisher *et al.* (2008) do not reflect tree mortality. This is because up to 50% of individual tree deaths occur without any gap formation taking place (Liebemann *et al.* 1985). Thus, although the analysis of gap frequencies may provide a good indication of larger tree and clustered mortality events, they also overlook the many more frequent deaths of smaller trees and those trees that die standing. The results of Fisher *et al.* (2008) would also be more realistic if they were to have conceptualized the many differences between random (background) disturbance events attributable to natural tree death and those due to exogenous disturbances such as extreme winds (Lugo & Scatena 1996). Indeed, it is by no means clear that infrequent disturbances occurring at scales greater than the 0.05 ha values reported in Fig. 1 of Fisher *et al.* (2008) should be modelled by a simple extrapolation of a relationship observed for small-scale disturbances. Considerable caution needs to be exercised when applying power-law functions to data, even when an apparently good fit is obtained (Clauset *et al.* 2007). This is especially the case for Fisher *et al.* (2008) who extrapolated forest disturbance size and frequency relationships several orders of magnitude beyond the values at which calibrating measurements were made.

Fisher *et al.* (2008) also supported their conclusions through noting the importance of large-scale catastrophic events in shaping Amazon forest dynamics. However, using satellite data, Nelson *et al.* (1994) reported that very large blowdowns (> 30 ha) occur only *c.* 10 times y^{-1} across 3.9×10^6 km^2 of Brazilian Amazonia. Thus large-scale disturbances are a very rare phenomenon. This is especially the case when one considers that most of the blowdowns observed in Nelson *et al.* (1994) were clustered in an area centred *c.* 65°W with that area probably being unique in occurring directly in the path of occasionally long-lived Amazon squall lines (Garstang *et al.* 1998). Often water-logged and unusually shallow forest soils also occur in much of this area (Fritsch *et al.* 2006; Quesada *et al.* 2009). This may also make the forests in this region unusually susceptible to catastrophic wind damage.

In short, the conclusions of Fisher *et al.* (2008) are unlikely to be correct. Several underlying assumptions of their model are questionable – even more so are the statistics used. Thus, given our current understanding of the importance of infrequent larger disturbances on tropical forest dynamics, is it not possible to say that the documented increases in Amazon forest biomass may have been caused by a simple sample-size artefact as claimed.

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