Competition, exogenous disturbances and senescence shape tree size distribution in tropical forest: evidence from tree mode of death in Central Amazonia

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Abstract

Questions: What processes shape the size–density distribution of tropical trees? Are these processes affected by topographic position?

Location: Reserva Ducke, Central Amazonia, Manaus, Brazil.

Methods: We identified tree mode of death in a 5-yr census interval (2003–2008) in 72 1-ha permanent plots distributed over 64 km^2, and calculated the proportion of standing and fallen modes of deaths across size classes and by topographic position. Lowess regression was used to identify the dominance of standing or fallen modes across tree sizes. We used this information to separate the size–density distribution of trees into two parts hypothetically shaped by different processes. We fitted several models and tested the metabolic theory's prediction that size–density distribution scales with stem diameter to the -2 power.

Results: Most dead trees <22 cm DBH and ≥ 48 cm DBH died standing, while trees between 22 and 48 cm DBH uprooted or snapped. Mode of death varied among topographic positions. On plateaux, standing death predominated across all tree size classes, while on slopes standing death dominated for small trees (<14 cm DBH), while fallen deaths dominated for intermediate to large trees ($14 \leq$ DBH <46 cm). In valleys, fallen modes of death dominated across all size classes. Scaling and negative exponential functions with a quadratic term fitted better the size–density distribution of all trees. The scaling function fitted better the distribution of small to intermediate-sized trees while the negative exponential function and functions with a quadratic term showed the best fit to distribution of intermediate to large trees.

Conclusions: Competition is the major source of mortality for small- to intermediate-sized trees, while exogenous disturbances and senescence predominate for intermediate to large trees. Modes of death, and presumed sources of mortality, change according to topographic position, but the shape of size–density distributions is not affected, demonstrating that unknown mechanisms with different processes not assumed in the metabolic theory can produce similar distributions for tropical trees. Understanding the mechanisms that determine tropical forest structure will allow us to predict forest dynamics under future climate change scenarios.

Introduction

Tropical forests worldwide share similarities in structure, which suggests that general principles determine the size–density distribution of trees. Metabolic theory strives to explain the physiology and performance of individual organisms and the structures of populations, communities and ecosystems using principles of physics, chemistry and biology (Brown et al. 2004). This theory has been extended to tree-dominated communities, and predicts that the number of individuals scales as the -2 power of tree diameter. Enquist & Niklas (2001) argued that the form of this relationship is relatively constant over gradients of latitude, species diversity, biomass and geographic

sampling area. However, several studies have highlighted limitations of metabolic theory, for which a number of assumptions were not applicable to temperate and tropical forests (Coomes et al. 2003; Muller-Landau et al. 2006a,b; Coomes & Allen 2007a,b). Metabolic theory assumes that competition is the dominant process driving mortality across all tree sizes and that resources are equally available (energy equivalence assumption) for all trees, regardless of their size (Enquist & Niklas 2001; Enquist et al. 2009). Assuming energy equivalence is not coherent for old-growth tropical forests since canopy trees compete asymmetrically with small trees dramatically decreasing light availability in the understorey (Montgomery & Chazdon 2001). Also, the metabolic theory lacks an incorporation of exogenous disturbances, even though tropical forests suffer several types of such disturbances, such as fragmentation, wind storms, droughts, lightning, fire and herbivory by large mammals (Nelson et al. 1994; Magnusson et al. 1996; Laurance et al. 2001; Muller-Landau et al. 2006a; Chambers et al. 2007; Negrón-Juárez et al. 2010).

Coomes et al. (2003) have proposed that more than one process shapes size–density distribution of trees. They analysed large data sets from forests worldwide and from New Zealand and showed that competition shapes size–density distribution of small trees (<18 cm DBH) and exogenous disturbances shape the distribution of large trees (>18 cm DBH). Since asymmetrical competition for light may be high under the shade of large trees, a scaling relationship is expected for size–density distribution of small trees. Nonetheless, for intermediate and large trees, competition for light is low or absent (Muller-Landau et al. 2006a,b; Coomes & Allen 2007a) and exogenous disturbances and senescence are expected to kill those trees (Alvarez-Buylla & Martinez-Ramos 1992; Gale & Barfod 1999; Gale & Hall 2001; Chao et al. 2008, 2009). If intermediate and large trees are predominantly affected by exogenous disturbances, tree mortality should be constant across size classes, and a negative exponential function would best describe size–density distribution of these trees. Although well reported for temperate forests (e.g. Coomes et al. 2003; Coomes & Allen 2007a,b), no study in tropical forests has empirically determined which tree size classes have mortality driven by competition, senescence or exogenous disturbances.

Although causes of tree mortality may be difficult to identify, much information on causal factors can be inferred from tree mode of death. Trees can die standing due to pathogen attack (Franklin et al. 1987), termites (Tho 1982), senescence (Alvarez-Buylla & Martinez-Ramos 1992), liana infestation (Putz 1984), drought (Ashton & Hall 1992), lightning (Magnusson et al. 1996) and flooding (Mori & Becker 1991). Standing death is also expected for understorey and sub-canopy trees under high

asymmetric competition for light because these trees have no large canopy to stress stems. Large trees also die standing, but of the many causes that could cause trees to die slowly, senescence is argued to be the most important (Alvarez-Buylla & Martinez-Ramos 1992; Chao et al. 2008, 2009). On the other hand, trees killed by exogenous disturbances, such as wind storms, are often found uprooted or snapped (Nelson et al. 1994; Gale & Barfod 1999; Gale & Hall 2001; Chao et al. 2009). Falling trees snap and uproot other trees (Ferry et al. 2010; Toledo et al. 2012), which is an indirect effect of exogenous disturbances. Therefore, information on tree mode of death can be used to infer which tree size classes are predominantly affected by competition, exogenous disturbances or senescence.

Tree mode of death is related to topography in several tropical forests (Durrieu de Madron 1994; Gale & Barfod 1999; Gale & Hall 2001; Ferry et al. 2010; Toledo et al. 2012). Standing and snapped dead trees are found more frequently on deep and well-drained soils, while uprooting is common in valleys with waterlogged soils and on steep slopes with shallow soils. Nevertheless, few studies in tropical forests have related tree size to mode of death (Chambers et al. 2000; Gale & Hall 2001; Chao et al. 2009), and we are not aware of any study that has investigated variation in mode of death in different size classes across topographic gradients and the implications for forest structure.

Here we ask: (1) what processes shape the size–density distribution of tropical trees through effects on mortality? We hypothesized that small- and intermediate-sized trees experience high competition, while larger trees are affected mainly by exogenous disturbances and senescence. Also, (2) are these processes affected by topographic position? We hypothesized that variation in soil properties related to topography generates spatial differences in the proportions of modes of death. Standing death is expected to be frequent on plateaux while uprooting and snapping may be higher on slopes and in valleys. Thus, competition can be more important on plateaux and exogenous disturbances dominant on slopes and in valleys, which will cause differences in the size–density distribution of trees related to topographic position.

Methods

Study site

The study was carried out in Reserva Ducke, which is managed by the Instituto Nacional de Pesquisas da Amazônia (INPA). The 10 000-ha reserve is covered by primary *terra firme* tropical moist forest and is located at the periphery of the city of Manaus, Amazonas, Brazil (2°55′ S, 59°59′ W; see Toledo et al. 2011 for details). The forest has a closed canopy of 30–37 m, with emergent trees reaching 45 m and an understorey with abundant acaulescent palms. The

dominant tree families are Fabaceae, Burseraceae, Sapotaceae, Lecythidaceae, Chrysobalanaceae, Moraceae and Lauraceae (Ribeiro et al. 1999).

Annual average temperature is 26 °C and the average annual rainfall from 1979 to 2008 was 2524 mm, with a dry season from July to September, during which monthly rainfall is often around 100 mm (Coordenação de Pesquisas em Clima e Recursos Hídricos – CPCRH – INPA, unpubl. data). Topography is hilly, with elevation varying from 40 to 140 m a.s.l. (Ribeiro et al. 1999). Soil characteristics are related to topography, especially with respect to clay, which is largest in the higher parts of the relief (Chauvel et al. 1987; Castilho et al. 2006). Oxisols (*Latossolo amarelo distrófico* in the Brazilian classification system) predominate on plateaux, ultisols (*Argissolo vermelho amarelo distrófico*) are more common on slopes, and spodosols (*Espodossolo cárbico hidromórfico*) predominate in valleys, usually near water. These soils are acidic and poor in phosphorus, calcium, magnesium, sodium and potassium, while often high in aluminium (Chauvel et al. 1987).

Sampling design

A grid of 9 × 9 8-km trails, each separated by 1 km, covers an area of 64 km^2 in Reserva Ducke. Between December 2000 and February 2003, 72 1-ha permanent plots were established along the east–west trails at least 1 km from each other. These plots are long and narrow (250 m × 40 m) and follow the topographic contours, thereby maintaining a constant elevation, minimizing variation in soil type and depth to the water table within the plot (Magnusson et al. 2005; Costa & Magnusson 2010).

Castilho et al. (2006) used a hierarchical design to sample trees and palms such that sampling area was defined by DBH. Trees with DBH ≥ 1 cm were sampled in 0.1 ha (250 m × 4 m) and those with DBH ≥ 10 cm were sampled in 0.5 ha (250 m × 20 m). Large trees with DBH ≥ 30 cm were sampled in 1 ha (250 m × 40 m). The DBH was measured to the nearest 1 mm at 1.3 m above the ground. When deformities or buttresses were present, DBH was measured 50 cm above them. All trees were mapped and marked with aluminium numbered tags.

Tree mode of death data

We used mortality data from a 5-yr interval between initial plot establishment (2000–2003) and subsequent recensuses, with mortality observation in 2003–2005 and 2006–2008 (see Toledo et al. 2012 for details). Dead recruits were not included. Trees were defined as dead by the absence of leaves, sap and loss of bark. Stems that were broken or had no sap below the point of DBH measurement also were marked as dead. In the second and third census, all dead trees ≥ 4 cm DBH were classified in the following modes of death: (1) Standing – dead trees with intact crown branches on their standing stem or with crown debris symmetrically scattered around the tree base; (2) Snapped – dead trees with a broken trunk and a downed stem, often with branches attached; (3) Uprooted – the root plate is upturned with soil attached; (4) Pushed – trees that were physically under a fallen tree, large branches or lianas, and were assumed to have died at the same time as the fallen material on them; and (5) Others – pushed trees and those trees that could not be located, trees cut by humans and those unidentifiable due to advanced stages of stem decomposition.

Topographic positions

In order to assess differences in modes of death in relation to topographic position, we classified plots as plateau, slope or valley using field observation and data on altitude, slope and percentage of clay, which are available online through the Brazilian Biodiversity Research Program (*Programa de Pesquisa em Biodiversidade* - PPBio) at http://ppbio.inpa. gov.br. Altitude varied from 39.38 m a.s.l. to 109.80 m (76.06 ± 20.10 m, mean ± SD), slope varied from 0.67° to 27° (9.97 ± 7.46°) and soil clay content from 1.62% to 87.74% (47.44 ± 33.32%). Plots with altitude ≥ 65 m a.s.l. and slope <12° were classified as plateaux, those with altitude <65 m and slope <12° were classified as valleys, and plots with ground angle ≥ 12° were classified as slopes. However, not all valleys are at low altitudes. Therefore, we compared this classification to subjective impressions obtained in the field. When doubt arose as to the classification, we applied an additional criterion using percentage of clay: plots on soils with clay <20% were taken as in valleys, those with clay ≥ 60% were on plateaux and plots with clay between 20 and 60% were on slopes. Thus, 27 plots were classified as plateaux, 28 as slopes and 17 as valleys. Although the edge of some plots may encompass other topographic positions, the overlapping is minimized because of the land contour-oriented plot design. Our definition of valley plot extends to plots found on flat or concave terrain in the bottomlands, predominantly on sandy soils and generally near water. Slope plots are those on sandy to clayey soils on medium to steep slopes and plateaux plots are those on deep and well-drained clayey soils on a flat terrain on the upper parts of the relief.

Data analysis

We divided data on trees ≥ 4 cm DBH pooled from all plots in 2-cm size class bins. Least-squares regression was used to fit several models to size–density distributions of all trees

($4 \leq$ DBH < 100 cm), and separately for small and large trees, defining the point of division between small and large using information on mode of death. Additionally, we fitted models separately for trees on plateau, slope and valley. The range of size classes was restricted to trees with DBH < 100 cm for the full data set and <80 cm for data divided by topographic positions; larger size classes often have less than five stems, increasing variance and violating homogeneity of variance assumptions in least-squares regression. We tested the fit of four candidate models as suggested in Coomes et al. (2003): (1) a scaling function, Log $N = a\log dbh + c$; (2) a scaling function with a quadratic term, Log $N = a\log dbh + b\log dbh^2 + c$; (3) a negative exponential function, Log $N = a\ dbh + c$; and (4) a negative exponential function with a quadratic term, Log $N = a\ dbh + b\ dbh^2 + c$, where N is the number of stems in a size class with a determined dbh midpoint and logarithms (Log) are base 10. Thus, we assessed whether the size–density distribution of trees is likely shaped mainly by competition and is better fitted by a scale function (as predicted by the metabolic theory), or is more likely shaped by exogenous disturbances and is better described by a negative exponential function. If size–density distributions are better fitted with scaling or exponential models with a quadratic term, multiple processes (competition plus exogenous disturbances or other processes) are probably affecting the distributions. Akaike's information criterion (AIC) was used to rank the models from the best to the worst fitting; the best fitting has the smallest AIC value (Burnham & Anderson 2002). We calculated Δ_i, the differences between the AIC value of each model and the AIC of the best-fitting model, and used rules of thumb of Burnham & Anderson (2002) to evaluate models with $\Delta_i \leq 2$ as having substantial support, those with $\Delta_i > 10$ as having no support, and models with $2 < \Delta_i \leq 10$ as having marginal support. The Akaike weight (w_i) was also calculated to furnish an approximate probability for the fit of each model among all tested models.

In order to assess the contribution of each mode of death across tree sizes, the proportion of each mode of death was calculated for tree size-class bins 6 cm to 50 cm wide, such that each class included at least 100 dead trees. We also pooled dead trees in narrower size-class bins (from 2-cm to 28-cm wide for all data and from 2 cm to 46 cm for data divided in topographic positions) including at least ten dead trees, and calculated the proportion of each mode of death. For these data, we used Lowess (Locally weighted scatterplot smoothing) regression (Zuur et al. 2009) to fit smoothing lines to the relationships between DBH midpoint of each size-class bin and percentage of standing dead trees in order to determine which mode of death (standing or fallen) predominates across tree sizes. We used size-class bin midpoint as a continuous variable in analyses of covariance

(ANCOVA) to test for differences between modes of death and to test for differences in percentage of standing dead trees related to topographic position. All analyses were performed using the R Program (v. 2.8.1, R Foundation for Statistical Computing, Vienna, AT, http://www.R-project.org).

Results

Mode of death across tree sizes

The standing mode of death predominated across all tree size classes (Fig. 1, Appendix S1). Standing dead trees constituted the highest proportion of mortality ($51 \pm 3.8\%$; mean $\pm$ SD), followed by snapped ($26 \pm 3.5\%$) and uprooted dead trees ($16 \pm 6.5\%$) (ANCOVA: significant effect for mode of death, $F_{2,14} = 90.6$, $P < 0.001$). Standing dead was also higher (ANCOVA: marginal significant effect of mode of death, $F_{1,9} = 3.9$, $P = 0.08$) than the sum of snapped, uprooted and pushed dead trees ($43 \pm 9.1\%$).

The predicted values from Lowess regression for percentage of standing dead trees were higher ($53 \pm 1.5\%$; one-tailed t-test: $t = 5.3$, $df = 8$, $P < 0.001$) than 50% in size classes up to 22 cm DBH (Fig. 2), suggesting predominance of standing mode of death for smaller trees. Observed values of percentage of standing dead trees were also higher than 50% in these size classes ($52 \pm 4\%$; difference marginally significant: $t = 1.6$, $df = 8$, $P = 0.08$). Between 22 and 48 cm DBH, predicted values were smaller than 50% ($49 \pm 0.67\%$; $t = -6.8$, $df = 12$, $P < 0.001$), but for trees between 48 and 72 cm DBH the predicted values again surpassed 50% ($53 \pm 1.9\%$; $t = 4.8$, $df = 7$,
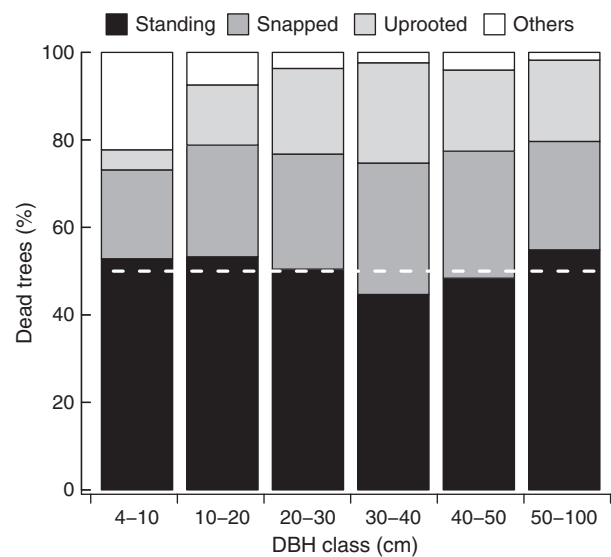

Fig. 1. Proportion of modes of death across tree size classes containing at least 100 dead trees. Data are from a 5-yr census interval pooled from 72 1-ha plots in Reserva Ducke, Central Amazonia. The white dashed line shows the point of 50% for each bar.
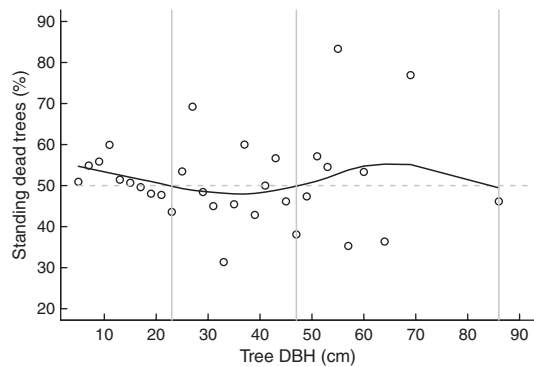
Fig. 2. Percentage of standing dead trees across tree sizes with at least ten dead trees per size-class bins varying from 2-cm to 28-cm wide. Data are from a 5-yr census interval pooled from 72 1-ha plots in Reserva Ducke, Central Amazonia. The dark line was predicted by Lowess regression with span equals to 0.75. The grey vertical lines show at which midpoints of DBH size class (23 cm, 47 cm and 86 cm) the predicted values (<50%) are closest to 50%.

$P = 0.001$). However, observed values did not differ significantly from 50% for either trees 22–48 cm DBH ($49 \pm 9.7\%$; $t = -0.6$, $df = 12$, $P = 0.29$) or trees 48–72 cm DBH ($56 \pm 17.2\%$; $t = 0.91$, $df = 7$, $P = 0.20$), suggesting contributions of processes that cause both standing and fallen death for larger trees.

Influence of topography on standing death

Percentage of standing dead trees across size classes was influenced by topographic position (ANCOVA: topographic position effect, $F_{2,56} = 8.6$, $P < 0.001$). On plateaux the standing mode of death predominated across tree size classes (Fig. 3a), while on slopes standing death dominated for small trees and fallen deaths for intermediate to large trees (Fig. 3b), and in valleys the fallen modes of death dominated across tree size classes (Fig. 3c). Predicted values from Lowess regression for percentage of standing dead trees on plateaux were higher than 50% for trees up to 32 cm DBH ($57 \pm 2.5\%$; one-tailed t-test: $t = 9.3$, $df = 12$, $P < 0.001$) as well as for trees more than 34 cm DBH ($58 \pm 6.3\%$; $t = 2.7$, $df = 4$, $P = 0.03$). Observed values showed the same pattern ($57 \pm 5.1\%$; $t = 5$, $df = 12$, $P < 0.001$ for trees up to 32 cm DBH; $60 \pm 5.9\%$; $t = 3.6$, $df = 4$, $P = 0.01$ for trees >34 cm DBH). On slopes, for small trees (<14 cm DBH) the predicted ($53 \pm 2.2\%$; $t = 3.3$, $df = 4$, $P = 0.02$) and the observed ($54 \pm 4.6\%$; marginally significant: $t = 2$, $df = 4$, $P = 0.06$) values were higher than 50%, and for trees between 14 and 46 cm DBH, the predicted ($44 \pm 2.4\%$; $t = -9$, $df = 11$, $P < 0.001$) and the observed ($44 \pm 6.7\%$; $t = -3.3$, $df = 11$, $P = 0.003$) values were smaller than 50%. In the valleys, the highest percentage of standing dead trees
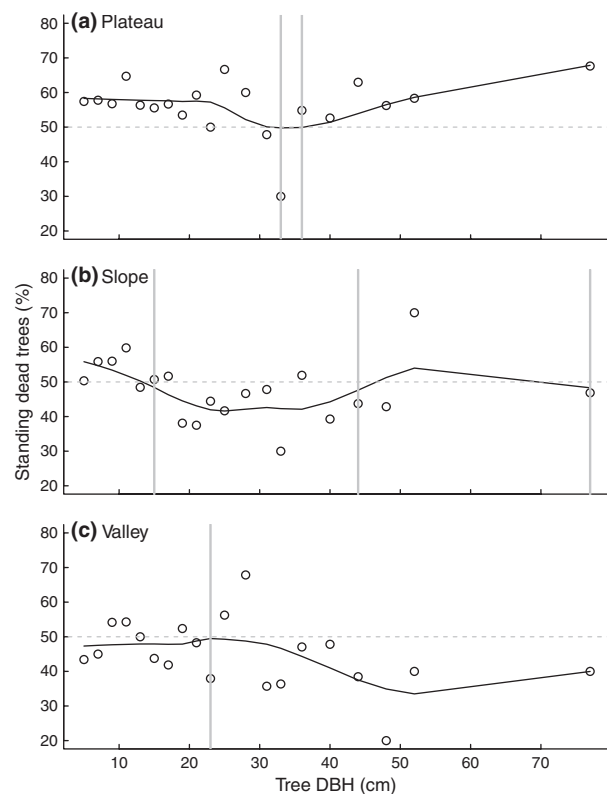

Fig. 3. Percentage of standing dead trees across tree sizes with at least ten dead trees per size-class bins varying from 2-cm to 46-cm wide. The percentages were calculated in three topographic positions: (**a**) plateau (**b**) slope and (**c**) valley. Data are from a 5-yr census interval pooled from 72 1-ha plots in Reserva Ducke, Central Amazonia. The numbers of 1-ha plots on plateaux, slopes and valleys were 27, 28 and 17, respectively. Dark lines were predicted by Lowess regressions with span equals to 0.75. The grey vertical lines show for which midpoints of DBH size class (33 and 36 cm for plateaux, 15, 44 and 77 cm for slopes and 23 cm for valleys) the predicted values (<50%) are closest to 50%.

(49.5%) appears in the size-class bin of 22–24 cm DBH. Below and above this size-class bin both the predicted ($48 \pm 0.64\%$ below and $42 \pm 5.8\%$ above; $t < -4$, $df = 9$, $P < 0.005$) and the observed ($47 \pm 5.6\%$ below and $43 \pm 12.9\%$ above; $t < -1.6$, $df = 9$, $P < 0.07$) values were lower than 50%. However, results from Lowess for plateaux and valleys should be considered with some caution because of unequal variances across tree sizes (Appendix S2).

Size–density distribution

Neither the scaling function nor the negative exponential function provided the best fit to size–density distribution of all trees ($4 \leq DBH < 100$ cm) in Reserva Ducke (Table 1). An exponential function with a quadratic term showed the best fit ($\Delta_i = 0$), and high certainty ($P = 0.9858$) as indicated by Akaike weight (w_i). The size–

density distribution was downwardly curved on log-log axes (Fig. 4a), and the number of small trees (<14 cm DBH) was overestimated by the scaling function and underestimated by the negative exponential function (both with no support, $\Delta_i > 10$).

Since patterns in mode of death suggested more intense competition among trees with $4 \leq$ DBH < 22 cm and greater importance of exogenous disturbances and senescence effects for trees with $22 \leq$ DBH < 100 cm, we fitted models separately for these two size ranges. For small trees, the scaling function and functions with a quadratic term received high support ($\Delta_i < 2$) as best-fitting models (Fig. 4b, Table 1), and the negative exponential function received marginal support ($\Delta_i = 9.2$). Functions with a quadratic term fitted better ($\Delta_i < 2$) for larger trees (Table 1), while the negative exponential function received marginal support ($\Delta_i = 2.2$), and the scaling function was unsupported ($\Delta_i = 58.1$) and overestimated the number of trees < 34 cm DBH (Fig. 4c).
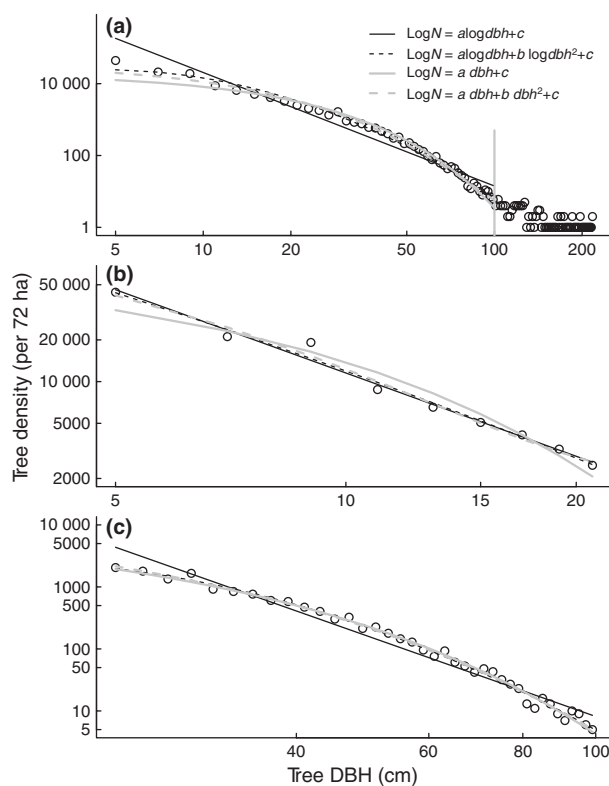

Fig. 4. Size–density distributions on log-log axes. Four models were used to fit the distributions of (**a**) all trees ($4 \leq$ DBH < 100 cm), (**b**) small ($4 \leq$ DBH < 22 cm) and (**c**) intermediate to large trees ($22 \leq$ DBH < 100 cm) from data pooled from 72 1-ha plots in Reserva Ducke, Central Amazonia. Data above the grey vertical line in (a) have less than five individuals per 2-cm size-class bin and were excluded from the analyses. Parameter estimates for each equation are in Table 1.

Size–density distributions of all trees ($4 \leq$ DBH < 80 cm) assessed separately for plateaux, slopes and valleys were best fitted ($\Delta_i = 0$) by the scaling function with a quadratic term (Fig. 5, Table 2), followed by the negative exponential function with a quadratic term ($\Delta_i < 2$ for slopes and valleys and $\Delta_i = 7.5$ for plateaux). However, only on plateaux was there no uncertainty ($P = 0.9768$) about the best-fitting model.

On plateaux, size–density distribution of trees with $4 \leq$ DBH < 32 cm was best fitted by the scaling function (Fig. 5a) and by functions with a quadratic term ($\Delta_i < 1$; Table 3), while on slopes, all models received strong support ($\Delta_i \leq 2$) to describe the distribution of trees with $4 \leq$ DBH < 14 cm DBH (Table 3, Fig. 5b). Distributions of trees with $32 \leq$ DBH < 80 cm DBH on plateaux (Fig. 5a) and of trees with $14 \leq$ DBH < 80 cm DBH on slopes (Fig. 5b) were better described by the negative exponential function and the version of this function with a quadratic term ($\Delta_i < 2$; Table 3). In valleys, the scaling function and the version of this function with a quadratic term fitted better ($\Delta_i \leq 2$) the distribution of trees with $4 \leq$ DBH < 24 cm DBH, while the two functions with a quadratic term and the negative exponential function fitted better ($\Delta_i < 2$) the distribution of trees with $24 \leq$ DBH < 80 cm DBH (Table 3, Fig. 5c). No certainty ($P < 0.65$) was given to any model.

The scaling exponent for size–density distribution of all trees was smaller than -2 (exponent = $-3.16 \pm$ SE = 0.12; $t = 9.67$, $df = 46$, $P < 0.001$), but differed over size classes. For large trees, the exponent was much smaller than -2 (exponent = -4.28 ± 0.131; $t = 17.4$, $df = 37$, $P < 0.001$), but approximated -2 for small trees (exponent = -1.996 ± 0.094; $t = -0.04$, $df = 7$, $P = 0.52$), consistent with metabolic theory's prediction.

Scaling exponents for all trees on plateau, slope and valley, treated separately, were smaller than -2.6 (and significantly lower than -2; $t > 6$, $df = 36$, $P < 0.001$), giving no support to the metabolic theory's prediction. However, scaling exponents for smaller trees on plateau (-2.02 ± 0.068), slope (-2.08 ± 0.261) and valley (-1.83 ± 0.113) were not different from -2 ($t = -1.5$ to 0.31, $df = 3$ to 12, $P > 0.3$), but exponents for large trees were smaller than -2 (exponents < -3.5; $t > 10$, $df = 22$ to 31, $P < 0.001$).

Discussion

Mode of death across tree sizes

The dominance of standing mode of death, followed by snapping and uprooting, is similar to overall results for a plot-based analysis for the same data set (Toledo et al. 2012), but here we find consistent patterns across tree sizes. In a nearby Amazonian forest, trees killed by wind and standing dead trees were on average larger than living

Table 1. Parameter estimates and model selection statistics for models describing size–density distributions. Four models were used to fit the distributions of all trees and small and large trees in which the point of division between both was 22 cm DBH. Least-squares regression was used to fit the models and the best-fitting model was chosen using Akaike's information criterion (AIC). Models are ranked from the best to worst according to AIC values. Δ_i is the difference in AIC between each model and the best-fitting model, and w_i is the Akaike weight, which provides an approximate probability that a given model shows the best fit.

| Size–density distribution	Model	df	$a \pm 1$ SE	$b \pm 1$ SE	$c \pm 1$ SE	r^2	AIC	Δ_i	w_i
All trees (4 ≤ DBH < 100 cm)	$LogN = a\,dbh + b\,dbh^2 + c$	45	-0.052 ± 0.0023	0.00014 ± 0.000022	4.56 ± 0.052	0.99	-77.8	0.0	0.9858
	$LogN = a\log dbh + b\log dbh^2 + c$	45	2.63 ± 0.405	-1.99 ± 0.14	3.52 ± 0.286	0.99	-69.3	8.5	0.0142
	$LogN = a\,dbh + c$	46	-0.038 ± 0.00073		4.29 ± 0.043	0.98	-48.2	29.6	<0.0001
	$LogN = a\log dbh + c$	46	-3.16 ± 0.12		7.47 ± 0.194	0.94	11.5	89.3	<0.0001
Small trees (4 ≤ DBH < 22 cm)	$LogN = a\log dbh + c$	7	-1.996 ± 0.094		6.06 ± 0.103	0.98	-22.7	0.0	0.5070
	$LogN = a\log dbh + b\log dbh^2 + c$	6	-1.27 ± 1.112	-0.35 ± 0.543	5.70 ± 0.553	0.99	-21.3	1.4	0.2540
	$LogN = a\,dbh + b\,dbh^2 + c$	6	-0.15 ± 0.022	0.0028 ± 0.00084	5.30 ± 0.130	0.99	-21.1	1.5	0.2339
	$LogN = a\,dbh + c$	7	-0.075 ± 0.006		4.89 ± 0.084	0.96	-13.5	9.2	0.0051
Large trees (22 ≤ DBH < 100 cm)	$LogN = a\log dbh + b\log dbh^2 + c$	36	9.87 ± 1.232	-4.15 ± 0.361	-2.45 ± 1.042	0.99	-93.0	0.0	0.4453
	$LogN = a\,dbh + b\,dbh^2 + c$	36	-0.040 ± 0.003	0.000048 ± 0.000024	4.24 ± 0.085	0.99	-92.8	0.2	0.4041
	$LogN = a\,dbh + c$	37	-0.035 ± 0.00051		4.08 ± 0.033	0.99	-90.8	2.2	0.1505
	$LogN = a\log dbh + c$	37	-4.28 ± 0.131		9.46 ± 0.231	0.97	-34.9	58.1	<0.0001
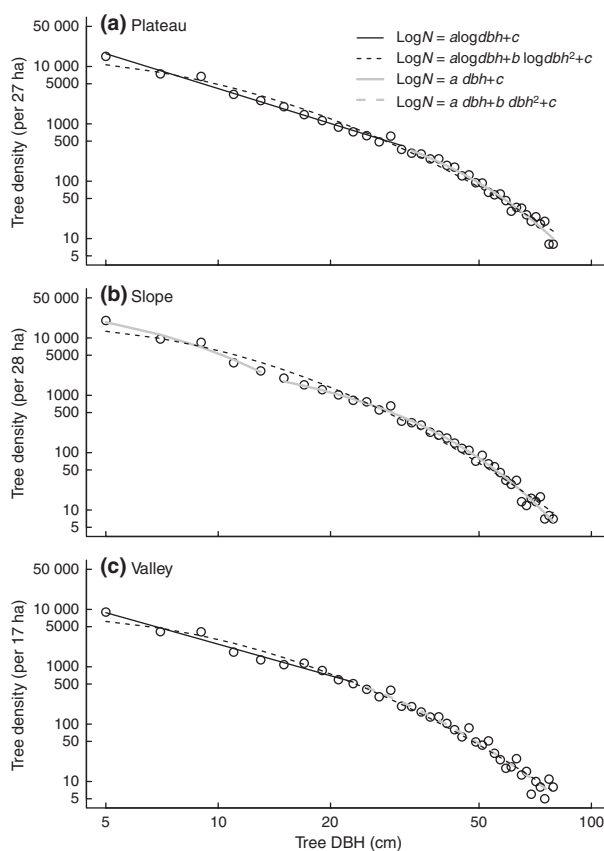
Fig. 5. Size–density distribution on log-log axes in three topographic positions. Distributions are from trees with $4 \leq$ DBH <80 cm from (**a**) 27 1-ha plots on plateaux, (**b**) 28 on slopes and (**c**) 17 in valleys in Reserva Ducke, Central Amazonia. Lines denote only the best model for each distribution of all trees and for parts of the distribution separated (in 32, 14 and 24 cm DBH for plateaux, slopes and valleys, respectively) based on information about mode of death. Parameter estimates of each equation are in Tables 2 and 3.

trees, while trees killed in treefalls were smaller than living trees, indicating size-specific differences in mortality related to mode of death (Chambers et al. 2000). Also, the relationship between size and mode of death is dependent on site characteristics. Large trees often die standing in northeastern Amazonian forests (Venezuela), while they frequently uproot in Western Amazonia (Peru) due to differences in wood density, soil and climate (Chao et al. 2009). Northeastern forests are under a stable climate, soils are poor and well drained and wood density is high, but western forests are constantly disturbed, soils are young and wood density is low. In Andalau forest (North Borneo), standing death predominated on well-drained soils

Table 2. Parameter estimates and model selection statistics for models describing size–density distributions in three topographic positions. Four models were used to fit the distributions of all trees with $4 \leq DBH < 80$ cm from 27 1-ha plots on plateaux, 28 on slopes and 17 in valleys in Reserva Ducke, Central Amazonia. Least-squares regression was used to fit the models and the best-fitting model was chosen using Akaike's information criterion (AIC). Models are ranked from the best to worst according to AIC values. Δ_i is the difference in AIC between each model and the best-fitting model, and w_i is the Akaike weight, which provides an approximate probability that a given model shows the best fit.

Topographic Position	Model	df	$a \pm 1$ SE	$b \pm 1$ SE	$c \pm 1$ SE	r^2	AIC	Δ_i	w_i
Plateau	$\text{Log } N = a \log dbh + b \log dbh^2 + c$	35	1.30 ± 0.432	-1.43 ± 0.155	3.82 ± 0.291	0.99	-63.3	0.0	0.9768
	$\text{Log } N = a\, dbh + b\, dbh^2 + c$	35	-0.056 ± 0.0035	0.00021 ± 0.000041	4.16 ± 0.065	0.98	-55.8	7.5	0.0232
	$\text{Log } N = a\, dbh + c$	36	-0.038 ± 0.0011		3.89 ± 0.050	0.97	-36.5	26.8	<0.0001
	$\text{Log } N = a \log dbh + c$	36	-2.67 ± 0.096		6.41 ± 0.150	0.96	-18.1	45.2	<0.0001
Slope	$\text{Log } N = a \log dbh + b \log dbh^2 + c$	35	1.78 ± 0.498	-1.70 ± 0.178	3.70 ± 0.335	0.99	-52.5	0.0	0.6516
	$\text{Log } N = a\, dbh + b\, dbh^2 + c$	35	-0.059 ± 0.0038	0.00021 ± 0.000044	4.28 ± 0.069	0.99	-51.3	1.3	0.3484
	$\text{Log } N = a\, dbh + c$	36	-0.042 ± 0.0011		4.01 ± 0.051	0.98	-34.2	18.3	0.0001
	$\text{Log } N = a \log dbh + c$	36	-2.94 ± 0.112		6.77 ± 0.176	0.95	-5.8	46.7	<0.0001
Valley	$\text{Log } N = a \log dbh + b \log dbh^2 + c$	35	1.66 ± 0.499	-1.59 ± 0.179	3.41 ± 0.336	0.98	-52.3	0.0	0.5737
	$\text{Log } N = a\, dbh + b\, dbh^2 + c$	35	-0.059 ± 0.0037	0.00024 ± 0.000043	4.0 ± 0.069	0.98	-51.7	0.6	0.4263
	$\text{Log } N = a\, dbh + c$	36	-0.039 ± 0.0012		3.69 ± 0.055	0.97	-29.4	22.9	<0.0001
	$\text{Log } N = a \log dbh + c$	36	-2.75 ± 0.107		6.28 ± 0.168	0.95	-9.4	43.0	<0.0001

across tree size classes, but on poorly drained soils, standing death was predominant only for smaller trees (<36 cm DBH), while uprooting was frequent for larger trees (Gale & Hall 2001). Variation in predominance of modes of death across tree sizes related to site differences indicates that processes shaping size–density distribution of trees are not constant across forests, which explains in part deviation from metabolic theory's prediction (Coomes et al. 2003; Muller-Landau et al. 2006a).

Evidence for competition, exogenous disturbances and senescence

We showed that standing death predominated for trees <22 cm DBH in Reserva Ducke, corroborating the hypothesis that competition shapes size–density distribution of small and intermediate trees. For these trees, the metabolic theory's prediction was held, as the scaling exponent was not different from -2. However, functions downwardly curved on log-log axes also showed a good fit, indicating that other processes than competition are affecting small- to intermediated-sized trees. Indeed, 34% of dead trees <20 cm DBH died fallen, showing that mechanical disturbances may also influence those trees.

Competition for light can slow growth of intermediate-sized trees (15–25 cm DBH) exposed to high densities of taller individuals (Coomes & Allen 2007a) and liana–tree competition has stronger negative effects on growth of trees with sun-exposed canopies (Ingwell et al. 2010). Also, intermediate-sized trees may compete for nutrients (Coomes & Allen 2007a) and water in the dry period, resulting in standing death (Gale & Barfod 1999; Gale & Hall 2001).

Standing dead trees represented less than half of all dead trees between 22 and 48 cm DBH in Reserva Ducke; therefore, exogenous disturbances may act more intensely on those trees. In agreement with this hypothesis, functions downwardly curved on log-log axes and the negative exponential function fitted better the size–density distribution of intermediate to large trees. Trees that reach the canopy are more exposed to wind and may be vulnerable during storms. In a nearby forest, trees killed by wind are on average larger than live trees (Chambers et al. 2000), suggesting that intermediate to large trees are prone to be killed by wind and rain. However, senescence rather than exogenous disturbances or competition is probably the major cause of mortality for trees more than 48 cm DBH, which died mostly standing and decreased in number more than predicted by the metabolic theory. Further, wind and rain are often proximal causes of death and kill trees already weakened by pathogens, drought, flooding or competition (Brokaw 1985; Franklin et al. 1987; Coomes & Allen 2007b). Proximal causal agents of death may have an influence on different modes of death. Chao et al. (2009) detected that a previous decrease in growth can precede both standing death and uprooting, but this depends on site characteristics and species traits. Slow-growing trees die standing in forests on nutrient-poor and well-drained soils with a stable climate, and trees are uprooted on nutrient-rich and poorly structured soils under an unstable climate. Nonetheless, despite the uncertainties around ultimate causes of death as interpreted from proximal mode of death, exogenous disturbances and senescence emerge as the main causes of death for intermediate to large trees in Central Amazonia (Chambers et al. 2000; Toledo et al. 2012).

Table 3. Parameter estimates and model selection statistics for models describing size–density distributions in three topographic positions. Four models were used to fit the distributions of small and large trees in which the point of division was determined using the percentage of standing dead trees for 27 1-ha plots on plateaux, 28 on slopes and 17 in valleys in Reserva Ducke, Central Amazonia. Least-squares regression was used to fit the models and the best-fitting model was chosen using Akaike's information criterion (AIC). Models are ranked from the best to worst according to AIC values. Δ_i is the difference in AIC between each model and the best-fitting model, and w_i is the Akaike weight, which provides an approximate probability that a given model shows the best fit.

Topographic position (size–density distribution)	Model	df	$a \pm 1$ SE	$b \pm 1$ SE	$c \pm 1$ SE	r^2	AIC	Δ_i	w_i
Plateau									
$4 \le$ DBH < 32 cm	Log $N = a$ log dbh $+ c$	12	-2.02 ± 0.068		5.63 ± 0.083	0.99	-35.4	0.0	0.3718
	Log $N = a$ log dbh $+ b$ log dbh$^2 + c$	11	-1.18 ± 0.658	-0.374 ± 0.292	5.19 ± 0.358	0.99	-35.3	0.05	0.3632
	Log $N = a$ dbh $+ b$ dbh$^2 + c$	11	-0.12 ± 0.0101	0.0017 ± 0.00028	4.68 ± 0.081	0.99	-34.7	0.7	0.2650
	Log $N = a$ dbh $+ c$	12	-0.057 ± 0.0039		4.24 ± 0.078	0.95	-16.1	19.3	<0.0001
$32 \le$ DBH < 80 cm	Log $N = a$ dbh $+ c$	22	-0.033 ± 0.001		3.64 ± 0.063	0.98	-52.9	0.0	0.5673
	Log $N = a$ dbh $+ b$ dbh$^2 + c$	21	-0.029 ± 0.010	-0.00004 ± 0.00009	3.52 ± 0.273	0.98	-51.1	1.8	0.2335
	Log $N = a$ log dbh $+ b$ log dbh$^2 + c$	21	13.45 ± 4.627	-5.11 ± 1.347	-6.13 ± 3.959	0.98	-50.7	2.1	0.1981
	Log $N = a$ log dbh $+ c$	22	-4.08 ± 0.175		8.85 ± 0.304	0.96	-40.2	12.6	0.0010
Slope									
$4 \le$ DBH < 14 cm	Log $N = a$ dbh $+ c$	3	-0.11 ± 0.012		4.82 ± 0.113	0.97	-8.2	0.0	0.4381
	Log $N = a$ log dbh $+ c$	3	-2.08 ± 0.261		5.78 ± 0.246	0.95	-6.9	1.3	0.2314
	Log $N = a$ dbh $+ b$ dbh$^2 + c$	2	-0.13 ± 0.111	0.0012 ± 0.0061	4.90 ± 0.467	0.97	-6.3	1.9	0.1686
	Log $N = a$ log dbh $+ b$ log dbh$^2 + c$	2	1.09 ± 4.158	-1.76 ± 2.292	4.38 ± 1.845	0.97	-6.2	2.0	0.1619
$14 \le$ DBH < 80 cm	Log $N = a$ dbh $+ c$	31	-0.038 ± 0.00071		3.82 ± 0.036	0.99	-71.1	0.0	0.5617
	Log $N = a$ dbh $+ b$ dbh$^2 + c$	30	-0.042 ± 0.004	0.00004 ± 0.000042	3.89 ± 0.085	0.99	-70.0	1.0	0.3362
	Log $N = a$ log dbh $+ b$ log dbh$^2 + c$	30	7.50 ± 1.108	3.51 ± 0.352	-0.74 ± 0.860	0.99	-67.7	3.4	0.1021
	Log $N = a$ log dbh $+ c$	31	-3.52 ± 0.141		7.75 ± 0.232	0.95	-21.5	49.6	<0.0001
Valley									
$4 \le$ DBH < 24 cm	Log $N = a$ log dbh $+ c$	8	-1.83 ± 0.113		5.22 ± 0.127	0.97	-20.0	0.0	0.6495
	Log $N = a$ log dbh $+ b$ log dbh$^2 + c$	7	-1.79 ± 1.318	-0.017 ± 0.629	5.20 ± 0.670	0.97	-18.0	2.0	0.2391
	Log $N = a$ dbh $+ b$ dbh$^2 + c$	7	-0.13 ± 0.027	0.0025 ± 0.00093	4.51 ± 0.168	0.96	-16.3	3.7	0.1028
	Log $N = a$ dbh $+ c$	8	-0.064 ± 0.0062		4.10 ± 0.094	0.93	-11.4	8.6	0.0086
$24 \le$ DBH < 80 cm	Log $N = a$ dbh $+ b$ dbh$^2 + c$	25	-0.051 ± 0.0095	0.00016 ± 0.000091	3.82 ± 0.232	0.97	-38.5	0.0	0.4065
	Log $N = a$ log dbh $+ b$ log dbh$^2 + c$	25	5.42 ± 3.594	-2.78 ± 1.080	0.47 ± 2.972	0.96	-38.2	0.3	0.3480
	Log $N = a$ dbh $+ c$	26	-0.034 ± 0.0014		3.42 ± 0.074	0.96	-37.1	1.3	0.2100
	Log $N = a$ log dbh $+ c$	26	-3.81 ± 0.161		8.08 ± 0.273	0.96	-33.6	4.9	0.0355

Effect of topography

The proportion of modes of death across tree sizes varies locally between topographic positions. Predominance of standing dead trees on plateaux suggests that competition is the major determinant of size–density distribution of small- to intermediate-sized trees (4 ≤ DBH < 32 cm), and that senescence is shaping size–density distribution of intermediate to large trees (32 ≤ DBH < 80 cm). In valleys, exogenous disturbances are the predominant cause of mortality for all tree sizes. On slopes, competition influences mortality only for smaller trees (4 ≤ DBH < 14 cm), while trees with 14 ≤ DBH < 46 cm are predominantly affected by exogenous disturbances.

Standing deaths are frequent on deep and well-drained soils (Gale & Barfod 1999; Gale & Hall 2001; Ferry et al. 2010) such as those found on plateaux. Strong anchorage provided by clayey soils (Dupuy et al. 2007), frequent in Reserva Ducke (Chauvel et al. 1987; Castilho et al. 2006), may enable trees to withstand uprooting by wind or falling trees. Also, trees on clayey soils on the high parts of the relief may be more susceptible to drought events (Ashton & Hall 1992) and die standing, but there has been no detailed investigation on the interaction between soil type, drought and mode of death.

In valleys, standing mode of death was less frequent for intermediate to large trees (≥ 24 cm DBH), which often died uprooted (22%). In Reserva Ducke, waterlogged soils in valleys also have high sand content (91%), which can be an additional constraint to root anchorage (Dupuy et al. 2007). Snapping of intermediate to large trees ≥ 24 cm DBH was also high in valleys (29%) in Reserva Ducke. Fungi and insects may weaken stem resistance to wind and rain and trigger stem snapping (Arriaga 1988). Wood density is a significant predictor of death by snapping (Putz et al. 1983; Chao et al. 2009). Trees with high wood density are supposed to be less prone to snap because they are less susceptible to pathogenic infections (Romero & Bolker 2008) and are more resistant to mechanical breakage (van Gelder et al. 2006). In Reserva Ducke, plot mean wood density is lower in valleys (J.J. Toledo, unpubl. data), which may contribute to increase tree snapping.

Slopes have clayey soils (Chauvel et al. 1987) with good conditions for root anchorage, but trees often uproot because crowns grow asymmetrically, searching for light in the downslope direction (Young & Perkocha 1994). Also, the shallow water table in the transition between slope and valley (Tomasella et al. 2008) can contribute to increase uprooting due to reduction of root–soil adherence. These factors may explain why trees ≥ 24 cm DBH uprooted on slopes (27%) more frequently than in valleys in Reserva Ducke.

Despite the differences in patterns of mode of death across tree sizes related to topographic position, we detected no differences in the choice of best-fitting size–density models related to topographic position (Tables 2 and 3). Since all size–density distributions were downwardly curved on log-log axes, they were described by versions of scaling and negative exponential functions with a quadratic term, indicating that more than one process is shaping size–density distributions. On plateau and slope, competition is probably the most important process for small trees, as most of them died standing, and for intermediate to large trees exogenous disturbances and senescence are more important. However, in the valley, fallen dead trees contributed to more than half of dead trees across the size spectrum. A negative exponential function should be the best fit for size–density distribution in valleys since the higher percentage of fallen deaths shows that exogenous disturbances are the preponderant source of tree mortality. Further, forests in valleys show higher mortality and less biomass than forests on slopes and plateaux (Castilho et al. 2006; Toledo et al. 2011), due to higher disturbance rates and treefall mortality (Toledo et al. 2012). Nevertheless, the similar shape of size–density distributions for all topographic positions suggests that different processes driving mortality can lead to similar size–density distributions. Therefore, assuming competitive thinning as the main source of mortality in tropical forests (Enquist et al. 2009) is not adequate even for small trees. Although the scaling exponents for small trees in all topographic positions were not different from −2, consistent with metabolic theory's prediction, competitive thinning was not the main source of mortality in Reserva Ducke. The mechanisms that contribute to the structure of tropical forests described here are not described totally by the metabolic theory.

The shape of size–density distributions

White et al. (2008) showed that cumulative distribution functions and maximum likelihood methods performed better than the linear binning method to estimate scaling exponents. They reanalysed original data used in Enquist & Niklas (2001) and found a scaling exponent closer to −2.5 using maximum likelihood, instead of −2 as found with linear binning. Despite the limitations of the linear binning method, we also found scaling exponents smaller than −2 for all trees and larger trees in Reserva Ducke; if maximum likelihood methods produced lower exponent values in the current study, this would only strengthen our interpretations.

The size–density distribution of all trees (4 ≤ DBH < 100 cm) in Reserva Ducke did not match the predictions of the metabolic theory, since the scaling exponent estimated for our data (−3.16) was much smaller than −2 (Enquist & Niklas 2001; Enquist et al. 2009). Coomes et al. (2003) also found smaller scaling exponents when reanalysing the

forest data set used by Enquist & Niklas (2001) and for a New Zealand forest data set. Also, the scaling exponent was significantly different from −2 in 13 of 14 tropical forest sites investigated by Muller-Landau et al. (2006a). The scaling function often overestimates the number of small and large individuals because metabolic theory does not incorporate higher mortality among small and large trees caused by exogenous disturbances and senescence. Therefore, tree size–density distributions are generally better represented by functions downwardly curved on log-log axes (Coomes et al. 2003; Muller-Landau et al. 2006a; present study).

In Reserva Ducke, the scaling exponent for small trees only was close to −2. However, the scaling exponent for small trees (1 ≤ DBH < 20 cm) was not different from −2 in only one of 14 tropical forest sites worldwide (Muller-Landau et al. 2006a). Metabolic theory focuses on competition as the main cause of mortality, but does not incorporate the effect of asymmetric competition on mortality and growth. Asymmetric competition between canopy trees and understorey individuals increases chances of death for stems in small size classes more than expected under competitive thinning dynamics assumed by metabolic theory (Enquist et al. 2009).

Scaling exponents for intermediate to large trees from other studies in tropical forests are often smaller than −2, probably due to disturbances not accounted for by metabolic theory (Coomes et al. 2003; Muller-Landau et al. 2006a; Coomes & Allen 2007b). Although Central Amazonian forests are not highly dynamic compared to forests of Western Amazonia (Phillips et al. 2004; Laurance et al. 2009), blowdowns (Nelson et al. 1994; Chambers et al. 2007; Negrón-Juárez et al. 2010) and droughts (Laurance et al. 2001) influence structure and composition of these forests. Studies have already reported the predominance of snapping and uprooting modes of death using long-term data from forests ca. 60 km north of Reserva Ducke (Chambers et al. 2000; D'Angelo et al. 2004). Also, high wind-driven tree mortality was reported ca. 50 km northwest of Reserva Ducke in 2005 (Negrón-Juárez et al. 2010). Therefore, storms may play a significant role in forest dynamics in Central Amazonia. Nevertheless, standing death accounted for more than 50% of dead trees in Reserva Ducke (Toledo et al. 2012), indicating that competition for light, nutrients or water may also significantly affect forest dynamics. As climate change models predict more frequent storms and droughts in the near future (Cox et al. 2008; Marengo et al. 2009), a general theory for forest structure should include factors linked to climatic disturbances.

Conclusions

Size–density distribution of trees <22 DBH is shaped mainly by sources of mortality that result in standing death, while trees ≥ 22 cm DBH are affected mainly by processes that cause uprooting and snapping. The size–density distribution of small to intermediate-sized trees was better fitted by the scaling function, while the negative exponential function and functions with a quadratic term showed the best fit to distribution of intermediate to large trees, consistent with our results for mode of death, and suggesting that competition and exogenous disturbances play important roles in shaping some parts of tree size distributions. Furthermore, mode of death, and presumably the effect of competition and exogenous disturbances changes with topographic position, but the shape of size–density distributions are almost invariant, suggesting that unknown mechanisms with different processes not assumed in the metabolic theory can produce similar size distributions for tropical trees. Understanding these mechanisms will allow us to make better predictions on forest dynamics under future climate change scenarios.

Acknowledgements

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Supporting Information

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

Appendix S1. Number of dead trees according to mode of death across tree sizes.

Appendix S2. Relationships between residuals and fitted values from results of Lowess regressions.

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