



## How much variation in tree mortality is predicted by soil and topography in Central Amazonia?

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### ABSTRACT

Tree mortality in Amazonia has been related to regional variation in soil, topography and climatic disturbances, but the magnitude of the effect of these factors on tree mortality at local and mesoscales remains poorly determined. We investigated tree mortality in 72 1-ha permanent plots spanning 64 km<sup>2</sup> of tropical moist forest in Reserva Ducke, Manaus, Brazil. Plots were censused three times (2000–2003, 2003–2005, and 2005–2008), resulting in two census intervals. The relationships of soil and topography to tree mortality were dependent on tree size. Small- and medium-sized trees ( $1 \leq \text{dbh} < 30 \text{ cm}$ ) had similar relationships of mortality with soil and topography, while large trees ( $\text{dbh} \geq 30 \text{ cm}$ ) showed different (or no) relationships. The effects of soil and topography on tree mortality also varied temporally. In the second census interval after storms, soil and topography explained about one-fourth of the spatial variation in mortality of small- and medium-sized trees ( $< 30 \text{ cm dbh}$ ), whereas no effects were detected in the first census interval. In particular, soil fertility was the most important predictor of tree mortality in the study area. Topography alone (altitude and slope) was associated with only 12% of the spatial variation in tree mortality and the magnitude of the effect of soil and topography on tree mortality also increased after storms. In general, plots on more fertile soils, on steep slopes and sandy soils in valleys showed greater tree mortality than those on plateau with well-drained clayey soils. Therefore, disturbance history and tree size should be included when scaling up tree mortality from local to regional scales. As much variation remains unexplained, other landscape features, such as watershed morphology and wind exposure, may be necessary to make more precise predictions on patterns of tree mortality in Central Amazonia.

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### 1. Introduction

Variation in tree mortality is related to soil and topography in Amazonia at regional scale (Phillips et al., 2004; Quesada et al., 2009a). Mortality is higher on the fertile soils of Western Amazonia, than on the infertile ones of Central and Eastern Amazonia. However, tree mortality variation within regions (local scale and mesoscale) is poorly understood (e.g., Williamson et al., 2000; Ferry et al., 2010). Empirical studies have shown that soil and topography influence the spatial distribution of above-ground live biomass (Laurance et al., 1999; Castilho et al., 2006) and plant species composition (e.g., Harms et al., 2001; Russo et al., 2005; John et al., 2007; Costa et al., 2005) at a mesoscale (10–100 km) in Amazonia. Nevertheless, soil and topography have small effects on decomposition and nutrient cycling processes (Luizão et al., 2004; Toledo et al., 2009). In French Guiana, differences in biomass

across topographic compartments (hilltops to bottomlands) are larger than differences in tree mortality (Ferry et al., 2010). Although some studies indicate that tree mortality may be related to specific environmental conditions, such as topographic position, slope angle, soil shear strength, soil texture, depth to water table, wind exposure and drought (e.g., Gale and Barford, 1999; Gale, 2000; Nepstad et al., 2007; Chao et al., 2009; Ferry et al., 2010), the magnitude of the effect of variables of soil and topography on tree mortality were estimated only at regional scales (Quesada et al., 2009a), and more precise estimates are required to scale up tree mortality or biomass losses from plots to large scale.

Soil fertility may affect tree mortality indirectly because light-demanding and fast-growing pioneer species are favored under higher nutrient supply (Lawrence, 2003; Ferry et al., 2010), and are more frequent in forest gaps, where soil fertility may be higher due to decomposition of debris (Denslow, 1987). Thus, large forest patches under regeneration dominated by pioneer species may suffer higher mortality by wind throw or neighboring falling trees than hard-wood species, since pioneers have low wood density

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and shorter lifespan (Alvarez-Buylla and Martinez-Ramos, 1992; Chao et al., 2008). However, nutrient effects on tree mortality are questionable because it is difficult to disentangle them from the effect of soil texture. Few studies have shown strong evidence of correlation between soil chemical properties and species composition in tropical forests (Sollins, 1998; John et al., 2007). However, Quesada et al. (2009a) found strong correlations between soil features and tree turnover rates across Amazonia, but correlations were stronger when only soil physical properties were considered. In general, the effects of fertility are easier to detect when there is large amplitude of nutrient variation (Sollins, 1998; Phillips et al., 2004; Quesada et al., 2009a), but variation in nutrient concentration also is related to soil texture.

Several studies associate tree mortality with topography (e.g., Gale and Hall, 2001; Gale and Barfod, 1999; Madelaine et al., 2007; Quesada et al., 2009a; Ferry et al., 2010), but topography in Amazonia is often a surrogate for the effects of soil because differences in elevation are not as extreme as in montane forests (Bellingham and Tanner, 2000). Higher mortality is found on lower parts of the relief due to sandy soils and shallow water table in valleys, which provide low adherence and prevent roots to penetrate deep in the soil (Madelaine et al., 2007; Ferry et al., 2010). However, slope can be a causal effect on tree mortality since trees in steeper areas can develop longer branches towards downslope, and asymmetrical crowns increase the probability of a tree falling down towards the gravity center of the crown (Young and Perkoča, 1994). Also, slow soil movement (soil creep) inducing tree trunks to curve downslope, landslides and even small wind exposure during storms and droughts can contribute to higher tree mortality on slopes (Harker, 1996; Gale and Barfod, 1999; Gale, 2000; Sasaki et al., 2000; Gale and Hall, 2001).

Spatial patterns of tree mortality, biomass, floristic composition and wood density described for Amazonia were obtained for trees with diameter at breast height (dbh)  $\geq 10$  cm (Baker et al., 2004; Phillips et al., 2004, 2009) and trees with dbh  $> 25$  cm or  $> 31.8$  cm measured in large forest inventories from FAO and Projeto RadamBrasil (ter Steege et al., 2006; Nogueira et al., 2008). However, the effect of tree size on the relationship between tree mortality and environmental variables was not evaluated. Most of analyses of tree mortality divided trees in small (dbh  $< 10$  cm) and large (dbh  $\geq 10$  cm) size classes. More recent analyses of tropical forest data have been based on a division in two other size classes (dbh  $< 18$  cm and  $\geq 18$  cm) in which the mortality of smaller trees are thought to be caused mainly by competition, whereas the mortality of larger trees are due to exogenous disturbances such as storms (Coomes et al., 2003; Muller-Landau et al., 2006). However, the effectiveness of such divisions using tree mortality has not yet been tested.

Several studies have reported marked increases in tree mortality in Amazonian forests following severe droughts (Williamson et al., 2000; Laurance et al., 2001; Nepstad et al., 2007; Phillips et al., 2009) and after climatic disturbances associated to wind and rain (blowdowns) (Nelson et al., 1994; Chambers et al., 2007). Climatic disturbances may influence the relationships of tree mortality with soil and topography, hence adding temporal variation on the predictability of tree mortality using soil and topography as surrogates. However, there are no studies of the effect of climatic disturbances on these relationships in Amazonia.

Here, we use a dataset on tree mortality and environmental variables (soil and topography) gathered in 72 1-ha permanent plots during 2000–2008 in a primary tropical moist forest in Central Amazonia to test the following hypotheses: (i) soil and topography are able to explain some of the variation in tree mortality and, (ii) the relationships of mortality with soil and topography depend on tree size. In 2005, the forest was struck by unusual storms which allow us to test the hypotheses that (iii) relationships be-

tween mortality and characteristics of soil and topography increase in magnitude following storms.

## 2. Material and methods

### 2.1. Site description

The study was carried out in the Reserva Florestal Adolpho Ducke (hereafter Reserva Ducke), which is managed by the Instituto Nacional de Pesquisas da Amazônia (INPA). The reserve (10,000 ha) 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 Supplementary Material Fig. S1). The forest has a closed canopy, with canopy height ranging from 30 to 37 m in height. Emergent trees can reach 45 m in height, and the understory is abundant with acaulescent palms. The dominant tree families are Fabaceae, Burseraceae, Sapotaceae, Lecythydaceae, 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 – CPRH – INPA, unpublished data). Topography is hilly with elevation varying from 40 to 140 m above sea level (m.a.s.l.) (Ribeiro et al., 1999). Soil characteristics are related to topography, especially with respect to clay which is greatest in the higher parts of the relief (Chauvel et al., 1987; Castilho et al., 2006). Oxisols (*Latosolo amarelo distrófico* in the Brazilian classification system) predominate on the plateaux, ultisols (*Argissolo vermelho amarelo distrófico*) are more common on the slopes and spodosols (*Espodosolo cárbico hidromórfico*) predominate in the valleys, usually near streams. All soils in Reserva Ducke are acidic and poor in phosphorus, calcium, magnesium, sodium and potassium, while often high in aluminum (Chauvel et al., 1987).

### 2.2. Sampling design

A grid of 188-km trails, each separated by 1 km, was installed in Reserva Ducke, encompassing 64 km<sup>2</sup> (Supplementary Material Fig. S1). 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 × 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 and Magnusson, 2010).

Castilho et al. (2006) used a hierarchical design to sample trees and palms (hereafter collectively called trees) in which the dbh was used to define the sampling area. Trees with dbh  $\geq 30$  cm were sampled in 1 ha (250 × 40 m), while trees with dbh  $\geq 10$  cm and dbh  $\geq 1$  cm were sampled in 0.5 ha (250 × 20 m) and 0.1 ha (250 × 4 m), respectively. 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 aluminum numbered tags.

### 2.3. Mortality data

Three censuses were undertaken: the first census was carried out when plots were established (2000–2003), the second was done between February 2003 and February 2005, and the third (thought the time interval has begun in March 2005), between August 2006 and February 2008. The first census interval, between the first and second censuses, averaged  $2 \pm 0.03$  years (mean  $\pm$  standard deviation,

range 1.98–2.21 years for the 72 plots) and the second census interval, between the second and third census, was  $3.1 \pm 0.2$  years (2.9–3.6 years). The total census interval between the first and third censuses averaged  $5.1 \pm 0.2$  years (4.9–5.8 years).

Tree mortality was determined in the second and third censuses. Trees were defined as dead by the absence of leaves, sap and loss of bark. Also classified as dead were those trees that disappeared and those whose stems had broken or had no sap below the point of dbh measurement.

The equation described by Sheil et al. (1995) was used to calculate the mortality rates for each plot:  $m = 1 - [1 - (N_0 - N_1)/N_0]^{1/t}$ , where  $m$  is given as percent of trees dead per year,  $N_0$  and  $N_1$  are the number of stems at the beginning and end of the time interval  $t$ . Tree mortality rates were calculated for the first ( $\sim 2$  years), second ( $\sim 3$  years) and total census interval ( $\sim 5$  years).

#### 2.4. Soil and topography data

Along the center of each plot, six superficial soil sub-samples (0–5 cm deep) were collected at 50-m intervals, and these were mixed to form a composite sample per plot. Soil samples were dried at 105 °C, cleaned by removing stones and fine roots and then sieved (2-mm mesh size). Soil texture and pH were measured in the Soil Laboratory of the INPA Agronomy Department and soil chemical measurements were carried out at the EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) soil chemistry laboratory in Manaus. We used 15 soil variables: clay, silt and sand (particles <0.002, 0.002–0.05 and 0.05–0.2 mm, respectively), pH, available phosphorus (P), K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup>, Cu<sup>+</sup>, Fe<sup>2+</sup>, Mn<sup>2+</sup>, Zn<sup>2+</sup>, exchangeable aluminum (Al<sup>3+</sup>) and potential acidity (Al<sup>3+</sup> + H<sup>+</sup>). More detailed descriptions of these variables are given in Castilho et al. (2006).

Altitude and slope were used as topographic variables. A professional surveyor determined altitude (m.a.s.l.) using a theodolite. Slope was estimated with a clinometer at five points along the plot and the average slope was used for each plot (Castilho et al., 2006). The data described here are available online through the Brazilian Biodiversity Research Program (Programa de Pesquisa em Biodiversidade – PPBio) at <<http://www.ppbio.inpa.gov.br/Eng/inventarios/ducke/pterrestrre>>.

#### 2.5. Statistical analyses

We used principal components analysis (PCA) to reduce the dimensionality of the 15 topsoil variables. Multiple regression analysis was used to test for the combined effects of the first two PCA resultant components (PC1 and PC2) and the topographic variables on tree mortality rates. Since altitude and the soil textural gradient (PC1) were strongly correlated ( $r = 0.82$ ;  $df = 70$ ;  $P < 0.001$ ), they were not included in the same model. Altitude and the soil fertility gradient (PC2) were not correlated ( $r = -0.15$ ;  $df = 70$ ;  $P = 0.21$ ), and slope was only moderately correlated with PC1 ( $r = -0.26$ ;  $df = 70$ ;  $P = 0.03$ ), PC2 ( $r = -0.36$ ;  $df = 70$ ;  $P = 0.002$ ) and altitude ( $r = -0.35$ ;  $df = 70$ ;  $P = 0.002$ ). We used only altitude and slope in a model to determine if topographic variables alone could explain the spatial variation in tree mortality.

We divided trees into seven dbh size classes ( $1 \leq dbh < 10$  cm, ...,  $50 \leq dbh < 60$  cm and  $dbh \geq 60$  cm) and assessed the relationships of soil and slope with tree mortality calculated for each class (minimum of five stems per plot). The significance of each model was primarily used to identify which tree size classes had mortality rates related to the environmental gradients. The standard partial coefficients ( $b$ ) of the soil gradients and slope (extracted from the regression models of each size class) were used to identify dbh size classes for which mortality rates are similarly related to the environmental gradients. The  $b$  shows the magnitude and nat-

ure (negative or positive) of the effect of the predictive variable on the response variable. We grouped the dbh size classes in which mortality was similarly related to soil and slope. For all calculations and statistical analyses we used the software R version 2.8.1 (R Development Core Team, 2008).

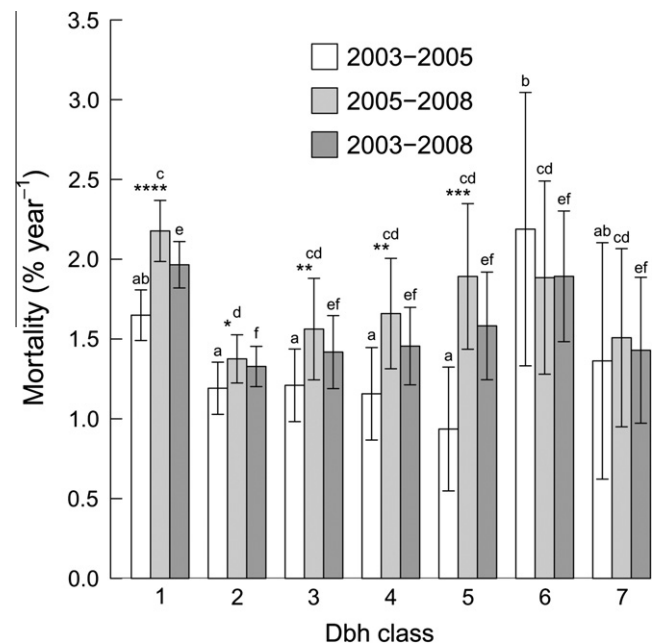
### 3. Results

#### 3.1. Soil gradients

Two soil gradients were summarized by the ordination analysis (Supplementary Material Table S1). The first axis (PC1) explained 37% of the variation of the original variables and described a textural gradient between plots with greater clay content and those with greater sand content. This axis was also positively correlated with K<sup>+</sup>, Na<sup>+</sup>, Mg<sup>2+</sup>, Al<sup>3+</sup>, Al<sup>3+</sup> + H<sup>+</sup>, Fe<sup>2+</sup> and Mn<sup>2+</sup> and negatively correlated with pH. A fertility gradient was described by the second axis (PC2), which explained 22% of the variation and was positively associated with P, K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>, Zn<sup>2+</sup>, Mn<sup>2+</sup> and pH, and negatively with Fe<sup>2+</sup>.

#### 3.2. Tree mortality and its relationship with soil and topography

There was a significant temporal variation in tree mortality. The mortality rate of all trees with  $dbh \geq 10$  cm combined was 1.39% year<sup>-1</sup> (95% CI:  $\pm 0.13$ ) for the total census interval, and 1.20% year<sup>-1</sup> ( $\pm 0.14$ ) and 1.49% year<sup>-1</sup> ( $\pm 0.17$ ) in the first and second census intervals, respectively. Tree mortality was dependent on tree size in the first (ANOVA:  $F_{6,485} = 3.20$ ;  $P = 0.004$ ), second ( $F_{6,481} = 1.97$ ;  $P = 0.07$ ) and total ( $F_{6,485} = 2.89$ ;  $P = 0.009$ ) census interval (Fig. 1). Trees with  $10 \leq dbh < 20$  cm showed substantially lower mortality than trees with  $1 \leq dbh < 10$  cm, but in general



**Fig. 1.** Mean tree mortality rates ( $\pm 95\%$  CI, vertical lines) for seven size classes ( $1 = 1 \leq dbh < 10$  cm,  $2 = 10 \leq dbh < 20$ ,  $3 = 20 \leq dbh < 30$ ,  $4 = 30 \leq dbh < 40$ ,  $5 = 40 \leq dbh < 50$ ,  $6 = 50 \leq dbh < 60$  and  $7 = dbh \geq 60$  cm) in the three census intervals. Asterisks indicate significant differences (paired  $t$ -test) between the first and second intervals ( $*P < 0.1$ ,  $**P < 0.05$ ,  $***P < 0.01$ , and  $****P < 0.001$ ). Differences among size classes within each census interval are indicated by different lower case letters (letters ab, cd and ef for the first, second and total census intervals, respectively) after Tukey HSD post hoc test.

there was a steady increase in mortality from trees with  $10 \leq \text{dbh} < 20$  cm up to trees with  $50 \leq \text{dbh} < 60$  cm, with exception of the first census interval since trees with  $40 \leq \text{dbh} < 50$  cm showed slightly lower mortality than other size classes above 10 cm dbh. Also, mortality estimates for large trees were less accurate than for small and intermediate size trees since the number of large individuals was small, less than 25 individuals  $\text{ha}^{-1}$  for trees  $\geq 40$  cm dbh (Supplementary Material Table S2).

The effects of the gradients of soil and topography on tree mortality rates were dependent on tree size and varied temporally (Supplementary Material Table S3). In the first census interval, tree mortality was weakly related to soil and topography. However, there was an increase in the effects of the gradients of soil and topography on mortality rates mainly for those trees with  $\text{dbh} < 30$  cm in the second census interval.

The standard partial coefficients extracted from the regression models for the second census interval only (Fig. 2) indicated that mortality rates in tree size classes from 1 to 30 cm dbh are mainly positively related to the gradients of fertility (PC2) and slope, and negatively related to the soil textural gradient (PC1). Therefore, trees with  $\text{dbh} < 30$  cm form a natural group of trees for which mortality rates show a similar pattern across the gradients of soil and topography. However, tree mortality in the size classes with  $\text{dbh} \geq 30$  cm either had different relationships with soil and slope than the smaller size classes, or lacked any significant relationship (Fig. 2). Mortality of trees  $\geq 60$  cm dbh was positively correlated to soil textural gradient, but this is probably an artifact of the small number of trees in this size class. Trees with  $\text{dbh} \geq 30$  cm constitute a group with different characteristics and higher variation compared to smaller trees, or they form more than one group which cannot be distinguished using the available data. Although most of the regression models were not statistically significant using mortality rates calculated for the first census interval, the patterns were quite similar to those obtained for the second interval. The total interval mirrored the pattern revealed in the second

interval (Supplementary Material Table S3). Therefore, we can separate trees into two groups that show differentiated patterns of spatial variation in mortality rates: small- and medium-sized trees ( $1 \leq \text{dbh} < 30$  cm) and large trees ( $\text{dbh} \geq 30$  cm).

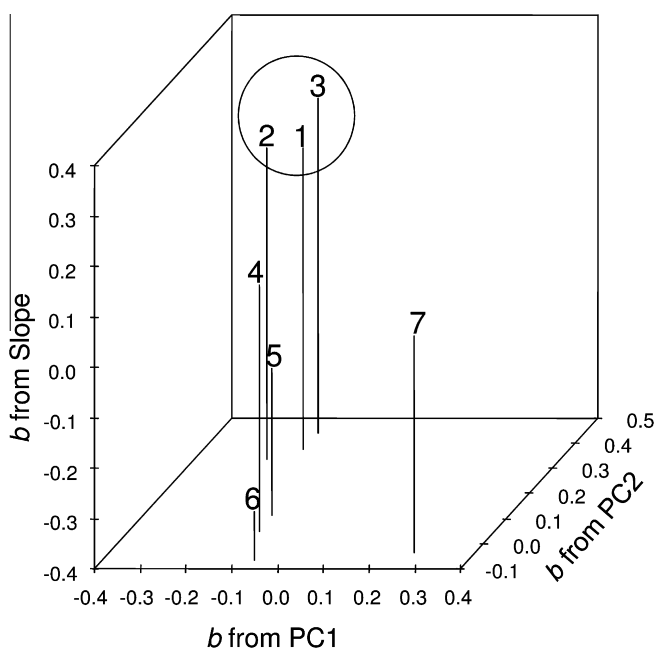
In the second census interval, the gradients of soil and slope explained 25% of the variation of the mortality of trees with  $1 \leq \text{dbh} < 30$  cm ( $F_{3,68} = 7.55$ ;  $P < 0.001$ ). The magnitude of the effect of soil fertility gradient was the greatest, followed by slope and soil texture (Table 1). Mortality rates were negatively related to the soil textural gradient ( $t = -2.23$ ;  $P = 0.03$ ), indicating lower mortality on more clayey soils (Fig. 3a). Moreover, mortality was positively related to the gradient of soil fertility ( $t = 3.67$ ;  $P < 0.001$ ) and slope ( $t = 2.12$ ;  $P = 0.04$ ), indicating higher mortality on soils with higher nutrient concentrations (Fig. 3b) and steeper slopes (Fig. 3c). The relationship between mortality and altitude also increased in the second census interval (Table 1). Altitude and slope explained only 12% of the variation in mortality of trees with  $1 \leq \text{dbh} < 30$  cm ( $F_{2,69} = 4.70$ ;  $P = 0.01$ ). Altitude was negatively related to mortality ( $t = -2.71$ ;  $P = 0.008$ ), indicating that mortality was lower on higher parts of the relief (plateaux), which have clayey soils (Fig. 3d).

The relationships between mortality and the gradients of soil and topography in the total census interval were similar to the pattern observed in the second interval, except for both a slight decrease in the variance explained and the magnitude of the effect of the gradients on mortality rates. There was no relationship between mortality rates of trees with  $\text{dbh} \geq 30$  cm and the gradients of soil and topography in any census interval (Table 1).

## 4. Discussion

### 4.1. The importance of soil and topography

We were able to separate small- and medium-sized trees ( $1 \leq \text{dbh} < 30$  cm) from large trees ( $\text{dbh} \geq 30$  cm) utilizing as a criterion the magnitude of the effect of soil and topography on tree mortality. Coomes et al. (2003) claimed that competition determines mortality of trees with  $\text{dbh} < 18$  cm, and exogenous disturbances affect mortality of trees with  $\text{dbh} \geq 18$  cm. We believe that similar factors (perhaps competition is the most important) are driving mortality of trees above the size limit suggested by Coomes et al. (2003) since similar relationships of mortality with soil and topography were found in all size classes with  $\text{dbh} < 30$  cm. Exogenous disturbances, however, may be the main factors affecting mortality of trees  $\geq 30$  cm dbh because those trees are expected to be more exposed to wind and storms. Furthermore, asymmetrical competition for light is expected to be negatively related to tree size (Coomes and Allen, 2007). The small number of larger trees added high variation in mortality rates and may have contributed to separate large trees from small trees. However, on average, trees  $30 \leq \text{dbh} < 40$  cm and  $40 \leq \text{dbh} < 50$  cm had more than 50 and more than 20 individuals per plot, respectively (Supplementary Material Table S2), which is reasonable for estimates of mortality (Condit et al., 1995), and even so these tree classes were separated from smaller trees and showed weak relationship with soil and topography. Only mortality of trees with  $1 \leq \text{dbh} < 30$  cm was significantly related to soil and topography. Therefore, the relationships between tree mortality and variables of soil and topography in local and regional scale in Amazonia (Phillips et al., 2004; Quesada et al., 2009a; Ferry et al., 2010) may be restricted to some tree size-classes. Moreover, spatial distribution patterns of mortality of large trees (Phillips et al., 2004, 2009), and perhaps biomass, floristic diversity and wood density (Baker et al., 2004; ter Steege et al., 2006; Nogueira et al., 2008), may not be extended to small trees.



**Fig. 2.** Relationships between standard partial regression coefficients ( $b$ ) of gradients of soil texture (PC1), soil fertility (PC2) and slope obtained from multiple regressions on mortality rates calculated in seven tree size classes (1 =  $1 \leq \text{dbh} < 10$  cm, 2 =  $10 \leq \text{dbh} < 20$ , 3 =  $20 \leq \text{dbh} < 30$ , 4 =  $30 \leq \text{dbh} < 40$ , 5 =  $40 \leq \text{dbh} < 50$ , 6 =  $50 \leq \text{dbh} < 60$  and 7 =  $\text{dbh} \geq 60$ ) in the second census interval (2005–2008). The circle shows tree size classes which have similar relationships of mortality with soil and slope.



**Table 1**

Results of multiple regressions relating gradients of soil texture (PC1), soil fertility (PC2), slope, and topography alone (altitude and slope), to tree mortality rates in two dbh size classes in three census intervals: first (2003–2005); second (2005–2008); and total census interval (2003–2008)

Classes of dbh (cm)	Census interval	Standard partial slope ( <i>b</i> )				<i>F</i> <sup>a</sup>	<i>P</i>	<i>R</i> <sup>2</sup>
		PC1	PC2	Slope	Altitude			
≥1, <30	1st	-0.15	0.10	0.11	-0.08	1.10	0.36	0.05
	1st			0.09		0.65	0.53	0.02
	2nd	-0.24**	0.42****	0.25**		7.55	<0.001	0.25
	2nd			0.05	-0.33***	4.70	0.01	0.12
	Total	-0.23**	0.36***	0.23 <sup>†</sup>		6.45	<0.001	0.22
	Total			0.07	-0.28**	3.76	0.03	0.10
≥30	1st	-0.13	0.05	0.12	-0.12	0.88	0.46	0.04
	1st			0.09		1.12	0.33	0.03
	2nd	-0.10	0.06	-0.01		0.30	0.83	0.01
	2nd			-0.04	-0.09	0.24	0.79	0.01
	Total	-0.16	0.09	0.07		0.91	0.44	0.04
	Total			0.07	-0.16	0.97	0.38	0.03

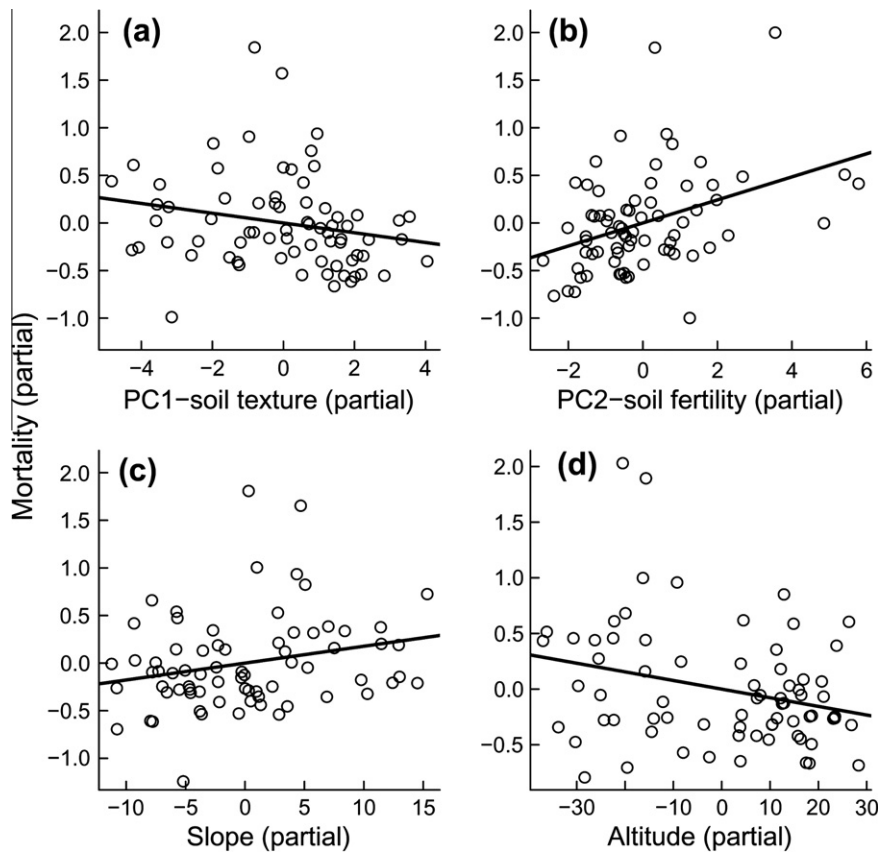
<sup>†</sup> *P* < 0.1.

\*\* *P* < 0.05.

\*\*\* *P* < 0.01.

\*\*\*\* *P* < 0.001.

<sup>a</sup> Three and 68 degrees of freedom for models of soil and slope, and two and 69 for models of altitude and slope.



**Fig. 3.** Partial regressions testing for the effects of gradients of (a) soil texture, (b) soil fertility, (c) slope and (d) altitude on mortality rates of small- and medium-sized trees (1 ≤ dbh < 30 cm) in the second census interval (2005–2008). Partial of altitude are from a model only with slope. Lines denote significant partial regressions.

The gradient of soil fertility was positively related to tree mortality and the magnitude of the effect of this variable on mortality was higher than soil texture and slope. However, there is little support for the hypothesis that topsoil nutrient variations have a strong effect on forest dynamics at a local scale. Topsoil nutrient concentration is influenced by vegetation that produces organic

matter and recycles nutrients using a dense root system coupled with mycorrhiza to absorb nutrient promptly. Nevertheless, how deep roots can reach in tropical forests is dependent on soil type, since roots are found deeper in clayey soils than in sand soils (Schenk and Jackson, 2002). Although we are not sure about the effect of nutrients on root depth, biomass and production of fine

roots (<5 mm in diameter) are higher in poor soils than in fertile ones (Espeleta and Clark, 2007). Trees produce possibly more roots in poor soils to maximize nutrient uptake, thereby the stems stand better against uprooting in poor soils than in rich ones. However, there is evidence of high root proliferation in organic soil layers because these horizons have higher nutrient concentration and larger water-holding capacity (Schenk and Jackson, 2002), but this probably occurs when soils are poor in the deeper horizons.

The effect of soil fertility on forest dynamics is easier to detect when nutrient concentration varies widely over large areas (Sollins, 1998; Phillips et al., 2004; Quesada et al., 2009a). The strong correlations between soil fertility and tree turnover rates across Amazonia found by Quesada et al. (2009a) can be supported by the hypothesis that competition and disturbances shape community structure together. On more fertile soils, fast-growing species are adapted and dominate the community because nutrient availability is not a limiting factor to growth and competition for light is high. Fast-growing species invest little in structure and have light wood which make stems more susceptible to breakage (Alvarez-Buylla and Martinez-Ramos, 1992; Chao et al., 2008). However, the disadvantages of light wood species to resist against stem breakage are under question since a fat trunk of low-density wood can achieve greater strength at lower construction cost than a thin trunk of high-density wood (Larjavaara and Muller-Landau, 2010). Furthermore, light-wood species such as *Cecropia* have shorter lifespan (Alvarez-Buylla and Martinez-Ramos, 1992). Therefore, higher mortality on fertile soils may not be entirely related to wood density. Fertile soils in Amazonia are also frequently shallow, some contain rocks on the surface layers and others have high concentration of plithite which often changes irreversibly to hard pans (Quesada et al., 2009b). These soils do not provide good adherence and prevent roots to penetrate deeply. Furthermore, these characteristics make difficult to determine which factor may affect tree mortality. However, in Reserva Ducke, deep soils are generally infertile independent of soil type and topography (Chauvel et al., 1987). Therefore, tree mortality is possibly influenced by other unmeasured variables associated with soil fertility, such as depth to the water table, structural properties of the soil or topographical characteristics of the watershed.

A combination of several factors may explain the positive relationship of tree mortality with slope in Reserva Ducke. Soil creep induces tree trunks to curve downslope and may weaken tree root systems, causing trees to uproot on slopes (Harker, 1996; Sasaki et al., 2000). Although slopes also have clayey soils in Reserva Ducke, the water table is shallow in the transition between slope and valley (Tomasella et al., 2008), which reduces root adherence to soil due to high moisture. Also, trees may uproot more often on slopes due to shallow soils and high wind exposure (Gale and Barfod, 1999; Gale, 2000; Gale and Hall, 2001).

The negative relationship between tree mortality and the soil textural gradient indicated lower mortality on clayey soils on plateau than on sandy soils in valleys. Although clayey soils are frequent on plateau, which are more exposed to wind, they provide better anchorage for roots (Gale and Hall, 2001; Dupuy et al., 2007). In a nearby site, Williamson et al. (2000) did not detect a significant relationship between clay content and tree mortality. However, variation in clay content (30–66%) was smaller than reported in our study (2–88%), probably because they had no sites near streams. Moreover, soil variation within plots could be high since they used 1-ha square plots. Higher tree mortality in valleys is probably due to a high sand content and shallow water table (Tomasella et al., 2008; Quesada et al., 2009a). Empirical and simulation studies have shown that tree root systems are less resistant to uprooting in sandy soils (Dupuy et al., 2007). In tropical moist forests, productivity of fine roots and rooting depth are smaller in sandy soils and soils with

high moisture content (Schenk and Jackson, 2002; Espeleta and Clark, 2007). Therefore, uprooting is more frequent in poorly drained soils (Gale and Barfod, 1999). As waterlogging is frequent in valleys, the tree root system may be weakened or killed due to low oxygen levels in soils (Drew, 1997). Even tree species adapted to hypoxic conditions may have depressed metabolism under flooding (Fernandez et al., 1999), weakening root systems and favoring uprooting.

#### 4.2. Implications for estimates of tree mortality

We found that tree mortality is size dependent, as has been reported in other tropical forests (e.g., Condit et al., 1995, 1999; Muller-Landau et al., 2006; Nepstad et al., 2007). In Barro Colorado Island, Panamá, Condit et al. (1995) showed that mortality of smaller trees ( $1 \leq \text{dbh} < 10 \text{ cm}$ ) was higher than larger trees ( $\geq 10 \text{ cm dbh}$ ). In Pasoh, Malaysia, and also in BCI, a more detailed study which used small size class bins revealed that mortality varied mainly among small trees (1–5 cm dbh), while mortality was fairly constant among larger trees (Condit et al., 1999). An analysis of large datasets from 10 different tropical forests sites showed that mortality in general has a U-shaped pattern where smaller and larger trees show higher mortality than intermediate size trees (Muller-Landau et al., 2006). However, variation in mortality through size class can increase due to climatic disturbances. In East-Central Amazonia, Nepstad et al. (2007) showed that increase in mortality after an experimental drought was higher for larger trees ( $\geq 30 \text{ cm dbh}$ ) than for smaller ones, while mortality rates were constant in a control plot. In contrast, Chao et al. (2008) found a constant mortality probability through size classes in a highly dynamic forest in northwestern Amazonia, whereas mortality increased from smaller to larger trees in northeastern Amazonia. However, the absence of relationship between size and mortality in northwestern Amazonia can be attributed to the absence of trees <10 cm dbh and to the small number of plots (five 1-ha plots). Laurance et al. (2009) also found no relationship between mortality and size for trees  $\geq 10 \text{ cm dbh}$  from a large dataset in a nearby Central Amazonia forest. Therefore, the range of tree size can influence the patterns of mortality across size classes.

The dependence of the relationship of mortality with soil and topography on tree size may be a consequence of differences in tree attributes through the mesoscale and across size classes. Variation in tree composition related to soil and topography at mesoscale is well reported for tropical forests (e.g., Clark et al., 1999; Russo et al., 2005; John et al., 2007). Analyses of tree community in Reserva Ducke also suggests changes in composition from plateau to valley (C.V. Castilho, unpublished data). Tree compositional differences may be linked to changes in wood density and other attributes such as lifespan, tolerance to drought and waterlogging, and light requirements, which in turn can directly influence tree mortality. Wood density as indicator of susceptibility of tree death is questionable (Larjavaara and Muller-Landau, 2010), but gradients of tree resistance to drought and waterlogging may be intrinsically related to changes in tree community composition. A substitution of tree species through size classes may occur, thereby increasing the differences in tree mortality across size classes. Chao et al. (2008) suggested that tree attributes may be stronger determinants of tree mortality than environmental drivers such as soil, topography and climatic disturbances. However, it is difficult to disentangle environmental effects from the effects of species attributes since changes in species composition are influenced by environmental features. The pattern we found is most likely to be an outcome from the effect of soil, topography and past disturbances on tree species distribution through the local scale, and also from the direct effect of factors like wind, drought and waterlogging on tree mortality.

The ability of soil and topographic variables to predict the variation in tree mortality increased from the first census interval to the second census interval. The higher mortality after 2005 in Central Amazonia may not be entirely attributable to hydrological stress as it was suggested by Phillips et al. (2009). Marengo et al. (2008) showed that Central Amazonia did not suffer anomalies in precipitation. In Reserva Ducke, precipitation in the dry season of 2005 (June–October) was a total of 478 mm, which is only 20% lower than the average (616 mm) observed for that season over 30 years (CPCRH – INPA, unpublished data). In contrast, the severe El Niño drought of 1997 resulted in precipitation 40% lower than the average in the same region (Williamson et al., 2000; Laurance et al., 2001). In the latter census interval (2005–2008), blowdowns increased forest disturbance across Central Amazonia (Chambers et al., 2007). A higher increase in the mortality of large trees might be expected under the effect of storms. However, large trees are mainly found on deep clayey soils in Reserva Ducke (Castilho et al., 2006), which provide better tree anchorage. Even a small increase in mortality of large trees can cause significant increase in the mortality of smaller ones. In fact, the proportion of snapped or uprooted small trees (<30 cm dbh) doubled in the second census interval, probably as a result of a slight increase in the mortality of larger trees (J.J. Toledo, unpublished data). Empirical studies have shown that multiple death events are important in Amazonian forests (Gale, 2000; Ferry et al., 2010) and may contribute with half of the mortality of trees killed from stem breakage (Chao et al., 2009). The temporal variation in the relationships between tree mortality and variables of soil and topography indicates the need for constant monitoring of mortality. Although our study encompassed a short time period, our findings indicate that patterns found at local or regional scales (Phillips et al., 2004; Quesada et al., 2009a; Ferry et al., 2010) may change over time and relationships found today may differ from those that will occur under potential changes in climate.

Ferry et al. (2010) showed that mortality increased by a factor of two from hilltops to bottomlands in French Guiana. Scaling up mortality from local to regional scales using this type of information is difficult due to the need for previous classification of the landscape in topographic classes, which implies in loss of information. The approach used by Quesada et al. (2009a) and in the present study (using continuous variables of soil and topography rather than categorical variables) is suitable for modeling of mortality over the landscape because the magnitude of the effect can be estimated with higher precision.

Quesada et al. (2009a) showed that soil physical properties explained 52% of the variation in tree turnover at regional scale in Amazonia. However, variation in soil types is far greater than in Reserva Ducke. Here we showed that variation in tree mortality explained by soil and topography is low for trees <30 cm dbh, even after an increased power following storms, only 25% of variation in tree mortality was explained for trees <30 cm dbh, and the models were not significant for trees  $\geq$  30 cm dbh. When only altitude and slope were used, less variation was explained (12%). Tree size-classes <30 cm dbh in which mortality was related to soil and topography contribute for about 98% of all stems, but represent only nearly 40% of above ground tree biomass in Central Amazonia (Nascimento and Laurance, 2002; Castilho et al., 2006). As most of the biomass is stored in trees  $\geq$  30 cm dbh, in which mortality was not related to soil and topography, the prediction of biomass loss is also limited. Therefore, it is not possible to estimate mortality with high precision in Central Amazonia using variables of soil and topography. Other landscape features such as watershed morphology and wind exposure, may be necessary to improve predictions of spatial variation in tree mortality.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.03.039.

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