

Growth and wood density predict tree mortality in Amazon forests

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Summary

1. Tree mortality is an important process in forest ecology. We explored the extent to which tropical tree death is a predictable outcome of taxon and individual level properties by means of mixed-species logistic regression, for trees ≥ 10 cm in diameter. We worked in two lowland forest regions with markedly different floristic composition and dynamic regimes – the high wood density, low-mortality northeastern (NE) Amazon (in eastern Venezuela), and the low wood density, high-mortality northwestern (NW) Amazon (in northern Peru).

2. Among those genera that are shared between regions there were no detectable regional differences in mortality rates. This suggests that floristic compositional differences are a major driver of the twofold regional contrast in stand-level mortality.

3. In NE forests, mortality risk of individual trees is best predicted by low taxon-level wood density, slow relative growth, and large size, reflecting phylogenetically determined life-history strategy, physiological stress and senescence.

4. In NW forests, trees with low wood density and slow relative growth are also at most risk, but probability of death is independent of tree size, indicating that senescence is unimportant in this region.

5. *Synthesis.* This study shows that despite fundamental floristic and dynamic differences between the two Amazonian regions, mortality risk can be predicted with mixed-species, individual-based statistical models and that the predictors are remarkably similar, such that tree growth and wood density both play important roles.

Key-words: forest dynamics, logistic regression, relative growth rate, tree mortality, tree size, tropics, wood density

Introduction

Tree death influences forest nutrient cycling, structure, composition and dynamics. As such, an understanding of its causes can help to reveal how forests function (Harmon *et al.* 1986; Franklin *et al.* 1987; Lugo & Scatena 1996). In the most biodiverse and productive forest region of all, Amazonia (Gentry 1988; Field *et al.* 1998; Malhi *et al.* 2004), previous studies have shown strong gradients in mortality (Phillips *et al.* 2004), wood density (Baker *et al.* 2004; ter Steege *et al.*

2006), biomass (Baker *et al.* 2004; Malhi *et al.* 2006), productivity (Lewis *et al.* 2004a; Malhi *et al.* 2004) and species diversity (ter Steege *et al.* 2006). Mortality and growth rates of trees ≥ 10 cm diameter are lower in eastern than western Amazonia (Lewis *et al.* 2004a; Phillips *et al.* 2004). These dynamic differences are mirrored by a northeast–southwest (Guiana Shield to the lowland Andean foreplain) gradient in wood density and species diversity, such that the low-mortality forests have much denser wood and lower diversity than the high-mortality forests (Baker *et al.* 2004; ter Steege *et al.* 2006). This suggests floristic composition could be a driving factor of forest dynamics.

While the mechanisms driving tree death across Amazonia remain unclear, they are likely to reflect both taxon- and individual-level properties. Most tropical species exist at very low density (number of stems per unit area), so it is rarely

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Table 1 Proposed mortality predictors for the high-mortality northwestern (NW) and the low-mortality northeastern (NE) Amazonian forests

Attribute	High risk factor		Region	
			NW	NE
A. Taxon wood density	Low wood density	Fast-turnover strategy	✓	✓
B. Tree growth	Slow growth	Physiological stress	Minor effect	✓
C. Tree size	Small	Competition	Minor effect	✓
	Large	Senescences/structural instability	Minor effect	✓

feasible to build species-specific regression models (Vanclay 1990). However, different species have distinct life-history strategies; wood density, in particular, may indicate mortality risk (Nascimento *et al.* 2005; King *et al.* 2006b; van Gelder *et al.* 2006). This trait reflects trade-offs between resource acquisition (e.g. short life span and fast growth in height and stem size) and survival investment (e.g. longevity, slow growth and damage-resistant stems; Loehle 1987; Nascimento *et al.* 2005; King *et al.* 2006b; van Gelder *et al.* 2006). Wood density is also under substantial phylogenetic control (Baker *et al.* 2004; Chave *et al.* 2006), and may be used to reflect intrinsic, taxon-based properties.

Various individual-level attributes may also influence the probability of tree death, notably tree vigour (van Mantgem *et al.* 2003) and size (Yao *et al.* 2001). Slow growing trees are likely to be unhealthy, exhibit physiological stress and be prone to infection or death (van Mantgem *et al.* 2003; Bigler *et al.* 2004). Size partially reflects the age or competitive ability of a tree (Vanclay 1990; Yao *et al.* 2001). Most temperate-zone studies confirm that tree vigour and/or tree size are good indicators of mortality (e.g. Monserud & Sterba 1999; Yao *et al.* 2001; Coomes & Allen 2007).

Within tropical forests, a number of previous studies have described relationships between tree mortality and tree vigour and size, but these are based on a single variable (e.g. Lieberman & Lieberman 1987; Swaine *et al.* 1987; Carey *et al.* 1994; Korning & Balslev 1994), a single census (Barlow *et al.* 2003), or use discrete species functional groups (Vanclay 1990; Davies 2001). To evaluate the various causes of mortality within and across regions, it may be preferable to use a multivariable statistical analysis approach, a longer term census data set, and a trait continuum. To tackle these concerns in particular, we applied methodological and data improvements for tropical studies, notably: (i) logistic regression (Hosmer & Lemeshow 2000), in which the features of tree status (alive or dead) are modelled as the binary response variable in a multivariate regression; (ii) a newly compiled tree-by-tree data base from the RAINFOR project, consisting of long-term census records (Malhi *et al.* 2002; Peacock *et al.* 2007); (iii) a newly compiled species wood density data base (Baker *et al.* 2004; Chave *et al.* 2006) to provide a continuous predictor variable to represent the inherent functional strategy for individual trees.

We aimed to determine the relationships between tree attributes and mortality in two regions of Amazonia with distinct forest characteristics – one with higher average wood density, lower diversity, slower growth rates, and lower mortality rates, and another hyper-diverse region with lower wood density species, faster growth rates and higher mortality rates. For each region, we developed and evaluated multivariate mixed-species logistic regression models of tree mortality, using both taxon- and individual-level predictors. A logical corollary of the Amazon mortality gradient is that in the fast turnover forests trees die younger, and therefore death may be more stochastic and less dependent on individual performance than in the slow turnover forests. We therefore hypothesized that mortality predictors should differ between regions with contrasting dynamic regimes, such that in high-mortality forests rapid tree turnover would reflect *species functional composition*, but in low-mortality forests the *individual physiological status* of trees would also be important. We predicted that in high-mortality forests tree death is largely stochastic and explicable only by wood density (a proxy for a taxon-level functional strategy). We also predicted that in low-mortality forests tree death is less stochastic and is pre-determined by wood density, slow growth rate (an indicator of poor vigour) and small size (an indicator of competitive disadvantage) or large size (an indicator of senescence or structural instability) (Table 1).

Methods

STUDY PLOTS

We examined mortality processes in plots located in northwestern (NW) and northeastern (NE) Amazonia. We selected those plots located in mature, humid, unflooded tropical forests and with three or more censuses (each census interval is 4–5 years; period is 1996–2005 in the NW and 1971–2004 in the NE) in order to compute growth rates through time.

In NW Amazonia, we worked in five *c.* 1-ha plots in northern Peru. Two plots at Allpahuayo (ALP-A and ALP-B, 3°57'S, 73°26'W) were established in 1990 (Vásquez Martínez & Phillips 2000). One plot at Yanamono (YAN-01, 3°26'S, 72°51'W), and two plots at Sucusari (SUC-01 and SUC-02, 3°26'S, 72°54'W) were established in 1983 and 1992, respectively (Vásquez Martínez 1997). Soils are predominantly ultisols (Malhi *et al.* 2004). The climate is

almost aseasonal (on average < 1 month receiving < 100 mm rain), and annual precipitation ranges between 2600 and 3000 mm (Phillips *et al.* 2004). Dominant families in terms of basal-area are Fabaceae, Myristicaceae, Moraceae, Lecythidaceae and Euphorbiaceae. These include some of the most diverse forest plots in the world (up to 300 species > 10 cm diameter per hectare, e.g. ter Steege *et al.* 2003).

In NE Amazonia we worked in three 0.5-ha plots in eastern Venezuela – two at El Dorado (ELD-01/02 and -03/04, 6°05'06"N, 61°24'W) and one at Rio Grande (RIO-01/02, 8°06'N, 61°41'W). These plots were established in 1971 (Veillon 1985). Soils consist of igneous-derived inceptisols and ultisols (Carey *et al.* 1994). There is a short-dry season of < 1.5 months; annual average precipitation is between 2500 and 3200 mm (Carey *et al.* 1994). Dominant families are Fabaceae, Burseraceae, Chrysobalanaceae, Lecythidaceae and Euphorbiaceae. In both regions, all trees larger than 10 cm diameter have been tagged, measured, identified and regularly re-measured since the plots were established.

STAND-LEVEL MORTALITY PATTERNS

Stand-level mortality rate was estimated by the exponential mortality coefficient $\lambda = \ln(N_b/N_e)/(t_e - t_b)$ (Sheil *et al.* 1995), where N_b and N_e are population counts at the beginning time t_b and at the end time t_e . This function is obtained by integration of the differential equation, $dN/dt = -\lambda N$, assuming an exponential population decline. To account for potential long-term and inter-annual variation and control for possible census-interval effects (Lewis *et al.* 2004b), we standardized to two different lengths of census interval of *c.* 4 and *c.* 10 years.

INDIVIDUAL-LEVEL MORTALITY MODELS

Statistical models of individual-level mortality were developed by logistic regression (Hosmer & Lemeshow 2000), which describes the conditional probability P that a tree dies ($Y = 1$) during a given period of time, given predictors X_1, \dots, X_n as:

$$P(Y = 1 | X_1, \dots, X_n) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n)}} \quad \text{eqn 1}$$

where the linear function, $\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n$ (analogous to similar terms in linear regression) is termed the *logit link function*. We estimated parameters of this regression by maximizing the logarithm of the likelihood function (see Appendix S1 in Supplementary Material).

We tested for **taxon-** and **individual-level** mortality predictors only. Stand-level parameters, such as stand basal area (Vanclay 1990) or soil properties (Shen *et al.* 2001) were not used, because the small number of plots would risk over-parameterizing the individual-tree mortality model (Monserud & Sterba 1999).

Models were developed in a four-step process (Fig. 1). In Step 1, we prepared candidate predictor variables, classified into three groups, **A. Taxon wood density**, **B. Tree growth** and **C. Tree size**. Wood density is a measure of functional behaviour. Tree growth variables are based on long-term, prior-to-death diameter measurements and represented by both absolute and relative growth rates. Tree size variables are prior-to-death diameter measurements and represented by diameter, basal area and relative size. In Step 2, we selected the best predictor for each group using univariate logistic regression and Akaike weights (w_i), derived from Akaike's information criterion (AIC) (Akaike 1973). In Step 3, a full multivariate model was developed using these selected variables. Finally, in Step 4, the Akaike weights (w_i) were applied to evaluate the set of full and reduced models. Details of each step are described in turn.

Step 1: Data processing

Tree status (alive or dead) was coded at census time t_2 (see Table S1 in Supplementary Material for census dates and periods used). Only trees with diameter measurements at both t_0 and t_1 , prior to census time t_2 , were selected for modelling. Palms (Arecaceae) were excluded, because they lack secondary growth and have different growth patterns than dicotyledonous trees (Heywood *et al.* 2007).

For NW Amazonia, we used the most recent census period, 1996–2005 ('C'), with an average (\pm SD) census interval of 4.1 ± 0.0 years between t_1 and t_2 . The NE Amazonian plots are small but have long monitoring sequences. To maximize the sample size, we pooled data from three non-overlapping periods: 1971–81 ('A'), 1981–91 ('B'), and 1994–2004 ('C'), with an average census interval of 4.6 ± 0.2 years between t_1 and t_2 . Considering census interval as a factor in the models did not lower the value of AIC, so chronological variation in mortality models in this study was not pronounced.

Three attribute groups are:

Taxon-level predictor

Attribute A. Taxon wood density

A1. ρ_i (g cm⁻³): Wood density of tree i was estimated from the RAINFOR functional trait data set, consisting of wood density values for more than 2000 Neotropical species (Baker *et al.* 2004; Chave *et al.* 2006; Lopez-Gonzalez *et al.* 2006). In cases where species-level wood density was unavailable, Neotropical averages for the genus (28% of 4748 individuals), or family (4%) were used. For unidentified trees (3%) and trees in families without wood density data (< 1%), the average wood density of the available species in the plot, on a stem basis, was used. We assumed that there is no within-species variation in wood density across regions, as in Chave *et al.* (2006).

Individual-level predictors

Attribute B. Tree growth

- B1.** GR (mm per year) = $((DBH_{t_1} - DBH_{t_0}) \times 10)/(t_1 - t_0)$: annual diameter growth rate prior to death. Following Sheil *et al.* (1995), we excluded trees with diameter growth rates < -2 or > 40 mm year⁻¹, as representing possible measurement error.
- B2.** $BAGR$ (cm² per year) = $((BA_{t_1} - BA_{t_0}) \times 10\,000)/(t_1 - t_0)$: annual basal area growth rate prior to death.
- B3.** $relGR$ (% per year) = $((GR/10)/DBH_{t_0}) \times 100$: relative diameter growth rate prior to death. Trees with $relGR < -1\%$ year⁻¹ were excluded.
- B4.** $relBAGR$ (% per year) = $((BAGR/10\,000)/BA_{t_0}) \times 100$: relative basal area growth rate prior to death.

Attribute C. Tree size

- C1.** DBH (cm): diameter at 1.3 m (or above buttresses) of tree at time t_1 .
- C2.** BA (m²): basal area of tree at time t_1 .
- C3.** DBH (cm) & DBH^2 (m²): transformed diameter, diagnostic of a U-shaped mortality probability.
- C4.** RS = $(\Sigma BA \text{ of trees smaller than the target tree } i)/(\Sigma BA \text{ of all trees})$: relative size of tree i in a plot at time t_1 . For the biggest tree in a plot RS is close to 1, and for the smallest tree it is 0 (cf. Vanclay 1990; Monserud & Sterba 1999).

Step 2: Variable selection

To prevent potential collinearity, only one variable was selected from each attribute category, using univariate logistic regression, and evaluated by AIC (Akaike 1973) (see Appendix S1). Low AIC indicates a relatively better model than other models. Ranking

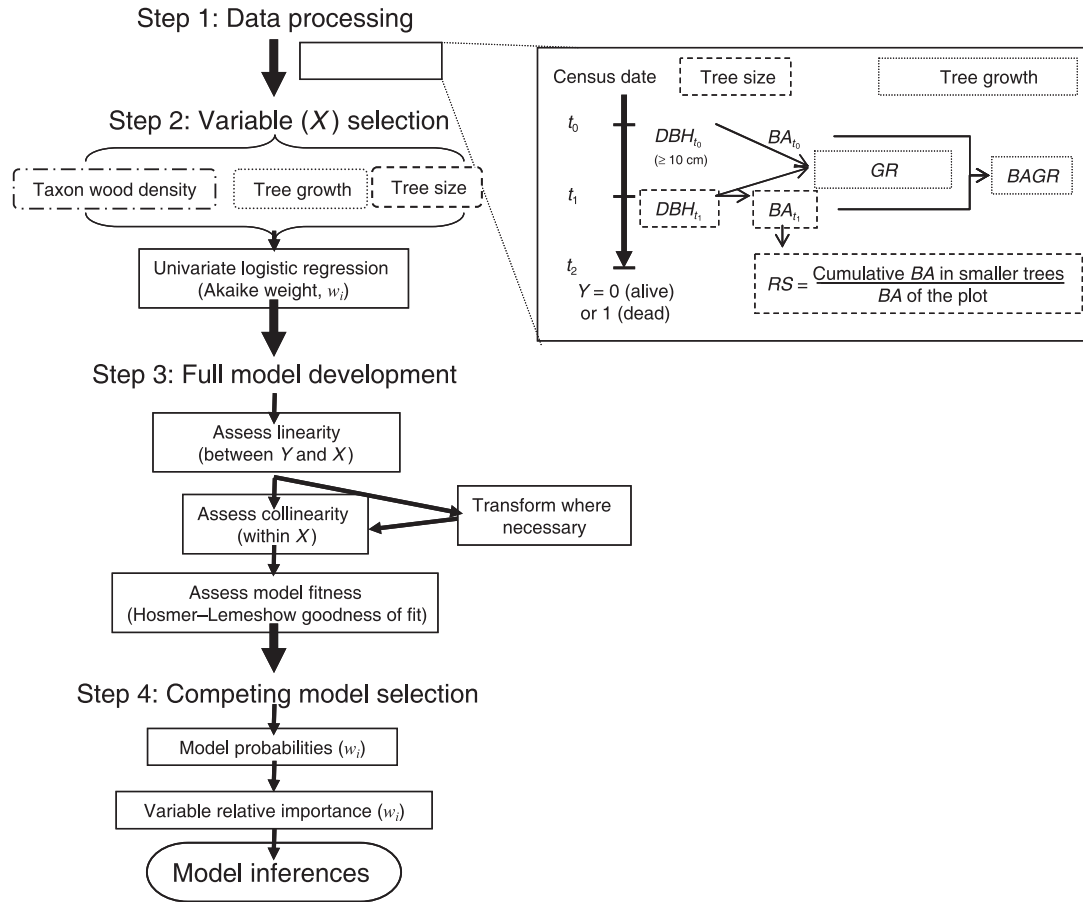


Fig. 1. Scheme of the four steps of model development. In the data-processing step, wood density was used to represent the taxon functional trait, and long-term diameter measurements were used to derive the tree size and tree growth attributes. In the inset box, census date t_2 is defined as the census at which tree status (alive or dead) is modelled. Two previous DBH measurements at t_0 and t_1 were selected to calculate tree growth (dotted square) and tree size (dashed square). In the variable selection step only one predictor variable was selected for each attribute group using univariate logistic regressions. In the full model development step, all selected variables were used to develop a full multivariate model, which was examined and transformed where necessary. In the last model selection step, the Akaike weights (w_i) were applied to evaluate the set of competing models.

was based on Akaike weights (w_i) which can be interpreted as the probability that model i is the best model for the observed data, given the candidate set of models (Burnham & Anderson 2002). Therefore, in each attribute category the variable with the greatest w_i (i.e. the lowest AIC) was selected for the next step.

Step 3: Full model development

Our 'initial full model' comprised all the selected variables (i.e. multivariate). Potential numerical problems (nonlinearity and collinearity, see Appendix S1) were examined and predictor variables were transformed where necessary. The transformed model, termed 'final full model', was evaluated by the Hosmer–Lemeshow goodness-of-fit statistic (Hosmer & Lemeshow 2000).

Step 4: Competing model selection

The final full model and all derived two-predictor, reduced models were further ranked by w_i . Where no single mortality model attained $w_i \geq 0.90$, a confidence set of models was obtained by summing w_i from the largest to smallest until that sum was just ≥ 0.90 ; the

corresponding subset of models is the 90% confidence model set (Burnham & Anderson 2002). The relative importance (RI) for each variable X_i was estimated by summing w_i across all the competing models where the variable X_i occurs (Burnham & Anderson 2002).

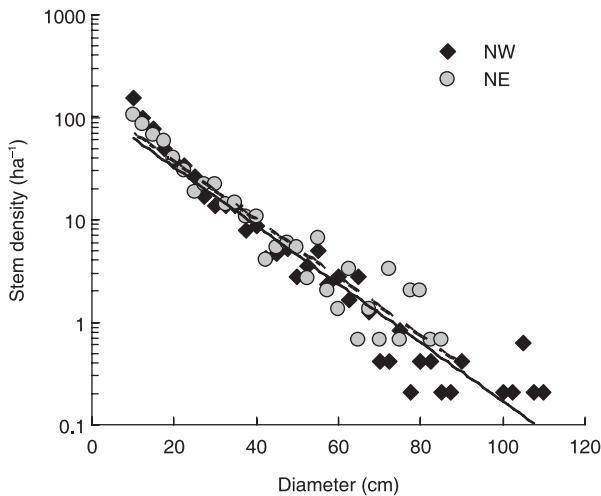
Results

STAND-LEVEL MORTALITY PATTERNS

The size distributions of trees in the NW and NE plots are similar (Fig. 2), and the differences in basal area between regions are not significant (Mann–Whitney test, $P = 0.161$; Table 2), although the NW plots have slightly higher stem numbers than the NE plots (Mann–Whitney test, $P = 0.032$; Table 2). Exponential mortality coefficients ($\lambda\%$), based on *c.* 10-year census intervals, are lower in our NE than our NW plots (Fig. 3a, Mann–Whitney test, $P = 0.025$). This is consistent with the general finding (Phillips *et al.* 2004) that most eastern Amazonian forests experience much lower mortality than most western Amazonian forests. Similarly, over

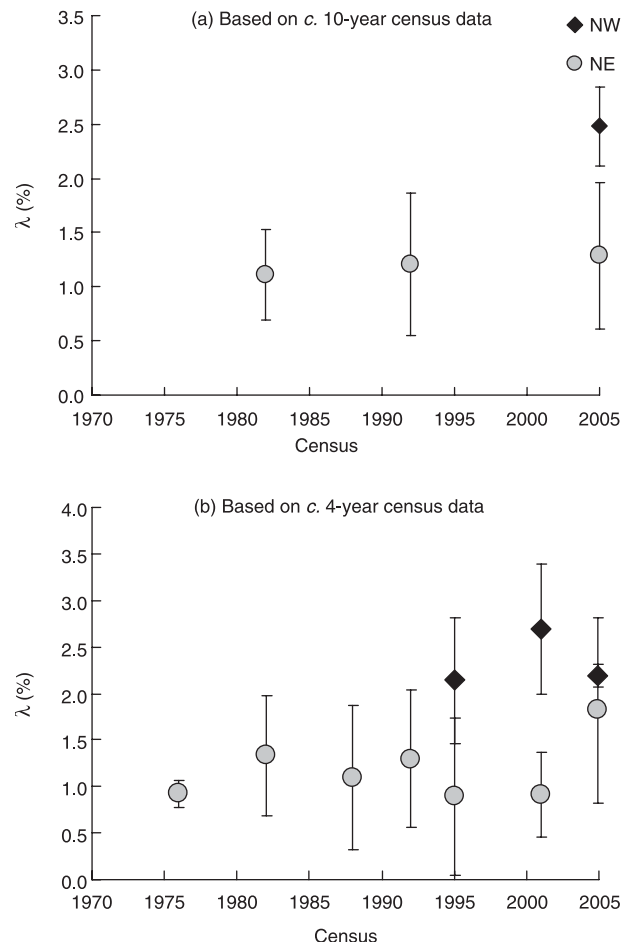
Table 2. Characteristics of studied plots in northwestern and northeastern Amazonia (\pm SD)

	Northwest	Northeast
Plot (three census)	($n = 15$) (1996, 2001, 2005)	($n = 9$) (1994, 2000, 2004)
Exponential mortality coefficient ($\lambda\%$)	2.34 ± 0.31	1.21 ± 0.53
Tree density (stem ha^{-1})	594.4 ± 23.0	560.4 ± 34.7
Basal area ($\text{m}^2 \text{ha}^{-1}$)	28.1 ± 1.6	31.3 ± 4.8
Individual tree (after data processing)	($n = 2307$)	($n = 2441$)
Average wood density (g cm^{-3})	0.63 ± 0.15	0.71 ± 0.14
Average growth rate (mm year^{-1})	2.4 ± 3.2	2.1 ± 2.4
Average relative growth rate ($\% \text{year}^{-1}$)	1.2 ± 1.8	1.0 ± 1.2

**Fig. 2.** Diameter distributions of northwestern (2005) and northeastern (2004) Amazon plots on log-linear axes. Lines are fitted exponential functions for the NW (solid) data and NE (dashed), respectively. Forests in the two regions have similar size-structure distributions for trees ≥ 10 cm diameter.

c. 4-year census intervals, exponential mortality coefficients ($\lambda\%$) of NE plots were also generally lower than that of NW plots (Fig. 3b, Mann–Whitney test, $P = 0.005$).

Few species (19 out of 783) were shared between the studied plots in the two regions, and only three species had more than five individuals recorded in each region; this is insufficient for mortality comparisons at the species level. At the genus level, there is a greater taxonomic overlap across regions: 55 out of 309 genera are shared between the studied plots in the two regions. Among those genera with at least five individuals recorded in each region ($n = 19$), no regional difference in the c. 10-year-based λ could be detected (Wilcoxon signed rank test, $P > 0.26$; mean \pm 1SE: $\lambda = 2.33 \pm 0.44\%$ in NW Amazonia and $\lambda = 2.34 \pm 0.83\%$ in NE Amazonia in census period C). For genera shared between the two regions, we also calculated a genus-level average from available species-level wood density values (a proxy for functional strategy) for each region. The wood densities did not differ significantly between regions ($0.67 \pm 0.04 \text{ g cm}^{-3}$ in the NW and 0.69 ± 0.04 in the NE (average \pm 1SE); Wilcoxon signed ranks test ($n = 15$), $P \geq 0.14$).

**Fig. 3.** Exponential mortality coefficient ($\lambda\%$, average \pm 95% CI) of the northwestern (NW) and northeastern (NE) plots, (a) based on c. 10-year census data and (b) based on c. 4-year census data. x-axis is the year of census (detailed dates as in Table S1).

INDIVIDUAL-LEVEL MORTALITY MODELS

After data processing for individual-based mortality model development (Step 1), there were 2307 individuals from the northwest (2119 alive and 188 dead) and 2441 trees from the northeast (2281 alive and 160 dead). The differences of individual growth rate and relative growth rate are not significant in the two regions, but wood density is significantly greater in the northeast than in the northwest (Mann–Whitney test,

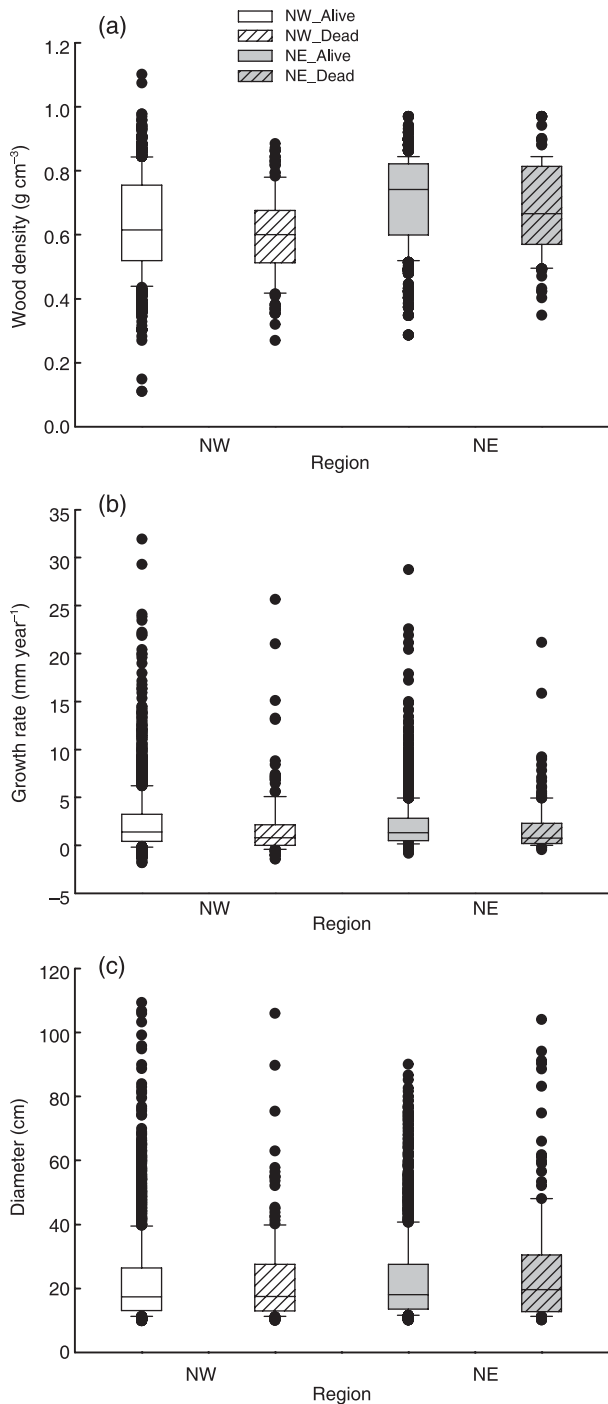


Fig. 4. Live and dead trees in the northwestern (NW) and northeastern (NE) plots compared by (a) wood density (ρ_i), (b) growth rate (GR), and (c) diameter (DBH). Wood densities of dead trees were generally lower than live trees (Mann–Whitney test, $P = 0.013$ in NW, and $P = 0.005$ in NE). Prior-to-death growth rates of dead trees were significantly lower than live tree growth rates (both regions have P -values ≤ 0.001). However, in neither region was there a significant difference in diameter between dead trees and live trees. (These box plots show the median, 10th, 25th, 75th and 90th percentiles of the data.)

$P < 0.001$; Table 2). Comparisons between dead and live trees in the two regions showed that dead trees did not necessarily have larger or smaller diameter than surviving trees, but did tend to have slower growth and lower wood density (Fig. 4).

In the high-mortality NW Amazonia

Correlations among variables in different attribute groups were low (Spearman's rank correlation coefficients, all $r_s < 0.7$), but were high among variables within the same group (all $r_s > 0.7$, $P < 0.002$), suggesting variables had been appropriately assigned to attribute groups (see Table S2a). During variable selection (Step 2, Table 3), of the tree growth category, relative growth rate ($relGR$) had the highest w_i (the probability of the model being the best in a given set) so was selected. Of the size variables, DBH , basal area (BA) and relative size (RS) were all identified as potentially the best variable (i.e. with similar w_i , Table 3), indicating that these variables explain similar variation in the data set. Because of the high within-attribute correlations, only BA , which had marginally superior w_i , was selected to represent this category.

The 'initial full model' was developed using wood density (ρ_i), $relGR$ and BA (AIC = 1286.12). In this model, both ρ_i and $relGR$ were not linearly related to the dependent variable ($P = 0.035$ and $P \leq 0.001$, respectively), so transformations were applied. The 'final full model' for the northwest, termed NW-1, incorporated a quadratic transformation for ρ_i and a logarithmic transformation for $relGR$. This model marginally fitted the observed data (Hosmer–Lemeshow goodness-of-fit, $\chi^2 = 14.06$, $P = 0.080$ ($P > 0.05$ suggests no significant difference between observed and predicted data)). We ranked the final full multivariate model (NW-1) against all reduced models derived from it (NW-2: $relGR$ and BA , NW-3: ρ_i and BA , and NW-4: ρ_i and $relGR$) and the null model (NW-null), by comparing their w_i values (Table 4a). Mortality was best modelled by NW-4 followed by NW-1, which together were almost certain (99% probable) to be the best models (Table 4a). The model containing only ρ_i and $relGR$ was most favoured (the variables both have a RI of 1.00); in this region mortality is not strongly influenced by tree size (RI = 0.29) (Table 4a). There was no interaction between ρ_i and $relGR$ (Wald test, $P = 0.348$). The predicted probability (P) for a tree to die in *c.* 4.1 years census interval, by NW-4 is:

$$\text{logit link function } (P) = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n \quad \text{eqn 2} \\ = -1.51 + (-1.48 \times \rho_i^2) + (-0.64 \times \ln(relGR + 1))$$

where ρ_i^2 is the quadratic-transformed wood density (ρ_i , g cm^{-3}) and $\ln(relGR + 1)$ is the logarithmic-transformed relative growth rate +1. The predicted results marginally fitted the observed data (Hosmer–Lemeshow goodness-of-fit, $\chi^2 = 14.62$, $P = 0.067$). Both predicted and observed probabilities showed that trees with low wood density (Fig. 5a) or low relative growth rate (Fig. 5b) tended to experience a high risk of mortality, but no differences occur between tree size classes (Fig. 5c).

In the low-mortality NE Amazonia

Variables within the same attribute group were closely correlated with one another ($r_s > 0.7$, $P < 0.002$), but less so

Table 3. Variable selection by univariate logistic regression of NW and NE Amazonia (Step 2 in model development)

Attribute and variable*	NW				NE			
	K^\dagger	AIC‡	$\Delta AIC§$	w_i^\parallel	K^\dagger	AIC‡	$\Delta AIC§$	w_i^\parallel
A. Taxon wood density								
A. ρ_i (g cm ⁻³)	2	1299.83	–	–	2	1178.72	–	–
B. Tree growth								
B1. <i>GR</i> (mm year ⁻¹)	2	1298.47	6.17	0.03	2	1182.07	10.52	0.00
B2. <i>BAGR</i> (cm ² year ⁻¹)	2	1306.22	13.91	0.00	2	1184.06	12.51	0.00
B3. <i>relGR</i> (% year ⁻¹)	2	1292.30	0.00	0.66	2	1171.55	0.00	0.58
B4. <i>relBAGR</i> (% year ⁻¹)	2	1293.86	1.55	0.31	2	1172.26	0.70	0.41
C. Tree size								
C1. <i>DBH</i> (cm)	2	1306.84	0.10	0.29	2	1179.19	4.49	0.05
C2. <i>BA</i> (m ²)	2	1306.75	0.00	0.31	2	1175.60	0.90	0.30
C3. <i>DBH</i> (cm)& <i>DBH</i> ² (m ²)	3	1308.68	1.94	0.12	3	1174.70	0.00	0.46
C4. <i>RS</i>	2	1306.91	0.16	0.28	2	1176.49	1.79	0.19

Wood density (ρ_i) and other variables with the highest w_i from each attribute category (marked in bold) are selected and used in further multivariate model development for each region.

* ρ_i , wood density of tree *i*; *GR*, growth rate; *BAGR*, basal area growth rate; *relGR*, relative growth rate; *relBAGR*, relative basal area growth rate; *DBH*, diameter at 1.3 m; *BA*, basal area; *RS*, relative size.

†Total number of estimated parameters including the constant.

‡Akaike's information criterion (AIC).

§Difference between the AIC value of model *i* and the minimum AIC value in a given set.

¶Probability of model being the best in a given set.

Table 4. Competing model and relative importance (RI) of predictor variables for NW and NE Amazonia (Step 4 in model development)

(a) NW Model	Variable*								
	ρ_i^2	$\ln(\text{relGR} + 1)$	<i>BA</i>	χ^2^\dagger	<i>P</i> ‡	<i>K</i> §	AIC¶	ΔAIC^{**}	$w_i^{\dagger\dagger}$
NW-4	–	–		14.62	0.067	3	1272.51	0.00	0.71
NW-1	–	–	+	14.06	0.080	4	1274.36	1.85	0.28
NW-2	–	–	+	10.73	0.217	3	1283.59	11.08	0.00
NW-3	–	–	+	10.92	0.206	3	1299.89	27.38	0.00
NW-null						1	1304.98	32.47	0.00
RI	1.00	1.00	0.29						
(b) NE Model	Variable*								
	ρ_i	$\ln(\text{relGR} + 1)$	<i>DBH</i> ²						
NE-1	–	–	+	6.98	0.538	4	1150.22	0.00	0.96
NE-4	–	–		13.71	0.090	3	1157.92	7.69	0.02
NE-2	–	–	+	19.30	0.013	3	1158.06	7.84	0.02
NE-3	–	–	+	12.63	0.125	3	1170.23	20.01	0.00
NE-null						1	1183.27	33.05	0.00
RI	0.98	1.00	0.98						

Symbol + indicates a positive relationship and – indicates a negative relationship of the independent variable with the dependent variable.

Variables selected from Table 3 were transformed where appropriate. RI of each variable X_i was estimated by summing the Akaike weights across all the competing models where the variable X_i occurs. An adjustment of 1 was added to each *relGR* value in models of both regions to set all *relGR* values as > 0 and thus suitable for log transformation. In the NE models, because the β value of *DBH* was not significant (Wald test, $P = 0.129$), only *DBH*² was retained.

* ρ_i : wood density of tree *i*; *GR*: growth rate, *BAGR*: basal area growth rate, *relGR*: relative growth rate, *relBAGR*: relative basal area growth rate, *DBH*: diameter at 1.3 m, *BA*: basal area, *RS*: relative size.

† χ^2 of the Hosmer–Lemeshow goodness-of-fit statistic.

‡*P*-value of the Hosmer–Lemeshow goodness-of-fit statistic.

§Total number of estimated parameters including the constant.

¶Akaike's information criterion (AIC).

**Difference between the AIC value of model *i* and the minimum AIC value in a given set.

††Probability of model being the best in a given set.

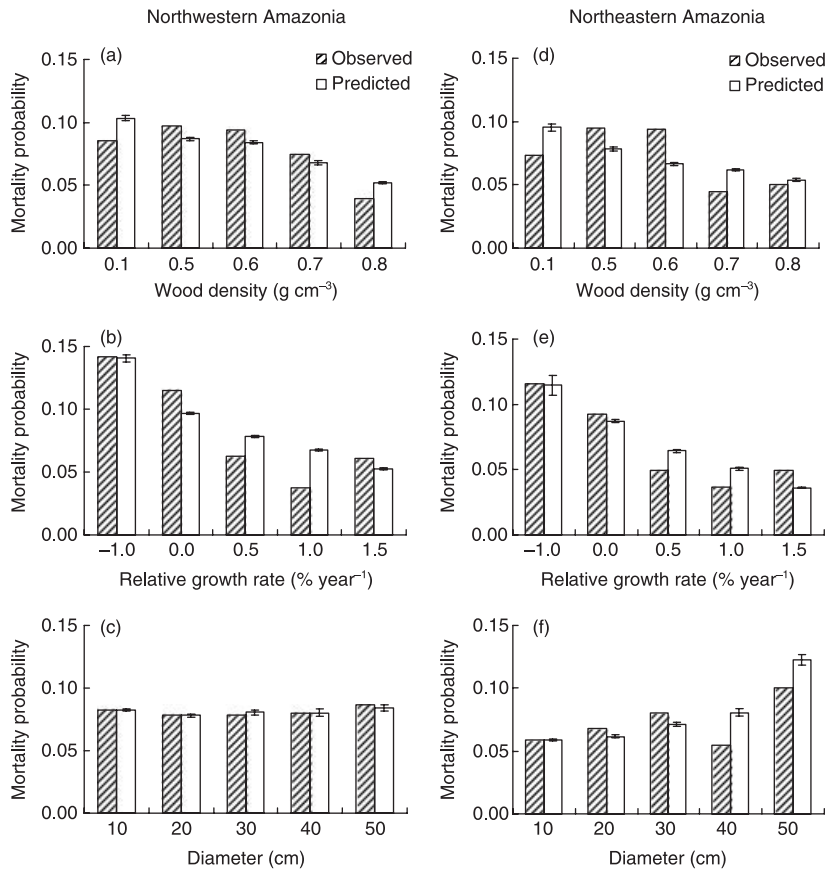


Fig. 5. Observed and predicted individual mortality probability for northwestern Amazonia (a–c, per 4.1 year) and northeastern Amazonia (d–f, per 4.6 year) against wood density (ρ_i , (a, d)), relative growth rate ($relGR$ (b, e)), and diameter (DBH (c, f)). Predicted mortality probability (with standard error) was calculated using model NW-4 for northwest plots and model NE-1 for northeast plots. The standard error of predicted probability is the variation range in an attribute interval. Observed probabilities are calculated as the number of dead trees divided by the total number of trees and do not have statistical variation value. In northwest Amazonia, tree mortality decreases as both the wood density and relative growth rate increase, but is independent of tree size ($n = 2307$). In northeast Amazonia, tree mortality decreases as both wood density and relative growth rate increase, and increases as the size increases ($n = 2441$). x -axis labels represent the lower limits of each variable.

with variables from other groups (all $r_s < 0.7$, see Table S2b), similar to those for NW Amazonia. During variable selection (Step 2), $relGR$ had the highest w_i of the growth variables and DBH & DBH^2 had the highest w_i of the size variables (Table 3), so both were selected for the next step.

The 'initial full model' included one variable from each attribute: ρ_i , $relGR$ and DBH & DBH^2 (AIC = 1156.82). Two further transformations were made to the model: (i) $relGR$ is nonlinear with the dependent variable ($P = 0.002$), so was transformed logarithmically to generate the most linear relationship; and (ii) only DBH^2 was retained, because including both DBH and DBH^2 resulted in model collinearity (Variance Inflation Factor > 12) and the β value of DBH was not significant (Wald test, $P > 0.12$). The 'final full model', termed NE-1, fitted the observed data well (Hosmer–Lemeshow goodness-of-fit, $\chi^2 = 6.98$, $P = 0.538$, Table 4b).

We again ranked the final full multivariate model (NE-1) against all reduced models derived from it (NE-2: $relGR$ and DBH , NE-3: ρ_i and DBH , and NE-4: ρ_i and $relGR$) and the null model (NE-null), using their w_i values. NE-1 had the highest probability of being the 'best' model ($w_i = 0.96$) (Table 4b), containing one variable from each attribute. There was no interaction between $relGR$ and ρ_i (Wald test, $P = 0.915$), or between DBH^2 and ρ_i (Wald test, $P = 0.130$). The predicted probability (P) for a tree to die in *c.* 4.6 years census interval is:

$$\text{logit link function } (P) = -1.03 + (-1.87 \times \rho_i) + (-0.95 \times \ln(relGR + 1)) + (1.97 \times DBH^2) \quad \text{eqn 3}$$

where ρ_i (g cm⁻³) is wood density of tree i ; $\ln(relGR + 1)$ is a logarithmic-transformed relative growth rate +1; DBH^2 (m²) is a quadratic transformed diameter. The RI of each variable is high ($w_i \geq 0.98$, Table 4b), suggesting that all are important for predicting mortality risk. Both the predicted results by NE-1 and observed data show that trees with low wood density (Fig. 5d), slow relative growth (Fig. 5e) and large size (Fig. 5f), were at greater risk of death.

Discussion

Based on long-term field data, this study presents mixed-species mortality models suitable for the highly diverse Amazon forest, in which wood density is applied as a surrogate for a taxon-level function. Three distinct groups of attributes were selected to examine the determinants of tree mortality. Although the two regions have very different dynamic regimes, both tree growth (physiological status) and wood density (functional strategy) are shown to have predictive value for tree death (Fig. 6). However, tree size (age or competitive ability) only predicts mortality in the low-mortality region. These insights help to provide a basic framework for understanding and modelling tree dynamics in tropical forests.

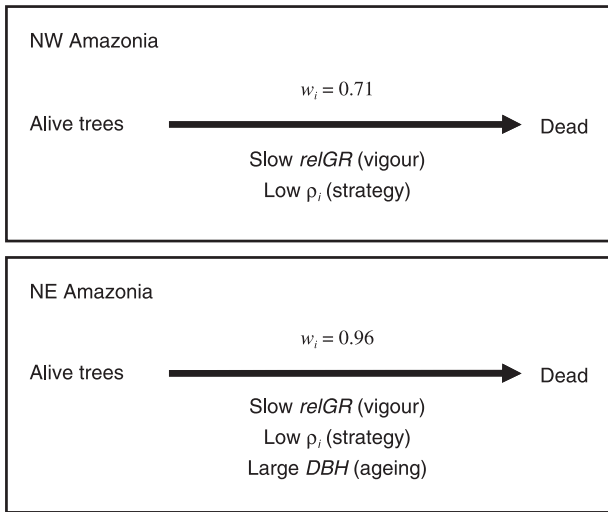


Fig. 6. Summary of the relationships between tree status and attributes. In northwestern Amazonia, dead trees are characterized by slow prior-to-death relative growth (*relGR*) and low wood density (ρ_i), whereas in northeastern Amazonia, dead trees are also characterized by large diameters (*DBH*). Models as listed in Table 4.

ECOLOGICAL IMPLICATION OF PREDICTOR VARIABLES

Tree growth

In both regions, tree growth is the most informative predictor category. We expected that in the slow-turnover northeast, tree survivorship would be related to slow or declining vigour prior to death (Table 1). This is evidently the case: including *relGR* improves the mortality models. Unexpectedly, in the dynamic NW forests tree growth was also a good predictor of mortality risk, suggesting that physiological stress plays a significant role here too. Moreover, *relative* growth rate is a better predictor than the *absolute* growth rate (Table 3), a commonly used predictor (e.g. Yao *et al.* 2001; van Mantgem *et al.* 2003). Using *relative* growth rate reduces the confounding effect of tree size on growth and so gives a more precise measure of tree vigour (Bigler *et al.* 2004). Our results confirm that in tropical forests a tree's probability of dying is predictable in advance by its vigour.

Taxon wood density

Wood density was the second best predictor variable of tree death in both regions. In NW Amazonia, we expected that a leading factor determining mortality risk would be wood density, as forests here have high-mortality and are disproportionately composed of low wood-density taxa (Baker *et al.* 2004). The results showed that in both regions this functional trait can predetermine mortality risks. The negative correlation between wood density and mortality is consistent with the view that the trait reflects the fundamental trade-off between taxon-level resource acquisition and investment in survival (Loehle 1987; King *et al.* 2006b). Some trees (36%) in our analyses lacked species-level wood density values,

and were substituted by genus-, family- or plot-level means. Although this introduces some uncertainties to our analyses, the large majority of species-level wood density variation is determined at the genus-level and at the family-level (Chave *et al.* 2006), indicating that wood density is strongly conserved phylogenetically. Therefore, using this predictor as a taxon-based functional trait can improve the representation of mortality in highly diverse tropical forests where taxon-level parameterisation is usually impossible. Other taxon-level traits, such as maximum height and maximum growth rate, are also potential predictors for tree death. An extensive functional trait data base would be needed to test the applicability of such traits.

Tree size

In low-mortality NE Amazonia, we had predicted high mortality for both small and very large trees (Table 1), which would be represented by a U-shaped function consisting of *DBH* and *DBH*². Our results showed that the bigger trees in this region did indeed run a greater mortality risk, indicating mechanisms related to senescence or structural instability. Carey *et al.* (1994), working in the same region, report that the dominant mortality mode here is 'standing dead', suggesting that tree death is primarily driven by senescence rather than structural instability. However, the U-shaped pattern was not strongly supported as the β value of *DBH* was not significant, perhaps because trees ≥ 10 cm in diameter have already escaped from serious competition. Incorporating smaller trees might reveal a clearer U-shaped pattern in the size-related probability of death (cf. Muller-Landau *et al.* 2006; Coomes & Allen 2007).

In the high-mortality NW Amazonia, as predicted, tree size did not determine tree death. A potential weakness of mixed-species models is that they may obscure species-specific mortality patterns as species differ in these relations and in adult stature (e.g. Davies 2001; King *et al.* 2006a). However, when using wood density to represent species functional variation, we found no interaction between the trait and tree size ($P = 0.349$) in the full model NW-1. Other tropical forest studies show unclear or inconsistent relationships between mortality and size, suggesting variously that they are independent (Lieberman & Lieberman 1987; Manokaran & Kochummen 1987; Swaine *et al.* 1987; Carey *et al.* 1994; in a drought period, Condit *et al.* 1995), negatively correlated (in a non-drought period, Condit *et al.* 1995) or positively correlated (King *et al.* 2006a). The relationship between tree size and mortality in the tropics may be highly dependent on the local context of taxon functional composition and stand dynamic regime.

Tree death linked to a decline in vigour should be predictable by its growth pattern before death, but tree death caused by disturbance, such as wind, is less likely to be predictable. These two processes would result in different modes of death – one standing, the other broken or uprooted. Developing separate models for different modes of death could therefore improve the understanding of mortality mechanisms in the

two regions. Besides, the relatively weak goodness-of-fit for the best northwest model suggests either that mortality here is a more stochastic process, or that we have not included some vital predictors.

REGIONAL VARIATIONS IN NE AND NW AMAZONIA

The Amazonian forests studied have several distinct characteristics, such that NE Amazonia has lower tree species diversity (ter Steege *et al.* 2006), lower productivity (Malhi *et al.* 2004) and is composed of trees with relatively high wood density (Baker *et al.* 2004). However, the two regions have no significant differences in tree size-distribution and basal area (this study, for trees ≥ 10 cm diameter). Large trees in the NE plots have higher mortality probability (this study), which may result in similar or even higher mortality output in basal area and thus the overall basal area in the two regions are not significantly different, despite NE plots having relatively low mortality rates. Because the two regions have similar forest structure, the major difference in mortality for trees ≥ 10 cm is likely to be caused by species composition.

In both regions, we found that wood density is a generally good predictor of mortality risk, such that lower wood density trees run a greater risk of death. This supports our hypothesis that functional trait can determine mortality risks. Therefore, forests composed of low wood-density species would be expected to have high-mortality rates. In turn, high-mortality rates would create more canopy gaps that favour low wood-density species. Thus, we propose that the mortality regime in Amazonia may be both a cause and an effect of forest floristic composition.

Other factors, such as environmental driver effects, cannot be discounted because some environmental differences between regions do exist, notably a slightly more marked dry season in the northeast (Sombroek 2001) as well as a tendency for gentler topography, deeper rooting-depth and poorer soil fertility (C. A. Quesada, unpubl. data). The fundamental factors that influence species compositional differences may still relate to environmental drivers as has been shown at smaller scales in forests elsewhere (e.g. Ashton & Hall 1992; Russo *et al.* 2005). Yet, while stand-level mortality rates are generally twice as great in the northwest, among those genera that are actually shared between the regions there was no evidence for differing mortality rates (this study). This implies that any environmental differences between the regions may have limited importance in explaining the contrasting dynamic regimes. Rather, the very large compositional differences observed may be a direct driver of the regional dynamic differences, and potentially the macroecological gradient in forest dynamics across Amazonia (cf. Phillips *et al.* 2004).

Conclusions

Tree death is often a consequence of multiple factors (Franklin *et al.* 1987), which poses challenges for understanding mortality patterns. To help understand mortality in the world's largest and most diverse tropical forests we adopted

a mixed-species, multivariate approach. In spite of twofold differences in stand-level mortality rates, individual tree death can be predicted from wood density (a proxy for functional strategy) and relative growth rate (indicator of vigour) in both forests. In the northeast, tree death is also dependent on tree size, but in the northwest it is not, suggesting that senescence plays an important role only where ecological process rates are slower. The best model for the northwest only marginally fits the observed data, indicating a substantial element of chance in tree death, possibly related to external disturbance. The similarity in mortality rates of genera shared across regions suggests an important role for floristic composition, such that high stand-level mortality in the northwest may be the inevitable destiny of forests composed of predominantly low-wood-density species.

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Supplementary material

The following supplementary material is available for this article:

Table S1 Census year of studied plots.

Table S2 Correlation among variables in NW and NE Amazonia.

Appendix S1 Statistic methods.

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