

## How do trees die? Mode of death in northern Amazonia

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### Abstract

**Question:** How do trees die in high-mortality and low-mortality Amazonian forest regions? Why do trees die in different ways?

**Location:** Humid, lowland forests in Amazonian Peru and Venezuela.

**Methods:** Patterns of multiple treefall and mode of death (standing, broken or uprooted) were recorded for trees  $\geq 10$  cm in diameter in permanent plots. Logistic regression was used to relate mode of death to tree diameter, relative growth rate and wood density.

**Results:** Frequency of multiple death events was higher in high-mortality northwestern (NW) than in low-mortality northeastern (NE) Amazonia, but these events were small, averaging two trees killed per multiple death event. Breakage was the dominant *known* mode of death ( $51 \pm 8\%$ ) in the NW, with half of fatal breakages caused by other treefalls or breakages. Small and slow-growing trees were more prone to breaking than uprooting. In NE Amazonia, the dominant *known* mode of death was standing ( $48 \pm 10\%$ ); these trees tended to be relatively large and slow growing. Broken trees in NE forests have a lower wood density than uprooted trees.

**Conclusions:** The major mortality mechanisms differ in the two regions. In the NW it involves an interaction between *physiological failure* and *mechanical failure* (small size, slow growth and broken mode). In the NE it is mainly driven by *physiological failure* (large size, slow growth and standing mode). We propose that by creating different-sized gaps the different dominant modes of death would favour species from different functional groups and so help to maintain the contrasting functional composition and mortality rates of the two regions.

**Keywords:** Broken tree; Canopy gap; Forest dynamics; Mortality mechanism; Relative growth rate; Standing

dead tree; Tree size; Tropical forests; Uprooted tree; Wood density.

**Abbreviations:** AIC<sub>c</sub> = second order Akaike's information criterion; B = broken dead tree; DBH = diameter at breast height; NE = northeast; NW = northwest; *relGR* = relative growth rate; S = standing dead tree; U = uprooted dead tree;  $\rho_i$  = wood density of tree *i*;  $w_i$  = Akaike weights.

### Introduction

Tree death is one of the critical processes in forest ecosystems, due to its influence on forest structure, composition, dynamics and carbon and nutrient cycles (Franklin et al. 1987; Lugo & Scatena 1996). A long-term research project in Amazonia, RAINFOR (Malhi et al. 2002; Peacock et al. 2007) has shown that mortality rates of trees  $\geq 10$  cm diameter are twice as high in western as in eastern Amazonia (Phillips et al. 2004). Why this difference should occur is unclear. Chao et al. (2008) examined possible predictors of mortality probabilities for trees in some Amazonian RAINFOR plots. They found that mortality probabilities are determined by both slow individual growth and low, taxon-level wood density. To develop a mechanistic understanding of the actual processes involved in tropical tree death, an important next step is to test whether the ways in which trees die – including standing, broken and uprooted – are similar across forests or are expressed differently in different localities.

The mechanisms causing tree death are often complicated and cumulative (Franklin et al. 1987), but knowledge of death mode can help to explain these mechanisms (Putz et al. 1983). For example,

Carey et al. (1994) proposed that a standing death may indicate intrinsic loss of vigour and/or senescence. Some extrinsic agents, e.g. competition from larger trees or lianas (Putz 1984; Phillips et al. 2005) or drought stress (Nakagawa et al. 2000), might also cause a tree to gradually die while standing. On the other hand, trees that are uprooted or broken by wind, rain-load or another treefall may die immediately (van der Meer & Bongers 1996). A Central American study showed that whether a tree dies from uprooting or snapping is partly determined by its anchorage and wood properties (Putz et al. 1983). However, in stands with a high proportion of multiple treefall events (trees dying together with other fallen trees), it is less easy to predict which trees are likely to die.

The dominant mode of tree death differs from region to region (Putz et al. 1983; Carey et al. 1994; Gale & Barfod 1999). Since different modes of death can affect subsequent gap formation and forest dynamics (Denslow 1980; Krasny & Whitmore 1992), it is important to identify the dominant mode and the controlling factors within an area.

The aim of this study was to examine modes of death and multiple treefall events in the north-western (NW, Peru) and northeastern (NE, Venezuela) RAINFOR plots. In particular, we asked: (Q<sub>1</sub>) how do trees die in NE and NW Amazonia? (Q<sub>2</sub>) Why do trees die in different ways (standing, broken or uprooted)? We hypothesised (H<sub>1</sub>) that forests with high mortality are subject to a greater amount of disturbance-related deaths. Therefore, we predicted (P<sub>1</sub>) a higher proportion of broken or uprooted deaths and multiple treefall events in NW Amazonia than in NE Amazonia. We also hypothesised (H<sub>2</sub>) that standing tree death is a gradual process, caused by physiological failure, and that broken and uprooted tree deaths are relatively immediate and stochastic processes, related to disturbance events and tree structural properties. Therefore, we predicted (P<sub>2-1</sub>) that standing tree deaths would be preceded by slow growth, but that broken and uprooted deaths would not. We also expected (P<sub>2-2</sub>) that broken trees have lower wood densities than uprooted trees, as wood density is related to wood strength (van Gelder et al. 2006).

## Methods

### Study sites

Modes of tree death were recorded in five long-term 1-ha plots in NW Amazonia, Peru (ALP-A,

ALP-B, YAN-01, SUC-01 and SUC-02) and three long-term 0.5-ha plots in NE Amazonia, Venezuela (ELD-01/02, ELD-03/04 and RIO-01/02) (see detailed plot descriptions in Chao et al. 2008). These regions are relatively unaffected by major catastrophic disturbance (e.g. cyclones, floods, fires or landslips). Dominant families are Fabaceae, Myristicaceae and Moraceae in the NW plots, and are Fabaceae, Burseraceae and Chrysobalanaceae in the NE plots. Both regions are rich in tree species; in particular, our NW forests include some of the most speciose plots on Earth (Vásquez Martínez & Phillips 2000). Slopes of subplots (typically 20 m × 20 m) are mostly <25° in both regions. The regional proportions of subplot slope degree classes (<10; <25; ≥25°) are, respectively, 63, 38 and 0% in the NE plots, and 46, 48 and 6% in the NW plots. The NW subplots are more topographically varied (more valley and slope subplots) than those in the NE. The proportions of subplot slope position (plateau, valley, slope or ridge) are 58, 0, 42 and 0% in the NE, and 7, 35, 55 and 4% in the NW, respectively.

### Field methods (how do trees die?)

All trees ≥ 10 cm in diameter at breast height (DBH) have been recorded and re-measured every 4-5 years. Modes of tree death were recorded in a census in 2005 for NW Amazonian plots, and were recorded at every ca. 5-year interval census from 1971 to 2004 for the NE Amazonian plots. We allocated deaths to one of the three major modes (Gale & Barfod 1999). (1) *Standing dead* trees are those with intact crown branches on their standing trunks, or those with crown debris scattered in all directions around the tree stump. (2) *Broken* trees are characterised by a broken stump and a fallen bole with crown branches attached. Trees that broke close to ground level were classified as “broken” rather than “uprooted”. (3) *Uprooted* trees have upturned root plates, with some soil attached. Where the mode of tree death could not be identified, an *unspecified* class was assigned. This includes those trees whose remains could not be found in the previously recorded location; those too decomposed to identify the mode of death with a reasonable degree of confidence; and those not easy to distinguish between standing dead and broken or between broken and uprooted. Trees dying as a result of human activity were not considered in this study.

Patterns of multiple treefall events were investigated in the most recent census (2004 in NE and 2005 in NW Amazonia). Dead trees were classified into four categories: solitary death, “multiple death

– killer” (a large tree lying on top of other trees  $\geq 10$  cm in diameter), “multiple death – killed” (physically below another uprooted tree, broken tree or large fallen branches) and “unidentified” (unclear if died alone or together with other trees). The magnitude of each multiple death event was quantified by grouping those trees killed by each killer tree. When trees were missing in the vicinity of a recent treefall event, the individuals were classified as dying in a separate event rather than being killed. Some scenarios – a group of diseased, standing dead trees and deaths associated with liana infestation – were considered as solitary death events.

*Model development (why do trees die in different ways?)*

#### Data selection

Analysis for NW Amazonian plots was confined to trees that died during the census period 2001–2005. NE Amazonian plots are small but have extremely long monitoring sequences; therefore we used all available mode of tree death data in every ca. 5-year interval census (1971, 1976, 1981, 1986, 1991, 1994, 2000 and 2004) to maximise the sample size of dead trees in this region. Three major census periods, 1971–1980 (c1, recorded by J.P. Veillon), 1980–2000 (c2, J. Serrano) and 2000–2004 (c3, K.-J.C.), were used in all NE models as categorical control variables to allow for the fact that trees with the same attributes may have different probabilities of specific death mode from one census period to another. During the 1980–2000 interval, trees dying standing or broken were mostly noted as “either standing or broken”, and were not used for statistical model development.

Five data selection criteria were applied prior to model development. (1) Trees noted as *unspecified* death modes were not included due to their uncertainty. (2) Palms (Arecaceae,  $n = 20$ ) were excluded because they have different diameter growth patterns and mode of death to dicotyledonous trees (Gale & Barfod 1999). (3) Topographic classes of insufficient sample size [slope class 3 ( $n = 6$ ) and in a “ridge” slope position ( $n = 4$ )] were excluded. (4) Trees lacking two diameter measurements prior to death, necessary to calculate growth rates, were excluded. (5) Trees with absolute growth rates  $< -2$  or  $> 40$  mm year<sup>-1</sup> or relative growth rate  $< -1\%$  (as defined in Table 1) were excluded ( $n = 5$  in the NW,  $n = 1$  in the NE) to minimise the impact of measurement error (cf. Sheil et al. 1995).

**Table 1.** Definitions of tree attributes for the multivariate logistic regression models. \*In the NE plots the census dates are 1971, 1976, 1981, 1986, 1991, 1994, 2000 and 2004. In the NW plots census dates are 1996, 2001 and 2005.

Attribute	Definition
<i>DBH</i> (cm)	Individual tree size and age indicator. Diameter at 1.3 m (or above buttresses) at the prior to death census $t_1^*$
<i>relGR</i> (% year <sup>-1</sup> )	Individual tree vigour indicator. Relative diameter growth rate at time $t_1$ . $relGR = (GR / DBH_{t_0}) \times 100\%$ , where $GR$ is the growth rate ( $GR = (DBH_{t_1} - DBH_{t_0}) / (t_1 - t_0)$ ), $t_1$ is the prior to death census, $t_0$ is the second prior to death census*
$\rho_i$ (g cm <sup>-3</sup> )	Taxon-level property indicator. Wood density of tree $i$ was obtained for each species (62% of 328 individuals) from the RAINFOR functional trait dataset (Baker et al. 2004; Chave et al. 2006; Lopez-Gonzalez et al. 2006). In cases where wood density data were unavailable, averages for that neotropical genus (30%) or family (5%) were used. For unidentified individuals (3%), the average wood density of the plot was applied.

#### Multivariate models

Three continuous tree attributes, including one taxon-level variable and two individual-level variables, were used as predictors of mode of death (Table 1). We did not develop multi-level models (cf. Jutras et al. 2003) as a very large sample size is needed for hierarchical data structure (Paterson & Goldstein 1991). Two types of models were developed in each region. Model S&BU (model for standing and “broken and uprooted” deaths) tests prediction  $P_{2-1}$  that standing dead trees have lower prior to death growth than “broken and uprooted” dead trees. Model B&U (model for broken and uprooted dead trees) tests prediction  $P_{2-2}$  that broken trees have a lower wood density than uprooted trees. Logistic regression was applied for model development because dependent variables are dichotomous (Hosmer & Lemeshow 2000) (see also App. 1). Models were ranked by Akaike weights ( $w_i$ ) (Burnham & Anderson 2002) (App. 1).

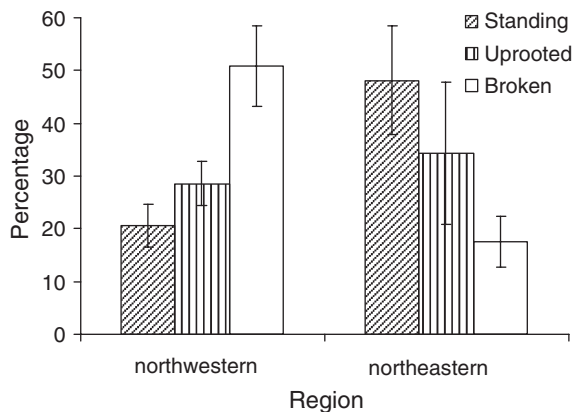
#### Results

##### How do trees die?

In NW Amazonia the predominant mode of death is broken, followed by uprooted, whereas in NE Amazonia the predominant mode is standing, followed by uprooted (Table 2). When trees with an *unspecified* death mode are excluded (Fig. 1), these differences are even more pronounced: in the NW  $51 \pm 8\%$  of trees die broken, in the NE  $48 \pm 10\%$  die standing. In both studied plots, topography has little effect on death mode ( $\chi^2$  test of slope class:  $P = 0.271$

**Table 2.** Average percentage ( $\pm 1$  SE) of *all* modes of death in northwestern (NW, number of plots = 5, census period 2001–2005) and northeastern (NE, number of plots = 3, census period 1971–2004) Amazonia. Modes of death in the NE plots were recorded by J.P. Veillon for census period 1971–1980, J. Serrano for census period 1980–2000, and K.-J.C. for census period 2000–2004. During the 1980–2000 census period, mode of tree death was mostly noted as “either standing or broken” or “uprooted”, so the proportion of standing or broken is higher than in other census periods. <sup>§</sup>Trees that were missing or were too decomposed to identify.

Region	Census period	Standing	Uprooted	Broken	Standing or broken	Uprooted or broken	Others <sup>§</sup>	<i>n</i>
NW	2001–2005	13.5 $\pm$ 3.1	19.2 $\pm$ 3.8	32.6 $\pm$ 5.0	16.3 $\pm$ 4.3	1.0 $\pm$ 1.0	17.4 $\pm$ 2.5	234
NE	1971–2004	40.3 $\pm$ 12.5	24.9 $\pm$ 7.4	14.3 $\pm$ 4.4	17.0 $\pm$ 9.0	–	5.1 $\pm$ 3.9	328
	1971–1980	63.3 $\pm$ 7.8	16.7 $\pm$ 10.7	16.8 $\pm$ 2.6	3.2 $\pm$ 2.1	–	–	76
	1980–2000	20.2 $\pm$ 5.6	39.6 $\pm$ 2.7	5.7 $\pm$ 2.2	34.0 $\pm$ 4.7	–	0.4 $\pm$ 0.4	194
	2000–2004	37.4 $\pm$ 13.8	18.4 $\pm$ 5.6	20.5 $\pm$ 11.3	13.9 $\pm$ 6.2	–	9.9 $\pm$ 9.9	58



**Fig. 1.** Plot-level percentage of *known* modes of tree death in northwestern and northeastern Amazonia ( $\pm 1$  SE). The dominant mode of death in the northwest is broken, whereas in the northeast it is standing.

in the NW, and  $P = 0.183$  in the NE; slope position:  $P = 0.222$  in the NW, and  $P = 0.436$  in the NE).

Patterns of multiple treefall events differ in NW and NE Amazonia. Magnitudes (number of trees being killed) per multiple death event are low and statistically indistinguishable, only  $1.5 \pm 0.1$  (mean  $\pm 1$  SE) in the NW and  $2.5 \pm 1.3$  in the NE. The missing or rotten trees (17% of dead trees in the NW plots and 5% of dead trees in the NE) were not considered attributable to any multiple death events, so the estimates of magnitudes are slightly conservative. The frequency of multiple death events (number of killer trees) per area per year is greater in the NW ( $1.0 \pm 0.2$  stem  $\text{ha}^{-1}$  year $^{-1}$ ) than in the NE ( $0.2 \pm 0.2$  stem  $\text{ha}^{-1}$  year $^{-1}$ ) (Mann-Whitney  $U$  test,  $P = 0.037$ ). Therefore, multiple treefalls are more frequent, but are typically very small in magnitude in the NW. In both regions, trees that died broken were mostly related to the fall of other trees or branches (47% of broken trees in the NW and 80% in the NE).

### Why do trees die in different ways?

For each region and each prediction ( $P_{2-1}$  and  $P_{2-2}$ ), eight models were developed with a combination of all three attributes. In NW Amazonia, standing and “broken and uprooted” death events were not easily distinguished: no NW-S&BU model had a clearly higher explanatory power than any other (Table 3). In contrast, standing and “broken and uprooted” death events in NE Amazonia are, as expected, best explained using relative growth rate and also diameter (NE-S&BU-2, Table 3), such that trees with a large diameter and slow growth prior to death tend to die standing.

Unexpectedly, for trees that died broken and uprooted in the NW, the differences in modes were best explained by a model using both *DBH* and *relGR* (NW-B&U-2, Table 4), such that small diameter and slow-growing trees tend to die broken. However, in NE Amazonia the probability of a tree dying broken was best explained by wood density,  $\rho_i$  (NE-B&U-7, Table 4), such that trees with a low wood density tend to die broken. These results show that the same mode of death has different characteristics in the two regions. Modes of death and tree attributes of dominant families are listed in App. S1, available as Supporting Information.

## Discussion

### Patterns of mode of death

This study provides insight into how trees die in Amazonia. The results support our prediction ( $P_1$ ) that the regional difference in stand-level mortality rates is related to the frequency of death modes and multiple treefall events. NW plots have a higher proportion of broken tree death, and a higher frequency, and possibly a smaller magnitude, of multiple treefall events compared to NE plots. Al-

**Table 3.** Multivariate logistic regression for “standing” (S,  $Y = 1$ ) and “broken and uprooted” (BU,  $Y = 0$ ) dead trees in northwestern (NW,  $n = 124$ ) and northeastern (NE,  $n = 204$ ) Amazonia. Models are listed in descending order of  $w_i$  and the best models are in bold.  $w_i$  is the probability of the selected model being the best model compared with other given models. The same model number indicates the same combination of variables in the NW and NE. \*For variable definitions see Table 1. †Hosmer-Lemeshow goodness-of-fit statistic and ‡its  $P$  value ( $P > 0.05$  indicates no significant differences between predicted and observed results). ¶The Akaike weights, which provide an approximate probability that a given model is the best fitting. #c2 and c3 denote census period 2 (1980-2000) and census period 3 (2000-2004), as control variables for NE Amazonian data. Census period 1 (1971-1980) is the reference category.

Model	Variable* coefficients					$\chi^{2\dagger}$	$P^\ddagger$	$w_i^\¶$
	<i>DBH</i>	<i>relGR</i>	$\rho_i$	c2 <sup>#</sup>	c3 <sup>#</sup>			
NW-S&BU-null								0.37
NW-S&BU-5	-0.01					6.68	0.57	0.15
NW-S&BU-6		-0.08				6.33	0.61	0.15
NW-S&BU-7			+0.53			13.81	0.09	0.14
NW-S&BU-2	-0.01	-0.08				10.34	0.24	0.06
NW-S&BU-3	-0.01		+0.49			4.52	0.81	0.06
NW-S&BU-4		-0.07	+0.42			17.55	0.03	0.05
NW-S&BU-1	-0.01	-0.07	+0.39			7.43	0.49	0.02
<b>NE-S&amp;BU-2</b>	+0.03	-0.55		-1.23	-1.06	10.18	0.25	<b>0.71</b>
NE-S&BU-1	+0.03	-0.55	+0.09	-1.23	-1.06	9.39	0.31	0.25
NE-S&BU-6		-0.50		-1.15	-0.95	14.85	0.06	0.02
NE-S&BU-5	+0.03			-1.02	-0.81	10.54	0.23	0.01
NE-S&BU-4		-0.50	-0.23	-1.14	-0.95	6.23	0.62	0.01
NE-S&BU-3	+0.03		+0.56	-1.03	-0.82	11.23	0.19	0.00
NE-S&BU-7			+0.22	-0.86	-0.73	9.00	0.34	0.00
NE-S&BU-null				-0.95	-0.73			0.00

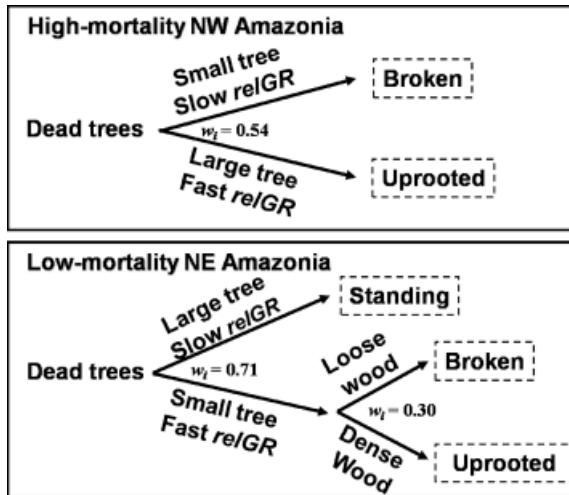
**Table 4.** Multivariate logistic regression for broken (B,  $Y = 1$ ) and uprooted (U,  $Y = 0$ ) dead trees in northwestern (NW,  $n = 99$ ) and northeastern (NE,  $n = 121$ ) Amazonia. \* † ‡ ¶ # For definitions see Tables 1 and 3.

Model	Variable* coefficients					$\chi^{2\dagger}$	$P^\ddagger$	$w_i^\¶$
	<i>DBH</i>	<i>relGR</i>	$\rho_i$	c2 <sup>#</sup>	c3 <sup>#</sup>			
<b>NW-B&amp;U-2</b>	-0.05	-0.42				8.74	0.37	<b>0.54</b>
NW-B&U-1	-0.05	-0.46	-1.64			9.22	0.32	0.27
NW-B&U-5	-0.05					7.34	0.50	0.12
NW-B&U-3	-0.05		-0.57			4.44	0.82	0.04
NW-B&U-6		-0.42				5.56	0.70	0.02
NW-B&U-4		-0.43	-0.89			15.65	0.05	0.01
NW-B&U-null								0.00
NW-B&U-7			-0.01			12.94	0.11	0.00
<b>NE-B&amp;U-7</b>			-2.77	-3.07	-0.46	5.72	0.68	<b>0.30</b>
NE-B&U-null				-3.06	-0.47			0.23
NE-B&U-3	+0.01		-2.70	-3.11	-0.52	9.98	0.27	0.12
NE-B&U-4		-0.02	-2.81	-3.07	-0.47	8.87	0.35	0.10
NE-B&U-5	+0.01			-3.11	-0.53	10.43	0.24	0.10
NE-B&U-6		+0.06		-3.04	-0.43	8.62	0.38	0.08
NE-B&U-1	+0.01	-0.02	-2.73	-3.12	-0.53	9.50	0.30	0.04
NE-B&U-2	+0.01	+0.07		-3.09	-0.49	12.14	0.15	0.03

though the small sample size of plots limits interpretation, it appears that the high proportion of broken tree deaths and frequency of multiple tree deaths (indicating higher frequency of disturbances) is one of the drivers of the high mortality in the NW. We failed to detect a relationship between topography and death mode, but further systematic sampling along topographic gradients could help clarify this (cf. Gale & Barford 1999).

#### *Tree attributes, mode of death and death mechanisms*

Previous modelling of tree mortality, in which live and dead trees are compared (e.g. Shirakura et al. 2006; Wunder et al. 2007; Chao et al. 2008), showed that wood density, prior to death growth and tree size can all help to explain the probability of death. Our study further demonstrates that there is also an important variation in



**Fig. 2.** Summary of the relationships between tree attributes and modes of death in northwestern and northeastern Amazonia. There are no special characteristics of standing dead trees in NW Amazonia, whereas standing dead trees are characterised by low-relative growth rate and large size in NE Amazonia. Broken trees are characterised by small diameters (*DBH*) and slow relative growth (*relGR*) in NW Amazonia, and by low-wood density ( $\rho$ ) in NE Amazonia. Model details are given in Tables 3 and 4.

tree attributes among different death modes (as summarised in Fig. 2), and reveals possible mortality mechanisms in each region. Here, we discuss the mortality risk factors and their ecological implications one-by-one.

### Tree size

Large trees in NE Amazonia tend to die standing, whereas those in NW Amazonia are prone to dying uprooted. This implies that large trees die due to old age in the NE, but due to an interaction between structural balance and wind disturbance in the NW. Since large trees are potentially the major gap-makers in forests, and standing dead trees create smaller gaps than broken and uprooted trees (Krasny & Whitmore 1992; Gale 2000), such differences in death modes will result in very different forest dynamics.

### Tree vigour

In NE Amazonia, reduced vigour (slow relative growth rate) is a precursor to trees dying standing, whereas broken and uprooted dead trees show no prior loss of vigour. This confirms our prediction  $P_{2-1}$  that standing death results from loss of vigour.

Unexpectedly, in NW Amazonia, trees with low relative growth rates also tend to die broken, which is inconsistent with our predictions  $P_{2-1}$  and  $P_{2-2}$ . These slow-growing trees may have been predisposed to be vulnerable to external disturbances, such as wind or the fall of other trees. Therefore, the mechanism for mortality in these trees in the NW appears to be an interaction between physiological failure and mechanical failure.

### Wood density

Wood density is substantially a species-specific trait (Baker et al. 2004), and high wood density has been associated with other life-history features, including greater mechanical strength (van Gelder et al. 2006), better protection from pathogens and pests (Turner 2001) and lower mortality probabilities (Chao et al. 2008) for tropical trees. The prediction  $P_{2-2}$  that low wood density species tend to die broken is supported in the NE, showing that broken and uprooted modes of death are related to wood properties in this region. However, in the NW, where trees generally have a lower wood density (Mann-Whitney *U* test,  $P < 0.001$ ) (see also Baker et al. 2004), we could not detect any effect of wood density on mode of death.

### Implications for forest structure, composition and dynamics

We found that in tropical forests with twofold differences in mortality rates, mortality mechanisms also differed markedly. Here, we propose that these differences in mortality mechanisms can help to maintain differences in forest composition in the two regions. NW Amazon forests are composed of low wood density species (Baker et al. 2004; ter Steege et al. 2006), prone to die broken and uprooted, creating relatively large gaps so favouring the same low density species. In contrast, NE forests are composed of high wood density species (Baker et al. 2004; ter Steege et al. 2006), tending to die standing, with a small impact on the forest canopy. This would further favour the regeneration of the same shade-tolerant, high-density species. Thus, forest structure, composition and dynamics in Amazonia may be determined partly by feedback processes in which mode of death plays a direct and prominent role. 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 NE (Sombroek 2001), with gentler topography, deeper soils and poorer soil fertility (C.A. Quesada, unpubl. data). While the ultimate driver might be environmental factors, the dominant modes of death and functional composition help to maintain the contrasting mortality rates in the two regions.

#### *Classification of mode of tree death*

Different modes of tree death imply quite different patterns of forest dynamics, so it is important to determine these correctly (Gale & Hall 2001), particularly for standing and broken dead trees, where the greatest potential for confusion lies. For example, during the census period 1980–2000 in the NE plots, both uprooted and “either standing or broken” are the dominant modes of death. This is partly due to lack of discrimination among standing and broken dead trees in this period. Here, we rearranged the traditional descriptions of mode of death available in the literature (e.g. Putz et al. 1983; Gale & Barfod 1999) and synthesised these with our field observations (e.g. the orientation of saprophytic fungi and the presence of resprouts) into a new key to assist future field classification of tree death modes in Amazonian forests (App. 2). Using this standardised key should help facilitate future cross-comparison among sites and research teams in the Amazon and across the tropics.

#### **Conclusions**

Death modes and tree attributes together help to understand the mechanisms of tree mortality and were found to differ in two parts of Amazonia. The results are consistent with our first hypothesis ( $H_1$ ) that high mortality forests are dominated by the broken mode of death. In NE Amazonia, slow-growing trees tend to die standing and low wood density trees tend to die broken, supporting hypothesis  $H_2$  that standing death is caused by *physiological failure* (slow growth) and broken death is related to low wood strength. Moreover, large trees in NE Amazonia are likely to die standing (indicating ageing), whereas large trees in NW Amazonia are likely to die uprooted (indicating structural imbalance). However,  $H_2$  is not supported by the results from NW Amazonia, where broken trees had unusually slow growth prior to death, suggesting a mortality mechanism caused by an interaction between *physiological failure* and *mechanical failure*. This region is dominated by softwood species (*weak mechanical strength*), which

may help explain the dominance of the broken mode. Thus, similar tree attributes can result in dissimilar modes of death, depending on the context of local dynamic regimes. Death modes reflect the different underlying causes of tree death and are likely, in turn, to affect subsequent forest dynamic processes and forest composition.

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### App. 1. Multivariate Models: Logistic Regression

Logistic regression (Hosmer & Lemeshow 2000) describes the conditional probability  $P$  that  $Y = 1$  during a given period of time and given predictors  $X_1, \dots, X_n$  as:

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

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*. In our study, models were assessed using two steps. (1) Testing the fitness of models by the Hosmer-Lemeshow goodness-of-fit statistic (Hosmer & Lemeshow 2000). (2) Ranking models according to Akaike weights ( $w_i$ ), which indicate the probability that model  $i$  is the best model for the observed data, given the candidate set of

models (Burnham & Anderson 2002). The Akaike weights ( $w_i$ ) are derived from a second-order Akaike's information criterion (AIC<sub>c</sub>), designed for small sample sizes (Burnham & Anderson 2002). All analyses were conducted in SPSS Version 13.0.

### Supporting Information

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

**Appendix S1:** Mode of death and average ( $\pm$  SD) tree attributes of the dominant families in northwestern and northeastern Amazonia.

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### App. 2. Key to the Mode of Tree Death.

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1. Main trunk standing with attached fine branches (not resprouts) . . . *Standing*
  1. Main trunk fallen on the ground . . . 2
  2. A fallen main trunk with standing stump . . . 3
  2. A fallen main trunk without obvious stump . . . 6
  3. Stump without resprouts . . . 4
  3. Stump with resprouts . . . 5
  4. Crown branches lying next to the standing stump, major branches scattered around, the standing stump with smooth and soft end, the fallen trunk with fungi growing perpendicular to the ground, and vegetation damage not noticeable . . . *standing (then broken afterwards)*
  4. Crown branches at the end of the fallen trunk, one major trunk on the ground, the standing stump with jagged end, the fallen trunk with fungi growing horizontal to the ground, and vegetation damage noticeable . . . *broken*
  5. Resprout(s) < 5 cm in diameter . . . *broken*
  5. Stump with attached resprout(s) > 5 cm in diameter . . . *standing (breakage is not the ultimate cause)*
  6. Root bole at least partially raised ('tip-up') with some soil exposed . . . *uprooted*
  6. Root bole not raised . . . 7
  7. Roots more decayed than the main trunk, vegetation damage not noticeable, and/or with fungi perpendicular to the ground . . . *standing (roots decomposed and then fallen, e.g. palms)*
  7. Roots equally decayed as the main trunk, vegetation damage noticeable, the fallen trunk with fungi growing horizontal to the ground, and/or have with resprout(s) . . . *broken at 0 m*
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