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Revealing the causes and temporal distribution of tree mortality in Central Amazonia

Clarissa G. Fontes^a Jeffrey Q. Chambers^b Niro Higuchi^c

Abstract

Tree mortality is a critical process in forest ecosystems, as it influences floristic composition, structure, dynamics, carbon storage, and forest nutrient cycling. However, the mechanisms behind tree death in tropical regions are still poorly characterized. This lack of information is mainly because tree mortality data come from long-interval inventories and studies that measured tree death seasonally are scarce. Here we offer novel insights into the power of fine temporal scale observations and we use a natural history approach to understand the processes and mechanism of tree mortality. We monitored tree mortality every month during one year, in 10 ha of terra-firme forest. To determine the pathways of mortality, we considered the state of the tree at the start of the investigation and the pre and post-mortem characteristics. From November 2010 to October 2011, 67 out of 5808 trees died. Despite the 2010 drought, mortality was highly correlated with monthly rainfall ($r = 0.85$). In total, six pathways of mortality were assessed. Storms were the main cause of mortality, killing 45% of all dead trees, followed by Biotic/abiotic factors accounting for 30% of tree mortality. The high mortality registered in the rainy season was mostly (78%) due to healthy trees dying uprooted or snapped. Finally, we would benefit from studies that assess mortality on a monthly basis and in combination with quantitative long-term data, we can substantially improve our understanding of the mechanisms behind tree death in the tropics.

Keywords: Causes of tree death, 2010 drought, Seasonality, Storms, Tree mortality, Tropical forest, Climatic disturbances

1. Introduction

What are the main agents of trees mortality in tropical regions and which climatic factors (i.e. storms or drought) have a greater impact on tree mortality? Even though tree mortality is one of the most studied processes in forest ecosystems, the answers to these questions are still unknown. First, very few studies directly assess causes of tree mortality during forest plot surveys, particularly in tropical forests. Second, tree mortality data come mostly from long-interval inventories and mortality information originates from permanent plots that are revisited, when frequent, once a year (most are re-measured with greater intervals of time; Phillips et al., 2010). In this study, we offer important insights into the power of fine temporal scale observations to understand the processes and mechanism behind tree mortality. We suggest a novel way of assessing tree death, and in combination with quantitative long-term data, it can substantially improve our understanding of tree mortality in the tropics.

Tree mortality is a critical process in forest ecosystems, as it influences floristic composition, structure, dynamics, carbon storage and forest nutrient cycling (Franklin et al., 1987, Chao et al., 2009, Toledo et al., 2013). Studies show a rise of tree mortality and turnover rates in the Amazon Basin (Phillips and Gentry, 1994, Phillips et al., 2004, Laurance et al., 2009, Toledo et al., 2011, Feldpausch et al., 2016) and this increase may be partially explained by changes in climate (Malhi & Wright, 2004). While some studies indicate that the intensification of the dry period (i.e. drought) is the main agent behind the increase of tree mortality (Allen et al., 2010, Phillips et al., 2010, Saatchi et al., 2013, Doughty et al., 2015), others suggest that an increase in storm intensity may also play an important role in elevated forest dynamism (Chambers et al., 2009, Espírito-Santo et al., 2010, Negrón-Juarez et al., 2010, Chambers et al., 2013).

Forests of the Amazon basin are estimated to store 86–96 Pg of carbon in aboveground biomass (Malhi et al., 2006, Saatchi et al., 2007) and a small increase in tree mortality can have great impact on atmospheric CO² concentration, accelerating the warming of the climate system (Phillips et al., 2009, Espírito-Santo et al., 2014). Furthermore, earth system models (ESMs) predict an increase in the frequency and intensity of the dry season and storm events for the Amazon region (Marengo et al., 2009, IPCC, 2014). Therefore, understanding how climatic factors influence tree mortality has become increasingly important.

In addition to climatic factors, other natural agents such as biotic elements (i.e. competition, senescence, insect, fungi and liana infestation), mechanical injury, and lightning strike can also have a significant effect on tree mortality (Magnusson et al., 1996, Dangelo et al., 2004, van Mantgem and Stephenson, 2007, Ingwell et al., 2010, Toledo et al., 2013, van der Heijden et al., 2015). However, the importance of these agents and how they will affect mortality under a changing climate is still unknown, mainly because detailed and frequent assessments of tree death are still missing in the tropics.

Most researchers measure tree mortality through long-interval inventories (plots are re-visited once a year or more often at a greater interval of time) and studies that measured tree death seasonally are scarce (e.g. Laurance et al., 2009). The lack of studies that monitor mortality during short intervals of time is surprising, particularly considering the improvement these fine-scale data can generate (i.e. a mechanistic representation of tree death). Long intervals between measurements (a year or more) are useful for estimating average rates, yet they fail to generate fine-scale information on proximal causes of mortality. A new approach to study tree death focused on short-term inventories is needed (Acker et al., 2015), especially in the face of changes in climate and associated increases in drivers of mortality. Therefore, with short-interval inventories (e.g. monthly) mortality patterns throughout the year can be assessed, including the effects of seasonal

(climatic) variation on tree mortality and the reliable elucidation of causes of tree death.

In this perspective, we assessed tree mortality bi-monthly during a one-year period in 10 ha of *terra-firme* forest in Central Amazonia to answer the following questions: (i) what are the patterns of tree mortality distribution throughout the year? (ii) What are the main pathways of mortality in this forest? To answer these questions, 5808 trees (≥ 10 cm DBH) were monitored continuously for a year and the preconditions and post-mortem of the individuals were analyzed in order to identify the detailed cause of their death. We predict that if seasonal variation in climate throughout the year (i.e. dry vs. wet season) is the strongest driver of mortality, more trees will die uprooted and snapped during the rainy season when the soil is saturated and heavy rain and windstorms are more frequent (Brokaw, 1982, Whitmore, 1990). Also, if the 2010 drought had a significant effect on tree mortality, trees will die standing with no signs of other proximate causes of mortality (e.g. lianas, fungi or insect infestation and/or mechanical injuries).

2. Materials and methods

2.1. Study area

The study was conducted in two 5 ha transects located at Estação Experimental de Silvicultura Tropical (EEST; 02°37'S, 60°11'W) of Instituto Nacional de Pesquisas da Amazônia (INPA), Amazonas, Brazil (Fig. 1). The transects are permanent plots installed in 1995 by the Jacaranda project (INPA/JAICA) and since 1998 their vegetation has been monitored every two years.

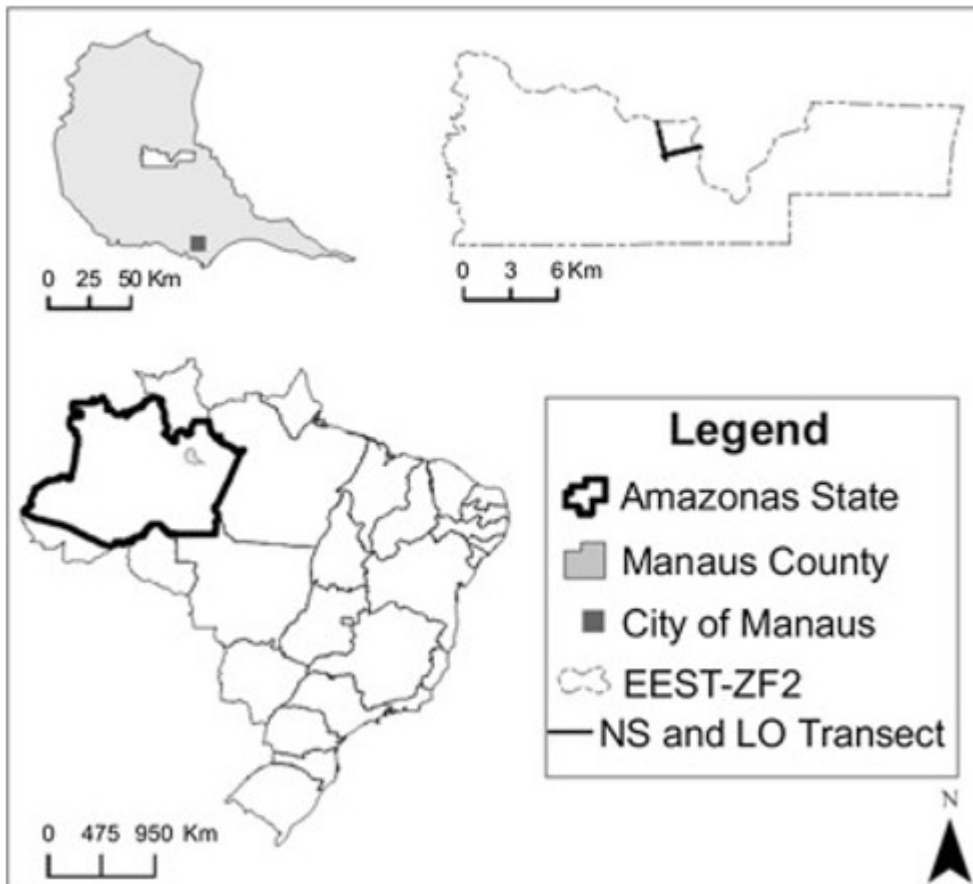


Fig. 1. The study was carried out in two transects (North-South- NS and East-West -LO) located in Estação Experimental de Silvicultura Tropical (EEST) in Central Amazon, NNW of the city of Manaus-AM, Brazil. The site is run by Instituto Nacional de Pesquisas da Amazônia (INPA).

There are three macro and mesoscale mechanisms which determine rainfall in the region: diurnal convection resulting from surface heating; instability lines propagating from N-NE inland, from the Atlantic coast; and mesoscale and large-scale aggregated convection associated with frontal systems from S-SE (Fisch et al., 1998). Annual rainfall is around 2000–2600 mm, with the rainy season from December to May, when mean monthly rainfall exceeds 300 mm (Sombroek, 2001, Higuchi et al., 2011). The drier months are from July to September when rainfall can be less than 100 mm per month. The air humidity ranges from 77 to 88%, with an annual average of 84%. The mean monthly temperature is 26 °C, minimum 19 °C in April and maximum 39 °C in September (Sombroek, 2001). Localized wind gusts in strong storms can produce windthrow of trees in so-called blowdowns (Nelson et al., 1994).

The transects have three distinct topographic compartments, upland plateaus, slopes, and valleys and they are equally represented in the study area, occupying respectively 34, 32 and 34% of the total area. Plateaus have high clay content soils (Oxisols) and are located on a higher elevation while the valley areas are characterized by sandy soils (Spodosols) with the water

table near the surface and subject to seasonal flooding. The maximum altitudinal difference between plateau and valley areas is about 140 m. There is no slope failure in the area such as landslides or mudflows. The area is covered by *terra firme* forest and there was no evidence of human intervention for at least the previous 100 years. *Terra firme* forests are characterized by a closed canopy with a high diversity of woody and herbaceous species. The understory is dense with abundant acaulescent palms on plateaus and canopy palm species in valleys (Kahn, 1986). During the last floristic inventory of the transects (in 2010) 879 species were found, belonging to 61 families.

2.2. Sampling design

The two transects have a total area of 10 ha (5 ha each; 20 × 2500 m) and all trees with a diameter at breast height (DBH) ≥ 10 cm were recorded (palms and ferns were excluded). Each transect was visited every other month during a period of one year (November 2010 to October 2011) and a total of 5808 living trees were monitored.

To determine pathways of mortality with improved accuracy, it is important to describe the state of all live trees at the start of the investigation. With this information we assessed in detail the condition the trees were before their death, and thus could better determine the causes of mortality. Pathways of mortality were not determined *a priori*, but rather were classified after the fieldwork was complete, and pre and post characteristics of tree mortality were analyzed. The characteristics of the living trees we monitored bi-monthly were: percentage of leaf loss in the crown, signs of mechanical damage (crown and trunk) and the presence of lianas, fungi, and insects (in the crown and trunk). During every measurement, a number from 1 to 4 was assessed for each of these characteristics, 1 being excellent condition and 4 very poor condition. For example, in the case of 'percentage of leaf loss', the number 1 means: 0–25% of leaf loss, 2: 25–50% of leaf loss, 3: 50–75% of leaf loss, and 4: 75–100% of leaf loss. The other characteristics were assessed in a similar way. After a tree was diagnosed dead, its mode of death was assessed: standing, uprooted or snapped (for description see Putz et al., 1983). All trees uprooted and snapped below 1.30 m height were considered dead. To determine the pathway of mortality we considered the state of the tree at the start of the investigation, the numbers from 1 to 4 assessed for each characteristic analyzed on each of the months (amount of leaves, signs of mechanical damage and presence of lianas, fungi, and insects) and the mode of death.

2.3. Data analysis

Annual mortality rate was calculated as suggested by Sheil et al. (1995). The taxonomic system used was the Angiosperm Phylogeny Group (APG III 2009) and names were standardized according to the List of Species of the Brazilian Flora (2013). All fungi present on dead tree's trunk/crown/root were collected and taken to the Laboratório de Patologia da Madeira at INPA. The

specimens were oven dried (50–60 °C), packed and identified by specialists. A Chi-square test (χ^2) was used to investigate if causes of tree death were independent of time.

The precipitation data were obtained from the micrometeorological K34 tower located at Reserva Biológica do Cuieiras - LBA, around 2 km (on average) away from the transects. The relationship between tree mortality and precipitation was analyzed using a correlation test. Tree fall direction (trees that died snapped or uprooted) was measured with a compass. The software Oriana (Kovach Computing Services) was used to make the circular histograms of tree fall direction. The Rao's Spacing Test of Uniformity (Rao, 1967) was used to test the null hypothesis that tree fall was uniformly distributed.

3. Results

3.1. Tree mortality and its relationship with climatic factors

In the period of one year, 67 trees died (6.7 dead trees per hectare). This translates into an annual mortality rate of 1.15%. There was no predominant mode of death (24 trees died uprooted, 23 standing and 20 snapped) however, uprooted trees accounted for 55.2% of the basal area of the dead trees (standing dead: 30% and snapped: 14.8%). Trees with $10 \leq \text{dbh} < 20$ cm showed substantially higher mortality than trees with $\text{dbh} \geq 20$ cm (Fig. 2a), indicating smaller trees are more vulnerable to death. Mean annual growth did not significantly differ between the three modes of death (Fig. 2b; T-test p-value ranges from 0.0532 to 0.0612). In addition, 24% of the trees died in the Plateau area, 39 in the slopes and 37% died in the Valleys. Around 18% of the dead trees belonged to the Fabaceae family, followed by Burseraceae (16.4%) and Rubiaceae (10.5%) and 47 species out of 55 documented occurred only one time (S1. Supplemental information).

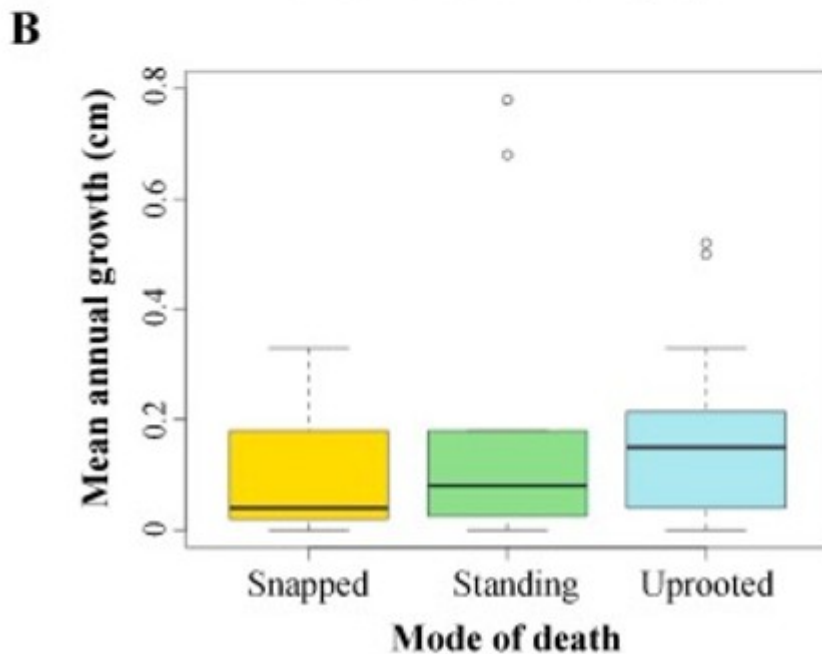
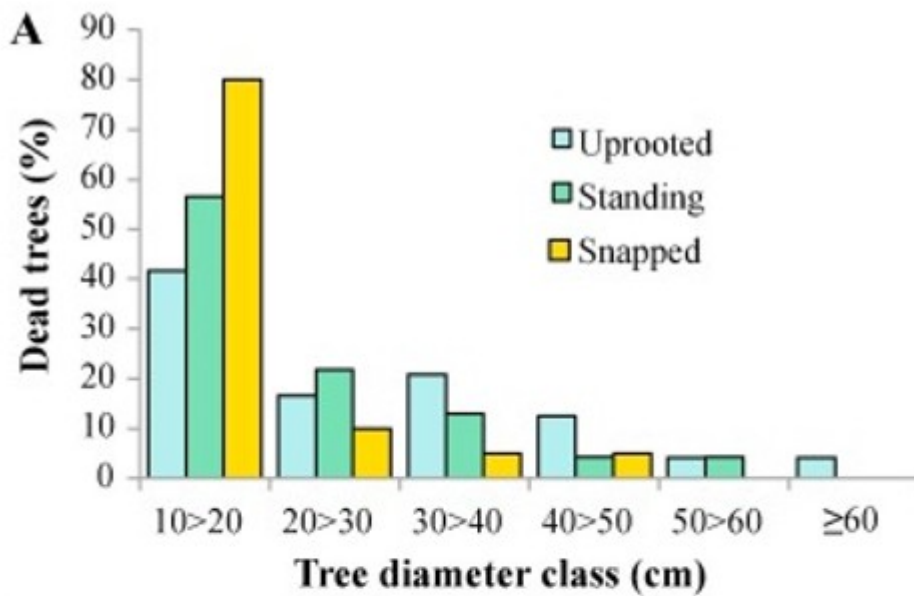


Fig. 2. (a) Proportion of dead trees in each category of mode of death (uprooted, standing or snapped) per DBH (diameter of breast height) class during November 2010 to October 2011 in a Central Amazonian forest. (b) Mean annual growth from 2006 to 2010 from the trees that died snapped, standing and uprooted during the study period (T-test p-value ranged from 0.532 to 0.0612).

Tree mortality was strongly and positively correlated with monthly rainfall ($r = 0.85$; p -value = 0.001; Fig. 3) even when only uprooted and snapped trees were considered ($r = 0.84$; $r^2 = 0.71$; p -value = 0.0006). In addition, the direction of tree fall (snapped or uprooted) was non-random (Fig. 4; 95% confident limit). During our study (November 2010 to October 2011), tree mortality was greater from January to April 2011. This period also corresponds to the months of highest precipitation in the area. April was the

month with the highest rainfall (Fig. 3a) and was also when 9 individual trees fell in one single event (Fig. 4a). These results suggest that Central Amazonian trees are highly vulnerable to strong rain and windstorms.

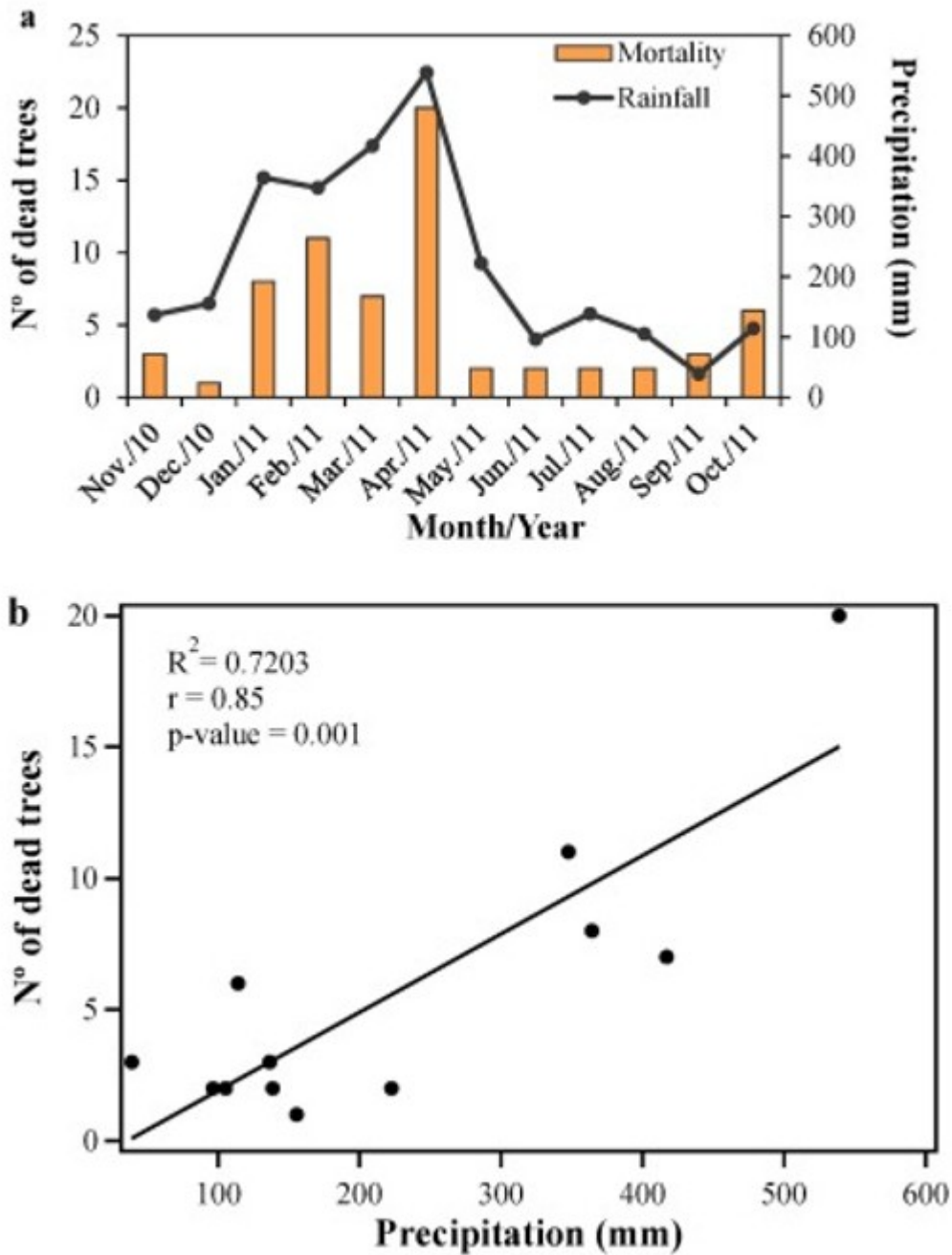


Fig. 3. (a) Tree mortality and precipitation, and (b) the relationship between these two variables throughout one year of measurements (November 2010 to October 2011) in a primary Amazonian forest in Brazil.

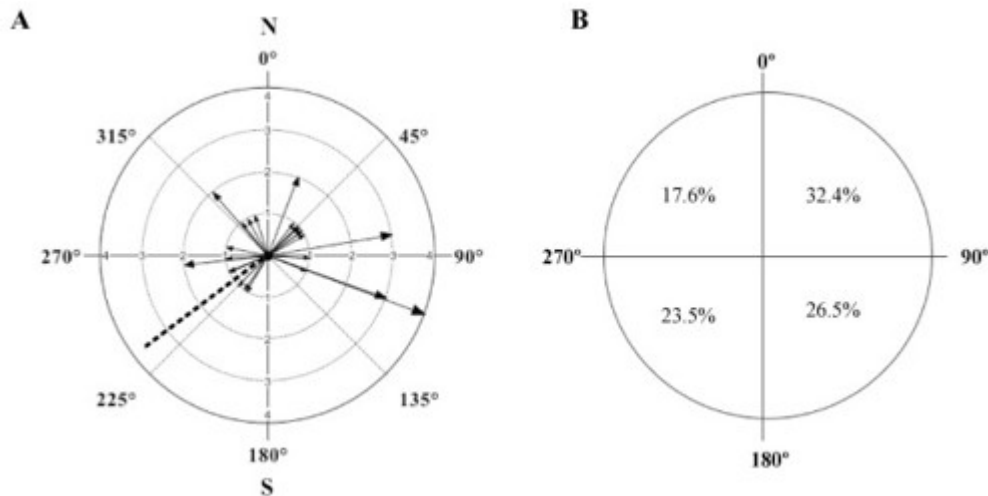


Fig. 4. (a) Circular histogram of tree fall direction (trees that died uprooted or snapped). The size of the lines corresponds to the number of trees that fell in that direction and the dashed line represents the dominant slope direction in the study area; (b) The percentage of dead trees that fell in each of the quadrants during November 2010 to October 2011 in a primary forest of Central Amazon, Brazil.

3.2. Pathways of tree mortality

A total of six categories of pathways of tree mortality were assessed, two of them being combinations (initial factor is different from the final factor; Table 1). *Storms*, which are the impact of wind and rain events on tree mortality, were the main pathway of mortality, killing 45% of all dead trees (Table 1). When a microburst of wind impact a forest area, all trees fall simultaneously and is very hard to separate these events from when large trees top smaller ones, therefore, trees uprooted and snapped in groups (domino effect) were put into the *storms* category. *Biotic/abiotic factors* were also important accounting for 30% of tree mortality.

Table 1. The six pathways of mortality assessed from November 2010 to October 2011 in a Central Amazonian forest, AM-Brazil. Their description and number of dead trees in each category are also found.

Causes of tree death	# of Trees	Description
Storms	30	Trees that died snapped or uprooted and were in a good condition* (trunk and crown) before dying.
Biotic/abiotic factors	20	- Trees that died standing and had no mechanical damage or signs of infestation by lianas, insects or fungi. Their death was probably due to resource availability (e.g. competition, drought, flooding, light, and others); - Standing dead trees that clearly died due to insects, fungi or/and lianas infestation (crown and/or trunk).

Causes of tree death	# of Trees	Description
Combination 1: Physical injury + biotic/abiotic factors	10	Trees that since the first measurement had a broken crown. After the breakage, trees released sprouts suggesting a recovery, but they eventually died due to biotic/abiotic factors.
Combination 2: Biotic/abiotic factors + physical injury	3	Trees that died snapped or uprooted and were already in a bad condition before dying. Before uprooting or snapping the individuals had few leaves in their crown, mechanical injury, and/or signs of insect, lianas, and fungi infestation.
Lightning	3	Trees that died in groups of two or more and were in good condition* before being hit. Most of the understory trees also died and the trees belonged to more than one species (not featuring a pathogen attack).
Crushing by a falling dead tree	1	Trees that died snapped or uprooted and were hit by a dead tree that was in an advanced stage of decomposition.

*

Good condition = Normal amount (more than 75%) of leaves in their crown, no mechanical damage (recent or old) and no lianas, insects or fungi infestation.

Trees can also die due to a combination of different factors (initial factor is different than the final factor). In this case, the first factor (initial cause) weakens the tree, which becomes more vulnerable to the second factor (final cause). During this study, two combinations were detected between *storms* and *biotic/abiotic factors* (**1** - *physical injury + biotic/abiotic factors* and **2** - *biotic/abiotic factors + physical injury*). In these combinations, physical injury is directly or indirectly associated with *storms* and even though the same factors are important for the tree's death, the two combinations differ in their initial and final pathway of mortality (the order of events matter; see Table 1 for description). Another difference is the mode of tree death, on the first combination (**1**) trees died standing while in the second (**2**) they were uprooted or snapped. Association **2** was more frequent during that year (15% of dead trees; Table 1) and 90% of the individuals in this category were smaller than 20 cm DBH. Therefore, *storms* and *biotic/abiotic factors*, as well as their combinations, account for 94% of tree death, indicating that these factors can be the main drivers of tree mortality in this tropical forest.

During one year of monthly measurements, a lightning event was documented and was responsible for killing three individuals (Table 1). A lightning hit was identified on one of the dead trees and no fungus was present on the root material we collected. This is one of the first works to register lightning events in Amazonian forests. The last significant pathway of mortality was *crushing by a falling dead tree* killing one (DBH \geq 10 cm) of the 67 dead trees.

Pathways of mortality were not independent of time (period of the year; $\chi^2 = 105.61$; $df = 55$; $p = 0.00005$). Trees killed by *biotic/abiotic factors* were more common in February while the ones killed by *storms* were more frequent during the rainy season (February to June), reaching its maximum in April. Thus, pathways of mortality (and in consequence mode of death) are related to seasonal variation, suggesting that intensity and duration of a specific season can have great effects on tree mortality and forest structure.

4. Discussion

The most severe drought registered in at least the last 100 years in the Amazon region occurred between July and September 2010 (Lewis et al., 2011, Xu et al., 2011), just a few months before our mortality assessments started (November 2010). We monitored 10 ha of *terra firme* forest monthly for a year (November 2010 to October 2011) after the 2010 drought, but we did not register many trees that could have died from its effects. Instead, mortality was higher during the rainy season (Fig. 3).

It can be argued that the effect of water deficit can persist for months after the end of the dry season (Phillips et al., 2010) and thus, the mortality assessed in the rainy period (January to April 2011) could be a late effect of the drought. However, the trees in the transects were monitored at short intervals of time and it is possible to affirm that the high mortality registered in the rainy season was mostly (78%) due to healthy trees dying uprooted or snapped. Therefore, even though forests in Central Amazon experienced a strong drought in 2010, *storms* were assessed as the main agent of tree mortality during 2010–2011 in ZF-2 forests. Nonetheless, studies have shown that tree mortality increases, and forest biomass and productivity decrease with long-term droughts (Nepstad et al., 2007, Brando et al., 2008). Thus, it would be interesting to monitor causes of tree death over long-term droughts to be able to better characterize their effect on forest structure and composition.

Storms can be partitioned into wind and rain and can have a great impact on tree mortality (Laurance et al., 2009, Marra et al., 2014). Forces to uproot or snap a healthy tree are very large (130,828–191,558 N.m; Ribeiro et al., 2016) and since we do not have any landslides or mudflows in the area, the only processes that can generate forces that large is high wind events associated with rainfall (Sellier & Fourcaud 2009). Heavy rain associated with wind bursts can change the tree's gravity center and cause it to fall (Young and Hubbell, 1991, Young and Perkocho, 1994, Ribeiro et al., 2016). Furthermore, our findings corroborates a study conducted in a nearby area (~10 km away) that found tree size (DBH) but not topographic position was a significant predictor of critical turning moment (rotational force at the moment a tree snaps or uproots) for all of the species they analyzed (Ribeiro et al., 2016), indicating that tree diameter is a better predictor of tree failure (snap or uproot) than topography in this area.

Wind velocity and direction are very dynamic and can vary over small spatial scales. The topography and canopy height at the transects can generate a wind airflow regime much too complex to be captured by standard measurement system like a single tower (Tóta et al., 2012). We found that trees that died uprooted or snapped fell non-randomly, in a similar direction (Northeast and East) of the prevailing winds (Zhuang et al., 2017). Furthermore, the number of trees that snapped and uprooted was considerably higher at the peak of the rainy season, with 9 out of 14 trees that died in this period (April) falling in one single event. Using the model proposed by Chambers et al. (2013) the return time of tree fall events with 13 trees (4 were outside our plots) in 10 ha is around 5.5 years. In conclusion, storm effects are stochastic events difficult to be predicted and our study, among others (Arriaga, 2000, Fisher et al., 2008, Marra et al., 2014), have shown the impacts of these events on forest structure and composition. The documentation of these events helps to quantify their size and frequency (Frolking et al., 2009), improving gap mortality models and carbon flux estimates (Keane et al., 2001, Saleska et al., 2003).

Biotic/abiotic factors were also an important pathway of mortality during our study. Unlike *storms*, this cause of mortality is a gradual process culminating in the physiological death of trees (Franklin et al., 1987, Chao et al., 2009). Agents of mortality in this category are difficult to determine because often multiple factors are involved. Yet, three individuals probably died due to fungi infestation in this category. One tree was probably killed by hemiepiphyte (*Coussapoa trinervia* Spruce ex Mildbr.) and another three probably died due to fungi infestation (two were attacked by *Gonoderma* sp. and one by *Auricularia delicata* Fries). In temperate forests, trees often die from pathogen attack (Harcombe and Marks, 1983, Rizzo et al., 2000, van Mantgem et al., 2009), while in tropical forests due to their high diversity these attacks are not commonly registered (Phillips & Gentry 1994). However, as documented here and in a few other studies (Freckleton & Lewis 2006) tropical trees can die due to fungi infestation. In the transects, two fungi species (*Gonoderma* sp. and *Auricularia delicata*) were responsible for killing three individuals. These fungi species are known for their pathogenicity and they can cause necrotic lesions that spread rapidly in the xylem of their hosts (Pearce 1996). Our study is one of the first to quantify fungi importance on tropical tree mortality, opening new research opportunities in the tropics.

Also, one tree probably died due to liana (*Coussapoa trinervia* Spruce ex Mildbr.) infestation in the category of *Biotic/abiotic factors*. Because of their indirect effect on tree mortality (e.g. resource competition and suppression of tree growth), it can be difficult to determine when lianas are the proximal cause of tree death (van der Heijden et al., 2008, Ingwell et al., 2010). Yet, there are species that are known for their aggression like the hemiepiphyte *C. trinervia* (Oliveira et al., 2008) and despite their small representation in the transects, studies indicate a positive correlation between tree mortality

and liana abundance (Grauel and Putz, 2004, Schnitzer et al., 2005, van der Heijden et al., 2008, van der Heijden et al., 2015).

The remaining trees (16) that were in the *Biotic/abiotic factors* category, died without apparent reasons (however some did have small liana infestation). Many studies have attributed these kinds of deaths to senescence, (Chao et al., 2008, Chao et al., 2009, Lines et al., 2010, Toledo et al., 2013) and one of the individuals (*Tachigali* cf. *myrmecophila*) probably died due to monocarpic senescence. Yet, there is no clear evidence that perennial trees can die from programmed (physiological) senescence (Mencuccini et al., 2005, Munne-Bosch, 2008, Stephenson et al., 2011) and researchers should use caution in attributing mortality of perennials to senescence (Lee & Muzika 2014). The primary agent of these trees' mortality is hard to determine but causes such as competition, light availability, nutrient acquisition, physiological constraints, and drought may be playing a role.

Lightning was also a pathway of mortality observed in the transects during the study period. These events usually occur at the beginning of the rainy season when a great amount of aerosols is still present in the atmosphere (Davidson et al., 2012). A single event of lightning killed three individuals during our study (DBH \geq 10 cm) and despite its low representation, mortality by lightning can be more frequent than first imagined (Magnusson et al., 1996). Death by lightning is usually difficult to detect after a few months of its occurrence and only short-interval inventories are able to identify these events. Therefore, long-interval inventory may fail to identify lightning strike mortality in the forest, attributing those deaths to biological factors, competition or senescence.

5. Final considerations

Pathways of mortality in tropical forests can be reliably determined if live tree conditions (e.g. amount of leaf, signs of mechanical injury and liana/fungi infestation) are frequently monitored. For Central Amazonian forests, a three-month interval between censuses should be enough. However, researchers should ponder how dynamic the forest is before choosing the measurement interval time. Mode of tree death is strongly related to the proximate cause of mortality and is important to consider. In addition, dividing the cause of death into initial and final may help determine the factors behind tree's mortality.

Finally, we would benefit from studies that assess mortality on a monthly basis. These short-interval inventories in combination with long-term observations can give us new insights on the effects of climatic variables (e.g. wind, rain, and drought), and thus climate change, on tree mortality. In conclusion, short-interval inventories are more expensive and time-consuming than long-interval assessments, however, it is the only way to generate fine-scale data that are vital for tree mortality models, conservation policies, and forest management.

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