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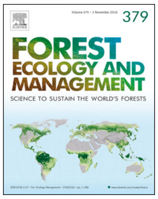

Revealing the causes and temporal distribution of tree mortality in Central Amazonia

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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.

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 & 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 CO^2 concentration, accelerating the warming of the climate system (Phillips et al,. 2009; Espirito-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

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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 & 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.

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).

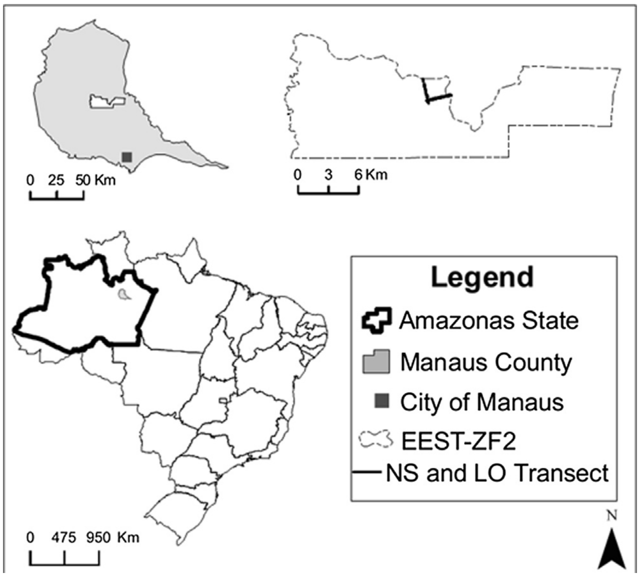

Fig. 1. The study was carried out in two transects (North-South- NS and East-West –LO) located in Estação Experimental de Silvicultura Tropical (EEST) in Central Amazon, NNW of the city of Manaus-AM, Brazil. The site is run by Instituto Nacional de Pesquisas da Amazônia (INPA).

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