Trees, Forests and People 7 (2022) 100180

Contents lists available at ScienceDirect

Trees, Forests and People

journal homepage: www.sciencedirect.com/journal/trees-forests-and-people

Primary modes of tree mortality in southwestern Amazon forests

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A R T I C L E I N F O

Keywords:
Tree mortality
Forest dynamics
Amazon rainforest

A B S T R A C T

Tree mortality rates and the modes of tree death have recently been extensively investigated in the Amazon. However, efforts to describe these processes have not been well distributed across the basin. No study has yet investigated in depth tree mortality process in the unique low, open, bamboo-dominated forests of southwestern Amazonia, a region with a distinct climate and the epicenter of recent severe drought events. Here, we investigated the leading ways that trees die in the *terra-firme* forests of the southwestern Brazilian Amazon, to understand whether the dynamics of mortality differ from those recorded in other parts of the basin. Using data from six permanent plots located in southwestern Amazonia, we calculated the mortality rate for three main modes of tree death: standing, broken and uprooted. We thus identified the predominant mode of death over a 14 year period (2002–2016). We found that trees in the southwestern Amazon died mainly standing (325 trees, 0.8% year^{-1}) and broken (362 trees, 0.8% year^{-1}); significantly fewer trees died uprooted (156 trees, 0.4% year^{-1}, equivalent to less than one in five of all trees dying). During the study period, the tree mode of death with the greatest proportion in the region alternated between standing and broken trees. Forest characteristics of the southwestern Amazon, like presence and high density of bamboo culms, and the fact that the region was subject to severe droughts in 2005 and 2010, may be affecting how trees die in southwestern Amazon. The presence of these factors makes the forest dynamics of the southwestern Amazon different from other regions of the Amazon basin.

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https://doi.org/10.1016/j.tfp.2021.100180
Received 27 September 2021; Received in revised form 11 December 2021; Accepted 18 December 2021
Available online 4 January 2022

1. Introduction

Mortality is a key element of forest dynamics - for example, the death of early successional tree species may create the space needed for late-successional species to develop and dominate (Lewis et al., 2004a; Holm et al., 2014). Similarly, the mortality of a large tree makes room for the development of understory trees (Laurance et al., 2009; Holm et al., 2014). Monitoring the dynamics of tree assemblages through the analysis of mortality allows for an understanding of vegetation responses to climatic phenomena, changes in land use, and interactions with biological agents (*e.g.* fungi, insects, mammals) (Swaine et al., 1987; Sheil et al., 2000). Some examples of vegetation responses identified in previous studies are: (i) larger trees die more frequently due to xylem cavitation; (ii) trees of early successional species tend to die faster, grow faster, and have shorter life-cycles; and (iii) tree assemblages located on more fertile soils tend to have higher mortality rates (Swaine et al., 1987; Caspersen, 2004; Toledo et al., 2011; Giardina et al., 2018). In addition, long-term studies with the monitoring of permanent plots show that, over the decades, the dynamics of tropical forests are accelerating, mainly due an increase in mortality and recruitment rates and, consequently, an increase in the rate of forest turnover (Phillips et al., 2008, 2016a, 2016b). Changes in climatic regimes appear to be modifying and shaping tropical vegetation structure, leading to changes in species composition and mortality rates (Swaine et al., 1987; Phillips et al., 2004; Esquivel-Muelbert et al., 2018).

How trees die – *i.e.*, their mode of death - influences forest dynamics, and each mode of death has a specific cause or results from an interaction of different processes. Through observation of tree modes of death, it is possible to characterize the forest dynamics of a region (Chao et al., 2009; Esquivel-Muelbert et al., 2020). Understanding the relation between the causes and modes of death in the Amazon forest over geographic and temporal gradients is important for parameterizing and validating models that predict changes in global biogeochemical cycles (water, carbon), global temperature, rain patterns (biotic pump) and ecosystem functions (cycling and regeneration) (Laurence et al., 2009; Esquivel-Muelbert et al., 2018; Aleixo et al., 2019). Moreover, studies of this kind provide information about the events that kill more trees (*e.g.* winds, droughts and pathogens), and can help identify which taxonomic or functional groups of plants that are harmed or favored by changes in mortality patterns.

The causes and modes of death also vary over time and between different regions with similar vegetation because the structure and floristic composition of the forest, as well as being affected by biotic agents and stochastic natural phenomena, is also conditioned by geographic and temporal gradients (Swaine et al., 1987; Phillips et al., 2004; Esquivel-Muelbert et al., 2020). For that reason, studying modes of death in areas that have not yet been investigated and with different physical and biological characteristics is essential. Amazonia, an almost 6 million square kilometers expanse of tropical forest, is particularly challenging to characterize but may be expected to have great ecosystem variety. In the Amazon, mortality rates are usually much higher in the western and southern parts (2.3–2.9% year^{-1}) than in the northern, eastern and central portions (0.8–1.1% year^{-1}; Chao et al., 2009; Fontes et al., 2018). Further, the mortality rates in the forests from Northwest of the basin is higher than in Central Amazon, where the productivity (Malhi et al., 2004) and biomass (Baker et al., 2004) are lower.

This variation in mortality can be largely attributed to the characteristics of the species that compose each region. In the western and southern parts, trees have lower basic wood density than those in eastern and central areas, and in general wherever the community is dominated by species trees with high wood density, there are relatively low mortality rates (Chao et al., 2009; Toledo et al., 2011). Regarding the temporal variation, an example is the 68% increase in the mortality rate in the central Amazon region from 1981 to 2003, potentially due to precipitation anomalies and the increase in temperature as well as underlying increases in productivity (Phillips and Gentry, 1994; Brienen et al., 2015; Phillips et al., 2004; Laurance et al., 2009).

Forest regions with distinct ecosystem structure and dynamics may be expected to have different mortality rates and dominant mode of death compared to others. The southwestern Amazon, a region also known as MAP, which encompasses the tri-national frontier between Madre de Dios (Peru), Acre (Brazil) and Pando (Bolivia) (Nelson, 1994; Vasconcelos et al., 2005; Southworth et al., 2011), is characterized by the predominance of open bamboo-dominated forests. Here, natural dynamics may be affected by endogenous disturbance processes driven by bamboo (*Guadua* spp.), which tends to colonize disturbed areas due to its aggressiveness and the ability to colonize open areas, and has a characteristic fixed life-cycle before dying back (Griscom and Ashton, 2003; Silveira, 2005; Smith and Nelson 2011; Medeiros et al., 2013). In addition, the southwestern Amazon has experienced strong effects of climate change, being the epicenter of two recent severe droughts in 2005 and 2010 (Aragão et al., 2007; Lewis et al., 2011). While these characteristics of the southwestern Amazon may lead to different characteristics in tree mode of death compared to elsewhere, this remains unstudied. To identify patterns in modes of death, we used a database of long-term forest inventory plots located in the southwestern Amazon, all established and monitored by some of the authors, and analyzed tree mortality over a 14-year period to answer the following question: what are the most frequent modes of tree death in southwestern Amazonia?

2. Material and methods

2.1. Study area and database

The study was carried out using data from long-term forest inventory plots accessed via the ForestPlots.net repository, which aggregates information from permanent plots in tropical regions and provides cooperation and collaboration through data sharing for studies of vegetation dynamics in tropical regions (Lopez-Gonzalez et al., 2011; Blundo et al., 2021). Six permanent plots located in Brazil were selected to represent the southwestern Amazon, chosen because they contain multiple inventories carried out in communities with homogeneous forest structures (Table 1). There are others plots in southwestern Amazon located in Bolivia and Peru, but these are mostly towards the Andean and dry forest and savanna fringes of Amazonia-Cerrado, or lack multiple censuses, making them unsuitable for our analyses. The region features a tropical monsoon climate (Am), according to the Köppen classification, with average annual rainfall of 1600–2500 mm and with average annual temperature of 22–26 °C (Table 1; Alvares et al., 2013).

2.2. Data collection

We used plot data covering a period between 2002 and 2016, *i.e.* the first year in which mode of death was recorded until the most recent data available in the database at the time of data collection (Table 1). Plots monitoring followed a standard RAINFOR (Amazon Forest Inventory Network) protocol (Phillips et al., 2016a, 2016b). Briefly, in each forest inventory all trees and palms that have a stem diameter at breast height (DBH; 1.3 m) ≥ 10 cm are measured, tagged and identified. Tree conditions including stem inclination, stem bifurcation, presence of lianas and other features are also recorded (Flag 1); if a tree or a palm is dead, their mode of death and probable causes of mortality are identified and recorded (Flag 2) (Table 2).

For the plots selected in this study (Table 1), the time span used to calculate mortality rates were those available in the ForestPlots.net repository: 2002–2003, 2003–2006, 2006–2009, 2009–2010, 2010–2011, 2011–2013 and 2013–2016. After evaluating the periods available we verified that the period 2009–2010 was registered only in one plot (DOI-01) and excluded this period from the analysis so as not to bias our results. We evaluated the modes of death based on Flag 2 data (Phillips et al., 2016a, 2016b; Table 2). Flag 2 presents a field classification that aims to infer the tree mode and cause of death, following protocols

Table 1
Characteristics of the six selected permanent plots in southwestern Amazon: [a]OOWB - Open Ombrophilous Forest with Bamboo; [b]DOF - Dense Ombrophilous Forest; [c]OFWPB - Open Ombrophilous Forest with Palms and Bamboo. The classification of forest typologies follows that established by the Ecological Economic Zoning promoted by the Government of Acre (Acre, 2010).

Plot code	Area	Size	Decimal coordinates	Annual average temperature	Average annual rainfall	Elevation	Forest typology
DOI-01	1 ha	10 × 1000 m	latitude -10.57, longitude -68.32	25.8 °C	1830 mm	203 m	OOWB[a]
DOI-02	1 ha	20 × 500 m	latitude -10.55, longitude -68.31	25.8 °C	1830 mm	203 m	OOWB[a]
FEC-01	1 ha	400 × 25 m	latitude -10.07, longitude -67.62	25.9 °C	1921 mm	170 m	DOF[b]
POR-01	1 ha	10 × 1000 m	latitude -10.82, longitude -68.77	25.1 °C	1661 mm	268 m	DOF[b]
POR-02	1 ha	10 × 1000 m	latitude -10.80, longitude -68.77	25.1 °C	1661 mm	268 m	DOF[b]
RFH-01	1 ha	200 × 50 m	latitude -9.75, longitude -67.67	26.0 °C	1940 mm	176 m	OFWPB [c]

Table 2
Grouping of flags in the four main tree modes of death in the southwestern Amazon forests.

Flags	Description	Mode of deaths
a	Standing dead	Standing dead
b	Broken (broken trunk)	Broken dead
c	Uprooted (root facing up)	Uprooted dead
d	Standing or broken (probably died standing)	Standing dead
e	Standing or broken (probably died broken)	Broken dead
f	Standing or broken dead	Others
g	Broken or uprooted (probably uprooted)	Uprooted dead
h	Broken or uprooted (probably broken)	Broken dead
i	Broken or uprooted	Others
k	Disappeared	exclude
l	Assumed dead	exclude
m	It is not known how	exclude

established by Chao et al. (2009), in addition to recording the number of trees involved in the mortality event (Table 2).

We initially grouped Flag 2 items into three main modes of death (standing, broken and uprooted) and we created a category called "other", which includes trees that do not clearly fit into those modes (Table 2). We categorized individuals in flags by mode of death for each year that a remeasurement was performed. We employed data filtering, such that trees not found (k), or whose geographic coordinates were incorrectly reported in the initial inventory (l) or were so damaged that they did not allow the identification of the mode of death (m) were excluded from the statistical analysis.

2.3. Data analysis

After filtering the data, we counted the number of trees by mode of death and calculated the overall mortality rate (m) for each type of mode of death in each remeasurement, and the mortality rate for each mode of death in the total time interval. For that, we used Eq. (1) (Sheil et al., 1995) because the forest inventories were carried out at irregular intervals of time and each plot had a different number of individuals.

$$m = 1 - [1 - (N_0 - N_1)/N_0]^{\frac{1}{t}} \quad (1)$$

where: N_0 = number of individuals in the initial time; N_1= number of individuals in the final time; t = time span measured in years.

As Eq. (1) Sheil et al., 1995) implicitly assumes that individuals in plots are homogeneous in terms of their dynamics, we applied an empirical correction (m_c) proposed by Lewis et al. (2004b); (Eq. (2)) to the mortality rate to allow comparisons among plots with different species and different census intervals (see correlation between mortality rates calculated by Eqs. (1) and ((2) in Appendix 2).

$$m_c = m{\cdot}t^{0.08} \quad (2)$$

Where: m = mortality rate; t = time span between plots remeasurement, in years.

Since we evaluated different modes of death in the same six plots over time, we used a one-way analysis of variance (ANOVA) for repeated measures, using the aov function in R, to compare the average annual mortality rates between the three modes of death (standing, broken and uprooted). As our data are in percentage, *i.e.* proportion, we performed a logarithmic transformation (Log_{10}) of the mortality rate values, which made possible the use of ANOVA. After completing the repeated measures ANOVA, we checked the normality of the residuals (Shapiro-Wilk test; shapiro.test function), and confirmed they were normally distributed. Subsequently, we performed a Tukey test with the TukeyHDS function to contrast the averages and check for possible differences between modes of death. We performed all statistical analyzes in the software R 3.6.2 (R Core Team 2019) using the base packages.

3. Results

In the six plots we found 540 species (521 tree species and 19 palm species), distributed among 62 families (Appendix 1). The 10 most dominant species were *Tetragastris altissima* (Aubl.) Swart (33 individuals ha^{-1}), *Euterpe precatoria* Mart. (28 ha^{-1}), *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr. (11 ha^{-1}), *Pausandra trianae* (Müll. Arg.) Baill. (9 ha^{-1}), *Irartea deltoidea* Ruiz & Pav. (8 ha^{-1}), *Rinoreocarpus ulei* (Melch.) Ducke (8 ha^{-1}), *Metrodorea flavida* K. Krause (8 ha^{-1}), *Acacia polyphylla* DC. (6 ha^{-1}), *Pouteria* sp. (6 ha^{-1}) and *Trichilia* sp. (6 ha^{-1}).

Between 2002 and 2016, we recorded an average of 440.4 ± 43.4 trees (mean ± standard deviation) alive per hectare in the six plots evaluated (Fig. 1a). In the same period, we registered a total 852 dead individuals across all plots and time periods (Fig. 1b), distributed in four main modes of death: standing (325 or 27.8%), broken (362 or 31%), uprooted (156 or 13.3%), other (9 or 0.8%) and unknown (317 or 27.1%). The 852 dead individuals were distributed across 250 species and 52 families, of which the species with the highest proportions of dead individuals were *E. precatoria* (76 individuals; 8.9%), *A. polyphylla* (35 individuals; 4.1%) and *P. trianae* (22 individuals; 2.6%) (Appendix 3). The plots with the lowest number of living individuals over the evaluation period were DOI-02 and RFH-01, with annual averages of 306 and 376 individuals, respectively (Fig. 1a). The plots with the highest numbers of dead individuals, on the other hand, were POR-02 (37), POR-01 (28) and FEC-01 (27; Fig. 1b).

The average annual mortality rates for the standing, broken, uprooted, other and unknown tree modes of death were, respectively, 0.8, 0.8, 0.4, 0.02 and 0.7% year^{-1} for the entire period evaluated (2002–2016), accounting for a total mortality rate of 2.72% year^{-1}. Mortality rate for each time period was higher than the total mortality rate (2.72% year^{-1}), due the variation of the number of individuals alive and dead in each plot and also because trees whose modes of death were not identified are included. The time intervals with the highest mortality rates were 2002–2003, 2003–2006 and 2013–2016 with, respectively, 7.8%, 4.0% and 3.7% year^{-1}. The other time periods evaluated had average mortality rates varying between 3.0% and 3.6% year^{-1} (2009–2010 = 3.6% year^{-1}; 2010–2011 = 3.3% year^{-1}; 2006–2009 = 3.2% year^{-1}; and 2011–2013 = 3.0% year^{-1}).

The proportion of dead individuals varied between time periods during the study, with the highest number recorded of dead individuals in 2016 (22.6%; 192 trees), 2006 (15.5%; 132 trees), and 2011 (15.2%; 129 trees). Regarding the mode of death in the evaluated time span

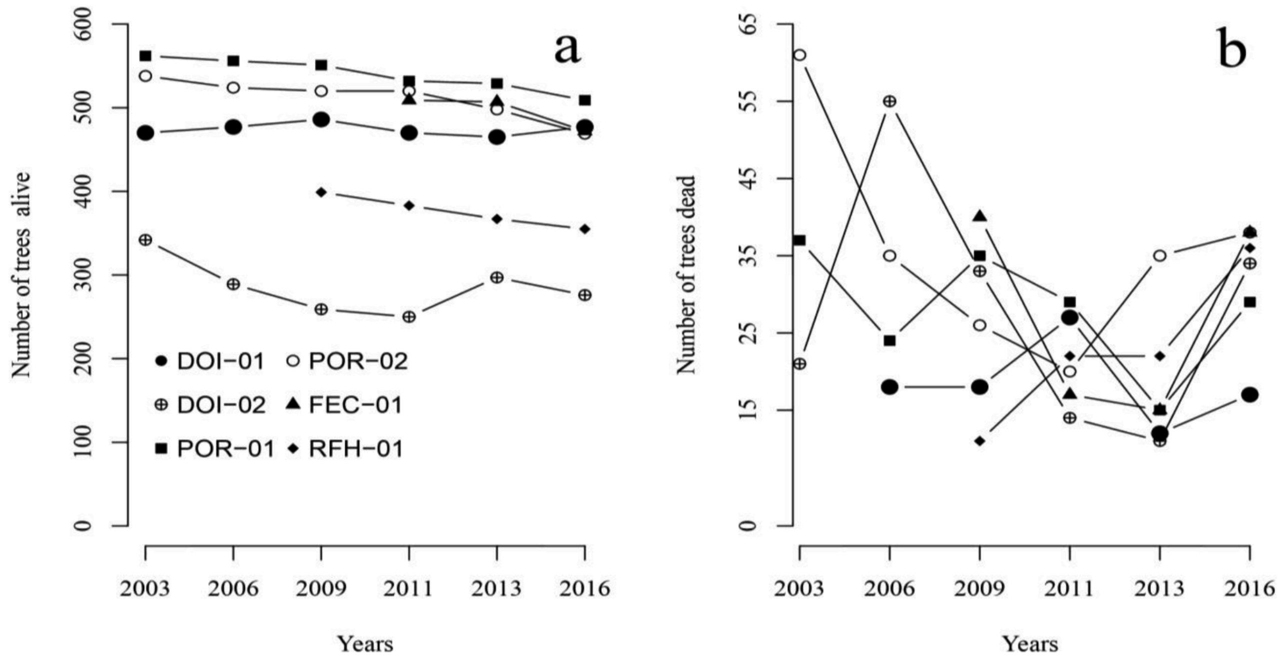

Fig. 1. Variation in the number of living (a) and newly dead (b) individuals between 2003 and 2016, in the six evaluated plots in the southwestern Amazon forests.

(2002–2016), the proportion of dead standing trees varied between 23% and 52%; the proportion of dead individuals by breaking varied between 19% and 57%; and the proportion of uprooted dead individuals ranged between 12% and 25%. The category "others" was registered only twice, and its proportion was low (Table 3).

We detected a difference between the tree modes of death in southwestern Amazon ($F_{2,10} = 6.08$, $p = 0.0187$; Error: $F_{2,3} = 1.148$, $p = 0.426$). The mode of death "uprooted" had an average annual mortality rate lower than the modes of death "standing" and "broken", which had no difference between them (Fig. 2).

4. Discussion

The results of our study revealed that standing and broken are the most frequent modes of death in the southwestern Amazon, having equivalent proportions. The mode of death uprooted, on the other hand, was less frequent than the others. In this sense, the standard mode of death in southwestern Amazon differs from other regions of the Amazon where studies of modes of tree mortality have been conducted. In the northeastern (southern Venezuela) and central Amazon (Manaus, Brazil), trees die in greater proportions standing; however, in northwestern Amazon (northern Peru), trees die in a greater proportion broken (Chao et al., 2009; Toledo et al., 2012; Esquivel-Muelbert et al., 2020). According to Chao et al. (2009), trees that have higher wood density and larger sizes (height and diameter), are more likely to die standing, while trees with lower basic wood density and smaller sizes

Table 3
Average percentage proportion of dead trees (± SE *) among the modes of death assessed over 14 years in six plots in southwestern Amazon forests: * SE = standard error.

Time span	Proportion of individuals by mode of death			
	Standing	Broken	Uprooted	Others
2002–2003	28.8 ± 4.6%	48.0 ± 4.1%	23.2 ± 3.2%	–
2003–2006	52.3 ± 4.2%	19.7 ± 3.0%	25.7 ± 4.8%	2.3 ± 14.2%
2006–2009	44.5 ± 5.4%	35.8 ± 3.4%	17.3 ± 3.7%	2.4 ± 14.2%
2009–2010	40.0 ± 10.0%	45.0 ± 6.1%	15.0 ± 5.8%	–
2010–2011	30.2 ± 5.4%	53.5 ± 3.9%	16.3 ± 3.0%	–
2011–2013	23.6 ± 5.4%	57.3 ± 4.8%	19.1 ± 3.1%	–
2013–2016	45.3 ± 5.0%	42.2 ± 2.6%	3.5 ± 2.7%	–

tend to die broken. Therefore, our findings for the southwestern Amazon, where trees have lower wood density, are in accordance with previous literature, as trees in the central and northeastern Amazon have a higher wood density than trees in the northwestern Amazon (Toledo et al., 2012; Chao et al., 2009).

In southwestern Amazonia, forests often have large canopy openings and an abundance of bamboo and palm trees (Valverde et al., 2006; Castro et al., 2013). The trees in the region are smaller than in the other parts of the Amazon basin due to edaphoclimatic characteristics, as well as lower precipitation rates and high soil fertility, which promote high turnover rates (Wadt, 2002; Acre, 2010; Quesada et al., 2012). Considering the typology and forest dynamics of southwestern Amazon (Griscom; Ashton, 2003; Chao et al., 2009; Castro et al., 2013), trees were expected to die more often broken; this study confirmed the predominance of that mode of death (Table 3). However, there was an almost equivalent proportion of trees dying broken (42.5%) and standing (38.1%), a similarity that was not expected considering the characteristics of the forests in the study area (Chao et al., 2009). Thus, there are possibly other factors that may be contributing to this situation. In a study of tree mode of death across Amazonia, (Esquivel-Muelbert et al., 2020) found that trees across the whole of western Amazonia die most frequently broken or uprooted, a pattern that differs from our findings. However, (Esquivel-Muelbert et al., 2020) defined the western Amazon as a very broad area (including parts of Bolivia, Brazil, Peru, Ecuador, Colombia and Venezuela), a much larger and more climatically variable region than our region. Severe droughts and the high density of bamboo culms are factors that influence forest dynamics and could shape tree mortality distinctly in the southwestern Amazon (Griscom and Ashton, 2006; Allen et al., 2010; Lewis et al., 2011; Medeiros et al., 2013). Studies evaluating the mortality caused by severe droughts show that in these situations, more trees die while standing (*e.g.* Corlett, 2016; Choat et al., 2018; Giardina et al., 2018). This mode of death is due to xylem cavitation (embolisms). That can drive death directly, or be associated with carbon starvation, reducing plant metabolism, culminating eventually in the death of the individual; in either case, the tree is likely to die standing, and remain erect until suffering mechanical damage *post-mortem* (Corlett, 2016; Feldpausch et al., 2016; Hammond et al., 2019; Kono et al., 2019).

In the plots evaluated in this study, the time periods of 2003–2006

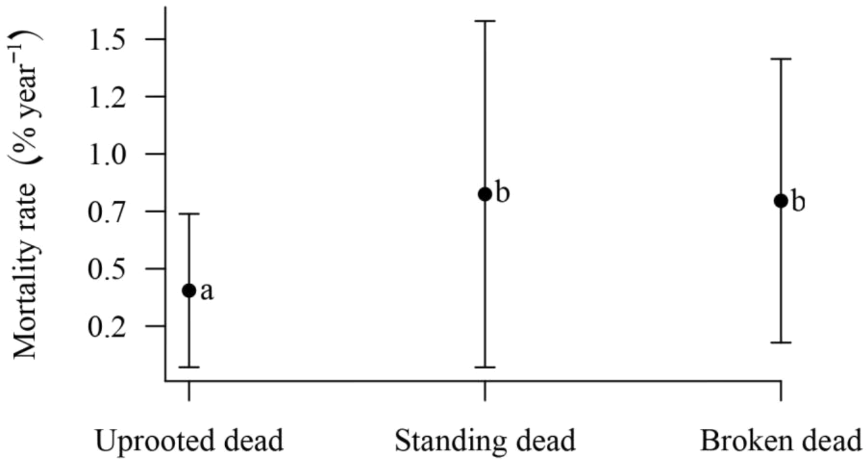

Fig. 2. Average difference in annual mortality rates (% year^{-1}) for the main modes of tree death in southwestern Amazon forests. Different letters indicate different means according to the Tukey test; the central point of each letter indicates the average of the mortality rate and the ends of the graph the standard deviation of the average of the mortality rates.

and 2006–2009 were, respectively, those with the highest proportions of standing dead trees. The first period includes the drought year of 2005 and the second immediately followed it (Aragão et al., 2007). However, in the 2010–2011 and 2011–2013 time periods, which also included a severe drought year (2010), the predominant mode of death in southwestern Amazon was broken, which does not fit to the expected mode of death while standing. Lewis et al. (2011) described the 2010 drought as having a broader geographic in scope, but three epicenters, of which the southwestern Amazon was one. Therefore, the effects of the 2010 drought in the southwestern Amazon may not have been as intense as those generated by the 2005 drought. In addition, mortality due to drought has a time-lag that induces mortality not immediately following the occurrence of drought, but often taking time (up to 5 years) for drought damage to culminate in forest mortality (Feldpausch et al., 2016). Other possibilities are that trees in the southwestern region had not reached the critical limit of water deficits (above 50% loss of hydraulic conductivity; Choat et al., 2018), or that another unknown factor influenced tree mortality during the period 2010–2013 (Esquivel-Muelbert and Baker, 2018; Feldpausch and Phillips, 2016).

In the plots evaluated, the species with the highest mortality rates were *E. precatoria, A. polyphylla, P. trianae, T. paniculata* and *Sclerolobium* sp. (Appendix 3). Among them, *E. precatoria* is a palm tree with distinct characteristics (*e.g.* fasciculated roots that reach depths of up to 80 cm in the soil, a non-lignified stem and leaves only at the apex of the shoot), which makes it more vulnerable to water stress and mechanical damage to the stem (Svenning, 2001; Rocha, 2004). On the other hand, *A. polyphylla, T. paniculata, Sclerolobium* sp. (Fabaceae) and *P. trianae* (Euphorbiaceae), have shorter life cycles and are generally found in secondary forests (Laurance et al., 2004; Souza et al., 2004; Coelho et al., 2013; Abdo and Valeri, 2017). In this sense, the higher proportion of mortality of these species is probably due their susceptibility to water deficits (Uhl et al., 1988; Esquivel-Muelbert et al., 2018). That is, its hydrological safety may be at more risk than slower-growing plants. While the latter may successfully down-regulate hydraulic conductivity and prioritize survival over growth, (Hammond and Adams, 2019; Powers et al., 2020), faster-growing species may be unable to survive, where even reductions of 30% in conductivity may result in physiological failure leading to death (Choat et al., 2018; Powers et al., 2020).

Another factor that could also be shaping tree mortality in the southwestern Amazon is the high density of bamboo culms (Nelson, 1994; Griscom and Ashton, 2003). Two of the six plots (DOI-02 and RFH-01; Table 1) have a notably higher density of bamboo and a lower tree density than the others. The bamboo growth habit places a heavy load on trees, causing damage to the stems and overloading the canopy, increasing mortality due to breaking (Griscom and Ashton, 2006). The presence of bamboo can be a key factor that explains the distinct relative proportions among mode of deaths found in southwestern Amazon (Griscom et al., 2007; Larpkern et al., 2011).

Previous studies have shown that individual explanations are often not the dominant cause of a certain mode of death; instead, there is an interplay between explanations that results in differences in dynamics from place to place (Esquivel-Muelbert et al., 2020). Therefore, we believe the dynamics of tree modes of death in the southwestern Amazon are most likely to be regulated by a combination of vegetation structure and tree species composition, by the abundance of bamboo (*Guadua* spp.), and by events of severe droughts that impacted the region.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was carried out as a collaborative effort of the ForestPlots.net meta-network, a cyber- initiative that unites contributing scientists and their permanent plot records from the world's tropical forests. This paper is an outcome of ForestPlots.net approved Research Project #40. We thank our colleagues who made this work possible by helping in the field and later with data management. We are thankful to Dr. Jean Carlo Gonçalves Ortega for his collaboration in interpreting the data and statistical analysis and to Dr. Oliver L. Phillips for revising the whole manuscript. We also want to express our appreciation to the editor and reviewer for their insightful comments, which have helped us to significantly improve the paper.

Funding

This work was funded by U.S. Agency for International Development under the Partnerships for Enhanced Engagement in Research (PEER) program of the National Academies of Science.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2021.100180.

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