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RESEARCH ARTICLE

Climate and crown damage drive tree mortality in southern Amazonian edge forests

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Abstract

1. Tree death is a key process for our understanding of how forests are and will respond to global change. The extensive forests across the southern Amazonia edge—the driest, warmest and most fragmented of the Amazon regions—provide a window onto what the future of large parts of Amazonia may look like. Understanding tree mortality and its drivers here is essential to anticipate the process across other parts of the basin.
2. Using 10 years of data from a widespread network of long-term forest plots, we assessed how trees die (standing, broken or uprooted) and used generalised mixed-effect models to explore the contribution of plot-, species- and tree-level factors to the likelihood of tree death.
3. Most trees died from stem breakage (54%); a smaller proportion died standing (41%), while very few were uprooted (5%). The mortality rate for standing dead trees was greatest in forests subject to the most intense dry seasons.
4. While trees with the crown more exposed to light were more prone to death from mechanical damage, trees less exposed were more susceptible to death from drought.
5. At the species level, mortality rates were lowest for those species with the greatest wood density. At the individual tree level, physical damage to the crown via branch breakage was the strongest predictor of tree death.
6. *Synthesis*. Wind- and water deficit-driven disturbances are the main causes of tree death in southern Amazonia edge which is concerning considering the predicted increase in seasonality for Amazonia, especially at the edge. Tree

mortality here is greater than any in other Amazonian region, thus any increase in mortality here may represent a tipping point for these forests.

KEYWORDS
climate change, disturbance, forest dynamics, forest structure, growth rate, tree death, water deficit, wood density

1 | INTRODUCTION

Tree mortality is a critical ecological process with fundamental implications for forest dynamics and carbon storage (e.g. McDowell et al., 2018). High mortality rates are known to strongly limit aboveground tropical forest biomass and carbon (e.g. Johnson et al., 2016; McMahon et al., 2019) and impact the structure and composition of ecological communities (Esquivel-Muelbert et al., 2019). Thus, a better understanding of the causes of tree death is fundamental for the mechanistic understanding of global change impacts on the carbon sink capacity of tropical forests (Brienen et al., 2015). However, the factors that determine tree mortality in forests across Amazonia remain unclear. This is especially so in the forests at the hyperdynamic southern edge, which have unusually high rates of tree mortality when compared to other tropical forests and other regions of Amazonia (Esquivel-Muelbert et al., 2020; Marimon et al., 2014).

Southern Amazonian edge forests have a unique species composition, due in part to the overlap of species between this and the adjacent biome, the Cerrado (savanna) (Morandi et al., 2016). These forests have been suffering from advances in agriculture, which has considerably increased habitat fragmentation and carbon loss in recent decades (Covey et al., 2021; Gatti et al., 2021; Silva Junior et al., 2020). In addition to the high levels of fragmentation, the remaining forests have been affected by increasing temperatures, frequent fires, drought events and the long-term lengthening of the dry season (e.g. Araújo et al., 2021; Reis et al., 2018; Silvério et al., 2019)—making this now the hottest, driest and most degraded region in the Amazon (e.g. Alvares et al., 2013; Covey et al., 2021; Matricardi et al., 2020; Sombroek, 2001).

Recurrent extreme drought events or prolonged water stress can cause a short-term increase in tropical tree mortality, especially by hydraulic failure and potentially by carbohydrate deficiency (Bennett et al., 2021; Feldpausch et al., 2016; McDowell et al., 2011, 2018; Phillips et al., 2010; Rowland et al., 2015). Habitat fragmentation due to deforestation and burning can also promote tree death by increasing the exposure of trees to the wind, which can cause damage, followed by death, mainly of taller trees (Haddad et al., 2015; Laurance et al., 2000a, 2000b; Silvério et al., 2019). Other factors, such as lightning (Fontes et al., 2018; Yanoviak et al., 2020), liana abundance (e.g. McDowell et al., 2018) and light competition (e.g. McDowell et al., 2018), may also promote tree mortality.

The likelihood and cause of tree death vary across different canopy layers (Camac et al., 2018). Competition for light is likely to impact especially trees growing in the understorey that are shaded by neighbours and are potentially close to their carbon compensation point (Camac et al., 2018; McDowell et al., 2018; Wright et al., 2010; Zuleta et al., 2021). Sub-canopy trees may be more susceptible to death from mechanical damage generated by canopy trees' death or breakage and extreme weather events (Toledo et al., 2012; Yang et al., 2003). On the other hand, canopy trees are more sensitive to climatic conditions (drought, lightning, high rainfall and storms) because of their exposed position in the canopy (Aleixo et al., 2019; Costa et al., 2010; Gora & Esquivel-Muelbert, 2021; Yanoviak et al., 2020).

Lianas can also affect the availability of light for support trees. When lianas reach tree crowns, they produce a dense cover of leaves that tend to reduce light availability. The stress generated by the reduction of light affects the trees' growth rate (e.g. Reis et al., 2020) and may lead to tree death (McDowell et al., 2018). Lianas can also cause mortality by damaging the branches or trunk of the supporting trees (Clark & Clark, 1990; Fontes et al., 2018; Putz, 1984; Visser et al., 2018).

The breakage of branches and trunks can also be caused by wind disturbances (Aleixo et al., 2019; Arriaga, 2000; Ribeiro et al., 2016). Broken trees are more susceptible to drought and wind events and to attack by herbivores and pathogens, as well as having reduced growth rates due to the loss of photosynthetic area, all of which are factors that can elevate mortality risk (Fontes et al., 2018; Franklin et al., 1987). While a recent study revealed that crown damage is the main factor determining tree death in Malaysia (Arellano et al., 2019), little is known about whether and how crown breakage affects tree death in Neotropical forests. The studies that exist are concentrated in experimental areas with logging (Shenkin et al., 2015) or subject to burning (Silvério et al., 2019), or are limited to two plots in the central Amazon (Fontes et al., 2018) and one each in Colombia and Panama (Zuleta et al., 2021).

Characteristics of species also exert significant control on the probability of tree death. For example, wood density is a key species-level trait that is strongly controlled by phylogeny and has been shown to indicate the likelihood of a tree to die, with those of less dense wood being at higher risk (Chao et al., 2008, 2009; Esquivel-Muelbert et al., 2020; Putz et al., 1983). At the individual tree level, tree size and growth rate are considered good predictors of tree death (Chao et al., 2008; Esquivel-Muelbert et al., 2020;

Franklin et al., 1987; Zuleta et al., 2021). Trees growing slowly may be responding to challenging environmental conditions and so likely to be more susceptible to disease, pathogen attack and eventually death (Bigler et al., 2004; Chao et al., 2008; Dobbertin, 2005; Yang et al., 2003). Mortality risk also varies with tree size, as the smallest and largest tropical forest trees are typically more likely to die than those of intermediate size (Coomes & Allen, 2007; Iida et al., 2014; Rozendaal et al., 2020; Yang et al., 2003). However, the relationship between mortality and tree size is not always clear and seems to depend substantially on a given location's disturbance regime (Chao et al., 2008; Lieberman et al., 1985).

Here we evaluate the drivers of tree mortality on a large scale across the forests in the hyperdynamic southern edge of Amazonia. We consider potential determinants of tree mortality operating at the plot level (e.g. water deficit, fragmentation, forest structure), the species level (wood density) and the individual level (e.g. liana infestation, canopy breakage and canopy exposure to light). We also assessed how trees died by examining the standardised mode of death records (standing, broken or uprooted), as this can provide insights into the underlying causes of tree death.

2 | MATERIALS AND METHODS

2.1 | Study area

We assessed tree mortality in 19 permanent plots in forests located across the southern edge of the Brazilian Amazon (Figure 1). All plots are in intact remnants of mature, evergreen or semi-deciduous tropical forests, on private properties or in conservation units (see Reis et al., 2018, 2020 for more details). The region's climate covers types of Aw and Am according to the Köppen classification (Alvares et al., 2013). The total annual rainfall ranges from ~1500 to 2400 mm and mean monthly temperature from ~24.0 to 27.3°C (see details in Table S1).

All plots are of 1 ha, except for VCR-01 with 0.64 ha (Table S1). In each plot, we tagged, measured and identified all plants (trees, palms and lianas) with a diameter at breast height (*DBH* 1.3 m) ≥ 10 cm following the protocol of the RAINFOR network (http://www.rainfor.org/; Phillips et al., 2018). We revisited each plot every 1–4 years and measured the living plants, including recruits that had reached the inclusion limit (Table S1), and recorded any death events using identical protocols.

2.2 | Data processing

2.2.1 | Modes of tree death

We evaluated tree mode death in all 19 plots for which we had data from two or more inventories (Table S1). For each plot, we used all possible time intervals since 2008 to maximise the sample size while standardising the measurement years as much as possible. The time intervals adopted here (mean = 2.4 years) are deliberately kept shorter than is typical for tropical forest permanent plots, as longer intervals are less helpful in identifying how trees die (e.g. Lieberman et al., 1985) or detecting changes in mortality rates (McMahon et al., 2019). We classified the mode of death as (1) standing—trees with all or part of the branches (dry) in the crown; (2) broken—trees whose broken stem was live when broken; (3) uprooted—trees prone on the forest floor and with exposed roots; and (4) unidentified—trees with the cause of death unidentifiable (see Chao et al., 2009; Phillips et al., 2018). This ensures a standardised and repeatable approach to mortality characterisation that is comparable across our study. Data are stored and managed via ForestPlots.net (ForestPlots.net et al., 2021).

2.2.2 | Tree mortality

We calculated the mean annual mortality rates (*M*) for each forest for different time intervals (Table S1), as:

$$M = \left(1 - \left(\frac{N_{t1}}{N_{t0}}\right)^{\frac{1}{T}}\right) \times 100, \tag{1}$$

where *T* is the time between two inventories, N_{t0} the initial number of individuals and N_{t1} the number of individuals who survived within the time interval (Sheil et al., 2000). We calculated the mean mortality rate of the different intervals for those plots with more than two inventories between 2008 and 2017. To remove small potential biases associated with varying interval lengths, we applied the correction factor proposed by Lewis et al. (2004):

$$Mcorr = M \times T^{0.08}, \tag{2}$$

where *M* is the mortality rate and *T* is the census interval length in years.

We also used Equation 1 to calculate the mean annual mortality rates for standing or broken dead trees and for each class of liana infestation index (*LII*), canopy damage index (*CDI*) and crown illumination index (*CII*).

2.2.3 | Drivers of tree mortality

Plot level

To assess the effect of forest structure on tree mortality at the plot level (Table 1), we calculated the stand density of trees (*TD*) and of large lianas (*LL*) separately, as well as the total basal area (*TBA*) that trees occupied in each plot. We further calculated the 95th percentile of the diameter (*D95*) and height (*H95*) of all stems in each plot. We extracted total annual precipitation values from the TerraClimate database (Abatzoglou et al., 2018). We also calculated the Maximum Cumulative Water Deficit for each plot (*MCWD*; Aragão et al., 2007), *MCWD* based on the calendar year (Jan–Dec), considering the different sampling intervals for each one (Table S1). To calculate *MCWD*,

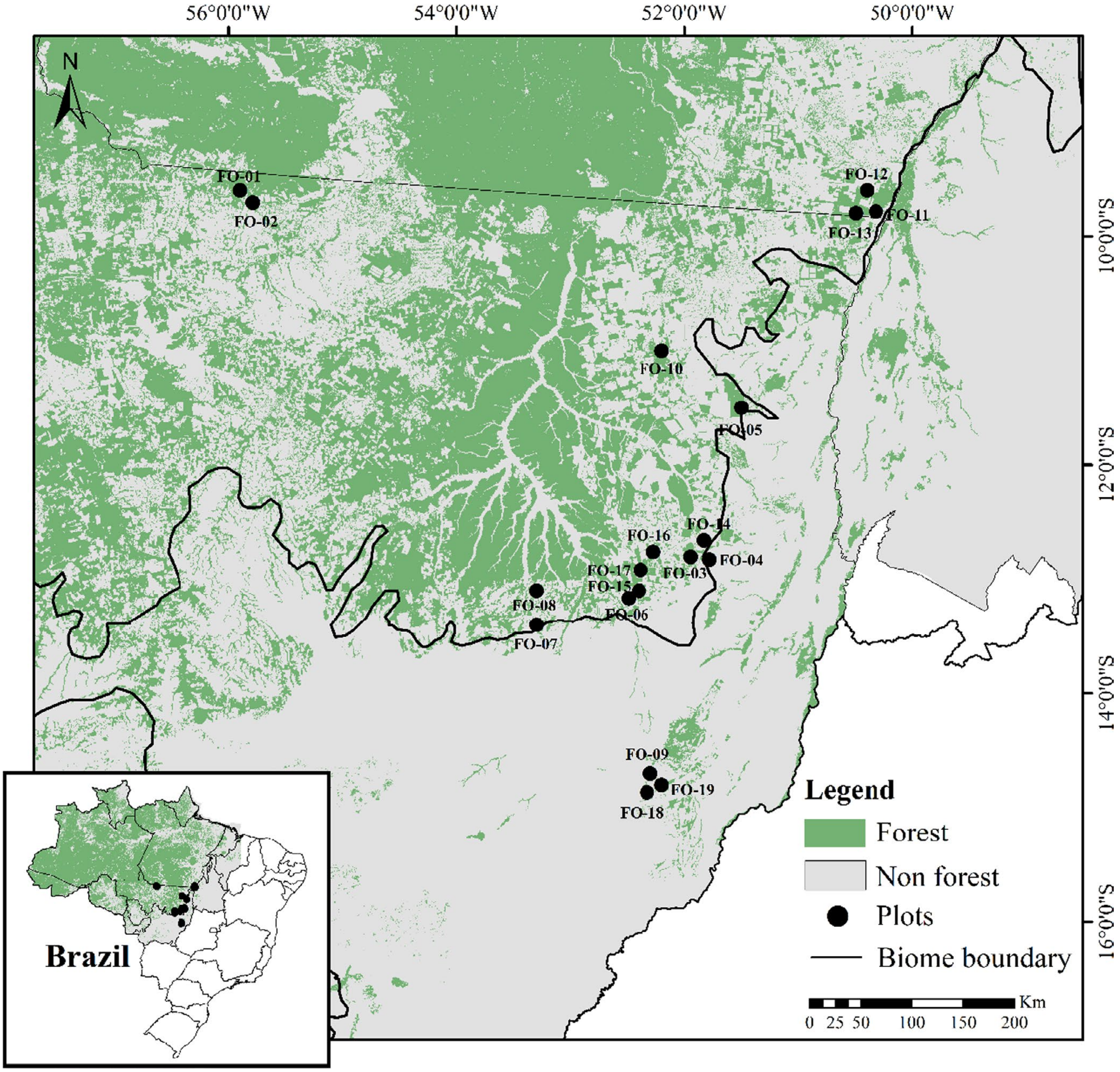

FIGURE 1 Location of the sampled plots (black points) in the southern Amazon edge, in the Brazilian Amazon states of Mato Grosso and Pará. The continuous black line represents the approximate separation between Amazonia and Cerrado biomes, according to IBGE (2004). The classification of forest and non-forest was based on the PRODES project (INPE, 2016). For display purposes, we have slightly separated points where plots are overlapping. FO indicates numbered *forest plots* (see Table S1 to see the names of each)

we used monthly precipitation values from the TerraClimate database and considered the standardised evapotranspiration (*ET*) value for tropical forests of 100 mm month^{-1} (Aragão et al., 2007). To represent the fragmentation effect, we calculated the total area of the fragment (*FA*) where each plot was located and each plot's distance to the nearest edge (*ED*) of the fragment (Table S1).

Species and individual level

To assess which predictors at the species (*WD*) and individual (*tree size*, *growth*, *LII*, *CII* and *CDI*) level were related to tree death (Table 1), we first selected the forests that had three (t_0, t_1 and t_2) or more censuses (Table S1), to assess the growth of the tree before death, that is, between the antepenultimate (t_0) and penultimate (t_1) census. We used the data from tree size, *LII*, *CII* and *CDI* from the last census before death (t_1) (Table 1). We excluded from the analysis trees that died between t_0 and t_1 as we lacked any growth history. We also excluded palm trees (Arecaceae) as they lack secondary growth and lianas.

We obtained wood density values for each species from the Wood Density Database (Chave et al., 2009; Zanne et al., 2009). When species-level wood density was not available, we used the appropriate mean genus-level (44.7% of species) or family-level (2.4%)

TABLE 1 Potential drivers of tree mortality at the plot level (all trees, standing and broken trees), species level and tree level across the southern edge of Amazonia. t_0 = antepenultimate census, t_1 = penultimate census

Mortality drivers	Specific variables	Variable description
Plot level		
Climate	*Prec*	Maximum precipitation (mm)
	MCWD	Maximum climatological water deficit (mm)
Fragmentation	*FA*	Fragment area (ha)
	ED	Distance to edge (m)
Forest structure	*D95*	Diameter 95th percentile (cm)
	H95	Height 95th percentile (m)
	TBA	Total basal area (m^2)
	TD	Tree density
	LL	Large lianas ≥10 cm DBH
Species level		
Species traits	*WD*	Wood density ($g\ cm^{-3}$)
Individual level		
Tree growth (between t_0 and t_1)	*relBAGR* (% $year^{-1}$)	Relative basal area growth rate before death
Tree size (t_1)	*BA* (m^2)	Basal area before death
Crown damage (t_1)	*CDI*	Crown damage index before death
Liana infestation (t_1)	*LII*	Liana crown occupancy index before death
Light (t_1)	*CII*	Crown illumination index before death

wood density, following Flores and Coomes (2011). For those trees in our plots that were only identified to genus level (9.7% of species) or to family level (0.3%), we used the mean wood density of the confirmed group identity. We used the mean value of the community's wood density for a small proportion of individuals (0.5% of the species) belonging to families for which we had no data.

We calculated the basal area (tree size) and the relative growth in basal area (tree growth) as:

$$BA = \left(\frac{\pi}{4}\right) \times (D)^2, \tag{3}$$

$$relBAGR\,(\%) = \left(1 - \left(\frac{BA_{t1} - BA_{t0}}{BA_{t0}}\right)^{\frac{1}{T}}\right) \times 100, \tag{4}$$

where *D* is the tree's diameter, *T* the time elapsed between the two censuses, BA_{t0} the basal area at the beginning and AB_{t1} the basal area at the end (Sheil et al., 2000). Our final dataset consisted of 9928 trees, of which 9266 were alive throughout, and 662 had died.

We visually estimated liana infestation using the five categories of the *LII* (van der Heijden et al., 2010), where 0 = no lianas in the crown, 1 = 1%–25% of the crown covered by liana leaves, 2 = 26%–50% of the crown covered, 3 = 51%–75% of the crown covered and 4 = >75% of the crown covered. This semi-quantitative index of crown occupation by lianas has been shown to accurately measure individual liana loads at tree level and plot level (van der Heijden et al., 2010). For the analysis, we included only three categories of liana infestation (0%–25% of the crown covered by lianas, 26%–50% and >50%) according to Reis et al. (2020).

Crown damage index was classified into five categories, where 0 = unbroken crown, 1 = 1%–25% of crown broken, 2 = 26%–50% of crown broken, 3 = 51%–75% of crown broken and 4 = >75% of crown broken (crown formation index; please see Phillips et al., 2018 and his references). We also estimated the level of light incidence on the crowns visually using a crown illumination index (*CII*): 1 = no direct light, 2a = low, 2b = medium and 2c = high lateral light–*Low light*; 3a = some vertical light (<50%) and 3b = high vertical light (>50%)–*Medium light*; 4 = crown fully exposed to vertical light and 5 = crown fully exposed to vertical and lateral light–*High light* (details in Clark & Clark, 1992; Keeling & Phillips, 2007).

2.3 | Statistical analysis

2.3.1 | How did the trees die?

We compared the mean annual mortality rates in the three modes of death categories (standing, broken and uprooted) using the Kruskal–Wallis test associated with Dunnett's post hoc test (Zar, 2010).

2.3.2 | What are the drivers of tree mortality in southern Amazonian edge forests?

Plot level

We performed Generalised Linear Models (GLM, family = Gaussian) to assess the influence of precipitation, fragment area, edge distance, *MCWD* and forest structure (e.g. basal area) on mean annual mortality rates considering all dead trees together and separately for trees that had either died broken or standing. We tested the correlation between the mortality of broken or standing trees vs. mortality for trees in different crown light conditions (*CII*), using Kendal tau correlation.

Species and individual level

We constructed Generalised Mixed-Effect Models (GLMM, family = binomial) to better understand species' importance and individual-level drivers of mortality (dead or alive during time interval) (see Table 1). We included species (*WD*) characteristics and individuals (*relBAGR*, *BA*, *CDI*, *LII* and *CII*) as fixed variables. As individual trees are clustered within plots, we also included the intercept of plot as random effects.

For both models (plot level and species and individual level), we checked possible collinearity among predictors using Variance Inflation Factors and pairwise correlations. We removed *D95*, *BA* and *LL* to plot level, as these variables correlated with H95. After that, the collinearity between the variables was weak ($r < 0.6$ and VIF < 3) (Quinn & Keough, 2002). We fitted all subsets of the model using the MuMIn package in R (Barton, 2019). The best model was the one with the smallest AICc. We conducted all analyses using R 3.6.0 (R Core Team, 2019), and adopted a 5% significance level.

3 | RESULTS

3.1 | How did trees die?

Of all trees that died, 76% ($N = 1134$) were classified as having died standing, broken or uprooted. Of these, most died broken ($N = 610$, 54%; $KW = 59.1$, $p < 0.001$, followed by standing dead ($N = 462$, 41%). Only 62 (5%) died uprooted (Figure 2). Between 2009 and 2013, some forests (e.g. SAA-01, TAN-02, TAN-03 and VCR-02) had higher mortality rates for standing dead individuals, but between 2013 and 2015, they had more broken deaths (Table S2). Of those most abundant species with more than 20 individuals and where the mode of death was identified, the mode of death varied: more than 70% of the dead trees of *Xylopia aromatica* (Annonaceae) and *Matayba guianensis* (Sapindaceae) died broken (Table S3), while by contrast more than 80% of the dead trees of *Tachigali vulgaris* (Fabaceae) died standing.

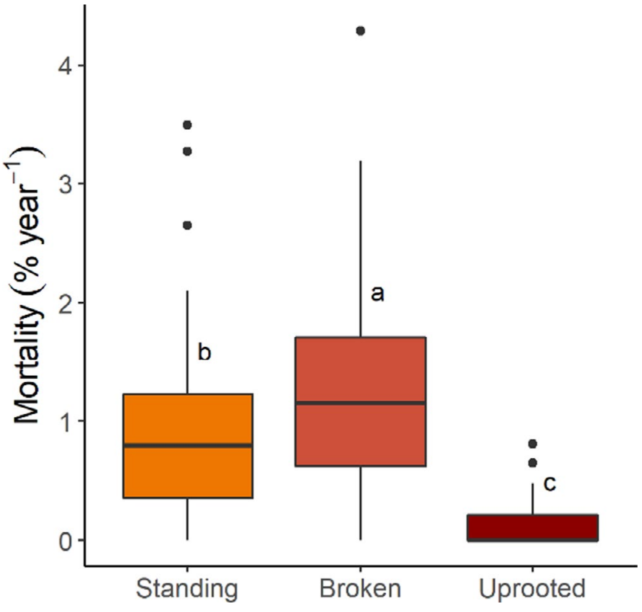

FIGURE 2 Mortality rates for each mode of tree death in southern Amazonian edge forests. Different letters denote significant differences according to the Dunnett's post hoc test

3.2 | What are the drivers of tree mortality in southern Amazonian edge forests?

3.2.1 | Plot level

The annual mortality rate varied between 1.2 and 6.7% year^{-1}, with a mean of 3.4% year^{-1}. This great variability in mortality rates was explained by precipitation when considering all trees ($R^2 = -0.57$, $p = 0.01$). Maximum monthly precipitation was the only variable that significantly explained mortality rates, with lower rates in forests with greater maximum precipitation (Figures 3a, Figure S4; Table S5). However, mortality rates of standing death (Figures 3b,c, Figure S4; Table S5) were lower in forests with greater maximum height (Figure 3b) and greater in forests under more intense water deficit (Figure 3c). For those trees which died broken, none of the candidate predictors emerged as a statistically significant factor (Table S5).

The mortality rates for broken trees were correlated positively with the mortality for trees with the crown more exposed to light (High and Medium light) (Figure 4e,f). The mortality rates of standing trees were correlated positively with the mortality for trees with the crown less exposed to light (Low and Medium light; Figure 4a,b). Additionally, the mortality for trees with the crown less exposed to light (Medium light) was correlated negatively with precipitation (Figure S4).

3.2.2 | Species and individual level

Both species-level and individual tree-level characteristics were significant predictors of tree mortality (Figure 5; Table S6). The best model included characteristics of the individuals (*LII*, *relBAGR* and *CDI*) and the species (*WD*), performing better than when variables measured at the level of the species, or the individual were included in the model independently (Table S6). Crown damage index (ΔAICc = 272.44 in model without *CDI*) followed by the species-level wood density (ΔAICc = 114.25 in model without *WD*) were the most important factors in determining tree death in forests in the southern Amazon edge (Figure 5; Table S6).

The mortality rate was much higher for trees with more than 75% of the crown broken ($KW = 30.66$; $p < 0.001$; Figure 5a), with approximately 30% of the trees in the highest proportion of the crown broken in t_1 dying by t_2. Tree mortality probability decreased with tree relative growth rate and wood density (Figure 5). Although liana infestation was an essential variable in our model (Table S6),

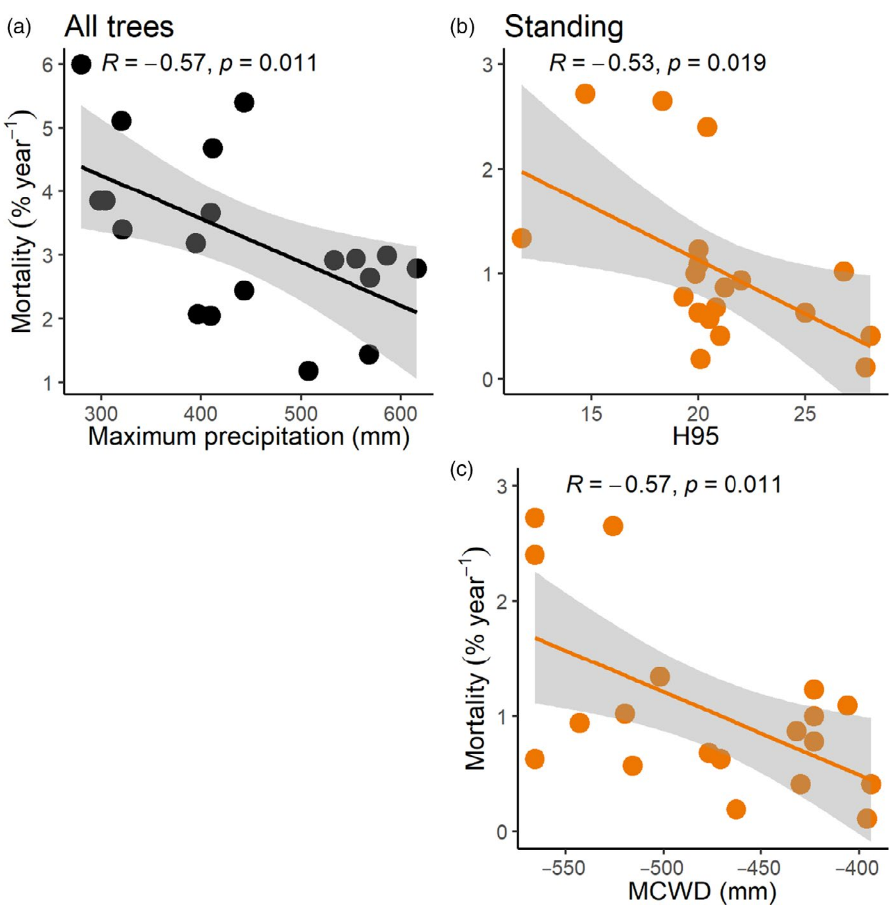

FIGURE 3 Selected predictors of plot-level tree mortality. Data are shown for the models including all trees (mean mortality rate and maximum month precipitation during census interval (a)) and standing trees (mean mortality rate and height 95th percentile (m) (b) and maximum climatological water deficit (c)) across southern Amazonia. Note that the scale of the *y*-axis of (a) is different from the others to facilitate visualisation. Coefficients from each model and model outputs for the selected generalised linear models are shown in Table S5

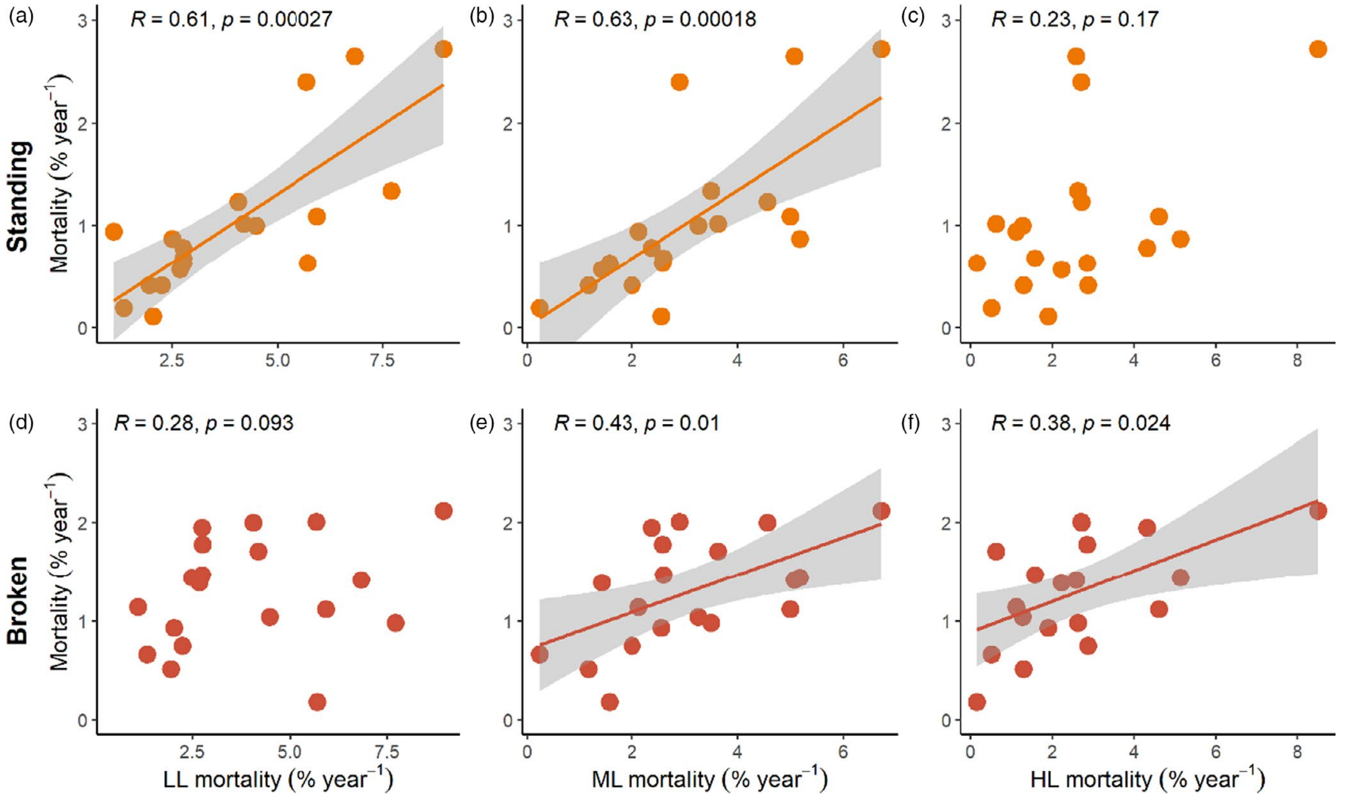

FIGURE 4 The relationship between the mortality rates within different modes of death (i.e. broken and standing) and the mortality rates at different crown illumination index (*CII*). LL, low *CII*; ML, medium *CII*; HL, high *CII*

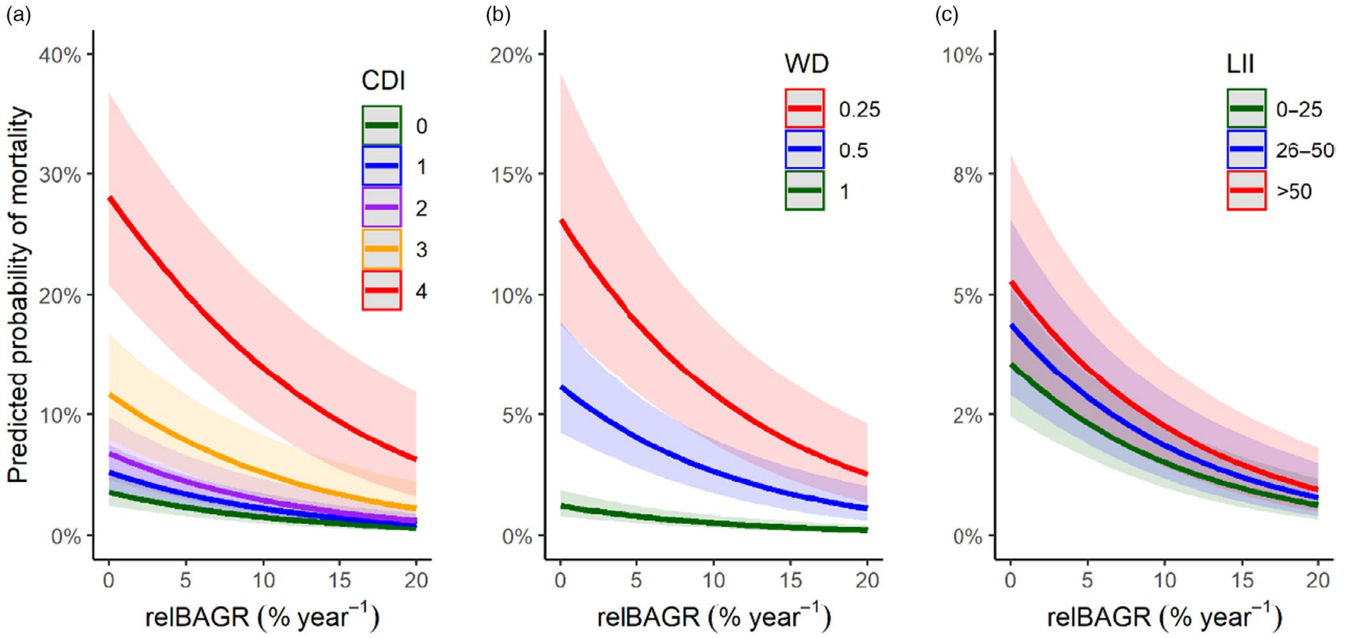

FIGURE 5 Predicted effects of tree-level mortality probability across southern Amazonia edge. Mortality probability as a function of relative growth rate (*relBAGR*) within different classes of (a) crown damage index (*CDI*), (b) species-level wood density (*WD*) and (c) liana crown occupancy index (*LII*). Lines represent the marginal means from models and shaded areas indicate the 95% credible interval. Model coefficients are shown in Table S6. Note that for visualisation purposes the *y*-axes of figures (b) and (c) are shown on a different scale from (a)

mortality did not vary significantly among liana infestation classes (Figure 5c).

When the most abundant species (those with ≥20 individuals) were analysed, the percentage of dead trees declined with increasing wood density (Figure S7). Among the 16 most frequent species that occurred in ≥50% of the plots, *Tapirira guianensis* (Anacardiaceae) and *Miconia pyrifolia* (Melastomataceae) had the greatest mortality rates (Table S8). On the other hand, not one individual of *Hymenaea courbaril* (Fabaceae) died in any of the plots, and *Hirtella glandulosa* (Chrysobalanaceae) and *Pouteria ramiflora* (Sapotaceae) both experienced low mortality (0.8% year^{-1}).

4 | DISCUSSION

Climate and crown damage were the most critical predictors of tree death in the hyperdynamic forests of the southern edge region of Amazonia. In general, more than half of the dead individuals were classified as 'broken dead'. This is a much greater fraction than in most other Amazonia regions, such as central Amazonia (26%; Toledo et al., 2012) except the northwest where it has been estimated by Chao et al. (2009) at 51%. Also, the combined percentage of broken and uprooted dead trees (59%) in our analysis of the southern Amazon edge was greater than the pan-Amazon mean (51%) and the value for the large southern Amazon region (44%) analysed by Esquivel-Muelbert et al. (2020). Crown damage was the most important predictor of tree death (Tables S6), with 71% of the dead trees having some crown breakage in the pre-death inventories. These results indicate that trees in the Amazon-edge forests are particularly susceptible to disturbances, such as high winds (Arriaga, 2000; Putz, 1984; Ribeiro et al., 2016), and they show that the exceptional stem mortality rates observed in these forests (Marimon et al., 2014) are related to high rates of crown and trunk breakage. These forests are more subject to habitat fragmentation due to the conversion of forested areas to agricultural areas (Covey et al., 2021). These forests also exist in drier climates, with less annual rainfall and more intense seasonal water deficits, than most of Amazonia (Brando et al., 2014; Malhi et al., 2015). These factors separately or together may contribute to higher mortality in this region.

Broken trees are susceptible to water stress, wind events, attack by herbivores and pathogens (Franklin et al., 1987). We observed in the field that broken individuals rarely regrow after breaking, which may explain their high mortality rate here, while other authors elsewhere have shown reduced growth due to less CO_2 assimilation associated with loss of photosynthetic area (Dobbertin, 2005; McDowell et al., 2018), factors that may contribute to increased mortality risk.

The mortality for trees with a high crown illumination index (CII) was enhanced by mechanical damage, while for the low CII trees mortality was more associated with physiological stress. The high mortality of high *CII* trees due to damage suggests that these forests suffer the effects of habitat fragmentation and high wind speed (Aleixo et al., 2019; Laurance et al., 2000a, 2000b). These trees have crowns most exposed to light, making them more susceptible to water stress caused by intense droughts or lengthening of dry seasons (Aleixo et al., 2019; Costa et al., 2010). Thus, the mortality of these trees may be caused by a combination of physiological and mechanical factors (Zuleta et al., 2021). Our results suggest that the stress generated by drought may be increasing the predisposition of trees to break just as much as it kills directly via hydraulic failure. This appears to be the case as the standing death mode was more dominant during intervals that included the 2010 drought, while in intervals following this drought, most trees died broken (Table S2).

Nevertheless, unlike the pattern for trees dying broken, standing tree mortality was greater for those trees which had crowns less exposed to light. We expected that trees less exposed to the sun—experiencing higher humidity, lower leaf temperatures and lower vapour pressure deficits—would be less impacted by drought than exposed trees (Bennett et al., 2015; Costa et al., 2010). It seems plausible that the greater competition for light and reduced CO_2 assimilation experienced in the understorey (McDowell et al., 2018; Muller-Landau et al., 2006; Wright et al., 2010) may increase their risk of death by water stress. However, it is equally true that small trees have shallower roots and therefore more limited access to deep water than bigger trees (Waring & Powers, 2017), potentially increasing the risk of drought-induced tree mortality (Condit et al., 1996; Esquivel-Muelbert et al., 2019; Fauset et al., 2012; Gora & Esquivel-Muelbert, 2021).

Those forests with strongest dry seasons and the shortest trees experienced the most standing tree mortality. Seasonal water deficits vary across Amazonia but are typically most intense in the southern edge (Brando et al., 2014; Malhi et al., 2015; Marimon et al., 2020), explaining the strong influence of this variable on the death of shorter trees in this region. Under high *MCWD*, trees are more susceptible to hydraulic failure and carbohydrate deficiency due to the high evaporative demand and stomatal closure, respectively (McDowell et al., 2011, 2018), which may affect tree growth (Cailleret et al., 2017; Dobbertin, 2005; Feldpausch et al., 2016; Phillips et al., 2009) and may be exacerbated by high maximum temperatures in the region (Sullivan et al., 2020).

As observed in previous tropical forest studies, our analyses show lower rates of tree mortality for those species with greater wood density (e.g. Chao et al., 2008; Esquivel-Muelbert et al., 2020; Kraft et al., 2010; Putz et al., 1983). Here, those species with the greatest mortality from breakage (*Xylopia aromatica*; 71%) or standing (*Tachigali vulgaris*; 84.5%) are light wooded (Table S3; 0.56 and 0.52 g cm^{-3}). Both are pioneers and have short life cycles, consistent with the broader growth-mortality trade-off in tropical trees (Chao et al., 2008; Esquivel-Muelbert et al., 2020; Kraft et al., 2010; Putz et al., 1983). Our works indicates these species are especially prone to death due to water deficit and to wind-related disturbances. However, the mean stand-level wood density in our plots (0.63 ± 0.14, mean and SD, $n = 383$ species) is identical to the pan-Amazon forest mean (0.63 ± 0.08, $n = 165$ plots, Phillips et al., 2019), so while species-level growth-mortality trade-offs and wood density variation help explain variation in risk among trees in our region, they are not plausible explanations for the exceptional mortality rates that our forests experience in general.

5 | CONCLUSIONS

Analysis of monitoring plots across the southern Amazonia edge confirms that they are exceptionally dynamic compared to other tropical forests and shows that their uniquely high tree mortality rates among all of Amazonia are driven by crown breakage and seasonal water deficit. In our region, individual species with low wood density experience the greatest mortality and are especially susceptible to both drought and wind disturbances. Overall, water deficits favour the widespread mortality of shorter trees. On the other hand, tree mortality rates substantially reflect the mortality of broken trees for trees with exposed canopy to light. The significant impact of climatic water deficits on mortality is particularly concerning because climate modelling studies predict more intense and prolonged seasonality for Amazonia (Boisier et al., 2015; Prevedello et al., 2019), which may result in high and potentially unprecedented mortality rates for trees of the southern edge region, growing as they do in an environment that is already on the edge of suitability for forests climatically (Marimon et al., 2014; Reis et al., 2018). Furthermore, these forests suffer from the high fragmentation of habitats, enhancing the effects of climate change (Reis et al., 2018; Silvério et al., 2019). High baseline rates of mortality already impact forest structure and, consequently, carbon storage here, and any increase in mortality brings a risk of positive feedback processes which are likely to constrain carbon storage further (e.g. Gatti et al., 2021). High mortality would favour the establishment of species with lower wood density, which store less carbon and which our analysis shows are, in turn, intrinsically more prone to mortality.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

S.M.R. wrote the manuscript with input from all authors (B.S.M., B.H.M.Jr., P.S.M., F.E., E.A.O., A.E.-M., D.G., T.R.F., I.O., Y.M. and O.L.P); B.S.M. and O.L.P. were involved in planning and supervised the work; S.M.R., B.S.M., B.H.M.Jr., P.S.M., E.A.O., F.E. and A.E.-M. performed the field measurements; S.M.R., A.E.-M., P.S.M. and F.E. performed the analyses and made the figures. All authors discussed the results and contributed to the final manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data are available as a data package on ForestPlots.net: https://doi.org/10.5521/forestplots.net/2022_1 (Reis et al., 2022). The tree-level data used in Figure 5 are available on request from ForestPlot.net: https://www.forestplots.net/en/join-forestplots/working-with-data

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