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RESEARCH ARTICLE

Interaction between extreme weather events and megadams increases tree mortality and alters functional status of Amazonian forests

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Abstract

- Forest responses to changes in drought frequency is a critical matter for the future of Amazon forests under climate change, but equally important is the much less studied response to large floods, which may also increase tree mortality and change forest functionality. Further, forest vulnerability to flood is being exacerbated by large hydroelectric dams on Amazon rivers that put upland environments not adapted to flood at unique risk.
- 2. To address this critical knowledge gap, we evaluated the effects of the extreme 2014 rainfall coupled with the newly constructed Jirau hydroelectric dam on tree survival and forest functionality, in the upper Madeira River basin. We used surveys of campinarana white-sand forests (stems >1 cm in seven 1 ha plots) conducted before and after the extreme flood to test trait-based ecological theory predictions of the impact of flood on overall community function.
- 3. We found that flooding increased mortality by nearly five-fold (from 3.2% to 15.1%), mostly in smaller trees. This large mortality induced significant and consistent shifts in community function, towards species with conservative life strategies: direct comparison of trait differences between surviving and dying trees showed that survivors had smaller, high density stomata, and higher leaf dry matter content, wood density and root tissue density (RTD). Size and density of stomata and RTD were the most important predictors of species mortality rates.
- 4. Synthesis and applications. Although focused on a single event in one type of forest, this work highlights the general importance, and need for further study, of interaction between climate change and mega-dams in Amazon forests. In particular, we expect that continued expansion of hydroelectric dams in Amazonia will likely intensify the impact of large floods on forests made newly vulnerable by these dams, with substantial effect on future forest functionality in expanded floodplain areas across the Basin. Hence, these interaction analyses should be required in the Brazilian legal instruments such as the environmental impact assessments and its accompanying Environmental Impacts Reports for large infrastructure projects in Amazon.

K E Y W O R D S

dams, flood tolerance, functional traits, global warming, precipitation anomaly, root tissue density, stomata density, tree mortality

1 | INTRODUCTION

Climatic change is increasing the frequency of droughts (Marengo & Espinoza, 2016), but also the frequency of large floods in the Amazon (Barichivich et al., 2018; Ovando et al., 2016). The effects of longer and more frequent droughts are being widely studied, and reports have shown an increase in tree mortality (Condit, Hubbell, & Foster, 1995; Flores et al., 2017), as well as loss of biomass (Brienen et al., 2015; Phillips et al., 2009), in association with the large El Niño Southern Oscillation and Tropical North Atlantic events of the last two decades (Marengo & Espinoza, 2016). However, the effects of large floods have received far less attention, despite being just as frequent and widespread in the basin, albeit generally confined to the margins of rivers. Moreover, large hydroelectric dams have been built in major Amazonian rivers with the corresponding potential to exacerbate the negative effects of extreme floods (Finer & Jenkins, 2012; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016). Recent research has shown that long-lasting floods associated with changes in the hydrological regime caused by large dams have affected tree survival with large-scale impacts on floodplain vegetation (Assahira et al., 2017; Resende et al., 2019).

The interaction arising from the coupling of climate change and the construction of large hydroelectric power dams has pushed flood waters toward upland sites (Ovando et al., 2016) where the vegetation has not been evolutionarily selected to withstand such pressure. Therefore, this study aimed to examine the effects of the 2014 flood on upland sites of the upper Madeira River basin in southern Amazonia where the Jirau hydroelectric mega-dam was built. This dam began to fill the reservoir in 2013/2014, a timeframe which coincided with elevated precipitation in the Amazon basin in association with warming of the Indo-Pacific and subtropical southern Atlantic Oceans (Espinoza et al., 2014). This interaction caused a record-setting discharge in the Madeira River (58,000 m^3/s), rising to the highest level (19.2 m) ever registered in the historical series (ANA, 2018), as previous records were 49,000 m³/s and 17.2 m in 1984 (Figure 1a,b). This record-setting rise in water level resulted in flooding a large expanse of uplands from Bolivia to the southern Brazilian Amazon (Ovando et al., 2016), reaching terra-firme sites where large-scale floods have never been registered before.

We examined the effects of this severe 2014 flood on the upland vegetation of *campinaranas* of the upper Madeira River basin. *Campinaranas*, also known as white sand forests, are considered a reservoir of endemic specialist species (García-Villacorta, Dexter, & Pennington, 2016). This vegetation type dominates the Negro River basin, but it also occurs in small patches across other Amazonian regions. The small patches and low fertility of *campinaranas* make this vegetation especially susceptible to disturbance with slow recovery rates (Adeney, Christensen, Vicentini, & Cohn-haft, 2016). In the study area, *campinaranas* have a natural seasonal fluctuation in water table levels, which come very close to the surface during the rainy season, but then retreat to a depth of 4-5 m in the dry season. After the Jirau hydroelectric dam started operations in the upper Madeira River, the water table under *campinaranas* rose to a higher average height above typical water table fluctuation (Figure 1c,d).

Unusual floods are expected to increase tree mortality, according to species traits and the intensity and duration of the flood (Colmer & Voesenek, 2009; Wittmann et al., 2006). In seasonally flooded forests, plant species have been selected for this regular and predictable stress. However, in the upland environment, plants have not been selected for it, and we, therefore, expected that unnatural flooding, such as that in 2014, would filter species according to traits related to: hydraulics, as represented by stomata size and density (SS and SD), xylem vessel area and density (A and VD), vessel mean hydraulic diameter (D_{mb}), vessel size to number ratio (S) and wood density (WD), as well as resource acquisition responses, such as specific leaf area (SLA), leaf dry matter content (LDMC), and specific root length (SRL). Moreover, plant size (height, H) and the capacity to conduct oxygen in roots (root tissue density, RTD) are critical to survival. Flooding dramatically reduces oxygen levels in soils, leading to a switch to the much less efficient fermentative metabolism (Parent, Capelli, Berger, Crèvecoeur, & Dat, 2008). In such extreme conditions, absence of oxygen and accumulation of toxic metabolites lead to the death of fine roots (Taiz & Zeiger, 2006). Lower energy and impaired root systems then lead to impaired supply of water and nutrients to the plant. These conditions would be particularly stressful for plants of rapid growth with correspondingly high demand for water and nutrients, as higher respiration rates may quickly consume any stored reserves. Thus, plants with more conservative metabolism (lower SLA and SRL, but higher LDMC; Cornelissen et al., 2003), safer hydraulic systems (lower WD and lower vessel and SS; Drake et al., 2017; Poorter et al., 2010) and better capacity to escape flooding stress (lower RTD and higher H) (Cornelissen et al., 2003; Ryser, Gill, & Byrne, 2011) should be better suited to survive after flooding compared to plants with the opposite traits. The capacity of roots to continue receiving oxygen may be critical to survival in prolonged flooding, and this may depend on having lower tissue density, i.e. more empty spaces through which air can more easily flow. Taller plants would have obvious advantages to escape some of the stresses of flooding, such as total coverage of leaves by water.

We expected that the extreme floods would kill trees selectively, according to species traits as described above, leading to a change in the functional composition of these forests towards more slowgrowing plants, which, on the one hand, would make *campinaranas* more resilient in the event of new floods, but could, on the other hand, decrease its short-term capacity for carbon sequestration besides lowering forest richness and diversity. We herein followed the FIGURE 1 Hydrological regime of the upper Madeira River. (a) Historical series of discharge from 1967 to 2017 of the Madeira River at the Porto Velho Station. (b) Historical series of river level from 1967 to 2017 (ANA, 2018), Arrows, Dotted lines in (a) and (b) represent historical averages of peak discharge and river level (ANA, 2018). (c) Fluctuation of the water level at two monitoring stations (Abunã and Mutum) next to the study area on the upper Madeira River from 2009 to 2017, showing an increase in both minimum and maximum levels after the operation of the Jirau hydroelectric dam (Source: Energia Sustentável do Brasil). (d) Water table level in seven forest plots measured with piezometers. Lines represent averages per site (Abunã and Mutum)



dynamics of these forests for 5 years, documenting the mortality levels for the whole tree community, by species and according to species traits. Specifically, we asked (a) how the extreme 2014 floodinduced mortality was related to plant size?; (b) which plant traits were related to increase in mortality rate for a range of 28 most abundant species?; and (c) how the community functional properties changed after the extreme 2014 flooding?

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in *campinaranas* that occur in the area of influence of the Jirau hydroelectric dam located in the upper Madeira River basin, southwestern Amazonia. The climate is tropical hyper-thermal humid (Cochrane & Cochrane, 2010), with the highest average annual temperature ranging from 31.3 to 34.3°C, the lowest annual temperature ranging from 19.3 to 22.8°C and mean annual precipitation between 1,700 and 2,000 mm (INMET, 2019). The predominant vegetation is open *terra firme* forest growing in latosols, which occupy most of the upland in the left margin of the Madeira River (facing

downstream). Patches of *campinaranas* occur on the right bank of the river in silty, hydromorphic soil that is subject to seasonal waterlogging caused by the elevation of the water table (Perigolo, Medeiros, & Simon, 2017). *Campinaranas* comprise stunted forests that vary in the density of the tree stratum, ranging from forests up to 20 m in height and 25% canopy opening to areas with sparse trees 3–5 m tall with 42% canopy opening and a dense herbaceous layer of predominantly Cyperaceae family (Perigolo et al., 2017).

The Madeira is classified as a white-water river, and under natural conditions, it has flood pulses of approximately 10 m high (Junk et al., 2011; Figure 1b). Because the river occurs in a deep catchment, seasonal natural flooding is restricted to a narrow strip of land on its banks. However, the filling of the Jirau reservoir, which occurred at the end of 2013, modified the river flooding regime, with an average increase in the river level of 4.2 m in the rainy season and 5.2 m in the dry season (Figure 1c). In 2014, an extreme flood event was recorded in southwestern Amazonia, in association with the heating of the Pacific-Indian Ocean and subtropical southern Atlantic (Espinoza et al., 2014), causing an intense precipitation in the main tributaries of the upper Madeira River basin. This flood coincided with the beginning of the operation of the Jirau hydroelectric dam and boosted flooding in the upper Madeira River, which reached the highest level observed in the last five decades (Figure 1b). The flood spread mainly on the flat terrain along the right bank of the river, flooding large expanses of *campinaranas*, as well as *terra firme* forests and other upland environments. The water column reached a maximum of 2.4 m from ground in the *campinaranas*, and the duration of the flood varied across the sampled plots between 49 and 130 days as a consequence of topographic variation (Table S1 in Appendix S2). In later years, the *campinaranas* were not flooded by the overflow of the Madeira River, but the water table became shallower in the dry season, as a result of the operation of the Jirau hydroelectric dam (Figure 1d). Descriptive statistics of discharge before and after the filling of the Jirau dam, following the Indicators of Hydrologic Alteration method (Richter, Baumgartner, Powell, & Braun, 1996), are presented in Supporting Information (Appendix S1), and reinforce the patterns presented in Figure 1.

2.2 | Field sampling

We sampled seven 1 ha permanent plots under the vegetation monitoring programme carried out in the area affected by the Jirau reservoir (Moser et al., 2014; Oliveira, Medeiros, Simon, Hay, & ter Steege, 2018; Perigolo et al., 2017). Plots were allocated following RAPELD (Magnusson et al., 2005) sampling modules distributed systematically along the area of influence of the Jirau reservoir, upstream of the dam, and perpendicular to the Madeira River. Vegetation sampling (trees with diameter at breast height >1 cm) was performed biannually before (2011 and 2013) and after the filling of the reservoir (2015) when demography was recorded, including mortality rates. We measured functional attributes of the most abundant species, representing >80% of the abundance per plot as in the 2011 survey (Cornelissen et al., 2003). We measured 12 functional attributes of leaves, stem and roots in February 2017, for a total of 271 individuals (Tables S4 and S5 in Appendix S2). Palms were not included. Brosimum acutifolium, Lacistema aggregatum, Meriania urceolata, Miconia prasina, Miconia sp. and Ternstroemia dentata, although within 80% of plot abundance, were not sampled for functional attributes because of extremely high mortality rates after the 2014 flood. Although most trait measurements were taken after flood (except plant height), we assume that this had no effect in our analysis since traits measured showed limited intraspecific variation (see Tables S4 and S5 in Appendix S2).

2.3 | Functional attributes

We selected 12 functional attributes to describe the functional composition of forest communities and understand the impacts of flooding according to plant traits. Traits were related to resource acquisition responses (leaf and root), hydraulics (vessel and wood) and plant size (Fortunel, Ruelle, Beauchêne, Fine, & Baraloto, 2014; Kramer-Walter et al., 2016; Poorter et al., 2010; Wright et al., 2004). To measure leaf, stomata and xylem vessels attributes, we collected a branch of approximately 1 m for each individual. Immediately after collection, the base of the branch was wrapped in a moist paper towel and conditioned in a plastic bag to maintain hydration until reaching the laboratory. The number of individuals collected for each attribute varied with species. This variation occurred because of the high mortality of some species after the 2014 flooding. For SLA, LDMC, WD, SRL and RTD, the number of individuals per species ranged from 1 to 30. For stomata and xylem vessels, three individuals per species were measured, except *Brosimum rubescens* and *Parinari* sp., for which only one individual was measured.

The measures of the functional attributes followed the protocol of Cornelissen et al. (2003). SLA was calculated by the ratio between fresh leaf area and dry mass (mm²/mg). LDMC as the ratio between the leaf dry mass and the wet mass (mg/g). The number and length of stomata were examined under the microscope with 40× magnification. SRL was obtained by the ratio between root length and root dry mass (m/g). Roots with high RTD was calculated by the ratio between tween root dry mass and fresh volume (g/cm³).

The Basic WD was obtained by the equation $D_b = [1/(P_f - P_s/P_s) + 1/G_s]$ (Smith, 1954), where P_f is the weight of the saturated mass, P_s is the dry mass, and G_s is a constant that represents the average density of the "wood substance" equivalent to 1.53 g/cm³. Xylem vessels we counted and measured in a microscope with 56× magnification. From these measurements, we calculated mean A (mm²); VD, given by the number of vessels per area (n/mm^2); mean hydraulic diameter of the vessel [$D_{mh} = (\sum D4/n)1/4$ (mm²)], where n is the number of vessels and D is the vessel diameter calculated by $D = (4A/\pi)1/2$ (Scholz, Klepsch, Karimi, & Jansen, 2013); and vessel size-to-number ratio (S), given by the relation between size and number of vessels (S = A/VD; Zanne et al., 2010).

Plant height mean (*H*) was obtained based on the total number of individuals per species measured in the 2011 inventory with a telescopic measuring rod or laser hypsometer. Further details about how the functional attributes were obtained are available in Supporting Information (Appendix S2).

2.4 | Data analysis

We calculated species mortality rates (Sheil, Burslem, & Alder, 1995), based on inventories carried out before (2011/2013) and after the filling of the reservoir (2013/2015). The variation in the mortality rate given by the difference between the mortality before and after the flood (*Mort* = $M_{2013/2015}$ - $M_{2011/2013}$) was used as an estimate of increment in mortality as a result of the 2014 flood.

Statistical comparisons of plant height and diameter between individuals that died and survived flooding were obtained by the Mann-Whitney non-parametric test. The relationship between the functional attributes was summarized with a principal component analysis (PCA), using standardized variables for the relative Z-score scale. We used a Generalized Linear Model (GLM) to test the relationship between mortality rate (response variable) and functional attributes (predictor variables). The model was set with a combination of predictors pre-selected from those with stronger loadings in the PCA, including one predictive variable representing each relevant plant component: LDMC (representing the leaves), WD (wood), A (xylem vessels), SD (stomata), RTD (roots) and H (plant size).

To understand changes in the functional composition of the community along time, we calculated the plot community weighted mean (CWM, the average of each attribute weighted by the abundance of each species; Violle et al., 2007) of each attribute for each census time. The CWM was obtained with the average value of each attribute collected in 2017 for each species and weighted by species abundance obtained in the 2011, 2013 and 2015 inventories, resulting in three measurements of CWM over time, with FD package (Laliberté, Legendre, & Shipley, 2014). We used PCA to summarize and visualize the trajectory of the community in each plot based on the CWM calculated for 2011, 2013 and 2015. To evaluate the effect of flooding on the community functional attributes, we also calculated the relative changes of each plot before and after flooding, where $\Delta = [(CWM_{2015} - CWM_{2011})/CWM_{2011}] \times 100$ (Carreño-Rocabado et al., 2012). Differences between CWM_{2011} and CWM_{2015} were tested with a paired t test. For the CWM calculations, all 28 species representing 80% of the community's abundance were used. In the PCA analysis and GLM model, only 25 species were considered since we chose not to include the three species with the lowest abundance in 2011 (≤10 individuals), thus avoiding a bias in the mortality rate that may have occurred as a result of random processes not related to flooding. All analyses were performed in R platform (R Core Team, 2018).

3 | RESULTS

3.1 | Tree mortality

Plots flooded by the rising waters of the upper Madeira River in 2013/2014 had highly increased annual mortality rates after the flood (average 10.5%) compared to the previous period (1.9%; Figure 2a; Table S1 in Appendix S2). Plants that died after the

flood were smaller, with lower diameter (U = 1,274,100, p < .001; Figure 2b) and height (U = 1,429,800, p < .001; Figure 2c) than survivors. Flooding reached a maximum height of 2.4 m from the ground in some sites, as measured by the flood marks on tree trunks, and individuals below this size had all their leaves submerged. Although flood intensity varied between plots (Table S1 in Appendix S2), we found no correlation between increment in mortality rate and the number of flooded days (p > .05).

3.2 | Differential mortality across species

At the species level, large differences in tolerance to flooding were observed. *Iryanthera juruensis*, *Clusia* sp. and *Licania caudata* suffered high mortality (>38%), while 12 species had low mortality (<1%), including *Ruizterania retusa*, which is dominant in the studied forests with almost a third of all individuals (Table S2 in Appendix S2).

3.3 | Relationship among the functional traits

The axis PCA 1 described a gradient that was positively correlated with the *S*, *H*, SRL, *A* and D_{mh} and that was negatively correlated with the VD. The axis PCA 2 described a gradient that was positively correlated with the LDMC, WD and RTD and that was negatively correlated with the SLA and SS (Figure 3; Table S3 in Appendix S2). Descriptive statistics of the 12 functional traits for the 28 species are provided in Tables S4 and S5 in Appendix S2.

3.4 | Best predictors of mortality

Although several traits were associated with the differential mortality of species, a general linear model retained SD and RTD as the most important predictors (Table 1); mortality increases with low *SD*



FIGURE 2 Tree mortality in seven forest plots in the upper Madeira River basin, southern Amazonia. (a) Average mortality rates before (2011–2013) and after the 2014 record flood (2013–2015) in seven forest plots. (b) Average diameter at breast height (DBH) and (c) height of trees that survived or died after 2014 extreme flood (N = 4,920). U = Mann–Whitney non-parametric test



FIGURE 3 Principal component analysis of 12 functional traits of 25 tree species affected by the extreme 2014 flood in the upper Madeira River basin, southern Amazonia. Contribution of each variable to the ordination is displayed proportional to arrow size. A, mean vessel area; $D_{\rm mh}$, vessel mean hydraulic diameter; *H*, height; LDMC, leaf dry matter content; RTD, root tissue density; *S*, vessel size to number ratio; SD, stomata density; SLA, specific leaf area; SRL, specific root length; SS, stomata size; VD, vessel density; WD, wood density

TABLE 1 General linear model describing the effect of traits onthe variation of mortality rate of 25 tree species affected by the2014 extreme flood in the upper Madeira River basin, southernAmazonia

	Estimate	SE	t Value	Р
(Intercept)	10.313	2.960	3.484	.003
Leaf dry matter content	-4.596	4.765	-0.965	.349
Wood density	1.836	4.468	0.411	.687
Vessel area	-0.497	3.377	-0.147	.885
Stomata density	-8.350	3.438	-2.429	.027
Root tissue density	-8.625	3.420	-2.522	.022
Tree height	-1.978	3.722	-0.532	.602

and RTD. SD is negatively correlated with SS (r = -.56), and both traits strongly affect stomatal conductance and therefore photosynthesis (Farquhar & Sharkey, 1982).

3.5 | Community level changes

The increased selective mortality of species resulting from the extreme 2014 flood led to a change in the functional composition of tree community. This change encompasses a significant increase in the CWMs of leaf dry matter content, WD, vessel size to number ratio, SD and plant height, as well as a decrease in SS (Figure 4). This represented a directional change in the functional trajectory of these forests towards a more conservative functional composition (Figure 5; Table S4 in Appendix S2).

4 | DISCUSSION

The interaction between the new Jirau mega-dam and the above-average precipitation anomaly in 2014 resulted in flood waters covering areas not previously subjected to inundation before dam construction, and a long-lasting flooding (49–130 days; Table S1 in Appendix S2). In this study, we have shown that this mega-flood caused a significant increase in tree mortality rates in the *campinaranas* of the upper Madeira River basin and that this mortality was selective, affecting mostly trees with lower height, acquisitive resource strategies and potentially lower stomatal control. The surviving community changed directionally towards conservative strategies.

Tree mortality induced by the interaction between the Jirau reservoir and the extreme rainfall event in 2014 was 5 times higher (up to 15.1%) than that observed in natural conditions and normal years (up to 3.2%). Background mortality rates in tropical rainforests are around 2% per year while moratilty rates >5% per year are considered catastrophic (Lugo & Scatena, 1996). The mortality level found here is comparable to that observed under the record windthrows of 2005 in central Amazonia, which increased mortality by 23% and, when scaled to the landscape, included 0.32 million dead trees (Negrón-Juárez et al., 2010). Effects of droughts have been variable, depending on drought intensity and region, being around two times higher than background levels across the Amazon (McDowell et al., 2018) and central Amazonia (Williamson et al., 2000). These comparisons show that mortality levels by extreme rainfall events that drive flooding in human-modified contexts, such as hydroelectric reservoirs, are just as deleterious, or more so, than other climate-induced changes in the Amazon and have the potential to change the landscape of river margins. Although largely confined to the margins of rivers, the upscaling of these effects to the basin may reach non-trivial values, as the area covered by riverine vegetation is estimated to be 12% of the seven million square kilometers of the Amazon basin (Junk et al., 2011). For example, the combined effects of 2014 extreme rainfall and the installation of the two mega hydroelectrics Jirau and Santo Antônio (located ca. 100 km downstream from Jirau) resulted in an estimated flooded area of more than 800 km² across the upper Madeira River basin (Cochrane, Matricardi, Numata, & Lefebvre, 2017).

Although subject to seasonal flooding by groundwater fluctuation, *campinaranas* in the study area have not evolved under the pressure of river inundations. Consequently, species are not as morphologically or physiologically adapted to this stress as plants that evolved in the river margins subjected to predictable annual river floods. Under the unexpected long-standing 2014 flood, plant species with acquisitive strategies associated with higher



FIGURE 4 Relative change in the community weighted mean (CWM) of traits in seven forest plots (and averaged across all plots, horizonal line) associated with the 2014 record flood in the upper Madeira River basin, southern Amazon. Bars represent the percent difference in each CWM trait in each plot before and after the flood; the statistical significance is tested using paired *t* test across all plots. *A*, mean vessel area; *D*_{mh}, vessel mean hydraulic diameter; *H*, height; LDMC, leaf dry matter content; RTD, root tissue density; *S*, vessel size to number ratio; SD, stomata density; SLA, specific leaf area; SRL, specific root length; SS, stomata size; VD, vessel density; WD, wood density

energetic demands that become too costly in the new flooded conditions were especially affected and had increased mortality. The oxygen reduction in flooded soils leads to a change to the much less efficient fermentative metabolism (Parent et al., 2008). In this condition, carbohydrate reserves may be quickly used, and the plant may enter into carbon starvation. Soil hypoxia and anoxia reduce root permeability and hydraulic conductivity in non-tolerant species, actually causing symptoms similar to those seen in drought conditions (Parent et al., 2008). Acquisitive plants also have larger transpiration surfaces, given the higher leaf surface-to-mass relationship, which can increase the stress caused by decreased water conductance from roots. Under these circumstances, acquisitive plants exhaust their carbohydrate reserves, water absorption by roots is inhibited, and transpiration is high, while their large stomata are not efficient to control water loss. These multiple stresses may kill plants by both carbon starvation and hydraulic failure (McDowell et al., 2008).

Plant height was also important to determine plant fate under the extreme 2014 flood. Greater heights may help plants escape flooding and increase survival, since submersion of the canopy restricts contact of leaves with oxygen and light (Parolin & Wittmann, 2010), decreasing or ceasing gas exchange and photosynthesis (Colmer & Voesenek, 2009). Plant species that evolved under periodic flooding are adapted to submergence (Fernández, 2006), but not *terra firme* or *campinarana* species. Small plants that were submerged in *campinaranas* experienced the stresses of soil anoxia, overlapped with the stress of leaf submergence and were those that suffered the most, with high mortality levels.

Size and density of stomata and RTD were the most important predictors of species mortality rates (Figure S1 in Appendix S2).



FIGURE 5 Functional trajectories of seven forest plots from before (2011, 2013, arrow tail) to after (2015, arrow head) the 2014 record flood in the upper Madeira River basin, southern Amazonia. Each data point corresponds to principal component analysis (PCA) scores based on 12 community weighted mean (CWM) traits. Functional traits that contributed most to each PCA axis are displayed: RTD, root tissue density; *S*, vessel size to number ratio; SLA, specific leaf area; and WD, wood density

Small stomata can open and close faster, given the higher proportion of cell membrane to volume (Drake et al., 2017), making it possible to better adjust to unfavorable conditions. Plants with good stomatal control can reduce stomatal conductance up to 30% under experimental flooding (Lopez & Kursar, 1999) in response to the lowered water absorption by roots in anoxic soils (Pezeshki, 1993). Low oxygen supply and accumulation of toxic compounds in flooded soils deteriorate roots of non-adapted plants, lowering root growth and, in worst cases, cause rotting, thus opening the door to invasion of pathogens (Kozlowski, 1997). In general, thin and light roots (i.e. lower RTD) are more susceptible to these conditions, and species with this trait had higher mortality rates.

At the community level, the selective mortality imposed by the extreme flood in 2014 filtered out acquisitive species, directionally changing the functional structure towards conservative strategies, a phenomenon that ultimately led to changes in the functioning of this forest ecosystem. A more conservative tree community may be more resistant to new flood events in the future, but will have a lower carbon sequestration capacity in the short to medium term. If new floods are not controlled and strike again in the same regions, the new community/functional composition and carbon sequestration pattern may become a permanent state, as predicted by alternative states theory. Flores et al. (2017) suggested that flooded forests may be the most vulnerable forest in the Amazon due to the synergism of droughts and fire. But here we showed that forests in the margins of rivers, not subject to regular flooding, are also vulnerable to synergies of climate change and large infrastructure projects, that may lead these ecosystems to irreversible tipping points. Additionally, the loss of sensitive species reduces the functional diversity of the forest, which may lead to decreased ecosystem services, such as resources to the fauna, with still unsuspected cascading effects.

The negative effects of flooding on Amazonian ecosystems have increased in the last decades owing to increased construction of hydroelectric dams (Finer & Jenkins, 2012). In 2013/2014, the filling of

the Jirau hydroelectric dam reservoir coincided with precipitation anomalies in the upper Madeira River basin that exceeded average rainfall by around 100% (Espinoza et al., 2014). Such unprecedented rainfall was associated with the warming of the Indo-Pacific and with exceptionally warm conditions in subtropical southern Atlantic Oceans, which, in turn, increased the transport of humidity over southwestern Amazonia (Espinoza et al., 2014). The walls of Jirau and Santo Antônio hydroelectrics dammed the excess precipitation in 2014, and the flood spread over more than 800 km², covering an area 64.5% larger than predicted by environmental impact studies (Cochrane et al., 2017). This flood also lasted much longer than the typical annual floods, stressing even the varzea (seasonally flooded) forests. The interaction between the expanded construction of hydroelectric dams and the increased frequency of extreme climatic events owing to climate change (Barichivich et al., 2018; Marengo & Espinoza, 2016) is likely to make the conditions that produce mega-floods, such that in 2014, a more frequent occurrence in the Amazon. The increase in frequency and duration of floods implies a change in the annual river flood pattern, affecting the dynamics of forests in the river margins, with increased mortality and altered functionality. Our findings suggest that decisions on the building of new dams and also the operation of those already in place (eg. Resende et al., 2019) should be re-evaluated in the light of the dramatic negative effects demonstrated here.

Our results suggest that tree mortality caused by the combination of extreme rainfall/river discharge associated with damming is substantially higher than average mortality in floodplain forests (eg. Homeier, Kurzatkowski, & Leuschner, 2017; Nebel, Kvist, Vanclay, & Vidaurre, 2001). Even during unusually severe flooding seasons, tree mortality in tropical riparian forests seems to be lower than detected here, probably because flooding intensity is within species flooding tolerance. For example, mortality rates associated with extreme floods in riparian forests in the Paraguai River (4.1% per year; Damasceno-Junior, Semir, Santos, & Leitão-Filho, 2004) and in southeastern Brazil (2.2% per year; Silva, Berg, Higuchi, & Nunes, 2011) suggest that natural floods alone are unlikely to generate levels of mortality as high as reported in our study site.

In tropical forests, tree mortality has increased in recent decades as a consequence of severe droughts, competition with lianas, fires and windstorms, with implications for both biodiversity conservation and maintenance of the carbon cycle (McDowell et al., 2018). In line with recent studies (Assahira et al., 2017; Resende et al., 2019), we have shown that flooding anomalies are also important drivers of tree mortality in the Amazon, with effects that are comparable to other major drivers such as drought and windstorms. The interaction effect between extreme climatic events and the construction of hydroelectric dams is likely to increase the frequency of major floods, leading to higher tree mortality and changes in the functional composition of forest communities. Hence, these interaction analyses should be required in the Brazilian legal instruments such as the environmental impact assessments and its accompanying Environmental Impacts Reports for large infrastructure projects in Amazon.

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AUTHORS' CONTRIBUTIONS

P.M., M.B.d.M., M.F.S. and F.R.C.C. designed the study, P.M., M.F.S., and F.R.C.C. analysed data with input from M.B.d.M. and A.B.G. P.M., M.F.S. and F.R.C.C. wrote the paper, with input from M.B.d.M. and A.B.G.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/ dryad.8041f4r (Moser, Simon, Medeiros, Gontijo, & Costa, 2019).

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SUPPORTING INFORMATION

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