

## **I. Title page**

**Statement of authorship:** GVG, JSP, WA, and EH conceived the idea. GVG, JSP, and EH designed the sampling scheme. GVG and HM performed data collection. JSP, EH, HM, and TEW contributed data. TR, HM, and GVG performed data curation. GVG performed data analysis with the input of WA. GVG wrote the first draft of the manuscript. All authors provided feedback on subsequent versions and edited the manuscript.

**Data accessibility:** All FIA, LiDAR, and trait data compiled for this work are publicly available and we indicate such sources in the manuscript. In addition, the hydraulic trait data for this study will be deposited in the Xylem Functional Traits Database (<https://xylemfunctionaltraits.org/>) upon publication. The compiled data associated with each research question and the R code used for statistical analysis in this study will be deposited in a DRYAD public repository upon acceptance of the manuscript. We have removed the geospatial information extracted with forest plot locations from the publicly available data used for statistical analyses due to landowner privacy rights considered in the United States Food Security Act of 1985 (P.L. 99-198, also known as the 1985 U.S. Farm Bill).

**Title: Aridity and forest age mediate landscape scale patterns of tropical forest resistance to cyclonic storms**

German Vargas G.; School of Biological Sciences, University of Utah, Salt Lake City, UT 84112, United States; [gevargu@gmail.com](mailto:gevargu@gmail.com)

Humfredo Marcano; USDA Forest Service, Southern Research Station, Knoxville, TN 37919, United States; [humfredo.marcano@usda.gov](mailto:humfredo.marcano@usda.gov)

Tom Ruzycki; Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, CO 80525, United States; [tom.ruzycki@colostate.edu](mailto:tom.ruzycki@colostate.edu)

Tana E. Wood; USDA Forest Service, International Institute of Tropical Forestry, San Juan, PR 00926, United States; [tana.e.wood@usda.gov](mailto:tana.e.wood@usda.gov)

28 William R. L. Anderegg; School of Biological Sciences, University of Utah, Salt Lake City, UT  
29 84112, United States; Wilkes Center for Climate Science and Policy, University of Utah, Salt Lake  
30 City, UT 84112, United States; [anderegg@utah.edu](mailto:anderegg@utah.edu)  
31 Jennifer S. Powers; Department of Plant and Microbial Biology, University of Minnesota, St. Paul,  
32 MN 55108, United States; [powers@umn.edu](mailto:powers@umn.edu)  
33 Eileen H. Helmer; USDA Forest Service, International Institute of Tropical Forestry, San Juan, PR  
34 00926, United States; [eileen.helmer@usda.gov](mailto:eileen.helmer@usda.gov)  
35 Running title:  
36 **Keywords:** climate change, drought tolerance, forest inventory analysis, functional diversity,  
37 hurricanes, tree mortality.  
38 **Type of article:** Letters  
39 **Number of words:** Abstract (150), Main text (4991)  
40 **Number of references:** 69  
41 **Number of figures:** 3  
42 **Number of tables:** 2  
43 Author for correspondence:  
44 German Vargas G.  
45 School of Biological Sciences  
46 The University of Utah  
47 Telephone: +1 617 459 2792  
48 Email: [gevargu@gmail.com](mailto:gevargu@gmail.com)  
49

## **II. Abstract page**

Ecological theory holds that tropical forest resistance to hurricanes should increase with stand age and aridity. However, limited data beyond a handful of long-term monitoring sites makes it hard to link resistance to hurricanes with environmental gradients. We address this by using trait data for 410 tree species, remote sensing metrics of canopy structure, and 339 plots to assess whether forest age and aridity mediate the impacts of two hurricanes in Puerto Rico. Hurricanes caused a 45% and 21% decrease in forest canopy height and cover, respectively, with a 25% increase in tree mortality. Old forest stands in wetter regions as well as those with tall canopies dominated by low wood density species were the most affected. Interestingly, high resistance to hurricanes was related to enhanced drought tolerance. These results highlight crucial complexity to include when forecasting the fate of tropical forests to increasingly stronger hurricanes in a changing climate.

### III. Main text

#### Introduction

Climate change is expected to cause an increase in the intensity of cyclonic storms, hereafter hurricanes, in tropical regions due to increases in ocean heat energy (Seneviratne *et al.* 2021). Hurricanes play a significant role in mediating tropical forest ecosystem processes and forest structure (Lugo 2008). Predicting the response of tropical forests to changes in hurricane intensity is a challenging task due to their high biological diversity and environmental complexity (McLaren *et al.* 2019; Uriarte *et al.* 2019; Lin *et al.* 2020). Given this complexity, forest resistance to hurricanes is likely to vary across the environmental gradients shaping forest structure and function. In E.P. Odum's seminal paper '*The strategy of ecosystem development*,' he theorizes that, as ecosystems age, their attributes will favor slower energy exchange with greater ecosystem homeostasis (*e.g.* resistance and/or resilience) (Odum 1969). However, this framework might not fully represent all of the factors mediating tropical forest resistance to hurricanes across environmental gradients (Vitousek & Reiners 1975; Uriarte *et al.* 2009; Feng *et al.* 2020). It is crucial then to evaluate whether the factors influencing tropical forests' characteristics mediate resistance to hurricanes.

During hurricane disturbances, two main mechanisms lead to tree mortality: uprooting and stem breakage (Lugo 2008). Tall tree species with low wood density (WD) have higher immediate mortality through either mechanism (Zimmerman *et al.* 1994; Ogle *et al.* 2006; Curran *et al.* 2008; Uriarte *et al.* 2019; Taylor *et al.* 2023). Yet other factors, such as aridity, can influence traits like WD. This raises the question of whether known patterns of trait variation can mediate forest resistance to hurricanes irrespective of forest age. It is well known that community-level patterns of functional traits, such as WD, vary across gradients of water availability (*i.e.*, aridity) (Bruehlheide *et al.* 2018). For instance, in arid regions plant species tend to show shorter stature, deep roots, high WD, and xylem tissue resistant to drought stress (Olson *et al.* 2018; Tumber-Dávila *et al.* 2022; Vargas G. *et al.* 2022). These characteristics represent a 'slow growing-hydraulically safe' physiological strategy (Reich 2014; Díaz *et al.* 2016; Oliveira *et al.* 2021),

which is associated with higher tree survival during periods of extreme drought (Anderegg *et al.* 2016). Forest stand age also affects these patterns of trait variation because, in tropical forests, low WD species usually dominate young stands at the wet end of the aridity spectrum while high WD species dominate young stands at the dry end (Poorter *et al.* 2019) (Fig. 1, a). Thus, the patterns of stand-level plant traits conferring resistance to hurricanes should depend on forest age and interactions with other environmental filters such as aridity.

Beyond the major effects on tree mortality and changes in forest structure, hurricanes also impact plant community composition. After a hurricane, there is an increase in the number of forest gaps (Lugo 2008), potentially favoring fast-growing drought-vulnerable plant species (Alonso-Rodríguez *et al.* 2022; Smith-Martin *et al.* 2022). Changes in the light environment can also lead to increases in phylogenetic relatedness in the seedling community (Comita *et al.* 2018). However, in tropical forests located at the dry end of aridity gradients, recruitment after hurricanes mostly occurs through the re-sprouting of snapped trees, and large re-organizations of the plant community are rarely seen (Van Bloem *et al.* 2007; Curran *et al.* 2008). These lines of evidence indicate that the trajectory (*i.e.*, increase or decrease) and the rate of change in functional composition (*e.g.*, trait velocities) after a hurricane may consequently follow many alternative routes depending on environmental factors and surviving tree species characteristics (Fig. 1, b) (Lugo 2008; Trugman *et al.* 2020). The combined effect of forest stand age and climate on these responses remains uncertain as no study has explored this extensively (Lin *et al.* 2020).

The factors that contribute to hurricane resistance at broad geographic scales are not yet fully understood. Recent remote sensing analyses suggest that large reductions in canopy greenness and increases in non-photosynthetic vegetation may be associated with tall forest canopies, hurricane exposure, old stand age, or wetter forests (Van Beusekom *et al.* 2018; Feng *et al.* 2020; Hall *et al.* 2020; Leitold *et al.* 2022). However, only one study performed a ground validation of impacts using limited ( $n < 30$ ) forest plot data in which canopy height was the most important forest characteristic explaining biomass loss during hurricanes (Hall *et al.* 2020). This highlights two major areas that require further research. First, the extent to which remotely

observed changes are linked to actual tree mortality remains unclear. Second, to our knowledge, no studies consider forest age and community-level functional traits in determining the severity of hurricane impacts.

We tested whether remotely sensed losses in canopy height and canopy cover were linked to an increase in plot forest mortality and investigated whether these patterns differed depending on the forest's functional composition, aridity, and age. We leveraged forest basal area data from a network of 339 long-term permanent inventory plots from Forest Inventory Analysis (FIA) data in the archipelago of Puerto Rico collected before and after Hurricanes Irma and Maria. We hypothesized that resistance to hurricane disturbances would increase with aridity and decrease with stand age, even after accounting for the differences in topographic slope and proximity to the eye of the storm (Feng *et al.* 2020). We further hypothesized that aridity would limit the increase in community-level trait values indicative of vulnerability to drought (*i.e.*, low WD) following hurricane disturbance. Specifically, we asked: 1) How do climate and stand age mediate forest diversity, structure, and community-level trait values? 2) How did forest structure, mortality, community-level traits, and trait velocities change after Hurricanes Irma and Maria in 2017? 3) Do climate and stand age determine the trajectory of trait velocities after the hurricanes? 4) Are hurricane-related changes in forest mortality directly and indirectly mediated by community-level traits?

## **Materials and methods**

### *Study region and forest inventory*

We used the network of 369 long-term permanent plots (0.067 ha each) from the U.S. Department of Agriculture Forest Service Forest Inventory Analysis Program (FIA) that were established between 2001-2004 for Puerto Rico, Vieques, Culebra, and U.S. Virgin Islands (Brandeis *et al.* 2009). We selected 339 plots with a forest condition class covering >30% of a given plot's area (Trugman *et al.* 2020) and excluded plots in mangrove forests. The selected plots span a steep rainfall gradient from 700 to 4600 mm, a mean temperature gradient from 19

to 29 °C (Daly *et al.* 2003), and a mosaic of forest stands of different ages recovering from near total deforestation in the 1950s followed by agricultural land abandonment and further socioeconomic development (Wadsworth 1950; Birdsey & Weaver 1987; Brandeis *et al.* 2007). On the selected plots, we calculated the Shannon diversity index (diversity), basal area in m<sup>2</sup> ha<sup>-1</sup> (BA), and the ratio between above-ground biomass and stem density (SDI). Dense stands with small trees have small SDI, while a large SDI indicates forest stands composed of large stems. We calculated forest mortality as the percentage of dead BA at the end of the interval (BA<sub>dead</sub>) in relation to the plot total BA at the beginning of the interval (BA<sub>total</sub>) divided by the time in years between each census (MR<sub>dead/alive</sub> in % yr<sup>-1</sup>) (Equation 1) for each census interval for each plot. This mortality calculation excluded trees that died from fire or non-natural causes.

$$MR_{dead/alive} = \frac{(BA_{dead}/BA_{total}) * 100}{t_f - t_i} \quad \text{Equation 1,}$$

#### *Remote sensing metrics of forest structure*

We complemented the FIA data with remotely sensed forest canopy height, cover, and stand age. We summarized plot-level changes in canopy height and cover from 1-m spatial resolution maps of those variables for the years 2016 and 2018 developed by Rounds *et al.* (2023) from airborne LiDAR data collected by the U.S. Geological Survey. From these maps, we used average canopy height values of 1-m pixels in each 0.065 ha plot and the proportion of pixels with forest cover for canopy cover. To determine stand age, we used data combining land-cover maps from the years 1951-2000 with plot status (forest or nonforest) since then (Helmer *et al.* 2023).

#### *Forest functional composition*

We characterize functional composition with four plant traits that together indicate species' growing strategies (e.g., fast vs. slow) and drought tolerance (Table S1). Fast-slow traits include wood density (WD) and specific leaf area (SLA), which provide a proxy of species'

resource acquisition strategies in which low WD and high SLA indicate a fast-growing acquisitive strategy (Díaz *et al.* 2016). Drought tolerance traits include the stem water potentials at leaf turgor loss point ( $\Psi_{\text{TLP}}$ ) and at 50% loss of hydraulic conductivity or 50% accumulation of embolisms ( $\Psi_{\text{P50}}$ ), which describe the thresholds of leaf and xylem function under drought (Vargas G. *et al.* 2022). While most trait data come from previously published sources, we collected data on drought tolerance traits for nine species during February-March 2020 (Methods S1). For each plot, we calculated trait community-weighted means, community-weighted standard deviation, and the rate of change of traits through time (*i.e.*, ‘trait velocities’). Trait velocities provide information on the functional trajectories of plant communities in which directionality is associated with environmental filters such as drought events or successional gradients (Trugman *et al.* 2020).

#### *Climatic predictors*

We used two complementary metrics to characterize climatic water availability. First, we referred to a previously published 30-year record of mean annual potential evapotranspiration to precipitation ratio (Daly *et al.* 2003), which provides insight into the level of aridity for any specific plot in the FIA inventory. Second, we calculated the minimum value of the standardized precipitation evapotranspiration index ( $\text{SPEI}_{\text{min}}$ ) for the five years leading up to each FIA census (Methods S2). This approach allowed us to gauge the intensity of drought during a given census interval, as drought events can have short-term effects that differ from long-term climate (Anderegg *et al.* 2015). By considering both short and long-term climates, we were able to construct a more nuanced understanding of the climatic drivers of forest characteristics for each FIA plot.

#### *Statistical analysis*

To test whether stand age and climate mediate forest diversity, structure, and functional composition, we fitted a series of linear mixed-effect models with the community-weighted means,



canopy cover, canopy height, SDI, and diversity as response variables, and stand age, aridity, and SPEI<sub>min</sub> as fixed effects. In this model, a joint categorical variable that included geological class (alluvial volcanic sedimentary, karst, serpentine) and forest type for a given life zone (dry, moist, wet, lower montane), with a total of 12 levels, was used as a random effect given that forests grouped by these two categorical variables share similarities in species composition and forest structure (Brandeis *et al.* 2009). We started by fitting the model with all the possible interactions among explanatory variables and then selected the model with the lowest AIC. If two models showed AIC values with a difference  $< 2$ , we selected the model with the higher number of explanatory variables. Predictor variables were standardized to allow comparison of model  $\beta$  coefficients. For this analysis, we used all the FIA plot data during the last census for a given plot before September 17<sup>th</sup>, 2017 (Hurricane Maria).

We identified 180 out of the original 339 plots with inventory data before and after September 17<sup>th</sup>, 2017. On these plots, we employed a four-step process to explore the impacts of hurricanes Irma and Maria. First, we compared values of canopy height, cover, MR<sub>dead/alive</sub>, species diversity, and community traits before and after the impact of the hurricanes using a series of paired Wilcoxon signed rank tests with continuity correction, given the lack of normality in our response variables. This analysis was complemented with forest-type specific tests for dry, moist, and wet forests. We excluded lower montane forests from these tests due to the low sample size ( $n < 30$ ). We then calculated the rate of change ( $\Delta$ ) of canopy height, cover, MR<sub>dead/alive</sub>, and functional traits from the last census before September 17<sup>th</sup>, 2017 to the census after that.

Second, we fitted a series of linear mixed models exploring whether  $\Delta$ MR<sub>dead/alive</sub>, canopy cover ( $\Delta$ CC), and height ( $\Delta$ CH) were explained by trait community-weighted means, their standard deviations, proximity to hurricane eye track (obtained from the National Hurricane Center's Tropical Cyclone Reports, [www.nhc.noaa.gov](http://www.nhc.noaa.gov), accessed September 2022) (Fig. S7), stand age, canopy height, or topographic slope. Additionally, we fitted linear mixed models to explore whether the  $\Delta$ CH predicted  $\Delta$ MR<sub>dead/alive</sub> and  $\Delta$ CC. We used the combination of geological

classes and life zones as random effects. The models using community-weighted means and standard deviation were weighted such that plots with higher trait BA coverage (*i.e.*, relative BA of the species for which we have trait data) had higher weight in the analysis. Because these models consider only one predictor, we did not standardize the explanatory variables before the analysis.

Third, we assessed whether climate and stand age explained increases or decreases in community trait values. To do this, we fitted a generalized mixed-effect model in which the response variable is binomially distributed where 1 represents decreases in trait values (negative trait velocity) and 0 increases in trait values (positive trait velocity) after the impacts of the hurricanes. We fitted the model using a complementary log-log link function and then calculated the risk ratio as the ratio between the probability of observing a negative trait velocity over the probability of observing a positive trait velocity. We used the combination of geological classes and life zones as random effects.

Last, we assessed the direct and indirect effects on forest resistance to hurricane disturbances using a piecewise structural equation model (SEM) (Lefcheck 2016). We built a single SEM that included all three metrics of the impact of Hurricane Maria ( $\Delta MR_{\text{dead/alive}}$ ,  $\Delta CC$ , and  $\Delta CH$ ) as response variables. Direct or indirect predictors included climate (aridity), topography (proximity to hurricane eye, slope), forest structure (stand age, canopy height, SDI), species diversity, and functional composition (community-weighted mean and standard deviation for WD). The selection of predictors was a two-fold process. First, we selected predictors based on the previous analyses to explain both forest characteristics and hurricane impacts. This provided an initial structure of hypothesized causal paths in the SEM (Fig. S4). Second, we selected predictors that were poorly related to each other (Spearman's  $\rho < 0.5$ ) as multicollinearity might confound the outcome of the SEM (Garrido *et al.* 2022). We assessed model fit using Shipley's test of directed separation (Shipley 2000). This tests the assumption that all variables are conditionally independent by calculating Fisher's C and whether the considered causal relationships are consistent with the data ( $p > 0.05$ ) (Lefcheck 2016). High Fisher's C

values indicate strong discrepancies between the proposed model and the observed variation in the data (Shipley 2000; Lefcheck 2016). We then obtained standardized estimates of the direct, indirect, and mediator effects of the predictors on all the response variables in the model. In all models with random effects, we calculated the variance explained by the fixed effects ( $R_m^2$ ), and the variance explained by both fixed and random effects ( $R_c^2$ ) (Nakagawa & Schielzeth 2013; Nakagawa *et al.* 2017). All data management and analyses were done using R 4.2.1 (R Core Team 2022) with packages tidyverse (Wickham *et al.* 2019), SPEI (Baquería & Vicente-Serrano 2017), piecewiseSEM (Lefcheck 2016), semeff (Murphy 2022), lmer4 (Bates *et al.* 2015), and MuMin (Bartón 2022).

## Results

### *Drivers of forest structure and function*

Aridity and stand age explained variations in forest structure and function: species diversity, canopy height, canopy cover, and SDI increased with stand age (Table 1). Stand age effects on canopy height varied based on aridity levels, as evidenced by a strong interaction effect (Table 1). Canopy height increases less with age in dry regions (~3.5-7 m) than in wetter ones (~8-20 m). Short-term drought stress (SPEI<sub>min</sub>) moderately ( $p = 0.01$ ) affected diversity (Table 1), in which plots that experienced severe drought conditions (SPEI<sub>min</sub> < -2) in the five years before September 2017 were on average 12 % less diverse.

With increasing aridity, there was a 10% increase in community-weighted WD and a decrease of 8% for  $\Psi_{TLP}$  and 10% for  $\Psi_{P50}$ . This can be seen in the dry forests of Southwestern Puerto Rico and outlying Vieques and Culebra Islands (Fig. S1), where drought tolerant tree species are more prevalent (average  $\Psi_{P50}$ : -7.5 MPa,  $\Psi_{TLP}$ : - 2.9 MPa), contrasting with the wetter Northeast (average  $\Psi_{P50}$ : -2.5 MPa,  $\Psi_{TLP}$ : - 1.7 MPa). As for stand age, older forests had lower SLA and more negative  $\Psi_{TLP}$  and  $\Psi_{P50}$ . Aridity modulated the effects of stand age on WD, SLA, and  $\Psi_{TLP}$ , in drier regions community-weighted means did not change with stand age and the opposite occurred in wetter regions as evidenced by the presence of interaction effects (Table 1).

*Effects of Hurricanes Irma and Maria*

Before September 2017,  $MR_{\text{dead/alive}}$  averaged 2.7% of forest basal area per year, canopy height averaged 3.9 m in the dry end and 12 m in the wetter end, and canopy cover averaged 84% (Fig. 2). After hurricanes Irma and Maria, we found strong evidence of a ~25% increase in  $MR_{\text{dead/alive}}$ , ~21% decrease in canopy cover, and ~45% decrease in canopy height (Fig. 2) and the impacts varied among dominant forest types (Fig. 2). We only found evidence of an increase in the community-weighted standard deviation of SLA in wet forests (Table S2). Additionally, the probability of a decline in community-weighted mean WD after the hurricanes was lower in drier areas. (Table S3, Fig S3, & Fig. S4).

*Factors mediating hurricane effects on tropical forests*

From the univariate analyses, we found that the main predictors of  $\Delta MR_{\text{dead/alive}}$  were distance to the hurricane track (*e.g.*, the shorter the distance the greater the increase in  $MR_{\text{dead/alive}}$ ) and forest stand age (*e.g.*, older stands showed greater increases in  $MR_{\text{dead/alive}}$ ) (Table 2). Plots in flat terrain suffered major decreases in canopy cover compared with plots on steep terrain (Table 2). Species diversity and community-weighted standard deviation for WD were associated with the change in canopy cover, whereas less diverse plots experienced the biggest reductions in canopy cover (Table 2). Eight out of the 14 variables individually explain changes in canopy height. First, plots in older forest stands with taller canopies and closer to the hurricane track showed the greatest reductions in canopy height (Table 2). Second, plots dominated by species with fast-growing, drought-sensitive trait values (high SLA; low WD,  $|\Psi_{\text{TLP}}|$  or  $|\Psi_{\text{P50}}|$ ) showed the greatest reductions in canopy height. Edaphic conditions and forest types were only important for the models predicting the change in canopy height (Table 2).

Structural equation models (SEMs) allowed us to quantify direct and indirect drivers of the effects of hurricane disturbance and the mediators of such effects. The first model included only the univariate relations shown in SI Appendix Fig S5 and Tables 1 & 2 yielding poor

goodness of fit (Fisher's  $C = 260.47$ , d.f.= 76,  $p < 0.0001$ ) (SI Appendix Fig S6). We obtained the final SEM model (Fisher's  $C = 53.43$ , d.f.= 68,  $p = 0.902$ ) after updating the model to account for missing paths found in the test of direct separation and to exclude weak paths ( $p > 0.1$ ). The final SEM showed that  $\Delta MR_{\text{dead/alive}}$  was higher in older forest stands that experienced larger losses in canopy cover (lower  $\Delta CC$ ), were located closest to the eye of the hurricanes, and were on flat terrain (Fig. 3, a). Canopy height, WD, and the  $\Delta CH$  had an indirect effect on  $\Delta MR_{\text{dead/alive}}$  in which forests with short canopies, low WD, and negative  $\Delta CH$  experienced the highest  $\Delta MR_{\text{dead/alive}}$  (Fig. 3, b). Interestingly, WD was the common mediator for the paths explaining these three metrics of hurricane impacts ( $\Delta CC$ ,  $\Delta CH$ , and  $\Delta MR_{\text{dead/alive}}$ ).

## Discussion

Using the FIA plot network, we comprehensively analyzed how aridity and forest age mediate forest properties conferring resistance to hurricanes. Hurricanes caused a 45% decrease in canopy height and a 21% decrease in forest canopy cover, leading to a 25% increase in stand-level tree mortality. After considering the proximity of the storms, we found that older forest plots and those with tall canopies were most affected. Importantly, tall forests dominated by fast-growing, drought-vulnerable tree species (high SLA, low WD, low  $|\Psi_{\text{TLP}}|$ , and low  $|\Psi_{\text{P50}}|$ ) were found in wetter environments. Stands in wetter environments were also 50% more likely to show a decrease in community-weighted WD than forests located in drier regions. Our findings emphasize the positive relationship between a community's ability to tolerate drought and its resistance to hurricanes across broad ecological gradients. These discoveries highlight factors to take into consideration when forecasting how forests will respond to increasingly severe hurricanes.

### *Variation in forest structure and function*

Both aridity and stand age influenced forest properties associated with resistance to hurricanes. Species diversity increased with stand age but decreased with  $\text{SPEI}_{\text{min}}$ ,

demonstrating strong controls of environmental factors on species diversity even over short periods (Anderegg *et al.* 2013; Batllori *et al.* 2020). Aridity had a negative effect on canopy height, which underscores the role of water availability in limiting plant size in dry environments (Olson *et al.* 2018; Stovall *et al.* 2019). Canopy height was also affected by the interaction of aridity and forest age (Table 1). In arid regions of Puerto Rico, the canopy height of young and old stands can be similar (~4 m) (Van Bloem *et al.* 2007). In wetter regions, canopy height increases along with stand age (Drew *et al.* 2009). Canopy cover and SDI both increased with age, which was expected as older forest stands tended to have closed canopies and fewer stems.

We observed increases in community drought tolerance (high WD and more negative  $\Psi_{TLP}$  and  $\Psi_{P50}$ ) with aridity, following expected patterns (Vargas G. *et al.* 2022). However, besides the sap flux velocity (Bretfeld *et al.* 2018), to our knowledge, no previous study has linked tropical forest stand age with community-weighted metrics of drought tolerance. Here we showed that community-level  $\Psi_{TLP}$  and  $\Psi_{P50}$  became more negative with forest age (Table 1), highlighting potential linkages between slow-growing species and increased drought resistance as expected in Odum's hypothesis (Odum 1969; Reich 2014; Oliveira *et al.* 2021). Decreases in SLA with forest age were expected, given that species with a 'slow' resource use strategy may dominate old stands (Díaz *et al.* 2016; Muscarella *et al.* 2017).

We also observed an interaction between stand age and aridity for WD, SLA, and  $\Psi_{TLP}$ . Trees with a conservative growing strategy dominate young forest stands in arid areas while wet environments typically show the opposite pattern (Lohbeck *et al.* 2013; Poorter *et al.* 2019, 2021). The interaction effects between aridity and forest age were not present for  $\Psi_{P50}$ . There are two possible explanations for this trend. First, in Caribbean arid regions precipitation is fairly low (< 1500 mm yr<sup>-1</sup>) when compared to other tropical forests (Schwartz *et al.* 2020), limiting the presence of drought-sensitive species regardless of forest age (Vargas G. *et al.* 2021, 2022). Second, drought-resistant xylem usually has denser wood via increased vessel density and thickened pit membranes (Isasa *et al.* 2023).

### *Hurricane impacts across environmental gradients*

The hurricane caused a 25% increase in forest mortality rates, a 21% decrease in canopy cover, and a 45% decrease in canopy height across Puerto Rico (Fig. 2). While the changes in canopy height and cover were equal among the dominant forest types, increases in mortality rates were not (Fig. 2). Together with previous remote sensing work (Feng *et al.* 2020; Hall *et al.* 2020), these patterns suggest that hurricane impacts are milder in the dry forests. However, vegetation indices from 30-m satellite imagery do not show the nuances driving the observed impacts of hurricanes Irma and Maria. While mortality ( $\Delta MR_{\text{dead/alive}}$ ) increased with canopy-cover loss, it was only indirectly related to changes in canopy height (Fig. S5), at least until 2021. Likely because most stem snapping does not cause tree death (Taylor *et al.* 2023). These results highlight the importance of ground validation with extensive plot data such as the FIA database (Hoque *et al.* 2017), which addresses the sampling coverage limitations of long-term field observations (Hall *et al.* 2020).

### *Direct and indirect drivers of hurricane forest damage*

The univariate models allowed us to directly link remote sensing metrics of hurricane impacts with ground-level observations of forest structure and function (Table 2). Forest stands with greater species diversity and community-level variation in WD lost less canopy cover during the storms. Although in some cases more diverse forests can experience greater impacts (Tanner & Bellingham 2006), in Puerto Rico low diversity forests tend to be dominated by non-native tree species more susceptible to hurricane disturbances (*e.g.*, *Spathodea campanulata*) (Helmer *et al.* 2018). Functional strategies were particularly important in determining canopy height reductions. Stands dominated by fast-growing, drought-vulnerable tree species (high SLA, low WD, low  $|\Psi_{\text{TLP}}|$ , and low  $|\Psi_{\text{P50}}|$ ) showed greater reductions in canopy height. This pattern links remote sensing observations with classic work on species-specific hurricane responses (Zimmerman *et al.* 1994). Additionally, it suggests there might be a tradeoff between fast-growing, hydraulically vulnerable strategies and resistance to wind disturbances.

We were only able to detect an effect of aridity on the directionality of trait velocities for WD. Forest plots in wetter environments showed a higher probability of displaying a decrease in WD than plots in dry environments (Table S3 & Fig. S3). Though regeneration in wet tropical forests can favor the recruitment of low WD species (Lohbeck *et al.* 2013), it is yet to be tested whether observed patterns are a product of recruitment or a reflection of the surviving plant community. This uncertainty illustrates the limitations of exploring the impacts of hurricanes on community-level traits at short temporal scales (< 5 years). It also implies that changes in the plant community composition might only become apparent over longer periods or when considering the seedling layer (Comita *et al.* 2018; Alonso-Rodríguez *et al.* 2022; Smith-Martin *et al.* 2022; Umaña *et al.* 2023).

From the final SEM model, it was evident that older forest stands that faced a considerable reduction in canopy cover and were situated on flat terrain closer to the storms' center, had a significantly higher  $\Delta MR_{\text{dead/alive}}$  (Fig. 3). Such patterns point out three key factors driving the impacts of hurricanes. First, exposure to hurricane winds plays an important role in determining the damage during storms (McLaren *et al.* 2019; Feng *et al.* 2020; Zhang *et al.* 2022). This was evidenced by the higher increase in  $MR_{\text{dead/alive}}$  in forests closer to the hurricane track and in lowland flat areas compared with steep slopes, some of which may be more protected from winds (McLaren *et al.* 2019; Zhang *et al.* 2022; Helmer *et al.* 2023). Second, older forest stands showed greater increases in mortality. This result challenges Odum's views of greater homeostasis with increases in the ecosystem age (Odum 1969). In Northeast Puerto Rico, older forest stands might not or will never reach a stable state due to frequent disturbances favoring plant communities with a mosaic of both early succession and late succession specialist tree species (Uriarte *et al.* 2009). On the other hand, it might be possible that these patterns are shaped by the widespread presence of non-native species that also tend to have lighter wood, making them less resistant to hurricanes (Helmer *et al.* 2018, 2023). In contrast to results from intensively studied, old forest sites, here younger forests (with widespread species introductions) showed more homeostasis in that regional CWM traits changed little. Another example of young



forests being more resistant to hurricane disturbance is the disturbance-adapted Sierra palm forest areas that expanded after Hurricane Georges in 1998. They were more resistant to Hurricanes Maria and Irma (Zhang *et al.* 2022).

The indirect effects from the SEM revealed that across Puerto Rico forests with low WD, tall canopies and large reductions in canopy height showed the largest increases in  $MR_{\text{dead/alive}}$  (Fig. 3). Interestingly, WD was the common mediator variable for the observed impacts ( $\Delta CH$ ,  $\Delta CC$ , and  $\Delta MR_{\text{dead/alive}}$ ). A mediator variable modulates the effect of a given predictor on a response (MacKinnon *et al.* 2000). A good example of this can be observed in the effects of CH and WD on  $\Delta CH$  (Fig. 3). These results link, for the first time, the well-documented species-specific patterns of hurricane resistance in relation to higher WD and shorter height with landscape scale responses across aridity gradients obtained from the FIA plot network and airborne LiDAR (Zimmerman *et al.* 1994; Ostertag *et al.* 2005; Ogle *et al.* 2006; Lin *et al.* 2018; Uriarte *et al.* 2019; Feng *et al.* 2020; Hall *et al.* 2020; Helmer *et al.* 2023). We showed here that aridity and forest age gradients, plant communities dominated by species with high WD tend to be shorter in stature and have overall greater resistance to hurricane winds (Fig. 3). These plant communities also tend to be dominated by species with higher drought tolerance (more negative  $\Psi_{\text{TLP}}$  &  $\Psi_{\text{P50}}$ ) (Fig S8). This evidence suggests that improved drought tolerance could lead to greater resilience against hurricane disruption, even after accounting for the differences in proximity to the storm eye (*i.e.*, storm intensity). However, we acknowledge that uncertainties still exist when considering storm frequency in shaping the observed patterns (Hogan *et al.* 2018).

## Conclusions

This work allowed us to understand how the interaction between aridity and stand age mediate forest characteristics that explain landscape scale variability in the impacts of hurricanes across environmental gradients (Eppinga & Pucko 2018; Uriarte *et al.* 2019; Zhang *et al.* 2022; Umaña *et al.* 2023) and why LiDAR-based changes in canopy cover better gauge hurricane-related mortality than height changes. We also show that an increase in forest age does not

necessarily imply increased resistance to hurricanes, which highlights important considerations when linking ecosystem age with resistance to disturbances (Odum 1969; Uriarte *et al.* 2009; Lin *et al.* 2020). In addition, we propose that the changing climate and projected increased aridity for tropical regions (Seneviratne *et al.* 2021) may limit the increase of exploitative drought-sensitive species that dominate recruitment after hurricanes in wet tropical forests (Smith-Martin *et al.* 2022; Umaña *et al.* 2023). Overall, we show that linking successional theory with plant functional ecology is a promising avenue to identify nuances essential for predicting forests' responses to increasingly stronger cyclonic storms.

## **Acknowledgments**

German Vargas G. was supported by the NOAA Climate and Global Change Postdoctoral Fellowship Program, administered by UCAR's Cooperative Programs for the Advancement of Earth System Science (CPAESS) under the NOAA Science Collaboration Program award # NA21OAR4310383. Additional funding by the United States Department of Energy to Tana Wood awards # 89243018S-SC-000014 and DE-SC0022095 and to Jennifer Powers # DESC0020344. Eileen Helmer and Jennifer S. Powers acknowledge support by USDA Forest Service-University of Minnesota Joint Venture Agreement 19-JV-11120101-037. William R.L. Anderegg acknowledges funding from the David and Lucille Packard Foundation and US National Science Foundation grants 1802880, 2003017, 2044937, and IOS-2325700. The USDA Forest Service's International Institute of Tropical Forestry (IITF) provided additional support. All research at IITF is conducted in collaboration with the University of Puerto Rico – Río Piedras. We thank Rubi del Mar Santiago, James Rauschendorfer, Iana Grullón-Penkova, Megan E. Berberich, Rob Tunison, and interns Ixia Aviles-Vaszuez, Aral Green, Helena Kleiner, Veronica Lourich, Carolina May, Megan Muller-Girard, Casey Menick, Rosanise Odell, Luis Ortiz-Lopez, Virginia-Rose Seagal, Wade Tinkham, and Ivan Vicens for help in collecting trait data. We also thank the administrative staff at the USDA Forest Service Sabana Field Research Station, and the USDA Forest Service Forest Inventory Analysis field crew for outstanding help in forest data

collection. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

## References

- Alonso-Rodríguez, A.M., Wood, T.E., Torres-Díaz, J., Cavaleri, M.A., Reed, S.C. & Bachelot, B. (2022). Understory plant communities show resistance to drought, hurricanes, and experimental warming in a wet tropical forest. *Front. For. Glob. Change*, 5, 733967.
- Anderegg, L.D.L., Anderegg, W.R.L. & Berry, J.A. (2013). Not all droughts are created equal: translating meteorological drought into woody plant mortality. *Tree Physiol*, 33, 672–683.
- Anderegg, W.R.L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F.A., Choat, B., *et al.* (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *PNAS*, 113, 5024–5029.
- Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., *et al.* (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349, 528–532.
- Baquería, S. & Vicente-Serrano, S.M. (2017). SPEI: Calculation of the Standardised Precipitation-Evapotranspiration Index.
- Bartón, K. (2022). MuMIn: Multi-Model Inference.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.
- Batllori, E., Lloret, F., Aakala, T., Anderegg, W.R.L., Aynekulu, E., Bendixsen, D.P., *et al.* (2020). Forest and woodland replacement patterns following drought-related mortality. *PNAS*, 117, 29720–29729.
- Birdsey, R.A. & Weaver, P.L. (1987). *Forest Area Trends in Puerto Rico* ( No. SO-RN-331). U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA.

493 Brandeis, T.J., Helmer, E.H., Marciano-Vega, H. & Lugo, A.E. (2009). Climate shapes the novel  
 494 plant communities that form after deforestation in Puerto Rico and the U.S. Virgin Islands.  
 495 *Forest Ecology and Management*, 258, 1704–1718.

496 Brandeis, T.J., Helmer, E.H. & Oswalt, S.N. (2007). The status of Puerto Rico's forests, 2003.  
 497 *Resour. Bull. SRS-119. Asheville, NC: U.S. Department of Agriculture Forest Service,*  
 498 *Southern Research Station. 72 p., 119.*

499 Bretfeld, M., Ewers, B.E. & Hall, J.S. (2018). Plant water use responses along secondary forest  
 500 succession during the 2015–2016 El Niño drought in Panama. *New Phytologist*, 219,  
 501 885–899.

502 Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M., *et al.*  
 503 (2018). Global trait–environment relationships of plant communities. *Nat Ecol Evol*, 2,  
 504 1906–1917.

505 Comita, L., Uriarte, M., Forero-Montaña, J., Kress, W., Swenson, N., Thompson, J., *et al.* (2018).  
 506 Changes in Phylogenetic Community Structure of the Seedling Layer Following Hurricane  
 507 Disturbance in a Human-Impacted Tropical Forest. *Forests*, 9, 556.

508 Curran, T.J., Gersbach, L.N., Edwards, W. & Krockenberger, A.K. (2008). Wood density predicts  
 509 plant damage and vegetative recovery rates caused by cyclone disturbance in tropical  
 510 rainforest tree species of North Queensland, Australia. *Austral Ecology*, 33, 442–450.

511 Daly, C., Helmer, E.H. & Quiñones, M. (2003). Mapping the climate of Puerto Rico, Vieques and  
 512 Culebra: CLIMATE MAPPING. *Int. J. Climatol.*, 23, 1359–1381.

513 Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., *et al.* (2016). The  
 514 global spectrum of plant form and function. *Nature*, 529, 167–171.

515 Drew, A.P., Boley, J.D., Zhao, Y., Johnston, M.H. & Wadsworth, F.H. (2009). Sixty-two years of  
 516 change in subtropical wet forest structure and composition at el verde, Puerto Rico.  
 517 *Interciencia*, 34, 34–40.

518 Eppinga, M.B. & Pucko, C.A. (2018). The impact of hurricanes Irma and Maria on the forest  
 519 ecosystems of Saba and St. Eustatius, northern Caribbean. *Biotropica*, 50, 723–728.

520 Feng, Y., Negrón-Juárez, R.I. & Chambers, J.Q. (2020). Remote sensing and statistical analysis  
521 of the effects of hurricane María on the forests of Puerto Rico. *Remote Sensing of*  
522 *Environment*, 247, 111940.

523 Garrido, M., Hansen, S.K., Yaari, R. & Hawlena, H. (2022). A model selection approach to  
524 structural equation modelling: A critical evaluation and a road map for ecologists.  
525 *Methods in Ecology and Evolution*, 13, 42–53.

526 Hall, J., Muscarella, R., Quebbeman, A., Arellano, G., Thompson, J., Zimmerman, J.K., *et al.*  
527 (2020). Hurricane-Induced Rainfall is a Stronger Predictor of Tropical Forest Damage in  
528 Puerto Rico Than Maximum Wind Speeds. *Sci Rep*, 10, 4318.

529 Helmer, E.H., Kay, S.L., Marciano-Vega, H., Powers, J.S., Wood, T.E., Zhu, X., *et al.* (2023).  
530 Multiscale predictors of small tree survival across a heterogeneous tropical landscape.  
531 *PLOS ONE*, 18, e0280322.

532 Helmer, E.H., Ruzyski, T.S., Wilson, B.T., Sherrill, K.R., Lefsky, M.A., Marciano-Vega, H., *et al.*  
533 (2018). Tropical Deforestation and Recolonization by Exotic and Native Trees: Spatial  
534 Patterns of Tropical Forest Biomass, Functional Groups, and Species Counts and Links  
535 to Stand Age, Geoclimate, and Sustainability Goals. *Remote Sensing*, 10, 1724.

536 Hogan, J., Zimmerman, J., Thompson, J., Uriarte, M., Swenson, N., Condit, R., *et al.* (2018). The  
537 Frequency of Cyclonic Wind Storms Shapes Tropical Forest Dynamism and Functional  
538 Trait Dispersion. *Forests*, 9, 404.

539 Hoque, M.A.-A., Phinn, S. & Roelfsema, C. (2017). A systematic review of tropical cyclone  
540 disaster management research using remote sensing and spatial analysis. *Ocean &*  
541 *Coastal Management*, 146, 109–120.

542 Isasa, E., Link, R.M., Jansen, S., Tezeh, F.R., Kaack, L., Sarmiento Cabral, J., *et al.* (2023).  
543 Addressing controversies in the xylem embolism resistance–vessel diameter relationship.  
544 *New Phytologist*, 238, 283–296.

545 Lefcheck, J.S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology,  
546 evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579.

547 Leitold, V., Morton, D.C., Martinuzzi, S., Paynter, I., Uriarte, M., Keller, M., *et al.* (2022). Tracking  
 548 the Rates and Mechanisms of Canopy Damage and Recovery Following Hurricane Maria  
 549 Using Multitemporal Lidar Data. *Ecosystems*, 25, 892–910.

550 Lin, S.-Y., Shaner, P.-J.L. & Lin, T.-C. (2018). Characteristics of Old-Growth and Secondary  
 551 Forests in Relation to Age and Typhoon Disturbance. *Ecosystems*, 21, 1521–1532.

552 Lin, T.-C., Hogan, J.A. & Chang, C.-T. (2020). Tropical Cyclone Ecology: A Scale-Link  
 553 Perspective. *Trends in Ecology & Evolution*, 35, 594–604.

554 Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H., *et al.*  
 555 (2013). Successional changes in functional composition contrast for dry and wet tropical  
 556 forest. *Ecology*, 94, 1211–1216.

557 Lugo, A.E. (2008). Visible and invisible effects of hurricanes on forest ecosystems: an  
 558 international review. *Austral Ecology*, 33, 368–398.

559 MacKinnon, D.P., Krull, J.L. & Lockwood, C.M. (2000). Equivalence of the Mediation,  
 560 Confounding and Suppression Effect. *Prev Sci*, 1, 173.

561 McLaren, K., Luke, D., Tanner, E., Bellingham, P.J. & Healey, J.R. (2019). Reconstructing the  
 562 effects of hurricanes over 155 years on the structure and diversity of trees in two tropical  
 563 montane rainforests in Jamaica. *Agricultural and Forest Meteorology*, 276–277, 107621.

564 Murphy, M.V. (2022). semEff: Automatic Calculation of Effects for Piecewise Structural Equation  
 565 Models.

566 Muscarella, R., Lohbeck, M., Martínez-Ramos, M., Poorter, L., Rodríguez-Velázquez, J.E., van  
 567 Breugel, M., *et al.* (2017). Demographic drivers of functional composition dynamics.  
 568 *Ecology*, 98, 2743–2750.

569 Nakagawa, S., Johnson, P.C.D. & Schielzeth, H. (2017). The coefficient of determination R<sup>2</sup> and  
 570 intra-class correlation coefficient from generalized linear mixed-effects models revisited  
 571 and expanded. *Journal of The Royal Society Interface*, 14, 20170213.

572 Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from  
 573 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.

574 Odum, E.P. (1969). The Strategy of Ecosystem Development. *Science*, 164, 262–270.

575 Ogle, K., Uriarte, M., Thompson, J., Johnstone, J., Jones, A., Lin, Y., *et al.* (2006). Implications of  
576 vulnerability to hurricane damage for long-term survival of tropical tree species: a  
577 Bayesian hierarchical analysis. In: *Applications of computational statistics in the*  
578 *environmental sciences: hierarchical Bayes and MCMC methods*. Oxford University  
579 Press, Oxford, UK, pp. 198–117.

580 Oliveira, R.S., Eller, C.B., Barros, F. de V., Hirota, M., Brum, M. & Bittencourt, P. (2021). Linking  
581 plant hydraulics and the fast–slow continuum to understand resilience to drought in  
582 tropical ecosystems. *New Phytologist*, 230, 904–923.

583 Olson, M.E., Soriano, D., Rosell, J.A., Anfodillo, T., Donoghue, M.J., Edwards, E.J., *et al.* (2018).  
584 Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National*  
585 *Academy of Sciences*, 115, 7551–7556.

586 Ostertag, R., Silver, W.L. & Lugo, A.E. (2005). Factors Affecting Mortality and Resistance to  
587 Damage Following Hurricanes in a Rehabilitated Subtropical Moist Forest1: Predicting  
588 Resistance to Hurricane Damage. *Biotropica*, 37, 16–24.

589 Poorter, L., Rozendaal, D.M.A., Bongers, F., Almeida, de J.S., Álvarez, F.S., Andrade, J.L., *et al.*  
590 (2021). Functional recovery of secondary tropical forests. *Proceedings of the National*  
591 *Academy of Sciences*, 118, e2003405118.

592 Poorter, L., Rozendaal, D.M.A., Bongers, F., de Almeida-Cortez, J.S., Almeyda Zambrano, A.M.,  
593 Álvarez, F.S., *et al.* (2019). Wet and dry tropical forests show opposite successional  
594 pathways in wood density but converge over time. *Nat Ecol Evol*, 3, 928–934.

595 R Core Team. (2022). R: A language and environment for statistical computing.

596 Reich, P.B. (2014). The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto.  
597 *Journal of Ecology*, 102, 275–301.

598 Rounds, E., Patterson, S., Howard, S., Quiñones, M. & Schleicher, M. (2023). *Mapping canopy*  
599 *cover in the US Caribbean using airborne lidar data from 2016 and 2018* ( No. IITF-55).

600 Gen. Tech. Rep. U.S. Department of Agriculture Forest Service, Institute of Tropical  
601 Forestry, Río Piedras, Puerto Rico.

602 Schwartz, N.B., Lintner, B.R., Feng, X. & Powers, J.S. (2020). Beyond MAP: A guide to  
603 dimensions of rainfall variability for tropical ecology. *Biotropica*, 52, 1319–1332.

604 Seneviratne, S.I., Zhang, X., Adnan, M., Badi, W., Dereczynski, C., Di Luca, A., *et al.* (2021).  
605 Chapter 11: Weather and Climate Extreme Events in a Changing Climate. In: *Climate*  
606 *Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth*  
607 *Assesment Report of the Intergovernmental Panel on Climate Change*.

608 Shipley, B. (2000). A New Inferential Test for Path Models Based on Directed Acyclic Graphs.  
609 *Structural Equation Modeling: A Multidisciplinary Journal*, 7, 206–218.

610 Smith-Martin, C.M., Muscarella, R., Ankori-Karlinsky, R., Delzon, S., Farrar, S.L., Salva-Sauri, M.,  
611 *et al.* (2022). Hurricanes increase tropical forest vulnerability to drought. *New Phytologist*,  
612 235, 1005–1017.

613 Stovall, A.E.L., Shugart, H. & Yang, X. (2019). Tree height explains mortality risk during an  
614 intense drought. *Nature Communications*, 10, 4385.

615 Tanner, E.V.J. & Bellingham, P.J. (2006). Less diverse forest is more resistant to hurricane  
616 disturbance: evidence from montane rain forests in Jamaica. *Journal of Ecology*, 94,  
617 1003–1010.

618 Taylor, B.N., Stedman, E., Van Bloem, S.J., Whitmire, S.L. & DeWalt, S.J. (2023). Widespread  
619 stem snapping but limited mortality caused by a category 5 hurricane on the Caribbean  
620 Island of Dominica. *Forest Ecology and Management*, 532, 120833.

621 Trugman, A.T., Anderegg, L.D.L., Shaw, J.D. & Anderegg, W.R.L. (2020). Trait velocities reveal  
622 that mortality has driven widespread coordinated shifts in forest hydraulic trait  
623 composition. *PNAS*, 117, 8532–8538.

624 Tumber-Dávila, S.J., Schenk, H.J., Du, E. & Jackson, R.B. (2022). Plant sizes and shapes above  
625 and belowground and their interactions with climate. *New Phytologist*, 235, 1032–1056.



626 Umaña, M.N., Needham, J., Forero-Montaña, J., Nytch, C.J., Swenson, N.G., Thompson, J., *et*  
 627 *al.* (2023). Demographic trade-offs and functional shifts in a hurricane-impacted tropical  
 628 forest. *Annals of Botany*, mcad004.

629 Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., Murphy, L., Sabat, A.M., *et al.*  
 630 (2009). Natural disturbance and human land use as determinants of tropical forest  
 631 dynamics: results from a forest simulator. *Ecological Monographs*, 79, 423–443.

632 Uriarte, M., Thompson, J. & Zimmerman, J.K. (2019). Hurricane María tripled stem breaks and  
 633 doubled tree mortality relative to other major storms. *Nat Commun*, 10, 1362.

634 Van Beusekom, A., Álvarez-Berríos, N., Gould, W., Quiñones, M. & González, G. (2018).  
 635 Hurricane Maria in the U.S. Caribbean: Disturbance Forces, Variation of Effects, and  
 636 Implications for Future Storms. *Remote Sensing*, 10, 1386.

637 Van Bloem, S.J., Murphy, P.G. & Lugo, A.E. (2007). A link between hurricane-induced tree  
 638 sprouting, high stem density and short canopy in tropical dry forest. *Tree Physiology*, 27,  
 639 475–480.

640 Vargas G., G., Brodribb, T.J., Dupuy, J.M., González-M., R., Hulshof, C.M., Medvigy, D., *et al.*  
 641 (2021). Beyond leaf habit: generalities in plant function across 97 tropical dry forest tree  
 642 species. *New Phytologist*, 232, 148–161.

643 Vargas G., G., Kunert, N., Hammond, W.M., Berry, Z.C., Werden, L.K., Smith-Martin, C.M., *et al.*  
 644 (2022). Leaf habit affects the distribution of drought sensitivity but not water transport  
 645 efficiency in the tropics. *Ecology Letters*, 25, 2637–2650.

646 Vitousek, P.M. & Reiners, W.A. (1975). Ecosystem Succession and Nutrient Retention: A  
 647 Hypothesis. *BioScience*, 25, 376–381.

648 Wadsworth, F.H. (1950). Notes on the climax forests of Puerto Rico and their destruction and  
 649 conservation prior to 1900. *Caribbean Forester*, 11, 38–56.

650 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., *et al.* (2019).  
 651 Welcome to the Tidyverse. *Journal of Open Source Software*, 4, 1686.

652 Zhang, J., Heartsill-Scalley, T. & Bras, R.L. (2022). Forest Structure and Composition Are Critical  
653 to Hurricane Mortality. *Forests*, 13, 202.

654 Zimmerman, J.K., Iii, E.M.E., Waide, R.B., Lodge, D.J., Taylor, C.M. & Brokaw, N.V.L. (1994).  
655 Responses of Tree Species to Hurricane Winds in Subtropical Wet Forest in Puerto Rico:  
656 Implications for Tropical Tree Life Histories. *The Journal of Ecology*, 82, 911.

657

## Tables and Figure legends

**Table 1.** Results of linear mixed effect models for predicting forest structure and functional composition metrics before hurricanes Maria and Irma as a function of aridity, stand age (Age), and short-term drought stress (SPEI<sub>min</sub>). Forest structure was measured as Shannon diversity index (Species Diversity), LiDAR-derived canopy height, LiDAR-derived canopy cover, and stem density index. Functional composition was measured as community-weighted mean wood density (WD), specific leaf area (SLA), the absolute values of leaf water potential at turgor loss point ( $|\Psi_{TLP}|$ ), and water potential at 50% loss of conductivity or accumulation of embolisms ( $|\Psi_{P50}|$ ).  $\beta$  represents the standardized coefficient values and CI the 95% confidence interval. The marginal  $R^2$  ( $R_m^2$ ) represents the variance explained by the fixed effects, and the conditional  $R^2$  ( $R_c^2$ ) is the variance explained by both fixed and random effects.

Species Diversity				Canopy Height			
	B	CI	p		$\beta$	CI	p
Age	0.29	0.22 – 0.36	< 0.001	Age	1.45	0.92 – 1.97	< 0.001
SPEI <sub>min</sub>	0.08	0.02 – 0.13	0.009	Aridity	-1.27	-2.14 – -0.40	0.004
R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.20 / 0.40			Age : Aridity	-0.91	-1.35 – -0.47	< 0.001
				R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.17 / 0.48		
Canopy Cover				Stem Density Index			
	B	CI	p		$\beta$	CI	p
Age	0.06	0.04 – 0.09	< 0.001	Age	0.26	0.20 – 0.33	< 0.001
Aridity	-0.03	-0.07 – 0.01	0.108	Aridity	-0.09	-0.20 – 0.02	0.108
Age : Aridity	-0.05	-0.07 – -0.03	< 0.001	R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.18 / 0.30		
R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.15 / 0.23						
WD (g cm <sup>-3</sup> )				SLA (m <sup>2</sup> kg <sup>-1</sup> )			
	B	CI	p		$\beta$	CI	p
Age	0.00	-0.01 – 0.02	0.437	Age	-0.77	-1.12 – -0.42	< 0.001
Aridity	0.06	0.04 – 0.07	< 0.001	Aridity	-0.36	-0.88 – 0.16	0.174
Age : Aridity	-0.02	-0.03 – -0.01	< 0.001	SPEI <sub>min</sub>	-0.23	-0.50 – 0.05	0.106
R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.28 / 0.30			Age : Aridity	0.41	0.12 – 0.69	0.006
				R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.10 / 0.22		
Ψ <sub>TLP</sub>   (MPa)				Ψ <sub>P50</sub>   (MPa)*			
	B	CI	p		$\beta$	CI	p
Age	0.04	-0.01 – 0.08	0.054	Age	0.23	0.09 – 0.38	0.002
Aridity	0.15	0.11 – 0.20	< 0.001	Aridity	0.25	0.07 – 0.42	0.006
Age : Aridity	-0.06	-0.10 – -0.03	< 0.001	R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.14 / 0.15		
R <sup>2</sup> <sub>m</sub> / R <sup>2</sup> <sub>c</sub>	0.27 / 0.28						

\*For  $|\Psi_{P50}|$  we used the plots with a trait coverage of > 35% instead of weighing the analysis by the trait basal area coverage given the smaller sample size when compared to the other traits. This was done to avoid the presence of singularities when fitting the model.

**Table 2.** Standardized  $\beta$  coefficients from univariate linear mixed effect models of the changes ( $\Delta$ ) in mortality rates ( $MR_{\text{dead/alive}}$ ), canopy cover, and canopy height as a function of distance to hurricane eye ( $D_{\text{HT}}$ ), topographic slope, stand age (SA), canopy height (CH), species diversity, stem density index (SDI), community-weighted mean and standard deviation (SD) for wood density (WD), specific leaf area (SLA), leaf water potential at turgor loss point ( $|\Psi_{\text{TLP}}|$ ) and water potential at 50% embolism ( $|\Psi_{\text{P50}}|$ ). Marginal  $R^2$  ( $R_m^2$ ) and conditional  $R^2$  ( $R_c^2$ ) represent the variance explained only by fixed effects and by both fixed and random effects respectively.

	$\Delta MR_{\text{dead/alive}}$				$\Delta \text{Canopy Cover}$				$\Delta \text{Canopy Height}$			
	$\beta$	$R_m^2$	$R_c^2$	p	$\beta$	$R_m^2$	$R_c^2$	p	$\beta$	$R_m^2$	$R_c^2$	p
$D_{\text{HT}}$	<b>-0.1183</b>	<b>0.05</b>	<b>0.07</b>	<b>0.0040</b>	0.0095	0.02	0.12	0.1413	<b>0.3254</b>	<b>0.04</b>	<b>0.20</b>	<b>0.0196</b>
Slope	-0.0705	0.02	0.05	0.0784	<b>0.0137</b>	<b>0.03</b>	<b>0.10</b>	<b>0.0171</b>	-0.1865	0.01	0.26	0.1295
SA	<b>0.1246</b>	<b>0.05</b>	<b>0.13</b>	<b>0.0021</b>	-0.0003	0.00	0.08	0.9627	<b>-0.2961</b>	<b>0.03</b>	<b>0.32</b>	<b>0.0181</b>
CH	0.0163	0.00	0.01	0.6956	-0.0021	0.00	0.09	0.7368	<b>-1.5066</b>	<b>0.79</b>	<b>0.79</b>	<b>0.0001</b>
Diversity	0.0217	0.00	0.02	0.5859	<b>0.0152</b>	<b>0.04</b>	<b>0.08</b>	<b>0.0079</b>	-0.0151	0.00	0.26	0.9018
SDI	-0.0336	0.00	0.02	0.3952	-0.0059	0.01	0.09	0.2987	<b>-0.4596</b>	<b>0.07</b>	<b>0.31</b>	<b>0.0001</b>
SLA	-0.0065	0.00	0.06	0.8730	-0.0092	0.02	0.11	0.1374	<b>-0.4882</b>	<b>0.09</b>	<b>0.32</b>	<b>0.0001</b>
WD	0.0112	0.00	0.03	0.7894	0.0019	0.00	0.09	0.7660	<b>0.6110</b>	<b>0.14</b>	<b>0.24</b>	<b>0.0001</b>
$ \Psi_{\text{TLP}} $	0.0550	0.02	0.02	0.1369	0.0031	0.00	0.02	0.6118	<b>0.5205</b>	<b>0.12</b>	<b>0.39</b>	<b>0.0006</b>
$ \Psi_{\text{P50}} $	0.0606	0.03	0.29	0.2821	0.0107	0.04	0.21	0.2378	<b>0.5765</b>	<b>0.17</b>	<b>0.47</b>	<b>0.0045</b>
SD-SLA	0.0412	0.01	0.06	0.3293	-0.0004	0.00	0.11	0.9439	-0.1757	0.01	0.29	0.1771
SD-WD	0.0097	0.00	0.02	0.8061	<b>0.0120</b>	<b>0.03</b>	<b>0.09</b>	<b>0.0345</b>	0.1477	0.01	0.28	0.2139
SD- $ \Psi_{\text{TLP}} $	0.0598	0.03	0.03	0.1234	0.0086	0.02	0.03	0.1681	0.2520	0.03	0.41	0.0987
SD- $ \Psi_{\text{P50}} $	0.0708	0.04	0.32	0.1373	0.0091	0.03	0.02	0.2294	0.2320	0.03	0.47	0.1861

**Fig. 1.** Hurricanes act as a major disturbance agent in tropical forests. Panel **a**) shows the relation between CWM-WD and forest stand age for three forest types associated with climatic conditions for a given life zone in Puerto Rico, Vieques, and Culebra islands. Panel **b**) shows the hypothesized prediction that hurricanes will reinitiate the functional trajectory, but the resulting functional composition will depend on the available species pool given the effect of environmental drivers on forest age (Panel **a**)). In panel **b**), points represent CWM-WD through time, the gray shaded area represents the 95% confidence interval of the CWM-WD, the straight blue line is the mean trendline of CWM-WD against time, the vertical dashed line is the hurricane impact, and the three dashed lines represent hypothesized functional trajectories. Panel **c**) shows mortality rates ( $MR_{\text{dead/alive}}$ ), measured as the percentage basal area loss during the census interval before and after Hurricanes Irma and Maria for 179 Forest Inventory Analysis plots in Puerto Rico, Vieques, and Culebra islands. Additional maps were produced for community-weighted traits (Fig. S1).

**Fig. 2.** Comparison of mortality rates ( $MR_{\text{dead/alive}}$ ), canopy cover, and canopy height before and after the impacts of Hurricanes Irma and Maria. P-values were obtained using a paired Wilcoxon signed rank test with continuity correction across all forest types (Total), tropical dry (Dry), tropical moist (Moist), and tropical wet (Wet).

**Fig. 3.** Structural equation model (SEM) to determine the direct and indirect effects mediating tree mortality during Hurricanes Irma and Maria in Puerto Rico. Panel **a**) shows a diagram depicting the causal pathways exploring the effects of climate, topography, and forest function in mediating the impacts of Hurricane Maria measured as the changes ( $\Delta$ ) in mortality rates ( $MR_{\text{dead/alive}}$ ), LiDAR-derived canopy cover (CC), and LiDAR-derived canopy height (CH). Complete arrows and line thickness represent moderate ( $p < 0.05$ ) to strong ( $p < 0.001$ ) evidence of an effect, while dashed lines represent weak ( $p > 0.05$ ) evidence of an effect but still accounted for in the model. The  $R^2$  in each node represents the conditional  $R^2$  ( $R^2_c$ ), which shows the variance explained by both fixed and random effects. Panel **b**) shows the standardized effects of variables with either a

708 direct or indirect effect on  $\Delta MR_{\text{dead/alive}}$ . Points represent the median standardized estimate and  
709 error bars represent the 95% confidence interval obtained from 5000 bootstrapped samples. The  
710 gray color shows whether the 95% confidence interval overlaps with zero for a given predictor in  
711 the SEM. Additional direct and indirect standardized effects plots for  $\Delta CC$ ,  $\Delta CH$ , and  $CH$  are in  
712 Fig. S5.