Received: 27 October 2023 | Accepted: 1 August 2024

DOI: 10.1111/1365-2745.14437

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

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

German Vargas G.[1,2,3] | **Humfredo Marcano-Vega**[4] | **Tom Ruzycki**[5] | **Tana E. Wood**[6] | **William R. L. Anderegg**[1,7] | **Jennifer S. Powers**[8] | **Eileen H. Helmer**[6]

[1]School of Biological Sciences, University of Utah, Salt Lake City, Utah, USA; [2]Department of Botany & Plant Pathology, Oregon State University, Corvallis, Oregon, USA; [3]Department of Forest Ecosystems & Society, Oregon State University, Corvallis, Oregon, USA; [4]USDA Forest Service, Southern Research Station, Knoxville, Tennessee, USA; [5]Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, Colorado, USA; [6]USDA Forest Service, International Institute of Tropical Forestry, San Juan, Puerto Rico, USA; [7]Wilkes Center for Climate Science and Policy, University of Utah, Salt Lake City, Utah, USA and [8]Department of Plant and Microbial Biology, University of Minnesota, St. Paul, Minnesota, USA

Correspondence
German Vargas G.
Email: vargasgg@oregonstate.edu

Funding information
Biological and Environmental Research, Grant/Award Number: 89243018S-SC-000014, DE-SC0020344 and DE-SC0022095; University Corporation for Atmospheric Research; Directorate for Biological Sciences, Grant/Award Number: 1802880, 2003017, 2044937 and IOS-2325700; David and Lucile Packard Foundation; International Institute of Tropical Forestry; University Corporation for Atmospheric Research's Cooperative Programs for the Advancement of Earth System, Grant/Award Number: #NA21OAR4310383; USDA Forest Service, Grant/Award Number: 19-JV-11120101-037

Handling Editor: Albert Vilà-Cabrera

Abstract

1. Cyclonic storms, or hurricanes, are expected to intensify as ocean heat energy rises due to climate change. Ecological theory suggests that tropical forest resistance to hurricanes should increase with forest age and wood density. However, most data on hurricane effects on tropical forests come from a limited number of well-studied long-term monitoring sites, restricting our capacity to evaluate the resistance of tropical forests to hurricanes across broad environmental gradients.
2. In this study, we assessed whether forest age and aridity mediate the effects of hurricanes Irma and Maria in Puerto Rico, Vieques and Culebra islands. We leveraged functional trait data for 410 tree species, remotely sensed measurements of canopy height and cover, along with data on forest stand characteristics of 180 of 338 forest monitoring plots, each covering an area of 0.067 ha. The plots represent a broad mean annual precipitation (MAP) gradient from 701 to 4598 mm and a complex mosaic of forest age from 5 to around 85 years since deforestation.
3. Hurricanes resulted in a 25% increase in basal area mortality rates, a 45% decrease in canopy height and a 21% reduction in canopy cover. These effects intensified with forest age, even after considering proximity to the hurricane path. The links between forest age and hurricane disturbances were likely due the prevalence of tall canopies.
4. Tall forest canopies were strongly linked with low community-weighted wood density (WD). These characteristics were on average more common in moist and wet forests (MAP >1250 mm). Conversely, dry forests were dominated by short species with high wood density ($WD > 0.6\,g\,cm^{-3}$) and did not show significant increases in basal area mortality rates after the hurricanes.
5. *Synthesis*. Our findings show that selection towards drought-tolerant traits across aridity gradients, such as short stature and dense wood, enhances resistance to

hurricanes. However, forest age modulated responses to hurricanes, with older forests being less resistant across the islands. This evidence highlights the importance of considering the intricate links between ecological succession and plant function when forecasting tropical forests' responses to increasingly strong hurricanes.

KEYWORDS
climate change, drought tolerance, forest inventory analysis, functional diversity, hurricanes, tree mortality

1 | INTRODUCTION

Climate change is expected to increase the intensity of cyclonic storms, hereafter hurricanes, due to rising ocean heat energy (Seneviratne et al., 2023). Large areas of tropical forests experience hurricane disturbances, which strongly influences forest function and structure (Lugo, 2008). The high biological and functional diversity of these ecosystems poses challenges for predicting their response to increased hurricane intensity (Lin et al., 2020; McLaren et al., 2019; Uriarte et al., 2019). It is expected that forest resistance to hurricane disturbance will vary based on factors, such as forest age, water availability, structure, topography, land-use history and species composition (Feng et al., 2020; Uriarte et al., 2009). This complexity highlights the need for a unifying framework to study forest resistance to hurricanes across broad environmental gradients.

Classic ecological theory suggests that, as ecosystems age, their attributes will favour slower energy exchange with greater ecosystem homeostasis (Odum, 1969). This provides a framework that links ecological succession with ecosystem stability in the face of perturbations (Poorter et al., 2023). In the context of hurricane disturbances, this can be defined as an increase in forest resistance with forest age. However, for this to hold true, the functional properties of forests conferring resistance to hurricane disturbances should covary along with ecosystem development, which can be context dependent (Vitousek & Reiners, 1975; Zak, 2014). It is crucial, then, to evaluate whether the factors influencing tropical forest function along gradients of succession mediate resistance to hurricanes.

During hurricane disturbances, tree mortality primarily occurs through uprooting and stem breakage (Lugo, 2008), especially among tall tree species with low wood density (WD; Curran et al., 2008; Helmer et al., 2023b; Ibanez et al., 2024; Ogle et al., 2006; Taylor et al., 2023; Uriarte et al., 2019; Zimmerman et al., 1994). Community-level patterns of plant traits, such as WD or tree height, vary across gradients of water availability and forest age (Bruelheide et al., 2018). These traits link to species' growing strategies, where conservative traits such as high WD and short stature are found in 'slow-safe' species and the opposite in 'fast-risky' species (Díaz et al., 2016; Reich, 2014). For instance, in arid regions, plant species tend to show shorter stature, deep roots, high WD and xylem resistant to drought stress (Olson et al., 2018; Tumber-Dávila et al., 2022; Vargas G et al., 2022), representing a physiological strategy associated with higher survival during drought stress (Anderegg et al., 2016). Conversely, low WD species typically 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; Figure 1a).

The known variation in plant traits along aridity gradients suggests that many of the traits associated with drought tolerance, such as dense wood or deep roots, also enhance forest resistance to hurricanes. However, whether this assumption holds true across broad geographic scales remains an open question. 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 (Feng et al., 2020; Hall et al., 2020; Leitold et al., 2022; Van Beusekom et al., 2018). However, only one study to date has performed a ground validation of hurricane disturbances using a small sample size ($n < 30$) in which canopy height was the most important forest characteristic explaining biomass loss during hurricanes (Hall et al., 2020). Conversely, a global data synthesis of 74 forest plots confirmed the importance of WD in mediating tree damage caused by hurricane disturbances (Ibanez et al., 2024), yet the plots were located only in three types of forests (tropical montane, lowland tropical and lowland subtropical rainforests). This evidence underscores the need to investigate the contribution of forest age and community-level functional traits in determining the severity of hurricane disturbances across climatic gradients.

Climate and forest type may also be an important factor mediating how hurricanes affect plant community composition. In wet forests, hurricanes cause an increase in the number of forest gaps (Lugo, 2008), potentially favouring fast-growing drought-vulnerable plant species (Alonso-Rodríguez et al., 2022; Smith-Martin et al., 2022). However, in tropical dry forests, biomass recovery after hurricanes mostly occurs through the re-sprouting of snapped trees, and large re-organizations of the plant community are rarely seen (Curran et al., 2008; Van Bloem et al., 2007). These lines of evidence suggest that the functional composition of plant communities can follow many alternative routes depending on environmental factors and the characteristics of surviving tree species (Figure 1b). Identifying how environmental gradients affect the rate at which community-level trait values change

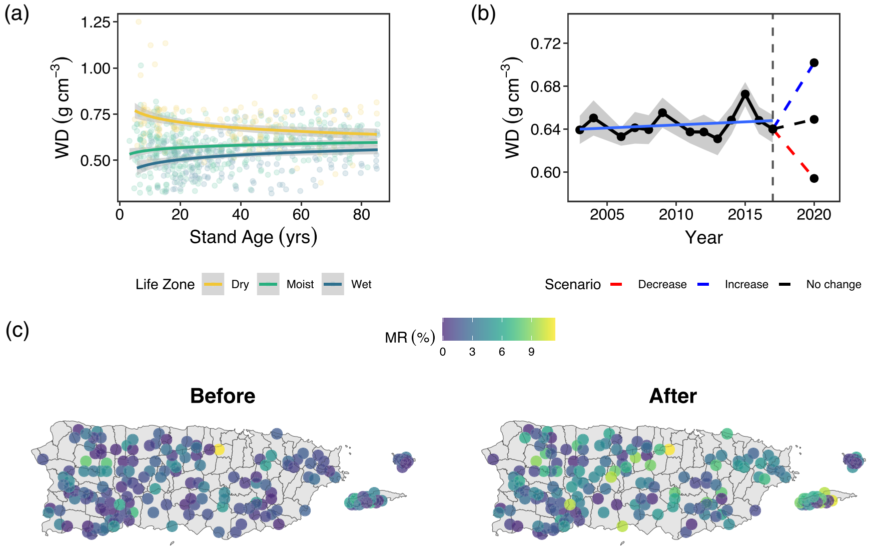

FIGURE 1 Hurricanes act as a major disturbance agent in tropical forests. (a) The relation between CWM-WD and forest stand age for three forest types associated with climatic conditions for a given life zone in Puerto Rico, Vieques and Culebra islands. (b) The hypothesized prediction that hurricanes 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 (b), points represent CWM-WD through time, the grey-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 represents a hurricane event and the three dashed lines represent hypothesized functional trajectories. (c) Basal area mortality rates (MR), measured as the percentage basal area loss during the census interval before and after Hurricane Maria for 180 Forest Inventory Analysis plots in Puerto Rico, Vieques and Culebra.

over time (e.g. trait velocities) can provide valuable information on whether plant communities become more resistant to future disturbances (Trugman et al., 2020). To our knowledge, no study has extensively explored community-level changes as a function of hurricane disturbances across broad gradients of forest stand age and aridity (Lin et al., 2020).

In this work, we evaluate key factors that influence the patterns of hurricane disturbance on forest ecosystems across broad environmental gradients. Specifically, we tested whether aridity, forest structure, stand age and functional composition explained the variability in basal area mortality rates, changes in canopy height and cover after Hurricanes Irma and Maria in the archipelago of Puerto Rico. We leveraged forest basal area mortality rates on 180 out of 338 permanent plots from U.S. Forest Inventory and Analysis (FIA) data with censuses before and after the hurricanes. We supplemented FIA data with functional traits for 410 tree species, along with remotely sensed measurements of canopy height, canopy cover and stand age. Given that wet and dry forests exhibit opposite trends in their wood density trajectories along succession (Lohbeck et al., 2013; Poorter et al., 2023), we hypothesized that tropical forest hurricane resistance patterns will converge in late successional stages along aridity gradients. Specifically, older wet forests will increase resistance due to the increasing abundance of high wood density species, while older dry forests will decrease resistance owing to the increasing abundance of low wood density species (Figure 1a). We expected these patterns to remain 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 do forest structure, basal area mortality, community-level traits and trait velocities change after Hurricanes Irma and Maria? (3) Do climate and stand age determine the trajectory of trait velocities after the hurricanes? (4) Are hurricane-related changes in forest basal area mortality directly and indirectly mediated by community-level traits?

2 | MATERIALS AND METHODS

2.1 | Study site and hurricanes

Puerto Rico, Vieques and Culebra are a group of islands in the Caribbean with a total land cover of ~8890 km^2, a steep rainfall gradient from 701 to 4598 mm and a mean temperature gradient from 19 to 29°C (Daly et al., 2003). Plant communities reflect the climatic conditions and have been classified into six major life zones of the subtropical forest: mangroves, dry, moist, wet, rain and lower montane (Ewel & Whitmore, 1973). In September of 2017, the islands were impacted by two major hurricanes. First Hurricane Irma, a category 5 hurricane with maximum sustained wind velocities of 298 km h^{-1}, passed approximately 97 km northeast of Puerto Rico (www.nhc.noaa.gov, accessed May 2024). Subsequently, Hurricane

Maria made landfall in Puerto Rico as a category 4 storm with maximum sustained wind velocities of 250 km h^{-1} (www.nhc.noaa.gov, accessed on May 2024).

2.2 | Forest inventory

We used the network of 369 long-term permanent plots from the U.S. Department of Agriculture Forest Service Forest Inventory Analysis Program (FIA) that were established between 2001 and 2004 (Brandeis et al., 2009). FIA plots comprise a cluster of four subplots each with a radius of 7.3 m, resulting in a total sampled area of 0.067 hectares for trees with a diameter at breast height (dbh) equal or higher than 12.5 cm (Burrill et al., 2019). Trees with a dbh equal or higher than 2.5 centimetres are measured within a 2.1-m radius microplot nested within each subplot. In this study, we aggregated data at the plot level. In FIA plots, the condition classifier accounts for changes in land use or changes that occur along distinct boundaries (Burrill et al., 2019). This allows for the classification of plot area between forest and non-forest conditions (e.g. pasture or water). Using this classification, we selected 338 plots with a forest condition class covering >30% of a given plot total area (Trugman et al., 2020). For each plot, we measured the distance from eye track of Hurricane Maria using track data obtained from the National Hurricane Center's Tropical Cyclone Reports (Figure S1; www.nhc.noaa.gov, accessed on September 2022).

On the selected plots, we calculated the Shannon diversity index (diversity), basal area in m^2 ha^{-1} (BA) and the ratio between stem density and above-ground biomass as a stem density index (SDI). Dense stands with small trees have a high SDI, while a low SDI indicates forest stands composed of large stems (Goring et al., 2016). SDI provides a metric of horizontal biomass distribution. We calculated basal area mortality rates (MR) as the percentage of dead BA at the end of the interval (BA$_{\text{dead}}$) in relation to the plot total BA at the beginning of the census interval (BA$_{\text{total}}$). We annualized our calculations by dividing the change in basal area mortality by the difference in years between each census ($t_f - t_i$) (Equation 1). We acknowledge the possible biases of our approach in estimating forest biomass losses due to small differences in sampling intervals among plots (Kohyama et al., 2019). However, this approach is similar to previous analyses of FIA data (McNellis et al., 2021; Trugman et al., 2020; Venturas et al., 2021) and allowed us to capture changes in naturally occurring MR before and after the hurricanes by leveraging FIA-reported mortality agents and excluding non-natural causes of tree death (Table S1; Burrill et al., 2019).

$$\text{MR} = \frac{\left(\text{BA}_{\text{dead}} / \text{BA}_{\text{total}}\right) * 100}{t_f - t_i} \quad (1)$$

2.3 | Forest stand age

The ~60% current forest cover encompasses 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 (Birdsey & Weaver, 1987; Brandeis et al., 2007; Wadsworth, 1950). We defined stand age as the number of years since land was last classified as non-forest. We analysed landcover maps from the years 1951–1952, 1977–1978, 1991–1992 and 2000–2003, along with forest versus non-forest classifications in air photos from 1936 to 1937. This approach allowed us to calculate the stand age at the beginning of the FIA censuses in 2001. Subsequently, we determined the final stand age based on the age in 2001 and whether a plot remained forested from 2001 to 2019. Additional details regarding the determination of stand age can be found elsewhere (Helmer et al., 2023a, 2023b).

2.4 | Canopy height and canopy cover

To assess the effects of Hurricanes Irma and Maria on forest structure, we utilized high-resolution canopy height and cover data derived from airborne LiDAR. LiDAR surveys were conducted in 2016 and 2018 by the U.S. Geological Survey (Rounds et al., 2023). Leveraging LiDAR data allowed us to analyse changes in canopy height and cover at the plot level for elapsed times before and after the hurricanes that are equal among all plots link these hurricane-related canopy properties with stand age and community-level trait values, and study the influence of such properties in hurricane-related MR. The LiDAR data had a 1-m spatial resolution, providing information on tree canopy presence (0, 1) and the height of each 1-m^2 pixel. To mitigate potential disturbances that could disproportionately affect values within FIA subplots (e.g. tree falls), we assessed canopy cover and height within a 10 m radius surrounding the subplot centre instead of using the 7.3-m radius. Subsequently, we calculated percent canopy cover (canopy-present pixels divided by total pixels in 10 m radius) and average pixel height over this radius. These values were then aggregated to the plot level by computing the average value for each FIA plot.

2.5 | Forest functional composition

We characterized functional composition with four plant traits that together indicate species' growing strategies (e.g. fast vs. slow) and drought tolerance (Table S2). 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 water potentials at leaf turgor loss point (Ψ_{TLP}) and at 50% loss of hydraulic conductivity or 50% accumulation of embolisms (Ψ_{P50}), which describe the thresholds of leaf and xylem function under drought (Vargas G et al., 2022). Most trait data we used come from previously published work carried out after the hurricanes in Puerto Rico (Table S2); we supplemented this data set with data we collected on drought tolerance traits for nine species during February–March 2020 (Methods S1). For each plot, we calculated trait community-weighted means (Figure S2), community-weighted standard deviation and the rate of change of trait community-weighted means over time (i.e. 'trait velocities').

2.6 | 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 ($SPEI_{min}$) for the 5 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.

2.7 | Statistical analysis

We used linear mixed-effect models to explore climate and stand age effects on forest diversity, structure and plant community functional composition (Question 1). Our response variables included trait community-weighted means, canopy cover, canopy height, SDI and diversity. Fixed effects comprised stand age, aridity and $SPEI_{min}$. Additionally, a 12-level categorical variable integrating geological class (alluvial volcanic sedimentary, karst, serpentine) and forest type (dry, moist, wet, lower montane) served as a random effect to address spatial similarities in forest properties (Brandeis et al., 2009). Models initially considered all two-way interactions between fixed effects predictors (Table S3), followed by stepwise selection to identify the model that maximized the log-likelihood function and minimized the second-order Akaike information criterion using the 'dredge()' function in MuMin (Bartón, 2022). We then selected the candidate model that did not delete significant terms. Standardized predictor variables facilitated model β coefficients comparison. We utilized FIA plot data up until the last census prior to September 6 of 2017.

To assess the effects of Hurricanes Irma and Maria in forest structure, MR, trait community-weighted means and trait velocities (Question 2), we identified 180 plots with FIA data before and after 20 September 2017. We employed paired Wilcoxon signed rank tests with continuity correction to compare canopy height, cover, MR, species diversity, community- weighted means and trait velocities and defined as the rate of change of trait community-weighted means through time. We also conducted additional tests for three forest types: dry, moist and wet forests. We excluded lower montane and mangrove forests from these tests due to their limited sample size ($n < 30$).

We assessed whether climate and stand age mediated how the hurricanes affected the trajectory of trait velocities (Question 3). The trajectory of trait velocities indicates whether the functional composition in the plant community becomes more sensitive or tolerant to drought following the hurricanes (Trugman et al., 2020). We fitted a generalized mixed-effect model, assuming a binomial distribution in the response variable, with 1 indicating decreases (negative trait velocity) and 0 indicating increases (positive trait velocity) in mean trait values following the hurricanes. Using a complementary log–log link function, we calculated the risk ratio as the probability of observing a negative trait velocity relative to a positive trait velocity. The model included the 12-level joint categorical combination of geological classes and life zones as random effect.

Last, we investigated whether forest diversity, structure and community-level trait values mediated changes in MR, canopy height and cover (Question 4). First, we calculated the rate of change (Δ) of canopy height, cover and MR. We did this by subtracting the values from the last census before 20 September 2017, from those of the first census after that date. We adjusted for differences in census interval lengths among plots by annualizing the calculations. Next, we performed both univariate and multivariate analyses to address this question comprehensively. In the univariate analysis, we fitted a series of linear mixed models exploring whether ΔMR, canopy cover (ΔCC), and height (ΔCH) were explained by trait community-weighted means, their standard deviations, proximity to hurricane eye track (Figure S1), stand age, canopy height or topographic slope. We used the combination of geological classes and life zones as a random effect. We weighted the linear mixed models involving community-weighted means and standard deviation using the basal area coverage, that is, relative basal area of the species for which we have trait data (Figure S4).

The multivariate approach involved assessing the direct and indirect effects on forest resistance to hurricane disturbances using a piecewise structural equation model (SEM) (Lefcheck, 2016). The SEM included all three metrics of hurricane disturbances (ΔMR, ΔCC and ΔCH) as response variables, with aridity, proximity to hurricane eye, topographic slope, forest stand age, canopy height, SDI, species diversity and the community-weighted mean and standard deviation for WD.

Predictor selection in the SEM was a twofold process. First, we selected predictors based on the previous analyses to explain both forest characteristics and hurricane disturbances. This provided an initial hypothesis for causal paths in the SEM (Figure S3). Then, we selected predictors weakly related to each other (Spearman's rho < 0.5) to avoid multicollinearity (Garrido et al., 2022). We selected WD over SLA, Ψ_{TLP} and Ψ_{P50} due to its greater basal area coverage in our data set (Figure S4). Moreover, at the plot level, WD is highly correlated with Ψ_{TLP} and Ψ_{P50} (Figure S5), serving as an integrated proxy for drought tolerance. We assessed model fit using Shipley's test of directed separation (Shipley, 2000), which 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 (Lefcheck, 2016; Shipley, 2000). We obtained standardized estimates of the direct, indirect and mediator effects of predictors on all response variables in the model.

In all models with random effects, we calculated the variance explained by the fixed effects (R^2_m), and the variance explained by both fixed and random effects (R^2_c) (Nakagawa et al., 2017; Nakagawa & Schielzeth, 2013). 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), lme4 (Bates et al., 2015) and MuMin (Bartón, 2022).

3 | RESULTS

3.1 | Drivers of forest structure and function

Aridity and stand age explained variations in forest structure and function. Short-term drought stress (SPEI_{min}) moderately ($p = 0.01$) affected diversity (Table 1), with plots experiencing severe drought conditions ($\mathrm{SPEI}_{min} < -2$) in the 5 years before September 2017 being, on average, 12% less diverse. As expected, canopy height increased with stand age and decreased with aridity (Table 1). However, the effects of stand age on canopy height varied based on aridity levels, as evidenced by a strong interaction effect ($p < 0.001$). This was shown by the much smaller differences in canopy height in dry regions, where both young and old forests had an average canopy ~4.5 m, while in wetter regions, young forests tend to have a canopy height of ~8 m and old forests ~20 m. Stand age had a strong positive effect on canopy cover ($p < 0.001$). For every unit increase in forest age, there was, on average, approximately a 7% increase in canopy cover (Table 1). A strong interaction with aridity ($p < 0.001$) highlights that increases in canopy cover between young and old forests occur differently along water availability gradients. SDI decreased with forest age, suggesting that young forest stands are denser with smaller trees. However, this model explained less than 1% in total SDI variance (Table 1).

With increasing aridity, there was a 10% increase in community-weighted WD, an 8% increase for $|\Psi_{TLP}|$ and a 10% increase for $|\Psi_{P50}|$. This pattern can be seen in the dry forests of South-western Puerto Rico and outlying Vieques and Culebra Islands (Figure S2), 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, SLA decreased with forest age, while $|\Psi_{TLP}|$ and $|\Psi_{P50}|$ increased (Table 1). In dry

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_{min}).

Species diversity

	β	CI	p
Age	0.29	0.22 – 0.35	<0.001
SPEI_{min}	0.08	0.02 – 0.13	0.008
R^2_m/R^2_c	0.20 / 0.40		

Canopy height

	β	CI	p
Age	1.44	0.92 – 1.96	<0.001
Aridity	−1.29	−2.16 – −0.43	0.004
Age : Aridity	−0.91	−1.35 – −0.47	<0.001
R^2_m/R^2_c	0.17 / 0.48		

Canopy cover

	β	CI	p
Age	0.07	0.04 – 0.09	<0.001
Aridity	−0.03	−0.07 – 0.01	0.067
Age : Aridity	−0.05	−0.07 – -0.03	<0.001
R^2_m/R^2_c	0.15 / 0.23		

Stem density index

	β	CI	p
Age	−0.04	−0.07 – −0.01	0.026
Aridity	0.01	−0.03 – 0.03	0.883
R^2_m/R^2_c	0.01 / 0.02		

WD (g cm^{-3})

	β	CI	p
Age	0.01	−0.01 – 0.02	0.376
Aridity	0.06	0.05 – 0.08	<0.001
Age : Aridity	−0.02	−0.03 – −0.01	<0.001
R^2_m/R^2_c	0.29 / 0.31		

SLA (m^2 kg^{-1})

	β	CI	p
Age	−0.73	−1.08 – −0.39	<0.001
Aridity	−0.38	−0.91 – 0.15	0.167
Age : Aridity	0.41	0.12 – 0.69	0.006
R^2_m/R^2_c	0.09 / 0.23		

$|\Psi_{TLP}|$ (MPa)

	β	CI	p
Age	0.04	0.002 – 0.08	0.039
Aridity	0.16	0.12 – 0.21	<0.001
Age : Aridity	−0.07	−0.10 – −0.03	<0.001
R^2_m/R^2_c	0.30 / 0.31		

$|\Psi_{P50}|$ (MPa)[a]

	β	CI	p
Age	0.23	0.09 – 0.37	0.002
Aridity	0.25	0.08 – 0.42	0.005
R^2_m/R^2_c	0.15 / 0.15		

[a] 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.

Note: 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 ($|\Psi_{P50}|$). β represents the standardized coefficient values and CI the 95% confidence interval, and highlighted in bold when significant effects were found. The marginal R^2 (R^2_m) represents the variance explained by the fixed effects, and the conditional R^2 (R^2_c) is the variance explained by both fixed and random effects. Predictors were selected using stepwise AIC, a complete list of candidate models can be found in Table S3.

regions, community-weighted means of WD, SLA and $|\Psi_{TLP}|$ did not change with stand age, contrary to wet regions where community-weighted values of these traits increased with forest age as evidenced by the presence of strong ($p < 0.01$) interaction effects (Table 1).

3.2 | Effects of hurricanes Irma and Maria

Before September 2017, MR 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% (Figure 2). After hurricanes Irma and Maria, we found strong evidence of an ~25% increase in MR, ~21% decrease in canopy cover and ~45% decrease in canopy height (Figure 2). These effects differed by forest type, where in tropical dry forests, we did not find evidence ($p > 0.1$) of changes in MR before and after the hurricanes (Figure 2). When testing for changes in community-weighted means, community-weighted standard deviations and trait velocities after hurricanes, we only found an increase in the community-weighted standard deviation of SLA in wet forests alone while all the other variables yet non-significant results (Table S4).

3.3 | Factors mediating hurricane disturbances on tropical forests

From the univariate analyses, we found that the main predictors of ΔMR were distance to the hurricane track (e.g. the shorter

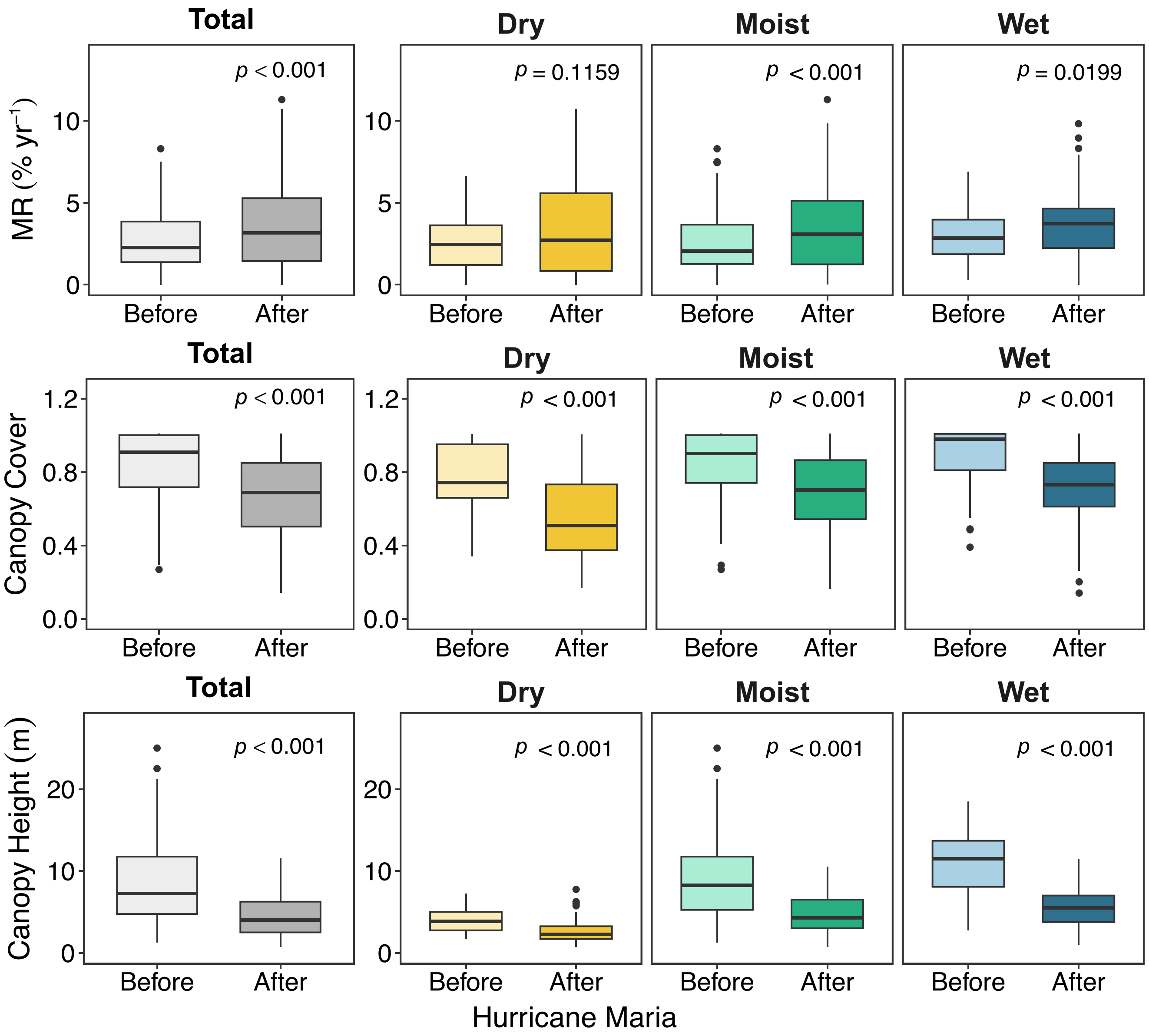

FIGURE 2 Comparison of basal area mortality rates (MR), canopy cover and canopy height in 180 FIA plots with surveys before and after Hurricanes Irma and Maria. Where p-values were obtained using a paired Wilcoxon signed-rank test with continuity correction across all forest types (Total), tropical dry (Dry), tropical moist (Moist) and tropical wet (Wet).

the distance the greater the increase in MR) and forest stand age (e.g. older stands showed greater increases in MR; Table 2). We observed a rise in ΔMR in plots that also showed decreases in canopy cover, but the same was not true for changes in canopy height (Figure S6). Plots in flat terrain suffered up to 40% losses in canopy cover compared up to 5% in plots found on steep terrain (>20% grade; 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 canopy height reductions of up to 8 m (Table 2). Second, plots dominated by species with fast-growing, drought-sensitive trait values (high SLA; low WD, $|\Psi_{\mathrm{TLP}}|$ or $|\Psi_{\mathrm{P50}}|$) showed on average 5 m reductions in canopy height, while plots dominated by more conservative species show little to no reductions in canopy height. The higher R^2_{c} relative to the R^2_{m} showed the importance of accounting for edaphic conditions and forest type in the models, which was particularly evident for the changes in canopy height (Table 2). Moreover, we found moderate evidence that aridity mediated the changes in community-weighted mean WD (Table S5), where the probability of a decline in WD after the hurricanes was 30% lower in dry regions than wet regions (Figure S7). Apart from $|\Psi_{\mathrm{P50}}|$, there was not sufficient evidence ($p > 0.1$) to suggest that these changes depended on the functional composition before the hurricanes (Figure S8).

Structural equation models (SEMs) allowed us to quantify direct and indirect drivers of hurricane-related changes in forest properties and the mediators of such changes. The first model included only the hypothetical causal relations shown in Figure S3, inferred from Tables 1 and 2, yielding poor goodness of fit (Fisher's $C = 260.47$, df = 76, $p < 0.0001$; Figure S9). We obtained the final SEM model (Fisher's $C = 53.43$, df = 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 ΔMR was higher in older forest stands that experienced larger reductions in canopy cover (more negative ΔCC), were located closest to the eye of the hurricanes and were on flat terrain (Figure 3a). Canopy height, WD and the ΔCH had an indirect effect on ΔMR in which forests with low WD and negative ΔCH experienced the largest increases in mortality (highest ΔMR; Figure 3b). Interestingly, WD was the common mediator for the paths explaining these three metrics of hurricane disturbance (ΔCC, ΔCH and ΔMR).

4 | DISCUSSION

Using the FIA plot network, we comprehensively analysed 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 canopy cover, leading to a 25% increase in MR. After considering the proximity of the storms, we found that older forest plots and those with tall canopies were

TABLE 2 Standardized β coefficients from univariate linear mixed effect models of the changes (Δ) in basal area mortality rates (MR) (MR at t − MR at $t - 1$), canopy cover and canopy height in 180 FIA plots with surveys before and after the Hurricanes Irma and Maria.

	Δ MR				**Δ canopy cover**				**Δ canopy height**			
	β	R^2_{m}	R^2_{c}	p	β	R^2_{m}	R^2_{c}	p	β	R^2_{m}	R^2_{c}	p
$\mathrm{D_{HT}}$	**−0.1183**	**0.05**	**0.07**	**0.0040**	0.0095	0.02	0.12	0.1413	**0.3254**	**0.04**	**0.20**	**0.0196**
Slope	−0.0705	0.02	0.05	0.0784	**0.0137**	**0.03**	**0.10**	**0.0171**	−0.1865	0.01	0.26	0.1295
SA	**0.1246**	**0.05**	**0.13**	**0.0021**	−0.0003	0.00	0.08	0.9627	**−0.2961**	**0.03**	**0.32**	**0.0181**
CH	0.0163	0.00	0.01	0.6956	−0.0021	0.00	0.09	0.7368	**−1.5066**	**0.79**	**0.79**	**0.0001**
Diversity	0.0217	0.00	0.02	0.5859	**0.0152**	**0.04**	**0.08**	**0.0079**	−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	**−0.4596**	**0.07**	**0.31**	**0.0001**
SLA	−0.0065	0.00	0.06	0.8730	−0.0092	0.02	0.11	0.1374	**−0.4882**	**0.09**	**0.32**	**0.0001**
WD	0.0112	0.00	0.03	0.7894	0.0019	0.00	0.09	0.7660	**0.6110**	**0.14**	**0.24**	**0.0001**
$\lvert\Psi_{\mathrm{TLP}}\rvert$	0.0550	0.02	0.02	0.1369	0.0031	0.00	0.02	0.6118	**0.5205**	**0.12**	**0.39**	**0.0006**
$\lvert\Psi_{\mathrm{P50}}\rvert$	0.0606	0.03	0.29	0.2821	0.0107	0.04	0.21	0.2378	**0.5765**	**0.17**	**0.47**	**0.0045**
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	**0.0120**	**0.03**	**0.09**	**0.0345**	0.1477	0.01	0.28	0.2139
SD-$\lvert\Psi_{\mathrm{TLP}}\rvert$	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-$\lvert\Psi_{\mathrm{P50}}\rvert$	0.0708	0.04	0.32	0.1373	0.0091	0.03	0.02	0.2294	0.2320	0.03	0.47	0.1861

Note: Univariate predictor variables are the distance to hurricane eye ($\mathrm{D_{HT}}$), 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 ($|\Psi_{\mathrm{TLP}}|$) and water potential at 50% embolism ($|\Psi_{\mathrm{P50}}|$). Marginal R^2 (R^2_{m}) and conditional R^2 (R^2_{c}) represent the variance explained only by fixed effects and by both fixed and random effects, respectively. Effects are highlighted in bold when significant effects were found.

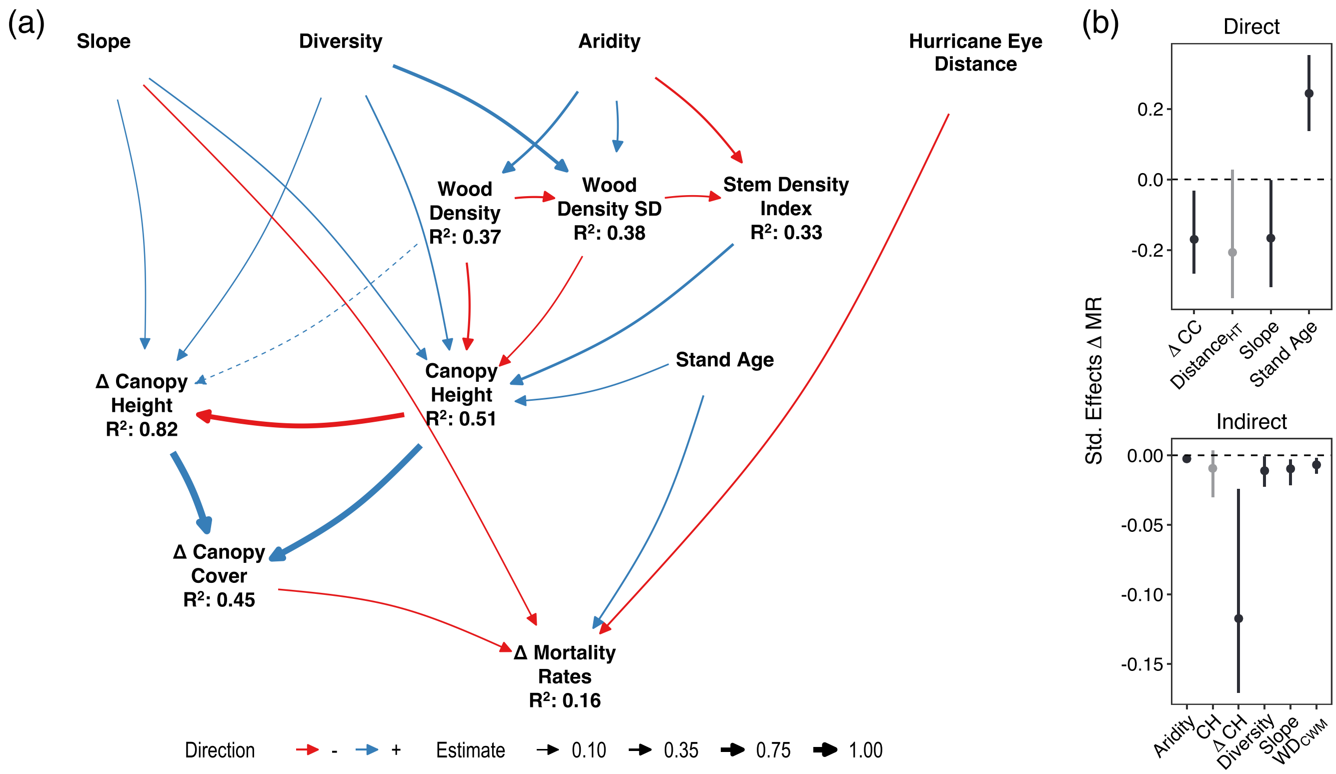

FIGURE 3 Structural equation model (SEM) to determine the direct and indirect effects mediating the observed changes in forests of Puerto Rico after Hurricanes Irma and Maria. (a) The causal pathways exploring the effects of climate, topography and forest function in mediating the changes (Δ) in basal area mortality rates (MR) (MR at t − MR at $t-1$), 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. (b) The standardized effects of variables with either a direct or indirect effect on ΔMR. Points represent the median standardized estimate and error bars represent the 95% confidence interval obtained from 5000 bootstrapped samples. The grey colour shows whether the 95% confidence interval overlaps with zero for a given predictor in the SEM. Direct and indirect standardized effects plots for Δ CC, Δ CH, and CH are shown in Figure S10.

most affected. Importantly, we observed that tall forests dominated by fast-growing, drought-vulnerable tree species (high SLA, low WD, high Ψ_{TLP} and high Ψ_{P50}) were primarily found in wet environments. Stands in wet environments were also 50% more likely to show a decrease in community-weighted WD than forests located in dry regions. These findings reveal a positive relationship between a community's ability to tolerate drought and its resistance to hurricanes across broad ecological gradients.

4.1 | 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 SPEI_{min}, suggesting strong controls of drought stress on species diversity even over a 5-year period (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). Aridity also explained the observed differences on the changes in canopy height with forest age (Table 1). In arid regions of Puerto Rico, the average canopy height of young and old stands was between 4 and 5 m (Van Bloem et al., 2007). In wetter regions, canopy height increased along with stand age from 8 m in young forests to 20 m in old forests (Drew et al., 2009). Canopy cover increased with age and SDI decreased, 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 Ψ_{TLP} and Ψ_{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 physiological traits indicative of drought tolerance. Here, we showed that community-level Ψ_{TLP} and Ψ_{P50} became more negative with forest age (Table 1). Our results highlight the potential linkages between slow-growing species and increased drought resistance as expected with the ecosystem development hypothesis (Odum, 1969; Oliveira et al., 2021; Reich, 2014). It is also important to highlight that human disturbances can affect such patterns (Berenguer et al., 2021), and more insight is needed from other tropical forests. 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 Ψ_{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). More conservative traits in young dry forests and a change towards more exploitative strategies as ecosystem develops suggest that the assumption of increasing resistance along with forest age may depend on other environmental pressures such as wet and dry tropical forest resistance forests suggest less resistance to disturbance as forest age in dry regions. The interaction effects between aridity and forest age were not present for Ψ_{P50}. This might be due to the fact that, in Caribbean arid regions, precipitation is fairly low (<1500 mm year^{-1}) 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).

4.2 | Hurricane disturbances across environmental gradients

The hurricanes caused a 25% increase in MR, a 21% decrease in canopy cover and a 45% decrease in canopy height across Puerto Rico (Figure 2). While the changes in canopy height and cover were consistent across forest types, increases in MR varied (Figure 2). In line with earlier remote sensing studies (Feng et al., 2020; Hall et al., 2020), hurricane-driven increases in non-photosynthetic vegetation were less in dry forests. Similarly, hurricane-related reductions in biomass were less in moist than in wet forests (Hall et al., 2020). We observed that ΔMR increased with canopy-cover loss. The trend was less evident considering declines in canopy height (Figure S6). It is likely that most stem snapping does not result in tree death (Taylor et al., 2023), a phenomenon also observed in hurricane-prone forests of Taiwan (Zuleta et al., 2023), yet reduces forest canopy height. These findings shed light on the mechanisms driving biomass changes, underscoring the importance of ground validation with geographically extensive plot networks such as the FIA database (Hoque et al., 2017). Ground plots add important insight into remotely sensed responses that are not otherwise evident.

While changes in forest structure and demographics were evident, changes in forest functional composition were more subtle or absent (Table S4). 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 S5 and Figure S7). Although regeneration in wet tropical forests can favour 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 how hurricanes affect 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 (Alonso-Rodríguez et al., 2022; Comita et al., 2018; Smith-Martin et al., 2022; Umaña et al., 2023).

4.3 | Drivers of hurricane forest damage

Forest stands exhibiting higher species diversity and greater community-level variation in WD experienced fewer reductions in canopy cover during the storms (Table 2). It has been observed that, in some cases, more diverse forests can show greater disturbance during a hurricane (Tanner & Bellingham, 2006). In Puerto Rico, forests with low diversity are often dominated by non-native tree species more susceptible to hurricane disturbances (e.g. *Spathodea campanulata*) (Figure S11; Helmer et al., 2018). Functional composition played an important role in determining canopy height reductions. Stands dominated by fast-growing, drought-vulnerable tree species (high SLA, low WD, low $|\Psi_{TLP}|$ and low $|\Psi_{P50}|$) showed on average a 4-m reduction in canopy height. This pattern links the observations of hurricane disturbances at the species level (Zimmerman et al., 1994) with the landscape-wide patterns at the stand level reported in this study, indicating a trade-off between fast-drought vulnerable growing strategies versus resistance to wind disturbances. Interestingly, neither functional composition nor functional diversity explained increases in MR, which was only higher in older forests and those closer to the hurricane track. The lack of direct linkages with MR highlights the complexity of these patterns at broad environmental gradients.

The SEM revealed that older forest stands (>50 years), those that faced a considerable reduction (>20%) in canopy cover and those situated on flat terrain closer (<40 km) to the storms' centre exhibited significantly higher ΔMR (Figure 3). Such patterns point out three key factors driving the hurricane disturbances in tropical forests. First, exposure to hurricane winds plays an important role in determining the damage during storms (Feng et al., 2020; Ibanez et al., 2024; McLaren et al., 2019; Zhang et al., 2022). This pattern was evidenced by the higher increase in MR 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 (Helmer et al., 2023b; McLaren et al., 2019; Zhang et al., 2022).

Second, older forest stands showed higher ΔMR. This result challenges the idea that, as ecosystems develop, their capacity to withstand perturbations increases (Odum, 1969; Poorter et al., 2023), at least in the context of ΔMR and hurricane disturbances. In Northeast Puerto Rico, older forest stands might not or will never reach a stable state due to frequent disturbances favouring plant communities with a mosaic of both early succession and late succession specialist tree species (Uriarte et al., 2009). In these tropical wet forest mosaics, tall trees with low WD will suffer the greatest mortality during hurricanes (Zimmerman et al., 1994). While in dry environments, the high prevalence of short stature trees with high WD can enhance survival during hurricanes (Van Bloem et al., 2007). 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; these forests were also more resistant to Hurricanes Maria and Irma (Zhang et al., 2022). Last, it might also be possible that these patterns are shaped by the widespread presence of non-native species that also tend to have lower wood density than native species (Figure S12), making them less resistant to hurricanes (Helmer et al., 2018, 2023b).

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 (Figure 3). Interestingly, WD was the common mediator variable for the observed changes (ΔCH, ΔCC and ΔMR). 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 canopy height and WD on ΔCH (Figure 3). These results link the well-documented species-specific patterns of hurricane resistance in relation to high WD and tree height with landscape scale responses across aridity gradients obtained from the FIA plot network and airborne LiDAR (Feng et al., 2020; Hall et al., 2020; Helmer et al., 2023b; Ibanez et al., 2024; Lin et al., 2018; Ogle et al., 2006; Ostertag et al., 2005; Uriarte et al., 2019; Zimmerman et al., 1994).

Our findings suggest that, across broad environmental gradients, plant communities dominated by species with high WD tend to be shorter in stature and have overall greater resistance to hurricane winds (Figure 3). Additionally, these plant communities are often dominated by species with higher drought tolerance, as indicated by the more negative values of Ψ_{TLP} & Ψ_{P50} (Figure S5). It is likely that the adaptations that enhance drought tolerance could lead to greater resistance against hurricane disturbances, even after accounting for the differences in proximity to the storm eye (i.e. storm intensity). However, our data cannot fully disentangle the possible interactions between hurricanes and droughts, which occur consecutively and simultaneously in Puerto Rico (Figure S13). As a whole, we acknowledge that uncertainties still exist regarding the influence of storm frequency in shaping the observed patterns (Hogan et al., 2018), and also the potential interactions with other disturbances such as drought events (Alonso-Rodríguez et al., 2022; Helmer et al., 2023b). Disentangling these interactions remains crucial given ongoing global environmental change.

5 | CONCLUSIONS

Our results reveal how aridity and stand age mediate forest characteristics that explain landscape scale variability in hurricane disturbances across environmental gradients (Eppinga & Pucko, 2018; Umaña et al., 2023; Uriarte et al., 2019; Zhang et al., 2022). We also show that stand age modulates hurricane resistance differently along water availability gradients. Where young dry forests show conservative community-weighted mean trait values enhancing resistance to disturbances, and the opposite occurs in young wet forests. Consequently, an increase in forest age does not necessarily imply increased resistance to hurricanes. This finding highlights important considerations when linking ecosystem age with resistance to disturbances (Lin et al., 2020; Odum, 1969; Uriarte et al., 2009). In addition, we propose that aridity 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.

AUTHOR CONTRIBUTIONS

German Vargas G., Jennifer S. Powers, William R. L. Anderegg and Eileen H. Helmer conceived the idea. German Vargas G., Jennifer S. Powers and Eileen H. Helmer designed the sampling scheme. German Vargas G. and Humfredo Marcano-Vega performed data collection. Jennifer S. Powers, Eileen H. Helmer, Humfredo Marcano-Vega and Tana E. Wood contributed data. Tom Ruzycki, Humfredo Marcano-Vega and German Vargas G. performed data curation. German Vargas G. performed data analysis with the input of WA. German Vargas G. wrote the first draft of the manuscript. All authors provided feedback on subsequent versions and edited the manuscript.

ACKNOWLEDGEMENTS

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.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14437.

DATA AVAILABILITY STATEMENT

The hydraulic trait data collected for this study, community-weighted mean trait values, community-weighted trait standard deviation values, proportion of deciduous species, proportion of native species and trait velocities can be found at the following Dryad repository: https://doi.org/10.5061/dryad.7pvmcvf39 (Vargas G et al., 2024). Due to the sensitive nature of some portions of the data used in the study and concerns regarding landowner privacy rights, certain portions of the processed data set should be exempt from public availability under the United States Food Security Act of 1985 (P.L. 99–198, also known as the 1985 U.S. Farm Bill). Specifically, any data that can be associated with the FIA plot geolocation should be considered confidential and protected from public disclosure. This involves any data derived from geospatial information that could potentially be used to identify the plot location, including aridity, minimum standardized precipitation evapotranspiration index, canopy cover, canopy height, topographic slope, forest stand age and distance to the hurricane track. The raw data from the FIA plot inventory, USGS LiDAR mission, distance to the hurricane track and trait data compiled for this work are publicly available as described in Table S6.

ORCID

German Vargas G. https://orcid.org/0000-0003-1738-0014
Humfredo Marcano-Vega https://orcid.org/0000-0001-7642-9151
Tana E. Wood https://orcid.org/0000-0001-6322-6224
William R. L. Anderegg https://orcid.org/0000-0001-6551-3331
Jennifer S. Powers https://orcid.org/0000-0003-3451-4803
Eileen H. Helmer https://orcid.org/0000-0003-3731-0056

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. *Frontiers in Forests and Global Change*, *5*, 733967. https://doi.org/10.3389/ffgc.2022.733967

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 Physiology*, *33*(7), 672–683. https://doi.org/10.1093/treephys/tpt044

Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(18), 5024–5029. https://doi.org/10.1073/pnas.1525678113

Anderegg, W. R. L., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., Ogle, K., Shaw, J. D., Shevliakova, E., Williams, A. P., Wolf, A., Ziaco, E., & Pacala, S. (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, *349*(6247), 528–532. https://doi.org/10.1126/science.aab1833

Baquería, S., & Vicente-Serrano, S. M. (2017). *SPEI*: *Calculation of the Standardised Precipitation-Evapotranspiration Index* (Version 1.7) [R package]. https://CRAN.R-project.org/package=SPEI

Bartón, K. (2022). *MuMIn*: *Multi-model inference* (version 1.47.1) [R package]. https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Batllori, E., Lloret, F., Aakala, T., Anderegg, W. R. L., Aynekulu, E., Bendixsen, D. P., Bentouati, A., Bigler, C., Burk, C. J., Camarero, J. J., Colangelo, M., Coop, J. D., Fensham, R., Floyd, M. L., Galiano, L., Ganey, J. L., Gonzalez, P., Jacobsen, A. L., Kane, J. M., … Zeeman, B. (2020). Forest and woodland replacement patterns following drought-related mortality. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(47), 29720–29729. https://doi.org/10.1073/pnas.2002314117

Berenguer, E., Lennox, G. D., Ferreira, J., Malhi, Y., Aragão, L. E. O. C., Barreto, J. R., Del Bon Espírito-Santo, F., Figueiredo, A. E. S., França, F., Gardner, T. A., Joly, C. A., Palmeira, A. F., Quesada, C. A., Rossi, L. C., de Seixas, M. M. M., Smith, C. C., Withey, K., & Barlow, J. (2021). Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(30), e2019377118. https://doi.org/10.1073/pnas.2019377118

Birdsey, R. A., & Weaver, P. L. (1987). *Forest Area Trends in Puerto Rico* (SO-RN-331; p. SO-RN-331). U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. https://doi.org/10.2737/SO-RN-331

Brandeis, T. J., Helmer, E. H., Marcano-Vega, H., & Lugo, A. E. (2009). Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the U.S. Virgin Islands. *Forest Ecology and Management*, *258*(7), 1704–1718. https://doi.org/10.1016/j.foreco.2009.07.030

Brandeis, T. J., Helmer, E. H., & Oswalt, S. N. (2007). The status of Puerto Rico's forests, 2003. *Resour. Bull. SRS-119. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 72 p., 119*. https://doi.org/10.2737/SRS-RB-119

Bretfeld, M., Ewers, B. E., & Hall, J. S. (2018). Plant water use responses along secondary forest succession during the 2015–2016 El Niño drought in Panama. *New Phytologist*, *219*(3), 885–899. https://doi.org/10.1111/nph.15071

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V. D., Schrodt, F., Mahecha, M. D., Peet, R. K., Sandel, B., Van Bodegom, P., Altman, J., Alvarez-Dávila, E., … Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature Ecology & Evolution*, *2*(12), 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Burrill, E. A., Wilson, A. M., Turner, J. A., Pugh, S. A., Menlove, J., Christensen, G., Conkling, B. L., & David, W. (2019). *The forest inventory and analysis*: *Database description and user guide for phase 2* (version 8.0). https://www.fs.usda.gov/research/understory/forest-inventory-and-analysis-database-user-guide-nfi

Comita, L., Uriarte, M., Forero-Montaña, J., Kress, W., Swenson, N., Thompson, J., Umaña, M., & Zimmerman, J. (2018). Changes in phylogenetic community structure of the seedling layer following hurricane disturbance in a human-impacted tropical forest. *Forests*, *9*(9), 556. https://doi.org/10.3390/f9090556

Curran, T. J., Gersbach, L. N., Edwards, W., & Krockenberger, A. K. (2008). Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of North Queensland, Australia. *Austral Ecology*, *33*(4), 442–450. https://doi.org/10.1111/j.1442-9993.2008.01899.x

Daly, C., Helmer, E. H., & Quiñones, M. (2003). Mapping the climate of Puerto Rico, Vieques and Culebra: CLIMATE MAPPING. *International Journal of Climatology*, *23*(11), 1359–1381. https://doi.org/10.1002/joc.937

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), Article 7585. https://doi.org/10.1038/nature16489

Drew, A. P., Boley, J. D., Zhao, Y., Johnston, M. H., & Wadsworth, F. H. (2009). Sixty-two years of change in subtropical wet forest structure and composition at el verde, Puerto Rico. *Interciencia*, *34*(1), 34–40.

Eppinga, M. B., & Pucko, C. A. (2018). The impact of hurricanes Irma and Maria on the forest ecosystems of Saba and St. Eustatius, northern Caribbean. *Biotropica*, *50*(5), 723–728. https://doi.org/10.1111/btp.12600

Ewel, J. J., & Whitmore, J. L. (1973). *Ecological life zones of Puerto Rico and the U.S. Virgin Islands* (Research Paper 18; ITF, p. 72). U.S. Department of Agriculture Forest Service, Institute of Tropical Forestry. https://scholar.google.com/scholar_lookup?title=Ecological+life+zones+of+Puerto+Rico+and+the+U.S.+Virgin+Islands&author=Ewel%2C+John+J.&publication_year=1973

Feng, Y., Negrón-Juárez, R. I., & Chambers, J. Q. (2020). Remote sensing and statistical analysis of the effects of hurricane María on the forests of Puerto Rico. *Remote Sensing of Environment*, *247*, 111940. https://doi.org/10.1016/j.rse.2020.111940

Garrido, M., Hansen, S. K., Yaari, R., & Hawlena, H. (2022). A model selection approach to structural equation modelling: A critical evaluation and a road map for ecologists. *Methods in Ecology and Evolution*, *13*(1), 42–53. https://doi.org/10.1111/2041-210X.13742

Goring, S. J., Mladenoff, D. J., Cogbill, C. V., Record, S., Paciorek, C. J., Jackson, S. T., Dietze, M. C., Dawson, A., Matthes, J. H., McLachlan, J. S., & Williams, J. W. (2016). Novel and lost forests in the upper midwestern United States, from new estimates of settlement-era composition, stem density, and biomass. *PLoS One*, *11*(12), e0151935. https://doi.org/10.1371/journal.pone.0151935

Hall, J., Muscarella, R., Quebbeman, A., Arellano, G., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2020). Hurricane-induced rainfall is a stronger predictor of tropical forest damage in Puerto Rico than maximum wind speeds. *Scientific Reports*, *10*(1), 4318. https://doi.org/10.1038/s41598-020-61164-2

Helmer, E. H., Kay, S. L., Marcano-Vega, H., Powers, J. S., Wood, T. E., Zhu, X., Gwenzi, D., & Ruzycki, T. S. (2023a). Forest age map, tree species traits and Landsat phenology metrics for Puerto Rico and the U.S. Virgin Islands. *Forest Service Research Data Archive*. https://doi.org/10.2737/RDS-2023-0004

Helmer, E. H., Kay, S. L., Marcano-Vega, H., Powers, J. S., Wood, T. E., Zhu, X., Gwenzi, D., & Ruzycki, T. S. (2023b). Multiscale predictors of small tree survival across a heterogeneous tropical landscape. *PLoS One*, *18*, e0280322. https://doi.org/10.1371/journal.pone.0280322

Helmer, E. H., Ruzycki, T. S., Wilson, B. T., Sherrill, K. R., Lefsky, M. A., Marcano-Vega, H., Brandeis, T. J., Erickson, H. E., & Ruefenacht, B. (2018). Tropical deforestation and recolonization by exotic and native trees: Spatial patterns of tropical Forest biomass, functional groups, and species counts and links to stand age, geoclimate, and sustainability goals. *Remote Sensing*, *10*(11), Article 11. https://doi.org/10.3390/rs10111724

Hogan, J., Zimmerman, J., Thompson, J., Uriarte, M., Swenson, N., Condit, R., Hubbell, S., Johnson, D., Sun, I., Chang-Yang, C.-H., Su, S.-H., Ong, P., Rodriguez, L., Monoy, C., Yap, S., & Davies, S. (2018). The frequency of cyclonic wind storms shapes tropical forest dynamism and functional trait dispersion. *Forests*, *9*(7), 404. https://doi.org/10.3390/f9070404

Hoque, M. A.-A., Phinn, S., & Roelfsema, C. (2017). A systematic review of tropical cyclone disaster management research using remote sensing and spatial analysis. *Ocean and Coastal Management*, *146*, 109–120. https://doi.org/10.1016/j.ocecoaman.2017.07.001

Ibanez, T., Bauman, D., Aiba, S., Arsouze, T., Bellingham, P. J., Birkinshaw, C., Birnbaum, P., Curran, T. J., DeWalt, S. J., Dwyer, J., Fourcaud, T., Franklin, J., Kohyama, T. S., Menkes, C., Metcalfe, D. J., Murphy, H., Muscarella, R., Plunkett, G. M., Sam, C., … Keppel, G. (2024). Damage to tropical forests caused by cyclones is driven by wind speed but mediated by topographical exposure and tree characteristics. *Global Change Biology*, *30*(5), e17317. https://doi.org/10.1111/gcb.17317

Kohyama, T. S., Kohyama, T. I., & Sheil, D. (2019). Estimating net biomass production and loss from repeated measurements of trees in forests and woodlands: Formulae, biases and recommendations. *Forest Ecology and Management*, *433*, 729–740. https://doi.org/10.1016/j.foreco.2018.11.010

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Leitold, V., Morton, D. C., Martinuzzi, S., Paynter, I., Uriarte, M., Keller, M., Ferraz, A., Cook, B. D., Corp, L. A., & González, G. (2022). Tracking the rates and mechanisms of canopy damage and recovery following hurricane Maria using multitemporal Lidar data. *Ecosystems*, *25*(4), 892–910. https://doi.org/10.1007/s10021-021-00688-8

Lin, S.-Y., Shaner, P.-J. L., & Lin, T.-C. (2018). Characteristics of old-growth and secondary forests in relation to age and typhoon disturbance. *Ecosystems*, *21*(8), 1521–1532. https://doi.org/10.1007/s10021-018-0238-0

Lin, T.-C., Hogan, J. A., & Chang, C.-T. (2020). Tropical cyclone ecology: A scale-link perspective. *Trends in Ecology & Evolution*, *35*(7), 594–604. https://doi.org/10.1016/j.tree.2020.02.012

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J. A., Paz, H., Pérez-García, E. A., Romero-Pérez, I. E., Tauro, A., & Bongers, F. (2013). Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, *94*(6), 1211–1216. https://doi.org/10.1890/12-1850.1

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

MacKinnon, D. P., Krull, J. L., & Lockwood, C. M. (2000). Equivalence of the mediation, confounding and suppression effect. *Prevention Science: The Official Journal of the Society for Prevention Research*, *1*(4), 173–181.

McLaren, K., Luke, D., Tanner, E., Bellingham, P. J., & Healey, J. R. (2019). Reconstructing the effects of hurricanes over 155 years on the structure and diversity of trees in two tropical montane rainforests in Jamaica. *Agricultural and Forest Meteorology*, *276–277*, 107621. https://doi.org/10.1016/j.agrformet.2019.107621

McNellis, B. E., Smith, A. M. S., Hudak, A. T., & Strand, E. K. (2021). Tree mortality in western U.S. forests forecasted using forest inventory and random Forest classification. *Ecosphere*, *12*(3), e03419. https://doi.org/10.1002/ecs2.3419

Murphy, M. V. (2022). *semEff: Automatic calculation of effects for piecewise structural equation models* (Version 0.6.1) [R package]. https://CRAN.R-project.org/package=semEff

Muscarella, R., Lohbeck, M., Martínez-Ramos, M., Poorter, L., Rodríguez-Velázquez, J. E., van Breugel, M., & Bongers, F. (2017). Demographic drivers of functional composition dynamics. *Ecology*, *98*(11), 2743–2750. https://doi.org/10.1002/ecy.1990

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, *14*(134), 20170213. https://doi.org/10.1098/rsif.2017.0213

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Odum, E. P. (1969). The strategy of ecosystem development. *Science*, *164*(3877), 262–270.

Ogle, K., Uriarte, M., Thompson, J., Johnstone, J., Jones, A., Lin, Y., McIntire, E. J. B., & Zimmerman, J. K. (2006). Implications of vulnerability to hurricane damage for long-term survival of tropical tree species: A Bayesian hierarchical analysis. In *Applications of computational statistics in the environmental sciences: Hierachical Bayes and MCMC methods* (pp. 98–117). Oxford University Press.

Oliveira, R. S., Eller, C. B., Barros, F. d. V., Hirota, M., Brum, M., & Bittencourt, P. (2021). Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist*, *230*(3), 904–923. https://doi.org/10.1111/nph.17266

Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., León-Gómez, C., Dawson, T., Camarero Martínez, J. J., Castorena, M., Echeverría, A., Espinosa, C. I., Fajardo, A., Gazol, A., Isnard, S., Lima, R. S., Marcati, C. R., & Méndez-Alonzo, R. (2018). Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(29), 7551–7556. https://doi.org/10.1073/pnas.1721728115

Ostertag, R., Silver, W. L., & Lugo, A. E. (2005). Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest1: Predicting resistance to hurricane damage. *Biotropica*, *37*(1), 16–24. https://doi.org/10.1111/j.1744-7429.2005.04052.x

Poorter, L., Amissah, L., Bongers, F., Hordijk, I., Kok, J., Laurance, S. G. W., Lohbeck, M., Martínez-Ramos, M., Matsuo, T., Meave, J. A., Muñoz, R., Peña-Claros, M., & Van Der Sande, M. T. (2023). Successional theories. *Biological Reviews*, *98*(6), 2049–2077. https://doi.org/10.1111/brv.12995

Poorter, L., Rozendaal, D. M. A., Bongers, F., Almeida, d. J. S., Álvarez, F. S., Andrade, J. L., Arreola Villa, L. F., Becknell, J. M., Bhaskar, R., Boukili, V., Brancalion, P. H. S., César, R. G., Chave, J., Chazdon, R. L., Dalla Colletta, G., Craven, D., de Jong, B. H. J., Denslow, J. S., Dent, D. H., … Westoby, M. (2021). Functional recovery of secondary tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(49), e2003405118. https://doi.org/10.1073/pnas.2003405118

Poorter, L., Rozendaal, D. M. A., Bongers, F., de Almeida-Cortez, J. S., Almeyda Zambrano, A. M., Álvarez, F. S., Andrade, J. L., Villa, L. F. A., Balvanera, P., Becknell, J. M., Bentos, T. V., Bhaskar, R., Boukili, V., Brancalion, P. H. S., Broadbent, E. N., César, R. G., Chave, J., Chazdon, R. L., Colletta, G. D., … Westoby, M. (2019). Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution*, *3*(6), Article 6. https://doi.org/10.1038/s41559-019-0882-6

R Core Team. (2022). *R: A language and environment for statistical computing* (Version 4.2.1) [R]. R Foundation for Statistical Computing. https://www.r-project.org/

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Rounds, E., Patterson, S., Howard, S., Quiñones, M., & Schleicher, M. (2023). *Mapping canopy cover in the US Caribbean using airborne lidar data from 2016 and 2018*. (IITF-55; Gen. Tech. Rep.). U.S. Department of Agriculture Forest Service, Institute of Tropical Forestry.

Schwartz, N. B., Lintner, B. R., Feng, X., & Powers, J. S. (2020). Beyond MAP: A guide to dimensions of rainfall variability for tropical ecology. *Biotropica*, *52*(6), 1319–1332. https://doi.org/10.1111/btp.12830

Seneviratne, S. I., Zhang, X., Adnan, M., Badi, W., Dereczynski, C., Di Luca, A., Ghosh, S., Iskandar, I., Kossin, J., Lewis, S., Otto, F., Pinto, I., Satoh, M., Vicente-Serrano, S. M., Wehner, M., & Zhou, B. (2023). Chapter 11: Weather and climate extreme events in a changing climate. In *Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assesment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York: Cambridge University Press, NY, USA. https://doi.org/10.1017/9781009157896

Shipley, B. (2000). A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling: A Multidisciplinary Journal*, *7*(2), 206–218. https://doi.org/10.1207/S15328007SEM0702_4

Smith-Martin, C. M., Muscarella, R., Ankori-Karlinsky, R., Delzon, S., Farrar, S. L., Salva-Sauri, M., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2022). Hurricanes increase tropical forest vulnerability to drought. *New Phytologist*, *235*(3), 1005–1017. https://doi.org/10.1111/nph.18175

Stovall, A. E. L., Shugart, H., & Yang, X. (2019). Tree height explains mortality risk during an intense drought. *Nature Communications*, *10*(1), Article 1. https://doi.org/10.1038/s41467-019-12380-6

Tanner, E. V. J., & Bellingham, P. J. (2006). Less diverse forest is more resistant to hurricane disturbance: Evidence from montane rain forests in Jamaica. *Journal of Ecology*, *94*(5), 1003–1010. https://doi.org/10.1111/j.1365-2745.2006.01149.x

Taylor, B. N., Stedman, E., Van Bloem, S. J., Whitmire, S. L., & DeWalt, S. J. (2023). Widespread stem snapping but limited mortality caused by a category 5 hurricane on the Caribbean Island of Dominica. *Forest Ecology and Management*, *532*, 120833. https://doi.org/10.1016/j.foreco.2023.120833

Trugman, A. T., Anderegg, L. D. L., Shaw, J. D., & Anderegg, W. R. L. (2020). Trait velocities reveal that mortality has driven widespread coordinated shifts in forest hydraulic trait composition. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(15), 8532–8538. https://doi.org/10.1073/pnas.1917521117

Tumber-Dávila, S. J., Schenk, H. J., Du, E., & Jackson, R. B. (2022). Plant sizes and shapes above and belowground and their interactions with climate. *New Phytologist*, *235*(3), 1032–1056. https://doi.org/10.1111/nph.18031

Umaña, M. N., Needham, J., Forero-Montaña, J., Nytch, C. J., Swenson, N. G., Thompson, J., Uriarte, M., & Zimmerman, J. K. (2023). Demographic trade-offs and functional shifts in a hurricane-impacted tropical forest. *Annals of Botany*, *131*, 1051–1060. https://doi.org/10.1093/aob/mcad004

Uriarte, M., Canham, C. D., Thompson, J., Zimmerman, J. K., Murphy, L., Sabat, A. M., Fetcher, N., & Haines, B. L. (2009). Natural disturbance and human land use as determinants of tropical forest dynamics: Results from a forest simulator. *Ecological Monographs*, *79*(3), 423–443. https://doi.org/10.1890/08-0707.1

Uriarte, M., Thompson, J., & Zimmerman, J. K. (2019). Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nature Communications*, *10*(1), 1362. https://doi.org/10.1038/s41467-019-09319-2

Van Beusekom, A., Álvarez-Berríos, N., Gould, W., Quiñones, M., & González, G. (2018). Hurricane Maria in the U.S. Caribbean: Disturbance forces, variation of effects, and implications for future storms. *Remote Sensing*, *10*(9), 1386. https://doi.org/10.3390/rs10091386

Van Bloem, S. J., Murphy, P. G., & Lugo, A. E. (2007). A link between hurricane-induced tree sprouting, high stem density and short canopy in tropical dry forest. *Tree Physiology*, *27*(3), 475–480. https://doi.org/10.1093/treephys/27.3.475

Vargas G, G., Brodribb, T. J., Dupuy, J. M., González-M, R., Hulshof, C. M., Medvigy, D., Allerton, T. A. P., Pizano, C., Salgado-Negret, B., Schwartz, N. B., Van Bloem, S. J., Waring, B. G., & Powers, J. S. (2021). Beyond leaf habit: Generalities in plant function across 97 tropical dry forest tree species. *New Phytologist*, *232*(1), 148–161. https://doi.org/10.1111/nph.17584

Vargas G, G., Kunert, N., Hammond, W. M., Berry, Z. C., Werden, L. K., Smith-Martin, C. M., Wolfe, B. T., Toro, L., Mondragón-Botero, A., Pinto-Ledezma, J. N., Schwartz, N. B., Uriarte, M., Sack, L., Anderson-Teixeira, K. J., & Powers, J. S. (2022). Leaf habit affects the distribution of drought sensitivity but not water transport efficiency in the tropics. *Ecology Letters*, *25*(12), 2637–2650. https://doi.org/10.1111/ele.14128

Vargas G, G., Marcano-Vega, H., Ruzycki, T., Wood, T. E., Anderegg, W. R. L., Powers, J. S., & Helmer, E. H. (2024). Data from: Aridity and forest age mediate landscape scale patterns of tropical forest resistance to cyclonic storms. *Dryad*. https://doi.org/10.5061/dryad.7pvmcvf39

Venturas, M. D., Todd, H. N., Trugman, A. T., & Anderegg, W. R. L. (2021). Understanding and predicting forest mortality in the western United States using long-term forest inventory data and modeled hydraulic damage. *New Phytologist*, *230*, 1896–1910. https://doi.org/10.1111/nph.17043

Vitousek, P. M., & Reiners, W. A. (1975). Ecosystem succession and nutrient retention: A hypothesis. *Bioscience*, *25*(6), 376–381. https://doi.org/10.2307/1297148

Wadsworth, F. H. (1950). Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribbean Forester*, *11*(1), 38–56.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Zak, D. R. (2014). Ecosystem succession and nutrient retention: Vitousek and reiners' hypothesis. *The Bulletin of the Ecological Society of America*, *95*(3), 234–237. https://doi.org/10.1890/0012-9623-95.3.234

Zhang, J., Heartsill-Scalley, T., & Bras, R. L. (2022). Forest structure and composition are critical to hurricane mortality. *Forests*, *13*(2), 202. https://doi.org/10.3390/f13020202

Zimmerman, J. K., Iii, E. M. E., Waide, R. B., Lodge, D. J., Taylor, C. M., & Brokaw, N. V. L. (1994). Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: Implications for tropical tree life histories. *The Journal of Ecology*, *82*(4), 911. https://doi.org/10.2307/2261454

Zuleta, D., Arellano, G., McMahon, S. M., Aguilar, S., Bunyavejchewin, S., Castaño, N., Chang-Yang, C., Duque, A., Mitre, D., Nasardin, M., Pérez, R., Sun, I., Yao, T. L., Valencia, R., Krishna Moorthy, S. M., Verbeeck, H., & Davies, S. J. (2023). Damage to living trees contributes to almost half of the biomass losses in tropical forests. *Global Change Biology*, *29*(12), 3409–3420. https://doi.org/10.1111/gcb.16687

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting information.

How to cite this article: Vargas G., G., Marcano-Vega, H., Ruzycki, T., Wood, T. E., Anderegg, W. R. L., Powers, J. S., & Helmer, E. H. (2025). Aridity and forest age mediate landscape scale patterns of tropical forest resistance to cyclonic storms. *Journal of Ecology*, *113*, 53–67. https://doi.org/10.1111/1365-2745.14437