

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

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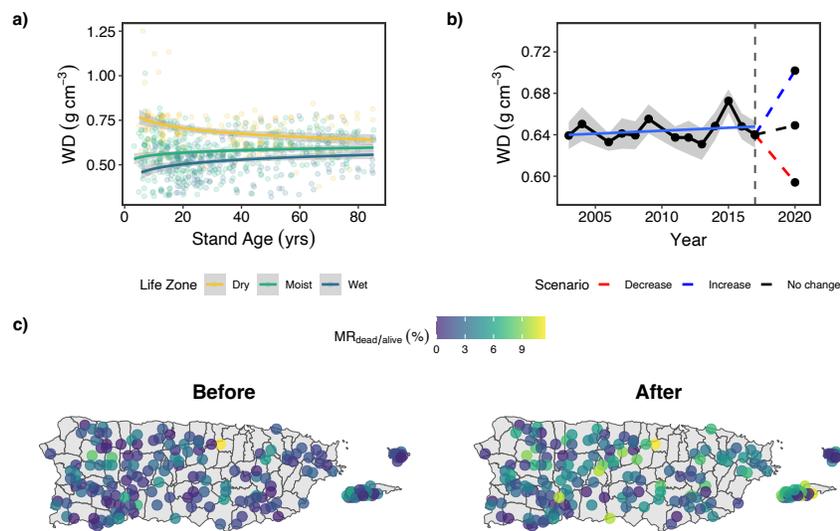
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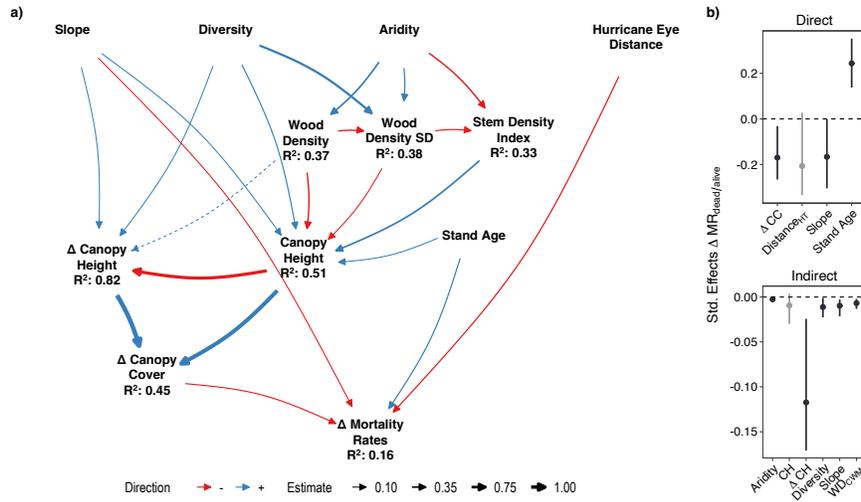
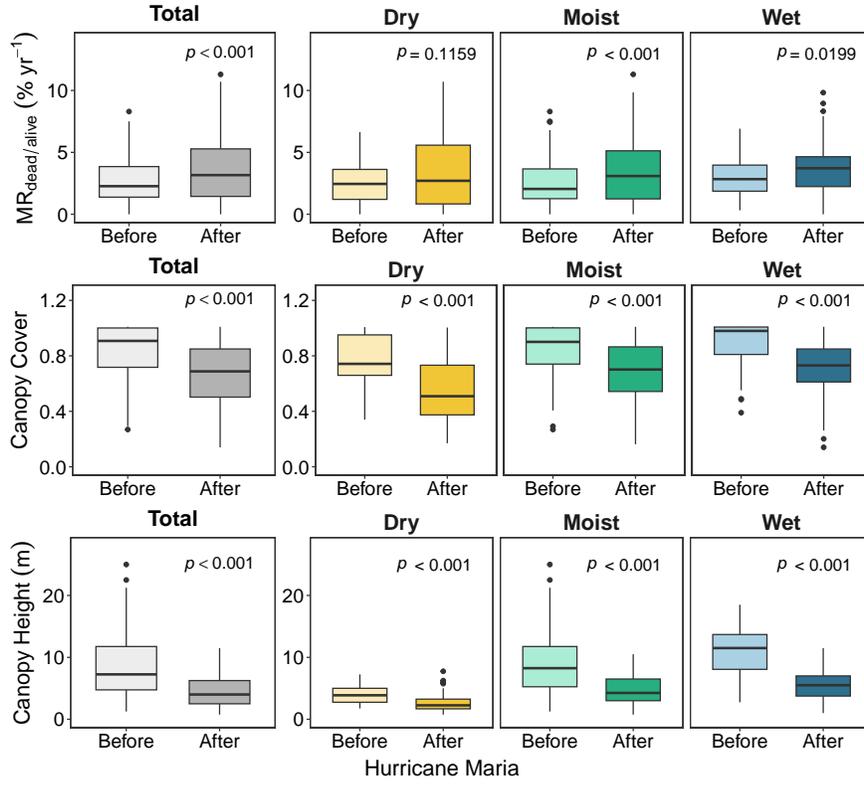
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Abstract

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.





1 **I. Title page**

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

7 **Data accessibility:** All FIA, LiDAR, and trait data compiled for this work are publicly available
8 and we indicate such sources in the manuscript. In addition, the hydraulic trait data for this study
9 will be deposited in the Xylem Functional Traits Database (<https://xylemfunctionaltraits.org/>) upon
10 publication. The compiled data associated with each research question and the R code used for
11 statistical analysis in this study will be deposited in a DRYAD public repository upon acceptance
12 of the manuscript. We have removed the geospatial information extracted with forest plot
13 locations from the publicly available data used for statistical analyses due to landowner privacy
14 rights considered in the United States Food Security Act of 1985 (P.L. 99-198, also known as the
15 1985 U.S. Farm Bill).

16

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

19

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50 **II. Abstract page**

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

62

63 **III. Main text**

64 **Introduction**

65 Climate change is expected to cause an increase in the intensity of cyclonic storms,
66 hereafter hurricanes, in tropical regions due to increases in ocean heat energy (Seneviratne *et al.*
67 2021). Hurricanes play a significant role in mediating tropical forest ecosystem processes and
68 forest structure (Lugo 2008). Predicting the response of tropical forests to changes in hurricane
69 intensity is a challenging task due to their high biological diversity and environmental complexity
70 (McLaren *et al.* 2019; Uriarte *et al.* 2019; Lin *et al.* 2020). Given this complexity, forest resistance
71 to hurricanes is likely to vary across the environmental gradients shaping forest structure and
72 function. In E.P. Odum's seminal paper '*The strategy of ecosystem development*,' he theorizes
73 that, as ecosystems age, their attributes will favor slower energy exchange with greater
74 ecosystem homeostasis (*e.g.* resistance and/or resilience) (Odum 1969). However, this
75 framework might not fully represent all of the factors mediating tropical forest resistance to
76 hurricanes across environmental gradients (Vitousek & Reiners 1975; Uriarte *et al.* 2009; Feng *et*
77 *al.* 2020). It is crucial then to evaluate whether the factors influencing tropical forests'
78 characteristics mediate resistance to hurricanes.

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

90 which is associated with higher tree survival during periods of extreme drought (Anderegg *et al.*
91 2016). Forest stand age also affects these patterns of trait variation because, in tropical forests,
92 low WD species usually dominate young stands at the wet end of the aridity spectrum while high
93 WD species dominate young stands at the dry end (Poorter *et al.* 2019) (Fig. 1, a). Thus, the
94 patterns of stand-level plant traits conferring resistance to hurricanes should depend on forest
95 age and interactions with other environmental filters such as aridity.

96 Beyond the major effects on tree mortality and changes in forest structure, hurricanes
97 also impact plant community composition. After a hurricane, there is an increase in the number of
98 forest gaps (Lugo 2008), potentially favoring fast-growing drought-vulnerable plant species
99 (Alonso-Rodríguez *et al.* 2022; Smith-Martin *et al.* 2022). Changes in the light environment can
100 also lead to increases in phylogenetic relatedness in the seedling community (Comita *et al.*
101 2018). However, in tropical forests located at the dry end of aridity gradients, recruitment after
102 hurricanes mostly occurs through the re-sprouting of snapped trees, and large re-organizations of
103 the plant community are rarely seen (Van Bloem *et al.* 2007; Curran *et al.* 2008). These lines of
104 evidence indicate that the trajectory (*i.e.*, increase or decrease) and the rate of change in
105 functional composition (*e.g.*, trait velocities) after a hurricane may consequently follow many
106 alternative routes depending on environmental factors and surviving tree species characteristics
107 (Fig. 1, b) (Lugo 2008; Trugman *et al.* 2020). The combined effect of forest stand age and climate
108 on these responses remains uncertain as no study has explored this extensively (Lin *et al.* 2020).

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

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

120 We tested whether remotely sensed losses in canopy height and canopy cover were
121 linked to an increase in plot forest mortality and investigated whether these patterns differed
122 depending on the forest's functional composition, aridity, and age. We leveraged forest basal
123 area data from a network of 339 long-term permanent inventory plots from Forest Inventory
124 Analysis (FIA) data in the archipelago of Puerto Rico collected before and after Hurricanes Irma
125 and Maria. We hypothesized that resistance to hurricane disturbances would increase with aridity
126 and decrease with stand age, even after accounting for the differences in topographic slope and
127 proximity to the eye of the storm (Feng *et al.* 2020). We further hypothesized that aridity would
128 limit the increase in community-level trait values indicative of vulnerability to drought (*i.e.*, low
129 WD) following hurricane disturbance. Specifically, we asked: 1) How do climate and stand age
130 mediate forest diversity, structure, and community-level trait values? 2) How did forest structure,
131 mortality, community-level traits, and trait velocities change after Hurricanes Irma and Maria in
132 2017? 3) Do climate and stand age determine the trajectory of trait velocities after the
133 hurricanes? 4) Are hurricane-related changes in forest mortality directly and indirectly mediated
134 by community-level traits?

135

136 **Materials and methods**

137 *Study region and forest inventory*

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

144 to 29 °C (Daly *et al.* 2003), and a mosaic of forest stands of different ages recovering from near
145 total deforestation in the 1950s followed by agricultural land abandonment and further
146 socioeconomic development (Wadsworth 1950; Birdsey & Weaver 1987; Brandeis *et al.* 2007).
147 On the selected plots, we calculated the Shannon diversity index (diversity), basal area in m² ha⁻¹
148 (BA), and the ratio between above-ground biomass and stem density (SDI). Dense stands with
149 small trees have small SDI, while a large SDI indicates forest stands composed of large stems.
150 We calculated forest mortality as the percentage of dead BA at the end of the interval (BA_{dead}) in
151 relation to the plot total BA at the beginning of the interval (BA_{total}) divided by the time in years
152 between each census (MR_{dead/alive} in % yr⁻¹) (Equation 1) for each census interval for each plot.
153 This mortality calculation excluded trees that died from fire or non-natural causes.

154
$$MR_{dead/alive} = \frac{(BA_{dead}/BA_{total}) * 100}{t_f - t_i} \quad \text{Equation 1,}$$

155

156 *Remote sensing metrics of forest structure*

157 We complemented the FIA data with remotely sensed forest canopy height, cover, and
158 stand age. We summarized plot-level changes in canopy height and cover from 1-m spatial
159 resolution maps of those variables for the years 2016 and 2018 developed by Rounds *et al.*
160 (2023) from airborne LiDAR data collected by the U.S. Geological Survey. From these maps, we
161 used average canopy height values of 1-m pixels in each 0.065 ha plot and the proportion of
162 pixels with forest cover for canopy cover. To determine stand age, we used data combining land-
163 cover maps from the years 1951-2000 with plot status (forest or nonforest) since then (Helmer *et*
164 *al.* 2023).

165

166 *Forest functional composition*

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

170 resource acquisition strategies in which low WD and high SLA indicate a fast-growing acquisitive
171 strategy (Díaz *et al.* 2016). Drought tolerance traits include the stem water potentials at leaf turgor
172 loss point (Ψ_{TLP}) and at 50% loss of hydraulic conductivity or 50% accumulation of embolisms
173 (Ψ_{P50}), which describe the thresholds of leaf and xylem function under drought (Vargas G. *et al.*
174 2022). While most trait data come from previously published sources, we collected data on
175 drought tolerance traits for nine species during February-March 2020 (Methods S1). For each
176 plot, we calculated trait community-weighted means, community-weighted standard deviation,
177 and the rate of change of traits through time (*i.e.*, ‘trait velocities’). Trait velocities provide
178 information on the functional trajectories of plant communities in which directionality is associated
179 with environmental filters such as drought events or successional gradients (Trugman *et al.*
180 2020).

181

182 *Climatic predictors*

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

193

194 *Statistical analysis*

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

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

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

218 Second, we fitted a series of linear mixed models exploring whether Δ MR_{dead/alive}, canopy
219 cover (Δ CC), and height (Δ CH) were explained by trait community-weighted means, their
220 standard deviations, proximity to hurricane eye track (obtained from the National Hurricane
221 Center's Tropical Cyclone Reports, www.nhc.noaa.gov, accessed September 2022) (Fig. S7),
222 stand age, canopy height, or topographic slope. Additionally, we fitted linear mixed models to
223 explore whether the Δ CH predicted Δ MR_{dead/alive} and Δ CC. We used the combination of geological

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

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

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

251 values indicate strong discrepancies between the proposed model and the observed variation in
252 the data (Shipley 2000; Lefcheck 2016). We then obtained standardized estimates of the direct,
253 indirect, and mediator effects of the predictors on all the response variables in the model. In all
254 models with random effects, we calculated the variance explained by the fixed effects (R_m^2), and
255 the variance explained by both fixed and random effects (R_c^2) (Nakagawa & Schielzeth 2013;
256 Nakagawa *et al.* 2017). All data management and analyses were done using R 4.2.1 (R Core
257 Team 2022) with packages tidyverse (Wickham *et al.* 2019), SPEI (Baquería & Vicente-Serrano
258 2017), piecewiseSEM (Lefcheck 2016), semeff (Murphy 2022), lmer4 (Bates *et al.* 2015), and
259 MuMin (Bartón 2022).

260

261 **Results**

262 *Drivers of forest structure and function*

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

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

278

279 *Effects of Hurricanes Irma and Maria*

280 Before September 2017, $MR_{\text{dead/alive}}$ averaged 2.7% of forest basal area per year, canopy
281 height averaged 3.9 m in the dry end and 12 m in the wetter end, and canopy cover averaged
282 84% (Fig. 2). After hurricanes Irma and Maria, we found strong evidence of a ~25% increase in
283 $MR_{\text{dead/alive}}$, ~21% decrease in canopy cover, and ~45% decrease in canopy height (Fig. 2) and
284 the impacts varied among dominant forest types (Fig. 2). We only found evidence of an increase
285 in the community-weighted standard deviation of SLA in wet forests (Table S2). Additionally, the
286 probability of a decline in community-weighted mean WD after the hurricanes was lower in drier
287 areas. (Table S3, Fig S3, & Fig. S4).

288

289 *Factors mediating hurricane effects on tropical forests*

290 From the univariate analyses, we found that the main predictors of $\Delta MR_{\text{dead/alive}}$ were
291 distance to the hurricane track (*e.g.*, the shorter the distance the greater the increase in
292 $MR_{\text{dead/alive}}$) and forest stand age (*e.g.*, older stands showed greater increases in $MR_{\text{dead/alive}}$)
293 (Table 2). Plots in flat terrain suffered major decreases in canopy cover compared with plots on
294 steep terrain (Table 2). Species diversity and community-weighted standard deviation for WD
295 were associated with the change in canopy cover, whereas less diverse plots experienced the
296 biggest reductions in canopy cover (Table 2). Eight out of the 14 variables individually explain
297 changes in canopy height. First, plots in older forest stands with taller canopies and closer to the
298 hurricane track showed the greatest reductions in canopy height (Table 2). Second, plots
299 dominated by species with fast-growing, drought-sensitive trait values (high SLA; low WD, $|\Psi_{\text{TLP}}|$
300 or $|\Psi_{\text{P50}}|$) showed the greatest reductions in canopy height. Edaphic conditions and forest types
301 were only important for the models predicting the change in canopy height (Table 2).

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

305 goodness of fit (Fisher's C = 260.47, d.f.= 76, $p < 0.0001$) (SI Appendix Fig S6). We obtained the
306 final SEM model (Fisher's C = 53.43, d.f.= 68, $p = 0.902$) after updating the model to account for
307 missing paths found in the test of direct separation and to exclude weak paths ($p > 0.1$). The final
308 SEM showed that $\Delta MR_{\text{dead/alive}}$ was higher in older forest stands that experienced larger losses in
309 canopy cover (lower ΔCC), were located closest to the eye of the hurricanes, and were on flat
310 terrain (Fig. 3, a). Canopy height, WD, and the ΔCH had an indirect effect on $\Delta MR_{\text{dead/alive}}$ in
311 which forests with short canopies, low WD, and negative ΔCH experienced the highest
312 $\Delta MR_{\text{dead/alive}}$ (Fig. 3, b). Interestingly, WD was the common mediator for the paths explaining
313 these three metrics of hurricane impacts (ΔCC , ΔCH , and $\Delta MR_{\text{dead/alive}}$).

314

315 **Discussion**

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

328

329 *Variation in forest structure and function*

330 Both aridity and stand age influenced forest properties associated with resistance to
331 hurricanes. Species diversity increased with stand age but decreased with SPEI_{min} ,

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

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

349 We also observed an interaction between stand age and aridity for WD, SLA, and Ψ_{TLP} .
350 Trees with a conservative growing strategy dominate young forest stands in arid areas while wet
351 environments typically show the opposite pattern (Lohbeck *et al.* 2013; Poorter *et al.* 2019, 2021).
352 The interaction effects between aridity and forest age were not present for Ψ_{P50} . There are two
353 possible explanations for this trend. First, in Caribbean arid regions precipitation is fairly low (<
354 1500 mm yr⁻¹) when compared to other tropical forests (Schwartz *et al.* 2020), limiting the
355 presence of drought-sensitive species regardless of forest age (Vargas G. *et al.* 2021, 2022).
356 Second, drought-resistant xylem usually has denser wood via increased vessel density and
357 thickened pit membranes (Isasa *et al.* 2023).

358

359 *Hurricane impacts across environmental gradients*

360 The hurricane caused a 25% increase in forest mortality rates, a 21% decrease in canopy
361 cover, and a 45% decrease in canopy height across Puerto Rico (Fig. 2). While the changes in
362 canopy height and cover were equal among the dominant forest types, increases in mortality
363 rates were not (Fig. 2). Together with previous remote sensing work (Feng *et al.* 2020; Hall *et al.*
364 2020), these patterns suggest that hurricane impacts are milder in the dry forests. However,
365 vegetation indices from 30-m satellite imagery do not show the nuances driving the observed
366 impacts of hurricanes Irma and Maria. While mortality ($\Delta MR_{\text{dead/alive}}$) increased with canopy-cover
367 loss, it was only indirectly related to changes in canopy height (Fig. S5), at least until 2021. Likely
368 because most stem snapping does not cause tree death (Taylor *et al.* 2023). These results
369 highlight the importance of ground validation with extensive plot data such as the FIA database
370 (Hoque *et al.* 2017), which addresses the sampling coverage limitations of long-term field
371 observations (Hall *et al.* 2020).

372

373 *Direct and indirect drivers of hurricane forest damage*

374 The univariate models allowed us to directly link remote sensing metrics of hurricane
375 impacts with ground-level observations of forest structure and function (Table 2). Forest stands
376 with greater species diversity and community-level variation in WD lost less canopy cover during
377 the storms. Although in some cases more diverse forests can experience greater impacts (Tanner
378 & Bellingham 2006), in Puerto Rico low diversity forests tend to be dominated by non-native tree
379 species more susceptible to hurricane disturbances (*e.g.*, *Spathodea campanulata*) (Helmer *et al.*
380 2018). Functional strategies were particularly important in determining canopy height reductions.
381 Stands dominated by fast-growing, drought-vulnerable tree species (high SLA, low WD, low
382 $|\Psi_{\text{TLP}}|$, and low $|\Psi_{\text{P50}}|$) showed greater reductions in canopy height. This pattern links remote
383 sensing observations with classic work on species-specific hurricane responses (Zimmerman *et*
384 *al.* 1994). Additionally, it suggests there might be a tradeoff between fast-growing, hydraulically
385 vulnerable strategies and resistance to wind disturbances.

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

396 From the final SEM model, it was evident that older forest stands that faced a
397 considerable reduction in canopy cover and were situated on flat terrain closer to the storms'
398 center, had a significantly higher $\Delta MR_{\text{dead/alive}}$ (Fig. 3). Such patterns point out three key factors
399 driving the impacts of hurricanes. First, exposure to hurricane winds plays an important role in
400 determining the damage during storms (McLaren *et al.* 2019; Feng *et al.* 2020; Zhang *et al.*
401 2022). This was evidenced by the higher increase in $MR_{\text{dead/alive}}$ in forests closer to the hurricane
402 track and in lowland flat areas compared with steep slopes, some of which may be more
403 protected from winds (McLaren *et al.* 2019; Zhang *et al.* 2022; Helmer *et al.* 2023). Second, older
404 forest stands showed greater increases in mortality. This result challenges Odum's views of
405 greater homeostasis with increases in the ecosystem age (Odum 1969). In Northeast Puerto
406 Rico, older forest stands might not or will never reach a stable state due to frequent disturbances
407 favoring plant communities with a mosaic of both early succession and late succession specialist
408 tree species (Uriarte *et al.* 2009). On the other hand, it might be possible that these patterns are
409 shaped by the widespread presence of non-native species that also tend to have lighter wood,
410 making them less resistant to hurricanes (Helmer *et al.* 2018, 2023). In contrast to results from
411 intensively studied, old forest sites, here younger forests (with widespread species introductions)
412 showed more homeostasis in that regional CWM traits changed little. Another example of young

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

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

433

434 *Conclusions*

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

440 necessarily imply increased resistance to hurricanes, which highlights important considerations
441 when linking ecosystem age with resistance to disturbances (Odum 1969; Uriarte *et al.* 2009; Lin
442 *et al.* 2020). In addition, we propose that the changing climate and projected increased aridity for
443 tropical regions (Seneviratne *et al.* 2021) may limit the increase of exploitative drought-sensitive
444 species that dominate recruitment after hurricanes in wet tropical forests (Smith-Martin *et al.*
445 2022; Umaña *et al.* 2023). Overall, we show that linking successional theory with plant functional
446 ecology is a promising avenue to identify nuances essential for predicting forests' responses to
447 increasingly stronger cyclonic storms.

448

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469

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657

658 **Tables and Figure legends**

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

Species Diversity				Canopy Height			
	B	CI	<i>p</i>		β	CI	<i>p</i>
Age	0.29	0.22 – 0.36	< 0.001	Age	1.45	0.92 – 1.97	< 0.001
SPEI _{min}	0.08	0.02 – 0.13	0.009	Aridity	-1.27	-2.14 – -0.40	0.004
R_m^2 / R_c^2	0.20 / 0.40			Age : Aridity	-0.91	-1.35 – -0.47	< 0.001
				R_m^2 / R_c^2	0.17 / 0.48		
Canopy Cover				Stem Density Index			
	B	CI	<i>p</i>		β	CI	<i>p</i>
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_m^2 / R_c^2	0.18 / 0.30		
R_m^2 / R_c^2	0.15 / 0.23						
WD (g cm⁻³)				SLA (m² kg⁻¹)			
	B	CI	<i>p</i>		β	CI	<i>p</i>
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 _{min}	-0.23	-0.50 – 0.05	0.106
R_m^2 / R_c^2	0.28 / 0.30			Age : Aridity	0.41	0.12 – 0.69	0.006
				R_m^2 / R_c^2	0.10 / 0.22		
Ψ_{TLF} (MPa)				Ψ_{P50} (MPa)*			
	B	CI	<i>p</i>		β	CI	<i>p</i>
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_m^2 / R_c^2	0.14 / 0.15		
R_m^2 / R_c^2	0.27 / 0.28						

669 *For $|\Psi_{\text{P50}}|$ we used the plots with a trait coverage of > 35% instead of weighing the analysis by the trait basal area
 670 coverage given the smaller sample size when compared to the other traits. This was done to avoid the presence of
 671 singularities when fitting the model.
 672

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

	$\Delta MR_{\text{dead/alive}}$				Δ Canopy Cover				Δ Canopy Height			
	β	R_m^2	R_c^2	p	β	R_m^2	R_c^2	p	β	R_m^2	R_c^2	p
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
$ \Psi_{\text{TLP}} $	0.0550	0.02	0.02	0.1369	0.0031	0.00	0.02	0.6118	0.5205	0.12	0.39	0.0006
$ \Psi_{\text{P50}} $	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- $ \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

680

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

693

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

698

699 **Fig. 3.** Structural equation model (SEM) to determine the direct and indirect effects mediating tree
700 mortality during Hurricanes Irma and Maria in Puerto Rico. Panel **a)** shows a diagram depicting
701 the causal pathways exploring the effects of climate, topography, and forest function in mediating
702 the impacts of Hurricane Maria measured as the changes (Δ) in mortality rates ($MR_{\text{dead/alive}}$),
703 LiDAR-derived canopy cover (CC), and LiDAR-derived canopy height (CH). Complete arrows and
704 line thickness represent moderate ($p < 0.05$) to strong ($p < 0.001$) evidence of an effect, while
705 dashed lines represent weak ($p > 0.05$) evidence of an effect but still accounted for in the model.
706 The R^2 in each node represents the conditional R^2 (R_c^2), which shows the variance explained by
707 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 ΔCC , ΔCH , and CH are in
712 Fig. S5.