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1 **Title: HURRICANES INCREASE TROPICAL FOREST VULNERABILITY TO**
2 **DROUGHT**

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41 **Summary**

- 42 • Rapid changes in climate and disturbance regimes, including droughts and hurricanes, are
43 likely to influence tropical forests, but our understanding of the compound effects of
44 disturbances on forest ecosystems is extremely limited. Filling this knowledge gap is
45 necessary to elucidate the future of these ecosystems under a changing climate.
- 46 • We examined the relationship between hurricane response (damage, mortality, and
47 resilience) and four hydraulic traits of 13 dominant woody species in a wet tropical forest
48 subject to periodic hurricanes.
- 49 • Species with high resistance to embolisms (low P_{50} values) and higher safety margins
50 ($SM_{P_{50}}$) were more resistant to immediate hurricane mortality and breakage, whereas
51 species with higher hurricane resilience (rapid post-hurricane growth) had high
52 capacitance and P_{50} values and low $SM_{P_{50}}$. During 26-years of post-hurricane recovery,
53 we found a decrease in community weighted mean values for traits associated with
54 greater drought resistance (leaf turgor loss point, P_{50} , $SM_{P_{50}}$) and an increase in
55 capacitance, which has been linked with lower drought resistance.
- 56 • Hurricane damage favors slow-growing, drought-tolerant species while post-hurricane
57 high resource conditions favor acquisitive, fast-growing but drought-vulnerable species,
58 increasing forest productivity at the expense of drought tolerance and leading to higher
59 overall forest vulnerability to drought.

60

61 **Keywords:** coastal tropical forests; cyclonic storm; Hurricane Hugo; forest succession; P₅₀
62 xylem optical vulnerability curves; plant–climate interactions; plant hydraulics; tropical trees and
63 palms
64
65

66 INTRODUCTION

67 Rapid changes in climate and disturbance regimes are likely to influence tropical forests
68 (Bonan, 2008; Chazdon, 2008; McDowell, N. G. *et al.*, 2020). Most models predict stronger
69 droughts across large areas in the tropics, including the Amazon (Joetzjer *et al.*, 2013), Central
70 America, and the Caribbean (Neelin *et al.*, 2006; Herrera & Ault, 2017). Increases in tree
71 mortality and growth declines have been associated with severe drought across several tropical
72 forests (Chazdon *et al.*, 2005; Uriarte, *et al.*, 2016a; Leitold *et al.*, 2018; Powers *et al.*, 2020).
73 Given that these ecosystems account for the majority of terrestrial aboveground biomass (Pan *et*
74 *al.*, 2011), declines in productivity coupled with high tree mortality could lead to large carbon
75 losses to the atmosphere, turning tropical forests from a carbon sink to a source, and creating a
76 positive feedback to climate warming (Gatti *et al.*, 2014; Brienen *et al.*, 2015; Hubau *et al.*,
77 2020). Beyond its effects on precipitation, climate change is also altering the frequency and/or
78 intensity of disturbances, including fires, cyclonic storms, insect outbreaks, and floods (Dale *et*
79 *al.*, 2001; Seidl *et al.*, 2017; DOE, 2018; Brando *et al.*, 2019; Knutson *et al.*, 2019).
80 Understanding the compound effects of droughts and more severe natural disturbance on
81 tropical forests is necessary to elucidate the future of these ecosystems under a changing
82 climate.

83 Cyclonic storms (known as hurricanes in the Atlantic and typhoons or cyclones
84 elsewhere) represent the dominant natural disturbance in many coastal tropical and sub-tropical
85 forests in the Atlantic coastal regions of Central and South America, through the Caribbean, Gulf
86 Coast region, the Indian subcontinent, Southeast Asia, Indo-Malaysia, and northern Australia
87 (Boose *et al.*, 1994; Everham & Brokaw, 1996; Lugo, 2008; Ibanez *et al.*, 2019). Since these
88 storms derive their energy from ocean heat and sea surface temperatures have increased in the
89 North Atlantic during the past decades, maximum wind speeds and rainfall rates are expected to
90 rise and storms to intensify more rapidly (Webster, 2005; Knutson *et al.*, 2010; Balaguru *et al.*,
91 2018). The expected shifts in the frequency and intensity of tropical storms, and their potential
92 interaction with other climate change stressors such as severe droughts, have profound
93 implications for the long-term resilience of tropical forests in these regions. Yet our
94 understanding of the compound effects of severe droughts and hurricanes on forests is extremely
95 limited (Beard *et al.*, 2005).

96 Forests undergoing post-hurricane disturbance may be particularly vulnerable to climate
97 stress from drought. Hurricanes cause widespread crown damage and mortality, opening up the
98 canopy and leading to rapid post-successional dynamics and community re-organization
99 (Vandermeer, 2000; Lugo, 2008; Tanner *et al.*, 2014; Imbert, 2018; Uriarte *et al.*, 2019). Canopy
100 damage results in elevated light and temperature in the understory (Comita *et al.*, 2009; Vargas
101 *et al.*, 2009), intensifying drought impacts. The high resource conditions that typically follow
102 hurricane disturbance result in large increases in seedling establishment and tree growth,
103 particularly for light-demanding species (Guzman-Grajales & Walker, 1991; Burslem *et al.*,
104 2000; Uriarte *et al.*, 2004; Uriarte *et al.*, 2005; Comita *et al.*, 2009). As a result, recovering
105 forests contain a greater proportion of pioneer and fast-growing tree species, whose
106 physiological characteristics may make them more vulnerable to drought (Bazzaz & Pickett,
107 1980; Phillips *et al.*, 2010; Lohbeck *et al.*, 2013; Greenwood *et al.*, 2017). Competition for
108 water, which may intensify under drought, is particularly high in regrowing forests as a result of
109 fast growth rates of understory vegetation, high stem densities, and dominance of water-
110 demanding species (Uriarte *et al.*, 2016b). Despite these potential vulnerabilities, research on the
111 factors that determine how drought may influence post-hurricane ecosystem recovery is lacking
112 (Anderson-Teixeira *et al.*, 2013; Uriarte *et al.*, 2016; Bretfeld *et al.*, 2018; McDowell, N. G. *et*
113 *al.*, 2020).

114 The fate of tropical forests exposed to severe droughts and hurricanes depends on
115 variation in species' responses to these events. Evidence suggests that forests subject to periodic
116 hurricane disturbance may have a greater proportion of species with traits (*e.g.*, shorter height,
117 high resistance to damage) that have been selected to withstand these repetitive large-scale
118 disturbances (Boose *et al.*, 2004; Griffith *et al.*, 2008; Ibanez *et al.*, 2019). Nevertheless, tree
119 species differ in their susceptibility to disturbance by a wind of a given intensity and the nature
120 of the damage they sustain (*i.e.*, resistance), as well in their recovery from wind disturbance, at
121 both the individual plant level through repair of damage, and at the population level through
122 reproduction, seedling establishment and growth response to enhanced light availability (*i.e.*,
123 resilience) (Boucher *et al.*, 1994; Canham *et al.*, 2010; Uriarte *et al.*, 2009; Walker, 1991;
124 Zimmerman *et al.*, 1994, Uriarte *et al.* 2019). Variability among species in their ability to resist
125 wind damage may not always align with life history classifications based on light-use strategies
126 (Zimmerman *et al.*, 1994; Lugo & Scatena, 1996; Uriarte *et al.*, 2004; Uriarte *et al.*, 2012;

127 Uriarte *et al.*, 2019). Although species with denser wood (Uriarte *et al.*, 2019) and deeper root
128 systems (Gresham *et al.*, 1991) generally suffer less damage and mortality, there are many
129 exceptions to these patterns (Uriarte *et al.*, 2019). Dense wood has also been associated with
130 greater drought tolerance (Powers *et al.*, 2020; Liang *et al.*, 2021), suggesting that resistance to
131 hurricanes and drought tolerance may be aligned across species. However, the fast-growing
132 light-demanding, hurricane resilient species are expected to possess a set of traits that make them
133 more vulnerable to drought. Species with strategies associated with greater resource
134 acquisitiveness that dominate post-disturbance recovery tend to have traits associated with
135 drought avoidance (high capacitance) and higher growth rates, whereas conservative species
136 favor greater drought tolerance (*i.e.*, low leaf turgor loss point, high resistance to xylem
137 embolisms, and larger safety margins) at the expense of lower growth (Oliveira *et al.*, 2021).
138 Forests recovering from hurricanes are expected to favor resource acquisitive species over
139 conservative ones due to high light conditions in the understory (Carreño-Rocabado *et al.*, 2012;
140 Subedi *et al.*, 2019), potentially leading to an increase in the overall level of forest susceptibility
141 to drought. Yet species-level responses to drought, and how they align with their responses to
142 disturbances are extremely variable and poorly understood (Umaña & Arellano, 2021).

143 Here we examine the relationship between drought avoidance and tolerance with
144 hurricane resistance (resistant to immediate hurricane mortality and stem break) and resilience
145 (rapid post-hurricane growth) for 12 common and broadly distributed tree species and one
146 dominant palm species in a forest in El Yunque National Forest in northeastern Puerto Rico. The
147 forest is subject to repeated hurricane disturbance with a return interval of approximately 50
148 years for severe storms (category 3-4 in the Saffir-Simpson scale) (Boose *et al.* 2004). After 57
149 years without a major storm, two severe storms, Hurricane Hugo in 1989 and Georges in 1998
150 struck the forest. We ask the following questions and test associated hypotheses:

151 Q1. Do resistance to hurricane damage (hurricane-induced mortality and stem damage)
152 and drought tolerance (embolism resistance and vulnerability to hydraulic failure) constitute
153 independent axis of plant function? We expect species that are more resistant to immediate
154 hurricane damage to also be more resistant to embolism and hydraulic failure.

155 Q2. Do resilience to hurricane damage (high post-hurricane growth) and drought
156 avoidance (high capacitance) constitute independent axes of plant function? We expect species

157 that are more resilient to hurricanes and grow more rapidly during post-hurricane recovery to
158 also be more vulnerable to embolisms and hydraulic failure and possess higher capacitance.

159 Q3. How does forest level vulnerability to drought change over 26 years of post-
160 hurricane recovery? We hypothesize that: 1) High light conditions in post-hurricane recovery
161 will favor acquisitive fast-growing, drought-avoiding species (high capacitance), with leaves that
162 wilt under lower drought stress (high turgor loss point— Ψ_{tlp}), are more vulnerable to embolisms,
163 and hydraulic failure, thus increasing forest productivity at the expense of drought tolerance. We
164 hypothesize that this change will lead to greater forest vulnerability to drought as the forest
165 recovers from disturbance.

166

167 **MATERIALS AND METHODS**

168 **Study site and species data**

169 This study was conducted at the Luquillo Experimental Forest (LEF) in northeastern Puerto
170 Rico. The LEF is an evergreen forest classified as subtropical wet forest in the Holdridge life
171 zone system (Ewel & Whitmore, 1973) with a mean annual temperature of 25.2°C and mean
172 annual rainfall is 3,500 mm. Soils are from volcanic origin and are classified as Oxisols and
173 Ultisols (Soil Survey Staff 1995). Although land use was extensive when the US Forest Service
174 acquired the land in 1932, the majority of the forest is considered old-growth, particularly at
175 elevations >350 m. These forests have a well-documented history of hurricane damage, with a
176 return interval of approximately 50 years for severe storms (category 3-4 in the Saffir-Simpson
177 scale) (Boose et al., 2004), although hurricane activity exhibits oscillations linked to Atlantic
178 Multidecadal Variability (Goldenberg et al., 2001). Early in the last century, in 1928 and 1932,
179 major hurricanes struck the LEF. After 57 years without a major storm, two severe storms, Hugo
180 in 1989, a category 3 storm with winds up to 166 km hr⁻¹ and Georges in 1998, also a category 3
181 storm with winds up to 144 km hr⁻¹, struck the forest. The compound effects of these two storms
182 led to rapid, post-hurricane dynamics (Uriarte *et al.*, 2005; Uriarte *et al.*, 2009; Zimmerman *et*
183 *al.*, 2010; Hogan *et al.*, 2016; Heartsill Scalley, 2017). Average canopy height is 30 m but
184 hurricane damage can lead to canopy height losses ranging between 5 and 10 m (Brokaw &
185 Gear, 1991; Leitold et al., 2021).

186 For our study, we selected 12 tree species and one palm species that encompass many of
187 the dominant species at this site (Table 1; Thompson *et al.*, 2002). Demographic and immediate

188 hurricane damage data was collected in the Luquillo Forest Dynamics Plot (LFDP; 18°20' N,
189 65°49'N; Thompson *et al.*, 2002). The LFDP is a 16-ha forest plot located near El Verde Field
190 Station in the LEF with an elevation range from 333 – 423 m. The plot was established in 1989
191 and censused at approximately 5-year intervals starting in 1990 through 2016 using standard
192 protocols (Condit, 1998). Briefly, all stems with diameter at breast height (DBH) of ≥ 1 cm are
193 mapped, measured, and identified to species. In each census, new stems are added, stems are re-
194 measured and their status (alive/dead) is updated. Prior to 1934 parts of the lower elevation forest
195 of the LDFP (<350m) were subjected to light logging and agriculture, but the forest structure and
196 canopy cover had recovered by the time H. Hugo made landfall (Thompson *et al.*, 2002).

197 The first LFDP census in 1990 included an initial survey of all stems ≥ 10 cm DBH to
198 prevent loss of data due to decomposition of trees killed or damaged by Hurricane Hugo
199 (Zimmerman *et al.*, 1994; Thompson *et al.*, 2002). During this census, immediate hurricane
200 mortality and damage (stem break) were also recorded (Zimmerman *et al.*, 1994; Thompson *et*
201 *al.*, 2002; Canham *et al.*, 2010). Surveys of all stems ≥ 1 and ≤ 10 cm in DBH in the first census
202 were conducted from 1990–1993, and capture post-successional recruitment. For this reason, we
203 only use stems ≥ 10 cm DBH to calculate comparable basal area across all censuses (Q3).
204 However, we use all stems ≥ 1 cm DBH to calculate growth rates (Q2). As the forest was
205 recovering from Hurricane Hugo, Hurricane Georges struck Puerto Rico in September 1998 with
206 winds up to 144 km hr⁻¹ (category 3; Miner Solá, 2000) but it was estimated to be a category 2
207 storm by the time it reached the forest. The effects of this second hurricane on the LFDP forest
208 area were less acute than those of Hugo (Uriarte *et al.*, 2019) and it had a limited effect on forest
209 structure and composition (Uriarte *et al.*, 2009; Uriarte *et al.*, 2019). Basal area was estimated to
210 average 36.7 m² ha⁻¹ at the time of Hurricane Hugo, 30.85 m² ha⁻¹ at the time Georges struck,
211 and 38.37 m² ha⁻¹ in 2016. Density of stems ≥ 10 cm DBH has remained stable ca. 1,000 stems
212 ha⁻¹ while density of small stems (1-10 cm DBH) ranged between 6,841 in 1993 to 2,444 stems
213 ha⁻¹ in 2016, reflecting continuous stem thinning through post-hurricane succession (Fig. S1).
214 The forest has not been censused since the passage of Hurricane Maria in 2017 so we use census
215 data collected through 2016. Altogether, our 13 target species represent ~50 – 60 % of the basal
216 area of the LFDP depending on the census (Table 1). For each of the 13 species, we calculated
217 two metrics of growth for the first five years after the hurricane: annual absolute growth
218 quantified as the increments in tree DBH between the initial and the first post-hurricane census

219 divided by census interval and relative growth, calculated as absolute growth divided by the
220 initial tree DBH. We also calculated relative growth in the same way using basal area instead of
221 DBH.

222

223 **Hydraulic traits**

224 For each species, we measured hydraulic traits on 5 to 13 mature canopy trees (Table S1) for a
225 total of 123 trees measured. We collected canopy branches that were >1.5 m long with a pole
226 pruner, immediately sealed branches in large plastic bags with wet paper towels, placed the
227 branches in large black plastic garbage cans filled with water as soon as possible, recut the
228 branches under water, and covered them with black plastic bags to minimize transpiration until
229 further processing. At the end of each collecting trip, we immediately took samples to the
230 laboratory where we conducted the hydraulic measurements. All hydraulic measurements were
231 conducted between July 2019 and August 2020.

232

233 *Leaf turgor loss point and leaf capacitance*

234 We characterized leaf turgor loss point and leaf water storage capacity using pressure-
235 volume curves. To do so, we used the bench dry method as described by Tyree and Hammel
236 (1972) and the protocol developed by Sack and Pasquet-Kok (2011). We let the branch rehydrate
237 overnight, excised a mature fully expanded healthy leaf from the branch with a sharp razor blade,
238 and immediately sealed it in a Whirl-Pak bag. As leaves dehydrated, we periodically measured
239 water potential (Ψ) with a Pressure Chamber Instrument (PMS Instrument Company, Albany,
240 OR, USA) and leaf weight. We continued to measure the leaves until $1/\Psi$ and water loss became
241 linear. Finally, we scanned the leaves, then oven-dried them at 65°C for at least 72 h and
242 weighed them to obtain leaf dry mass. We calculated leaf area with ImageJ software (National
243 Institute of Health, New York, NY, USA) and used the Sack and Pasquet-Kok (2011)
244 spreadsheet tool to construct pressure-volume curves from which we extracted leaf turgor loss
245 point (Ψ_{tlp}) and leaf capacitance at full turgor (C_{ft}).

246

247 *Leaf optical vulnerability curves*

248 We used the optical vulnerability technique to estimate xylem embolism accumulation in
249 leaves (Brodribb *et al.*, 2016). Briefly, for each branch immediately after it was brought back

250 from the field, we secured a leaf inside a custom-built three-dimensional printed clamp
251 (OpenSourceOV—OSOV) fitted with a small 8-megapixel Raspberry Pi camera and light-
252 emitting diodes operated by a Raspberry Pi microcomputer. Once the leaf was secured in the
253 clamps, we took a picture every two minutes of a 4 cm² leaf area until no embolism events were
254 recorded for at least 12 h (~72–96 h depending on the species). As the branch dehydrated, we
255 used a stem psychrometer (ICT International, Armidale, Australia) to record water potential
256 every 10 min. To attach the stem psychrometer, we removed a small section of bark from the
257 branch and clamped the psychrometer to the exposed xylem and created an air-tight seal with
258 Parafilm sealing film.

259 We used ImageJ to analyze the pictures of leaf embolisms following Brodribb *et al.*
260 (2016). We stacked all the images and converted them to 8-bit grayscale with pixel values
261 ranging from black (0) to white (255). Each image was subtracted from the next image in the
262 sequence to reveal embolisms that appear as changes in light intensity. Embolism accumulation
263 in each leaf was quantified as a cumulative total of embolized pixels in each image divided by
264 the total number of embolized pixels in the fully dried sample. To determine the water potential
265 (Ψ_x) at the time of image capture, we fitted a linear regression to the Ψ_x over time and extracted
266 the values at which 50% of the cumulative embolisms had occurred (P_{50} ; Fig. S2-S4). We also
267 measured xylem vulnerability in stems on the same branches at the same time as we measured
268 the leaves (Fig. S2-S4), however, we only use vulnerability curves from leaves because we
269 were unable, due to their stem anatomy, to measure stem xylem vulnerability for *Cecropia*
270 *schreberiana*, which has thick hollow stems and the palm, *Prestoea acuminata* var. *montana*. For
271 the 11 species for which we were able to measure P_{50} in both leaves and stems, there was no
272 significant difference between the two (Fig. S2-S4). Full details of the procedure, including an
273 overview of the technique, image processing, as well as ImageJ scripts, are available at
274 <http://www.opensourceov.org>.

275 We calculated safety margins (SM_{P50}) as the difference between leaf turgor loss point
276 (Ψ_{tlp}), which is a common proxy for stomatal closure (Brodribb *et al.*, 2003; Rodriguez-
277 Dominguez *et al.*, 2016; Martin-StPaul *et al.*, 2017; Ziegler *et al.*, 2019), and the water potential
278 at which 50% of total embolisms had occurred as defined by Martin-St Paul et al. 2017:

$$SM_{P50} = \Psi_{tlp} - P_{50}$$

280

281 **Data analysis**

282

283 We used linear regressions to evaluate if there were associations between species P_{50} and HSM
284 and the metrics of hurricane response: hurricane damage (mortality and broken stems) and post-
285 hurricane absolute and relative growth. To evaluate if there was a tradeoff between storage of
286 water in the tissue and embolism resistant and vulnerability to hydraulic failure, we fitted linear
287 regressions of species leaf capacitance (C_{ft}) vs. P_{50} and SM_{P50} .

288 To assess changes in forest level drought responses during post-hurricane recovery, we
289 calculated community-weighted mean (CWM) trait values for all of the species with measured
290 hydraulic traits for each census under the assumption that these traits are static through time. We
291 calculated CWM values for each trait t and each census c as: $CWM_{tc} = \sum_{i=1}^S a_{ic} \times t_i$, where
292 a_{ic} is the relative basal area of each species i for census c based on the total basal area of the
293 focal species. To evaluate how the individual CWM traits changed among censuses, we
294 calculated the percent of relative change between each census c as:

$$295 \quad [(CWM_c - CWM_{c-1}) \div CWM_{c-1}] \times 100.$$

296 We performed all analyses using R statistical software (Version 4.0.2; R Core Team, 2020).

297

298 **RESULTS**

299 Overall, our study species exhibited substantial variation in hydraulic traits. Turgor loss point
300 (Ψ_{tlp}), a proxy for leaf wilting point and stomatal closure, had significant variation across species
301 (Fig. **1a**; Table S2,S3). *Cecropia schreberiana* had the highest Ψ_{tlp} values, meaning that this
302 species wilts at a higher water potential while *Casearia arborea* wilted at the lowest water
303 potential. Species also exhibited large variation in water storage capacity in leaves (Fig. **1b**;
304 Table S2,S3), *C. schreberiana* and *Cordia borinquensis* had the highest capacitance followed by
305 the palm, *Prestoea acuminata* var. *montana*. *C. arborea*, *Dacryodes excelsa*, *Drypetes glauca*,
306 and *Micropholis guyanensis* had some of the lowest water storage capacitance. Resistance to
307 embolism formation (P_{50}) was also highly variable across species, with *C. schreberiana*, *D.*
308 *excelsa*, and *Alchornea latifolia* at the lowest range and *C. arborea* and *M. guyanensis* at the
309 highest end overall (Fig. **1c**; Table S2,S3). Species safety margins (SM_{P50}) also exhibited a broad
310 range of variation, with significant differences among species (Fig. **1d**; Table S2,S3). *C.*
311 *schreberiana* was the only species that exhibited a slightly negative SM_{P50} , suggesting that it is

312 particularly vulnerable to severe drought. Several other species also had very low SM_{P50} ,
313 indicating that they operate at thresholds that are very close to hydraulic failure, making them
314 highly susceptible to droughts. Specifically, *A. latifolia*, *Cyrilla racemiflora*, *D. excelsa*, *Inga*
315 *laurina*, *Ocotea leucoxylon*, *P. acuminata* var. *montana*, and *Sloanea berteriana* all had $SM_{P50} <$
316 1 MPa while *C. arborea*, *C. borinquensis*, *D. glauca*, and *Tabebuia heterophylla* had $SM_{P50} >$ 1
317 MPa, and *M. guyanensis* had the highest SM_{P50} of 2.6 MPa (Fig. 1d).

318 Across species, there was a trade-off between capacitance and P_{50} (Fig S5a; Table S4)
319 and SM_{P50} (Fig. S5b; Table S4). Drought-avoiding species (*i.e.*, higher capacitance) were also
320 more vulnerable to embolisms (*i.e.*, higher P_{50}) and hydraulic failure (*i.e.*, lower SM_{P50}) and thus,
321 less drought-tolerance, while the more embolism and drought-tolerance species had lower
322 capacitance. There was an association between vulnerability to hurricane damage and resistance
323 to embolisms and hydraulic failure. Species that had more negative P_{50} values also experienced a
324 lower percentage of immediate mortality (Fig. 2a) and stem breaks (Fig. 2b) during Hurricane
325 Hugo. Paralleling patterns observed for P_{50} , again species that had higher SM_{P50} also had lower
326 percentage of hurricane-induced immediate mortality (Fig. 2c) and stem break (Fig. 2d). In the
327 case of hurricane resilience, we found the opposite trend. There was a trade-off between
328 hurricane resilience and resistance to embolisms and hydraulic failure. The species that had less
329 negative P_{50} values also had the highest absolute and relative growth (Fig. 3a,b; Fig. S6a) during
330 the first five years after Hurricane Hugo and these hurricane resilient species also had low SM_{P50}
331 (Fig. 3c,d; Fig. S6b). However, we did not find this association between growth and capacitance
332 ($R^2 = 0.01$, $p = 0.806$). For example, *C. schreberiana* became more dominant during post-
333 hurricane recovery had the highest P_{50} narrowest SM_{P50} , and *Prestoea acuminata* var. *montana*
334 which had the highest hurricane resilience and eventually became the most dominant species
335 during post-hurricane recovery also had high P_{50} and low SM_{P50} (Fig. 4; Table S5). We also
336 found an association between percentage of hurricane-induced immediate mortality and absolute
337 (Fig. S7a) and relative growth (Fig. S7b).

338 In the first five years following Hurricane Hugo, basal area of stems ≥ 10 cm DBH of
339 most of the target species decreased or stayed the same (Fig. 4; Table S5). However, after 10 to
340 15 years of post-hurricane recovery there was an increase in the basal area of many species.
341 Three species in particular had very high hurricane resilience, *C. schreberiana*, *D. excelsa*, and
342 *P. acuminata* var. *montana*, with dramatic increases in basal area that exceeded pre-hurricane

343 levels 15 to 20 years after the hurricane. After 26 years of post-hurricane recovery, the basal area
344 of two of these species *C. schreberiana* and *P. acuminata* var. *montana* declined while *D.*
345 *excelsa* continued to increase (Fig. 4; Table S6).

346 Hurricane disturbance increased forest susceptibility to drought. Over the 26 years of
347 post-hurricane recovery, CWM trait values associated with drought avoidance (capacitance)
348 increased whereas CWM trait values associated with drought tolerance (P_{50} and $SM_{P_{50}}$) declined.
349 CWM for leaf turgor loss point (Ψ_{tlp}) decreased by $\sim 2.5\%$ during the first 10 years post-
350 disturbance, then leveled off, and started to increase during the last census interval (2011-2016;
351 Fig. 5a; Table S6). CWM capacitance (C_f) increased until it reached a peak in 2005, with a total
352 increase of $\sim 12.5\%$ over the 15-year period, and then started to decrease during the last census
353 (Fig. 5b; Table S6). CWM P_{50} decreased by $\sim 11\%$ during the 26-years of post-hurricane
354 recovery, although it leveled off and even started to increase by 2016 (Fig. 5c; Table S6). The
355 most pronounced post-hurricane change in our analyses was CWM hydraulic safety margins
356 ($SM_{P_{50}}$), with a 45% total decrease over the first 20 years post-hurricane, although it had leveled
357 off between the last two censuses (Fig. 5d; Table S6).

358

359 **DISCUSSION**

360 We examined the relationship between hurricane resistance and resilience and hydraulic traits of
361 13 dominant woody species in a wet tropical forest subject to periodic hurricane disturbance. We
362 found a large range in variation in hydraulic traits within the community and a trade-off between
363 capacitance and two metrics of drought tolerance, P_{50} and $SM_{P_{50}}$. Species that were more
364 resistant to embolisms (P_{50}) and hydraulic failure ($SM_{P_{50}}$) were also less vulnerable to immediate
365 hurricane damage (mortality and stem break), whereas species that had higher hurricane
366 resilience and regenerated rapidly after the hurricane had hydraulic traits that made them more
367 vulnerable to drought (high P_{50} values and low $SM_{P_{50}}$). Over the first five years of post-hurricane
368 recovery, we found a trade-off between growth and hydraulic safety, confirming a recently
369 proposed trade-off between growth and $SM_{P_{50}}$ that had not been tested in other forests outside
370 the Brazilian Amazon (Oliveira *et al.*, 2021). In particular, three species (*C. schreberiana*, *D.*
371 *excelsa*, and *P. acuminata* var. *montana*) with hydraulic traits linked to greater vulnerability to
372 drought also exhibited high hurricane resilience, with dramatic increases in basal area that
373 exceeded pre-hurricane levels. During 26-years of post-hurricane recovery, there was a decrease

374 in community weighted mean trait values associated with greater drought tolerance (Ψ_{t1p} , P_{50} ,
375 SM_{P50}) and an increase in capacitance, a trait that has been linked with lower drought tolerance
376 (Christoffersen *et al.*, 2016; Pivovarovoff *et al.*, 2018; Santiago *et al.*, 2018; Oliveira *et al.*, 2021).
377 Immediate hurricane damage in this forest favors slow-growing, drought-tolerant species.
378 However, the high resource conditions in the wake of a hurricane favors acquisitive, fast-
379 growing, drought-avoiding species that are more vulnerable to drought and hydraulic failure,
380 increasing forest productivity at the expense of potential higher forest vulnerability to drought.

381

382 *Species exhibited large variation in hydraulic traits and a trade-off between drought avoidance*
383 *and tolerance*

384 Species within our community exhibited a large range of variation in embolism resistance
385 and hydraulic safety. We found over a five-fold difference in P_{50} values across species and SM_{P50}
386 ranged from close to zero to around 2.5 MPa. Consistent with our findings, several studies have
387 observed a wide range in P_{50} values within tropical forest communities elsewhere (Santiago *et*
388 *al.*, 2018; Barros *et al.*, 2019; Oliveira *et al.*, 2019; Ziegler *et al.*, 2019; Fontes *et al.*, 2020;
389 Powers *et al.*, 2020). The wide range in SM_{P50} indicates that not all the species within our
390 community function at the edge of their hydraulic capacity, a fact that does not support the
391 expectation that species should operate with narrow SM_{P50} to sustain CO_2 assimilation for as
392 long as possible before closing their stomata as water becomes more limited (Tyree & Sperry,
393 1988; Choat *et al.*, 2012; Barros *et al.*, 2019; Fontes *et al.*, 2020). Although a growing number of
394 studies have found that wide SM_{P50} (1-5 MPa) are common within and across tropical forest
395 communities (Martin-StPaul *et al.*, 2017; Benito Garzón *et al.*, 2018; Barros *et al.*, 2019; Ziegler
396 *et al.*, 2019; Powers *et al.*, 2020; Smith-Martin *et al.*, 2020), eight of the 13 species we studied
397 had $SM_{P50} < -1$ MPa, indicating that the majority of species were operating close to their
398 maximum hydraulic capacity. *C. schreberiana* had slightly negative SM_{P50} , which should be
399 further investigated by direct measurements of stomatal conductance in response to drought as
400 the expectation is that no embolism occurs before full stomatal closure has occurred (Creek *et*
401 *al.*, 2020). Community-wide variation in turgor loss point was not as marked as for P_{50} . There
402 was only around a 1.5-fold difference in Ψ_{t1p} across species with 11 of our 13 species having Ψ_{t1p}
403 between -1.5 and -2 MPa suggesting greater convergence in this trait than embolism resistance
404 (over a five-fold difference in P_{50}). Our findings support the idea that the range in Ψ_{t1p} values is

405 lower than in P_{50} and $SM_{P_{50}}$. Ziegler *et al.* (2019) also found a range in $\Psi_{\text{tip}} \sim -1.5 - -2.0$ MPa
406 further supporting that this trait is less variable at least in wetter forests.

407 Our findings imply a trade-off between drought avoidance (high capacitance) and
408 drought tolerance (high embolism resistance and large $SM_{P_{50}}$). Among the species we studied,
409 there was over a three-fold difference in leaf capacitance, and some of the species with the
410 greatest water storage in their leaves also had the least negative P_{50} values and the lowest $SM_{P_{50}}$.
411 This pattern was particularly marked in *C. schreberiana*, *D. excelsa* and *P. acuminata* var.
412 *montana*. Our results coincide with previous findings of a synthesis of data from multiple sites
413 which found a trade-off between capacitance and P_{50} for tropical species (Christoffersen *et al.*,
414 2016); here we show this pattern operates at the community level. Environmental conditions
415 after a hurricane favor fast-growing species that take advantage of the increase in light
416 availability (Guzman-Grajales & Walker, 1991; Burslem *et al.*, 2000; Uriarte *et al.*, 2004; Uriarte
417 *et al.*, 2005; Comita *et al.*, 2009). Fast-growing species also tend to have higher hydraulic
418 conductance (Markesteijn *et al.*, 2011; McCulloh *et al.*, 2012), which has been shown to be
419 correlated with capacitance (Santiago *et al.*, 2018), potentially explaining the trade-off between
420 drought avoidance and drought tolerance in our forest.

421

422 *Coordination between drought tolerance and hurricane resistance*

423 We found that many of the species that suffered less immediate hurricane damage and
424 mortality were more drought tolerant. Wood density may be one of the species traits behind this
425 association. Species resistance to hurricanes depends in part on the strength of the wood and
426 previous studies have found that hurricane-induced mortality and stem break are lower for
427 species with denser wood (Zimmerman *et al.*, 1994; Uriarte *et al.*, 2019). Previous research at
428 our study site found that Hurricane Hugo broke, uprooted, and killed fewer individuals of species
429 with dense wood, which could explain the association we found between drought and hurricane
430 resistance as densely wooded species have been shown to be more drought-tolerant (Powers *et al.*
431 *et al.*, 2020; Liang *et al.*, 2021). Overall, this would mean that the direct effects of hurricanes and
432 drought favor the same group of old-growth, dense-wood, and drought-tolerant species.

433

434 *Trade-off between drought tolerance and hurricane resilience*

435 There was also a trade-off between post-hurricane growth and drought tolerance.
436 Specifically, we found a trade-off between stem diameter growth and the two metrics of drought
437 tolerance (P_{50} and SM_{P50}) during the first five years after the hurricane. Even if immediate
438 hurricane damage favors more drought-tolerant species, rapid forest reorganization and high
439 post-hurricane growth benefit species that favor productivity over hydraulic safety. Oliveira *et al.*
440 (2021) argue that the fast-slow economic spectrum also applies to SM_{P50} , reasoning that species
441 with high SM_{P50} are not operating at maximum growth capacity to achieve higher safety, and
442 thus, have a lower return on their carbon investment making them slower growing and better
443 suited for low resource environments. In contrast, species with low SM_{P50} that operate at
444 maximum capacity have a high return on their carbon investment, leading to fast growth and a
445 competitive advantage in high resource environment. Our findings support the trade-off between
446 SM_{P50} and growth proposed by Oliveira *et al.* (2021), showing that this pattern applies to another
447 forest aside from the Brazilian Amazon where this idea was originally tested and also applies to
448 the trade-off between P_{50} and growth. The degree to which this trade-off occurs in other tropical
449 forest ecosystems remains an open question.

450

451 *Post-hurricane successional forests are more vulnerable to drought*

452 Post-hurricane successional forests had high capacitance and low resistance to embolisms
453 and hydraulic failure. Assuming that traits remained stable over the 26-year period, we found a
454 decrease in community weighted mean trait values associated with drought tolerance (*i.e.*, Ψ_{tlp} ,
455 P_{50} , and SM_{P50}) and an increase in capacitance. These shifts in forest level traits were most
456 pronounced during the first 15 years post-disturbance, and in general, leveled off or started to
457 revert 26-years after the hurricane. This increase in drought vulnerability was largely driven by
458 increases in three of the species with the most drought-vulnerable hydraulic traits, *C.*
459 *schreberiana*, *D. excelsa*, and *P. acuminata* var. *montana*, which dominate post-disturbance
460 communities (Uriarte *et al.*, 2009; Uriarte *et al.*, 2019). Umaña and Arellano (2021) et al. studied
461 six tree species at the same location in Puerto Rico and found that *C. schreberiana* was the
462 species that had the highest growth reduction during drought consistent with our findings. In
463 their study, *D. excelsa* was not affected by severe drought and responded favorably to moderate
464 droughts (Umaña & Arellano, 2021). *D. excelsa* is known to have extensive root grafting (Basnet
465 *et al.*, 1993) that could allow trees to redistribute water and make them less susceptible to

466 drought. Our findings could have consequences for forest post-disturbance dynamics since
467 forests in Puerto Rico and the Caribbean are subject to periodic hurricanes and our study site was
468 recently hit by another category 4 hurricane in 2017, H. María (Uriarte *et al.*, 2019). A warming
469 climate is expected to lead to more intense hurricanes (Knutson *et al.*, 2010; Balaguru *et al.*,
470 2018), which coupled with expected increases in extreme drought events (Khalyani *et al.*, 2015;
471 Ramseyer *et al.*, 2019) could drastically change dynamics and species composition of Caribbean
472 forests.

473 Compound disturbances can interact in ways that cannot be predicted by the study of a
474 single disturbance (Paine *et al.*, 1998; Seidl *et al.*, 2017), potentially altering forest species
475 composition and successional pathways (Wu & Loucks, 1995; McDowell, Nate G. *et al.*, 2020).
476 Our results demonstrate that the temporal pattern of disturbance can play a key role in
477 determining forest vulnerability to drought. Hurricane disturbance favors species on the fast end
478 of the plant economic spectrum (Reich, 2014). Hurricane Hugo struck our study site in 1989
479 causing significant forest damage and favoring fast-growing but drought vulnerable pioneer
480 species. If this forest were to suffer a severe drought in the first few years after a recent
481 hurricane, this could result in rapid drought-induced mortality of hydraulically vulnerable species
482 and alter post-disturbance ecosystem successional trajectories (Beard *et al.*, 2005). A previous
483 study at the site found a decline in tree growth during a 2015 drought, (Feng *et al.*, 2018;
484 Schwartz *et al.* 2020), an effect that could potentially be exacerbated if the forest were in early
485 stages of recovery from severe hurricane damage. A substantial amount of research in temperate
486 forests has examined compound impacts of climate change stressors on ecosystems (Seidl *et al.*,
487 2017; Gaiser *et al.*, 2020). Disturbance can enhance resilience or increase vulnerability to other
488 global change factors (Turner, 2010). For example, drought exacerbates forest vulnerability to
489 bark beetle attacks (Negrón *et al.*, 2009; Netherer *et al.*, 2019) while insect damage can favor
490 species better adapted to warmer climates, reducing ecosystem vulnerability to subsequent
491 disturbances (Temperli *et al.*, 2013). However much less is known about the effect of compound
492 disturbances on tropical forests, especially about the interaction between wind disturbance and
493 drought. Since climate change has multiple and varied effects on ecosystems, anticipating
494 whether a disturbance will change vulnerability to other environmental stressors is an issue
495 ecologists must address if they are going to forecast the future of the biosphere (Gaiser *et al.*,
496 2020).

497

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508 A.-K., S.D., S.L.F., M.S.-S., J.T., J.K.Z. and M.U collected the data. C.M.S.-M. and M.U.
509 analyzed the data. C.M.S.-M. and M.U. wrote the manuscript and R.M., R. A.-K., S.D., S.L.F.,
510 M.S.-S., J.T. and J.K.Z. contributed to the final draft.

511

512 **Data availability statement:** All data that is not included in the main text and in the Supporting
513 Information can be found here: <https://luquillo.lter.network/data-catalog/>
514 Luquillo Forest Dynamics Plot (LFDP) census data here:

515 <https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.119.1545979>

516 Tree damage by Hurricane Hugo in the LFDP here:

517 <https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.57.583050>

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519 **REFERENCES**

520 **Anderson-Teixeira KJ, Miller AD, Mohan JE, Hudiburg TW, Duval BD, DeLucia EH.**

521 **2013.** Altered dynamics of forest recovery under a changing climate. *Global Change*
522 *Biology* **19**(7): 2001-2021.

523 **Balaguru K, Foltz GR, Leung LR. 2018.** Increasing magnitude of hurricane rapid
524 intensification in the Central and Eastern Tropical Atlantic. *Geophysical Research Letters*
525 **45**(9): 4238-4247.

526 **Barros FdV, Bittencourt PRL, Brum M, Restrepo-Coupe N, Pereira L, Teodoro GS,**
527 **Saleska SR, Borma LS, Christoffersen BO, Penha D, et al. 2019.** Hydraulic traits

528 explain differential responses of Amazonian forests to the 2015 El Niño-induced drought.
529 *New Phytologist* **223**(3): 1253-1266.

530 **Basnet K, Scatena FN, Likens GE, Lugo AE. 1993.** Ecological Consequences of Root Grafting
531 in Tabonuco (*Dacryodes excelsa*) Trees in the Luquillo Experimental Forest, Puerto
532 Rico. *Biotropica* **25**(1): 28.

533 **Bazzaz FA, Pickett STA. 1980.** Physiological Ecology of Tropical Succession: A Comparative
534 Review. *Annual Review of Ecology and Systematics* **11**: 287-310.

535 **Beard KH, Vogt KA, Vogt DJ, Scatena FN, Covich AP, Sigurdardottir R, Siccama TG,
536 Crowl TA. 2005.** Structural and functional responses of a subtropical forest to 10 years
537 of hurricanes and droughts. *Ecological Monographs* **75**(3): 345-361.

538 **Benito Garzón M, González Muñoz N, Wigneron J-P, Moisy C, Fernández-Manjarrés J,
539 Delzon S. 2018.** The legacy of water deficit on populations having experienced negative
540 hydraulic safety margin. *Global Ecology and Biogeography* **27**(3): 346-356.

541 **Bonan GB. 2008.** Forests and climate change: Forcings, feedbacks, and the climate benefits of
542 forests. *Science* **320**(5882): 1444-1449.

543 **Boose ER, Foster DR, Fluet M. 1994.** Hurricane Impacts to Tropical and Temperate Forest
544 Landscapes. *Ecological Monographs* **64**(4): 369-400.

545 **Boose ER, Serrano MI, Foster DR. 2004.** Landscape and regional impacts of hurricanes in
546 Puerto Rico. *Ecological Monographs* **74**(2): 335-352.

547 **Brando PM, Paolucci L, Ummenhofer CC, Ordway EM, Hartmann H, Cattau ME, Rattis
548 L, Medjibe V, Coe MT, Balch J 2019.** Droughts, Wildfires, and Forest Carbon Cycling:
549 A Pantropical Synthesis. In: Jeanloz R, Freeman KH eds. *Annual Review of Earth and
550 Planetary Sciences, Vol 47*, 555-581.

551 **Bretfeld M, Ewers BE, Hall JS. 2018.** Plant water use responses along secondary forest
552 succession during the 2015-2016 El Nino drought in Panama. *New Phytol* **219**(3): 885-
553 899.

554 **Brienen RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, Lloyd J, Lopez-Gonzalez
555 G, Monteagudo-Mendoza A, Malhi Y, Lewis SL, et al. 2015.** Long-term decline of the
556 Amazon carbon sink. *Nature* **519**(7543): 344-348.

- 557 **Brodribb TJ, Holbrook NM, Edwards EJ, Gutiérrez MV. 2003.** Relations between stomatal
558 closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell*
559 *& Environment* **26**(3): 443-450.
- 560 **Brodribb TJ, Skelton RP, McAdam SAM, Bienaimé D, Lucani CJ, Marmottant P. 2016.**
561 Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *New*
562 *Phytologist* **209**(4): 1403-1409.
- 563 **Burslem DFRP, Whitmore TC, Brown GC. 2000.** Short-term effects of cyclone impact and
564 long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of*
565 *Ecology* **88**(6): 1063-1078.
- 566 **Canham CD, Thompson J, Zimmerman JK, Uriarte M. 2010.** Variation in Susceptibility to
567 Hurricane Damage as a Function of Storm Intensity in Puerto Rican Tree Species.
568 *Biotropica* **42**(1): 87-94.
- 569 **Carreño-Rocabado G, Peña-Claros M, Bongers F, Alarcón A, Licona J-C, Poorter L. 2012.**
570 Effects of disturbance intensity on species and functional diversity in a tropical forest.
571 *Journal of Ecology* **100**(6): 1453-1463.
- 572 **Chazdon RL. 2008.** Beyond deforestation: Restoring forests and ecosystem services on
573 degraded lands. *Science* **320**(5882): 1458-1460.
- 574 **Chazdon RL, Brenes AR, Alvarado BV. 2005.** Effects of Climate and Stand Age on Annual
575 Tree Dynamics in Tropical Second-Growth Rain Forests. *Ecology* **86**(7): 1808-1815.
- 576 **Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS,**
577 **Gleason SM, Hacke UG, et al. 2012.** Global convergence in the vulnerability of forests
578 to drought. *Nature* **491**(7426): 752-755.
- 579 **Christoffersen BO, Gloor M, Fauset S, Fyllas NM, Galbraith DR, Baker TR, Kruijt B,**
580 **Rowland L, Fisher RA, Binks OJ, et al. 2016.** Linking hydraulic traits to tropical forest
581 function in a size-structured and trait-driven model (TFS v.1-Hydro). *Geoscientific Model*
582 *Development* **9**(11): 4227-4255.
- 583 **Comita LS, Uriarte M, Thompson J, Jonckheere I, Canham CD, Zimmerman JK. 2009.**
584 Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest.
585 *Journal of Ecology* **97**(6): 1346-1359.
- 586 **Condit R. 1998.** *Tropical Forest Census Plots*. Berlin, Heidelberg: Springer Berlin Heidelberg.

587 **Creek D, Lamarque LJ, Torres-Ruiz JM, Parise C, Burlett R, Tissue DT, Delzon S. 2020.**
588 Xylem embolism in leaves does not occur with open stomata: evidence from direct
589 observations using the optical visualization technique. *Journal of Experimental Botany*
590 71(3): 1151-1159.

591 **Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland**
592 **LC, Lugo AE, Peterson CJ, et al. 2001.** Climate Change and Forest Disturbances:
593 Climate change can affect forests by altering the frequency, intensity, duration, and
594 timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes,
595 windstorms, ice storms, or landslides. *Bioscience* 51(9): 723-734.

596 **DOE US. 2018.** Disturbance and Vegetation Dynamics in Earth System Models; Workshop
597 Report SC-0196: Office of Biological and Environmental Research, U.S. Department of
598 Energy Office of Science. [WWW document] URL
599 <https://ess.science.energy.gov/disturbance-workshop/> [accessed 24 July 2021]

600 **Everham EM, Brokaw NVL. 1996.** Forest damage and recovery from catastrophic wind. *The*
601 *Botanical Review* 62(2): 113-185.

602 **Ewel JJ, Whitmore JL. 1973.** *The ecological life zones of Puerto Rico and the U.S. Virgin*
603 *Islands*. Rio Piedras, P.R.: Institute of Tropical Forestry.

604 **Feng X, Uriarte M, González G, Reed S, Thompson J, Zimmerman JK, Murphy L. 2018.**
605 Improving predictions of tropical forest response to climate change through integration of
606 field studies and ecosystem modeling. *Global Change Biology* 24(1): e213-e232.

607 **Fontes CG, Fine PVA, Wittmann F, Bittencourt PRL, Piedade MTF, Higuchi N, Chambers**
608 **JQ, Dawson TE. 2020.** Convergent evolution of tree hydraulic traits in Amazonian
609 habitats: implications for community assemblage and vulnerability to drought. *New*
610 *Phytologist* 228(1): 106-120.

611 **Gaiser EE, Bell DM, Castorani MCN, Childers DL, Groffman PM, Jackson CR,**
612 **Kominoski JS, Peters DPC, Pickett STA, Ripplinger J, et al. 2020.** Long-Term
613 Ecological Research and Evolving Frameworks of Disturbance Ecology. *BioScience*
614 70(2): 141-156.

615 **Gatti LV, Gloor M, Miller JB, Doughty CE, Malhi Y, Domingues LG, Basso LS,**
616 **Martinewski A, Correia CSC, Borges VF, et al. 2014.** Drought sensitivity of

617 Amazonian carbon balance revealed by atmospheric measurements. *Nature; London*
618 **506(7486): 76-80.**

619 **Greenwood S, Ruiz-Benito P, Martínez-Vilalta J, Lloret F, Kitzberger T, Allen CD,**
620 **Fensham R, Laughlin DC, Kattge J, Bönisch G, et al. 2017.** Tree mortality across
621 biomes is promoted by drought intensity, lower wood density and higher specific leaf
622 area. *Ecology Letters* **20(4): 539-553.**

623 **Gresham CA, Williams TM, Lipscomb DJ. 1991.** Hurricane Hugo Wind Damage to
624 Southeastern U.S. Coastal Forest Tree Species. *Biotropica* **23(4): 420.**

625 **Griffith MP, Noblick LR, Dowe JL, Husby CE, Calonje MA. 2008.** Cyclone Tolerance in
626 New World Arecaceae: Biogeographic Variation and Abiotic Natural Selection. *Ann Bot*
627 **102(4): 591-598.**

628 **Guzman-Grajales SM, Walker LR. 1991.** Differential Seedling Responses to Litter After
629 Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23(4): 407-**
630 **413.**

631 **Heartsill Scalley T. 2017.** Insights on Forest Structure and Composition from Long-Term
632 Research in the Luquillo Mountains. *Forests* **8(6): 204.**

633 **Herrera D, Ault T. 2017.** Insights from a New High-Resolution Drought Atlas for the
634 Caribbean Spanning 1950-2016. *Journal of Climate* **30(19): 7801-7825.**

635 **Hogan JA, Zimmerman JK, Thompson J, Nytech CJ, Uriarte M. 2016.** The interaction of
636 land-use legacies and hurricane disturbance in subtropical wet forest: twenty-one years of
637 change. *Ecosphere* **7(8): e01405.**

638 **Hubau W, Lewis SL, Phillips OL, Affum-Baffoe K, Beeckman H, Cuni-Sanchez A, Daniels**
639 **AK, Ewango CEN, Fauset S, Mukinzi JM, et al. 2020.** Asynchronous carbon sink
640 saturation in African and Amazonian tropical forests. *Nature* **579(7797): 80-87.**

641 **Ibanez T, Keppel G, Menkes C, Gillespie TW, Lengaigne M, Mangeas M, Rivas-Torres G,**
642 **Birnbaum P. 2019.** Globally consistent impact of tropical cyclones on the structure of
643 tropical and subtropical forests. *Journal of Ecology* **107(1): 279-292.**

644 **Imbert D. 2018.** Hurricane disturbance and forest dynamics in east Caribbean mangroves.
645 *Ecosphere* **9(7): e02231.**

- 646 **Joetzjer E, Douville H, Delire C, Ciais P. 2013.** Present-day and future Amazonian
647 precipitation in global climate models: CMIP5 versus CMIP3. *Climate Dynamics* **41**(11-
648 12): 2921-2936.
- 649 **Khalyani AH, Gould WA, Harmsen E, Terando A, Quinones M, Collazo JA. 2015.** Climate
650 Change Implications for Tropical Islands: Interpolating and Interpreting Statistically
651 Downscaled GCM Projections for Management and Planning. *Journal of Applied*
652 *Meteorology and Climatology* **55**(2): 265-282.
- 653 **Knutson T, Camargo SJ, Chan JCL, Emanuel K, Ho C-H, Kossin J, Mohapatra M, Satoh**
654 **M, Sugi M, Walsh K, et al. 2019.** Tropical Cyclones and Climate Change Assessment:
655 Part I: Detection and Attribution. *Bulletin of the American Meteorological Society*
656 **100**(10): 1987-2007.
- 657 **Knutson TR, McBride JL, Chan J, Emanuel K, Holland G, Landsea C, Held I, Kossin JP,**
658 **Srivastava AK, Sugi M. 2010.** Tropical cyclones and climate change. *Nature*
659 *Geoscience* **3**(3): 157-163.
- 660 **Leitold V, Morton DC, Longo M, dos-Santos MN, Keller M, Scaranello M. 2018.** El Niño
661 drought increased canopy turnover in Amazon forests. *New Phytologist* **219**(3): 959-971.
- 662 **Liang X, Ye Q, Liu H, Brodribb TJ. 2021.** Wood density predicts mortality threshold for
663 diverse trees. *New Phytologist* **229**(6): 3053-3057.
- 664 **Lohbeck M, Poorter L, Lebrija-Trejos E, Martinez-Ramos M, Meave JA, Paz H, Perez-**
665 **Garcia EA, Romero-Perez IE, Tauro A, Bongers F. 2013.** Successional changes in
666 functional composition contrast for dry and wet tropical forest. *Ecology* **94**(6): 1211.
- 667 **Lugo AE. 2008.** Visible and invisible effects of hurricanes on forest ecosystems: an international
668 review. *Austral Ecology* **33**(4): 368-398.
- 669 **Lugo AE, Scatena FN. 1996.** Background and Catastrophic Tree Mortality in Tropical Moist,
670 Wet, and Rain Forests. *Biotropica* **28**(4): 585.
- 671 **Markestijn L, Poorte L, Paz H, Sack L, Bongers F. 2011.** Ecological differentiation in xylem
672 cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell &*
673 *Environment* **34**(1): 137-148.
- 674 **Martin-StPaul N, Delzon S, Cochard H. 2017.** Plant resistance to drought depends on timely
675 stomatal closure. *Ecology Letters* **20**(11): 1437-1447.

676 **McCulloh KA, Johnson DM, Meinzer FC, Voelker SL, Lachenbruch B, Domec Jc. 2012.**
677 Hydraulic architecture of two species differing in wood density: opposing strategies in
678 co-occurring tropical pioneer trees. *Plant, Cell & Environment* **35**(1): 116-125.

679 **McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L,**
680 **Clark JS, Dietze M, Grossiord C, Hanbury-Brown A, et al. 2020.** Pervasive shifts in
681 forest dynamics in a changing world. *Science* **368**(6494): eaaz9463.

682 **Miner Solá E. 2000.** *Historia de los huracanes en Puerto Rico*: E. Miner Solá, Puerto Rico.

683 **Neelin JD, Munnich M, Su H, Meyerson JE, Holloway CE. 2006.** Tropical drying trends in
684 global warming models and observations. *Proc Natl Acad Sci U S A* **103**(16): 6110-6115.

685 **Negrón JF, McMillin JD, Anhold JA, Coulson D. 2009.** Bark beetle-caused mortality in a
686 drought-affected ponderosa pine landscape in Arizona, USA. *Forest Ecology and*
687 *Management* **257**(4): 1353-1362.

688 **Netherer S, Panassiti B, Pennerstorfer J, Matthews B. 2019.** Acute Drought Is an Important
689 Driver of Bark Beetle Infestation in Austrian Norway Spruce Stands. *Frontiers in Forests*
690 *and Global Change* **2**(39): 1-21.

691 **Oliveira RS, Costa FRC, Baalen Ev, Jonge Ad, Bittencourt PR, Almanza Y, Barros FdV,**
692 **Cordoba EC, Fagundes MV, Garcia S, et al. 2019.** Embolism resistance drives the
693 distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New*
694 *Phytologist* **221**(3): 1457-1465.

695 **Oliveira RS, Eller CB, Barros FDV, Hirota M, Brum M, Bittencourt P. 2021.** Linking plant
696 hydraulics and the fast–slow continuum to understand resilience to drought in tropical
697 ecosystems. *New Phytologist* **230**(3): 904-923.

698 **Paine RT, Tegner MJ, Johnson EA. 1998.** Compounded Perturbations Yield Ecological
699 Surprises. *Ecosystems* **1**(6): 535-545.

700 **Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi P, Kurz W, Phillips O, Shvidenko A,**
701 **Lewis S, Canadell J, et al. 2011.** A large and persistent carbon sink in the Worlds
702 forests. *Science* **333**(6045).

703 **Phillips OL, van der Heijden G, Lewis SL, López-González G, Aragão LEOC, Lloyd J,**
704 **Malhi Y, Monteagudo A, Almeida S, Dávila EA, et al. 2010.** Drought-mortality
705 relationships for tropical forests. *The New Phytologist* **187**(3): 631-646.

706 **Pivovarov AL, Cook VMW, Santiago LS. 2018.** Stomatal behaviour and stem xylem traits are
707 coordinated for woody plant species under exceptional drought conditions. *Plant, Cell &*
708 *Environment* **41**(11): 2617-2626.

709 **Powers JS, G GV, Brodribb TJ, Schwartz NB, Pérez-Aviles D, Smith-Martin CM, Becknell**
710 **JM, Aureli F, Blanco R, Calderón-Morales E, et al. 2020.** A catastrophic tropical
711 drought kills hydraulically vulnerable tree species. *Global Change Biology* **26**(5): 3122-
712 3133.

713 **Ramseyer CA, Miller PW, Mote TL. 2019.** Future precipitation variability during the early
714 rainfall season in the El Yunque National Forest. *Science of The Total Environment* **661**:
715 326-336.

716 **Reich PB. 2014.** The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto.
717 *Journal of Ecology* **102**: 275–301.

718 **Rodriguez-Dominguez CM, Buckley TN, Egea G, Cires Ad, Hernandez-Santana V,**
719 **Martorell S, Diaz-Espejo A. 2016.** Most stomatal closure in woody species under
720 moderate drought can be explained by stomatal responses to leaf turgor. *Plant, Cell &*
721 *Environment* **39**(9): 2014-2026.

722 **Sack L, Pasquet-Kok J. 2011.** Leaf pressure–volume curve parameters. [WWW
723 document] URL [https://prometheusprotocols.net/function/water-relations/pressure-](https://prometheusprotocols.net/function/water-relations/pressure-volume-curves/leaf-pressure-volume-curve-parameters/)
724 [volume-curves/leaf-pressure-volume-curve-parameters/](https://prometheusprotocols.net/function/water-relations/pressure-volume-curves/leaf-pressure-volume-curve-parameters/) [accessed 16 July 2020] In
725 Prometheus.

726 **Santiago LS, De Guzman ME, Baraloto C, Vogenberg JE, Brodie M, Hérault B, Fortunel**
727 **C, Bonal D. 2018.** Coordination and trade-offs among hydraulic safety, efficiency and
728 drought avoidance traits in Amazonian rainforest canopy tree species. *New Phytologist*
729 **218**(3): 1015-1024.

730 **Scatena FN, Larsen MC. 1991.** Physical Aspects of Hurricane Hugo in Puerto Rico. *Biotropica*
731 **23**(4): 317.

732 **Schwartz NB, Feng X, Muscarella R, Swenson NG, Umaña MN, Zimmerman JK, Uriarte**
733 **M. 2020.** Topography and Traits Modulate Tree Performance and Drought Response in a
734 Tropical Forest. *Frontiers in Forests and Global Change* **3**(136): 1-14.

735 **Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli**
736 **D, Petr M, Honkaniemi J, et al. 2017.** Forest disturbances under climate change. *Nature*
737 *Climate Change* 7(6): 395-402.

738 **Smith-Martin CM, Skelton RP, Johnson KM, Lucani C, Brodribb TJ. 2020.** Lack of
739 vulnerability segmentation among woody species in a diverse dry sclerophyll woodland
740 community. *Functional Ecology* 34(4): 777-787.

741 **Subedi SC, Ross MS, Sah JP, Redwine J, Baraloto C. 2019.** Trait-based community assembly
742 pattern along a forest succession gradient in a seasonally dry tropical forest. *Ecosphere*
743 10(4): e02719.

744 **Tanner EVJ, Kapos V, Healey JR. 1991.** Hurricane Effects on Forest Ecosystems in the
745 Caribbean. *Biotropica* 23(4): 513.

746 **Tanner EVJ, Rodriguez-Sanchez F, Healey JR, Holdaway RJ, Bellingham PJ. 2014.** Long-
747 term hurricane damage effects on tropical forest tree growth and mortality. *Ecology*
748 95(10): 2974-2983.

749 **Temperli C, Bugmann H, Elkin C. 2013.** Cross-scale interactions among bark beetles, climate
750 change, and wind disturbances: a landscape modeling approach. *Ecological Monographs*
751 83(3): 383-402.

752 **Thompson J, Brokaw N, Zimmerman JK, Waide RB, Everham EM, Lodge DJ, Taylor CM,**
753 **García-Montiel D, Fluet M. 2002.** Land Use History, Environment, and Tree
754 Composition in a Tropical Forest. *Ecological Applications* 12(5): 1344-1363.

755 **Turner MG. 2010.** Disturbance and landscape dynamics in a changing world. *Ecology* 91(10):
756 2833-2849.

757 **Tyree MT, Hammel HT. 1972.** The Measurement of the Turgor Pressure and the Water
758 Relations of Plants by the Pressure-bomb Technique. *Journal of Experimental Botany*
759 23(1): 267-282.

760 **Tyree MT, Sperry JS. 1988.** Do Woody Plants Operate near the Point of Catastrophic Xylem
761 Dysfunction Caused by Dynamic Water Stress?: Answers from a Model. *Plant*
762 *Physiology* 88(3): 574-580.

763 **Umaña MN, Arellano G. 2021.** Legacy effects of drought on tree growth responses to
764 hurricanes. *Ecography* 44(11): 1686-1697.

765 **Uriarte M, Canham CD, Thompson J, Zimmerman JK. 2004.** Neighborhood analysis of tree
766 growth and survival in a hurricane-driven tropical forest. *Ecological Monographs* **74**(4):
767 591-614.

768 **Uriarte M, Canham CD, Thompson J, Zimmerman JK, Brokaw N. 2005.** Seedling
769 recruitment in a hurricane- driven tropical forest: light limitation, density- dependence
770 and the spatial distribution of parent trees. *Journal of Ecology*. **93**(2): 291-304.

771 **Uriarte M, Canham CD, Thompson J, Zimmerman JK, Murphy L, Sabat AM, Fetcher N,
772 Haines BL. 2009.** Natural disturbance and human land use as determinants of tropical
773 forest dynamics: results from a forest simulator. *Ecological Monographs* **79**(3): 423-443.

774 **Uriarte M, Clark JS, Zimmerman JK, Comita LS, Forero-Montaña J, Thompson J. 2012.**
775 Multidimensional trade-offs in species responses to disturbance: implications for
776 diversity in a subtropical forest. *Ecology* **93**(1): 191-205.

777 **Uriarte M, Lasky JR, Boukili VK, Chazdon RL. 2016a.** A trait-mediated, neighbourhood
778 approach to quantify climate impacts on successional dynamics of tropical rainforests.
779 *Functional Ecology* **30**(2): 157-167.

780 **Uriarte M, Schwartz N, Powers JS, Marín-Spiotta E, Liao W, Werden LK. 2016b.** Impacts
781 of climate variability on tree demography in second growth tropical forests: the
782 importance of regional context for predicting successional trajectories. *Biotropica* **48**(6):
783 780-797.

784 **Uriarte M, Schwartz N, Powers JS, Marin-Spiotta E, Liao WY, Werden LK. 2016.** Impacts
785 of climate variability on tree demography in second growth tropical forests: the
786 importance of regional context for predicting successional trajectories. *Biotropica* **48**(6):
787 780-797.

788 **Uriarte M, Thompson J, Zimmerman JK. 2019.** Hurricane María tripled stem breaks and
789 doubled tree mortality relative to other major storms. *Nature Communications* **10**(1):
790 1362.

791 **Vandermeer J. 2000.** Hurricane Disturbance and Tropical Tree Species Diversity. *Science*
792 **290**(5492): 788-791.

793 **Vargas R, Trumbore SE, Allen MF. 2009.** Evidence of old carbon used to grow new fine roots
794 in a tropical forest. *New Phytologist* **182**(3): 710-718.

795 **Webster PJ. 2005.** Changes in Tropical Cyclone Number, Duration, and Intensity in a Warming
796 Environment. *Science* **309**(5742): 1844-1846.

797 **Wu J, Loucks OL. 1995.** From Balance of Nature to Hierarchical Patch Dynamics: A Paradigm
798 Shift in Ecology. *The Quarterly Review of Biology* **70**(4): 439-466.

799 **Ziegler C, Coste S, Stahl C, Delzon S, Levionnois S, Cazal J, Cochard H, Esquivel-**
800 **Muelbert A, Goret J-Y, Heuret P, et al. 2019.** Large hydraulic safety margins protect
801 Neotropical canopy rainforest tree species against hydraulic failure during drought.
802 *Annals of Forest Science* **76**(4): 115.

803 **Zimmerman JK, Comita LS, Thompson J, Uriarte M, Brokaw N. 2010.** Patch dynamics and
804 community metastability of a subtropical forest: compound effects of natural disturbance
805 and human land use. *Landscape Ecology* **25**(7): 1099-1111.

806 **Zimmerman JK, Iii EME, Waide RB, Lodge DJ, Taylor CM, Brokaw NVL. 1994.**
807 Responses of Tree Species to Hurricane Winds in Subtropical Wet Forest in Puerto Rico:
808 Implications for Tropical Tree Life Histories. *The Journal of Ecology* **82**(4): 911.

809 **Zimmerman JK, Wood TE, González G, Ramirez A, Silver WL, Uriarte M, Willig MR,**
810 **Waide RB, Lugo AE. 2021.** Disturbance and resilience in the Luquillo Experimental
811 Forest. *Biological Conservation* **253**: 108891.

812

813 **Supporting Information single sentence legends**

814 **Fig. S1** Biomass and stem mortality from after Hurricane Hugo of the target species in the 16-ha
815 Luquillo Forest Dynamics Plot and over 26 years of post-hurricane succession.

816 **Fig. S2** Leaf and stem optical vulnerability curves.

817 **Fig. S3** Leaf and stem optical vulnerability curves.

818 **Fig. S4** Leaf and stem optical vulnerability curves.

819 **Fig. S5** Tradeoff between capacitance at full turgor and P_{50} and safety margins ($SM_{P_{50}}$) for all
820 measured individuals.

821 **Fig. S6** Associations between P_{50} and safety margins and relative basal area growth during the
822 first five years after Hurricane Hugo.

823 **Fig. S7** Associations between the proportion of stems with $DBH \geq 10\text{cm}$ for each of the 13 tree
824 species that were immediately killed by Hurricane Hugo and growth during the first five years
825 after H. Hugo.

826 **Table S1** Number of measured individuals per species for each of the hydraulic traits.

827 **Table S2** Mean and standard deviation of all the hydraulic traits and maximum tree height per
828 species.

829 **Table S3** F, p-values, and degrees of freedom from ANOVAs of hydraulic traits by species.

830 **Table S4** Results of linear regressions of capacitance at full turgor by P_{50} and safety margins.

831 **Table S5** Basal area of stems $\geq 10\text{ cm DBH}$ of the target species in the six censuses of the 16-ha
832 Luquillo Forest Dynamics Plot.

833 **Table S6** Percent of relative change of community-weighted mean trait values between each
834 census and the preceding one.

835

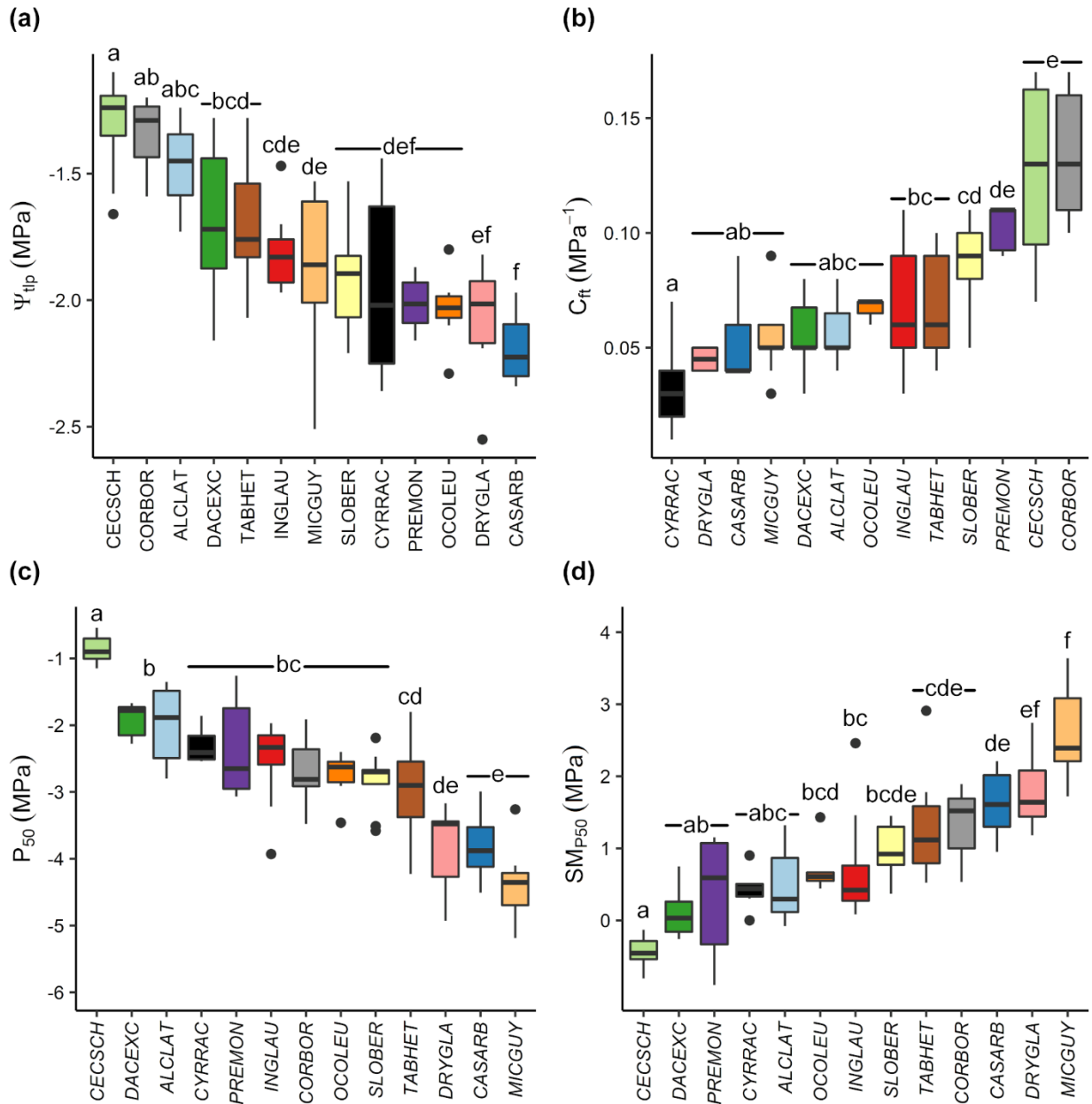
836 **Figures and Tables**

837 **Table 1** List of species used in this study, the code we used to represent them in some figures,
 838 their families, and the range of the percent of the total basal area of each species across six
 839 censuses of the 16-ha LFDP.

Species	Code	Family	Range of basal area (%)
<i>Alchornea latifolia</i>	ALCLAT	Euphorbiaceae	1.43–1.95
<i>Casearia arborea</i>	CASARB	Flacourtiaceae	2.99–4.94
<i>Cecropia schreberiana</i>	CECSCH	Moraceae	3.87–6.54
<i>Cordia borinquensis</i>	CORBOR	Boraginaceae	0.10–0.25
<i>Cyrilla racemiflora</i>	CYRRAC	Cyrillaceae	0.17–0.24
<i>Dacryodes excelsa</i>	DACEXC	Burseraceae	12.04–16.82
<i>Drypetes glauca</i>	DRYGLA	Euphorbiaceae	0.38–0.73
<i>Inga laurina</i>	INGLAU	Fabaceae	3.07–5.25
<i>Micropholis guyanensis</i>	MICGUY	Sapotaceae	0.01–0.02
<i>Ocotea leucoxydon</i>	OCOLEU	Lauraceae	0.60–0.94
<i>Prestoea acuminata</i> var. <i>montana</i>	PREMON	Arecaceae	13.44–24.44
<i>Sloanea berteriana</i>	SLOBER	Elaeocarpaceae	2.72–3.85
<i>Tabebuia heterophylla</i>	TABHET	Bignoniaceae	1.24–2.67
Total			50 – 60 %

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842

843 **Fig. 1** (a) Leaf turgor loss point (Ψ_{tip}), (b) leaf capacitance at full turgor (C_{ft}), (c) P_{50} , and (d)

844 safety margins (SM_{P50}) for all measured species. Letters indicate significant ($P < 0.05$)

845 differences among groups based on Tukey's HSD tests. Box plot midlines show medians, box

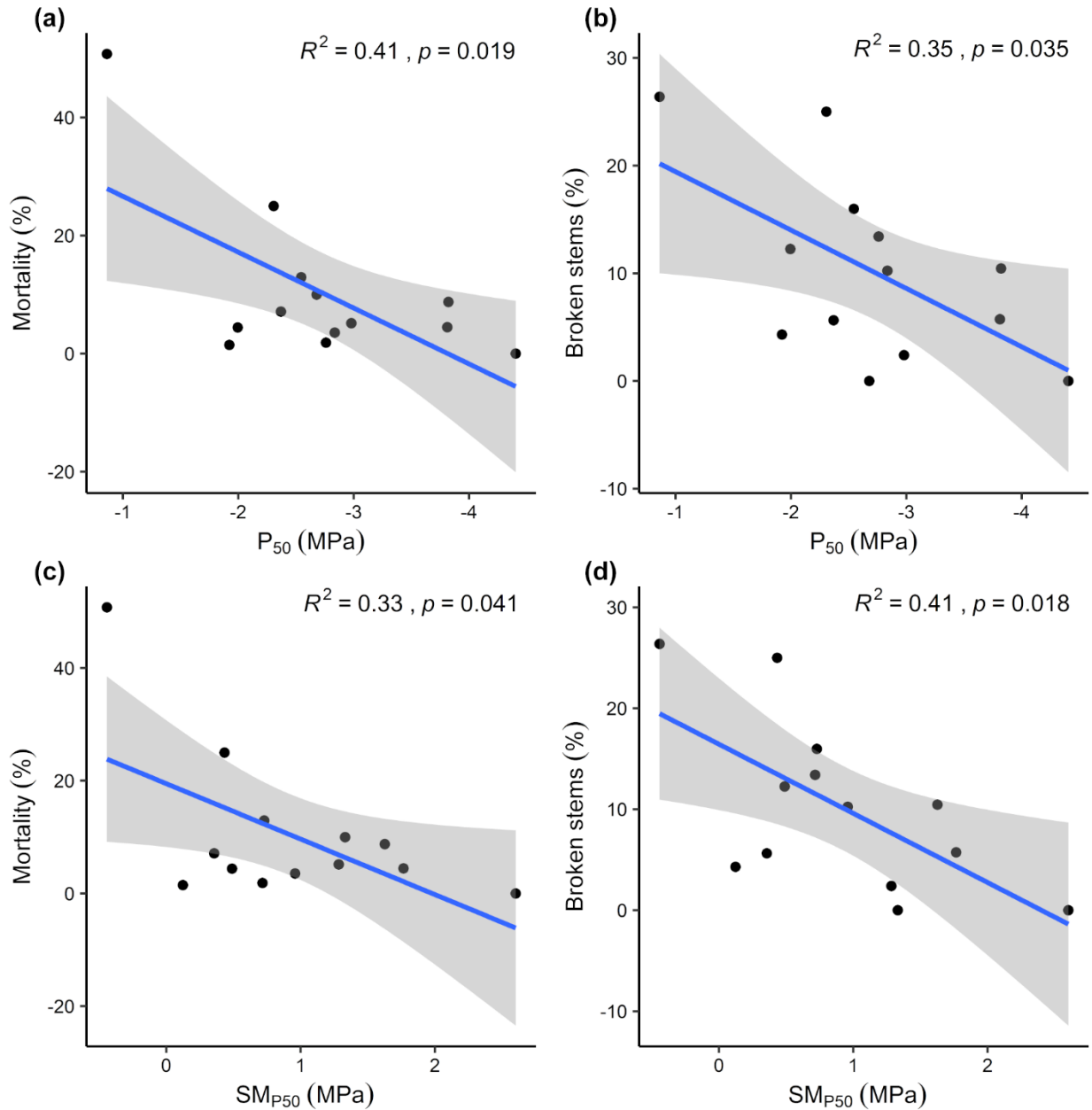
846 edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Each species

847 has a unique color to facilitate comparison across traits: *Alchornea latifolia* (ALCLAT),

848 *Casearia arborea* (CASARB), *Cecropia schreberiana* (CECSCH), *Cordia borinquensis*

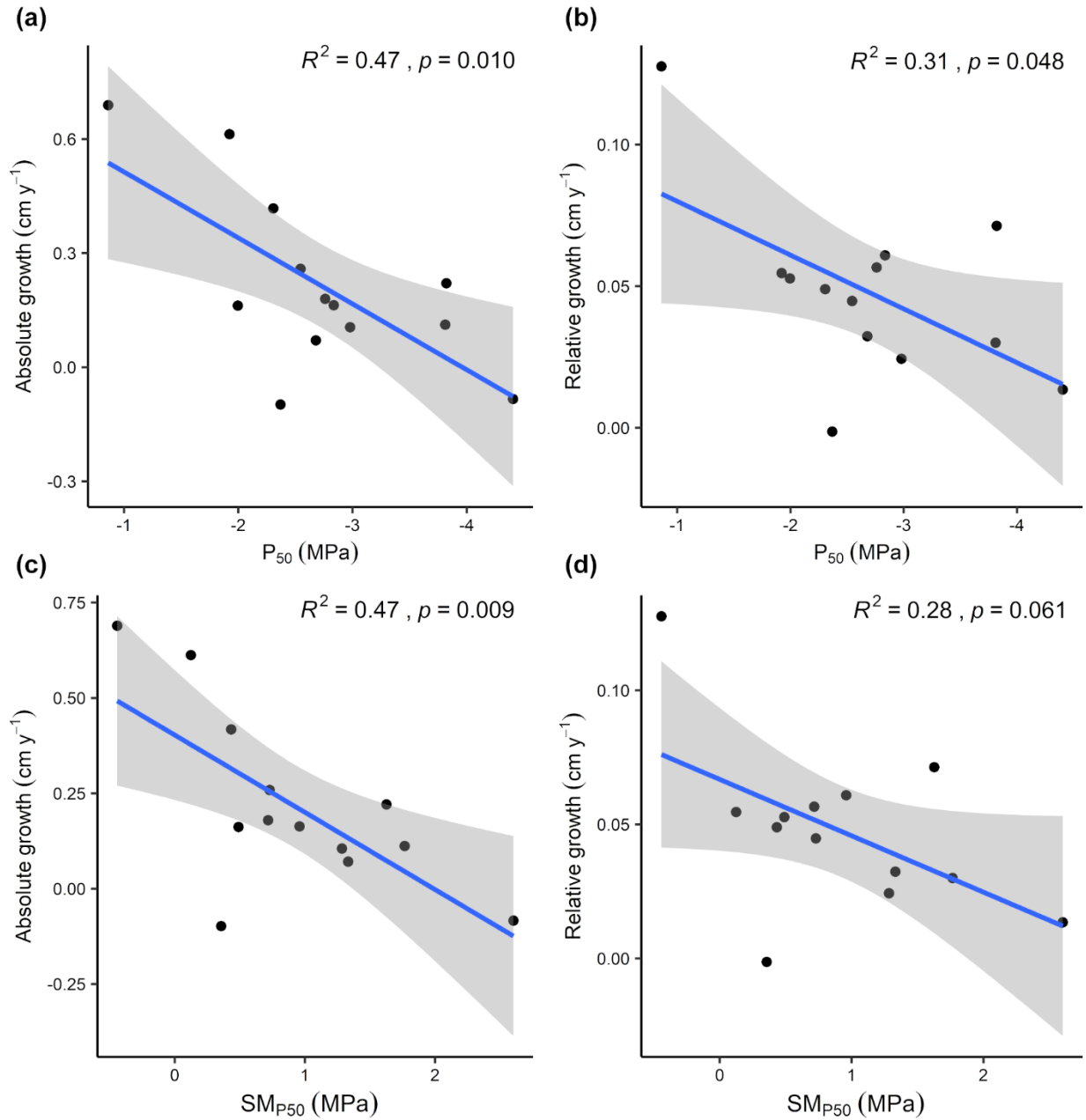
849 (*CYRRAC*), *Dacryodes excelsa* (DACEXC), *Drypetes glauca*

850 (DRYGLA), *Inga laurina* (INGLAU), *Micropholis guyanensis* (MICGUY), *Ocotea leucoxyton*
 851 (OCOLEU), *Prestoea acuminata* var. *montana* (PREMON), *Sloanea berteriana* (SLOBER),
 852 and *Tabebuia heterophylla* (TABHET).



853
 854 **Fig. 2** Associations between P_{50} and safety margins ($SM_{P_{50}}$) and proportion of stems with $DBH \geq$
 855 10cm for each of the 13 tree species that were immediately killed (a,c) or broken (b,d) by
 856 Hurricane Hugo. Blue lines depict linear regressions and shaded areas represent 95% confidence
 857 intervals.

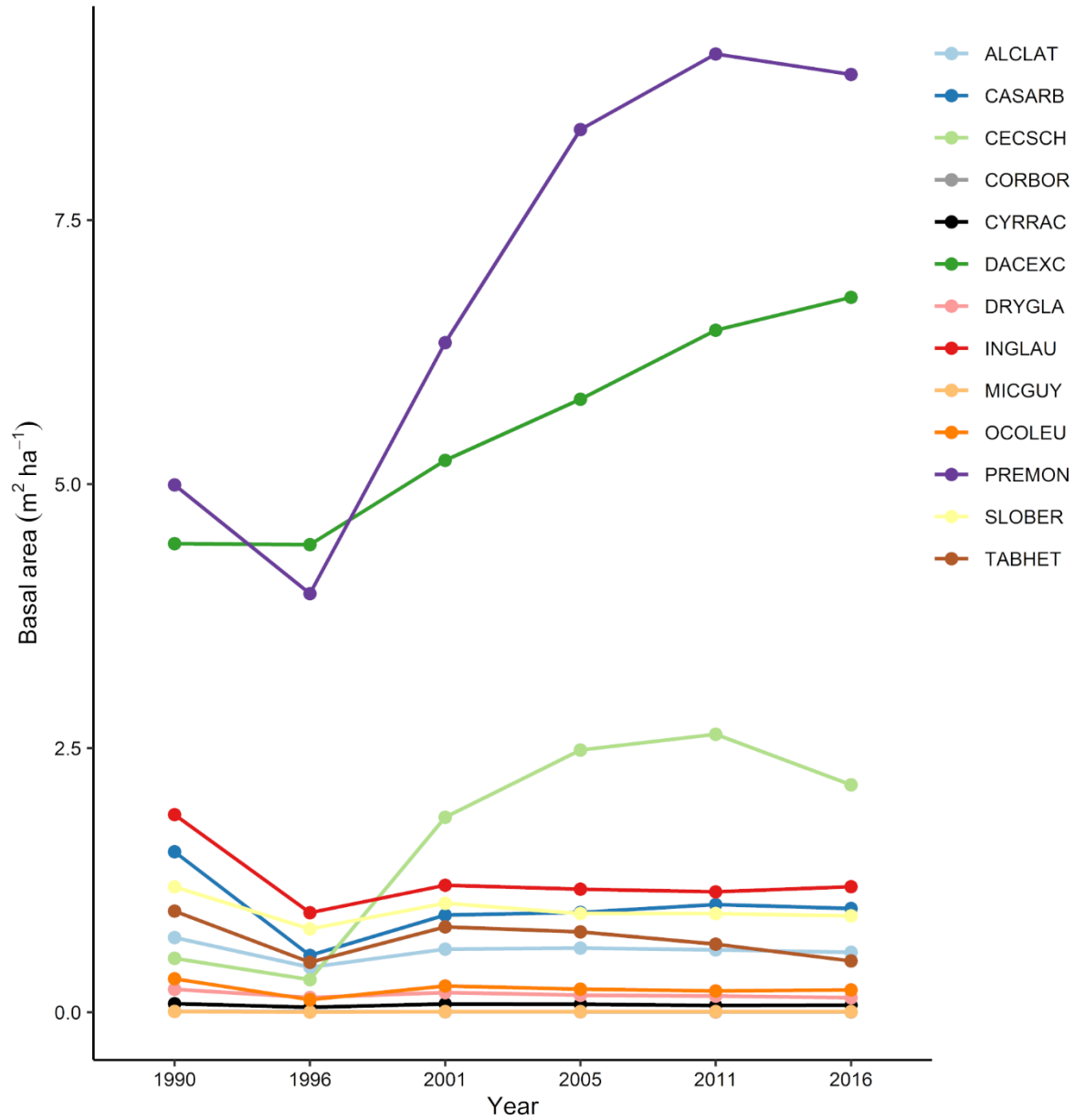
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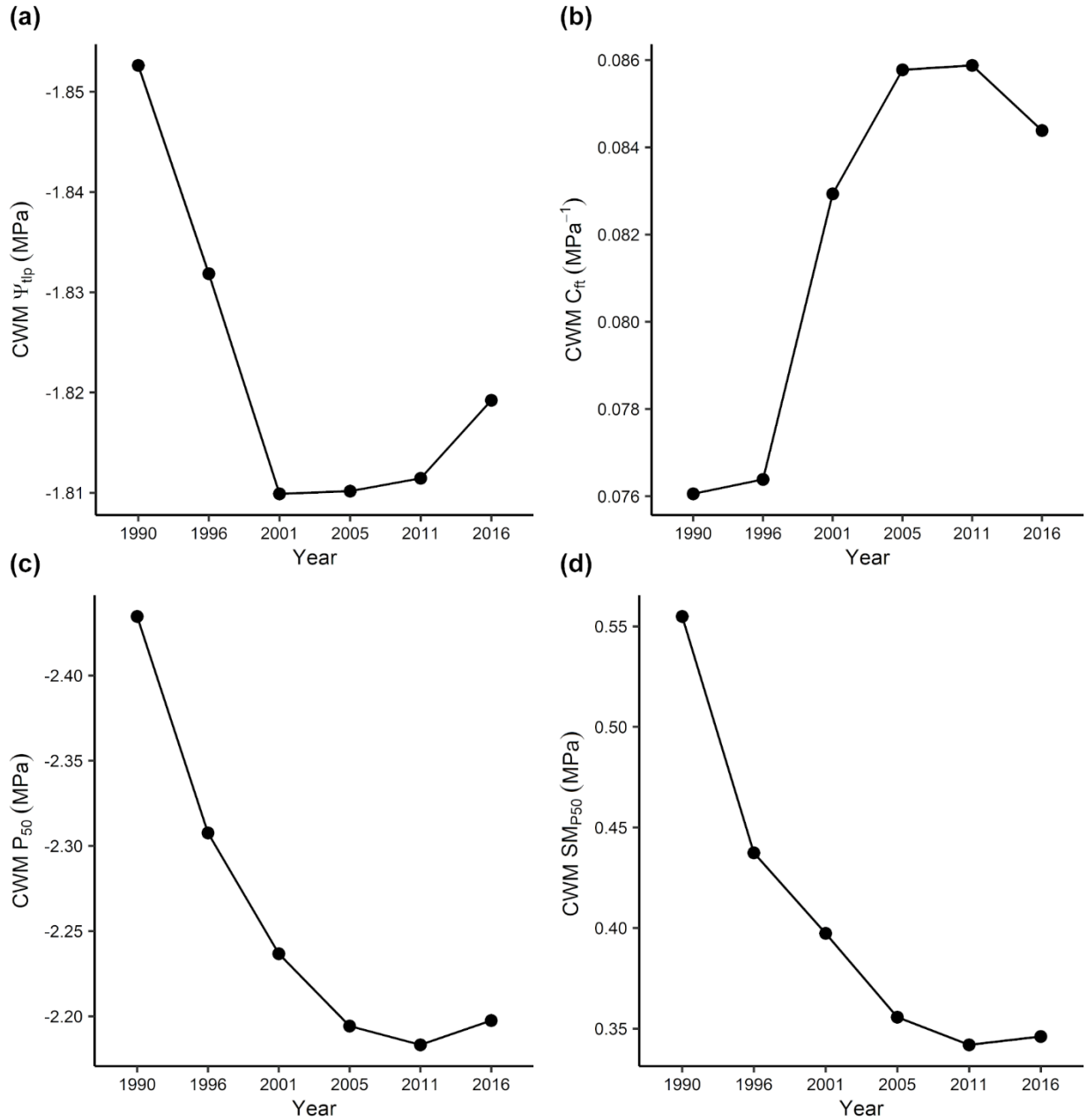
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860 **Fig. 3** Associations between P_{50} and safety margins (SM_{P50}) and absolute annual diameter
 861 growth **(a,c)** and relative annual growth **(b,d)** during the first five years after Hurricane Hugo.

862 Blue lines depict linear regressions and shaded areas represent 95% confidence intervals.



863
 864 **Fig. 4** Basal area of stems ≥ 10 cm DBH of the target species in the six censuses of the 16-ha
 865 Luquillo Forest Dynamics Plot from before Hurricane Hugo (year 1990) and over 26 years of
 866 post-hurricane succession. Plot censuses are conducted approximately every five years. Colors
 867 indicate species codes: *Alchornea latifolia* (ALCLAT), *Casearia arborea* (CASARB), *Cecropia*
 868 *schreberiana* (CECSCH), *Cordia borinquensis* (CORBOR), *Cyrilla racemiflora* (CYRRAC),
 869 *Dacryodes excelsa* (DACEXC), *Drypetes glauca* (DRYGLA), *Inga laurina* (INGLAU),
 870 *Micropholis guyanensis* (MICGUY), *Ocotea leucoxylon* (OCOLEU), *Prestoea acuminata* var.
 871 *montana* (PREMON), *Sloanea berteriana* (SLOBER), and *Tabebuia heterophylla* (TABHET).



872

873 **Fig. 5** Community-weighted mean (CWM) trait values of (a) leaf turgor loss point (Ψ_{tlp}), (b) leaf
 874 capacitance at full turgor (C_{ft}), (c) P_{50} , (d) safety margins (SM_{P50}) for 12 common tree species
 875 and one dominant palm species for each census from before Hurricane Hugo (year 1990) and
 876 then during 26 years of post-hurricane succession.