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Chris M. Smith-Martin[1] (iD), **Robert Muscarella**[2] (iD), **Roi Ankori-Karlinsky**[1] (iD), **Sylvain Delzon**[3] (iD),
Samuel L. Farrar[2], **Melissa Salva-Sauri**[1,4], **Jill Thompson**[5], **Jess K. Zimmerman**[4] and **María Uriarte**[1]

[1]Department of Ecology, Evolution and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA; [2]Plant Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Uppsala 752 36, Sweden; [3]INRA, BIOGECO, Université Bordeaux, Pessac 33615, France; [4]Department of Environmental Sciences, University of Puerto Rico, San Juan, PR 00925, USA; [5]UK Centre for Ecology & Hydrology Bush Estate, Penicuik, Midlothian, EH26 0QB, UK

Author for correspondence:
Chris M. Smith-Martin
Email: chrismsmithmartin@gmail.com

Summary

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

Introduction

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

more severe natural disturbance on tropical forests is necessary to elucidate the future of these ecosystems under a changing climate.

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

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

The fate of tropical forests exposed to severe droughts and hurricanes depends on variation in species' responses to these events. Evidence suggests that forests subject to periodic hurricane disturbance may have a greater proportion of species with traits (e.g. shorter height, high resistance to damage) that have been selected to withstand these repetitive large-scale disturbances (Boose *et al.*, 2004; Griffith *et al.*, 2008; Ibanez *et al.*, 2019). Nevertheless, tree species differ in their susceptibility to disturbance by a wind of a given intensity and the nature of the damage they sustain (i.e. resistance), as well in their recovery from wind disturbance, at both the individual plant level through repair of damage, and at the population level through reproduction, seedling establishment, and growth response to enhanced light availability (i.e. resilience) (Walker, 1991; Boucher *et al.*, 1994; Zimmerman *et al.*, 1994; Uriarte *et al.*, 2009, 2019; Canham *et al.*, 2010). Variability among species in their ability to resist wind damage may not always align with life history classifications based on light-use strategies (Zimmerman *et al.*, 1994; Lugo & Scatena, 1996; Uriarte *et al.*, 2004, 2012, 2019). Although species with denser wood (Uriarte *et al.*, 2019) and deeper root systems (Gresham *et al.*, 1991) generally suffer less damage and mortality, there are many exceptions to these patterns (Uriarte *et al.*, 2019). Dense wood has also been associated with greater drought tolerance (Powers *et al.*, 2020; Liang *et al.*, 2021), suggesting that resistance to hurricanes and drought tolerance may be aligned across species. However, the fast-growing light-demanding, hurricane-resilient species are expected to possess a set of traits that make them more vulnerable to drought. Species with strategies associated with greater resource acquisitiveness that dominate post-disturbance recovery tend to have traits associated with drought avoidance (high capacitance) and higher growth rates, whereas conservative species favor greater drought tolerance (i.e. low leaf turgor loss point, high resistance to xylem embolisms, and larger safety margins) at the expense of lower growth (Oliveira *et al.*, 2021). Forests recovering from hurricanes are expected to favor resource-acquisitive species over conservative ones due to high light conditions in the understory (Carreño-Rocabado *et al.*, 2012; Subedi *et al.*, 2019), potentially leading to an increase in the overall level of forest susceptibility to drough. Yet species-level responses to drought, and how they align with their responses to disturbances, are extremely variable and poorly understood (Umaña & Arellano, 2021).

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

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

Q2. Do resilience to hurricane damage (high post-hurricane growth) and drought avoidance (high capacitance) constitute independent axes of plant function? We expect species that are more resilient to hurricanes and grow more rapidly during post-hurricane recovery to also be more vulnerable to embolisms and hydraulic failure and possess higher capacitance.

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

Materials and Methods

Study site and species data

This study was conducted at the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico. The LEF is an evergreen forest classified as subtropical wet forest in the Holdridge life zone system (Ewel & Whitmore, 1973) with a mean annual temperature of

25.2°C and mean annual rainfall of 3500 mm. Soils are from volcanic origin and are classified as Oxisols and Ultisols (Soil Survey Staff, 1995). Although land use was extensive when the US Forest Service acquired the land in 1932, the majority of the forest is considered old-growth, particularly at elevations > 350 m. These forests have a well-documented history of hurricane damage, with a return interval of *c.* 50 yr for severe storms (category 3–4 in the Saffir–Simpson scale) (Boose *et al.*, 2004), although hurricane activity exhibits oscillations linked to Atlantic multidecadal variability (Goldenberg *et al.*, 2001). Early in the last century, in 1928 and 1932, major hurricanes struck the LEF. After 57 yr without a major storm, two severe storms, Hugo in 1989, a category 3 storm with winds up to 166 km h^{-1} and Georges in 1998, also a category 3 storm with winds up to 144 km h^{-1}, struck the forest (Zimmerman *et al.*, 2021). The compound effects of these two storms led to rapid, post-hurricane dynamics (Uriarte *et al.*, 2005, 2009; Zimmerman *et al.*, 2010; Hogan *et al.*, 2016; Heartsill Scalley, 2017). Average canopy height is 30 m, but hurricane damage can lead to canopy height losses ranging between 5 and 10 m (Brokaw & Grear, 1991; Gannon & Martin, 2014; Leitold *et al.*, 2021).

For our study, we selected 12 tree species and one palm species that encompass many of the dominant species at this site (Table 1; Thompson *et al.*, 2002). Demographic and immediate hurricane damage data were collected in the Luquillo Forest Dynamics Plot (LFDP; 18°20′N, 65°49′N; Thompson *et al.*, 2002). The LFDP is a 16 ha forest plot located near El Verde Field Station in the LEF with an elevation range from 333 to 423 m. The plot was established in 1989 and censused at *c.* 5 yr intervals starting in 1990 through 2016 using standard protocols (Condit, 1998). Briefly, all stems with diameter at breast height (DBH) of ≥ 1 cm are mapped, measured, and identified to species. In each census, new stems are added, stems are remeasured, and their status (alive/dead) is updated. Prior to 1934, parts of the lower elevation forest of the LDFP (< 350m) were subjected to light logging and agriculture, but the forest structure and canopy cover had

recovered by the time Hurricane Hugo made landfall (Thompson *et al.*, 2002).

The first LFDP census in 1990 included an initial survey of all stems ≥ 10 cm DBH to prevent loss of data due to decomposition of trees killed or damaged by Hurricane Hugo (Zimmerman *et al.*, 1994; Thompson *et al.*, 2002). During this census, immediate hurricane mortality and damage (stem break) were also recorded (Zimmerman *et al.*, 1994; Thompson *et al.*, 2002; Canham *et al.*, 2010). Surveys of all stems ≥ 1 and ≤ 10 cm in DBH in the first census were conducted from 1990 to 1993 and capture post-successional recruitment. For this reason, we only use stems ≥ 10 cm DBH to calculate comparable basal area across all censuses (Q3). However, we use all stems ≥ 1 cm DBH to calculate growth rates (Q2). As the forest was recovering from Hurricane Hugo, Hurricane Georges struck Puerto Rico in September 1998 with winds up to 144 km h^{-1} (category 3; Solá, 2000), but it was estimated to be a category 2 storm by the time it reached the forest. The effects of this second hurricane on the LFDP forest area were less acute than those of Hugo (Uriarte *et al.*, 2019), and it had a limited effect on forest structure and composition (Uriarte *et al.*, 2009, 2019). Basal area was estimated to average 36.7 m^2 ha^{-1} at the time of Hurricane Hugo, 30.85 m^2 ha^{-1} at the time Georges struck, and 38.37 m^2 ha^{-1} in 2016. Density of stems ≥ 10 cm DBH has remained stable at *c.* 1000 ha^{-1}, whereas the density of small stems (1–10 cm DBH) ranged between 6841 in 1993 and 2444 ha^{-1} in 2016, reflecting continuous stem thinning through post-hurricane succession (Supporting Information Fig. S1).

The forest has not been censused since the passage of Hurricane Maria in 2017, so we use census data collected through 2016. Altogether, our 13 target species represent *c.* 50–60% of the basal area of the LFDP, depending on the census (Table 1). For each of the 13 species, we calculated two metrics of growth for the first 5 yr after the hurricane: annual absolute growth quantified as the increments in tree DBH between the initial and the first post-hurricane census divided by census interval and relative growth, calculated as absolute growth divided by the initial tree DBH. We also calculated relative growth in the same way using basal area instead of DBH.

Hydraulic traits

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

Leaf turgor loss point and leaf capacitance We characterized leaf turgor loss point and leaf water storage capacity using

Table 1 List of species used in this study, the code we used to represent them in some figures, their families, and the range of the percentage of the total basal area of each species across six censuses of the 16 ha Luquillo Forest Dynamics Plot.

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

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

Leaf optical vulnerability curves We used the optical vulnerability technique to estimate xylem embolism accumulation in leaves (Brodribb *et al.*, [2016]). Briefly, for each branch immediately after it was brought back from the field, we secured a leaf inside a custom-built three-dimensional printed clamp (OpenSourceOV) fitted with a small 8 Mpx Raspberry Pi camera and light-emitting diodes operated by a Raspberry Pi microcomputer. Once the leaf was secured in the clamps, we took a picture every 2 min of a 4 cm^2 leaf area until no embolism events were recorded for at least 12 h (*c.* 72–96 h, depending on the species). As the branch dehydrated, we used a stem psychrometer (ICT International, Armidale, NSW, Australia) to record water potential every 10 min. To attach the stem psychrometer, we removed a small section of bark from the branch and clamped the psychrometer to the exposed xylem and created an airtight seal with Parafilm sealing film.

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

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

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

Data analysis

We used linear regressions to evaluate if there were associations between species P_{50} and safety margin $SM_{P_{50}}$ and the metrics of hurricane response: hurricane damage (mortality and broken stems) and post-hurricane absolute and relative growth. To evaluate if there was a trade-off between storage of water in the tissue and embolism resistance and vulnerability to hydraulic failure, we fitted linear regressions of species leaf capacitance C_{ft} vs P_{50} and $SM_{P_{50}}$.

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

$$\frac{CWM_c - CWM_{c-1}}{CWM_{c-1}} \times 100$$

We performed all analyses using R statistical software (v.4.0.2; R Core Team, [2020]).

Results

Overall, our study species exhibited substantial variation in hydraulic traits. Turgor loss point Ψ_{tlp}, a proxy for leaf wilting point and stomatal closure, had significant variation across species (Fig. 1a; Tables S2, S3). *Cecropia schreberiana* had the highest Ψ_{tlp} values, meaning that this species wilts at a higher water potential, whereas *Casearia arborea* wilted at the lowest water potential. Species also exhibited large variation in water storage capacity in leaves (Fig. 1b; Tables S2, S3): *C. schreberiana* and *Cordia borinquensis* had the highest capacitance, followed by the palm *P. acuminata* var. *montana*. *Casearia arborea*, *Dacryodes excelsa*, *Drypetes glauca*, and *Micropholis guyanensis* had some of the lowest water storage capacitance. Resistance to embolism formation P_{50} was also highly variable across species, with *C. schreberiana*, *D. excelsa*, and *Alchornea latifolia* at the lowest range and *C. arborea* and *M. guyanensis* at the highest end overall (Fig. 1c; Tables S2, S3). Species safety margins $SM_{P_{50}}$ also exhibited a broad range of variation, with significant
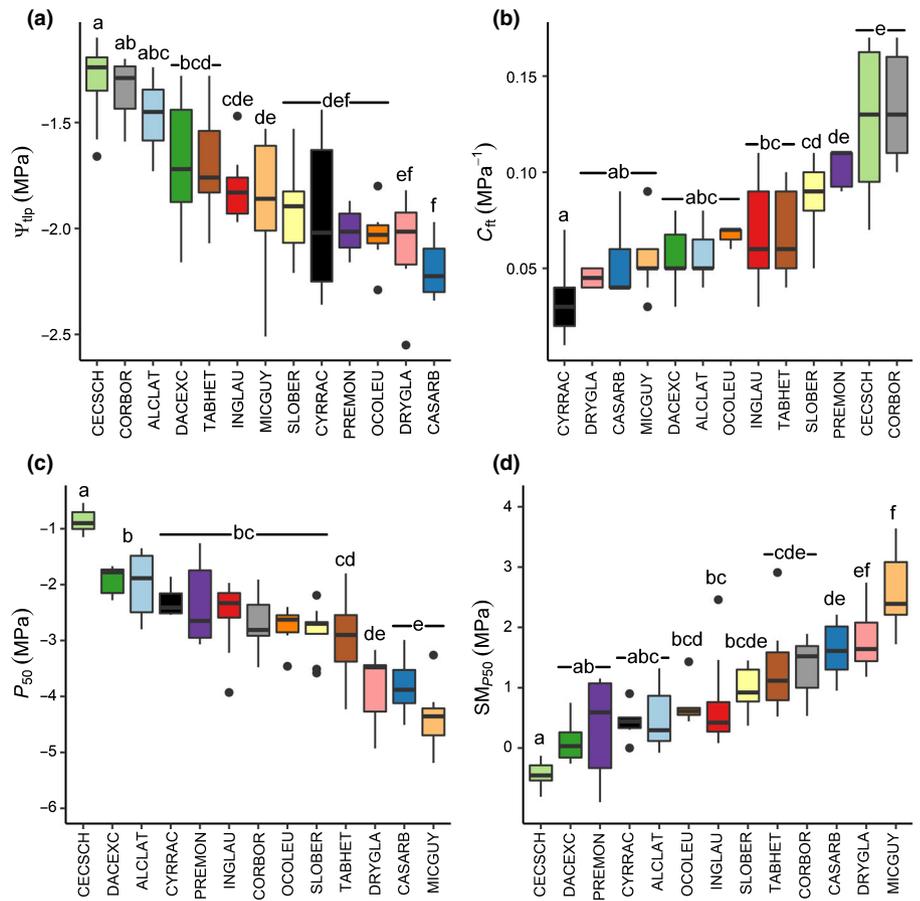
Fig. 1 (a) Leaf turgor loss point Ψ_{tlp}, (b) leaf capacitance at full turgor C_{ft}, (c) P_{50}, and (d) safety margins $SM_{P_{50}}$ for all species measured. Letters indicate significant ($P < 0.05$) differences among groups based on Tukey's honestly significant difference tests. Box plot midlines show medians, box edges show first and third quartiles, whiskers show minima and maxima, and points show outliers. Each species has a unique color to facilitate comparison across traits: ALCLAT, *Alchornea latifolia*; CASARB, *Casearia arborea*; CECSCH, *Cecropia schreberiana*; CORBOR, *Cordia borinquensis*; CYRRAC, *Cyrilla racemiflora*; DACEXC, *Dacryodes excelsa*; DRYGLA, *Drypetes glauca*; INGLAU, *Inga laurina*; MICGUY, *Micropholis guyanensis*; OCOLEU, *Ocotea leucoxylon*; PREMON, *Prestoea acuminata* var. *montana*; SLOBER, *Sloanea berteroana*; TABHET, *Tabebuia heterophylla*.

differences among species (Fig. 1d; Tables S2, S3). *Cecropia schreberiana* was the only species that exhibited a slightly negative $SM_{P_{50}}$, suggesting that it is particularly vulnerable to severe drought. Several other species also had very low $SM_{P_{50}}$, indicating that they operate at thresholds that are very close to hydraulic failure, making them highly susceptible to droughts. Specifically, *A. latifolia*, *Cyrilla racemiflora*, *D. excelsa*, *Inga laurina*, *Ocotea leucoxylon*, *P. acuminata* var. *montana*, and *Sloanea berteroana* all had $SM_{P_{50}} < 1$ MPa, whereas *C. arborea*, *C. borinquensis*, *D. glauca*, and *Tabebuia heterophylla* had $SM_{P_{50}} > 1$ MPa, and *M. guyanensis* had the highest $SM_{P_{50}}$ of 2.6 MPa (Fig. 1d).

Across species, there was a trade-off between capacitance and P_{50} (Fig. S5a; Table S4) and $SM_{P_{50}}$ (Fig. S5b; Table S4). Drought-avoiding species (i.e. higher capacitance) were also more vulnerable to embolisms (i.e. higher P_{50}) and hydraulic failure (i.e. lower $SM_{P_{50}}$), and thus less drought tolerance, whereas the more embolism resistant and drought-tolerant species had lower capacitance. There was an association between vulnerability to hurricane damage and resistance to embolisms and hydraulic failure. Species that had more negative P_{50} values also experienced a lower percentage of immediate mortality (Fig. 2a) and stem breaks (Fig. 2b) during Hurricane Hugo. Paralleling patterns observed for P_{50}, species that had higher $SM_{P_{50}}$ again also had lower percentage of hurricane-induced immediate mortality (Fig. 2c) and stem break (Fig. 2d). In the case of hurricane resilience, we found the opposite trend. There

was a trade-off between hurricane resilience and resistance to embolisms and hydraulic failure. The species that had less negative P_{50} values also had the highest absolute and relative growth (Figs 3a,b, S6a) during the first 5 yr after Hurricane Hugo, and these hurricane-resilient species also had low $SM_{P_{50}}$ (Figs 3c,d, S6b). However, we did not find this association between growth and capacitance ($R^2 = 0.01$, $P = 0.806$). For example, *C. schreberiana*, which became more dominant during post-hurricane recovery, had the highest P_{50} and narrowest $SM_{P_{50}}$, and *P. acuminata* var. *montana*, which had the highest hurricane resilience and eventually became the most dominant species during post-hurricane recovery, also had high P_{50} and low $SM_{P_{50}}$ (Fig. 4; Table S5). We also found an association between percentage of hurricane-induced immediate mortality and absolute (Fig. S7a) and relative growth (Fig. S7b).

In the first 5 yr following Hurricane Hugo, basal area of stems ≥ 10 cm DBH of most of the target species decreased or stayed the same (Fig. 4; Table S5). However, after 10–15 yr of post-hurricane recovery there was an increase in the basal area of many species. Three species in particular had very high hurricane resilience, *C. schreberiana*, *D. excelsa*, and *P. acuminata* var. *montana*, with dramatic increases in basal area that exceeded pre-hurricane levels 15–20 yr after the hurricane. After 26 yr of post-hurricane recovery, the basal area of two of these species, *C. schreberiana* and *P. acuminata* var. *montana*, declined whereas that of *D. excelsa* continued to increase (Fig. 4; Table S6).
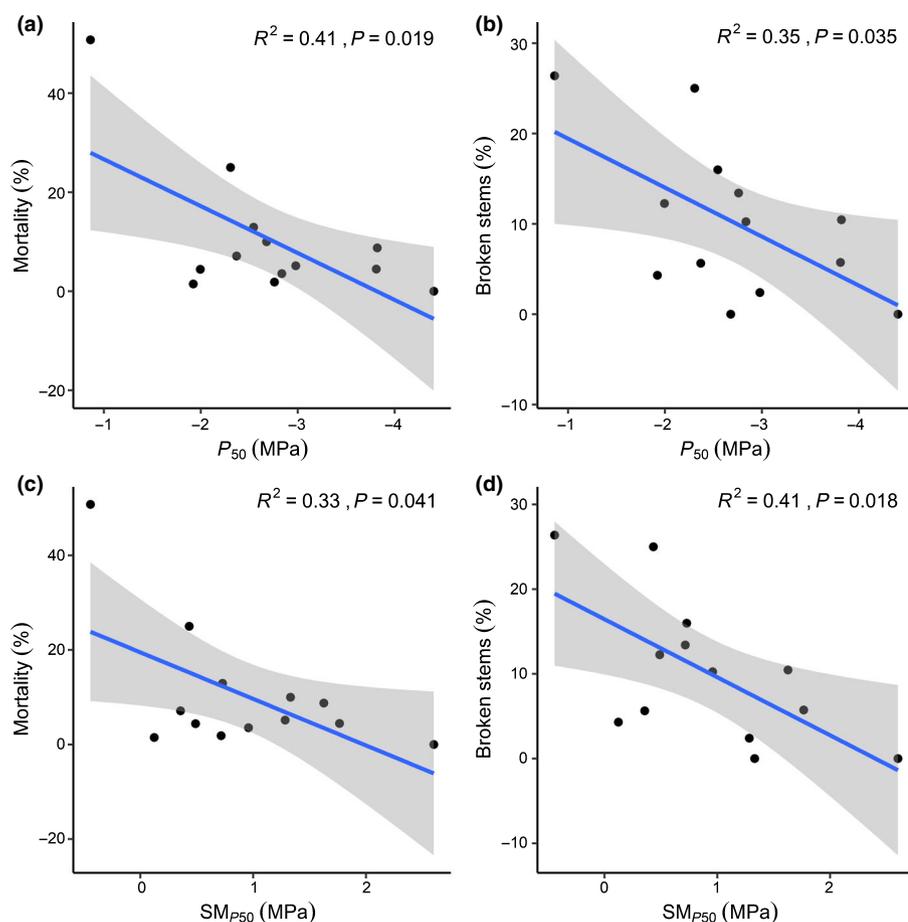
Fig. 2 Associations between P_{50} and safety margins $SM_{P_{50}}$ and proportion of stems with diameter at breast height $\geq$ 10 cm for each of the 13 tree species that were (a, c) immediately killed or (b, d) broken by Hurricane Hugo. Blue lines depict linear regressions and shaded areas represent 95% confidence intervals.

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

Discussion

We examined the relationship between hurricane resistance and resilience and hydraulic traits of 13 dominant woody species in a wet tropical forest subject to periodic hurricane disturbance. We found a large range in variation in hydraulic traits within the community and a trade-off between capacitance and two metrics

of drought tolerance, P_{50} and $SM_{P_{50}}$. Species that were more resistant to embolisms (P_{50}) and hydraulic failure ($SM_{P_{50}}$) were also less vulnerable to immediate hurricane damage (mortality and stem break), whereas species that had higher hurricane resilience and regenerated rapidly after the hurricane had hydraulic traits that made them more vulnerable to drought (high P_{50} values and low $SM_{P_{50}}$). Over the first 5 yr of post-hurricane recovery, we found a trade-off between growth and hydraulic safety, confirming a recently proposed trade-off between growth and $SM_{P_{50}}$ that had not been tested in other forests outside the Brazilian Amazon (Oliveira *et al.*, 2021). In particular, three species (*C. schreberiana*, *D. excelsa*, and *P. acuminata* var. *montana*) with hydraulic traits linked to greater vulnerability to drought also exhibited high hurricane resilience, with dramatic increases in basal area that exceeded pre-hurricane levels. During 26 yr of post-hurricane recovery, there was a decrease in community-weighted mean trait values associated with greater drought tolerance (Ψ_{tlp}, P_{50}, $SM_{P_{50}}$) and an increase in capacitance, a trait that has been linked with lower drought tolerance (Christoffersen *et al.*, 2016; Pivovaroff *et al.*, 2018; Santiago *et al.*, 2018; Oliveira *et al.*, 2021). Immediate hurricane damage in this forest favors slow-growing, drought-tolerant species. However, the high resource conditions in the wake of a hurricane favor acquisitive, fast-growing, drought-avoiding species that are more vulnerable to drought and hydraulic failure, increasing
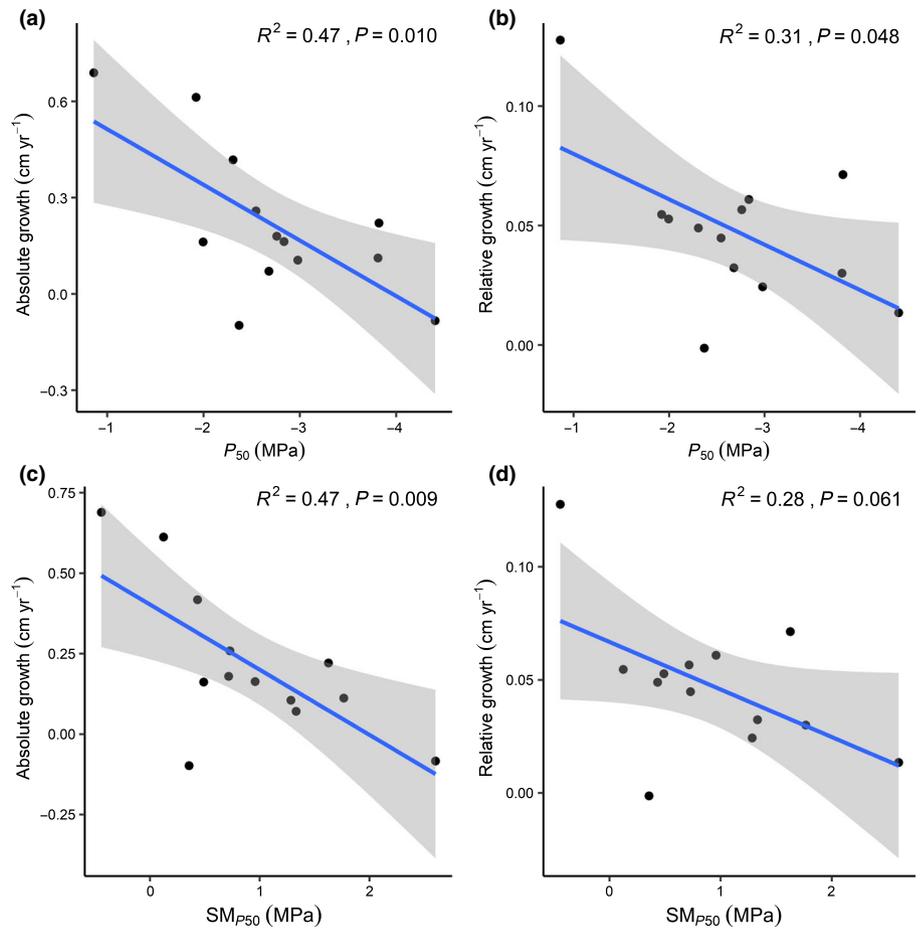
Fig. 3 Associations between P_{50} and safety margins $SM_{P_{50}}$ and (a, c) absolute annual diameter growth and (b, d) relative annual growth during the first 5 yr after Hurricane Hugo. Blue lines depict linear regressions and shaded areas represent 95% confidence intervals.

forest productivity at the expense of potential higher forest vulnerability to drought.

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

Species within our community exhibited a large range of variation in embolism resistance and hydraulic safety. We found over a five-fold difference in P_{50} values across species, and $SM_{P_{50}}$ ranged from close to zero to c. 2.5 MPa. Consistent with our findings, several studies have observed a wide range in P_{50} values within tropical forest communities elsewhere (Santiago *et al.*, 2018; Barros *et al.*, 2019; Oliveira *et al.*, 2019; Ziegler *et al.*, 2019; Fontes *et al.*, 2020; Powers *et al.*, 2020). The wide range in $SM_{P_{50}}$ indicates that not all the species within our community function at the edge of their hydraulic capacity, a fact that does not support the expectation that species should operate with narrow $SM_{P_{50}}$ to sustain CO_2 assimilation for as long as possible before closing their stomata as water becomes more limited (Tyree & Sperry, 1988; Choat *et al.*, 2012; Barros *et al.*, 2019; Fontes *et al.*, 2020). Although a growing number of studies have found that wide $SM_{P_{50}}$ values (1–5 MPa) are common within and across tropical forest communities (Martin-StPaul *et al.*, 2017; Benito Garzón *et al.*, 2018; Barros *et al.*, 2019; Ziegler *et al.*, 2019; Powers *et al.*, 2020; Smith-Martin *et al.*, 2020), eight

of the 13 species we studied had $SM_{P_{50}} < -1$ MPa, indicating that the majority of species were operating close to their maximum hydraulic capacity. *Cecropia schreberiana* had slightly negative $SM_{P_{50}}$, which should be further investigated by direct measurements of stomatal conductance in response to drought as the expectation is that no embolism occurs before full stomatal closure has occurred (Creek *et al.*, 2020). Community-wide variation in turgor loss point was not as marked as for P_{50}. There was only around a 1.5-fold difference in Ψ_{tlp} across species, with 11 of our 13 species having Ψ_{tlp} between −1.5 and −2 MPa, suggesting greater convergence in this trait than in embolism resistance (over a five-fold difference in P_{50}). Our findings support the idea that the range in Ψ_{tlp} values is lower than in P_{50} and $SM_{P_{50}}$. Ziegler *et al.* (2019) also found a range in Ψ_{tlp} of c. −1.5 to −2.0 MPa, further supporting that this trait is less variable, at least in wetter forests.

Our findings imply a trade-off between drought avoidance (high capacitance) and drought tolerance (high embolism resistance and large $SM_{P_{50}}$). Among the species we studied, there was over a three-fold difference in leaf capacitance, and some of the species with the greatest water storage in their leaves also had the least negative P_{50} values and the lowest $SM_{P_{50}}$. This pattern was particularly marked in *C. schreberiana*, *D. excelsa*, and *P. acuminata* var. *montana*. Our results coincide with previous findings of a synthesis of data from multiple sites that found a trade-off
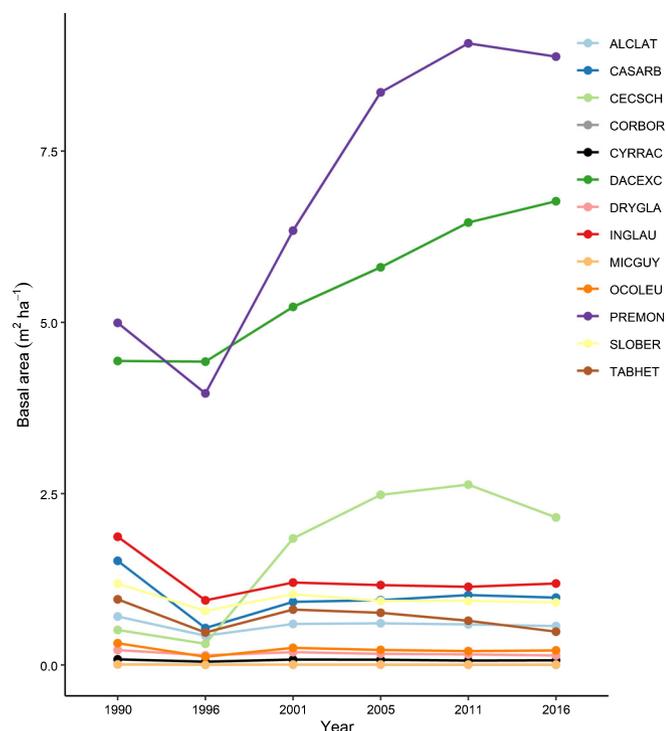
Fig. 4 Basal area of stems ≥ 10 cm diameter at breast height of the target species in the six censuses of the 16 ha Luquillo Forest Dynamics Plot from before Hurricane Hugo (year 1990) and over 26 yr of post-hurricane succession. Plot censuses are conducted approximately every 5 yr. Colors indicate species codes: ALCLAT, *Alchornea latifolia*; CASARB, *Casearia arborea*; CECSCH, *Cecropia schreberiana*; CORBOR, *Cordia borinquensis*; CYRRAC, *Cyrilla racemiflora*; DACEXC, *Dacryodes excelsa*; DRYGLA, *Drypetes glauca*; INGLAU, *Inga laurina*; MICGUY, *Micropholis guyanensis*; OCOLEU, *Ocotea leucoxylon*; PREMON, *Prestoea acuminata* var. *montana*; SLOBER, *Sloanea berteroana*; TABHET, *Tabebuia heterophylla*.

between capacitance and P_{50} for tropical species (Christoffersen *et al.*, 2016); here, we show this pattern operates at the community level. Environmental conditions after a hurricane favor fast-growing species that take advantage of the increase in light availability (Guzman-Grajales & Walker, 1991; Burslem *et al.*, 2000; Uriarte *et al.*, 2004, 2005; Comita *et al.*, 2009). Fast-growing species also tend to have higher hydraulic conductance (Markesteijn *et al.*, 2011; McCulloh *et al.*, 2012), which has been shown to be correlated with capacitance (Santiago *et al.*, 2018), potentially explaining the trade-off between drought avoidance and drought tolerance in our forest.

Coordination between drought tolerance and hurricane resistance

We found that many of the species that suffered less immediate hurricane damage and mortality were more drought tolerant. Wood density may be one of the species traits behind this association. Species resistance to hurricanes depends in part on the strength of the wood, and previous studies have found that hurricane-induced mortality and stem break are lower for species with denser wood (Zimmerman *et al.*, 1994; Uriarte *et al.*, 2019). Previous research at our study site found that Hurricane

Hugo broke, uprooted, and killed fewer individuals of species with dense wood, which could explain the association we found between drought and hurricane resistance, as densely wooded species have been shown to be more drought tolerant (Powers *et al.*, 2020; Liang *et al.*, 2021). Overall, this would mean that the direct effects of hurricanes and drought favor the same group of old-growth, dense-wood, and drought-tolerant species.

Trade-off between drought tolerance and hurricane resilience

There was also a trade-off between post-hurricane growth and drought tolerance. Specifically, we found a trade-off between stem diameter growth and the two metrics of drought tolerance (P_{50} and $SM_{P_{50}}$) during the first 5 yr after the hurricane. Even if immediate hurricane damage favors more drought-tolerant species, rapid forest reorganization and high post-hurricane growth benefit species that favor productivity over hydraulic safety. Oliveira *et al.* (2021) argue that the fast–slow economic spectrum also applies to $SM_{P_{50}}$, reasoning that species with high $SM_{P_{50}}$ are not operating at maximum growth capacity to achieve higher safety, and thus have a lower return on their C investment, making them slower growing and better suited for low-resource environments. By contrast, species with low $SM_{P_{50}}$ that operate at maximum capacity have a high return on their C investment, leading to fast growth and a competitive advantage in a high-resource environment. Our findings support the trade-off between $SM_{P_{50}}$ and growth proposed by Oliveira *et al.* (2021), showing that this pattern applies to another forest aside from the Brazilian Amazon where this idea was originally tested and also applies to the trade-off between P_{50} and growth. The degree to which this trade-off occurs in other tropical forest ecosystems remains an open question.

Post-hurricane successional forests are more vulnerable to drought

Post-hurricane successional forests had high capacitance and low resistance to embolisms and hydraulic failure. Assuming that traits remained stable over the 26 yr period, we found a decrease in community-weighted mean trait values associated with drought tolerance (i.e. Ψ_{tlp}, P_{50}, and $SM_{P_{50}}$) and an increase in capacitance. These shifts in forest level traits were most pronounced during the first 15 yr post-disturbance and, in general, leveled off or started to revert 26 yr after the hurricane. This increase in drought vulnerability was largely driven by increases in three of the species with the most drought-vulnerable hydraulic traits, *C. schreberiana*, *D. excelsa*, and *P. acuminata* var. *montana*, which dominate post-disturbance communities (Uriarte *et al.*, 2009, 2019). Umaña & Arellano (2021) studied six tree species at the same location in Puerto Rico and found that *C. schreberiana* was the species that had the highest growth reduction during drought, consistent with our findings. In their study, *D. excelsa* was not affected by severe drought and responded favorably to moderate droughts (Umaña & Arellano, 2021). *Dacryodes excelsa* is known to have extensive root grafting (Basnet
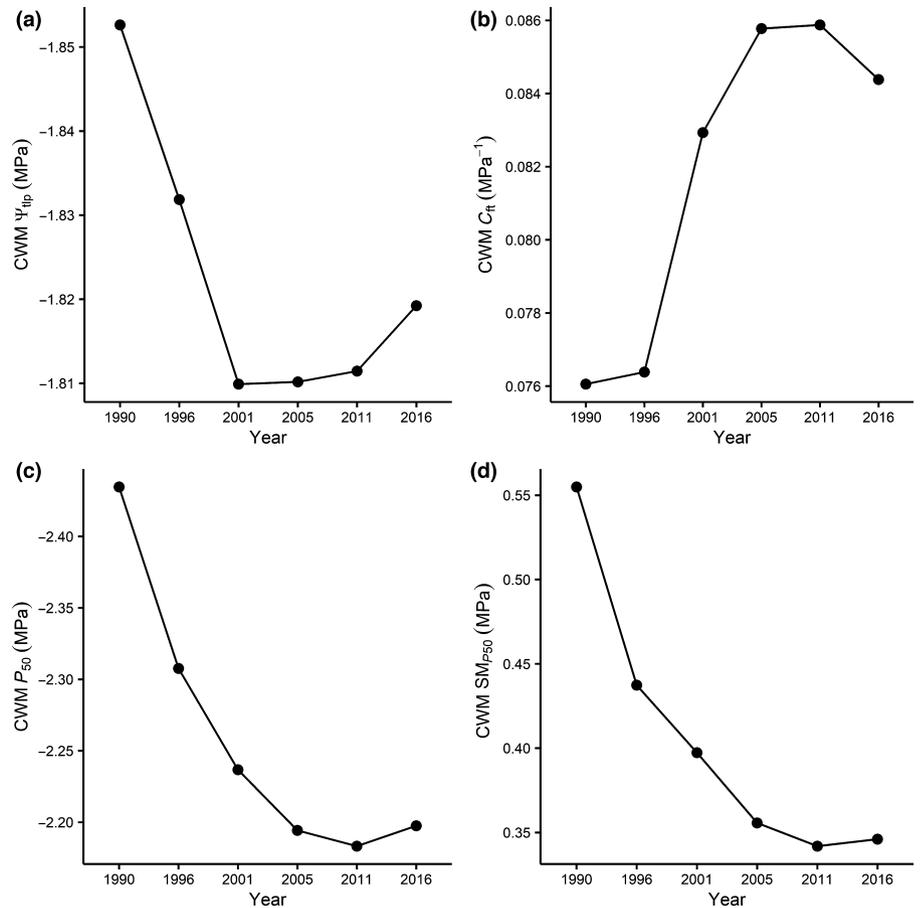
Fig. 5 Community-weighted mean (CWM) trait values of (a) leaf turgor loss point Ψ_{tlp}, (b) leaf capacitance at full turgor C_{ft}, (c) P_{50}, and (d) safety margins $SM_{P_{50}}$ for 12 common tree species and one dominant palm species for each census from before Hurricane Hugo (year 1990) and then during 26 yr of post-hurricane succession.

et al., 1993) that could allow trees to redistribute water and make them less susceptible to drought. Our findings could have consequences for forest post-disturbance dynamics, since forests in Puerto Rico and the Caribbean are subject to periodic hurricanes and our study site was recently hit by another category 4 hurricane in 2017, Hurricane María (Uriarte et al., 2019). A warming climate is expected to lead to more intense hurricanes (Knutson et al., 2010; Balaguru et al., 2018), which coupled with expected increases in extreme drought events (Khalyani et al., 2015; Ramseyer et al., 2019) could drastically change dynamics and species composition of Caribbean forests.

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

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Author contributions

CMS-M and MU conceptualized the project. CMS-M, RM, RA-K, SD, SLF, MS-S, JT, JKZ and MU collected the data. CMS-M and MU analyzed the data. CMS-M and MU wrote the manuscript and RM, RA-K, SD, SLF, MS-S, JT and JKZ contributed to the final draft.

ORCID

Roi Ankori-Karlinsky https://orcid.org/0000-0002-8277-8136
Sylvain Delzon https://orcid.org/0000-0003-3442-1711
Robert Muscarella https://orcid.org/0000-0003-3039-1076
Chris M. Smith-Martin https://orcid.org/0000-0002-6557-1432

Data availability

All data that are not included in the main text and in the Supporting Information can be found at https://luquillo.lter.network/data-catalog/. LFDP census data can be found at https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.119.1545979. Tree damage by Hurricane Hugo in the LFDP can be found at https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.57.583050.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

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

Fig. S2 Leaf and stem optical vulnerability curves.

Fig. S3 Leaf and stem optical vulnerability curves.

Fig. S4 Leaf and stem optical vulnerability curves.

Fig. S5 Trade-off between capacitance at full turgor and P_{50} and safety margins $SM_{P_{50}}$ for all measured individuals.

Fig. S6 Associations between P_{50} and safety margins and relative basal area growth during the first 5 yr after Hurricane Hugo.

Fig. S7 Associations between the proportion of stems with DBH ≥ 10 cm for each of the 13 tree species that were immediately killed by Hurricane Hugo and growth during the first 5 yr thereafter.

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

Table S2 Mean and SD of all the hydraulic traits and maximum tree height per species.

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

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

Table S5 Basal area of stems ≥ 10 cm DBH of the target species in the six censuses of the 16 ha Luquillo Forest Dynamics Plot.

Table S6 Percentage of relative change of community-weighted mean trait values between each census and the preceding one.

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