RESEARCH ARTICLE

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Hydraulic traits are not robust predictors of tree species stem growth during a severe drought in a wet tropical forest

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Abstract

1. Severe droughts have led to lower plant growth and high mortality in many ecosystems worldwide, including tropical forests. Drought vulnerability differs among species, but there is limited consensus on the nature and degree of this variation in tropical forest communities. Understanding species-level vulnerability to drought requires examination of hydraulic traits since these reflect the different strategies species employ for surviving drought.

2. Here, we examined hydraulic traits and growth reductions during a severe drought for 12 common woody species in a wet tropical forest community in Puerto Rico to ask: Q1. To what extent can hydraulic traits predict growth declines during drought? We expected that species with more hydraulically vulnerable xylem and narrower safety margins (SM_{P50}) would grow less during drought. Q2. How does species successional association relate to the levels of vulnerability to drought and hydraulic strategies? We predicted that early- and mid-successional species would exhibit more acquisitive strategies, making them more susceptible to drought than shade-tolerant species. Q3. What are the different hydraulic strategies employed by species and are there trade-offs between drought avoidance and drought tolerance? We anticipated that species with greater water storage capacity would have leaves that lose turgor at higher xylem water potential and be less resistant to embolism forming in their xylem (P_{50}).

3. We found a large range of variation in hydraulic traits across species; however, they did not closely capture the magnitude of growth declines during drought. Among larger trees (≥10 cm diameter at breast height—DBH), some tree species with high xylem embolism vulnerability (P_{50}) and risk of hydraulic failure (SM_{P50}) experienced substantial growth declines during drought, but this pattern was not consistent across species. We found a trade-off among species between drought avoidance (capacitance) and drought tolerating (P_{50}) in this tropical forest community. Hydraulic strategies did not align with successional associations. Instead, some of the more drought-vulnerable species were shade-tolerant

dominants in the community, suggesting that a drying climate could lead to shifts in long-term forest composition and function in Puerto Rico and the Caribbean.

1 | INTRODUCTION

Severe droughts have led to tree growth reductions and widespread plant mortality across many ecosystems, including tropical forests (Aleixo et al., 2019; Allen et al., 2015). Tropical forests account for the majority of terrestrial above-ground biomass (Pan et al., 2011) and growth declines and high tree mortality during drought could lead to large carbon losses to the atmosphere, turning these ecosystems from a carbon sink to a source and creating a positive feedback to climate warming (Feng et al., 2018; Gatti et al., 2014). Since natural drought events are anticipated to become more severe and last longer as the climate continues to change (Chadwick et al., 2016; Duffy et al., 2015; Feng et al., 2013), growth declines and high rates of tree mortality are likely to persist and even rise (Brodribb, Powers, et al., 2020).

Increases in tree mortality and growth declines have been associated with severe drought across several neotropical forests (Bretfeld et al., 2018; Engelbrecht et al., 2006; Leitold et al., 2018; Powers et al., 2020; Umaña & Arellano, 2021; Uriarte et al., 2016), which are expected to be exposed to increasing drought frequency and severity (Kooperman et al., 2018; Neelin et al., 2006). Even relatively short periods of decreased rainfall (≥10 days with no rainfall) during the wet season can increase seedling mortality (Engelbrecht et al., 2006). Drought impacts, however, differ among species and depend on species' hydraulic and functional traits. Pioneer and fast-growing tree species have physiological characteristics that may make them more vulnerable to drought (Bazzaz & Pickett, 1980; Greenwood et al., 2017; Lohbeck et al., 2013). For early-successional tree species, high rates of hydraulic conductance have been linked to leaf and wood functional traits that support the high rates of photosynthesis and transpiration, but also increase the risk of xylem embolism under drought (Aleixo et al., 2019; Markesteijn, Poorte, et al., 2011; McCulloh et al., 2011; Santiago et al., 2004). Shade-tolerant species with more conservative strategies (e.g. higher wood density) tend to be more drought resistant (Powers et al., 2020; Uriarte et al., 2016). However, responses of shade-tolerant species to drought are variable and not well understood. Since the majority of tree species in tropical rainforests are shade tolerant, our ability to forecast the likely impacts of increasing drought severity on tropical forest composition remains limited. Gaining a greater understanding of how tropical forests respond to drought requires a deeper understanding of species-level drought resistance within diverse communities.

To understand species-level vulnerability to drought, it is necessary to examine hydraulic traits, as these mediate responses to environmental conditions including drought events (Griffin-Nolan et al., 2018).

Species may have different strategies for surviving drought (Pivovaroff et al., 2014; Pockman & Sperry, 2000; Santiago et al., 2018), but see Gleason et al. (2016) and Liu et al. (2021). One strategy (capacitance) is to store water in tissues that can then be released during transpiration to avoid drops in xylem water potential (Ψ_x) during drought (Goldstein et al., 1998; Meinzer et al., 2003; Santiago et al., 2018; Ziemińska et al., 2020). A second strategy is to minimize the risk of hydraulic failure by regulating stomatal closure (i.e. turgor loss point, Ψ_{tlp}; Bartlett et al., 2016; Rodriguez-Dominguez et al., 2016; Martin-StPaul et al., 2017). A third strategy is to be able to function under low Ψ_x without risking air embolisms in the xylem, which block the movement of water (Sperry et al., 1988; Tyree & Sperry, 1989). Fourth, larger margins from the point when a plant closes its stomata or loses turgor in its leaves to when a plant has lost 50% of its water-conducting capacity due to xylem embolism (P_{50}), a metric known as safety margins (Choat et al., 2012; Martin-StPaul et al., 2017; Powers et al., 2020).

Species within a community will likely employ a combination of strategies to cope with drought. For example, greater water storage capacity has been associated with more efficient xylem but higher turgor loss point, whereas lower capacitance is associated with lower turgor loss point, high xylem safety and low xylem efficiency (Pivovaroff et al., 2018; Santiago et al., 2018), implying a trade-off between hydraulic safety and efficiency. Species with strategies associated with greater resource acquisitive tend to have traits associated with hydraulic efficiency whereas conservative species favour hydraulic safety (Reich, 2014). Nevertheless, linking different hydraulic strategies to performance under drought requires coupling species-level hydraulic trait measurements with performance (e.g. growth, mortality) during a drought event, which few studies have done for tropical forests.

Natural drought events offer unique opportunities to understand how hydraulic strategies translate into demographic performance during drought. Here, we take advantage of a severe drought in Puerto Rico in 2015 to examine the relationship between species hydraulic strategies and performance during drought in a wet tropical forest. To do so, we couple targeted hydraulic trait measurements for 12 dominant species representing ~50% of the forest basal area with growth data to address the following questions:

Q1. To what extent can hydraulic traits predict growth during drought? We expected that species with more hydraulically vulnerable xylem and narrower safety margins would grow less during drought.

Q2. How does successional association relate to the levels of vulnerability to drought and hydraulic strategies? We predicted that

early- and mid-successional species would exhibit more acquisitive strategies, making them more susceptible to drought than shade-tolerant species.

Q3. What are the different hydraulic strategies employed by species and are there trade-offs between drought avoidance and drought tolerance? We anticipated that species with greater water storage capacity (drought avoidance) would have leaves that lose turgor at higher xylem water potential and be less resistant to embolism forming in their xylem (drought tolerance).

2 | MATERIALS AND METHODS

2.1 | Study site and species selection

This study was conducted at Luquillo Experimental Forest (LEF) in north-eastern Puerto Rico. The permit to conduct research at the LEF is special use permit CNF-2047 authorized by the US Department of Agriculture Forest Service, El Yunque National Forest. The LEF is classified as an evergreen subtropical wet forest in the Holdridge life zone system (Ewel & Whitmore, 1973). Although land use was extensive when the US Forest Service acquired the land in 1932, the majority of the forest is considered old growth (Thompson et al., 2002). Current forest age ranges from >35 years to >80 years (Schwartz et al., 2020). Mean annual rainfall is 3700 mm. In 2015, rainfall was only 2035 mm, the second lowest on record since 1975 (Figure 1; Schwartz et al., 2020). For our study, we selected 11 tree species and one palm species that encompass many of the dominant species

at this site, are common in wet forests throughout Puerto Rico and represent 50–60% of the basal area depending on the census of the 16-ha Luquillo Forest Dynamics Plot (18°20′N, 65°49′N) located in LEF (Table 1; Thompson et al., 2002).

2.2 | Hydraulic traits

We sampled individual trees between 250 and 550 m. For each species, we measured hydraulic traits on 5–13 mature canopy trees with a diameter at breast height (DBH) ≥8 cm (Table S1). 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 them in large black plastic garbage cans with water, recut the branches under water and kept them covered with black plastic bags to minimize evapotranspiration until further processing. All branches were collected in the morning between 7:00 and 9:00 am local time. 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.

2.2.1 | Leaf turgor loss point and leaf and stem capacitance

We characterized leaf turgor loss point and water storage capacity of leaves and stems using pressure–volume curves. To do so, we
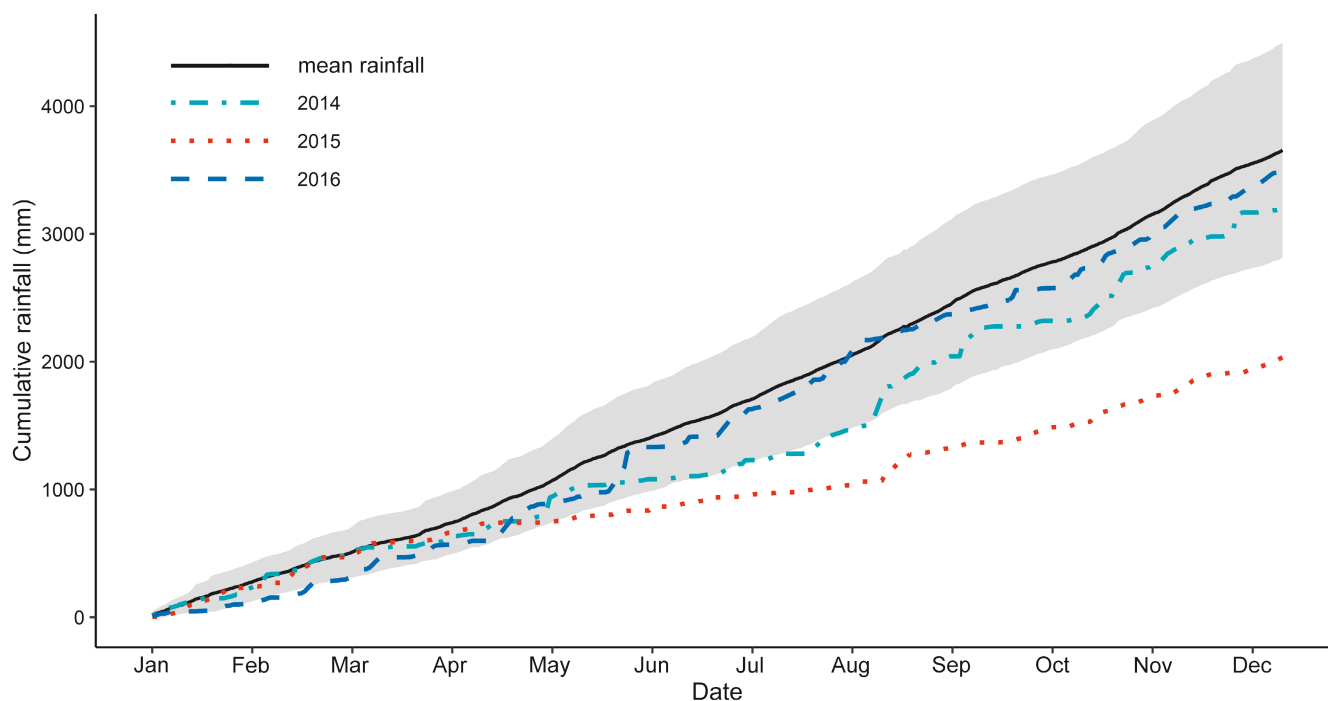

FIGURE 1 Cumulative daily rainfall at El Verde Field Station in the Luquillo experimental Forest. The black line shows 1975–2016 mean cumulative rainfall, the grey-shaded area represents mean cumulative rainfall plus/minus one standard deviation and dashed lines show cumulative rainfall for 2014, 2015 and 2016.

TABLE 1 Species used in this study, their families and the forest successional stage at which they predominantly occur—early-successional (early), mid-successional (mid) and late-successional (late), and the range of the per cent of the total basal area of each species across six censuses of the 16-ha Luquillo Forest Dynamics Plot

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

used the bench dry method described by Tyree and Hammel (1972). For leaves, 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 (Whirl-Pak). As leaves dehydrated, we periodically measured water potential (Ψ) with a Pressure Chamber Instrument (PMS Instrument Company) and leaf weight. We continued to measure the leaves until $1/\Psi$ and water loss became linear. Finally, we dried the leaves in an oven at 65°C for at least 72 h and weighed them to obtain leaf dry mass. We used Sack and 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 ($C_{ft,leaf}$).

For stems, we excised ~1–1.5 m long intact terminal branches immediately after the samples were brought back from the field, removed all the leaves, and sealed any cuts in the bark with Parafilm sealing film (Bemis Company). As the branch dehydrated, we used a stem psychrometer (ICT International) to record water potential every 10 min and periodically weighed the branch. 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 air-tight seal with Parafilm sealing film. We continued to measure the branches until $1/\Psi$ and water loss became linear. Finally, we oven-dried the branches at 65°C for a week and weighed them to obtain dry mass. We used the Sack and Pasquet-Kok (2011) tool to construct pressure–volume curves from which we extracted stem capacitance at full turgor ($C_{ft,stem}$). Because of its stem anatomy, we were unable to obtain stem capacitance data for the palm, *Prestoea acuminata* var. *montana*.

2.2.2 | Leaf and stem optical vulnerability curves

We used the optical vulnerability (OV) technique to estimate xylem embolism accumulation in leaves and stems as described by

Brodribb et al. (2016) and Brodribb et al. (2017). Briefly, for each branch immediately after it was brought back from the field, we secured a leaf and a small distal stem (~3–6 mm in diameter depending on the species) inside a custom-built three-dimensional printed clamp (OpenSourceOV—OSOV) fitted with a small 8-megapixel Raspberry Pi camera and six bright light-emitting diodes operated by a Raspberry Pi microcomputer. Details of materials and instructions for construction, image capturing and post-image processing using OSOV clamps are explained in detail at http://www.opensourceov.org. For the stems, we carefully removed a small area of bark (~2 cm^2) from a small distal branch with healthy foliage to expose the xylem. We then applied adhesive hydrogel (Tensive) to the exposed xylem to reduce surface reflection and aid light penetration into the xylem, covered the area with a round glass coverslip and secured the branch in the OSOV clamp. Once the leaf and stem were secured in the clamps, we took a picture every 2 min until no embolism events were recorded for at least 12 h (~72–96 h depending on the species). While the branches were drying, we used stem psychrometers to measure water potential every 10 min. Because of their stem anatomy, we were unable to obtain optical vulnerability data for stems of *Cecropia schreberiana* and the palm, *P. acuminata* var. *montana*. We chose to use the OV technique as it has been validated in many studies for many species and can be used simultaneously on leaves and stems (Brodribb et al., 2016; Brodribb et al., 2017; Brodribb, Carriquí, et al., 2020; Gauthey et al., 2020; Guan et al., 2021; Johnson et al., 2020; Pereira et al., 2020; Skelton et al., 2018; Smith-Martin et al., 2020).

We used ImageJ software (National Institutes of Health, USA) to analyse the pictures of leaf and stem embolisms following Brodribb et al. (2016) and Brodribb et al. (2017). Briefly, 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 (differences in pixel values). We removed

differences in pixels due to noise or artefacts (e.g. sample movements or shrinkage) using both the remove outlier function in ImageJ and manually. Embolism accumulation in each stem 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 at the time of image capture (Ψ_x), we fitted a linear regression to the water potential measurements over time and extracted the values at which 50% of the cumulative embolisms had occurred (P_{50}). We calculated this for both leaves (leaf P_{50}) and stems (stem P_{50}; Figures S1, S2 and S3). Full details of the procedure, including an overview of the technique, image processing, as well as ImageJ scripts, are available at http://www.opensourceov.org.

2.3 | Stem growth data

Stem growth data were collected in four forest plots, which are located at the edges of El Yunque National Forest (Table S2). These plots range in size from ~0.5 to 1 ha and vary in elevation from ~150 m to 550 m a.s.l (Schwartz et al., 2020). All stems ≥1 cm DBH have been mapped using standard protocols (Condit, 1998), identified to species and diameters were recorded annually between 2013 and 2016.

2.4 | Data analysis

2.4.1 | Stem growth

To quantify the impact of drought on annual growth, we used the ratio of growth (drought growth ratio) during the drought year (2015) to a non-drought year (2014). We selected these years to avoid potential lag effects of drought for the 2016 census. For each individual stem and year, we calculated relative growth rate (RGR) as follows:

$$RGR = \frac{\ln(DBH_{t2}) - \ln(DBH_{t1})}{t_2 - t_1}. \tag{1}$$

Size distributions and growth rates differ substantially among species and can obscure interannual differences driven by climate. To standardize growth rates among species and facilitate comparison, we calculated z-scores ($Z_{i,s}$) for all individuals across all years as:

$$Z_{i,s} = \frac{X_{i,s} - \mu_s}{\sigma_s}, \tag{2}$$

where $X_{i,s}$ is RGR of individual i in species s, μ_s is the species-level mean RGR and σ_s is the species-level standard deviation.

We used these standardized measurements for each stem to calculate the ratio of RGR during the drought year (2015) relative to an average, non-drought year (2014). We then calculated mean annual drought growth ratio per species for individuals with a DBH < 10 cm

and another for DBH ≥ 10 cm (Table S3). Values <1 indicate that a species grew less during the drought than the non-drought year. We used linear regression to determine if there was a correlation between the drought growth ratio with measured hydraulic traits. We also used linear regression to determine if there was a correlation between absolute annual diameter growth for the years 2014 (non-rainfall deficit year), 2015 (rainfall deficit year) and 2016 (post rainfall deficit year) with measured hydraulic traits.

2.4.2 | Hydraulic traits

We calculated safety margins in leaves ($SM_{P50,leaf}$) and stems ($SM_{P50,stem}$) as the difference between leaf turgor loss point (Ψ_{tlp}) and the water potential at which 50% of total embolisms had occurred as defined by Martin-StPaul et al. (2017):

$$SM_{P50} = \Psi_{tlp} - P_{50} \tag{3}$$

To determine if there were differences in hydraulic traits among species and successional life-history strategies, we used type-II analysis of variance using the CAR package followed by post hoc Tukey's HSD tests that we conducted with the EMMEANS package. To evaluate if there was a trade-off between the different hydraulic traits, we fitted linear regressions. We performed all analyses using R statistical software (Version 4.1.1; R Core Team, 2021). Data are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.fn2z34tzd (Smith-Martin et al., 2022).

3 | RESULTS

3.1 | Weak association of growth reduction with hydraulic traits

There was a weak association between declines in growth for larger trees (DBH ≥10 cm) during the 2015 drought and xylem embolism resistance and vulnerability to hydraulic failure. Specifically, we found a significant but noisy association between the drought growth ratio and leaf and stem P_{50} as well as leaf and stem SM_{P50}s in large trees but not in small ones (Figure 2; Table S4). These significant associations were mostly driven by one species, *M. guyanensis*, which was the most drought-resistant species. Large individuals of this species had above-average growth during the 2015 drought. None of the other hydraulic traits that we measured were associated with growth reductions during drought (Table S4). Nevertheless, most species experienced a decline in growth during the drought. However, small trees of *S. berteroana* and to a lesser degree small trees of *A. latifolia* and large trees of *M. guyanensis* grew more in 2015 drought year. We found no statistically significant association between leaf P_{50} (Figure S4) and SM_{P50}s (Figure S5) with absolute annual diameter growth for the years 2014, 2015 and 2016 of both small and large trees.
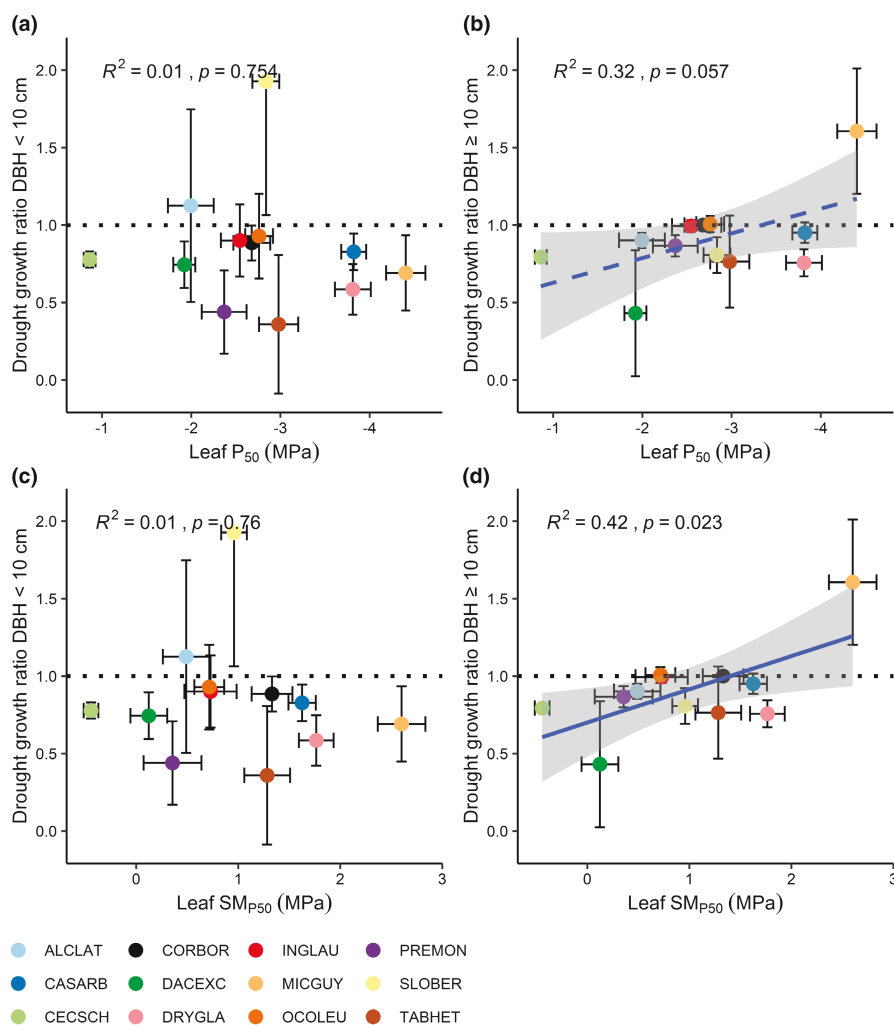
FIGURE 2 Associations between leaf P_{50} (a, b) and leaf safety margins (leaf SM_{P50}; c, d) and growth ratio between drought and non-drought conditions for small and large individuals. A drought growth ratio <1 (below black dashed line) indicates that a species grew less during the drought year than the non-drought year. Blue lines represent results of linear regressions and shaded areas 95% confidence intervals. Bars depict standard errors for each species. Species codes in Table 1.

Yet absolute annual diameter growth of small and large trees was lower during the 2015 rainfall deficit year than in the year before and the year after (Figures S4 and S5).

3.2 | Variation in hydraulic traits across species and successional association

Turgor loss point (Ψ_{tlp}) had low but significant variation across species (Figure 3a; Table S5). The two early-successional species had high Ψ_{tlp} values, as expected, but so did the late-successional species, *Cordia borinquensis*. However, while mid-successional species had the lowest Ψ_{tlp} values as a group, the range of variation across mid- and late-successional species was high (Figure 3a; Table S6). Interestingly, *Casearia arborea*, a mid-successional species, had the lowest Ψ_{tlp}.

Species also exhibited large variation in water storage capacity in both leaves and stems (Figure 3b,c; Table S5). Overall, early-successional groups had higher capacitance than mid- and late-successional ones (Table S6). The early-successional species *C. schreberiana* and the late-successional species *C. borinquensis* had the highest leaf capacitance followed by the palm *P. acuminata*, a

mid- to late-successional species (Figure 3b). The mid-successional species, *Casearia arborea*, and the late-successional species *Dacryodes excelsa*, *Drypetes glauca* and *Micropholis guyanensis* had some of the lowest leaf water storage capacitance, leading to no clear difference between mid- and late-successional groups (Table S6).

On average, stem capacitance was highest in the early-successional group, followed by the late-successional group, while the mid-successional group had the lowest (Figure 3c; Table S6). The early-successional species *Alchornea latifolia* had the greatest stem water storage capacity followed by the late-successional species *D. excelsa*. The mid-successional species *C. arborea* had the lowest value and the mid-successional group had the lowest values overall (Table S6).

Resistance to embolism formation and thus, xylem drought tolerance, was also highly variable, with only early-successional species being more vulnerable but with no distinct patterns between mid- and late-successional groups (Figure 3d,e; Tables S5 and S6). The two early-successional species and the late-successional species *D. excelsa* had the least embolism-resistant leaves and stems. The late-successional species, *M. guyanensis*, was the most embolism-resistant species overall.
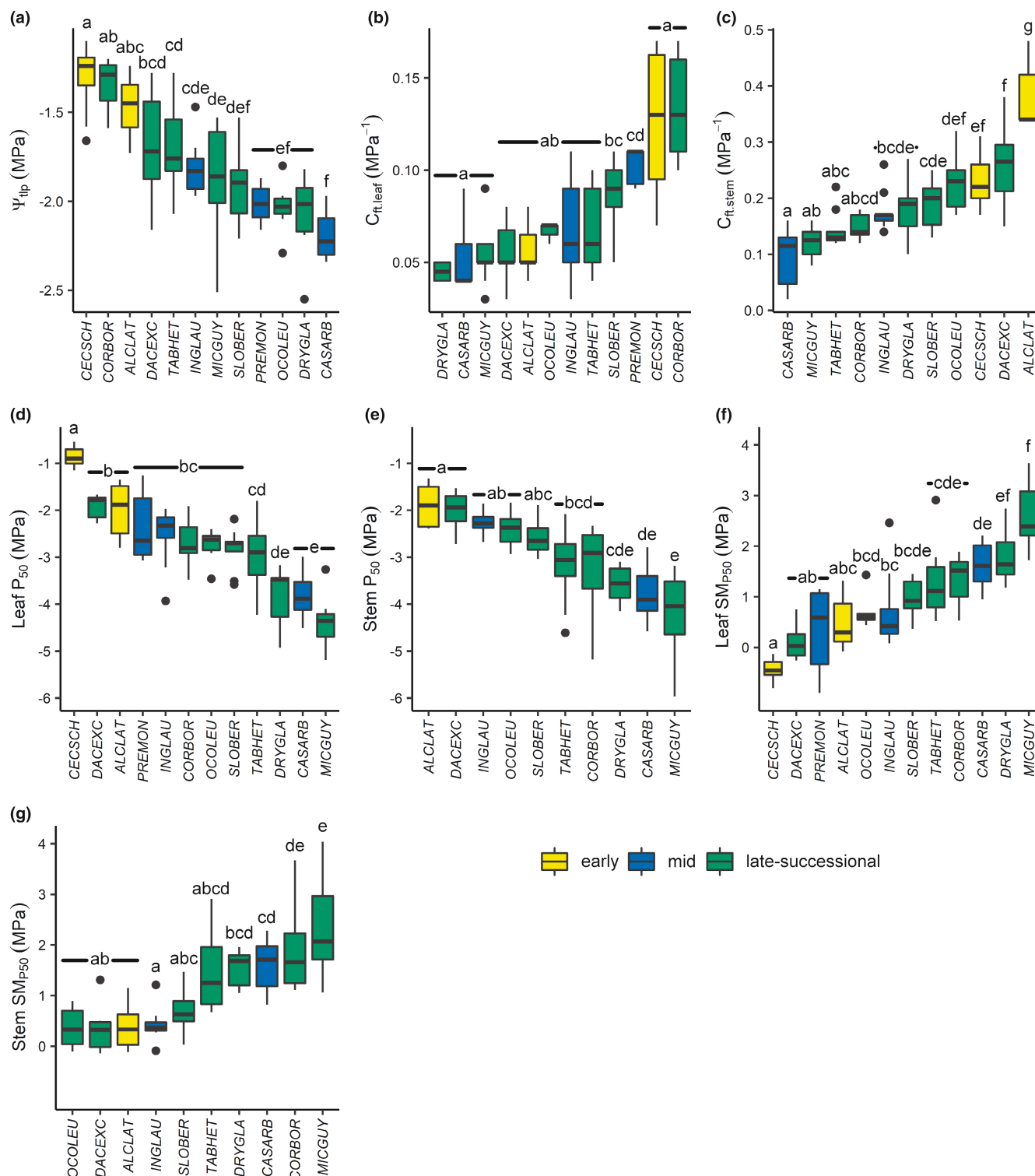
FIGURE 3 (a) Leaf turgor loss point (Ψ_{tlp}); (b) leaf capacitance at full turgor ($C_{ft,leaf}$); (c) stem capacitance at full turgor ($C_{ft,stem}$), (d) leaf P_{50}, (e) stem P_{50}, (f) leaf safety margins ($SM_{P50,leaf}$) and (g) stem safety margins ($SM_{P50,stem}$) for all measured species. Letters indicate significant ($p < 0.05$) differences among groups based on Tukey's HSD tests. Box plot midlines show medians; box edges, first and third quartiles; and whiskers, minima and maxima. Points show outliers. Species codes in Table 1.

Species safety margins (SM_{P50}) also exhibited a broad range of variation, with significant differences among species for both stems and leaves (Figure 3f,g; Tables S5 and S6). Several species had very low (i.e. <1 MPa) SM_{P50}s, indicating that they operate at

thresholds that are very close to hydraulic failure, making them highly susceptible to droughts. Specifically, *A. latifolia, D. excelsa, I. laurina, Ocotea leucoxylon, P. acuminata* and *Sloanea berteroana* all had $SM_{P50} < 1$ MPa (Figure 3f,g). While *C. arborea, C. borinquensis, D.*

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glauca and *T. heterophylla* had $SM_{P50} > 1$ MPa, and *M. guyanensis* had the highest with both leaf and stem SM_{P50}s of 2.3 MPa (Figure 3f,g). The pioneer *C. schreberiana* was the only species that we measured that exhibited a slightly negative SM_{P50}, suggesting that it is particularly vulnerable to severe drought.

3.3 | Hydraulic strategies

There was a trade-off between traits associated with drought avoidance and traits associated with drought tolerance. Drought-avoiding species (i.e. higher leaf and stem capacitance) were also more vulnerable to embolisms (i.e. higher P_{50}; Figure 4e,f). Species with lower Ψ_{tlp} had lower Leaf P_{50} values (Figure 4c), but there was no clear trend with Stem P_{50} (Figure 4d). There was not a robust association between Ψ_{tlp} and capacitance (Figure 4a,b). As expected, early-successional species tended to be drought avoiders. In contrast, hydraulic strategies for mid- and late-successional species fell along a gradient from more drought avoidant to more drought resistant.

4 | DISCUSSION

We examined hydraulic traits and growth declines during a drought for 12 common woody species in a wet tropical forest community. We found a large range of variation in hydraulic traits across species. Most species experienced a decline in growth during the drought. However, hydraulic traits were not robust predictors of observed growth declines. Hydraulic strategies also failed to clearly align with successional association. Although early-successional species were less drought tolerant (less negative P_{50} smaller SM_{P50}) as expected, several dominant mid- and late-successional species also had low drought tolerance. The most drought-tolerant species were not dominant in the community, suggesting that sustained and increasing drought frequency and severity could lead to shifts in species dominance with potential implications for long-term forest composition under a drying climate. Our analyses also uncovered a trade-off among species between drought avoidance (capacitance) and drought tolerance (P_{50}) in this tropical forest community.

4.1 | Hydraulic traits were not a robust predictor of growth reduction during drought

Plant hydraulic traits are important drivers of drought-induced mortality in many ecosystems (Anderegg et al., 2016; Johnson et al., 2022; Powers et al., 2020). However, we did not find a clear link among all species between hydraulic traits and growth declines during drought. Among larger trees, some of the more drought-resistant species did not reduce their growth as much as the less drought-resistant ones, which was the case for *M. guyanensis*, but this was not true for all species. This result suggests that while hydraulic traits, in particular P_{50} and safety margins, may be linked to drought-induced

mortality, this link may be less clear for growth reductions, at least in our site. Under non-drought conditions but across a water availability gradient in a Mediterranean climate where water is expected to be limited at least at some locations, Rosas et al. (2021) found that functional and hydraulic traits were poor predictors of tree growth—further supporting our findings that hydraulic traits are not necessarily good predictors of tree growth under drought conditions. Soft functional traits were also weak predictors of growth at our site during drought, with only species with denser wood having slightly less growth decline during drought and trees with higher specific leaf area having greater drought-induced growth declines on steep slopes where water is more limited (Schwartz et al., 2020).

The majority of the species in our study, however, had lower growth during drought. A recent study at the site using four of the same species found a decline on growth during the 2015 drought at higher elevation sites in the LEF for *C. schreberiana*, *C. borinquensis* and *S. berteroana*—results that were largely consistent with our findings (Umaña & Arellano, 2021). However, drought did not result in lower growth for *D. excelsa* in their study whereas we found that this keystone species, one of the most important species in Puerto Rican wet forests, also experienced one of the highest declines in growth during the 2015 drought, particularly for larger individuals. This difference in findings for *D. excelsa* may reflect variation in responses related to the location of the plots and the size distributions of trees in the samples.

Interestingly, a few species actually grew more during the drought. Smaller individuals of *A. latifolia* and especially of *S. berteroana* grew more during the drought while larger trees grew less, perhaps due to an increase in understorey light caused by high rates of leaf fall during the drought (Zimmerman, pers. obs.). This result aligns with studies elsewhere that found neutral or even positive effects of drought on small tree growth (Chen et al., 2019; Uriarte et al., 2016) or photosynthetic rates (Bartholomew et al., 2020) and greater growth declines during drought of larger trees (Bennett et al., 2015; Uriarte et al., 2016). One species, however, exhibited the opposite pattern; large individuals of *M. guyanensis* grew more during the drought whereas small individuals of the same species had lower growth rates during this period. This pattern may reflect a competitive advantage of this extremely drought-resistant species under dry conditions.

4.2 | Drought tolerance did not align with successional association

Early-successional species were vulnerable to drought but so were several mid- and late- successional ones. The two early-successional species studied, *C. schreberiana* and *A. latifolia*, both had traits associated with pioneer and fast-growing trees (Aleixo et al., 2019; Markesteijn, Poorter, et al., 2011; McCulloh et al., 2011; Santiago et al., 2004) of low resistance to xylem embolism formation, narrow hydraulic safety margin, high tissue water content and low-density wood (Uriarte et al., 2010), suggesting that these species should be

FIGURE 4 Association between leaf turgor loss point and leaf capacitance at full turgor (a), stem capacitance at full turgor (b), leaf P_{50} and stem P_{50}. Association between leaf capacitance at full turgor and leaf P_{50} (e) and between stem capacitance at full turgor and stem P_{50} (f) for all the measured species. Blue lines show results of linear regressions and shaded areas 95% confidence intervals. Bars depict standard errors for each species.
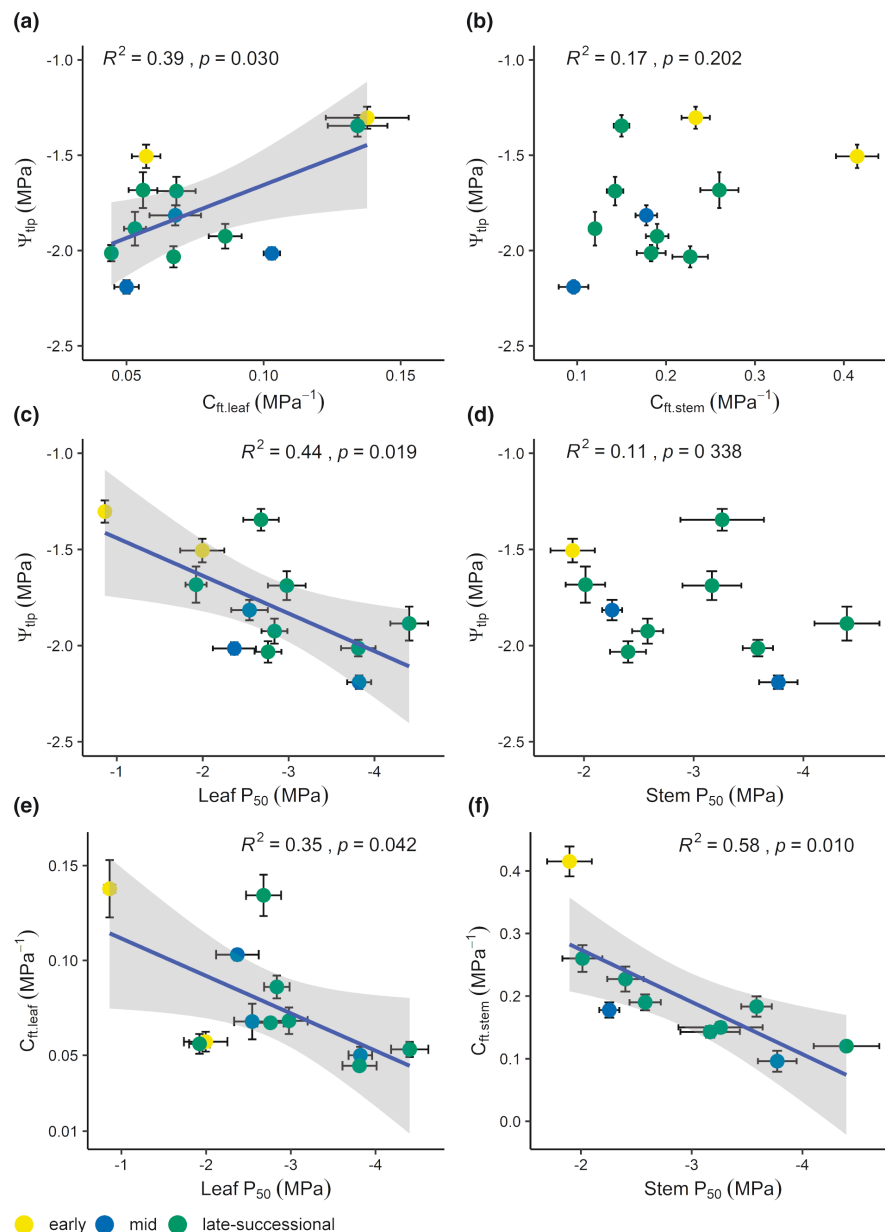
more susceptible to drought-induced mortality. What was surprising was that a number of mid- and late-successional species had similar characteristics. One mid-successional species, the palm *P. acuminata* var. *montana*, and the late-successional species, *D. excelsa*, had hydraulic traits similar to those of the early-successional species. All three of these species had safety margins under 1 MPa, P_{50} values higher than −3 MPa and a tendency to have high tissue water content, traits associated with reduced drought tolerance. In a greenhouse drought experiment with tropical dry forest species from Mexico (748 mm year^{-1}), there was no clear difference in loss of hydraulic conductivity between early- and late-successional species, instead, there was variation among species within each successional group (Pineda-Garcia et al., 2013). Two early-successional species from a seasonally dry tropical forest in Panama (~2100 mm year^{-1}) differed in their wood density, vulnerability to loss of hydraulic conductivity and water storage capacity (McCulloh et al., 2012).

However, in a Bolivian tropical dry forest (1160 mm year^{-1}), species seemed to align with life history; pioneer species tended to be more vulnerable to loss of hydraulic conductivity, had less dense wood and higher maximum hydraulic conductivity compared to shade-tolerant species, although there was still considerable trait variation within life-history groups (Markesteijn, Poorte, et al., 2011; Markesteijn, Poorter, et al., 2011).

Community-level diversity for drought resistance and variation in levels of drought resistance across species that are dominant at different stages of succession could lead to shifts in species composition due to drought. We found that some of the most dominant species within the community were actually the most vulnerable to drought. In contrast, some of the least abundant species, such as *M. guyanensis*, had the highest resistance to embolisms, the widest safety margins, with large trees of this species actually increased their growth during drought. Expected increases in extreme

drought events in tropical environments, including the Caribbean (Khalyani et al., 2015; Ramseyer et al., 2019), could lead to shifts in species composition in tropical forests, a change that is already occurring in some other ecosystems (Fauset et al., 2012; Trugman et al., 2020). Anderegg et al. (2018) showed that hydraulically diverse ecosystems responded better to drought than less diverse ones, and while we found a high level of hydraulic diversity in our community, the most drought-resistant species were all mid- and late-successional with lower levels of dominance within the community. *D. excelsa*, the key species in the mid-elevation subtropical wet forest and the palm, *P. acuminata var. montana*, which is by far the most dominant species in the tropical montane forests at our study site, had some of the lowest resistance to drought based on hydraulic traits. Under future increased drought scenarios, high mortality rates of these and other dominant species could lead to drastic changes in the composition and function of the forests in Puerto Rico and the Caribbean.

4.3 | Species exhibited large variation in hydraulic strategies and drought resistance

Species within our community fell along a gradient of levels of embolism and drought resistance. We found over a fivefold difference in P_{50} values across species and SM_{P50}s ranged from close to zero to around 2.5 MPa. Consistent with our findings, several studies have observed a wide range in P_{50} values within forest communities elsewhere (Barros et al., 2019; Fontes et al., 2020; Oliveira et al., 2019; Powers et al., 2020; Santiago et al., 2018; Ziegler et al., 2019). The wide range in SM_{P50}s 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_{P50}s to sustain CO_2 assimilation for as long as possible before closing their stomata as water becomes more limited (Barros et al., 2019; Choat et al., 2012; Fontes et al., 2020; Tyree & Sperry, 1988). Although a growing number of studies have found that wider SM_{P50}s are common within and across communities (Barros et al., 2019; Benito Garzón et al., 2018; Martin-StPaul et al., 2017; Powers et al., 2020; Smith-Martin et al., 2020; Ziegler et al., 2019), seven of the 12 species we studied did have SM_{P50}s < −1 MPa, indicating that the majority of species were operating close to their hydraulic capacity.

The large community-level variation in hydraulic traits in our study could be driven by a lack of uniform environmental pressure towards drought resistance since rainfall is typically high at our study site (~3700 mm year^{-1}) and largely aseasonal. We observed very large within-community ranges in P_{50} values (−0.86 to −4.40 MPa) and SM_{P50}s (−0.44 to 2.60 MPa). Two recent studies of lowland tropical rainforest canopy species of the Guiana Shield in French Guiana (~3102 mm year^{-1}) also found a large range of variation in P_{50} across 26 species (−1.86 to −7.63 MPa) and HSMs values (−0.09 to 5.64 MPa; Santiago et al., 2018; Ziegler et al., 2019). However, in

contrast to our findings, 15 of their studied species had P_{50} values below −3 MPa and 17 species had HSMs greater than 1 MPa, which potentially allow these species to withstand severe drought, whereas only three of our species had P_{50} values lower than −3 MPa and only five species SM_{P50}s greater than 1 MPa (Santiago et al., 2018; Ziegler et al., 2019). Working in a drier Central Amazonian rainforest near Manaus (2200 mm year^{-1}), Oliveira et al. (2019) found that 28 tree species had a range of P_{50} values of −0.88 to −4.18 MPa and only nine species had P_{50} lower than −3 MPa, similar to our findings. A second study at two different locations in Central Amazonian forests (2140 mm year^{-1} and 2376 mm year^{-1}) using a largely different set of species found a range in P_{50} values of only −0.59 to −2.59 MPa across 16 species with the majority of P_{50} values above −2 MPa suggesting that like ours, species in this community are not very embolism resistant (Fontes et al., 2020). Yet a third study conducted at two different Amazonian forest sites with contrasting precipitation patterns found similar trends in P_{50} and SM_{P50} in both forests despite the substantial difference in rainfall patterns (Barros et al., 2019). In the first site, a forest with low seasonality in Central Amazonia (2400 mm year^{-1}), P_{50} values ranged from −1.01 to −4.47 MPa across 17 species with only four species having values below −3 MPa and SM_{P50} ranged from −0.34 to 2.49 MPa with only three species above 1 MPa. In the second site, a seasonal forest in Eastern Amazonia (1900 mm year^{-1}), P_{50} ranged from −1.75 to −5.02 MPa across 12 species with again only four species having values lower than −3 MPa and SM_{P50} ranged from −1.44 to 3.79 with only four species having SM_{P50} above 1 MPa. Oliveira et al. (2019) had proposed that Central Amazonian rainforest species were more embolism resistant than expected for tropical rainforests (P_{50} values −0.18 to −6.30 MPa; mean − 1.55 MPa) based on a global meta-analysis (Choat et al., 2012) and suggested that such variation had arisen from species adaptations to local topographic and low-nutrient conditions. However, our findings and those of these recent studies (Barros et al., 2019; Oliveira et al., 2019; Santiago et al., 2018; Ziegler et al., 2019) suggest that wet tropical environments may have a greater range in levels of embolism resistance than previously thought.

To survive in drier environments, species must be drought resistant. In tropical wet forests, however, divergent biogeographical histories (Baker et al., 2020; Dick & Pennington, 2019) coupled with the lack of selective pressure from climate may be leading to this greater range in levels of drought resistance among forest species. This variation could make some species within these communities disproportionately vulnerable to extreme drought events and lead to changes in community composition. However, there is also great variation among wet rainforest communities in the preponderance of drought-resistant strategies with some forests dominated by drought-resistant species (e.g. some forests near Manaus, Central and Eastern Amazonia, and in French Guyana, Barros et al., 2019; Oliveira et al., 2019; Santiago et al., 2018; Ziegler et al., 2019) and others by drought vulnerable ones (e.g. Puerto Rico, other forests near Manaus; Fontes et al., 2020). The origins and causes of this variation offer an interesting research avenue.

4.4 | There was a trade-off between drought tolerance and drought avoidance

We found a clear trade-off between drought avoidance (high capacitance) and drought tolerance (high resistance to xylem embolisms). Among the species we studied, there was more than a threefold difference in leaf and stem capacitance, and some of the species with the greatest water storage in their leaves and stems also had the least negative P_{50} values. This pattern was particularly marked for the two early-successional species *A. latifolia* and *C. schreberiana* and two of the most dominant species at the site, *D. excelsa* and *P. acuminata* var. *montana*, which had high water storage capacitance and high xylem vulnerability to embolisms. Our results coincide with previous findings of a synthesis of data from multiple sites which found a trade-off between capacitance and P_{50} for tropical species (Christoffersen et al., 2016); here we show this pattern operates at the community level. Yet, in a lowland seasonal forest in French Guiana with a similar mean annual precipitation as our site, Santiago et al. (2018) did not find a correlation between stem capacitance and xylem vulnerability meaning that this trade-off may be site-specific.

5 | CONCLUSIONS

Climate models predict more severe droughts in the Caribbean region (Khalyani et al., 2015; Ramseyer et al., 2019), but few studies have considered how drought affects Caribbean forests but see (Reyer et al., 2017; Schwartz et al., 2019; Umaña & Arellano, 2021; Yu et al., 2007) and none have examined hydraulic strategies of tree species in the region. Our study shows that wet Puerto Rican forests are hydraulically diverse and that most species experienced a decline in growth during the drought. However, we found only a weak link between drought growth declines and hydraulic traits. Although hydraulic traits may not have proven to be a robust predictor of growth declines during drought at our site, some of the most dominant species in this forest had some of the lowest resistance to drought based on hydraulic traits. Increases in drought frequency could lead to sweeping changes in species composition and function in Puerto Rican and Caribbean forests.

CONFLICT OF INTEREST
The authors have no conflicts of interest.

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SUPPORTING INFORMATION

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