Received: 17 June 2023 | Accepted: 21 September 2023
DOI: 10.1111/1365-2435.14451

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Shifts in wood anatomical traits after a major hurricane

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Funding information
Carl Tryggers Foundation, Grant/Award Number: CTS 19:247; Swedish Phytogeographical Society; Vetenskapsrådet, Grant/Award Number: 2019-03758; US National Science Foundation, Grant/Award Number: 1546686, 1050957, 0620910 and DEB-1801315

Handling Editor: Antonella Gori

Abstract

1. Trait variation across individuals and species influences the resistance and resilience of ecosystems to disturbance, and the ability of individuals to capitalize on postdisturbance conditions. In trees, the anatomical structure of xylem directly affects plant function and, consequently, it is a valuable lens through which to understand resistance and resilience to disturbance.
2. To determine how hurricanes affect wood anatomy of tropical trees, we characterized a set of anatomical traits in wood produced before and after a major hurricane for 65 individuals of 10 Puerto Rican tree species. We quantified variation at different scales (among and within species, and within individuals) and determined trait shifts between the pre- and posthurricane periods. We also assessed correlations between traits and growth rates.
3. While the majority of anatomical trait variation occurred among species, we also observed substantial variation within species and individuals. Within individuals, we found significant shifts for some traits that generally reflected increased hydraulic conductivity in the posthurricane period. We found weak evidence for an association between individual xylem anatomical traits and diameter growth rates.
4. Ultimately, within-individual variation of xylem anatomical traits observed in our study could be related to posthurricane recovery and overall growth (e.g. canopy filling). Other factors, however, likely decouple a relationship between xylem anatomy and diameter growth. While adjustments of wood anatomy may enable individual trees to capitalize on favourable postdisturbance conditions, these may also influence their future responses or vulnerability to subsequent disturbances.

KEYWORDS
disturbance, hydraulic conductivity, Puerto Rico, tropical trees, wood anatomy

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1 | INTRODUCTION

Disturbances dramatically alter abiotic conditions, patterns of resource availability and competitive dynamics in local communities (Pickett & White, 1985). Much of the literature on ecological succession has focussed on arrival and establishment of new recruits and subsequent patterns of species turnover (Connell & Slatyer, 1977; Pacala & Rees, 1998) but surviving individuals also play a major role in postdisturbance community dynamics (Dietze & Clark, 2008; Uriarte et al., 2012). Better understanding the mechanisms that underpin how individuals and species respond to disturbance is critical for predicting the consequences of ecological disturbance.

Disturbance regimes in many tropical regions are dominated by cyclonic storms, which are predicted to occur with higher frequency and intensity under climate change (Balaguru et al., 2018). Strong storms cause defoliation, structural damage and tree mortality, which dramatically alter the structure, composition and resource conditions of forests (Leitold et al., 2021; Mitchell, 2013; Uriarte et al., 2004, 2019). However, increased levels of resource availability in the wake of storms (e.g. increased light availability, reduced belowground competition) can promote rapid growth of surviving trees. In Puerto Rico, for example, Walker (1991) showed that a majority of trees had recovered foliage just 7 weeks after hurricane Hugo. Umaña and Arellano (2021) reported increased diameter growth rates after hurricanes for some species, and Hogan et al. (2018) also showed elevated stand-level diameter growth rates following Hurricane Hugo. In Jamaica, Bellingham et al. (1995) reported diameter growth rates up to eight times higher shortly after Hurricane Gilbert than prehurricane periods. Tanner et al. (2014) subsequently showed that these elevated growth rates persisted for more than 20 years after Hurricane Gilbert, in particular for trees that suffered low amounts of crown damage from the hurricane. The large magnitude of growth rate changes following hurricanes raises questions about underlying anatomical features that might facilitate elevated growth rates among some trees.

Although a large literature deals with the physical properties of wood that confer resistance to wind damage (e.g. de Langre, 2008), very limited information is available on how individual trees may adjust anatomical traits in response to wind disturbance, including hurricanes. For one species (*Cyrilla racemiflora*) from wet forests of Puerto Rico, Drew (1998) reported elevated wood production and flowering after Hurricane Hugo that was associated with increased vessel density. We are not aware of other studies that have explored variation in wood anatomy with respect to wind disturbance. In general, however, Michaletz (2018) highlighted the response of xylem anatomy to disturbance as a research priority due to the broad consequences for ecosystem functioning and the resistance and resilience of trees to subsequent disturbances.

Based on the functional role of xylem anatomy, wood produced during posthurricane conditions may differ in predictable ways from wood produced in undisturbed conditions (Table 1). Within an individual tree, for example, anatomical traits that confer increased hydraulic conductivity (e.g. larger vessel diameters, more vessels, more highly grouped vessels) could enable it to rapidly capitalize on higher resource conditions after a storm (Martínez-Vilalta et al., 2012; Tyree & Zimmermann, 2013). In undisturbed conditions, an increase in vessel size at the trunk base is expected as a tree grows taller to make up for the increase in the total flow path resistance (due to increased tree height; Echeverría et al., 2019). However, in the context of short-term response to hurricane disturbance, when trees lose canopy area and total height (Leitold et al., 2021), an increase in vessel area could reflect a transient period where vessels are larger than expected for a given tree height to facilitate regeneration of the canopy (Olson et al., 2021). Phenotypic accommodation of vessel anatomy in response to hurricanes could, at least in the short term, lead to an increased rate of total carbon assimilation, and, potentially, increased diameter growth rate. Apart from long-distance water transport, wood performs other vital functions, particularly, radial transport of water and nutrients in ray parenchyma as well as water and nutrients storage in parenchyma (ray and axial) and living fibres. These tissues may also therefore be expected to change during the high-resource conditions following a hurricane. For example, we might expect wood produced after a hurricane to have lower fraction of living cells (i.e. parenchyma or living fibres) if relatively more carbon is devoted to growth as opposed to storage and metabolism of living cells (Chapin et al., 1990; Plavcová et al., 2016).

In September 2017, two major hurricanes (Irma and Maria) struck the Caribbean island of Puerto Rico and caused nearly complete defoliation, extensive damage to the forest canopy, and high levels of instantaneous tree mortality (Hall et al., 2020; Leitold et al., 2021; Uriarte et al., 2019). Here, we focus on individual trees and the variation in anatomical traits of wood produced before and after these hurricanes. We sampled 65 individuals representing 10 focal species that span a broad range of life-history strategies to address the following questions:

1. What is the magnitude of variation in wood anatomical traits expressed within individuals relative to within and among species before and after the 2017 hurricanes?
2. How did anatomical properties differ in wood produced before and after the 2017 hurricanes?
3. Are wood anatomical traits associated with tree diameter growth rates?

2 | MATERIALS AND METHODS

2.1 | Study site, focal species and tree selection

We conducted this study in the Luquillo Forest Dynamics Plot (LFDP; 18° 20′ N, 65° 49′ W) in El Yunque National Forest, Puerto Rico, with permission from the Luquillo LTER. The LFDP is located on volcanic soils at ca. 400 m a.s.l. The climate is mostly aseasonal with mean annual rainfall of ca. 3500 mm year^{-1} (Figure S1). All free-standing woody stems in the LFDP are tagged, identified and measured for diameter at 1.3 m above the ground (DBH)

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TABLE 1 Wood anatomical traits quantified in this study and their expected association with elevated posthurricane growth at the within-individual scale.

Trait [abbreviation] (units)	Predicted response to hurricane (elevated growth)	Rationale	References
Median vessel lumen area [A_{50}] (μm^2)	+	Rapid posthurricane growth should be facilitated by wider vessels	Fan et al. (2012), Hietz et al. (2017) and Poorter et al. (2010)
95th percentile of vessel lumen area [A_{95}] (μm^2)	+	Rapid posthurricane growth should be facilitated by wider vessels	(*see* A_{50})
Skewness of vessel distribution [V_{skew}]	−	Rapid posthurricane growth should be facilitated by more large vessels and fewer small vessels. More negative value of skewness indicates fewer small vessels	(*see* A_{50})
Area-based sum of theoretical conductivity [Kh_{area}] ($m^4/MPa^1\ s^1\ mm^2$)	+	Rapid posthurricane growth should be supported by higher conductivity	(*see* A_{50})
Vessel fraction [F_{ves}] ($\mu m^2/\mu m^2$)	No change	The expected increase in vessel area will be balanced off by decreased vessel number. Consequently, vessel fraction will not change	Zanne et al. (2010)
Fibre fraction [F_{fib}] ($\mu m^2/\mu m^2$)	+	Fibre fraction should increase if parenchyma fraction decreases	
Total parenchyma fraction [$F_{par(total)}$] ($\mu m^2/\mu m^2$)	−	Parenchyma fraction in posthurricane wood should decline if carbon used for parenchyma respiration or for carbohydrate storage could be used instead for growth. This trend is expected in the absence of living fibres, which also can store carbohydrates	Chapin et al. (1990) and Plavcová et al. (2016)
Axial parenchyma fraction [$F_{par(axial)}$] ($\mu m^2/\mu m^2$)	−	The expected decrease in total parenchyma fraction would be chiefly driven by decreases in axial parenchyma fraction	
Ray parenchyma fraction [$F_{par(ray)}$] ($\mu m^2/\mu m^2$)	+	Increased ray fraction in posthurricane wood would enhance radial movement of resources to be spent on growth and other maintenance processes	Pfautsch (2016)
Vessel density [V_{den}] (mm^{-2})	−	Vessel density is typically negatively correlated with vessel area. We expect wider vessels (at a lower density) to support rapid posthurricane growth	Zanne et al. (2010)
Vessel grouping index [V_{grp}]	+	Increased integration of hydraulic network (larger vessel groupings)	Lens et al. (2011), Martínez-Vilalta et al. (2012) but see Loepfe et al. (2007)

approximately every 5 years. For this study, we used DBH measurements from the 2011 and 2016 censuses to quantify prehurricane diameter growth rates.

We equipped a subset of trees that survived the 2017 hurricanes with metal band dendrometers in April–June 2018 ($Dendro_0$), 6–9 months after the hurricanes. Trees were given a score of physical hurricane damage (low, medium, high). Dendrometers were first measured in December/January 2018–2019 ($Dendro_1$), January/February 2020 ($Dendro_2$) and finally in July 2020 ($Dendro_3$), at the time of tree core collection (see below). We computed posthurricane growth rates based on measurements of DBH during installation of dendrometers and the final dendrometer measurement ($Dendro_3$). In designing our field sampling, we first identified trees with positive posthurricane growth to ensure that there was sufficient woody material to sample. We also focused on trees with relatively high posthurricane growth rates (relative to prehurricane growth rates) because we sought to evaluate anatomical characteristics that might facilitate high posthurricane growth rates. Nevertheless, growth rates of the sampled trees varied considerably during the pre- and posthurricane periods, and several trees had reduced growth rates in the posthurricane period (Figure 1).

2.2 | Field sampling and determination of pre- and posthurricane wood

In July 2020, potential focal trees were located in the field and excluded if they were dead, heavily damaged, leaning, on a steep slope or had an irregular shaped trunk. We selected 65 individuals, corresponding to 4–8 trees from each one of the 10 focal species for anatomical sampling (Table 2). For each tree, we recorded tree height, DBH and the dendrometer measurement ($Dendro_3$). We then

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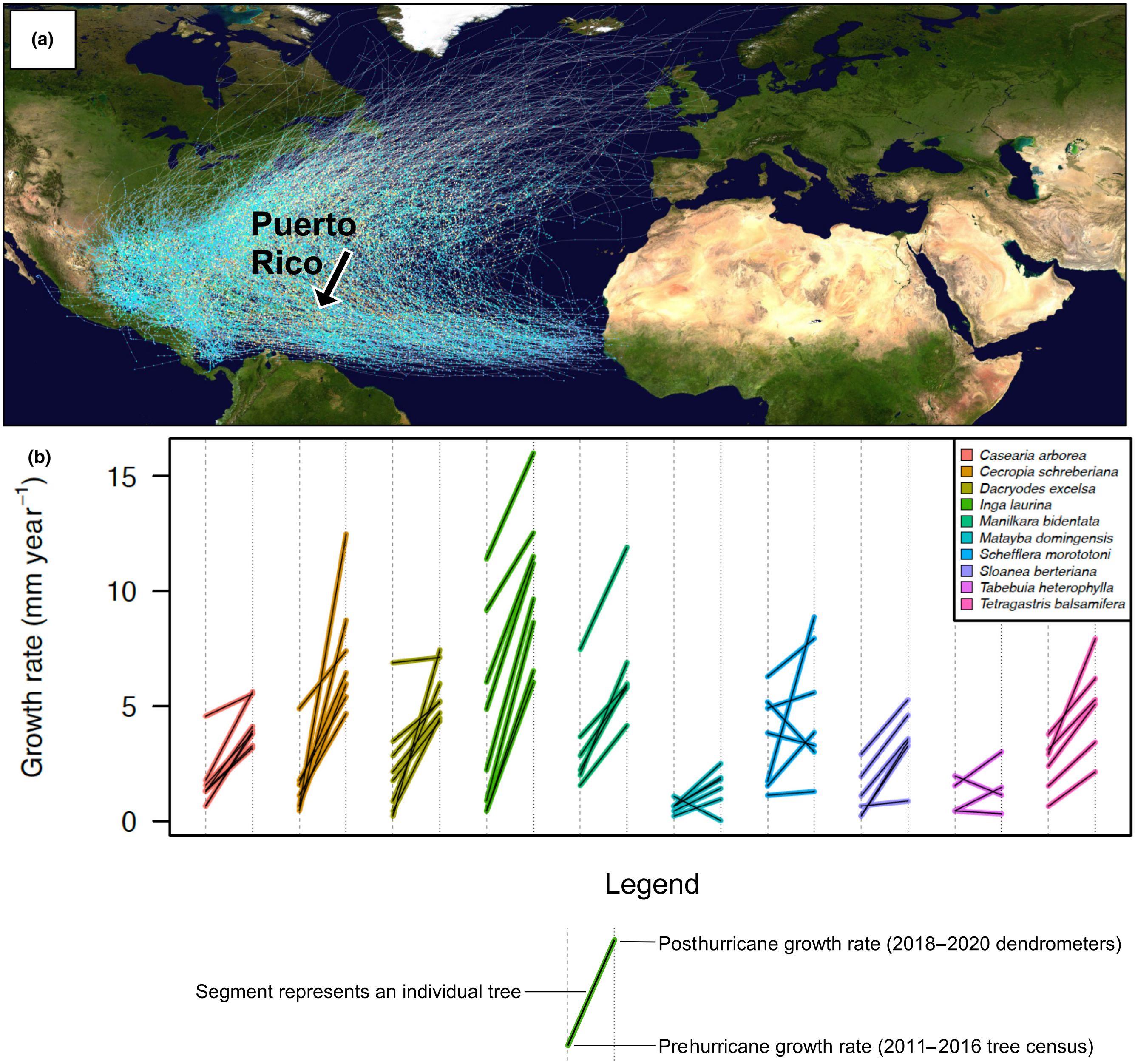

FIGURE 1 (a) Map of tracks for all Atlantic hurricanes from 1851 to 2012 based on data from the US National Hurricane Center. Image modified from en.wikipedia.org/wiki/Atlantic_hurricane#/media/File:Atlantic_hurricane_tracks.jpg. (b) Individual stem diameter growth rates before and after the 2017 hurricane season for sampled trees of 10 studied species.

collected two cores ca. 3 cm long using a 1-cm-diameter tenon plug cutter mounted on an electric drill from each focal tree at opposite sides of the main trunk and perpendicular to the terrain slope. Cores were taken at 1 m height and 10–20 cm below a dendrometer band. We stored wood samples in 70% ethanol until further processing.

To estimate the boundary between wood produced before and after the 2017 hurricanes, we computed a posthurricane diameter growth rate (mm day^{-1}) for each tree based on dendrometer readings from Dendro$_1$ (Dec/Jan 2018–19) to Dendro$_2$ (Jan/Feb 2020) (i.e. the growth interval closest to the hurricanes where we had consecutive dendrometer readings). We then estimated the location of the cambium when Hurricane Maria made landfall in Puerto Rico (20 September 2017) relative to the cambium at the time of sample collection (July 2020) by multiplying the posthurricane growth rates by the number of days between the first dendrometer measurement (Dendro$_1$) and the day hurricane Maria made landfall in Puerto Rico. We consider this as the putative boundary between wood produced before and after hurricane Maria (DBH$_{\text{Maria}}$). We restricted the prehurricane samples to wood produced between the 2011 LFDP census and DBH$_{\text{Maria}}$.

2.3 | Sample preparation and anatomical analyses

We made cross-sections of cores (ca. 20–40 μm thick) and imaged them with a ZEISS Axioscan 7 slide scanner to obtain digital

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TABLE 2 Species, families, number of trees per species sampled for anatomical traits in the Luquillo Forest Dynamics Plot, Puerto Rico. Successional status based on expert knowledge from the study area.

Family	Species	Authority	*N*	Successional status
Salicaceae	*Casearia arborea*	(Rich.) Urb.	8	Mid
Urticaceae	*Cecropia schreberiana*	Miq.	7	Early
Burseraceae	*Dacryodes excelsa*	Vahl	8	Late
Fabaceae	*Inga laurina*	(Sw.) Willd.	8	Mid
Sapotaceae	*Manilkara bidentata*	(A.DC.) A. Chev.	6	Late
Sapindaceae	*Matayba domingensis*	(DC.) Radlk.	6	Late
Araliaceae	*Schefflera morototoni*	(Aubl.) Maguire, Steyerm. & Frodin	7	Early
Elaeocarpaceae	*Sloanea berteroana*	Choisy ex DC.	6	Late
Bignoniaceae	*Tabebuia heterophylla*	(DC.) Britton	4	Mid
Burseraceae	*Tetragastris balsamifera*	(Sw.) Oken	6	Late

images of cross-sections at 0.195 μm^2 resolution. Vessels were autodetected and then manually confirmed and annotated using the QuPath software (Bankhead et al., 2017) and then exported as SVG files for downstream measurements in R v 4.0.3 (R Development Core Team, 2020; Figure 2).

With the annotated images, we measured vessel lumen area and diameter (from equivalent circle area), as well as the distance from each vessel to the cambium along the shortest path parallel to the rays. We then summarized a suite of anatomical traits in the wood corresponding to the pre- and posthurricane periods, separately. In particular, we measured the median and 95th percentile of vessel lumen area (A_{50} and A_{95}; μm^2), skewness of the distribution of vessel area (V_{skew}), vessel density, or number of vessels per unit area (V_{den}; N/mm^2) and the vessel group index (V_{grp}) (Scholz et al., 2013). To delineate vessel groups, we measured double vessel wall thickness on at least 70 vessels per species and used the species-mean values as thresholds to define grouped vessels (von Arx et al., 2013). V_{grp} quantifies the total number of vessels divided by the total number of vessel groupings; a sample with no grouped vessels has a $V_{grp}=1$, larger values indicate a greater degree of grouping. We calculated theoretical hydraulic conductivity (Kh) for each vessel as $Kh = pi * D^4/128 * \eta$, where D is equivalent circle diameter and η is the viscosity index of water (1.002×10^{-9} MPa s at 20°C; Scholz et al., 2013). Then, we computed an area-based metric of theoretical hydraulic conductivity, Kh_{area}, as the sum of Kh for vessels in a given portion of the sample (pre- or posthurricane) and then divided by the corresponding area in mm^2 (equivalent to "xylem specific conductivity" in Castagneri et al., 2020). Only one species (*Manilkara bidentata*) had tracheids (vasicentric sensu Carlquist, 2001; vascular sensu IAWA Committee, 1989), which were classified as vessels because they were impossible to discern from narrow vessels. We also measured vessel, fibre and parenchyma (total, axial and ray) fractions (F_{ves}, F_{fib}, $F_{par(total)}$, $Fpar_{(axial)}$, $F_{par(ray)}$; $\mu m^2/\mu m^2$) in the wood produced before and after the 2017 hurricanes for each sample. Seven species had septate fibres that contained starch (in some cases they were abundant), which we grouped with nonliving fibres in our measurements. In all species, the ground tissue fibres had minutely bordered pits (fibre-trachaids sensu Carlquist, 2001), which indicates that vessels (and tracheids in *M. bidentata*) were the only conductive cells. To quantify tissue fractions, we overlaid a grid of 0.16 mm^2 resolution on the image and manually determined the tissue type at each intersection point (Ziemińska et al., 2015). The mean (±SD) of the number of intersection points per sample (pre- and posthurricane portions are treated here as separate samples) was 329 (±230).

2.4 | Statistical analyses

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Population	Individual	4–8 individuals per species
Species	Individual	10 species

2.5 | Variance partitioning of anatomical traits

To address our first question about the structure of variation in wood anatomical properties, we used a nested variance partitioning approach (Messier et al., 2010). Specifically, we fit linear mixed models with a fixed intercept and nested random effects for species, tree and period (pre- vs. posthurricane). This approach quantified the variation expressed among species, within species, within individual trees, and residual variance corresponding to individual variation within wood produced during either the pre- or posthurricane period. All variables except for V_{skew} and tissue fractions were log-transformed prior to analysis to improve normality.

2.6 | Comparing traits in pre- and posthurricane wood

To address our second question about adjustments of individual trees in wood anatomy following hurricane disturbance, we fit

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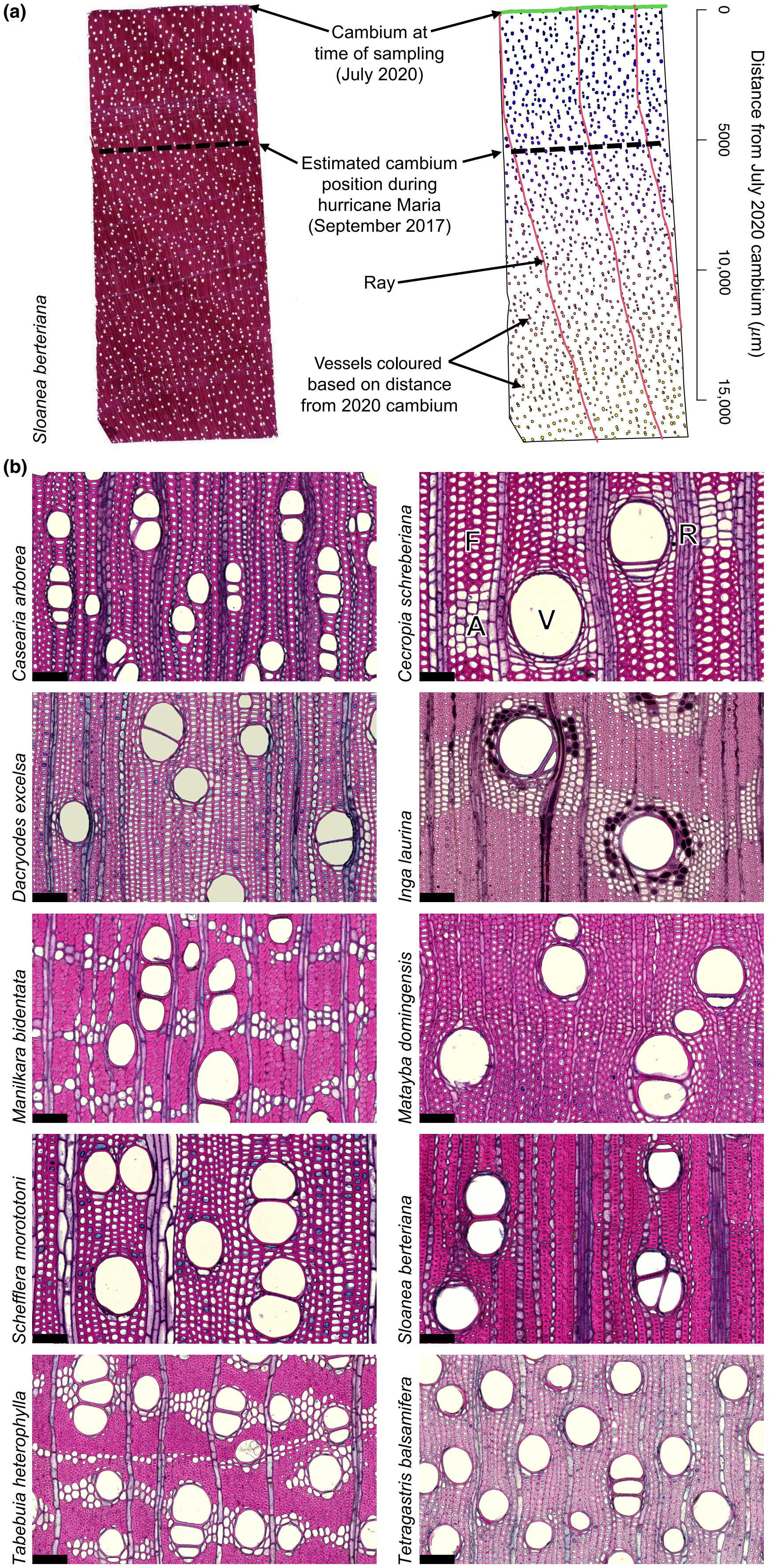
FIGURE 2 Example of our image processing and analysis workflow (a) and cross-sections of 10 studied species (b). Note that the putative location of the cambium at the time of the hurricane is shown, for convenience, as a line but in our calculations this was estimated perpendicular to the rays (see main text). Image of *Cecropia schreberiana* contains labels: V—vessel, A—axial parenchyma, R—ray, F—fibres. Scale bar: 100 µm.



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hierarchical Bayesian models to evaluate differences within trees for each anatomical trait in wood produced before and after the 2017 hurricanes. The first level took the form:

$$\Delta t_{is} \sim b_{0s} + b_1{}^{*}\, \Delta \mathrm{DBH}_{is} + b_2{}^{*}\, \mathrm{Damage}_{is} + \sigma \tag{1}$$

where Δt_{is} is the difference between the pre- and posthurricane values (postvalue minus prevalue) for a given anatomical trait in individual tree *i* of species *s*. The term b_{0s} represents a vector of species-specific intercepts (the mean shift in an anatomical variable between post- and prehurricane wood for all individuals of species *s*). The parameters b_1 reflects the average effect of tree diameter growth (ΔDBH; change in diameter during the posthurricane period) to control for expected increases in vessel size from increases in tree height due to the universal base-to-tip vessel tapering relationship (Olson et al., 2021). The parameter b_2 reflects the damage category assigned to the tree during dendrometer installation. We used ΔDBH instead of change in height because we lack measurements of tree height prior to the 2017 hurricanes, and σ represents a normally distributed error term. We modelled species-level intercepts (which reflect average shifts of individuals within species of anatomical traits from the pre- to posthurricane period) in a second level as:

$$b_{0s} \sim B_1 + e_s \tag{2}$$

where B_1 is the overall (i.e. interspecific) intercept and e_s are normally distributed random effects for species. Prior to model fitting, we standardized ΔDBH values within species to mean zero and unit standard deviation to facilitate model convergence and parameter interpretation. We interpret b_{0s} and B_1 as the species-average and interspecific responses (i.e. community-level), respectively, of a given wood anatomical trait, *t*, to hurricane disturbance. Positive (negative) values indicate higher (lower) values for the trait in wood produced after the 2017 hurricanes compared to wood produced before the hurricanes.

All parameters were given diffuse priors, and posterior sampling was conducted via Markov chain Monte Carlo (MCMC) using JAGS (Plummer, 2003) and the 'jagsUI' package (Kellner, 2015) in R v 4.0.3 (R Development Core Team, 2020). Model convergence was assessed based on the Rhat diagnostic. Estimated parameters were considered different from zero when 95% credible intervals did not overlap zero.

2.7 | Associations between anatomy and growth

To address our third question about the association between anatomical traits and growth rates, we used hierarchical Bayesian models (similar to those described above) to model individual tree diameter growth rates as a function of anatomical traits with separate models that compared (i) prehurricane growth rates with prehurricane traits, and (ii) posthurricane growth rates with posthurricane traits. The first level of these models took the form:

$$G_{is} \sim b_{0s} + b_{1s}{}^{*}\, t_{is} + b_2{}^{*}\, \mathrm{DBH}_{is} + b_3{}^{*}\, \mathrm{Damage}_{is} + \sigma \tag{3}$$

where G_{is} is the absolute growth rate (mm day^{-1}) of individual tree *i* of species *s*; b_0 is a vector of species-level intercepts; b_{1s} is a vector of species-level slopes that reflect the average association between growth rate and an anatomical trait, *t*, for a given species, *s*; b_2 and b_3 are interspecific (i.e. community-level) terms to account for differences in tree diameter at the beginning of the interval being modelled and damage category, and σ is a normally distributed error term. Note that the damage term was excluded from models analysing prehurricane growth and anatomy. Species-level terms were modelled in second level regressions as:

$$b_{0s} \sim B_0 + e_{0s} \tag{4}$$

$$b_{1s} \sim B_1 + e_{1s} \tag{5}$$

where B_0 and B_1 are the interspecific intercept and slope, and e_{0s} and e_{1s} are normally distributed random effects for species. As above, we standardized anatomical covariates and DBH values within species to mean zero and unit standard deviation prior to analysis. The b_{1s} and B_1 parameters reflect the species-level and interspecific associations, respectively, of growth rate to a given anatomical trait. We report results based on absolute diameter growth rates in the main text but we obtained similar results using basal area growth rates, presented in supplemental materials. Procedures for fitting these models followed those described for Question 2.

3 | RESULTS

Species exhibited substantial variation in wood anatomical parameters. For example, considering wood produced both before and after the 2017 hurricane season, A_{50} ranged more than an order of magnitude from about 3000 μm^2 for the mid-successional species, *Casearia arborea*, to ca. 32,000 μm^2 for the early successional species, *Cecropia schreberiana*. Diameter growth rates of the focal trees ranged from 0.21–11.4 mm year^{-1} in the prehurricane period to 0.02–16.0 mm year^{-1} in the posthurricane period (Figure 1b). Additional general comparisons of anatomical trait variation among the study species are illustrated for individual trees in Figure S2.

3.1 | Variance partitioning of anatomical traits

In general, the largest portion of trait variation occurred among species (41%–92%), with the exception of the parenchyma fraction ($F_{par(total)}$), which showed the largest portion of variation (47%) at the within-individual level, that is pre- vs posthurricane variation (Figure 3). Within-species variation accounted for 2%–38% of the total variation and the within-individual component accounted for 1%–47% of the total variation. Within-individual variation constrained to either the pre- or posthurricane period (termed 'within-period + residual' in Figure 3) consistently represented the smallest proportion of variation, explaining <5% per trait.

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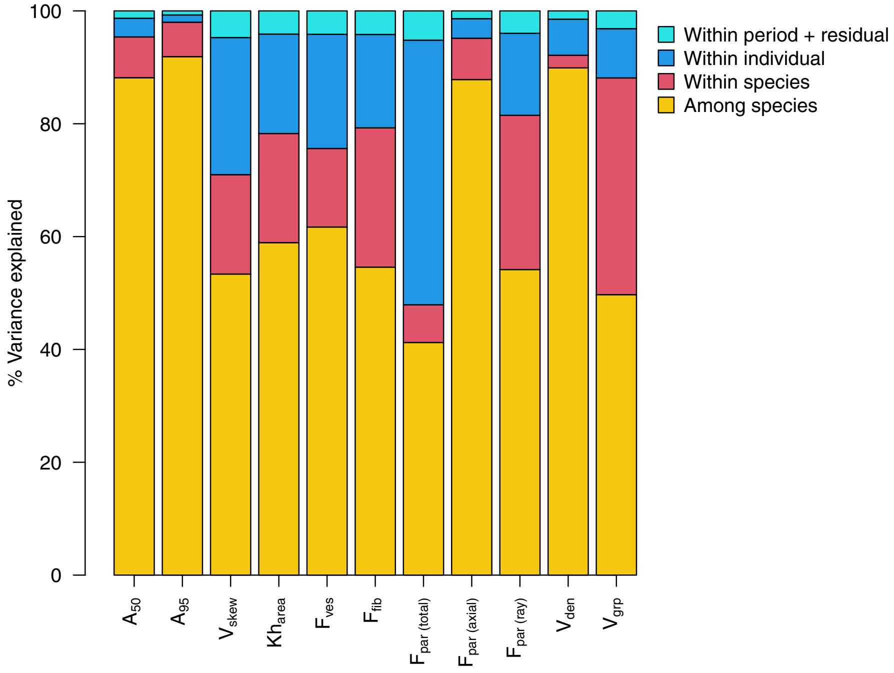

FIGURE 3 Variance partitioning for wood anatomical traits in 10 studied species. The proportion of within-individual variation includes anatomical data from wood produced before and after Hurricane Maria.

3.2 | Comparing traits in pre- and posthurricane wood

Among species (i.e. at the community-level), Kh_{area}, $F_{par(total)}$, $F_{par(ray)}$, and V_{den} were significantly higher in wood produced in the posthurricane period compared to the prehurricane period (Figure 4d,f,g,j; Figure S2), while F_{fib} was significantly lower (Figure 4f). There was also considerable support (i.e. 90% credible intervals did not overlap zero) for an increase in A_{95} (Figure 4b). Other anatomical traits did not show significant differences in pre- and posthurricane wood. Effects of ΔDBH on anatomical shifts were not statistically significant except that trees with higher ΔDBH had greater Kh_{area} and V_{den} in posthurricane wood compared to prehurricane wood (Figure S3). Effects of damage on anatomical shifts were not statistically significant except that more damaged trees tended to have lower A_{50} in posthurricane wood compared to prehurricane wood (Figure S3).

Shifts in anatomical traits were fairly consistent across species in the direction of their response but differed in terms of statistical significance. For instance, A_{50} and A_{95} showed a tendency to increase, indicating production of wider vessels in posthurricane wood compared to prehurricane wood (although the effect was only marginally significant for individuals of one species for A_{50}, and, for A_{95}, was significant in two species and marginally significant in another one, Figure 4a,b). V_{skew} tended to shift negatively across species (reflecting an increase in the size distributions of vessels in the posthurricane wood) but the effect was not significant for individual species (Figure 4c). Nine species showed a significant increase in Kh_{area} in wood produced after the hurricanes (Figure 4d). The tendency for F_{ves} to decrease was weak, with only one species showing a significant effect and another species showing a marginal significance (Figure 4e). F_{fib} tended to decrease after the hurricanes with three species showing significant effects and three showing marginally significant effects (Figure 4f). In terms of parenchyma fractions, $F_{par(total)}$ and $F_{par(ray)}$ consistently shifted towards increased values, with two species showing significant effects for $F_{par(total)}$, while for $F_{par(ray)}$ no individual species had a significant increase but six showed marginally significant increases (Figure 4g,i). There were no consistent or significant shifts in $F_{par(axial)}$ (Figure 4h). V_{den} tended to be higher in posthurricane wood for all species but the effect was significant for only three species and marginally significant for one (Figure 4j). There were no clear patterns (and no statistically significant species-level effects) for V_{grp} (Figure 4k).

3.3 | Coordination between growth and anatomy

We found few significant relationships between growth rates and anatomical traits when independently evaluating the pre- or posthurricane periods (Figure 5). Among species (i.e. at the community-level), there were no significant effects for any traits for the pre- and posthurricane periods. At the species level, we found significant associations between traits and growth rates only for *I. laurina* (five instances of significant and two marginally significant trait-growth relationships). Specifically, prehurricane growth rates were negatively associated with Kh_{area}, F_{ves} and V_{den} (Figure 5d,e,j). Posthurricane growth rates were positively associated with A_{50}, and $F_{par(total)}$, and negatively with F_{ves} and V_{den} (Figure 5a,e,g,j). For the remaining species, trait-growth relationships were not significant for either hurricane period. Although most species-level effects were non-significant for both the pre- and posthurricane periods, the range and variation of effects

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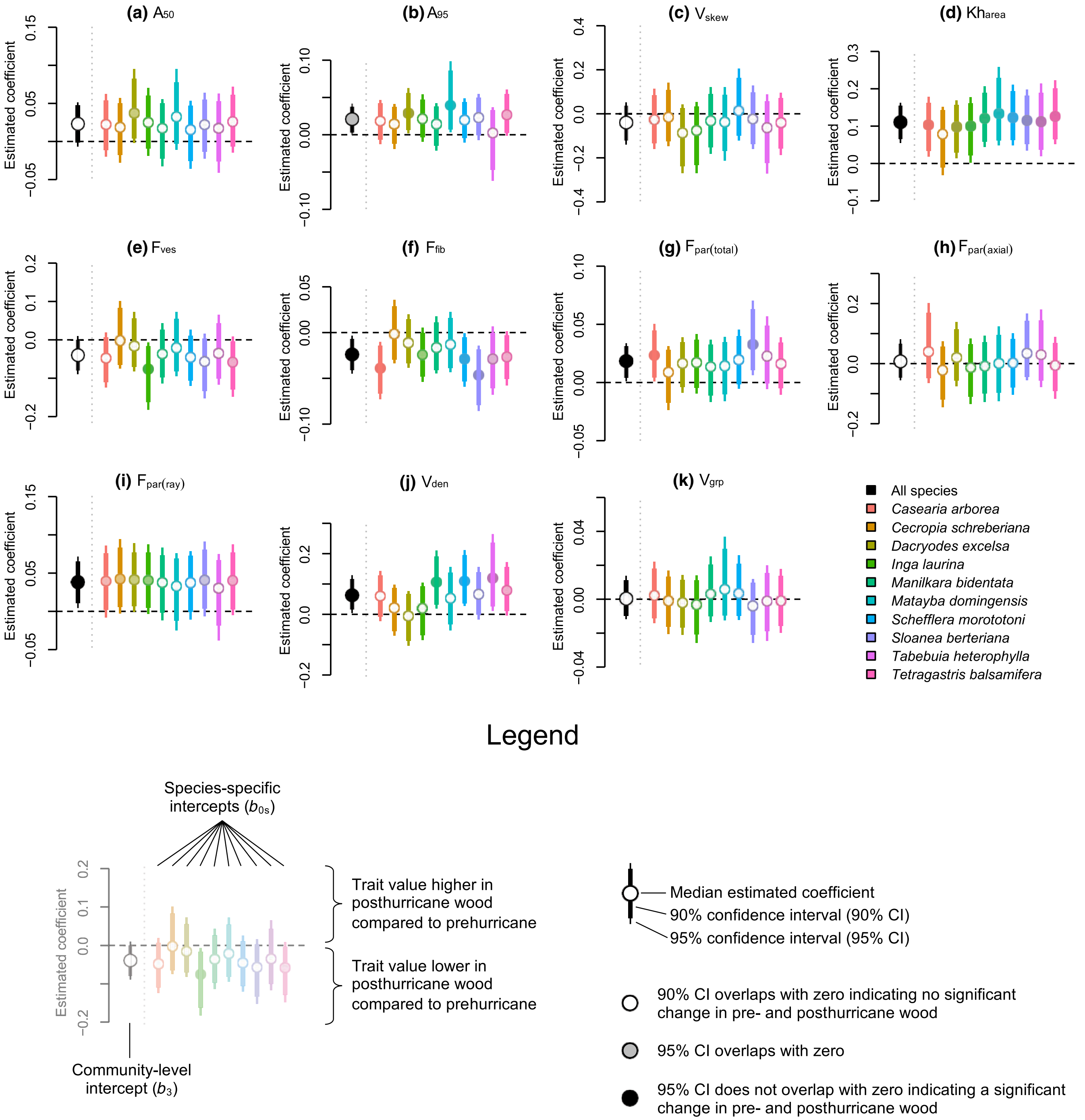

FIGURE 4 Estimated coefficients from hierarchical Bayesian models of shifts in 11 xylem anatomical parameters (panels a–k) before and after major hurricanes for 65 trees from 10 studied species. See Table 1 for abbreviations of anatomical parameters.

were notably larger for the posthurricane period. In general, larger trees tended to have higher prehurricane diameter growth rates than smaller trees, but the effect was not significant for posthurricane diameter growth rates and damage was not related to posthurricane growth rates in this study (Figure S4). Results for basal area growth rates were similar to those of diameter growth rate (Figure S5); although larger trees did tend to have high basal area growth rates in both the pre- and posthurricane periods (Figure S6).

4 | DISCUSSION

We characterized variation in xylem anatomy of wood produced before and after a major hurricane for 65 trees representing 10 species in Puerto Rico. Our main findings (1) reveal significant variation of anatomical traits within individual trees, suggesting that individual-level phenotypic accommodation in xylem anatomy can impact the response of tropical forest trees to hurricane disturbance; (2) provide evidence for directional shifts in xylem anatomical traits following hurricane disturbance that

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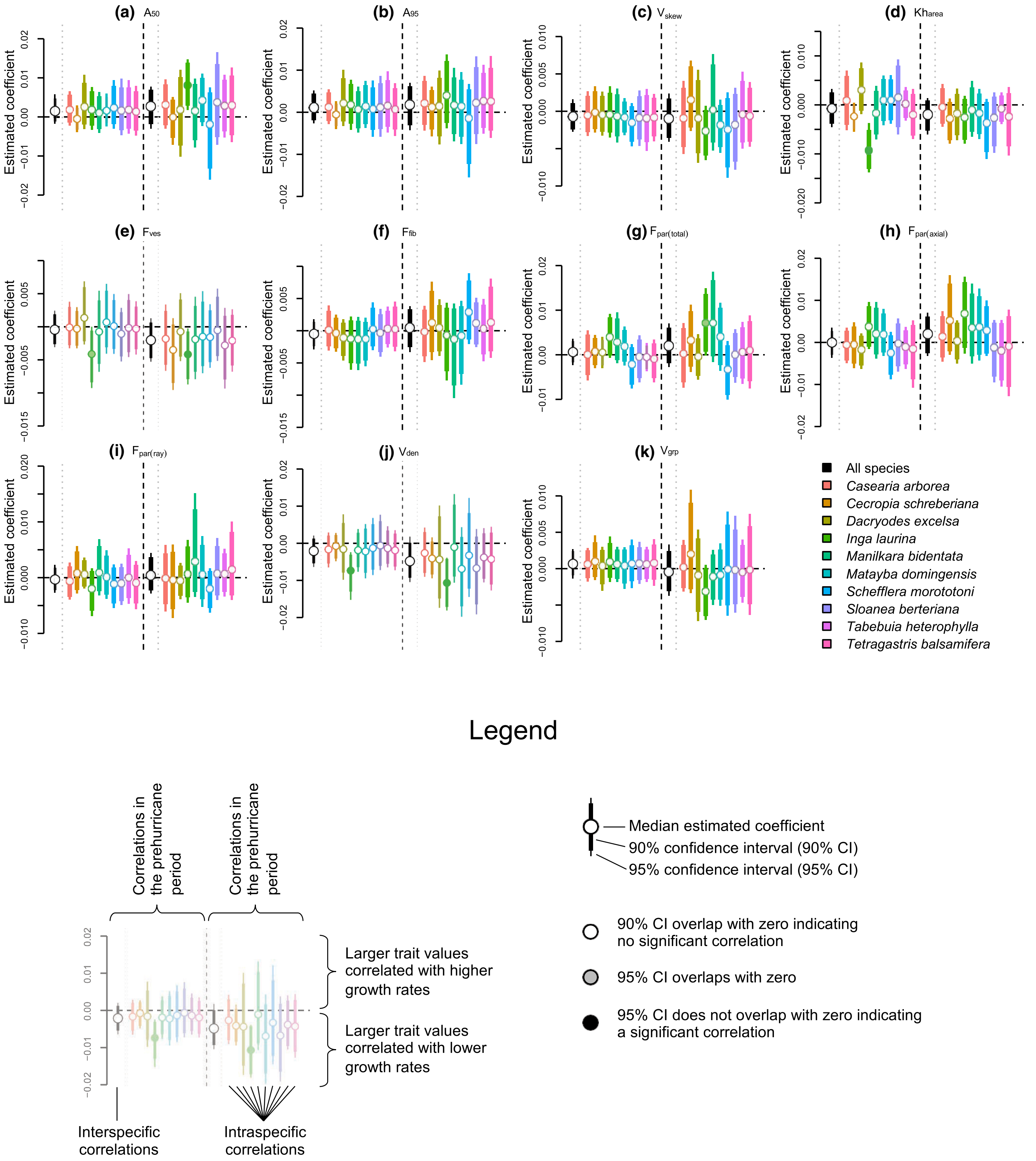

FIGURE 5 Correlations between stem diameter growth rates and anatomical traits in wood produced during the pre-hurricane (2011–2016) and posthurricane (2017–2020) periods for 65 trees from10 species of Puerto Rican trees, in models that include a term for size differences among individual trees.

were: (i) fairly consistent across species and (ii) generally associated with increased vessel area and density, theoretical hydraulic conductivity, total and ray parenchyma fractions and decreased fibre fraction; and (3) offer weak evidence for a direct association between individual tree diameter growth rates and wood anatomical traits.

4.1 | Structure of xylem anatomical variation

Because the species included in our study span a wide range of life-history strategies, exhibit high variation in previously measured functional traits, and have diverse responses to hurricanes

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(Uriarte et al., 2012; Zimmerman et al., 1994), we expected the majority of variation in xylem anatomical traits would occur among species. Nonetheless, previous research—including in our study area—has shown a high degree of trait variation within-species and within-individuals, which has important implications for population-level responses to environmental heterogeneity (Messier et al., 2010). Indeed, among-species variation represented the largest component of variation for all anatomical traits, explaining 41%–92% of the total variation in our measurements for a given trait. Overall, the magnitude of individual and within-species variation highlights the potential for intraspecific variation and phenotypic accommodation of anatomical traits to shape the response of trees to disturbance.

To some extent, the high degree of anatomical variation we found among species reflected our general understanding of life-history strategies across the focal species. Vessel lumen area, for example, was largest (by far) for the shade-intolerant pioneer, *C. schreberiana*, whereas several late successional, shade-tolerant species (e.g. *Manilkara bidentata*, *Matayba domingensis*) tended to have smaller vessels (Figure S2). However, another early successional species (*Schefflera morototoni*) had similar vessel sizes as some typically late-successional species (e.g. *Dacryodes excelsa* and *Sloanea berteroana*), while smallest vessels were observed in mid-successional species (*C. arborea*). It is important to note, however, that these descriptive generalizations do not account for differences in height of the trees sampled across species, which has a strong influence on vessel diameter (Olson et al., 2021). Future work focused on more general links between wood anatomy and tree life-history strategies will provide valuable additional context for our results.

4.2 | Directional shifts in anatomical traits following hurricanes

Dendrochronologists have long used within-individual variation of annual growth rings to study long-term climate variability. Although recent research has focused on detecting climate extremes and other environmental factors (e.g. fire, herbivore outbreaks) using xylem traits at inter- and intra-annual time scales, most studies have focused on temperate (often coniferous) forests with relatively few studies based on tropical angiosperms (but see e.g. Groenendijk et al., 2014; Zuidema et al., 2013).

We are aware of only one previous study (Drew, 1998)—based on one tree species in Puerto Rico (*Cyrilla racemiflora*, not included in our study)—that investigated response of wood anatomical traits to hurricane disturbance. Drew (1998) reported increased vessel diameter and vessel density in wood produced shortly after hurricane Hugo, corresponding to increased potential hydraulic conductivity, which was also associated with elevated wood production and flowering. In fact, Drew (1998) proposed that these patterns may reflect a general 'signature' of past hurricane disturbances.

Consistent with Drew (1998), we detected some directional shifts in xylem anatomical traits across individual trees and across species that correspond with increased hydraulic conductivity. The statistical significance of the species-level effects was mixed but rather consistent in terms of direction, at least for vessel traits related to hydraulic conductivity. Although increase in vessel size is expected as a means to offset an increase of total path length resistance due to height growth (Echeverría et al., 2019), we observed shifts in vessel traits and Kh_{area} even after taking into account shifts in DBH (used as a proxy for height growth). Moreover, while we lack individual-level data on height loss due to the hurricane for our focal trees, other research has shown that 73% of our study area lost ≥1 m in canopy height due to the 2017 hurricanes (mean loss 7.1 m) and showed that even by 2020, there remained a substantial net loss of canopy height (Leitold et al., 2021). These results suggest that most trees were likely shorter during the posthurricane period compared to the prehurricane period, despite continued diameter growth. Altogether, our analysis suggests that changes in vessel traits were more likely to be a response to disturbance rather than differences in tree size.

An increase in theoretical hydraulic conductivity may be favoured during postdisturbance periods because it facilitates greater transpiration per given leaf area and more rapid growth and recovery, provided water and nutrients supply is not limiting. Alternatively, higher theoretical conductivity may be a response to an increased water demand imposed by higher light availability. Wider vessels and associated traits (e.g. intervessel pit size, Wheeler et al., 2005) may increase the risk of hydraulic failure (Isasa et al., 2023; but see Lens et al., 2022). However, in our study, positive shifts in vessel area and density were small and likely their cumulative effect contributed to a larger shift in Kh_{area}. This shift may avoid risky changes that could lead to embolism, while still achieving increased conductivity.

Ray parenchyma fraction ($F_{par(ray)}$) tended to be higher in posthurricane wood and it showed the strongest and most consistent effects among all tissue fractions. Given that rays are main pathways of bidirectional radial water and nutrient transport, higher $F_{par(ray)}$ implies larger volumes of nutrients and water may move radially and facilitate hydraulic recovery, drought resistance, osmoregulation, defence, storage and new growth (Hartmann & Trumbore, 2016; Tomasella et al., 2019). The marginal increase in $F_{par(total)}$ was contrary to our expectation that lower total parenchyma fraction would be beneficial if more resources diverted from parenchyma maintenance or storage could be spent on growth. However, higher $F_{par(total)}$ was primarily driven by an increase in $F_{par(ray)}$, and the benefits of higher ray fraction may indeed outweigh the costs of higher $F_{par(total)}$. We observed no consistent significant shifts in $F_{par(axial)}$; this result is not straightforward to interpret because living fibres, which are functionally similar to axial parenchyma, were present in the xylem of seven out of ten of our study species and we did not quantify their fraction. As in other studies, it is possible that axial parenchyma and living fibres trade off in our study species (Plavcová et al., 2023).

We note that the prehurricane period considered in our study (2011–2016) encompasses a drought that peaked in 2015 (Hogan

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et al., 2019; Umaña & Arellano, 2021). Although we cannot fully separate the effects of hurricane and drought, we do not expect the 2015 drought to have strongly affected our results for several reasons. First, the drought represented a relatively short period during our prehurricane period, which integrated wood produced over a 5-year period (2011–2016). Second, the drought tended to reduce tree growth rate (Feng et al., 2018; Schwartz et al., 2020; Umaña & Arellano, 2021), so wood produced during that period should represent a relatively small proportion of the total wood produced during the prehurricane period, and therefore have a relatively minor contribution to the average prehurricane anatomical trait values. Nonetheless, a valuable direction for future work will be to explicitly untangle independent and interactive effects of drought and wind disturbance on wood anatomy.

4.3 | Direct coordination between growth rates and anatomical traits

We targeted individuals with higher posthurricane growth rates in part because they produced sufficient amounts of wood for anatomical analysis; however, there was substantial variation in these growth rates and prehurricane growth rates for these trees were representative of the larger population. Consequently, our posthurricane results should be interpreted as representative of the best performing individuals, not as general trends encompassing the entire range of growth responses (including reduced or no-change growth rates), which were observed in our study site (Umaña & Arellano, 2021).

We did not find strong evidence for an overall coordination between growth and anatomical traits, either for pre- or posthurricane periods. Prior studies in undisturbed forests reported similar lack of correlations between growth rates and vessel area (Osazuwa-Peters et al., 2017), or positive correlations of various strengths (Fan et al., 2012; Hietz et al., 2017; Poorter et al., 2010). Interestingly, although Kh_{area} increased after the hurricane, this increase did not translate to higher diameter growth. This suggests that more conductive wood may facilitate growth in different parts of the tree (new branches and foliage), or it is a response to higher water demand imposed by higher light availability, or actual stem conductivity is lower than our measured theoretical conductivity. Similar to other studies, we also found no significant associations between growth and tissue fractions (Osazuwa-Peters et al., 2017). Overall, despite different analytical approaches (e.g. Pearson's correlations vs models accounting for tree size, as used here) and growth measures (e.g. relative vs absolute), our results align with previous findings, suggesting that other factors (see below) may decouple a direct link between wood anatomy and growth independently of growth conditions. Interestingly, the range and variation of anatomy–growth effects was larger for the posthurricane period, suggesting that anatomy–growth relationships were more stochastic in the time after the hurricane.

Reasons for partial decoupling between growth rates and anatomy are manifold. First, stem diameter growth, as we measured, does not capture all aspects of tree growth (Hilty et al., 2021), some of which may be especially important in early posthurricane phases of recovery (e.g. canopy filling). Second, growth rate plasticity is affected by a suite of interacting factors both internal and external to the plant. In other words, growth rates of individual trees are highly stochastic and governed by interacting processes such that it may be overly simplistic to expect strong direct correlations with anatomical traits (Iida et al., 2014; Paine et al., 2015). Third, measurement precision and low temporal resolution may partly inhibit our ability to link growth rates and xylem anatomy. For example, error in our growth estimates may have been introduced by drought (see above) or small amounts of bark growth. Finally, the variation in the growth rates measured in our study was likely smaller than the overall variation across all trees, thus reducing our ability to detect putative growth–anatomy relationships.

5 | CONCLUSIONS

Overall, our results suggest that adjustments of xylem anatomy to hurricane disturbance may have implications for altered susceptibility to subsequent hurricanes, drought or other disturbances, but may not necessarily have a clear direct effect on posthurricane diameter growth. Further work on the response of xylem anatomy to disturbance may provide valuable insights into other aspects of tree growth, as well as hydraulic, nutrient transport and storage strategies that can influence future resistance and resilience of forest ecosystems.

AUTHOR CONTRIBUTIONS

Kasia Ziemińska and Robert Muscarella designed the study. Samuel Farrar collected wood samples. Kasia Ziemińska prepared and imaged anatomical samples. Silvia Bibbo and Kasia Ziemińska annotated images. María Uriarte, Jill Thompson and Jess K. Zimmerman provided data on tree growth and damage. Robert Muscarella and Kasia Ziemińska wrote the manuscript with input from all authors.

ACKNOWLEDGEMENTS

This work was supported by grants from the Carl Tryggers Foundation (CTS 19:247 to R.M. and K.Z.), the Swedish Research Council Vetenskapsrådet (2019-03758 to R.M.), and the Swedish Phytogeographical Society. Tree damage data were collected with support from US National Science Foundation award DEB-1801315 to M.U. and J.K.Z. Census data from the LFDP were collected with funding from US National Science Foundation awards 0620910, 1050957 and 1546686. We thank the many people who have been involved with field censuses, long-term maintenance, and administration of the LFDP.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

Data on individual tree growth rates and anatomical data derived from annotated images, as well as summary data used in analyses are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.31zcrjdsf (Muscarella et al., 2023) and will be hosted by the Luquillo LTER data catalogue (https://luquillo.lter.network/data-catalog/). Raw and annotated images are available upon request.

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REFERENCES

Balaguru, K., Foltz, G. R., & Leung, L. R. (2018). Increasing magnitude of hurricane rapid intensification in the central and eastern tropical Atlantic. *Geophysical Research Letters*, *45*(9), 4238–4247.

Bankhead, P., Loughrey, M. B., Fernández, J. A., Dombrowski, Y., McArt, D. G., Dunne, P. D., McQuaid, S., Gray, R. T., Murray, L. J., Coleman, H. G., James, J. A., Salto-Tellez, M., & Hamilton, P. W. (2017). QuPath: Open source software for digital pathology image analysis. *Scientific Reports*, *7*(1), 16878.

Bellingham, P. J., Tanner, E. V. J., & Healey, J. R. (1995). Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology*, *76*(8), 2562–2580.

Carlquist, S. (2001). *Comparative wood anatomy*. Springer Berlin Heidelberg.

Castagneri, D., Carrer, M., Regev, L., & Boaretto, E. (2020). Precipitation variability differently affects radial growth, xylem traits and ring porosity of three Mediterranean oak species at xeric and mesic sites. *The Science of the Total Environment*, *699*, 134285.

Chapin, F. S., Schulze, E.-D., & Mooney, H. A. (1990). The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics*, *21*, 423–447.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, *111*(982), 1119–1144.

de Langre, E. (2008). Effects of wind on plants. *Annual Review of Fluid Mechanics*, *40*(1), 141–168.

Dietze, M. C., & Clark, J. S. (2008). Changing the gap dynamics paradigm: Vegetative regeneration control on forest response to disturbance. *Ecological Monographs*, *78*(3), 331–347.

Drew, A. P. (1998). Growth rings, phenology, hurricane disturbance and climate in *Cyrilla racemiflora* L., a rain forest tree of the Luquillo mountains, Puerto Rico 1. *Biotropica*, *30*(1), 35–49.

Echeverría, A., Anfodillo, T., Soriano, D., Rosell, J. A., & Olson, M. E. (2019). Constant theoretical conductance via changes in vessel diameter and number with height growth in moringa oleifera. *Journal of Experimental Botany*, *70*(20), 5765–5772.

Fan, Z.-X., Zhang, S.-B., Hao, G.-Y., Ferry Slik, J. W., & Cao, K.-F. (2012). Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density. *The Journal of Ecology*, *100*(3), 732–741.

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

Groenendijk, P., Sass-Klaassen, U., & Bongers, F. (2014). Potential of tree-ring analysis in a wet tropical forest: A case study on 22 commercial tree species in Central Africa. *Forest Ecology and Management*, *323*, 65–78. https://www.sciencedirect.com/science/article/pii/S0378112714001911?casa_token=pzRh-yk-z4QAAAAA:FI1nIHH-Xm-vbxSVz8KVVkPTh9tHYMHrNHOwprdwLZ58O4GZf38p2NbGbnWIJKdyS4fmIR5IKeg

Hall, J., Muscarella, R., Quebbeman, A., Arellano, G., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2020). Hurricane-induced rainfall is a stronger predictor of tropical Forest damage in Puerto Rico than maximum wind speeds. *Scientific Reports*, *10*(1), 4318.

Hartmann, H., & Trumbore, S. (2016). Understanding the roles of nonstructural carbohydrates in forest trees—from what we can measure to what we want to know. *The New Phytologist*, *211*(2), 386–403.

Hietz, P., Rosner, S., Hietz-Seifert, U., & Wright, S. J. (2017). Wood traits related to size and life history of trees in a Panamanian rainforest. *The New Phytologist*, *213*(1), 170–180.

Hilty, J., Muller, B., Pantin, F., & Leuzinger, S. (2021). Plant growth: The what, the how, and the why. *The New Phytologist*, *232*(1), 25–41.

Hogan, J. A., McMahon, S. M., Buzzard, V., Michaletz, S. T., Enquist, B. J., Thompson, J., Swenson, N. G., & Zimmerman, J. K. (2019). Drought and the interannual variability of stem growth in an aseasonal, everwet forest. *Biotropica*, *51*(2), 139–154.

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

IAWA Committee. (1989). *IAWA list of microscopic features for hardwood identification*. IAWA Bulletin. https://www.iawa-website.org/uploads/soft/Abstracts/IAWA%20list%20of%20microscopic%20features%20for%20hardwood%20identification.pdf

Iida, Y., Kohyama, T. S., Swenson, N. G., Su, S.-H., Chen, C.-T., Chiang, J.-M., & Sun, I. F. (2014). Linking functional traits and demographic rates in a subtropical tree community: The importance of size dependency. *The Journal of Ecology*, *102*(3), 641–650.

Isasa, E., Link, R. M., Jansen, S., Tezeh, F. R., Kaack, L., Sarmento Cabral, J., & Schuldt, B. (2023). Addressing controversies in the xylem embolism resistance-vessel diameter relationship. *The New Phytologist*, *238*, 283–296. https://doi.org/10.1111/nph.18731

Kellner, K. (2015). *jagsUI: A wrapper around "rjags" to streamline "JAGS" analyses*. R package version 1.3.7. https://CRAN.R-project.org/package=jagsUI

Leitold, V., Morton, D. C., Martinuzzi, S., Paynter, I., Uriarte, M., Keller, M., Ferraz, A., Cook, B. D., Corp, L. A., & González, G. (2021). Tracking the rates and mechanisms of canopy damage and recovery following hurricane maria using multitemporal lidar data. *Ecosystems*, *25*, 892–910. https://doi.org/10.1007/s10021-021-00688-8

Lens, F., Gleason, S. M., Bortolami, G., Brodersen, C., Delzon, S., & Jansen, S. (2022). Functional xylem characteristics associated with drought-induced embolism in angiosperms. *The New Phytologist*, *236*(6), 2019–2036.

Lens, F., Sperry, J. S., Christman, M. A., Choat, B., Rabaey, D., & Jansen, S. (2011). Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. *The New Phytologist*, *190*(3), 709–723.

Loepfe, L., Martinez-Vilalta, J., Piñol, J., & Mencuccini, M. (2007). The relevance of xylem network structure for plant hydraulic efficiency and safety. *Journal of Theoretical Biology*, *247*(4), 788–803.

Martínez-Vilalta, J., Mencuccini, M., Alvarez, X., Camacho, J., Loepfe, L., & Piñol, J. (2012). Spatial distribution and packing of xylem conduits. *American Journal of Botany*, *99*(7), 1189–1196.

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Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, *13*, 838–848.

Michaletz, S. T. (2018). Xylem dysfunction in fires: Towards a hydraulic theory of plant responses to multiple disturbance stressors [review of *Xylem dysfunction in fires*: *Towards a hydraulic theory of plant responses to multiple disturbance stressors*]. *The New Phytologist*, *217*(4), 1391–1393.

Mitchell, S. J. (2013). Wind as a natural disturbance agent in forests: A synthesis. *Forestry*, *86*(2), 147–157.

Muscarella, R., Ziemińska, K., Bibbo, S., Uriarte, M., & Zimmerman, J. K. (2023). Data from: Shifts in wood anatomical traits after a major hurricane. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.31zcrjdsf

Olson, M. E., Anfodillo, T., Gleason, S. M., & McCulloh, K. A. (2021). Tip-to-base xylem conduit widening as an adaptation: Causes, consequences, and empirical priorities. *The New Phytologist*, *229*(4), 1877–1893.

Osazuwa-Peters, O. L., Wright, S. J., & Zanne, A. E. (2017). Linking wood traits to vital rates in tropical rainforest trees: Insights from comparing sapling and adult wood. *American Journal of Botany*, *104*(10), 1464–1473.

Pacala, S. W., & Rees, M. (1998). Models suggesting field experiments to test two hypotheses explaining successional diversity. *The American Naturalist*, *152*(5), 729–737.

Paine, C. E. T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H., Daïnou, K., de Gouvenain, R. C., Doucet, J. L., Doust, S., Fine, P. V. A., Fortunel, C., Haase, J., Holl, K. D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., … Hector, A. (2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *The Journal of Ecology*, *103*(4), 978–989.

Pfautsch, S. (2016). Hydraulic anatomy and function of trees—Basics and critical developments. *Current Forestry Reports*, *2*(4), 236–248.

Pickett, S. T. A., & White, P. S. (Eds.). (1985). *The ecology of natural disturbance and patch dynamics*. Academic Press.

Plavcová, L., Hoch, G., Morris, H., Ghiasi, S., & Jansen, S. (2016). The amount of parenchyma and living fibers affects storage of nonstructural carbohydrates in young stems and roots of temperate trees. *American Journal of Botany*, *103*(4), 603–612.

Plavcová, L., Olson, M. E., Jandová, V., & Doležal, J. (2023). Parenchyma is not the sole site of storage: Storage in living fibres. *IAWA Journal/International Association of Wood Anatomists*, -1(aop), 1–12.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. International workshop on Distributed Statistical Computing, (DSC 2003), March 20–22, Vienna, Austria. ISSN 1609–395X.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.-C., Peña-Claros, M., Sterck, F. J., Villegas, Z., & Sass-Klaassen, U. (2010). The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *The New Phytologist*, *185*, 481–492.

R Development Core Team. (2020). *R: A language and environment for statistical computing* (Version v 4.0.3) [Computer software]. R Foundation for Statistical Computing. http://www.R-project.org

Scholz, A., Klepsch, M., Karimi, Z., & Jansen, S. (2013). How to quantify conduits in wood? *Frontiers in Plant Science*, *4*, 56.

Schwartz, N. B., Feng, X., Muscarella, R., Swenson, N. G., Umaña, M. N., Zimmerman, J. K., & Uriarte, M. (2020). Topography and traits modulate tree performance and drought response in a tropical forest. *Frontiers in Forests and Global Change*, *3*, 136.

Tanner, E. V. J., Rodriguez-Sanchez, F., Healey, J. R., Holdaway, R. J., & Bellingham, P. J. (2014). Long-term hurricane damage effects on tropical forest tree growth and mortality. *Ecology*, *95*(10), 2974–2983.

Tomasella, M., Petrussa, E., Petruzzellis, F., Nardini, A., & Casolo, V. (2019). The possible role of non-structural carbohydrates in the regulation of tree hydraulics. *International Journal of Molecular Sciences*, *21*(1), 144. https://doi.org/10.3390/ijms21010144

Tyree, M. T., & Zimmermann, M. H. (2013). *Xylem structure and the ascent of sap* (2nd ed.). Springer.

Umaña, M. N., & Arellano, G. (2021). Legacy effects of drought on tree growth responses to hurricanes. *Ecography*, *44*, 1686–1697. https://doi.org/10.1111/ecog.05803

Uriarte, M., Canham, C. D., Thompson, J., & Zimmerman, J. K. (2004). A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecological Monographs*, *74*(4), 591–614.

Uriarte, M., Clark, J. S., Zimmerman, J. K., Comita, L. S., Forero-Montaña, J., & Thompson, J. (2012). Multidimensional tradeoffs in species responses to disturbance: Implications for diversity in a subtropical forest. *Ecology*, *93*(1), 191–205.

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

von Arx, G., Kueffer, C., & Fonti, P. (2013). Quantifying plasticity in vessel grouping—Added value from the image analysis tool ROXAS. *IAWA Journal/International Association of Wood Anatomists*, *34*(4), 433–445.

Walker, L. R. (1991). Tree damage and recovery from hurricane Hugo in Luquillo experimental forest, Puerto Rico. *Biotropica*, *23*(4), 379–385.

Wheeler, J. K., Sperry, J. S., Hacke, U. G., & Hoang, N. (2005). Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: A basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment*, *28*(6), 800–812.

Zanne, A. E., Westoby, M., Falster, D. S., Ackerly, D. D., Loarie, S. R., Arnold, S. E. J., & Coomes, D. A. (2010). Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany*, *97*(2), 207–215.

Ziemińska, K., Westoby, M., & Wright, I. J. (2015). Broad anatomical variation within a narrow wood density range—A study of twig wood across 69 Australian angiosperms. *PLoS ONE*, *10*, e0124892.

Zimmerman, J. K., Iii, E. M. E., Waide, R. B., Lodge, D. J., Taylor, C. M., & Brokaw, N. V. L. (1994). Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: Implications for tropical tree life histories. *The Journal of Ecology*, *82*(4), 911–922.

Zuidema, P. A., Baker, P. J., Groenendijk, P., Schippers, P., van der Sleen, P., Vlam, M., & Sterck, F. (2013). Tropical forests and global change: Filling knowledge gaps. *Trends in Plant Science*, *18*(8), 413–419.

SUPPORTING INFORMATION

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

Notes S1. Details of anatomical lab processing.

Figure S1. Walter and Lieth climate diagram generated by ClimateCharts.net (Zepner et al., 2020) for Río Grande, Puerto Rico, near the Luquillo Forest Dynamics plot. Climate data is drawn from CRU Time Series v4.05.

Figure S2. Shifts in wood anatomical traits before and after the 2017 hurricane season for 65 sampled trees of 10 species in the Luquillo Experimental forest, Puerto Rico. Each segment represents trait values calculated for each tree; the left side of line segments correspond to pre-hurricane trait values; the right side of segments correspond to post-hurricane trait values.

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Figure S3. Estimated coefficients for the effect of stem diameter growth, ΔDBH, and damage category (low, medium, high) on shifts in anatomical traits in wood produced before and after major hurricanes for 10 species of Puerto Rican trees (parameters *b*1 and *b*2 from Equation 1 of the main text).

Figure S4. Estimated coefficients for effects of tree size (a, b) and damage (c) on relationships between stem diameter growth rates and anatomical traits for pre-hurricane wood (a) and post-hurricane wood (b) for 10 species of Puerto Rican trees (parameters b_2 and b_3 from Equation 3).

Figure S5. Estimated relationships between the difference in basal area growth rates (post minus pre-hurricane values) and shifts in anatomical traits (post minus pre-hurricane values) at the community-level (black circles) and 10 tree species (colored points) in Puerto Rico. Points are filled if the 95% credible interval does not overlap zero. Positive coefficients indicate that larger shifts in anatomy are related with larger shifts in growth rates between the pre- and post-hurricane periods.

Figure S6. Estimated coefficients for effects of tree size (a, b) and damage (c) on relationships between basal area growth rates and anatomical traits for pre-hurricane wood (a) and post-hurricane wood (b) for 10 species of Puerto Rican trees (parameters *b*2 and *b*3 from Equation 3).

How to cite this article: Ziemińska, K., Bibbo, S., Farrar, S., Thompson, J., Uriarte, M., Ziaco, E., Zimmerman, J. K., & Muscarella, R. (2023). Shifts in wood anatomical traits after a major hurricane. *Functional Ecology*, *37*, 3000–3014. https://doi.org/10.1111/1365-2435.14451

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