

Species intraspecific variation drives tropical forest drought resistance

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Severe droughts are increasingly driving tree mortality, yet predicting forest resilience remains limited by a lack of understanding of within-species variation in drought resistance^{1–4}. Although hydraulic traits such as embolism resistance are central to drought survival, studies conducted primarily in temperate regions have reported little intraspecific variation^{5–12}, implying that there are evolutionary constraints in the adaptive potential of tree species. Here we test this assumption using a dataset comprising 11 hydraulic traits for 290 trees representing 18 species collected along Puerto Rico's fourfold rainfall gradient (1,000 to 4,000 mm per year). We find that substantial intraspecific variation, together with species turnover, drives coordinated shifts in drought resistance across the gradient. Most species exhibit substantially more embolism resistance and wider stomatal safety margins in drier forests, demonstrating a considerable level of intraspecific variation in tropical trees and a mechanism for adaptation to increasingly dry conditions. Species lacking such trait variability may be highly vulnerable under a future drier climate. Incorporating both interspecific and intraspecific trait variation into predictive models will advance our ability to forecast forest resilience to intensifying droughts.

Severe droughts have led to widespread tree mortality and growth declines across tropical forests^{1–4}. As these ecosystems account for the majority of terrestrial aboveground biomass¹³, elevated tree mortality could lead to large carbon losses to the atmosphere, transforming these forests from a carbon sink to a source and exacerbating climate warming¹⁴. As drought events are anticipated to intensify and lengthen¹⁵, high mortality rates are likely to persist and even rise¹⁶. However, drought impacts differ among tropical tree species, populations and communities⁴. These differences may lead to shifts in species composition and species geographic ranges^{17,18}. On the other hand, tree species may have enough intraspecific variation in drought resistance to withstand severe droughts. The capacity of tropical forests to mitigate climate change hinges on the capacity of tree species and communities to survive changing precipitation patterns¹⁹.

Understanding the extent of both interspecific and intraspecific variation in drought resistance, including traits related to drought tolerance and drought avoidance, is essential for predicting tropical forest responses to climate change. Previous studies show that co-occurring tropical tree species differ widely in their resistance to drought^{4,20,21}, influencing species abundance and distribution^{22–24}. While interspecific variation has been more thoroughly studied, intraspecific variation, particularly in hydraulic traits directly linked to physiological function, remains poorly understood. Many tropical tree species span broad rainfall gradients^{24,25}, yet intraspecific variation in hydraulic traits has rarely been examined across multiple species. Most work on intraspecific variation in hydraulic traits, such as xylem vulnerability to embolism, comes from temperate and Mediterranean regions, where studies

generally report no adjustment to climatic water availability^{5,7,8,26,27}. The few studies that have focused on tropical systems have measured only one or two species at a small spatial scale, limiting our ability to draw inferences at broader taxonomic and climate scales^{25,28}. Tropical studies with larger numbers of species have focused on morphological traits (such as specific leaf area and wood density) as proxies for physiological functions¹⁹, but these traits often fail to predict which species experience growth declines or mortality during severe droughts⁴. These limitations highlight the need for multispecies datasets on interspecific and intraspecific variation in hydraulic traits for predicting tropical forest responses to drought and constraining forecasts of changes in species composition, range shifts and ecosystem resilience under future climate scenarios^{19,29,30}.

To fill this knowledge gap, we studied tropical forests along a steep rainfall gradient (1,000–4,000 mm per year) in Puerto Rico. This island-wide system provides an ideal setting to evaluate the relative contribution of intraspecific variation and species turnover to forest drought resistance. We measured 11 plant hydraulic traits for 18 tree species in 6 different forest reserves spanning the island's rainfall gradient. Together, these species account for 18–75% of tree stems (≥ 5 cm diameter) depending on the site (Fig. 1, Extended Data Fig. 1, Extended Data Tables 1 and 2 and Supplementary Table 1). We included traits linked to drought avoidance, such as leaf and stem capacitance, saturated water content (SWC) and drought tolerance, such as leaf and stem xylem vulnerability to embolism (stem xylem water potential at 50% embolism accumulation (P_{50})) and stomatal safety margins ($SMP_{50} = \text{turgor loss point (TLP)} - P_{50}$). Traits were measured in as many of the 6 sites as each

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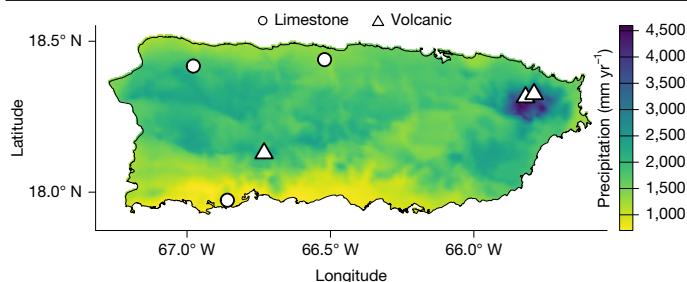


Fig. 1 | Island-wide precipitation gradient and study sites. Map of the island of Puerto Rico coloured by the gradient of MAP. The locations of the six study sites are shown as circles (limestone soils) or triangles (volcanic soils). Further details were reported previously^{36,49}.

species occurred, totalling 290 trees, with all species measured at 2–4 locations (Supplementary Table 2). Using this dataset, we examined (1) how hydraulic traits associated with different drought resistance strategies (that is, drought avoidance and drought tolerance) shifted across the island's steep rainfall gradient; and (2) the relative contribution of intraspecific variation versus species turnover to these shifts. This study represents a comprehensive assessment of intraspecific variation in hydraulic traits for tropical forest trees.

Drought avoidance and tolerance

Across the rainfall gradient, we observed a shift in dominant drought resistance strategies: trees at drier sites exhibited trait values associated with greater drought tolerance, while those at wetter sites displayed trait values associated with more pronounced drought avoidance. Species-level trait means revealed that drier forest sites had higher resistance to embolism and stomatal safety margins in both leaves and stems (Fig. 2a,b,d,e), whereas wetter sites had higher average leaf and stem capacitance, and greater stem SWC (Fig. 2h–k). There was no association between leaf TLP and rainfall (Fig. 2c), indicating that the observed association between stomatal safety margins and rainfall was driven by variation in P_{50} rather than TLP. There was no association between leaf saturated water content (Fig. 2f) and leaf capacitance at full turgor (Fig. 2g) and rainfall. Overall, our findings suggest that drought tolerance strategies are more successful in forests subject to prolonged and intense water stress, while drought avoidance traits are more common in wetter forests where water shortages are shorter and less severe. These patterns are consistent with previous work in temperate precipitation gradients in Australia, where species showed increasing drought tolerance (P_{50} and SMP_{50}) with decreasing rainfall^{31,32}. Our findings show that this pattern is also true for diverse tropical forests and offer a new dimension: drought avoidance traits also shift along rainfall gradients, increasing with higher rainfall.

The positive relationship between site-level drought tolerance and decreasing rainfall was stronger than the corresponding decrease in drought avoidance (Fig. 3 and Supplementary Tables 3 and 4). When accounting for intraspecific variation, most traits related to drought tolerance exhibited significant shifts across the rainfall gradient (Fig. 3a,b,d,e and Supplementary Tables 3 and 4), while most drought-avoidance traits did not (Fig. 3h–k and Supplementary Tables 3 and 4). This asymmetry may be partly explained by the difference in soil type and moisture retention. All three wetter sites, where drought avoidance dominates, have volcanic soil that retain moisture well^{33–35} and share relatively high mean rainfall (2,195–4,029 mm; Extended Data Table 1) and weak seasonality³⁶. As a result, trees at these sites probably experience similarly low levels of drought stress, contributing to comparable drought avoidance trait values. By contrast, the three drier sites at which drought tolerance is more prevalent all share limestone soil with poor water retention^{33–35}. These sites also experience higher vapour pressure deficit (Extended Data Table 1) and lower rainfall (mean

annual precipitation (MAP) = 1,004–2,017 mm), probably leading to greater variability in drought stress and stronger trait–environment associations^{33–35}. As soil type and rainfall are confounded in our study, all the wetter sites have volcanic-derived soil and all the drier sites have limestone-derived soil, we cannot fully disentangle their effects. However, the confounding of rainfall and soil type is inherent to the island's landscape and does not negate the biological signal.

Species turnover and intraspecific variation

Site-level drought resistance traits varied substantially across the precipitation gradient. For example, site-average leaf P_{50} ranged from -2.74 to -5.79 and leaf stomatal safety margins from 0.95 to 3.82 MPa among sites, reflecting a combination of species turnover and intraspecific trait variation (Supplementary Table 5). On average, species turnover accounted for 39% of the variance in hydraulic traits across sites, ranging from 18% for leaf capacitance at TLP (CTLTP) to 66% for leaf SWC (Supplementary Table 6). Intraspecific variation explained a smaller, yet significant, proportion of variance, averaging 13% across all traits, with values ranging from 1% for leaf SWC to 23% for stem capacitance at full turgor (CFT). Notably, leaf P_{50} and leaf SMP_{50} each showed 17% intraspecific contribution to the observed variation, which is substantial (Fig. 4 and Supplementary Table 6). Note that, owing to our sampling scheme, which focused on species that occurred at more than one of the six plots, we measured only a subset of species within each plot (Extended Data Fig. 1).

In analyses conducted at the individual species level, 17 out of the 18 study species exhibited statistically significant intraspecific variation across the rainfall gradient for at least 1 of the 11 hydraulic traits measured (Supplementary Tables 7 and 8). The number of traits with statistically significant levels of intraspecific variation per species ranged from one to ten (Supplementary Tables 7 and 8). Species with statistically significant intraspecific variation generally mirrored site-level trends, with increasing drought tolerance in drier sites (Fig. 3a,b,d,e and Supplementary Tables 7 and 8) and higher drought avoidance in wetter sites (Fig. 3h–k and Supplementary Tables 7 and 8). However, different species exhibited intraspecific variation in different combinations of traits and magnitudes. Traits most frequently exhibiting intraspecific variation included leaf P_{50} , stem P_{50} , leaf SMP_{50} , stem SMP_{50} , leaf CFT, stem SWC, stem CFT and stem CTLTP (Supplementary Tables 7 and 8). These traits are associated with embolism resistance, hydraulic safety and stem water storage, highlighting their central role in drought resistance across the island. Although studies have found limited intraspecific variation in morphological traits of tropical seedlings¹⁹, our findings reveal substantial variation in hydraulic traits among adult trees. This difference suggests that local water availability may exert stronger selective pressure on hydraulic traits²¹ than on morphological traits and stronger selective pressure on adult trees rather than seedlings.

Previous studies of intraspecific variation in hydraulic traits of tropical trees have been limited and have yielded mixed results. For example, one study²⁵ found substantial differences in P_{50} between wet and dry sites for *Cordia alliodora* (MAP = 4,200 mm and $P_{50} = -1.78$ (wet), and MAP = 1,460 mm and $P_{50} = -3.60$ (dry)), consistent with our findings for many more species spanning a broader rainfall gradient. By contrast, a study comparing two dominant Amazonian tree species across water table depths found increased embolism resistance in the drier site for only one species²⁸. Similarly, a long-term throughfall exclusion experiment in the Amazon³⁷ documented substantial osmotic adjustment in response to the imposed long-term drought but focused on a limited number of species at a single site, precluding extrapolation to a larger number of species across marked rainfall gradients. Collectively, these studies suggest that tropical trees may exhibit intraspecific variation in hydraulic traits in response to water availability, but their limited taxonomic scope and spatial extent have precluded broader generalization across marked rainfall gradients.

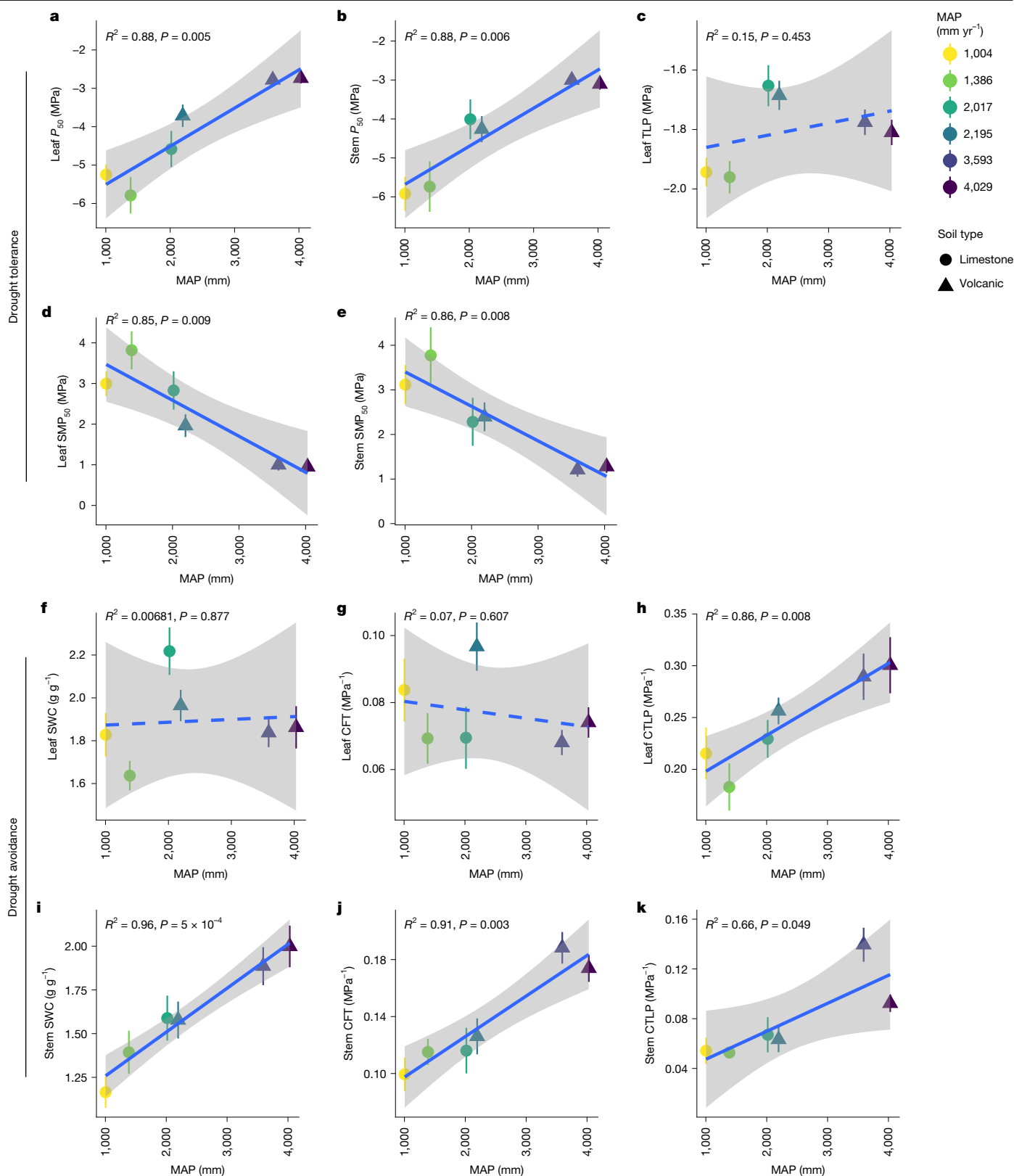


Fig. 2 | Association between MAP and hydraulic traits. a–k, Association between MAP and the site-level species means of leaf P_{50} (a); stem P_{50} (b); leaf TLP (c); leaf (d) and stem (e) stomatal safety margins ($SMP_{50} = TLP - P_{50}$); leaf SWC (f); leaf CFT (g); leaf CTLP (h); stem SWC (i); stem CFT (j); and stem CTLP (k). The blue lines show the results of linear regressions and the shaded

areas indicate the 95% confidence intervals. Data are mean $\pm$ s.e.m. Colours indicate each of the six sites where the measurements were conducted, and their respective MAP; the symbols indicate the soil type. $n = 290$ measured trees from 18 tree species.

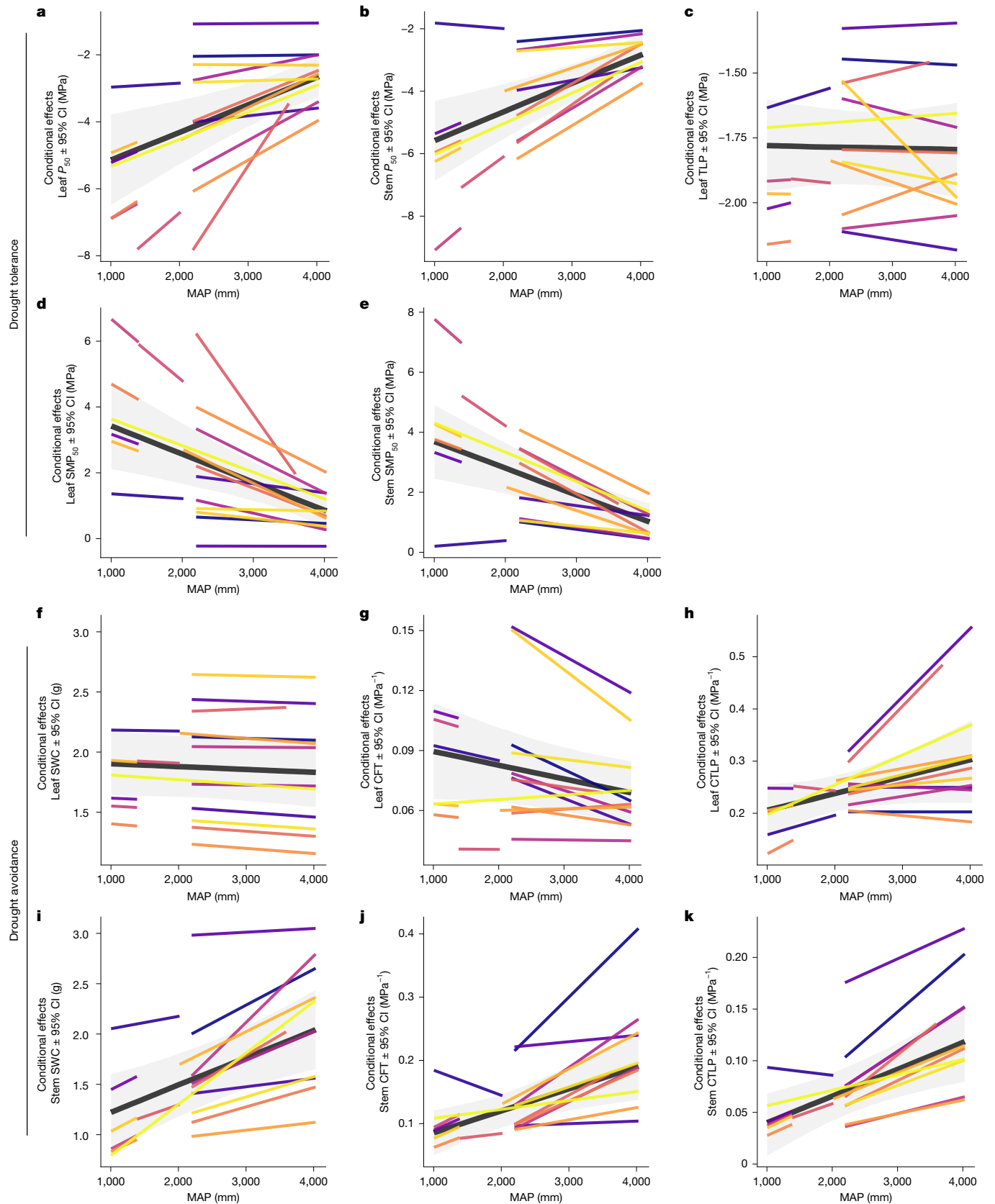


Fig. 3 | Conditional effects of hydraulic traits by MAP. a–k. The solid black lines depict the overall conditional effects from the Bayesian hierarchical models of leaf P_{50} (a); stem P_{50} (b); leaf TLP (c); leaf (d) and stem (e) SMP_{50} ; leaf SWC (f); leaf CFT (g); leaf CTLP (h); stem SWC (i); stem CFT (j); and stem CTLP (k) and scaled MAP. The shaded areas are the 95% credible intervals (CIs). The coloured lines show the species-specific posterior predictions for random

slope effects from the Bayesian hierarchical models for each hydraulic trait restricted to the sites where they occurred. Note that the hydraulic trait responses to the rainfall gradient are not the same across species, so colours represent different species among panels (details on species-level intraspecific variation are provided in Supplementary Tables 7 and 8). $n = 290$ measured trees from 18 tree species.

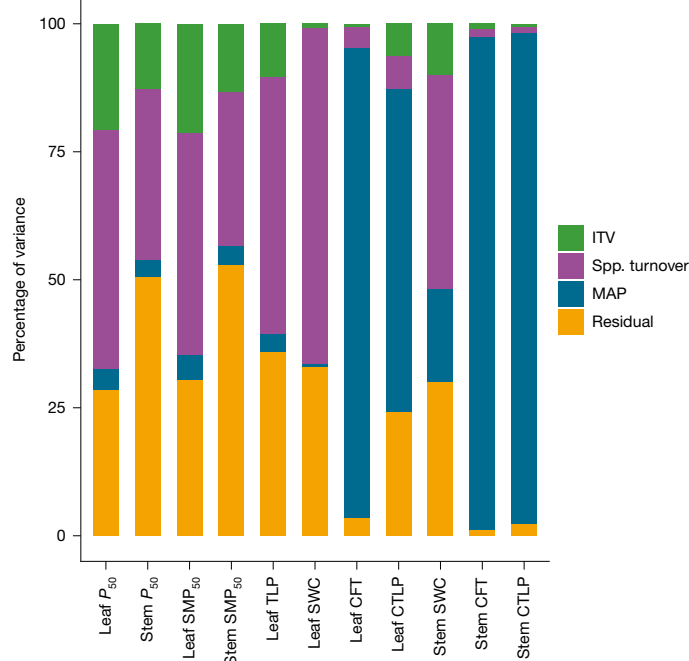


Fig. 4 | Variance partition. The percentage of variance from each of the Bayesian hierarchical models for each of the hydraulic traits that are explained by the random slopes of the models (intraspecific trait variation, ITV), the random intercepts of the models (species (Spp.) turnover), the fixed effect of MAP and the residual unexplained variance. The traits are leaf P_{50} and stem P_{50} , leaf and stem SMP_{50} , leaf TLP, leaf SWC, leaf CFT, leaf CTLP, stem SWC, stem CFT and stem CTLP. $n = 290$ measured trees from 18 tree species.

As empirical evidence from tropical forests remains limited, much of our current understanding of intraspecific variation in hydraulic traits derives from studies conducted in temperate and Mediterranean ecosystems. Across these systems, research on P_{50} and related hydraulic traits in both conifers and angiosperms report limited within-species variability or weak adaptive differentiation across aridity gradients, patterns often interpreted as evidence of strong genetic canalization under stabilizing selection^{5–12}. Instead, drought responses in these regions are thought to occur primarily through variation in allocation strategies (for example, leaf:sapwood ratios) and plasticity or adaptation in traits such as leaf mass per area, wood density and Huber values, rather than through changes in intrinsic xylem vulnerability to embolism^{5–8,38–40}. This body of work has contributed to a prevailing view that hydraulic traits are largely conserved within species, particularly in environments characterized by strong seasonality and repeated drought exposure. Against this backdrop, our results highlight a marked departure from the prevailing paradigm derived largely from temperate systems. We find that most tropical tree species exhibit greater xylem resistance to embolism (that is, more negative P_{50} values) and larger stomatal safety margins at drier sites, indicating substantial intraspecific variation in hydraulic traits across rainfall gradients. These patterns suggest that tropical tree species may possess greater hydraulic flexibility than their temperate counterparts, with intrinsic xylem properties varying in response to long-term differences in water availability. Such flexibility has important implications for predicting drought vulnerability in tropical forests, a biome that has a disproportionate role in global biodiversity and climate regulation, underscoring the need to explicitly incorporate intraspecific hydraulic variation into process-based vegetation models. In tropical wet forests, complex biogeographical histories^{41,42} combined with relatively weak and spatially heterogeneous climatic filtering may promote the maintenance of this variation within species. Understanding the origins, limits and consequences of such variation represents an important frontier

for improving predictions of tropical forest responses to intensifying drought under climate change.

The mechanisms generating observed intraspecific phenotypic variation in hydraulic traits probably include genetic differentiation, phenotypic plasticity and transgenerational environmental effects. Evidence from temperate and semi-arid systems shows that populations adapted to distinct rainfall regimes diverge in hydraulic and water use traits while retaining strong plasticity to short-term drought^{43–45}. Moreover, maternal environments can influence physiological performance in subsequent generations. For example, the offspring of *Eucalyptus grandis* trees from wetter origins exhibit higher growth and water use efficiency⁴⁶, suggesting that epigenetic inheritance may contribute to drought acclimation. A recent global meta-analysis, based largely on temperate species, found plastic adjustments in hydraulic traits under drier conditions, including increases in embolism resistance and sapwood per leaf area, and decreases in stem-specific hydraulic conductivity and leaf TLP⁴⁷. However, these adjustments were insufficient to offset declines in plant water potential, resulting in reduced hydraulic safety margins under drought⁴⁷. Such interactions among adaptation, plasticity and transgenerational effects imply that intraspecific trait variation in tropical trees could reflect both evolutionary divergence and environmental memory, enhancing species' ability to persist under non-stationary climates. Another possible explanation is that although drought occurs in both temperate and tropical environments, the nature of environmental filtering differs. In temperate and Mediterranean regions, recurrent and relatively predictable seasonal stresses—including drought and, in many systems, freezing—may impose strong stabilizing selection on hydraulic traits. In particular, temperature-related constraints on xylem structure associated with freezing risk are known to limit variation in conduit architecture and embolism resistance⁴⁸. By contrast, tropical forests experience relatively uniform temperatures and often more irregular drought regimes, which may weaken consistent selective pressures and allow greater phenotypic variation in hydraulic traits to be maintained within species. Future studies combining physiological, genomic and experimental approaches will be crucial to disentangle the relative contributions of these mechanisms to drought resistance in tropical forests.

Conclusion

By measuring hydraulic traits for a large number of tropical tree species across a steep rainfall gradient, we found that 17 out of 18 species exhibited significant directional shifts in hydraulic trait values, indicating that phenotypes can adjust in response to local water availability. Species exhibiting intraspecific variation in drought-related traits may be better equipped to cope with future climate scenarios with more frequent and intense droughts. By contrast, species lacking such variability may be less able to adapt, potentially leading to shifts in species geographical distributions and forest composition that favour those with greater trait phenotypic variation. Across both the site level and species level, drought-tolerant traits were more common in drier environments, while drought-avoidant traits predominated in wetter sites. The widespread occurrence of intraspecific variation in hydraulic traits suggests that tropical forests may possess greater adaptive capacity to changing rainfall regimes than previously recognized. This phenotypic variation could have a critical role in buffering forest function and maintaining biodiversity under climate change.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-026-10870-4>.

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Methods

Study site and species selection

Puerto Rico spans 8,740 km² and encompasses six Holdridge life zones. The MAP ranges from 800 mm in subtropical dry forests to more than 4,000 mm in subtropical rainforests^{28,50}. The primary soil types are derived from limestone and volcanic parent materials^{29,51,52}. Limestone soils, which have lower water-holding capacity and nutrients, are generally found in drier regions, and the volcanic soils, with higher water-holding capacity, occur in wetter areas^{28,30,49}. We selected six forest reserves distributed across the island spanning a MAP from around 1,000 to 4,000 mm. Three of the study sites are located on limestone soils and three on volcanic soils (Fig. 1 and Extended Data Table 1). On the basis of previous ecological studies at these sites, we identified tree species that occurred in at least two sites^{31,49}, and measured hydraulic traits (see below) for each species at all sites where it was present, ranging from two to four sites per species (Extended Data Table 2).

Environmental data

MAP was derived from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>, accessed 25 April 2023). Geological substrate (soil parent material) data were obtained from ref. 30.

Hydraulic traits

We collected two >1.5 m long canopy branches with a pole pruner from each individual tree. We sealed the branches in large black plastic bags with wet paper towels and transported them out of the forest. Once we reached our vehicle, we placed the branches in large plastic garbage cans with water, recut the branches under water, and kept them covered with the black plastic bags to minimize evapotranspiration while we transported them to the laboratory. All branches were collected in the morning between 07:00 and 09:00 a.m. local time. At the end of each collecting trip, we immediately took the samples to the laboratory where we conducted the hydraulic measurements. Depending on the distance from the site to the laboratory, this period was between 1 and 2 h. If we had to repeat any of the measurements, we would collect more branches from the same individual tree sampled before. The bulk of the hydraulic trait measurements were conducted between July 2019 and June 2021, with one final campaign in June 2023. Owing to the logistical challenges of transporting branches back to a laboratory within 2 h of collection, we first worked out of two laboratories on the north side of the island, where we sampled El Yunque 300–400 m, El Yunque 500–600 m and Cambalache. We then moved to a laboratory on the west side of the island to sample Guajataca, Guilarte and Guanica. We avoided sampling the drier sites, namely Cambalache, Guajataca and Guanica, during the peak of the dry season in March and April, so that all sites were sampled during the wet season (>100 mm of mean monthly precipitation). Although sites were sampled during the wet season, rainfall variability might have affected the hydraulic traits that potentially can adjust throughout the year, such as TLP⁵³.

Leaf and stem PV curves

We measured leaf TLP, leaf and stem SWC and water storage capacity of leaves and stems using pressure–volume (PV) curves. For the PV curves, we used the bench dry method described previously⁵⁴. For the leaf PV curves, we let the branch rehydrate overnight, then, using a razor blade, excised a mature fully expanded healthy leaf from the branch and sealed it in a Whirl-Pak bag. As the leaf dried, we periodically measured water potential (ψ) with a pressure chamber instrument (PMS Instruments) and leaf weight (3-decimal-point balance, OHAUS Scout). We continued to measure the leaf until the relationship between $1/\psi$ and water loss became linear. Lastly, we dried the leaf in an oven at 65 °C for more than 72 h and weighed it to obtain the leaf dry mass. We constructed the PV

curves used the ref. 55 spreadsheet tool, from which we extracted the leaf TLP, leaf SWC, leaf CFT and leaf CTLP.

For the stem PV curves, we excised approximately 1–1.5-m-long intact terminal branches immediately after the samples were brought back from the field, removed all the leaves from the branch, and wrapped Parafilm (Bemis) around any cuts in the bark to seal them. We attached a stem psychrometer (ICT International) to the branch by removing a small section of bark from the branch, washing the exposed xylem with deionized water, drying it with Kimwipes (Kimberly-Clark), clamping the psychrometer to the exposed xylem and creating an air-tight seal with Parafilm. We set the psychrometers to record water potential every 10 min. As the branch dried, we periodically weighed it (2-decimal-point balance, OHAUS Scout). We continued to log water potential and branch weight until $1/\psi$ and water loss became linear. Lastly, we dried the branch in an oven at 65 °C for 1 week and weighed it to obtain the branch dry mass. The same as with the leaves, we used a previously described tool⁵⁵ to construct the branch PV curves, from which we extracted the stem SWC, stem CFT and stem CTLP. We could not do stem PV curves for the palm, *Prestoea acuminata* var. *montana*, owing to its monocot anatomy.

Leaf and stem OV curves

We used the optical vulnerability (OV) technique to estimate xylem embolism accumulation in leaves and stems following refs. 56,57. For each branch, we clamped one leaf and a small distal stem (around 3–6 mm in diameter depending on the species) inside a custom-built clamp (OpenSourceOV, OSOV) with an 8-megapixel Raspberry Pi camera and 6 light-emitting diodes operated by a Raspberry Pi microcomputer. Further details for OSOV clamps construction, image capturing and post-image processing can be found online (<http://www.opensourceov.org>). In brief, for the leaves, we selected a healthy, fully expanded leaf, placed a microscope slide over the area to be imaged and clamped it onto the OSOV clamp. For stems, we removed a small area of bark (around 2 cm²) from a distal stem with healthy foliage to expose the xylem. We applied adhesive hydrogel (Tensive) to the exposed xylem to reduce surface reflection, help light penetration into the xylem and reduce desiccation. We covered the hydrogel with a round-glass coverslip and clamped it in the OSOV clamp. We set the OSOV clamps to take a picture every 5 min until no embolism events were recorded for at least 12 h (around 72–96 h depending on the species). We used stem psychrometers to measure water potential every 10 min as the branches dried. We were unable to obtain OV data for stems of *Cecropia schreberiana* and the palm, *P. acuminata* var. *montana*, owing to their anatomy. We chose to use the OV technique over other techniques for measuring xylem vulnerability to embolism, as it has been validated in many studies for many species and can be used simultaneously on leaves and stems^{56–64}.

We used ImageJ software (v.1.54p; National Institutes of Health) to process all the pictures of leaf and stem to extract embolisms following refs. 56,57. In brief, we stacked all the pictures in chronological order and converted them to 8-bit greyscale with pixel values ranging from black (0) to white (255). Each picture was subtracted from the next picture in the sequence to reveal embolisms, which appear in the image differences as changes in light intensity (differences in pixel values). We removed all the differences in pixels that were due to noise or artefacts (for example, sample movements or shrinkage) using both the remove outlier function in ImageJ and manually, leaving only the differences in pixels belonging to embolisms. The accumulation of embolisms in each leaf and stem was quantified as a cumulative total of embolized pixels in each picture divided by the total number of embolized pixels in the full stack of pictures from the dried sample. To estimate the water potential at the time of each picture capture (ψ_x), we fitted a linear regression to the water potential measurements over time. With this, we created the vulnerability curves and extracted the values at which 50% of the cumulative embolism had occurred (P_{50}). We calculated P_{50}

Article

for both leaves (leaf P_{50}) and stems (stem P_{50}). The complete details of the methods for the OV curves, including an overview of the technique, instructions for image processing, as well as ImageJ scripts, are available online (<http://www.opensourceov.org>). We calculated stomatal safety margins as leaf TLP – P_{50} . We chose to use P_{50} instead of Ψ_x at 88% of the cumulative embolism P_{88} because, in a previous study, we found that P_{88} exhibits substantially higher within-individual variability than P_{50} (ref. 65).

Data analysis

To assess shifts between drought avoidance and drought tolerance strategies across the rainfall gradient, we fitted linear regression models for each of the 11 hydraulic traits using species-level mean trait values per site as the response variable and MAP as the predictor. We recognize that leaf phenology is one axis of variation in drought avoidance and sampled all leaves for the two drought-deciduous species when they were fully leafed out. We examined how good a prediction we could obtain without the two drought-deciduous species, but as it did not change model fits, we did not consider this trait in the final analyses.

To evaluate species-level trait response to MAP across the different sites where each species was measured, we fitted separate mixed effects models for each species and trait combination, using trait values from all the individual trees with hydraulic traits as the response variables, MAP as the fixed effect, and site as a random intercept. Models were fitted using the lme4 (ref. 66) and lmerTest⁶⁷ packages. Using all the individual trait measurements allowed us to retain within-site variation, as no averaging was performed at the species by site level, while including site as a random intercept captured site level variation not accounted by MAP and avoided pseudoreplication.

To quantify the extent to which variation in hydraulic traits was driven by species turnover versus intraspecific variation across sites, we fitted a series of Bayesian hierarchical models (one for each hydraulic trait) using the brms package⁶⁸. For all the models, we used weakly informative normal priors, four Markov chain Monte Carlo chains with 4,000 total iterations and 50% of them as warmup iterations. Models were based on individual-level tree data for all traits and included as response variables hydraulic traits associated with drought tolerance (leaf P_{50} , stem P_{50} , leaf SMP₅₀, stem SMP₅₀ and Ψ_{TLP}) and those associated with drought avoidance (leaf SWC, leaf CFT, leaf CTLP, stem SWC, stem CFT and stem CTLP). All models included MAP as a fixed effect, but the four models differed in the inclusion and structure of the random effects. The first model (the baseline model) included only MAP, assuming no differences among species in average hydraulic trait values or responses to rainfall. The second model included only random intercepts for species, capturing variation across sites that can be attributed to species turnover, but assuming a uniform response to precipitation for all species. The third model included only random slopes to account for the fact that the association between drought strategies and MAP is also likely to vary by species (intraspecific variation) but no additional effect of species. Finally, the fourth model included both random intercepts and slopes, which accounts for species turnover and differences among species in their response to precipitation. We then calculated conditional R^2 (fixed + random effects), marginal R^2 (only the fixed effect of rainfall) and LOO elpd (leave-one-out cross-validation expected log posterior density) for each model. Higher LOO elpd values indicate a better fit of the model. Based on LOO elpd, we calculated elpd difference and LOO elpd standard error difference among models to determine the best model. A higher LOO elpd and conditional R^2 for the fourth model relative to the model that includes only random intercepts (that is, species turnover) and a fixed effect of rainfall indicate that intraspecific variation in hydraulic traits is a significant factor in structuring forest drought resistance. In other words, if the full mixed-effects model, which includes both species-level intercepts and species-specific

trait–rainfall slopes, has the highest LOO elpd and conditional R^2 , this indicates that allowing species to differ in their trait–environment responses (that is, intraspecific variation) substantially improves model performance. In all of the models, we scaled MAP to standardize the values and facilitate convergence. Using the insight package⁶⁹, we extracted the proportion of variance explained by slopes (intraspecific trait variation), intercepts (species turnover), fixed effect (MAP) and the residual unexplained variance from the fourth model, which included both random intercepts and slopes. We performed all analyses using R statistical software (R v.4.4.2). All data used for the analyses and the R code are available at Dryad (<https://doi.org/10.5061/dryad.r4xgxd2vb>)⁷⁰.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data have been deposited to the Dryad digital repository⁷⁰ (<https://doi.org/10.5061/dryad.r4xgxd2vb>).

Code availability

All R code has been deposited to the Dryad digital repository⁷⁰ (<https://doi.org/10.5061/dryad.r4xgxd2vb>).

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Author contributions C.M.S.-M., R.M. and M.U. conceived the study. C.M.S.-M. and M.U. collected the data. C.M.S.-M., R.M. and M.U. performed the analyses. C.M.S.-M. and M.U. wrote the manuscript with input from T.J.B. and R.M.

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Competing interests The authors declare no competing interests.

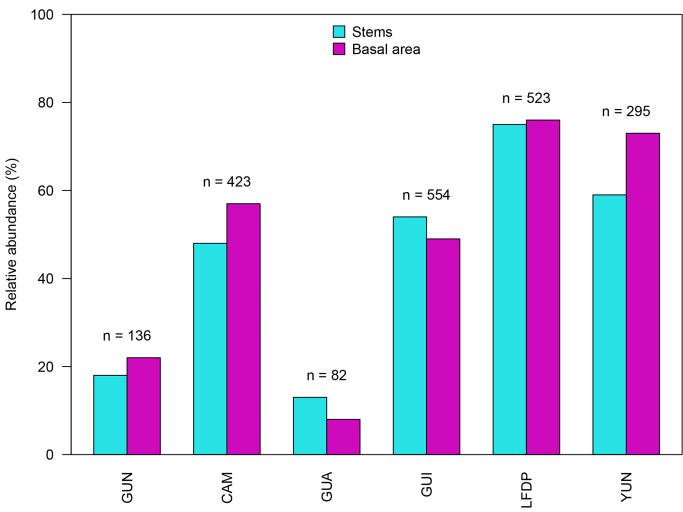
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-026-10870-4>.

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Extended Data Fig. 1 | Relative abundance (based on counts of individual stems and basal area of all trees with a diameter at breast height ≥ 5 cm) of species sampled for hydraulic traits in six plots.

Extended Data Table 1 | Characteristics of the six sites where we conducted the hydraulic measurements (MAP = mean annual precipitation, Tmax = maximum monthly temperature, VPD = vapour pressure deficit)

Site	Site Code	Soil type	MAP (mm yr ⁻¹)	Tmax (°C)	VPD (Pa)	Stem density (ha ⁻¹)	Mean canopy height (m)
Guanica	GUN	Limestone	1,004	30.5	1,290	5,856	6.8
Cambalache	CAM	Limestone	1,386	30.7	1,356	3,872	15.5
Guajataca	GUA	Limestone	2,017	29.1	1,110	3,138	21.2
Guilarte	GUI	Volcanic	2,195	25.6	912	2,454	18.5
El Yunque 300-400 m	LFDP	Volcanic	3,593	26.8	920	2,118	19.8
El Yunque 500-600 m	YUN	Volcanic	4,029	25.5	783	2,618	17.1

MAP and Tmax data are extracted from PRISM⁷¹; VPD is extracted from Chelsa Climate data⁷²; Stem density per ha is based on the trees ≥2.5 cm DBH⁴⁹. Mean canopy height is based on airborne lidar data from the plots³⁶.

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Extended Data Table 2 | List of the species measured, their families, species codes, leaf phenology (evergreen and drought-deciduous), sites where each species was measured, species-level maximum height⁷³, and relative basal area for the species in each given site

Species	Family	Phenology	Sites Code	Max height (m)
<i>Alchornea latifolia</i>	Euphorbiaceae	evergreen	GUI	15
<i>Alchornea latifolia</i>	Euphorbiaceae	evergreen	YUN	15
<i>Alchornea latifolia</i>	Euphorbiaceae	evergreen	LFDP	15
<i>Bursera simaruba</i>	Burseraceae	deciduous	CAM	12
<i>Bursera simaruba</i>	Burseraceae	deciduous	GUA	12
<i>Bursera simaruba</i>	Burseraceae	deciduous	GUN	12
<i>Casearia arborea</i>	Flacourtiaceae	evergreen	GUI	9
<i>Casearia arborea</i>	Flacourtiaceae	evergreen	YUN	9
<i>Casearia arborea</i>	Flacourtiaceae	evergreen	LFDP	9
<i>Cecropia schreberiana</i>	Moraceae	evergreen	GUI	21
<i>Cecropia schreberiana</i>	Moraceae	evergreen	YUN	21
<i>Cecropia schreberiana</i>	Moraceae	evergreen	LFDP	21
<i>Coccoloba diversifolia</i>	Polygonaceae	evergreen	CAM	9
<i>Coccoloba diversifolia</i>	Polygonaceae	evergreen	GUN	9
<i>Dacryodes excelsa</i>	Burseraceae	evergreen	GUI	30
<i>Dacryodes excelsa</i>	Burseraceae	evergreen	YUN	30
<i>Dacryodes excelsa</i>	Burseraceae	evergreen	LFDP	30
<i>Drypetes glauca</i>	Euphorbiaceae	evergreen	GUI	9
<i>Drypetes glauca</i>	Euphorbiaceae	evergreen	YUN	9
<i>Drypetes glauca</i>	Euphorbiaceae	evergreen	LFDP	9
<i>Erythroxylum rotundifolium</i>	Erythroxylaceae	evergreen	CAM	6
<i>Erythroxylum rotundifolium</i>	Erythroxylaceae	evergreen	GUN	6
<i>Faramea occidentalis</i>	Rubiaceae	evergreen	CAM	9
<i>Faramea occidentalis</i>	Rubiaceae	evergreen	GUA	9
<i>Guarea guidonia</i>	Meliaceae	evergreen	GUI	23
<i>Guarea guidonia</i>	Meliaceae	evergreen	LFDP	23
<i>Inga laurina</i>	Fabaceae	evergreen	GUI	21
<i>Inga laurina</i>	Fabaceae	evergreen	YUN	21
<i>Inga laurina</i>	Fabaceae	evergreen	LFDP	21
<i>Krugiodendron ferreum</i>	Rhamnaceae	evergreen	CAM	5
<i>Krugiodendron ferreum</i>	Rhamnaceae	evergreen	GUN	5
<i>Micropholis guyanensis</i>	Sapotaceae	evergreen	GUI	15
<i>Micropholis guyanensis</i>	Sapotaceae	evergreen	YUN	15
<i>Micropholis guyanensis</i>	Sapotaceae	evergreen	LFDP	15
<i>Ocotea leucoxylon</i>	Lauraceae	evergreen	GUA	15
<i>Ocotea leucoxylon</i>	Lauraceae	evergreen	GUI	15
<i>Ocotea leucoxylon</i>	Lauraceae	evergreen	YUN	15
<i>Ocotea leucoxylon</i>	Lauraceae	evergreen	LFDP	15
<i>Poitea florida</i>	Fabaceae	deciduous	CAM	15
<i>Poitea florida</i>	Fabaceae	deciduous	GUN	15
<i>Prestoea acuminata</i> var. <i>montana</i>	Arecaceae	evergreen	GUI	23
<i>Prestoea acuminata</i> var. <i>montana</i>	Arecaceae	evergreen	YUN	23
<i>Prestoea acuminata</i> var. <i>montana</i>	Arecaceae	evergreen	LFDP	23
<i>Sloanea berteriana</i>	Elaeocarpaceae	evergreen	GUI	28
<i>Sloanea berteriana</i>	Elaeocarpaceae	evergreen	YUN	28
<i>Sloanea berteriana</i>	Elaeocarpaceae	evergreen	LFDP	28
<i>Tabebuia heterophylla</i>	Bignoniaceae	evergreen	GUA	18
<i>Tabebuia heterophylla</i>	Bignoniaceae	evergreen	GUN	18
<i>Tabebuia heterophylla</i>	Bignoniaceae	evergreen	YUN	18
<i>Tabebuia heterophylla</i>	Bignoniaceae	evergreen	LFDP	18

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Software and code

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Data collection

For the leaf and stem optical vulnerability curves, we used the optical vulnerability technique using costume made Cavicams as described by Brodribb et al. (2016) , Brodribb et al. (2017) and at <https://www.opensourceov.org/>. We used ImageJ software (Version 1.54p; National Institutes of Health, USA) to analyze the pictures of leaf and stem embolisms. For the pressure volume curves we used the bench dehydration method as decried by Tyree & Hammel (1972) and Sack & Pasquet-Kok (2011).

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Data analysis

We performed all statistical analyses using R statistical software version R 4.4.2. The mixed effects models fitted using the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) packages. To fit the Bayesian hierarchical models, we used the brms package (Bürkner 2017) and the insight package (Lüdtke et al. 2019).

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All data used for the analyses and the R code are available here DOI: 10.5061/dryad.r4xgxd2vb. There is one CSV with all hydraulic trait data and mean annual precipitation that was derived from Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>, accessed 25 April 2023).

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Study description

We measured 11 plant hydraulic traits for 18 tree species in six different forest reserves spanning the island's rainfall gradient (Fig. 1 and Extended Data Table 1; 2). These included traits linked to drought avoidance—leaf and stem capacitance (C), saturated water content (SWC)—and drought tolerance—leaf and stem xylem vulnerability to embolisms (P50) and stomatal safety margins (SM).

Research sample

Based on previous ecological studies at these six sites, we identified abundant tree species that occurred at multiple of these sites (Muscarella et al. 2016, Muscarella et al. 2020). We identified 18 abundant species that occurred at multiple of the six sites. Traits were measured on as many of the 18 species that occurred at each of the six sites, totaling 290 trees, with all species measured at two to four locations.

References:

Muscarella, R., S. Kolyaie, D. C. Morton, J. K. Zimmerman, and M. Uriarte. 2020. Effects of topography on tropical forest structure depend on climate context. *JOURNAL OF ECOLOGY* 108:145-159.

Muscarella, R., M. Uriarte, D. L. Erickson, N. G. Swenson, W. J. Kress, and J. K. Zimmerman. 2016. Variation of tropical forest assembly processes across regional environmental gradients. *Perspectives in Plant Ecology, Evolution and Systematics* 23:52-62.

Sampling strategy	At each site, we measured leaf and stem pressure-volume curves and leaf and stem optical vulnerability curves on average on five trees of each species of the 18 species at each of the sites where that occurred (ED Table 3).
Data collection	We measured leaf and stem pressure-volume curves using 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, Madison, WI, USA). As leaves dehydrated, we periodically measured water potential (Ψ) with a Pressure Chamber Instrument (PMS Instrument Company, Albany, OR, USA) and leaf weight on a balance. We entered all the data as it was collected in Google spreadsheets. 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 (Parafilm sealing film, Bemis Company, Neenah, WI, USA). As the branch dehydrated, we used a stem psychrometer (ICT International, Armidale, Australia) to record water potential every 10 min and periodically weighed the branch with a balance. We entered the data into a Google spreadsheet and uploaded to Google Drive each of the data file outputs from the stem psychrometer data loggers. 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. While the branches were drying, we used stem psychrometers to measure water potential every 10 minutes. We uploaded to Google Drive all the photos and the data files from the stem psychrometers. References: Brodribb, T. J., M. Carriqui, S. Delzon, and C. Lucani. 2017. Optical Measurement of Stem Xylem Vulnerability. <i>Plant Physiology</i> 174:2054–2061. Brodribb, T. J., R. P. Skelton, S. A. M. McAdam, D. Bienaimé, C. J. Lucani, and P. Marmottant. 2016. Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. <i>New Phytologist</i> 209:1403–1409. Tyree, M. T., and H. T. Hammel. 1972. The Measurement of the Turgor Pressure and the Water Relations of Plants by the Pressure-bomb Technique. <i>Journal of Experimental Botany</i> 23:267–282.
Timing and spatial scale	All hydraulic measurements were conducted between July 2019 and June 2023. We did continues sampling from July 2019 and June 2022 and then a final sampling during June 2023.
Data exclusions	No data was excluded from the sampling.
Reproducibility	All details are described in the Methods section on how we selected the species, collected the leaf and stem pressure-volume curves, and the leaf and stem optical vulnerability curves. We measured on average 5 trees of each species at each site, and we have added these details in the Extended data (ED Table 3).
Randomization	Randomization was not relevant to our study as we were targeting specific species at each of the six study sites across the rainfall gradient.
Blinding	Blinding was not relevant to our study.
Did the study involve field work?	☒ Yes ☐ No

Field work, collection and transport

Field conditions	The study was conducted in six locations across the Caribbean Island of Puerto Rico spans 8,740 km ² and encompasses six Holdridge life zones. Mean annual precipitation ranges from 800 mm in subtropical dry forests to over 4,000 mm in subtropical rainforests. The primary soil types are derived from limestone and volcanic parent materials. Limestone soils, which have lower water-holding capacity and nutrients, are generally found in drier regions and the volcanic soils with higher water-holding capacity, occur in wetter areas.
Location	We selected six forest reserves distributed across the island, spanning a mean annual precipitation (MAP) from ca. 1,000 to 4,000 mm. Six sites with their soil parent material, rainfall and coordinates: Guanica, limestone 1,004 mm, 17°58'25.1"N 66°51'15.9"W Cambalache, limestone, 1,386 mm, 18°26'51.1"N 66°35'38.3"W Guajataca, limestone, 2,017 mm, 18°21'55.2"N 66°58'14.6"W Guilarte, volcanic, 2,195 mm, 18°06'33.4"N 66°44'49.8"W El Yunque 300–400 m, volcanic, 3,593 mm, 18°19'12.0"N 65°48'36.0"W El Yunque 500–600 m, volcanic, 4,029 mm, 18°19'18.1"N 65°48'11.8"W
Access & import/export	We worked under the umbrella of the Luquillo Long-Term Ecological Research Site.
Disturbance	Our sampling did not cause significant disturbances to the plot. Sun exposed terminal branches were collected using pole pruners.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Plants

Seed stocks

We worked with native tree species in Puerto Rico, so this does not apply.

Novel plant genotypes

We worked with native tree species in Puerto Rico, so this does not apply.

Authentication

We worked with native tree species in Puerto Rico, so this does not apply.