Limited intraspecific variation in drought resistance along a pronounced tropical rainfall gradient

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Assessing within-species variation in response to drought is crucial for predicting species' responses to climate change and informing restoration and conservation efforts, yet experimental data are lacking for the vast majority of tropical tree species. We assessed intraspecific variation in response to water availability across a strong rainfall gradient for 16 tropical tree species using reciprocal transplant and common garden field experiments, along with measurements of gene flow and key functional traits linked to drought resistance. Although drought resistance varies widely among species in these forests, we found little evidence for within-species variation in drought resistance. For the majority of functional traits measured, we detected no significant intraspecific variation. The few traits that did vary significantly between drier and wetter origins of the same species all showed relationships opposite to expectations based on drought stress. Furthermore, seedlings of the same species originating from drier and wetter sites performed equally well under drought conditions in the common garden experiment and at the driest transplant site. However, contrary to expectation, wetter-origin seedlings survived better than drier-origin seedlings under wetter conditions in both the reciprocal transplant and common garden experiment, potentially due to lower insect herbivory. Our study provides the most comprehensive picture to date of intraspecific variation in tropical tree species' responses to water availability. Our findings suggest that while drought plays an important role in shaping species composition across moist tropical forests, its influence on within-species variation is limited.

drought resistance | local adaptation | functional traits | reciprocal transplant experiment | common garden experiment

Tropical forests harbor the majority of Earth's terrestrial diversity and play a critical role in regional and global carbon and water cycles (1, 2). Increasingly, conservation and restoration of tropical forests are recognized as potential cost-effective natural climate solutions (3), given the vast amounts of carbon they store (4) and their biophysical effects on climate (5). However, large changes to rainfall regimes are predicted for the tropics over the 21st century (6), including both increases and decreases in mean annual rainfall as well as increased frequency of severe events, such as droughts (7). The ability of tropical forests to mitigate climate change and maintain biodiversity depends on how tree species and populations respond to altered precipitation patterns. Understanding how water availability in general, and drought specifically, affects tropical trees is therefore critical for predicting impacts of climate change on these highly diverse and valuable ecosystems (8, 9).

Previous research has shown that co-occurring tropical tree species vary widely in their sensitivity to seasonal drought (10, 11). At the species level, experimentally measured drought responses and key traits related to drought resistance [e.g., turgor loss point (12)] can predict tropical tree species abundance and distribution at local to regional scales (10, 13, 14). However, many tropical tree species grow across a range of rainfall conditions, and thus populations of the same species often experience marked differences in drought severity. This should lead to within-species variation in drought resistance as a result of local adaptation to drought stress (15), if selection is strong enough and gene flow among populations is low (16). An understanding of intraspecific variation in drought resistance is critical for accurately predicting species range shifts (17, 18), and thus changes in community composition, structure, and diversity under climate change. In addition, information on within-species variation in drought resistance can inform the design of forest restoration projects (e.g., selection of seed sources) to maximize resilience in the face of climate change (19).

Understanding local adaptation and identifying the environmental factors driving selection requires experimental approaches that tease apart the influence of genetic differentiation from plasticity (17). Such experiments are logistically difficult, and as a result, intraspecific variation in drought resistance across populations has been assessed experimentally in only

Significance

Under climate change, the ability of tropical forests to maintain biodiversity and provide key ecosystem services will depend on how tree species respond to predicted shifts in rainfall and drought stress. Using transplant experiments and trait measurements, we investigated variation in drought resistance for 16 native tree species across a strong rainfall gradient in Panama. While drought resistance varied widely among species, we found little evidence for variation in drought resistance within species. Our findings suggest that while drought shapes species composition along precipitation gradients, within-species variation is driven by other factors, such as herbivory. These findings have implications for predicting shifts in tropical tree species distributions and for the design of conservation and restoration efforts in tropical forests.

a handful of tropical tree species (20). These studies have focused on economically valuable species [e.g., timber species (21, 22)] or a single common species (23, 24) or family (25), and have produced mixed results. Experimental studies involving multiple species are needed to evaluate the extent of intraspecific variation in drought resistance in tropical tree communities and identify traits underlying differences in performance under drought conditions.

To fill this knowledge gap, we conducted a comprehensive study of intraspecific variation in drought resistance using reciprocal transplant and common garden experiments, measurements of key functional traits related to drought response, and estimates of genetic diversity, differentiation, and gene flow for 16 tropical tree species in lowland tropical moist forests in central Panama. These species occur along a strong precipitation gradient spanning ~65 km from the Pacific to the Caribbean coast (Fig. 1). Across the study area, mean annual rainfall ranges widely (ca. 1,800 to 3,000 mm, *SI Appendix*, Table S1), as does dry season severity (Fig. 1). Tree species in this region vary widely in drought resistance (10, 11), and these species-level differences in response to seasonal drought play an important role in structuring tree communities (10, 26, 27). However, whether the pronounced differences in dry season severity across the gradient lead to within-species variation in drought resistance is not known.

We collected seeds of our 16 focal species from multiple sites along the rainfall gradient (*SI Appendix*, Table S2) and germinated them in a screenhouse. The resulting seedlings were then used in two field experiments: a common garden experiment with drought and irrigation treatments, and a reciprocal transplant experiment including three sites along the rainfall gradient (Fig. 1). The common garden experiment allowed us to quantify intraspecific variation in drought resistance and test the hypothesis that seedlings originating from drier sites are more resistant to drought stress than seedlings of the same species from wetter sites. The reciprocal transplant experiment allowed us to assess adaptation to local site

conditions and test the hypothesis that, at the driest transplant site, seedlings originating from drier sites have higher growth and survival than seedlings of the same species originating from wetter sites [i.e., local vs. foreign comparison, sensu (16)]. Because we expected drought stress to be the main factor driving differences in performance among origins, we did not expect to see a local advantage for wetter origin seedlings at the wet transplant site. In addition, we measured a range of traits related to drought resistance (Table 1) on seedlings of different origins in the screenhouse and common garden. We also genotyped leaf tissue from adult trees collected at sites across the gradient to assess levels of population genetic differentiation, gene flow, and genetic diversity in our focal species.

Results

Performance in the Common Garden Experiment. In the common garden experiment, transplanted seedlings in the drought treatment were subjected to drought under rain-out shelters for two consecutive annual 4-mo dry seasons (including a severe El Niño dry season), while those in the irrigation treatment were watered during the dry seasons to minimize drought stress (*Methods*). Analyses of seedling survival in drought vs. irrigation treatment revealed large variation among species in their responses to drought (Fig. 2), consistent with previous studies (10). By comparison, variation within species tended to be relatively small, with seedlings originating from drier and wetter sites along the rainfall gradient showing similar responses to drought for most species (Fig. 2). Although a few species appeared to exhibit wide variation among origins in response to drought (e.g., *Cordia alliodora, Trichilia tuberulata;* Fig. 2), interactions between seedling origin and treatment were not significant for any species when analyzed separately (*SI Appendix*, Table S3).

When analyzing all species together, however, we found that origin did significantly influence seedling response to treatment for survival (Fig. 3 and *SI Appendix*, Table S4), but not growth (*SI Appendix*, Table S5). Unexpectedly, in the drought treatment, there was no difference in the performance of drier vs. wetter origin seedlings of the same species. Instead, we detected a significant survival difference between origins in the irrigation treatment: Seedlings originating from wetter sites had higher survival in irrigated plots than seedlings originating from drier sites (Fig. 3).

Performance in the Reciprocal Transplant Experiment. Results of the reciprocal transplant experiment were consistent with our findings from the common garden experiment. At the driest transplant site, there was no difference in survival or growth among origins of the same species (Fig. 4 and *SI Appendix*, Tables S6 and S7), indicating that local origin seedlings had no advantage at that site. However, at the wettest transplant site, a local origin advantage emerged when analyzing all species together: Seedlings originating from the wetter side of the rainfall gradient had higher survival (but not growth) than seedlings originating from drier sites (Fig. 4 and *SI Appendix*, Tables S6 and S7).

When species were analyzed individually, no significant effects of origin (i.e., local vs. foreign) on growth or survival were found at any of the reciprocal transplant sites (*SI Appendix*, Table S8), with the one exception. At the intermediate site, one species (*Posoqueria latifolia*) showed a significant effect of origin on growth, with intermediate origin seedlings of that species growing significant faster than wet (but not dry) origin seedlings (*SI Appendix*, Table S8). This resulted in a significant effect of origin on growth at the intermediate site when comparing intermediate vs. wet origin seedlings for all species combined (*SI Appendix*, Table S7). However, intermediate

Fig. 1. Variation in dry season water availability (assessed as the mean maximum cumulative dry season water deficit) across the rainfall gradient spanning the Isthmus of Panama. Gray squares represent the location of the reciprocal transplant sites, the black square shows the location of the common garden drought-irrigation experiment, and the black X marks the location of the screenhouse. The long-term average of the yearly maximum dry season water deficit was modeled based on rainfall data from 1961 to 1990 from 27 weather stations [data provided by the Meteorological and Hydrological Branch of the Panama Canal Authority and by the Physical Monitoring Program of the Smithsonian Tropical Research Institute; for details, see Condit et al. (26) and Browne et al. (28)].

Table 1. Traits assessed for each origin in the screenhouse and the common garden experiment

Trait	Unit	Expectation (drier vs. wetter origin)	Result-Screen house	Result-Common garden
Turgor loss point (TLP)	MPa	↓*	n.s.	
Maximum stomatal conductance (g_{max})	mmol/ $(m^2 * s)$	↓	n.s.	
Water potential at stomatal closure (WP_{crit})	MPa	↓*	n.s.	
Nonstructural carbohydrates (NSC)	% of stem DW	↑	↓ ($P = 0.01$)	
Stem density (D_{stem})	g/cm^3	↑*	n.s.	n.s.
Root density (D_{root})	g/cm^3	↑*	n.s.	
Leaf water content (WC_{leaf})	%FW	↑	n.s.	n.s.
Stem water content (WC_{stem})	%FW	↑	n.s.	n.s.
Root water content (WC_{root})	%FW	↑	n.s.	n.s.
Specific leaf area (SLA)	cm^2/g	↓*	↑ ($P = 0.004$)	n.s.
Leaf area ratio (LAR)	cm^2/g	↓	↑ ($P = 0.01$)	
Leaf weight ratio (LWR)	g/g	↓	n.s.	n.s.
Stem weight ratio (SWR)	g/g	↓	n.s.	n.s.
Root weight ratio (RWR)	g/g	↑	n.s.	n.s.

*indicates expectations that may flip direction for drought deciduous species
Arrows in the Expectation column indicate the direction of differences in trait values for drier compared to wetter origins of the same species expected under adaptation to drought. Results columns indicate the direction of significant trait differences (arrows) or lack of difference (n.s.) observed for driest vs. wetter origin seedlings based on linear mixed effect models for all focal species combined (see *SI Appendix,* Tables S9 and S10 for full model results). Empty cells indicate traits not measured in the common garden experiment. For species and their respective origins included in the analyses, see *SI Appendix,* Table S2.

origins of *P. latifolia* showed a trend of higher growth (relative to both wet and dry origins) at all sites and no significant effects of origin on survival were found at the intermediate site (*SI Appendix,* Table S6). Therefore, the results do not suggest local adaptation at the intermediate site.

Intraspecific Variation in Functional Traits. For the majority of the functional traits that we assessed, we found no differences among origins (Table 1 and *SI Appendix,* Tables S9 and S10). Notably, turgor loss point, i.e., the water potential at which leaf wilting occurs, a trait that is closely linked to drought resistance in tropical tree species (12), did not differ significantly between driest and wetter origins of the same species (Fig. 5A). Furthermore, of the 14 traits measured under common conditions in the screenhouse, only three exhibited a significant intraspecific difference between seedlings of drier and wetter origins (Table 1 and *SI Appendix,* Table S9). In each of these cases, however, the difference between origins was contrary to what would be expected if trait values were determined predominantly by adaptation to drought stress: values of specific leaf area and leaf area ratio were higher, and nonstructural carbohydrates lower, for drier compared to wetter origin seedlings for all species combined (Fig. 5). For traits measured on seedlings at the end of the common garden experiment, i.e., after being exposed to drought vs. irrigated conditions over two
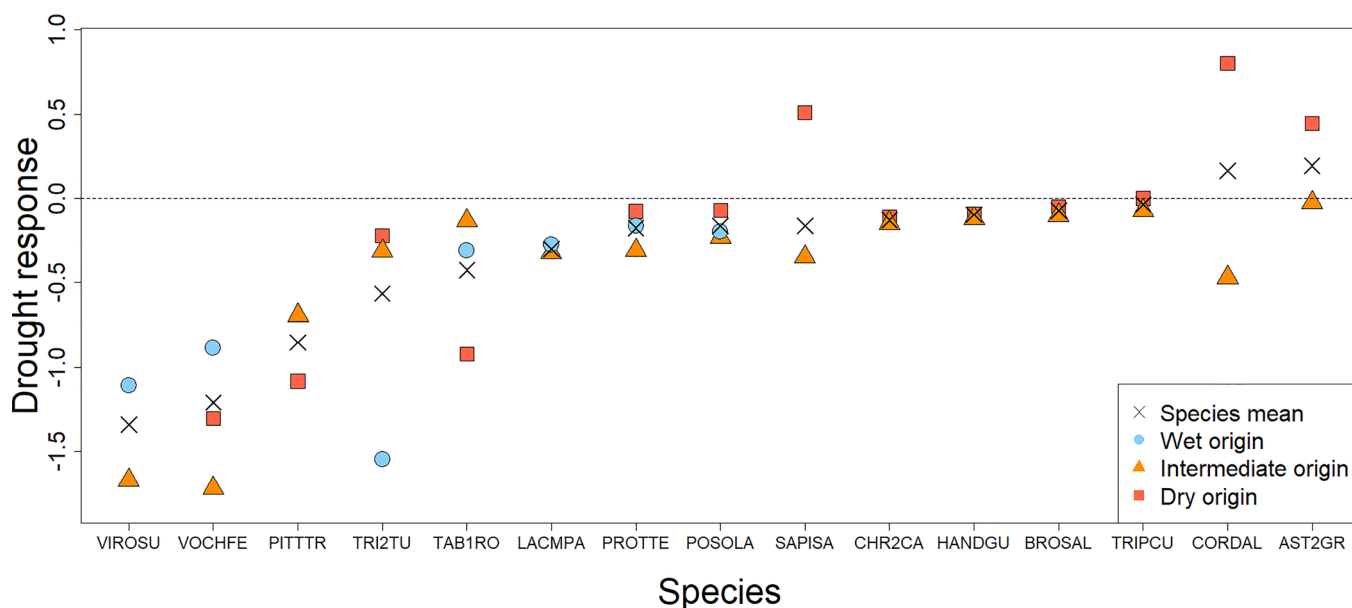
Fig. 2. Variation within and among tropical tree species in response to drought (i.e., drought resistance). Drought responses were quantified based on seedling survival in the common garden drought-irrigation experiment, with the response ratio calculated as ln (survival in drought treatment/survival in irrigated treatment). Drought response values of 0 indicate no difference in survival in irrigated vs. drought treatment (i.e., highly drought resistant), while negative values indicate lower survival under drought conditions (i.e., drought sensitive). Values shown for all origins of all focal species included in the common garden experiment, with the exception of *Anacardium excelsum*, which had very low survival in all treatments. Differences among origins in response to treatment were not significant in analyses of single focal species.
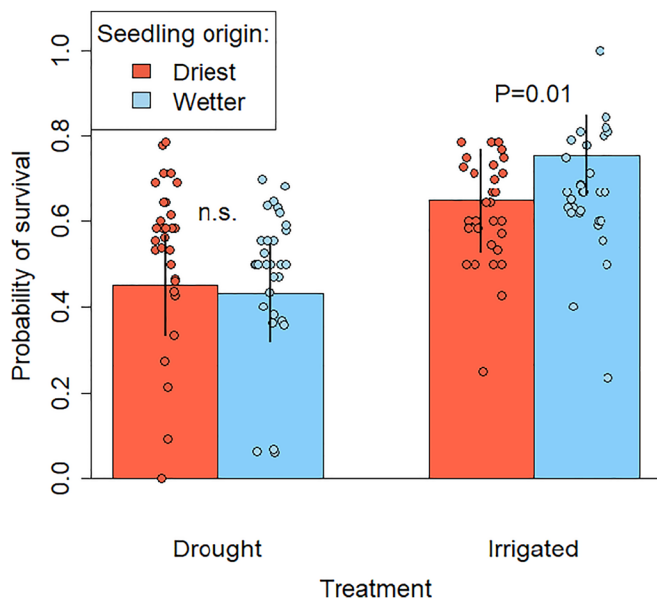
Fig. 3. Survival of transplanted seedlings of different origins in the drought and irrigated treatments of the common garden experiment for all 16 focal species combined. Bars show model-predicted survival (±1 SE) of seedlings originating from the driest section of the rainfall gradient of each focal species vs. seedlings originating from wetter sites where the species was present. Points correspond to observed survival in each of the 30 replicate plots per treatment. In the irrigated treatment, survival was significantly lower in the driest compared to the wetter origin seedlings, but there was no difference in survival between origins in the drought treatment. Survival was also significantly lower in the drought than in the irrigated treatment. See Fig. 2 for individual species response to experimental treatments.

dry seasons, we found no significant differences between wetter and drier origin seedlings (Table 1 and *SI Appendix*, Table S10). Additionally, we found no significant effect of irrigation treatment, and no treatment × origin interaction, on trait values (*SI Appendix*, Table S10), indicating overall low plasticity of traits in response to drought.

Gene Flow and Genetic Diversity among Populations. We performed genotype by sequencing and population genetic analyses on adults of 13 focal species to infer levels of gene flow and genetic structure across sites and to assess differences among sites in genetic

variation (i.e., single nucleotide polymorphisms). Among species, we found large differences in the amount of genetic clustering, genetic differentiation, and standing genetic diversity of adult trees across the gradient (*SI Appendix*, Table S11). However, some common trends emerged. First, for 11 of the 13 focal species, genetic clustering analyses (Bayesian Analysis of Population Structure, BAPS) indicated that individuals collected at sites spanning the gradient could be considered a single genetic population. Consistent with this, genetic differentiation among populations was generally low (mean G'st: 0.040; range: 0.015 to 0.066; *SI Appendix*, Table S11). Together, these results imply widespread panmictic mating and gene flow among sites for the majority of tree species examined. Second, we found that genetic diversity was higher at wetter sites compared to the driest site where the species occurred along the rainfall gradient for all species combined (mean$_{driest}$ = 0.24 vs. mean$_{wetter}$ = 0.27, t = 2.64, *P* = 0.017), with all but one species showing this trend (Fig. 6).

Discussion

Our analyses of seedling performance in common garden and reciprocal transplant experiments for 16 focal species, combined with measurements of key functional traits and estimates of population genetic structure and diversity, provide the most comprehensive picture to date of intraspecific variation in tropical tree species responses to water availability across sites. Contrary to our expectation, we found that, in general, seedlings originating from drier sites along the rainfall gradient are not better able to survive under drought conditions compared to populations of the same species from wetter sites—i.e., individuals from dry sites are not more drought resistant. Instead, seedlings originating from wetter sites appear to be better adapted to wetter conditions than seedlings originating from drier sites. While trends differed among species, our findings offer general insights into patterns of intraspecific variation in tropical tree species and optimal strategies for the conservation and restoration of tropical forests in the face of climate change.

Little Evidence for Within-Species Variation in Drought Resistance across the Gradient. Given the previously documented role of drought resistance in driving tree species distributions across the rainfall gradient in central Panama (10, 26, 27), we expected
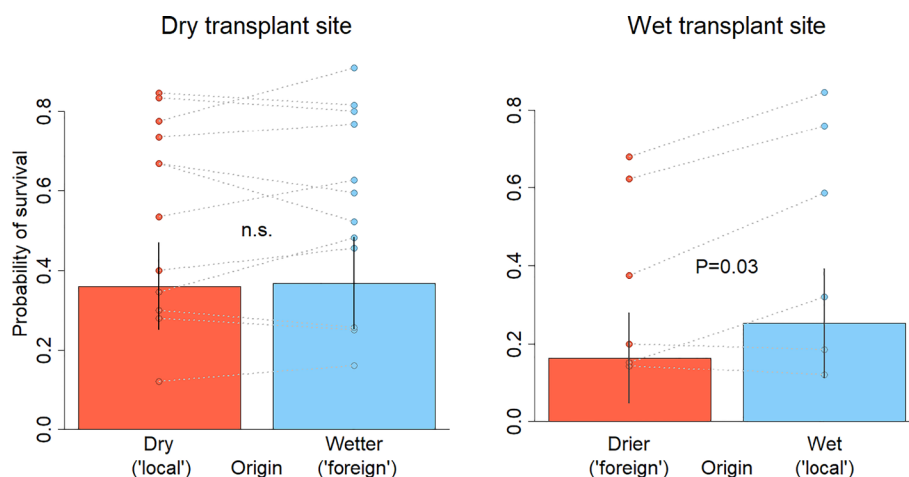
Fig. 4. Survival of transplanted seedlings of different origins at the dry and wet sites in the reciprocal transplant experiment. Bars show predicted survival (±1 SE) from a generalized linear mixed effects model with all focal species combined (total of 14 species at the dry site and 8 species at the wet site). Points connect with dashed lines show observed survival for the different origins of individual focal species having at least five survivors at the site. For the dry site, seedlings originating from the dry portion of the gradient (local) were compared to those originating from wetter sites (foreign). For the wet site, seedlings originating from the wet portion of the gradient (local) were compared to those originating from drier sites (foreign).
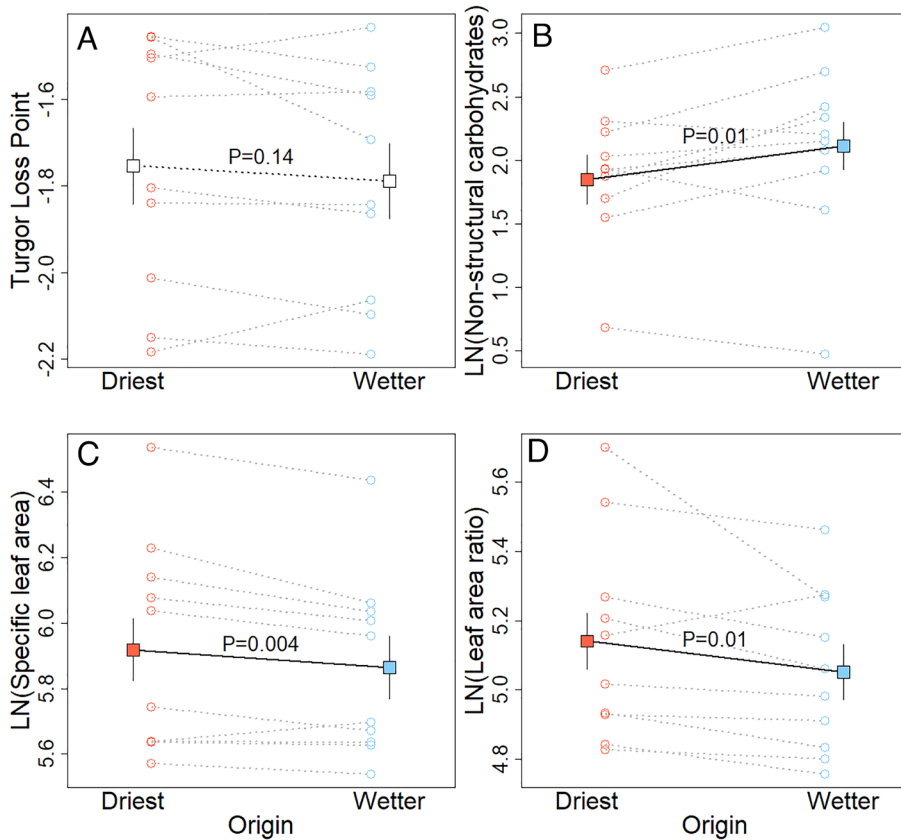
Fig. 5. Differences in trait values between the driest vs. wetter origin seedlings measured in the screenhouse for 10 focal species for (*A*) turgor loss point (MPa), (*B*) nonstructural carbohydrates (% of stem dry weight), (*C*) specific leaf area (cm²/g), and (*D*) leaf area ratio (cm²/g). Squares correspond to predicted trait values for all species combined (±1 SE) from linear mixed effects models, with filled squares connected by solid lines indicating a significant difference between origins (Table 1). Circles connected by dotted lines depict mean observed trait values for different origins of the same species.

to find differences in drought resistance among populations of the same species growing at wetter and drier sites along the same gradient. However, we found little evidence of intraspecific variation in drought resistance. Despite being exposed to drought stress over multiple dry seasons, including a severe dry season associated with an El Niño event (28), seedlings originating from wetter sites survived and grew just as well as seedlings of the same species originating from drier sites in the common garden drought treatment and at the dry transplant site. Thus, stronger seasonal drought stress at drier sites along the gradient does not appear to have selected for higher drought resistance at the within-species level. The low population genetic structure observed for the focal species (*SI Appendix,* Table S11) suggests that the strength of drought-mediated natural selection is not sufficient to counteract the homogenizing effect of gene flow across the gradient. However, our results suggest that selection by other factors is sufficiently strong to result in local adaptation at our wet site.

Our functional trait results further confirm that drought stress plays a limited role in driving within-species variation along this gradient. We found little evidence for intraspecific variation in trait values for the majority of functional traits examined in the screenhouse and common garden experiment, including for turgor loss point, which has been shown to correlate with drought resistance at the species level in our study system (12). Furthermore, the traits that did vary significantly among origins all showed relationships opposite to expectations based on drought stress (Table 1). These traits—specific leaf area, leaf area ratio, and nonstructural carbohydrates—are considered to be related to drought resistance (29, 30) but can be shaped by other factors, e.g., nutrients, light, and herbivore pressure (31–33). Both phosphorous and understory light availability tend to increase with drought stress along the gradient (26, 34). The higher values of specific leaf area and leaf area ratio, and lower concentrations of nonstructural carbohydrates, in drier vs. wetter origin seedlings suggest

that light and/or nutrient availability act as stronger selective forces than drought in this region (35).

Results from previous studies examining within-species differences in response to drought stress in tropical trees have been mixed. A reciprocal transplant experiment of six tree species in the Dipterocarp family in Malaysia found no evidence of local adaptation driven by topographic differences in water availability
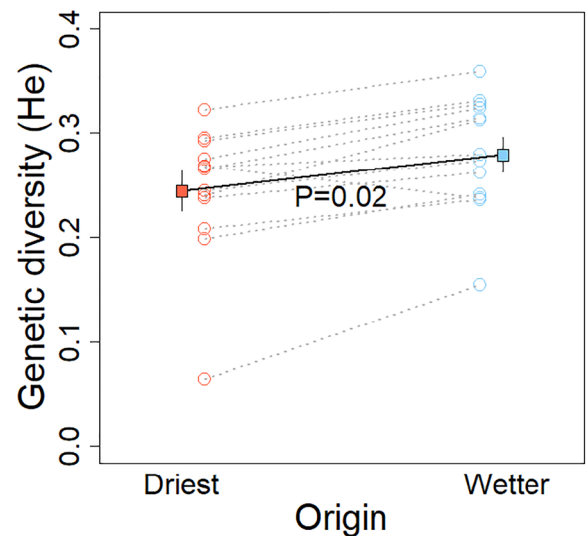
Fig. 6. Difference in genetic diversity (H$_e$) of trees found at the driest vs. wetter portion of the rainfall gradient, based on leaf tissue collected from adult trees of 13 focal species. Squares connected by the solid line correspond to predicted H$_e$ values (±1 SE) from a linear mixed effects model for all species combined, in which trees sampled in wetter areas had significantly higher genetic diversity than those sampled in wetter areas (*P* = 0.02). Circles connected by dotted lines depict mean observed H$_e$ values for the same species sampled at different sites.

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over relatively short distances (4.2 to 21.4 km) (25). In contrast, in field and greenhouse experiments on germination and seedling survival, Barton et al. (23) found evidence of intraspecific variation in drought resistance consistent with local adaptation in a widespread Hawaiian tree species. Compared to our study, the rainfall gradient covered was considerably steeper (1,150 to 4,460 mm mean annual rainfall), which may explain why intraspecific variation was found in that species despite its long seed dispersal distances (i.e., high gene flow). Intraspecific variation in traits related to drought resistance was reported in a tropical oak species (24). In that study, differences in annual rainfall among sites (1,014 to 2,683 mm) were more similar to our study; however, the geographical area covered was larger (>400 km), likely causing more limited gene flow between sites. Together with our results, these studies suggest within-species variation in drought resistance is influenced by both the steepness of the environmental gradient and the extent of gene flow between populations.

The species included in our study occur over larger geographic areas that span a wider range of environmental conditions than in our study region. It is therefore possible that intraspecific variation in drought resistance may be found in these species when including populations that experience more extreme climates or are more geographically isolated. However, the results of our multispecies study indicate that even across the same gradient, co-occurring species differ in the degree and direction of intraspecific variation in drought resistance among sites.

Evidence of Local Adaptation at Wetter Sites. While we found little evidence for within-species differences in response to drought, we found that seedlings originating from wetter sites had an advantage under wetter conditions, in both the common garden irrigation treatment and wet transplant site. This suggests that local adaptation within species does occur across this rainfall gradient due to differences in moisture, but only at the wetter site. All our study sites were on well-drained soils and the irrigation treatment was designed to alleviate drought stress but not cause waterlogging. Therefore, the advantage of wet origin seedlings at the wet transplant site and in the irrigation treatment is unlikely to be due to differences in tolerance to anoxia or any direct effect of water availability. Instead, the observed local advantage of wet origin seedlings under wetter conditions may be driven by biotic interactions. Specifically, in a related study, we assessed insect herbivore damage on seedlings in the same reciprocal transplant experiment as the current study and found that wetter origin seedlings experienced less herbivory than drier origin seedlings at the wet transplant site, but no differences in herbivory among origins were observed at the drier transplant sites (36). Local adaptation driven by herbivory is consistent with our finding of higher genetic diversity at wetter compared to drier sites (Fig. 6), because specialized herbivores can maintain high genetic diversity through balancing selection (37). Larger historical effective population sizes in wetter regions during past climatic changes followed by population expansion out of refugial wet forests after the last glacial maximum may also contribute to higher genetic diversity in wetter sites (38), along with lower human disturbance at the wetter vs. drier forest sites (39).

Implications for Conservation and Restoration of Tropical Forests. Changes in precipitation patterns are one of the main consequences of global climate change projected for the tropics (6). Our results offer several insights that can inform tropical forest conservation and restoration efforts under climate change. First, sensitivity to drought varies considerably more among species than within species for tropical trees, at least within our study region.

Thus, when designing restoration strategies for tropical forests at risk of increased drought stress, the primary focus should be on selecting more drought-resistant species, rather than on specific local populations or provenances. Nevertheless, in our study, some species showed a (nonsignificant) trend of higher drought resistance in drier origin seedlings, and local adaptation to drought stress has been reported in other tropical tree species (23). Therefore, if the goal is to protect or restore a particular species of ecological or economic importance, detailed studies of that species should be conducted to assess intraspecific variation. Our study also suggests that targeting drier populations as seed sources for restoration efforts could come at a cost, namely lower genetic diversity. Given the variety of different stressors tropical forests experience under current and future conditions, aiming for high species and genetic diversity will likely result in more resilient forests in the long term (40). Finally, the lack of local adaptation to drought that we observed suggests tropical tree species' range shifts under climate change in this region can be predicted based on species-level estimates of drought resistance and that populations in wetter parts of a species range may be able to persist under drier conditions in the future.

Materials and Methods

Study Site. The study was conducted in tropical moist lowland forests along the Isthmus of Panama, which exhibits a pronounced rainfall gradient from ca. 1,800 mm/y at the Pacific coast to nearly 3,000 mm/y at the Atlantic coast across a distance of 65 km. Dry season severity, assessed as the long-term average of the cumulative maximum dry season water deficit, varies with annual rainfall (Fig. 1 and *SI Appendix*, Table S1), as does typical dry season length (~145 d at the dry side vs. ~120 d on the wet side (10)). The gradient in seasonal drought severity has been found to be the primary driver of species distributions across the isthmus (10, 14, 26), leading to significant tree species turnover across sites (35, 41). Many species, however, are distributed either partway or all the way across the rainfall gradient, such that individuals of the same species growing at different sites experience different annual rainfall and dry season severity (26). Soil nutrient availability also varies across the region (26), while mean annual temperature varies little across the gradient [26.9 °C at both the Pacific and Caribbean sides (42)].

In this study, we divided the rainfall gradient into three sections: dry, intermediate, and wet (*SI Appendix*, Table S1). The study was conducted over ~1.5 y (September 2014 to July 2016), including two dry and one wet season. The second dry season was severe due to the 2015-16 El Niño event (28).

Species Selection. The study focused on 16 tree species (*SI Appendix*, Table S2), which are all native to the region, relatively common where they occur within the study area, and shade-tolerant (i.e., excluding light-demanding pioneer species). Species were chosen to include different distribution patterns across the rainfall gradient, i.e., species common in dry to intermediate rainfall sites, wet to intermediate, or occurring widely across entire whole rainfall gradient. Final species inclusion in each part of the study (e.g., experiments, trait measurements) depended on the availability of sufficient numbers of seeds and healthy seedlings of comparable size from at least two origins, including several mother trees per origin (see below; *SI Appendix*, Table S2).

Plant Material: Seeds, Seedlings, and Leaves. We collected seeds (to raise seedlings for experiments) and leaves (for genotyping) of each species from two or three sections of the rainfall gradient (dry, intermediate, wet sections; *SI Appendix*, Table S1) depending on the species' distribution (*SI Appendix*, Table S2). Previously established inventory plots (26) were used as guidance for locating the target species and fruiting individuals, and the search was expanded beyond the plots and along trails and forest roads. In each section of the gradient, leaves were collected for genotype analyses from 12 to 30 individuals per species and immediately placed in plastic bags with silica gel to dry.

Seeds were collected from at least three mother trees per species in lowland (<300 m) tropical forest within each section of the gradient. Fruits/seeds were usually collected from or under individual fruiting trees, so that the seeds could be assigned to seed lots representing a single likely mother tree. Sometimes fruits/seeds were collected from the ground in areas with several (2 to 8) fruiting

conspecifics. In such cases, seeds were considered one seed lot (and treated the same as a single mother) but may have come from several clumped trees. Mother trees/lots were located at least 40 m apart. Seeds were collected between December 2013 and October 2014, and then cleaned and raised in seedling trays in a screenhouse in a common substrate of local forest soil and sand (washed river sand; 3:1 mixture) at ca. 10% light under regular watering. In two species (VOCHFE and HADRGU), we did not find enough seeds and thus collected young seedlings from the field and raised them in the screenhouse under the same conditions until transplanting. From nearly 10,000 seedlings raised, we selected healthy seedlings for the field experiments and screenhouse trait measurements, minimizing size differences between origins (within species), and maintaining several mother trees per origin.

In this study, we focused on responses to water availability at the seedling stage. Seedlings are vulnerable to drought because their root systems do not reach deep, moist soil layers, and seedling survival shapes future forest composition. In our previous studies on interspecific drought resistance of tree species in this region, drought responses measured at the seedling stage (using a similar experimental approach) were correlated with species distributions across the rainfall gradient for adult trees (10) and with drought mortality of seedlings (28) and adults (Engelbrecht, unpublished data).

Seedling Transplanting. Seedlings were transplanted to the field experiments (for details, see below) to plots in the forest understory. Plots (1 × 1 m) were established within each area, in the understory of closed canopy forest on relatively flat terrain, excluding treefall and large branch-fall gaps and minimizing disturbance to the existing vegetation. Plots were 5 to 10 m apart from each other at each site. All plots were surrounded by open-top wire mesh cages (mesh holes 2.5 cm × 2.5 cm) to prevent herbivory from mammals, while allowing insect herbivory.

One seedling from each origin of each species was randomly assigned to each plot, and seedlings were transplanted into the field plots approximately 3 mo before the start of the dry season (September 2014), to allow enough time to establish root-soil contact before the start of the dry season. Seedlings were 1 to 7 mo old, and 6 to 18 cm tall depending on species, comparable to the age and size they would have reached in the field. Seedlings were independent of seed reserves, i.e., seeds had already fallen off in all species. Seedlings were transported to the field with their substrate to minimize stress, and the bare root seedlings were then transplanted directly into the local soil. Disturbance to the litter layer in transplanting was kept to a minimum.

Seedlings were planted in each plot in a 15 × 15 cm grid, spaced to minimize seedling overlap. Seedling mortality before the first census (December 2014/January 2015) was considered a transplant effect and those seedlings were excluded from analyses. When possible, such seedlings were replaced by a seedling of the same species and origin if still available in the screenhouse, to maximize sample sizes.

Experimental Design of the Field Experiments

Common Garden Drought-Irrigation Experiment. We conducted a drought-irrigation experiment with seedlings of the 16 focal species (2 to 3 origins each, see *SI Appendix,* Table S2) in the understory of a forest site in the center of the rainfall gradient (43) (Buena Vista, Fig. 1). Sixty plots were established in the understory, of which 30 were covered with transparent rain-out shelters and 30 were irrigated in the dry season to alleviate drought stress (for details, see below). We randomly selected one seedling of each origin of each species to transplant into each of the 60 plots. Due to a lack of available seedlings for some species and initial deaths due to transplant effects, the final sample sizes of each origin of each species varied, but numbers were similar for the irrigated and drought treatment (*SI Appendix,* Table S13). To ensure the same range of light conditions in both treatments, the plots were paired by similarity of initial light conditions as assessed by hemispherical photographs [Nikon Coolpix P5000 camera with a Fisheye Converter, analyzed with Gap Light Analyzer v2 (44)], and one plot of each pair was randomly assigned to each treatment.

In the drought treatment, plots were covered with clear plastic rainfall exclusion shelters (1.5 × 1.5 m square footprint) for the

duration of the dry seasons (3 January to 14 April 2015 and 21 January to 28 April 2016), excluding any dry season rainfall. Irrigation plots were watered regularly during the dry season. Irrigation levels necessary to avoid drought stress in the dry season are considerably higher than average wet season rainfall, because of elevated soil evaporation and transpiration of competing trees. Due to interannual and spatial variation of rainfall, relative air humidity, and competition, it was not useful to define irrigation levels a priori. Thus, plots were initially watered 5 d a week for a total equivalent to 209 mm/mo, and the amount was increased on a plot-by-plot basis up to 590 mm/mo as the dry season progressed, contingent on any visible wilting in the seedlings. Treatments were not applied during the wet season, when soil water availability in the forest understory is consistently high due to the high rainfall. The irrigation treatment successfully increased soil moisture and alleviated drought stress as indicated by significantly higher gravimetric soil water content, especially in the dry season (irrigated vs. drought treatment dry season plot means: t = –9.6645, df = 56.541, *P*-value = 1.405e-13; *SI Appendix,* Fig. S1) and higher survival and growth rates in the irrigated compared to the drought treatment (mean ± SE in irrigated vs. dry plots: proportion surviving = 0.65 ± 0.02 vs. 0.49 ± 0.03; RGR = 0.25 ± 0.05 vs. –0.15 ± 0.08).

Reciprocal Transplant Experiment across the Rainfall Gradient. We used a reciprocal transplant experiment across the rainfall gradient on seedlings of the 16 focal species (*SI Appendix,* Table S2) to test for differences in performance between origins indicative of a local origin advantage. The experiment included one site within each of the three sections of the rainfall gradient (wet, intermediate, and dry; Fig. 1 and *SI Appendix,* Table S1). For each focal species, we transplanted seedlings from two or three origins (wet, intermediate, and dry) reciprocally within their native range, i.e., into all three transplant sites along the rainfall gradient for widespread species and to two of the sites for species restricted to a portion of the gradient (*SI Appendix,* Table S2). Each experimental site contained 30 1 × 1 m plots. We randomly assigned one seedling from each origin of each species to each plot. As in the common garden experiment, there was some variation in the final sample sizes of each origin of each species due to a lack of available seedlings for some species and initial deaths due to transplant effects (*SI Appendix,* Table S13). Gravimetric soil moisture in the dry seasons decreased from the wettest to the driest site (*SI Appendix,* Fig. S1).

Performance Measurements. In both the common garden and reciprocal transplant experiments, seedlings were censused four times over ~1.5 y toward the beginning and end of the dry season: December 2014 to January 2015, May 2015 (September 2015 in PNM due to restricted site access), December 2015 to January 2016, and May 2016. In addition, the status (alive/dead) of seedlings in the reciprocal transplant experiment was assessed in September 2018 (seedlings in the common garden experiment were harvested in May 2016 for trait measurements; see below).

In each census, we recorded whether seedlings were alive or dead. Survival was monitored based on aboveground living biomass. Previous experiments have shown that seedlings in this system do not resprout once aboveground biomass has died (11). For surviving seedlings, we assessed plant height and leaf area. The length and width of each leaf were measured in the field, and missing or dead leaf area (e.g., due to pathogen or herbivory damage) on every leaf was recorded in 10% intervals. We calculated the area of each leaf from species-specific regression equations of direct leaf area measurements (leaf area meter LI-3100C, LiCor, NE) on the

product of leaf length and width (all $R^2 > 0.85$, $P < 0.001$) to derive "potential" leaf area, and then subtracted the damaged or missing leaf area. Relative growth rate based on leaf area change (RGR, $cm^2 cm^{-2} y^{-1}$) was calculated for each seedling as RGR = $(\ln[LA_{t1}] - \ln[LA_{t0}])/(t_1 - t_0)$ where LA is leaf area and t_0 and t_1 are the initial and final census.

Trait Measurements. We assessed 14 physiological, morphological, and whole plant traits that are known or hypothesized to be important for plant drought resistance (Table 1). The traits were measured under common screenhouse conditions on seedlings from 11 of our focal species (2 to 3 origins each, some traits could not be measured in all origins or species because of limited seedling availability (*SI Appendix*, Table S2). A subset of 8 traits was measured for 15 species with sufficient seedlings surviving in the dry and irrigated treatments at the end of the common garden experiment in May 2016 (*SI Appendix*, Table S2).

Seedlings for trait measurements in the screenhouse (located in Gamboa, at the center of the rainfall gradient, Fig. 1) were grown under fully watered conditions in 35 cm deep pots (D-40 Cone-tainers, Stewe and Sons) at ca. 10 % of full light in forest soil mixed with sand (equivalent to raising of seedlings, above). Seedlings were moved periodically to account for potential gradients of relative humidity and light in the screenhouse. At the time of measurement (February to March 2015) seedlings were 4 to 10 mo old, equivalent in age and size to seedlings naturally growing in the forest understory or in the field experiments at the start of their first dry season.

In the common garden experiment, aboveground traits were assessed for surviving individuals in 15 plots per treatment, and seedlings were dug up for belowground biomass in a subset of 10 plots per treatment.

Trait measurements followed Pérez-Harguindeguy et al. (45) when feasible (see details below). We aimed to measure each trait on at least five individuals per available species and origin. In the screenhouse, not all traits were measured on the same individuals, because some of the measurements were destructive and incompatible with each other. Traits measurements therefore give a composite picture of traits of origin × species combinations. Leaf traits were assessed on young, fully developed, healthy leaves, on 1 to 3 leaves per individual.

Leaf turgor loss point (π_{tlp}, MPa) was assessed following the method of Bartlett et al. (46) from measurements of leaf osmotic potential at leaf full turgor (π_o, MPa). Seedlings were rehydrated overnight, and osmotic potential was measured with an Osmometer (VAPRO 5600, Wescor, Logan, UT) on one mature leaf per individual after freezing in liquid N. We used the equation for woody species established by Bartlett et al. (46) to calculate the turgor loss point (π_{tlp}) from the measurements of osmotic potential at full turgor (π_o).

Maximum stomatal conductance (g_{max}, mmol m^{-2} s^{-1}) was measured in the morning (~6:00 to 9:00 am) with a steady-state diffusion leaf porometer (SC-1 Meter Group Inc. Pullman, WA).

To assess water potential at stomatal closure (WP_{crit}, MPa), we stopped watering and let the plants dry down in the screenhouse. We measured the stomatal conductance of the target leaves daily in the morning until stomatal conductance went below 10% of the maximum value (after 3 to 36 d). At that point, we measured its leaf water potential with a Scholander pressure chamber in the nearby laboratory (3000 Series Plant Water Status Console, Soil moisture Equipment Corp., Santa Barbara, CA).

For nonstructural carbohydrate content of stems (NSC_{stem}, % of total stem DW) plants were harvested in the morning (8:00 to 10:00 am), and the stem immediately dried in a microwave at

800 W for 5 min to stop any enzymatic activity and dried at 65 °C for 48 h (47). Analyses followed a modified version of the protocol of Hoch et al. (48) and Sala et al. (49). Stems were ground to a fine powder, and 12 mg sample material was extracted in 1.6 mL of distilled water in a 100 °C water bath. Fructose, sucrose, and starch were enzymatically hydrolyzed to glucose by consecutive enzymatic reactions (amyloglucosidase, glucose hexokinase, phosphoglucose isomerase, and invertase). The content of free sugars (glucose, fructose, sucrose) and starch was calculated from spectrophotometrical measurements obtained before and after the respective enzymatic reactions (microplate spectrophotometer, EPOCH, Biotek, Germany). Total nonstructural carbohydrate content, which has previously been linked to drought survival in tropical tree seedlings (30), was used in statistical analyses presented in the main text (see *SI Appendix*, Table S9 for results of separate analyses of starch and simple sugars).

Stem and root density (D_{stem}, D_{root}, g/cm^3) were determined for a ca. 2 to 3 cm long section of the stem and root (basal and upper section, respectively). The fresh volume was determined by the displacement method, i.e., the section was immersed in a water container on a balance (0.0001 g resolution) and the displacement weighed. Dry weight of the section was determined after oven drying (see below).

We also determined leaf, stem, and root water content (WC_{leaf}, WC_{stem}, WC_{root}, respectively, % fresh weight, FW), specific leaf area (SLA, cm^2/g), and whole plant allocation: leaf area ratio (LAR, cm2/g), and leaf, stem, and root weight ratios (LWR, SWR, RWR, respectively, g/g). To that end, we determined leaf area (leaf area meter LI-3100C, LiCOR, NE), fresh weight (FW) of leaves, stems, and roots of the fully watered plants (to 0.001 g), and the respective dry weights (DW) after drying to constant weight at 65 °C. Organ water contents were calculated as (FW-DW)/FW *100. Harvesting of the fully watered plants in the morning (at naturally high air moisture) ensured conditions close to full hydration and comparable across species.

Leaf Genotyping-by-Sequencing (GBS). We successfully genotyped trees of 13 of the 16 species from different origins along the rainfall gradient (*SI Appendix*, Table S11). We extracted the DNA from the dried leaves (see above) using 5 mg of dehydrated ground leaf tissue using the CTAB method with modifications (50) followed by a cleanup step using the solid-phase reversible mobilization (SPRI) method (51, 52). We normalized the DNA samples to a concentration of 20 ng/µL in a 96-well plate arrangement for each species for a total of 13 separate libraries. We digested DNA samples of each species library using the restriction enzyme *ApeKI*. Following digestion, we ligated indexed barcode adapters onto the DNA fragments to allow us to identify individuals for each species. After ligation, we pooled and cleaned each library. Then, we amplified the libraries for each species using PCR and primers that matched barcodes and universal adaptors and cleaned the libraries again (53). Subsequently, we sequenced the 13 libraries on one lane per species of either a HiSeq2000 (100-bp reads) or HiSeq3000 (150-bp reads) Illumina using a single-end reads at the CGRB facility in Oregon State University (http://core.cgrb.oregonstate.edu).

Statistical Analyses.
Survival and growth analyses. To model survival of transplanted seedlings, we used generalized linear mixed effects models with binomial errors to model the probability of an individual surviving from the initial census (December 2014/January 2015) to the final census in which mortality was assessed (May 2016 for common garden experiment; September 2018 for reciprocal transplant experiment). To model growth, we calculated relative growth rate

based on leaf area for each seedling that survived until the end of the experiment and used linear mixed effects models to model relative growth rates between the initial and final field census in which seedlings were measured (May 2016 for both experiments). In preliminary analyses, survival and growth results were qualitatively similar when using mixed effects Cox proportional hazards models or models with repeated measures of growth that included seedlings that died before the final census, respectively.

For the common garden experiment, we tested for an effect of treatment (irrigated vs. drought), origin, and an origin × treatment interaction on survival or growth. Because not all species had seedlings from all three origins (wet, intermediate, and dry), we tested for a difference between seedlings from the driest origin of each species and seedlings from wetter origins of the species (i.e., combining intermediate and wet origins for widespread species). We modeled all species combined and included species and species response to treatment as random slope and intercept terms, respectively.

Using survival data from the common garden experiment, we also calculated the response of survival to drought as an index of drought resistance (11) for each species and for each origin of each species separately (with the exception of *A. excelsum*, which had very low survival in all treatments). Drought response was assessed as DR = ln (survival in drought treatment/survival in irrigation treatment).

For the reciprocal transplant experiment, we analyzed each site separately because not all focal species were transplanted to all sites. For each site, we tested for performance differences between seedlings of "local" vs. "foreign" origin. Specifically, for the 14 focal species transplanted at the dry site, we tested for a difference in survival and growth of seedlings of dry (=local) origin relative to wetter origins (foreign, i.e., from intermediate and wet populations combined). For the eight focal species transplanted at the wet site, we tested for a difference in survival and growth of seedlings of wet (=local) origin compared to seedlings of drier origins (foreign, i.e., intermediate and dry populations combined). For the intermediate site, we compared growth and survival of intermediate (=local) vs. dry origins for the 14 focal species having seedlings from both intermediate and dry populations, and for intermediate (=local) vs. wet origins for the 8 focal species having seedlings from both the intermediate and wet populations. For the six widespread species, which had seedlings of all three origins transplanted to all three sites, we also ran models testing for survival differences between the three origins at each site, to check whether combining origins may have masked differences (*SI Appendix*, Table S14). Species was included as a random effect in all of these models.

For all of the above models, plot was included as a random effect to account for spatial variation in microhabitat, and initial size (height in the first census after transplantation) was included as a covariate to control for maternal effects and differences in seedling age at time of transplant. Seed lot was not included as a random effect in the final growth and survival models because it explained very little or no variation in preliminary analyses, and maternal effects should be captured (at least in part) by initial size. Because species varied widely in seedling size during the experiment, initial size values were log transformed and then standardized within species (by subtracting the mean and dividing by 1 SD) so that standardized values reflect the size of a seedling relative to other seedlings of the same species.

For growth and survival in both the common garden and reciprocal transplant experiments, we also ran models for each species separately using the same models as above (without species as a random effect), except in a few cases where the species had <5 survivors at a site or where models did not converge (e.g., due to insufficient number of survivors or growth observations

in one treatment or of one origin). To take into account multiple comparisons, we used the false discovery rate method (54) to adjust *P*-values based on the number of species in each analysis (e.g., 12 species analyzed separately for survival in the common garden experiment). Because the aim of the study was to assess general trends at the community level rather than within individual species, we focused on including as many species as logistically possible rather than having larger sample sizes for fewer species. Thus, we have more limited power to detect differences among origins for individual species.

Trait analyses. As in analyses of growth and survival, we tested for differences in trait values for the driest vs. wetter origins of each species (i.e., combining intermediate and wet origins for widespread species). For each of the 14 traits measured on seedlings of 10 to 11 species in the screenhouse (*SI Appendix*, Table S2), we used linear mixed effects models with seedling origin as a fixed effect and species and seed lot as random effects. For the 8 traits measured on seedlings of 15 species harvested at the end of the common garden experiment, we used linear mixed effects models to test for effects of origin and treatment, as well as an origin × treatment interaction. Species, seed lot, and seedling plot were included as random effects. For traits with skewed distributions, values were natural log or square-root transformed prior to analysis (*SI Appendix*, Tables S9 and S10). Because trait expectations may differ for tropical tree species with evergreen vs. drought deciduous leaf phenology (14), we confirmed that the results of the above trait analyses remained qualitatively similar when accounting for differences in leaf phenology (i.e., by excluding the two dry season deciduous species from the screenhouse trait analyses and by analyzing traits separately for the 5 drought deciduous species and 10 evergreen species in the field experiment). We did not run trait models for each species separately due to limited sample sizes for each origin and trait.

Survival, growth, and traits models were fit using the lme4 package (55) and lmerTest package (56) in R version 4.1.2 (57). *Analyses of genetic structure.* To process the raw reads of each of the species and to call SNPs, we used Stacks ver. 1.41 (58, 59) (*SI Appendix*, Table S12). None of the 13 species has a reference genome, so de novo assembly of SNP loci was required. In Stacks, we used Process_Radtags to demultiplex and discard reads with low-quality scores, incorrect barcodes, and ambiguous GBS sites. After this process, we ran the Stacks pipeline by hand, in the order: Ustacks, Cstacks, Sstacks, Rxstacks, rerun Cstacks, rerun Sstacks, and population. There is no prior information about polymorphisms or genome size for our focal species. Estimates of sequencing error and the depth of sequencing for each of the 13 species were used to delimit the optimal parameters in the Stacks analysis (58). Consequently, in 7 of 13 species (i.e., BROSAL, CHR2CA, PROTTE, PITTTR, TRIPCU, TRI2TU, and VOCHFE), we explored a range of values for two main parameters in the de novo pipeline that are associated with the final number of loci and their level of polymorphism recovered from our GBS. First, in Ustacks, we used values of 2, 3, 4, 5, and 10 for minimum depth of coverage of each stack (i.e., parameter –m, thus: m2, m3, m4, m5, m10). But we kept the number of mismatches allowed between Stacks by default (i.e., parameter M = 2). Moreover, in Cstacks, we tested values of one and three for the distance between catalog loci (i.e., parameter –n, thus: n1 and n3). Combining parameters –m and –n in Ustacks and Cstacks, we tested a total of 10 different combinations of parameters across the 8 species (58, 60). For each one of the 10 combinations, in Cstacks, we constructed a catalog for each one of the sampling locations, using the 10 individuals with a higher number of raw sequences. In Rxstacks, we used a threshold of –10 for the log

likelihood to remove loci with low coverage and high sequencing error and therefore correct genotypes and haplotype calls in the samples. Finally, in POPULATION, we selected the loci that were both present in all sample sites or habitat zones across the gradient and were genotyped at the 75% of individuals within each habitat. Moreover, to prevent linked SNPs, we selected a single SNP from any GBS locus.

We evaluated the optimal combination of parameters across eight species by calculating the genetic distance among individuals within each sampling site per species using Kinship in GENODIVE ver 2.0b27 (61). Assuming that individuals from the same geographic locality should be genetically more similar, we expected that best combination of parameters should maximize the number of SNPs recovered and, minimize the genetic distance among individuals collected in the same locality (60). We found no significant differences among mean genetic distance among 10 different combination parameters across all the eight species. Therefore, for later analysis across all 13 species, we decided to use the output data derived from the default parameter m = 3, and either n = 1 or n = 3 on each species, depending on which of those parameters recovered more SNPs.

Genetic diversity and population structure. Measures of population genetic diversity were determined using the program GENODIVE (62). We determined site and species level Observed Heterozygosity (Ho), Expected Heterozygosity (He), and Heterozygote deficit (Gis) (63). For each species, we calculated G'st a standardized measure of genetic differentiation (64). For all species combined, we tested for a significant difference in genetic diversity (He) between the driest site vs. wetter sites at which each species occurred using a linear mixed model with species as a random effect.

Population genetic structure was measured with a Bayesian clustering approach implemented in BAPS ver. 6 (65, 66). We used a mixture analysis with a spatially explicit model as a prior (i.e., the geographic coordinates of each sampling location) to determine the posterior probability (P) of cluster samples (K) from K = 1 to K = 10 for each one of the 13 species. Only in the cases when the higher posterior probability was for K > 1, we determined the level of admixture among sampled individuals using 100 iterations, 200 simulated nonadmixed reference individuals, and 20 iterations for each one of the reference individuals (*SI Appendix*, Table S11).

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