

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

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29

30 **Significance Statement**

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

40 **Abstract**

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

60

61 **Introduction**

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

73 Previous research has shown that co-occurring tropical tree species vary widely in their
74 sensitivity to seasonal drought (10, 11). At the species level, experimentally-measured drought
75 responses and key traits related to drought resistance (e.g., turgor loss point (12)) can predict
76 tropical tree species abundance and distribution at local to regional scales (10, 13, 14). However,
77 many tropical tree species grow across a range of rainfall conditions, and thus populations of the
78 same species often experience marked differences in drought severity. This should lead to
79 within-species variation in drought resistance as a result of local adaptation to drought stress
80 (15), if selection is strong enough and gene flow among populations is low (16). An
81 understanding of intraspecific variation in drought resistance is critical for accurately predicting
82 species range shifts (17, 18), and thus changes in community composition, structure, and

83 diversity under climate change. In addition, information on within-species variation in drought
84 resistance can inform the design of forest restoration projects (e.g., selection of seed sources) to
85 maximize resilience in the face of climate change (19).

86 Understanding local adaptation and identifying the environmental factors driving
87 selection requires experimental approaches that tease apart the influence of genetic
88 differentiation from plasticity (17). Such experiments are logistically difficult, and as a result,
89 intraspecific variation in drought resistance across populations has been assessed experimentally
90 in only a handful of tropical tree species (20). These studies have focused on economically
91 valuable species (e.g., timber species (21, 22)) or a single common species (23, 24) or family
92 (25), and have produced mixed results. Experimental studies involving multiple species are
93 needed to evaluate the extent of intraspecific variation in drought resistance in tropical tree
94 communities and identify traits underlying differences in performance under drought conditions.

95 To fill this knowledge gap, we conducted a comprehensive study of intraspecific
96 variation in drought resistance using reciprocal transplant and common garden experiments,
97 measurements of key functional traits related to drought response, and estimates of genetic
98 diversity, differentiation, and gene flow for 16 tropical tree species in lowland tropical moist
99 forests in central Panama. These species occur along a strong precipitation gradient spanning ~65
100 km from the Pacific to the Caribbean coast (Fig. 1). Across the study area, mean annual rainfall
101 ranges widely (ca. 1800-3000 mm, Table S1), as does dry season severity (Fig. 1). Tree species
102 in this region vary widely in drought resistance (10, 11), and these species-level differences in
103 response to seasonal drought play an important role in structuring tree communities (10, 26, 27).

104 However, whether the pronounced differences in dry season severity across the gradient lead to
105 within-species variation in drought resistance is not known.

106 We collected seeds of our 16 focal species from multiple sites along the rainfall gradient
107 (Table S2) and germinated them in a screenhouse. The resulting seedlings were then used in two
108 field experiments: a common garden experiment with drought and irrigation treatments, and a
109 reciprocal transplant experiment including three sites along the rainfall gradient (Fig. 1). The
110 common garden experiment allowed us to quantify intraspecific variation in drought resistance
111 and test the hypothesis that seedlings originating from drier sites are more resistant to drought
112 stress than seedlings of the same species from wetter sites. The reciprocal transplant experiment
113 allowed us to assess adaptation to local site conditions and test the hypothesis that, at the driest
114 transplant site, seedlings originating from drier sites have higher growth and survival than
115 seedlings of the same species originating from wetter sites (i.e., local vs. foreign comparison,
116 *sensu* (16)). Because we expected drought stress to be the main factor driving differences in
117 performance among origins, we did not expect to see a local advantage for wetter origin
118 seedlings at the wet transplant site. In addition, we measured a range of traits related to drought
119 resistance (Table 1) on seedlings of different origins in the screenhouse and common garden. We
120 also genotyped leaf tissue from adult trees collected at sites across the gradient to assess levels of
121 population genetic differentiation, gene flow, and genetic diversity in our focal species.

122 **Results**

123 ***Performance in the common garden experiment***

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

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

141 ***Performance in the reciprocal transplant experiment***

142 Results of the reciprocal transplant experiment were consistent with our findings from the
143 common garden experiment. At the driest transplant site, there was no difference in survival or
144 growth among origins of the same species (Fig. 4; Table S6, S7), indicating that local origin

145 seedlings had no advantage at that site. However, at the wettest transplant site, a local origin
146 advantage emerged when analyzing all species together: seedlings originating from the wetter
147 side of the rainfall gradient had higher survival (but not growth) than seedlings originating from
148 drier sites (Fig. 4; Table S6, S7).

149 When species were analyzed individually, no significant effects of origin (i.e., local vs
150 foreign) on growth or survival were found at any of the reciprocal transplant sites (Table S8),
151 with the one exception. At the intermediate site, one species (*Posoqueria latifolia*) showed a
152 significant effect of origin on growth, with intermediate origin seedlings of that species growing
153 significant faster than wet (but not dry) origin seedlings (Table S8). This resulted in a significant
154 effect of origin on growth at the intermediate site when comparing intermediate vs wet origin
155 seedlings for all species combined (Table S7). However, intermediate origins of *P. latifolia*
156 showed a trend of higher growth (relative to both wet and dry origins) at all sites and no
157 significant effects of origin on survival were found at the intermediate site (Table S6). Therefore,
158 the results, do not suggest local adaptation at the intermediate site.

159 ***Intraspecific variation in functional traits***

160 For the majority of the functional traits that we assessed, we found no differences among origins
161 (Tables 1, S9, S10). Notably, turgor loss point, i.e., the water potential at which leaf wilting
162 occurs, a trait that is closely linked to drought resistance in tropical tree species (12), did not
163 differ significantly between driest and wetter origins of the same species (Fig. 5a). Furthermore,
164 of the 14 traits measured under common conditions in the screenhouse, only three exhibited a
165 significant intraspecific difference between seedlings of drier and wetter origins (Table 1, S9). In

166 each of these cases, however, the difference between origins was contrary to what would be
167 expected if trait values were determined predominantly by adaptation to drought stress: values of
168 specific leaf area and leaf area ratio were higher, and non-structural carbohydrates lower, for
169 drier compared to wetter origin seedlings for all species combined (Fig. 5). For traits measured
170 on seedlings at the end of the common garden experiment, i.e., after being exposed to drought vs.
171 irrigated conditions over two dry seasons, we found no significant differences between wetter
172 and drier origin seedlings (Table 1, S10). Additionally, we found no significant effect of
173 irrigation treatment, and no treatment x origin interaction, on trait values (Table S10), indicating
174 overall low plasticity of traits in response to drought.

175 ***Gene flow and genetic diversity among populations***

176 We performed genotype by sequencing and population genetic analyses on adults of 13 focal
177 species to infer levels of gene flow and genetic structure across sites and to assess differences
178 among sites in genetic variation (i.e., single nucleotide polymorphisms). Among species, we
179 found large differences in the amount of genetic clustering, genetic differentiation, and standing
180 genetic diversity of adult trees across the gradient (Table S11). However, some common trends
181 emerged. First, for 11 of the 13 focal species, genetic clustering analyses (Bayesian Analysis of
182 Population Structure, BAPS) indicated that individuals collected at sites spanning the gradient
183 could be considered a single genetic population. Consistent with this, genetic differentiation
184 among populations was generally low (mean $G^{\prime}st$: 0.040; range: 0.015 – 0.066; Table S11).
185 Together, these results imply widespread panmictic mating and gene flow among sites for the
186 majority of tree species examined. Second, we found that genetic diversity was higher at wetter
187 sites compared to the driest site where the species occurred along the rainfall gradient for all

188 species combined ($\text{mean}_{\text{driest}}=0.24$ vs $\text{mean}_{\text{wetter}}=0.27$, $t=2.64$, $P=0.017$), with all but one species
189 showing this trend (Fig. 6).

190 **Discussion**

191 Our analyses of seedling performance in common garden and reciprocal transplant experiments
192 for 16 focal species, combined with measurements of key functional traits and estimates of
193 population genetic structure and diversity, provide the most comprehensive picture to date of
194 intraspecific variation in tropical tree species responses to water availability across sites.

195 Contrary to our expectation, we found that, in general, seedlings originating from drier sites
196 along the rainfall gradient are not better able to survive under drought conditions compared to
197 populations of the same species from wetter sites — i.e., individuals from dry sites are not more
198 drought resistant. Instead, seedlings originating from wetter sites appear to be better adapted to
199 wetter conditions than seedlings originating from drier sites. While trends differed among
200 species, our findings offer general insights into patterns of intraspecific variation in tropical tree
201 species and optimal strategies for the conservation and restoration of tropical forests in the face
202 of climate change.

203 ***Little evidence for within-species variation in drought resistance across the gradient***

204 Given the previously documented role of drought resistance in driving tree species distributions
205 across the rainfall gradient in central Panama (10, 26, 27), we expected to find differences in
206 drought resistance among populations of the same species growing at wetter and drier sites along
207 the same gradient. However, we found little evidence of intraspecific variation in drought
208 resistance. Despite being exposed to drought stress over multiple dry seasons, including a severe

209 dry season associated with an El Niño event (28), seedlings originating from wetter sites
210 survived and grew just as well as seedlings of the same species originating from drier sites in the
211 common garden drought treatment and at the dry transplant site. Thus, stronger seasonal drought
212 stress at drier sites along the gradient does not appear to have selected for higher drought
213 resistance at the within-species level. The low population genetic structure observed for the focal
214 species (Table S11) suggests that the strength of drought mediated natural selection is not
215 sufficient to counteract the homogenizing effect of gene flow across the gradient. However, our
216 results suggest that selection by other factors is sufficiently strong to result in local adaptation at
217 our wet site.

218 Our functional trait results further confirm that drought stress plays a limited role in
219 driving within-species variation along this gradient. We found little evidence for intraspecific
220 variation in trait values for the majority of functional traits examined in the screenhouse and
221 common garden experiment, including for turgor loss point, which has been shown to correlate
222 with drought resistance at the species level in our study system (12). Furthermore, the traits that
223 did vary significantly among origins all showed relationships opposite to expectations based on
224 drought stress (Table 1). These traits —specific leaf area, leaf area ratio, and non-structural
225 carbohydrates — are considered to be related to drought resistance (29, 30) but can be shaped by
226 other factors, e.g., nutrients, light, and herbivore pressure (31-33). Both phosphorous and
227 understory light availability tend to increase with drought stress along the gradient (26, 34). The
228 higher values of specific leaf area and leaf area ratio, and lower concentrations of non-structural
229 carbohydrates, in drier vs wetter origin seedlings suggest that light and/or nutrient availability act
230 as stronger selective forces than drought in this region (35).

231 Results from previous studies examining within-species differences in response to
232 drought stress in tropical trees have been mixed. A reciprocal transplant experiment of six tree
233 species in the Dipterocarp family in Malaysia found no evidence of local adaptation driven by
234 topographic differences in water availability over relatively short distances (4.2–21.4 km) (25).
235 In contrast, in field and greenhouse experiments on germination and seedling survival, Barton et
236 al. (23) found evidence of intraspecific variation in drought resistance consistent with local
237 adaptation in a widespread Hawaiian tree species. Compared to our study, the rainfall gradient
238 covered was considerably steeper (1150 - 4460 mm mean annual rainfall), which may explain
239 why intraspecific variation was found in that species despite its long seed dispersal distances
240 (i.e., high gene flow). Intraspecific variation in traits related to drought resistance were reported
241 in a tropical oak species (24). In that study, differences in annual rainfall among sites (1014 -
242 2683 mm) were more similar to our study, however the geographical area covered was larger
243 (>400 km), likely causing more limited gene flow between sites. Together with our results, these
244 studies suggest within-species variation in drought resistance is influenced by both the steepness
245 of the environmental gradient and the extent of gene flow between populations.

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

253 ***Evidence of local adaptation at wetter sites***

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

273 ***Implications for conservation and restoration of tropical forests***

274 Changes in precipitation patterns are one of the main consequences of global climate change
275 projected for the tropics (6). Our results offer several insights that can inform tropical forest
276 conservation and restoration efforts under climate change. First, sensitivity to drought varies
277 considerably more among species than within species for tropical trees, at least within our study
278 region. Thus, when designing restoration strategies for tropical forests at risk of increased
279 drought stress, the primary focus should be on selecting more drought resistant species, rather
280 than on specific local populations or provenances. Nevertheless, in our study, some species
281 showed a (non-significant) trend of higher drought resistance in drier origin seedlings, and local
282 adaptation to drought stress has been reported in other tropical tree species (23). Therefore, if the
283 goal is to protect or restore a particular species of ecological or economic importance, detailed
284 studies of that species should be conducted to assess intraspecific variation. Our study also
285 suggests that targeting drier populations as seed sources for restoration efforts could come at a
286 cost, namely lower genetic diversity. Given the variety of different stressors tropical forests
287 experience under current and future conditions, aiming for high species and genetic diversity will
288 likely result in more resilient forests in the long term (40). Finally, the lack of local adaptation to
289 drought that we observed suggests tropical tree species' range shifts under climate change in this
290 region can be predicted based on species-level estimates of drought resistance and that
291 populations in wetter parts of a species range may be able to persist under drier conditions in the
292 future.

293

294 **MATERIALS AND METHODS**

295 **Study site**

296 The study was conducted in tropical moist lowland forests along the Isthmus of Panama, which
297 exhibits a pronounced rainfall gradient from ca.1800 mm/year at the Pacific coast to nearly
298 3000 mm/year at the Atlantic coast across a distance of 65 km. Dry season severity, assessed as
299 the long-term average of the cumulative maximum dry season water deficit, varies with annual
300 rainfall (Fig. 1, Table S1), as does typical dry season length (~145 days at the dry side vs ~120
301 days on the wet side (10). The gradient in seasonal drought severity has been found to be the
302 primary driver of species distributions across the isthmus (10, 14, 26), leading to significant tree
303 species turnover across sites (35, 41). Many species, however, are distributed either partway or
304 all the way across the rainfall gradient, such that individuals of the same species growing at
305 different sites experience different annual rainfall and dry season severity (26). Soil nutrient
306 availability also varies across the region (26), while mean annual temperature varies little across
307 the gradient (26.9°C at both the Pacific and Caribbean sides (42)).

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

312

313 **Species selection**

314 The study focused on 16 tree species (Table S2), which are all native to the region, relatively
315 common where they occur within the study area, and shade-tolerant (i.e., excluding light-
316 demanding pioneer species). Species were chosen to include different distribution patterns across
317 the rainfall gradient, i.e., species common in dry to intermediate rainfall sites, wet to

318 intermediate, or occurring widely across entire whole rainfall gradient. Final species inclusion in
319 each part of the study (e.g., experiments, trait measurements) depended on the availability of
320 sufficient numbers of seeds and healthy seedlings of comparable size from at least two origins,
321 including several mother trees per origin (see below; Table S2).

322

323 **Plant material - seeds, seedlings, and leaves**

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

331 Seeds were collected from at least three mother trees per species in lowland (<300 m)
332 tropical forest within each section of the gradient. Fruits/seeds were usually collected from or
333 under individual fruiting trees, so that the seeds could be assigned to seed lots representing a
334 single likely mother tree. Sometimes fruits/seeds were collected from the ground in areas with
335 several (2 - 8) fruiting conspecifics. In such cases, seeds were considered one seed lot (and
336 treated the same as a single mother) but may have come from several clumped trees. Mother
337 trees/lots were located at least 40 m apart. Seeds were collected between December 2013 and
338 October 2014, and then cleaned and raised in seedling trays in a screenhouse in a common
339 substrate of local forest soil and sand (washed river sand; 3:1 mixture) at ca. 10% light under

340 regular watering. In two species (VOCHFE and HADRGU), we did not find enough seeds and
341 thus collected young seedlings from the field and raised them in the screenhouse under the same
342 conditions until transplanting. From nearly ten thousand seedlings raised, we selected healthy
343 seedlings for the field experiments and screenhouse trait measurements, minimizing size
344 differences between origins (within species), and maintaining several mother trees per origin.

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

352

353 **Seedling transplanting**

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

360 One seedling from each origin of each species was randomly assigned to each plot, and
361 seedlings were transplanted into the field plots approximately 3 months before the start of the dry

362 season (September 2014), to allow enough time to establish root-soil contact before the start of the
363 dry season. Seedlings were 1-7 months old, and 6-18 cm tall depending on species, comparable to
364 the age and size they would have reached in the field. Seedlings were independent of seed reserves,
365 i.e., seeds had already fallen off in all species. Seedlings were transported to the field with their
366 substrate to minimize stress, and the bare root seedlings were then transplanted directly into the
367 local soil. Disturbance to the litter layer in transplanting was kept to a minimum.

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

373

374 **Experimental design of the field experiments**

375 ***Common garden drought-irrigation experiment***

376 We conducted a drought-irrigation experiment with seedlings of the 16 focal species (2 - 3 origins
377 each, see Table S2) in the understory of a forest site in the center of the rainfall gradient (43)
378 (Buena Vista, Fig. 1). Sixty plots were established in the understory, of which 30 were covered
379 with transparent rain-out shelters and 30 were irrigated in the dry season to alleviate drought stress
380 (for details see below). We randomly selected one seedling of each origin of each species to
381 transplant into each of the 60 plots. Due to a lack of available seedlings for some species and initial
382 deaths due to transplant effects, the final sample sizes of each origin of each species varied, but
383 numbers were similar for the irrigated and drought treatment (see Table S13). To ensure the same

384 range of light conditions in both treatments, the plots were paired by similarity of initial light
385 conditions as assessed by hemispherical photographs (Nikon Coolpix P5000 camera with a
386 Fisheye Converter, analyzed with Gap Light Analyzer v2 (44)), and one plot of each pair was
387 randomly assigned to each treatment.

388 In the drought treatment, plots were covered with clear plastic rainfall exclusion shelters
389 (1.5 x 1.5m square footprint) for the duration of the dry seasons (3 January – 14 April 2015 and
390 21 January – 28 April 2016), excluding any dry season rainfall. Irrigation plots were watered
391 regularly during the dry season. Irrigation levels necessary to avoid drought stress in the dry season
392 are considerably higher than average wet season rainfall, because of elevated soil evaporation and
393 transpiration of competing trees. Due to inter-annual and spatial variation of rainfall, relative air
394 humidity, and competition, it was not useful to define irrigation levels *a priori*. Thus, plots were
395 initially watered five days a week for a total equivalent to 209 mm/month, and the amount was
396 increased on a plot-by-plot basis up to 590 mm/month as the dry season progressed, contingent on
397 any visible wilting in the seedlings. Treatments were not applied during the wet season, when soil
398 water availability in the forest understory is consistently high due to the high rainfall. The irrigation
399 treatment successfully increased soil moisture and alleviated drought stress as indicated by
400 significantly higher gravimetric soil water content, especially in the dry season (irrigated vs
401 drought treatment dry season plot means: $t = -9.6645$, $df = 56.541$, $p\text{-value} = 1.405e-13$; Fig. S1)
402 and higher survival and growth rates in the irrigated compared to the drought treatment (mean \pm
403 se in irrigated vs dry plots: proportion surviving = 0.65 ± 0.02 vs 0.49 ± 0.03 ; RGR = 0.25 ± 0.05
404 vs. -0.15 ± 0.08).

405

406 ***Reciprocal transplant experiment across the rainfall gradient***

407 We used a reciprocal transplant experiment across the rainfall gradient on seedlings of the 16
408 focal species (see Table S2) to test for differences in performance between origins indicative of a
409 local origin advantage. The experiment included one site within each of the three sections of the
410 rainfall gradient (wet, intermediate, and dry; Fig. 1, Table S1). For each focal species, we
411 transplanted seedlings from two or three origins (wet, intermediate, and dry) reciprocally within
412 their native range, i.e., into all three transplant sites along the rainfall gradient for widespread
413 species and to two of the sites for species restricted to a portion of the gradient (Table S2). Each
414 experimental site contained 30 1x1 m plots. We randomly assigned one seedling from each
415 origin of each species to each plot. As in the common garden experiment, there was some
416 variation in the final sample sizes of each origin of each species due to a lack of available
417 seedlings for some species and initial deaths due to transplant effects (Table S13). Gravimetric
418 soil moisture in the dry seasons decreased from the wettest to the driest site (Figure S1).

419

420 **Performance measurements**

421 In both the common garden and reciprocal transplant experiments, seedlings were censused four
422 times over ~1.5 years towards the beginning and end of the dry season: December 2014–January
423 2015, May 2015 (September 2015 in PNM due to restricted site access), December 2015–January
424 2016, and May 2016. In addition, the status (alive/dead) of seedlings in the reciprocal transplant
425 experiment was assessed in September 2018 (seedlings in the common garden experiment were
426 harvested in May 2016 for trait measurements; see below).

427 In each census, we recorded whether seedlings were alive or dead. Survival was monitored
428 based on aboveground living biomass. Previous experiments have shown that seedlings in this
429 system do not resprout once aboveground biomass has died (11). For surviving seedlings, we
430 assessed plant height and leaf area. The length and width of each leaf were measured in the field,
431 and missing or dead leaf area (e.g., due to pathogen or herbivory damage) on every leaf was
432 recorded in 10% intervals. We calculated the area of each leaf from species-specific regression
433 equations of direct leaf area measurements (leaf area meter LI-3100C, LiCor, NE, USA) on the
434 product of leaf length and width (all $R^2 > 0.85$, $P < 0.001$) to derive ‘potential’ leaf area, and then
435 subtracted the damaged or missing leaf area. Relative growth rate based on leaf area change (RGR,
436 $\text{cm}^2 \text{cm}^{-2} \text{year}^{-1}$) was calculated for each seedling as $\text{RGR} = (\ln[\text{LA}_{t1}] - \ln[\text{LA}_{t0}]) / (t_1 - t_0)$ where LA
437 is leaf area and t_0 and t_1 are the initial and final census.

438

439 **Trait measurements**

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

447 Seedlings for trait measurements in the screenhouse (located in Gamboa, at the center of
448 the rainfall gradient, Fig. 1) were grown under fully watered conditions in 35 cm deep pots (D-40

449 Cone-tainers, Stewe and Sons, USA) at ca. 10 % of full light in forest soil mixed with sand
450 (equivalent to raising of seedlings, above). Seedlings were moved periodically to account for
451 potential gradients of relative humidity and light in the screenhouse. At the time of measurement
452 (February - March 2015) seedlings were 4-10 months old, equivalent in age and size to seedlings
453 naturally growing in the forest understory or in the field experiments at the start of their first dry
454 season.

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

458 Trait measurements followed Pérez-Harguindeguy et al. (45) when feasible (see details
459 below). We aimed to measure each trait on at least 5 individuals per available species and origin.
460 In the screenhouse, not all traits were measured on the same individuals, because some of the
461 measurements were destructive and incompatible with each other. Traits measurements therefore
462 give a composite picture of traits of origin x species combinations. Leaf traits were assessed on
463 young, fully developed, healthy leaves, on 1-3 leaves per individual.

464 Leaf turgor loss point (π_{tlp} , MPa) was assessed following the method of Bartlett et al.
465 (2012) from measurements of leaf osmotic potential at leaf full turgor (π_o , MPa). Seedlings were
466 rehydrated overnight, and osmotic potential was measured with an Osmometer (VAPRO 5600,
467 Wescor, Logan, UT, USA) on one mature leaf per individual after freezing in liquid N. We used
468 the equation for woody species established by Bartlett et al. (46) to calculate the turgor loss point
469 (π_{tlp}) from the measurements of osmotic potential at full turgor (π_o).

470 Maximum stomatal conductance (g_{\max} , $\text{mmol m}^{-2} \text{ s}^{-1}$) was measured in the morning
471 (~6:00 – 9:00 am) with a steady-state diffusion leaf porometer (SC-1 Meter Group Inc. Pullman,
472 WA, USA).

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

479 For non-structural carbohydrate content of stems (NSC_{stem} , % of total stem DW) plants
480 were harvested in the morning (8:00 -10:00 am), and the stem immediately dried in a microwave
481 at 800W for 5 min to stop any enzymatic activity and dried at 65°C for 48h (47). Analyses
482 followed a modified version of the protocol of Hoch et al. (48) and Sala et al. (49). Stems were
483 ground to a fine powder, and 12 mg sample material was extracted in 1.6 ml of distilled water in
484 a 100°C water bath. Fructose, sucrose, and starch were enzymatically hydrolyzed to glucose by
485 consecutive enzymatic reactions (amyloglucosidase, glucose hexokinase, phosphoglucose
486 isomerase, and invertase). The content of free sugars (glucose, fructose, sucrose) and starch was
487 calculated from spectrophotometrical measurements obtained before and after the respective
488 enzymatic reactions (microplate spectrophotometer, EPOCH, Biotek, Germany). Total non-
489 structural carbohydrate content, which has previously been linked to drought survival in tropical
490 tree seedlings (30), was used in statistical analyses presented in the main text (see Table S9 for
491 results of separate analyses of starch and simple sugars).

492 Stem and root density (D_{stem} , D_{root} , g/cm³) were determined for a ca. 2 - 3 cm long section
493 of the stem and root (basal and upper section, respectively). The fresh volume was determined
494 by the displacement method, i.e., the section was immersed in a water container on a balance
495 (0.0001g resolution) and the displacement weighed. Dry weight of the section was determined
496 after oven drying (see below).

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

506

507 Leaf Genotyping-by-sequencing (GBS)

508 We successfully genotyped trees of 13 of the 16 species from different origins along the
509 rainfall gradient (see Table S11). We extracted the DNA from the dried leaves (see above) using
510 5 mg of dehydrated ground leaf tissue using the CTAB method with modifications (50) followed
511 by a cleanup step using the solid-phase reversible mobilization (SPRI) method (51, 52). We
512 normalized the DNA samples to a concentration of 20 ng/μl in a 96 -well plate arrangement for
513 each species for a total of 13 separate libraries. We digested DNA samples of each species

514 library using the restriction enzyme *ApeKI*. Following digestion, we ligated indexed barcode
515 adapters onto the DNA fragments to allow us to identify individuals for each species. After
516 ligation, we pooled and cleaned each library. Then, we amplified the libraries for each species
517 using PCR and primers that matched barcodes and universal adaptors and cleaned the libraries
518 again (53). Subsequently, we sequenced the 13 libraries on one lane per species of either a
519 HiSeq2000 (100-bp reads) or HiSeq3000 (150-bp reads) Illumina using a single-end reads at the
520 CGRB facility in Oregon State University (<http://core.cgrb.oregonstate.edu>).

521

522 **Statistical analyses**

523 Survival and growth analyses
524 To model survival of transplanted seedlings, we used generalized linear mixed effects models
525 with binomial errors to model the probability of an individual surviving from the initial census
526 (Dec 2014/Jan 2015) to the final census in which mortality was assessed (May 2016 for common
527 garden experiment; September 2018 for reciprocal transplant experiment). To model growth, we
528 calculated relative growth rate based on leaf area for each seedling that survived until the end of
529 the experiment and used linear mixed effects models to model relative growth rates between the
530 initial and final field census in which seedlings were measured (May 2016 for both experiments).
531 In preliminary analyses, survival and growth results were qualitatively similar when using mixed
532 effects Cox proportional hazards models or models with repeated measures of growth that
533 included seedlings that died before the final census, respectively.

534 For the common garden experiment, we tested for an effect of treatment (irrigated vs
535 drought), origin, and an origin x treatment interaction on survival or growth. Because not all

536 species had seedlings from all three origins (wet, intermediate, and dry), we tested for a
537 difference between seedlings from the driest origin of each species and seedlings from wetter
538 origins of the species (i.e., combining intermediate and wet origins for widespread species). We
539 modelled all species combined and included species and species response to treatment as random
540 slope and intercept terms, respectively.

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

546 For the reciprocal transplant experiment, we analyzed each site separately because not all
547 focal species were transplanted to all sites. For each site, we tested for performance differences
548 between seedlings of 'local' vs 'foreign' origin. Specifically, for the 14 focal species
549 transplanted at the dry site, we tested for a difference in survival and growth of seedlings of dry
550 (=local) origin relative to wetter origins (foreign, i.e., from intermediate and wet populations
551 combined). For the eight focal species transplanted at the wet site, we tested for a difference in
552 survival and growth of seedlings of wet (=local) origin compared to seedlings of drier origins
553 (foreign, i.e., intermediate and dry populations combined). For the intermediate site, we
554 compared growth and survival of intermediate (=local) vs dry origins for the 14 focal species
555 having seedlings from both intermediate and dry populations, and for intermediate (=local) vs
556 wet origins for the 8 focal species having seedlings from both the intermediate and wet
557 populations. For the 6 widespread species, which had seedlings of all three origins transplanted

558 to all three sites, we also ran models testing for survival differences between the three origins at
559 each site, to check whether combining origins may have masked differences (Table S14).
560 Species was included as a random effect in all of these models.

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

570 For growth and survival in both the common garden and reciprocal transplant
571 experiments, we also ran models for each species separately using the same models as above
572 (without species as a random effect), except in a few cases where the species had <5 survivors at
573 a site or where models did not converge (e.g., due to insufficient number of survivors or growth
574 observations in one treatment or of one origin). To take into account multiple comparisons, we
575 used the false discovery rate method (54) to adjust p-values based on the number of species in
576 each analysis (e.g., 12 species analyzed separately for survival in the common garden
577 experiment). Because the aim of the study was to assess general trends at the community level
578 rather than within individual species, we focused on including as many species as logically

579 possible rather than having larger sample sizes for fewer species. Thus, we have more limited
580 power to detect differences among origins for individual species.

581 Trait analyses

582 As in analyses of growth and survival, we tested for differences in trait values for the driest vs
583 wetter origins of each species (i.e., combining intermediate and wet origins for widespread
584 species). For each of the 14 traits measured on seedlings of 10-11 species in the screenhouse
585 (Table S2), we used linear mixed effects models with seedling origin as a fixed effect and species
586 and seed lot as random effects. For the 8 traits measured on seedlings of 15 species harvested at
587 the end of the common garden experiment, we used linear mixed effects models to test for
588 effects of origin and treatment, as well as an origin x treatment interaction. Species, seed lot, and
589 seedling plot were included as random effects. For traits with skewed distributions, values were
590 natural log or square-root transformed prior to analysis (Table S9, S10). Because trait
591 expectations may differ for tropical tree species with evergreen vs drought deciduous leaf
592 phenology (14), we confirmed that the results of the above trait analyses remained qualitatively
593 similar when accounting for differences in leaf phenology (i.e., by excluding the two dry season
594 deciduous species from the screenhouse trait analyses and by analyzing traits separately for the
595 five drought deciduous species and ten evergreen species in the field experiment). We did not
596 run trait models for each species separately due to limited sample sizes for each origin and trait.
597 Survival, growth, and traits models were fit using the lme4 package (55) and lmerTest package
598 (56) in R version 4.1.2 (57).

599 Analyses of genetic structure

600 To process the raw reads of each of the species and to call SNPs, we used STACKS ver. 1.41 (58,
601 59) (Table S12). None of the 13 species has a reference genome, so *de novo* assembly of SNP
602 loci was required. In STACKS, we used PROCESS_RADTAGS to demultiplex and discard reads with
603 low-quality scores, incorrect barcodes, and ambiguous GBS sites. After this process, we ran the
604 STACKS pipeline by hand, in the order: USTACKS, CSTACKS, SSTACKS, RXSTACKS, rerun
605 CSTACKS, rerun SSTACKS, and POPULATION. There is no prior information about polymorphisms
606 or genome size for our focal species. Estimates of sequencing error and the depth of sequencing
607 for each of the 13 species were used to delimit the optimal parameters in the Stacks analysis (58).
608 Consequently, in 7 of 13 species (i.e., BROSAL, CHR2CA, PROTTE, PITTR, TRIPCU,
609 TRI2TU, and VOCHFE), we explored a range of values for two main parameters in the *de novo*
610 pipeline that are associated with the final number of loci and their level of polymorphism
611 recovered from our GBS. First, in USTACKS, we used values of 2, 3, 4, 5 and 10 for minimum
612 depth of coverage of each stack (i.e., parameter $-m$, thus: m2, m3, m4, m5, m10). But we kept
613 the number of mismatches allowed between STACKS by default (i.e., parameter M=2). Moreover,
614 in CSTACKS, we tested values of one and three for the distance between catalog loci (i.e.,
615 parameter $-n$, thus: n1 and n3). Combining parameters $-m$ and $-n$ in USTACKS and CSTACKS, we
616 tested a total of ten different combinations of parameters across the eight species (58, 60). For
617 each one of the ten combinations, in CSTACKS, we constructed a catalog for each one of the
618 sampling locations, using the ten individuals with higher number of raw sequences. In RXSTACKS
619 we used a threshold of -10 for the log likelihood to remove loci with low coverage and high
620 sequencing error and therefore correct genotypes and haplotype calls in the samples. Finally, in
621 POPULATION, we selected the loci that were both present in all sample sites or habitat zones

622 across the gradient and were genotyped at the 75% of individuals within each habitat. Moreover,
623 to prevent linked SNPs, we selected a single SNP from any GBS locus.

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

634 Genetic diversity and population structure

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

641 Population genetic structure was measured with a Bayesian clustering approach
642 implemented in BAPS ver. 6 (65, 66). We used a mixture analysis with a spatially explicit model
643 as a prior (i.e., the geographic coordinates of each sampling location) to determine the posterior

644 probability (P) of cluster samples (K) from K=1 to K=10 for each one of the 13 species. Only in
645 the cases when the higher posterior probability was for $K > 1$, we determined the level of
646 admixture among sampled individuals using 100 iterations, 200 simulated non-admixed
647 reference individuals and 20 iterations for each one of the reference individuals (Table S11).

648

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655

656 **Data availability statement**

657 The performance, trait, and genetic data used in this study, along with R code use for analyses, are
658 archived on Dryad at <https://doi.org/10.5061/dryad.c2fqz61hv>.

659

660

661 **Figures & Tables**

662 **Figure 1.** Variation in dry season water availability (assessed as the mean maximum cumulative
663 dry season water deficit) across the rainfall gradient spanning the Isthmus of Panama. Grey
664 squares represent the location of the reciprocal transplant sites, the black square shows the
665 location of the common garden drought-irrigation experiment, and the black X marks the
666 location of the screenhouse. The long-term average of the yearly maximum dry season water
667 deficit was modelled based on rainfall data from 1961 to 1990 from 27 weather stations (data
668 provided by the Meteorological and Hydrological Branch of the Panama Canal Authority and by
669 the Physical Monitoring Program of the Smithsonian Tropical Research Institute; for details see
670 Condit et al. 2013 and Browne et al. 2021).

671 **Figure 2.** Variation within and among tropical tree species in response to drought (i.e., drought
672 resistance). Drought responses were quantified based on seedling survival in the common garden drought-
673 irrigation experiment, with the response ratio calculated as $\ln(\text{survival in drought treatment}/\text{survival in}$
674 $\text{irrigated treatment})$. Drought response values of 0 indicate no difference in survival in irrigated vs.
675 drought treatment (i.e., highly drought resistant), while negative values indicate lower survival under
676 drought conditions (i.e., drought sensitive). Values shown for all origins of all focal species included in
677 the common garden experiment, with the exception of *Anacardium excelsum*, which had very low
678 survival in all treatments. Differences among origins in response to treatment were not significant in
679 analyses of single focal species.

680 **Figure 3.** Survival of transplanted seedlings of different origins in the drought and irrigated treatments of
681 the common garden experiment for all 16 focal species combined. Bars show model-predicted survival
682 (+/- 1 SE) of seedlings originating from the driest section of the rainfall gradient of each focal species vs

683 seedlings originating from wetter sites where the species was present. Points correspond to observed
684 survival in each of the 30 replicate plots per treatment. In the irrigated treatment, survival was
685 significantly lower in the driest compared to the wetter origin seedlings, but there was no difference in
686 survival between origins in the dry treatment. Survival was also significantly lower in the drought than in
687 the irrigated treatment. See Fig. 2 for individual species response to experimental treatments.

688 **Figure 4.** Survival of transplanted seedlings of different origins at the dry and wet sites in the reciprocal
689 transplant experiment. Bars show predicted survival (+/- 1 SE) from a generalized linear mixed effects
690 model with all focal species combined (total of 14 species at the dry site and 8 species at the wet site).
691 Points connect with dashed lines show observed survival for the different origins of individual focal
692 species having at least 5 survivors at the site. For the dry site, seedlings originating from the dry portion
693 of the gradient (local) were compared to those originating from wetter sites (foreign). For the wet site,
694 seedlings originating from the wet portion of the gradient (local) were compared to those originating from
695 drier sites (foreign).

696 **Figure 5.** Differences in trait values between the driest vs wetter origin seedlings measured in the
697 screenhouse for 10 focal species for (a) turgor loss point (MPa), (b) non-structural carbohydrates (% of
698 stem dry weight), (c) specific leaf area (cm²/g), and (d) leaf area ratio (cm²/g). Squares correspond to
699 predicted trait values for all species combined (+/- 1 SE) from linear mixed effects models, with filled
700 squares connect by solid lines indicating a significant difference between origins (see Table 1). Circles
701 connected by dotted lines depict mean observed trait values for different origins of the same species.

702 **Figure 6.** Difference in genetic diversity (H_e) of trees found at the driest vs wetter portion of the rainfall
703 gradient, based on leaf tissue collected from adult trees of 13 focal species. Squares connected by the
704 solid line correspond to predicted H_e values (+/- 1 SE) from a linear mixed effects model for all species
705 combined, in which trees sampled in wetter areas had significantly higher genetic diversity than those

706 sampled in wetter areas ($P=0.02$). Circles connected by dotted lines depict mean observed H_e values for
707 the same species sampled at different sites.

708 **Table 1.** Traits assessed for each origin in the screenhouse and the common garden experiment. Arrows
709 in the Expectation column indicate the direction of differences in trait values for drier compared to wetter
710 origins of the same species expected under adaptation to drought. Results columns indicate the direction of
711 significant trait differences (arrows) or lack of difference (n.s.) observed for driest vs wetter origin seedlings
712 based on linear mixed effect models for all focal species combined (see Tables S9 & S10 for full model
713 results). Empty cells indicate traits not measured in the common garden experiment. For species and their
714 respective origins included in the analyses, see Table S2.

715

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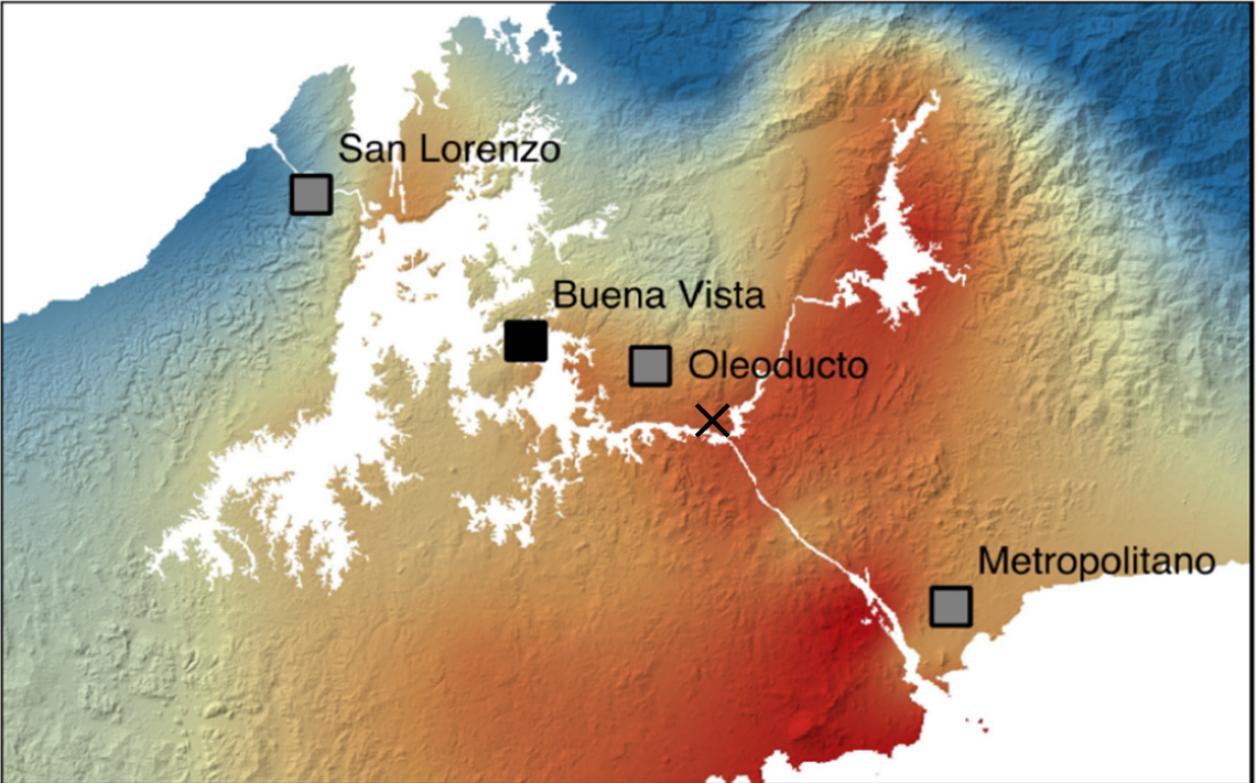
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863

Table 1. Traits assessed for each origin in the screenhouse and the common garden experiment. 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 Tables S9 & 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 Table S2.

Trait	Unit	Expectation (drier vs wetter origin)	Result- Screen house	Results- 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.	
Non-structural 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



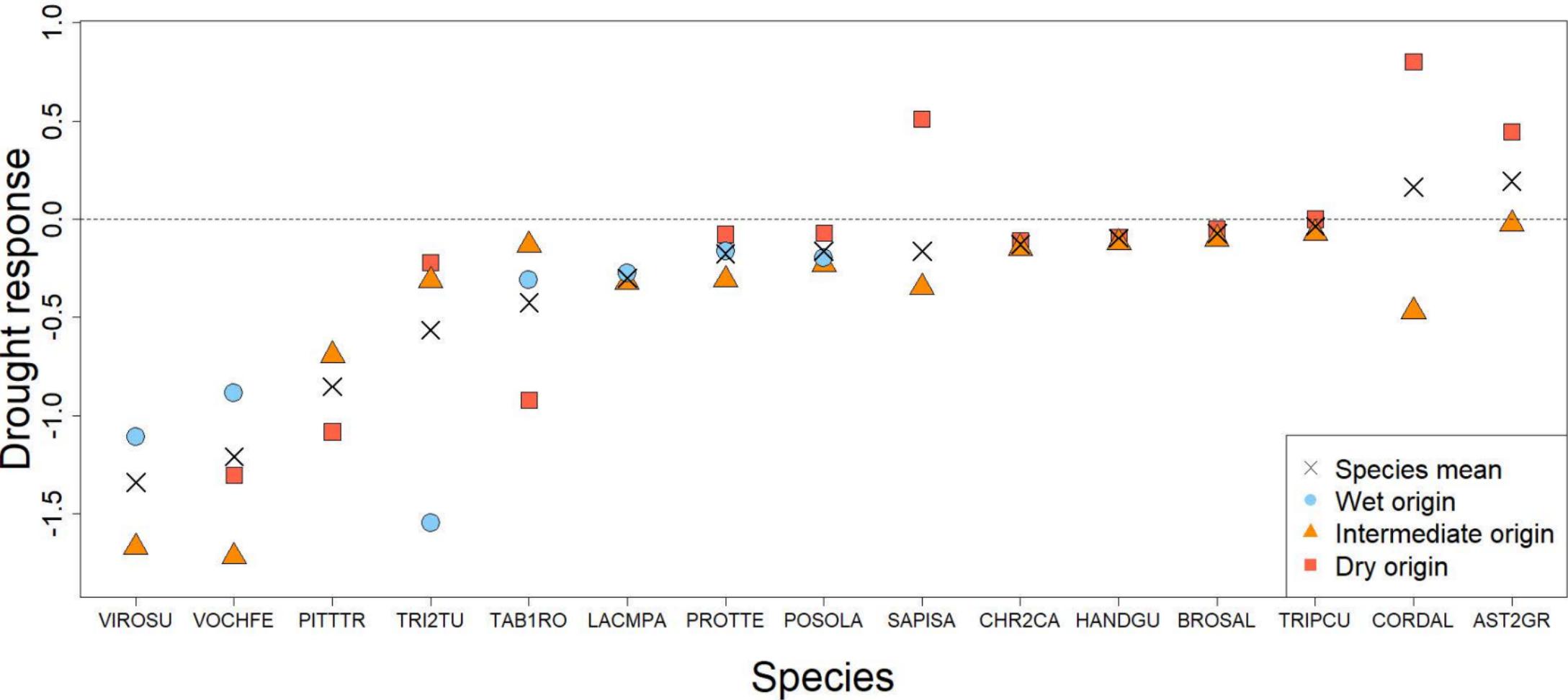
Dry season water availability
(1961-1990 average)

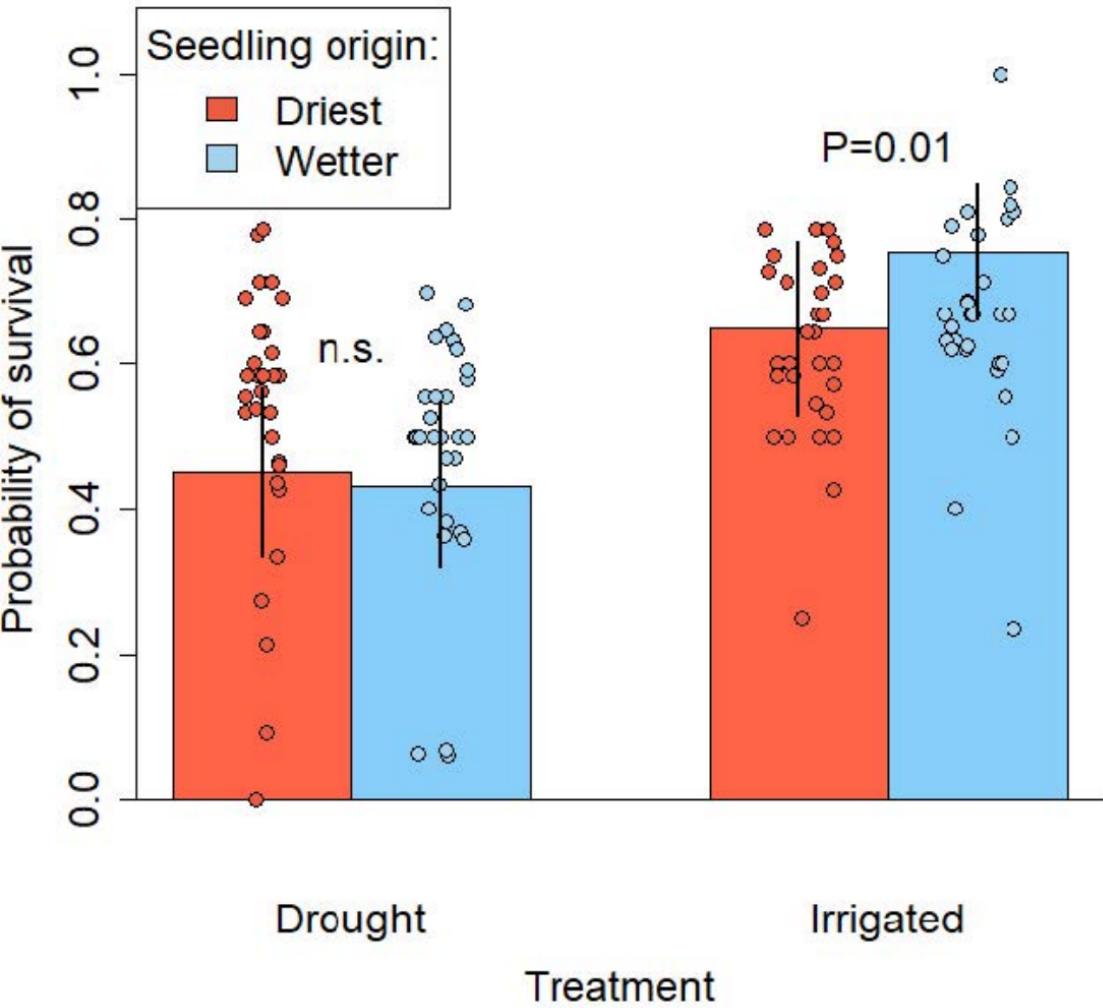


-250 mm

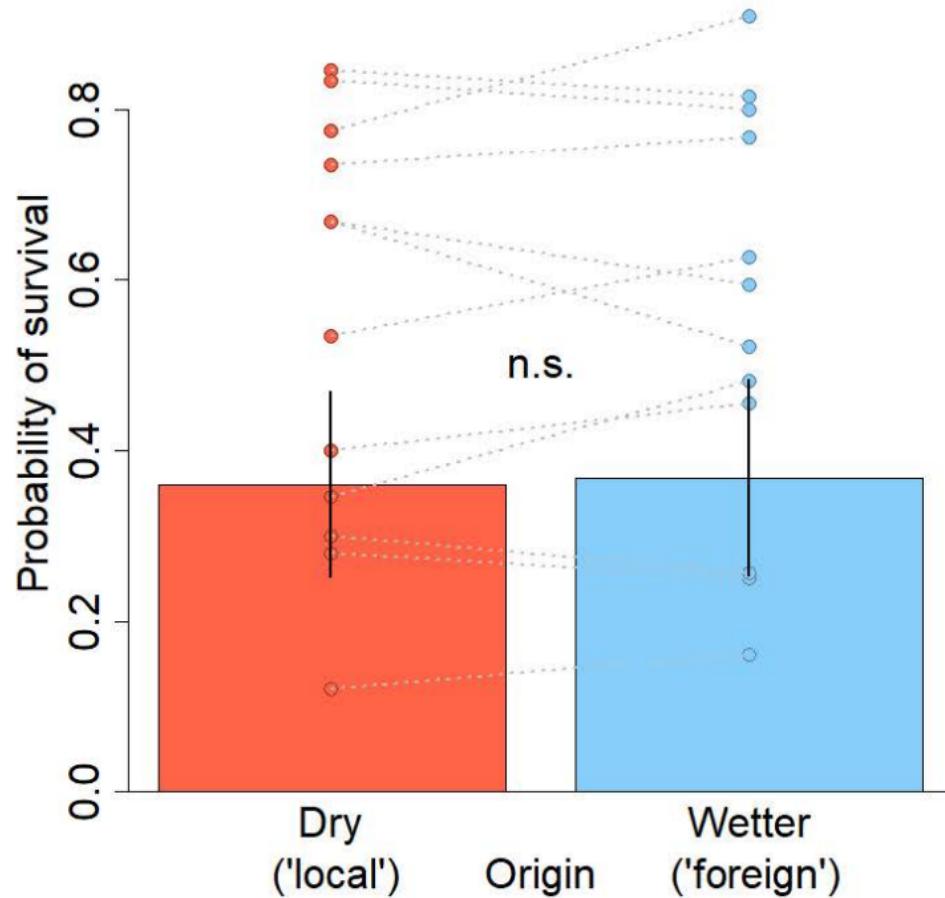
0 10 20 km







Dry transplant site



Wet transplant site

