


ARTICLE

Phenotypic plasticity and genetic diversity elucidate rarity and vulnerability of an endangered riparian plant

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Abstract

Environmental change, accelerated by anthropogenic activities, threatens many species and can be especially challenging for rare species given their potentially limited capacity for migration and adaptation relative to more common species. The ability to acclimate via phenotypic plasticity could provide an important path to species persistence in the face of such change. We investigated the responses of an endangered plant species endemic to a highly dynamic riparian habitat in southeastern Tennessee, USA, and its most widespread congener to environmental change to elucidate their current statuses and future vulnerability. Specifically, we compared the population- and species-level plasticity of rare *Pityopsis ruthii* and common *P. graminifolia* to contrasting light, temperature, and water conditions in a growth chamber experiment to evaluate their potential to acclimate to environmental change. Contrary to our expectations, *P. ruthii* had greater phenotypic plasticity than its common congener in response to both altered light and water availability. But this plasticity was not associated with increased fitness, suggesting that it was not adaptive. Concurrently, we genotyped these individuals at nine putatively neutral microsatellite loci to contrast genetic diversity across the range of each species. As expected, *P. ruthii* exhibited reduced genetic diversity relative to its more common congener. Overall, our findings accord with the narrow range and current habitat specificity of *P. ruthii*, especially its tolerance of highly variable water, and highlight its potential vulnerability to future environmental change.

KEYWORDS

acclimation, adaptation, endemic, genetic diversity, *Pityopsis graminifolia* (narrowleaf silkgrass), *Pityopsis ruthii* (Ruth's golden aster), plasticity

INTRODUCTION

Many ecosystems globally are experiencing unprecedented rates of anthropogenic environmental change,

which threatens populations, species, and overall biodiversity (Malhi et al., 2020). To persist in the face of such change, populations and species must successfully respond by migrating to more suitable habitats (Chen

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et al., 2011; Crickenberger & Wethey, 2018; Hickling et al., 2006; Parmesan, 2006), adapting to novel natural selection (Hamann et al., 2020; Jump & Peñuelas, 2005; Sheth et al., 2018), and/or acclimating to new conditions (Chevin et al., 2010; Nicotra et al., 2010; Seebacher et al., 2015). The capacity to persist through change can differ dramatically among species and particularly challenge those that are rare (Enquist et al., 2019; Xu et al., 2015). For example, models suggest that migratory potential depends on abundance near existing range boundaries, which could impede the potential for rare species to migrate (Iverson et al., 2004). Additionally, the limited genetic diversity characteristic of many rare species could constrain adaptation to environmental change (Cole, 2003; Gitzendanner & Soltis, 2000; Leimu & Fischer, 2008).

The capacity to acclimate in the face of rapid environmental change through phenotypic plasticity could be especially important for the persistence of species that have limited capacities for migration and adaptation. Plants generally exhibit high degrees of phenotypic plasticity relative to other types of organisms (Sultan, 2000), but plant populations and species can vary dramatically in their responses to environmental change due to variation in the extent of adaptive plasticity (Balaguer et al., 2001; Cleavitt, 2002; Dangremond et al., 2015; Godoy et al., 2012; Nicotra & Davidson, 2010; Osunkoya & Swanborough, 2001; Pohlman et al., 2005; Sultan, 2000; Valladares et al., 2000, 2007). For rare species characterized by low numbers and genetic diversity, high phenotypic plasticity could provide an important path to persistence in the face of environmental change. In contrast, low phenotypic plasticity combined with low numbers and genetic diversity could comprise a combination of limited acclimatory, migratory, and adaptive potential that could lead to extinction. Comparisons of rare and common species can elucidate factors that contribute to species rarity in a dynamic natural world and inform the conservation of biodiversity in a time of rapid environmental change (Bevill & Louda, 1999) while controlling for life history and phylogeny (Farnsworth, 2006; Murray et al., 2002). Studies comparing congeneric species in particular could be especially impactful to advancing our understanding of species' rarity by providing for control of the potential influences of life history and phylogeny on outcomes (Combs et al., 2013; Farnsworth, 2006; Godt & Hamrick, 2001; Kunin & Gaston, 1997; Murray et al., 2002).

Riparian habitats are characterized by disproportionately high amounts of biodiversity and ecosystem services (Capon et al., 2013). These unique systems also experience very high anthropogenic pressures and are among the most altered ecosystems in the world (Perry et al., 2012). The narrow endemic *Pityopsis ruthii* (Small

(Asteraceae; Ruth's golden aster) inhabits the banks of dammed rivers in southeastern Tennessee, USA, which are characterized by extreme events ranging from frequent, often prolonged droughts, to periodic high-flow events with total inundation (Moore et al., 2016). Changes in management practices along these rivers against an ongoing backdrop of climate and land use change have the potential to severely alter *P. ruthii* habitat in the future. In contrast, *P. graminifolia* (Michx.) Nutt. (narrowleaf silkgrass) is widespread throughout the southeastern United States and northern Central America across a variety of habitat types (Clewell, 1985; Duncan & Duncan, 1987; Radford et al., 1968; Wunderlin, 1998). Although not restricted to a strongly perturbed system like its rare congener, *P. graminifolia* is subject throughout its range to global change factors.

We contrasted *P. ruthii* and *P. graminifolia* to investigate the potential responses of rare and common species to environmental change. Specifically, we compared their phenotypic plasticity and genetic diversity. Given the narrow geographical distribution and habitat specificity of *P. ruthii*, we hypothesized that it would exhibit reduced plasticity and genetic diversity relative to *P. graminifolia*. Given the restricted distribution, we also expected lower intraspecific variation across *P. ruthii* populations in plasticity and genetic diversity than for the widespread congener *P. graminifolia*.

METHODS

Study system

Pityopsis ruthii is a historically rare plant species restricted primarily to soil-filled cracks in boulders on exposed banks and in the channel of a ~5.7-km section of the Hiwassee River (HR) and a ~4.6-km section of the Ocoee River in Polk County, Tennessee, USA (Appendix S1: Figure S1a), downstream of dams operated by the Tennessee Valley Authority (TVA) that divert water around *P. ruthii* habitat for hydroelectric power generation. The TVA has delineated 67 distinct occurrences of this species, which we treat as populations, ranging in size from <5 to ~1000 plants (A. Dattilo, Botanist, TVA, personal communication). Endemism is the most common type of species rarity (May, 1988; Rabinowitz, 1981), and we categorize *P. ruthii* as "endemic" based on its small geographic range, narrow habitat specificity, and large size of at least a single population (see Rabinowitz, 1981). Given its rarity and associated conservation concerns, *P. ruthii* is listed as both federally and state endangered (United States Fish and Wildlife Service [USFWS], 1985). In contrast, *P. graminifolia* is the most widespread species in the genus, occurring

throughout the southeastern United States (Appendix S1: Figure S1b) and northern Central America across a variety of habitat types including sandhills, flatwoods, old fields, bogs, grasslands, upland hardwood forests, and roadsides (Clewell, 1985; Duncan & Duncan, 1987; Radford et al., 1968; Wunderlin, 1998). This species is sometimes treated as five varieties that intergrade and hybridize when the ploidy level is the same (Semple & Bowers, 1985). We followed Weakley's (2020) taxonomy for *P. graminifolia*.

Seed collection and propagation

We collected seed from parent individuals of *P. ruthii* and common *P. graminifolia* throughout the ranges of *P. ruthii* and *P. graminifolia* to account for genetic and phenotypic variation within each species. Specifically, seeds of *P. ruthii* were collected from one population along the HR and three populations along the Ocoee River (O1, O2, O3; Polk County, Tennessee, USA; Appendix S1: Table S1). The sites for *P. ruthii* seed collection were determined in cooperation with the U.S. Fish and Wildlife Service with consideration of the endangered status of the species, population sizes and observed numbers of flowering individuals during recent monitoring, and site accessibility during the period in which seeds were present. The sampled populations are separated by at least 1 km such that gene flow between populations is unlikely (NatureServe, 2020). Given the restricted distribution and threatened status of this species, we cannot provide geographic coordinates for *P. ruthii* populations. Seeds of *P. graminifolia* were collected from five populations: Ocoee River (TN; Polk County, Tennessee, USA), Black Mountain Road (GA1; Stephens County, Georgia, USA), Currahee Mountain (GA2; Stephens County, Georgia, USA), Little Manatee River State Park (FL; Hillsborough County, Florida, USA), and Zube Park (TX; Harris County, Texas, USA; Appendix S1: Table S1). All *P. ruthii* seeds and *P. graminifolia* seeds from the Tennessee and Georgia populations were collected by the authors; *P. graminifolia* seeds from the Florida and Texas populations were collected by local contacts made through the biodiversity information platform *iNaturalist* (<http://inaturalist.org>). For both species, numerous seeds from each of 10–25 distinct parent individuals per population were collected in separate paper bags (i.e., to retain maternal information) and stratified in cold storage for 4 months prior to germination.

We identified viable seeds as described by Wadl et al. (2014) and sowed six to eight viable seeds representing half to full siblings per parent individual from each sampled population into each of four 7-cm² × 8.5-cm-deep pots filled with a potting medium (Pro-Mix Bx Biofungicide +

Mycorrhizae, Premier Tech Horticulture, Quakertown, PA, USA). Although this growth environment differs from the boulder cracks in which *P. ruthii* is generally found, our use of potting mix in pots was informed by previously successful protocol for growing *P. ruthii* (Wadl et al., 2014) with the consideration of the endangered status of this species and our limited seed supply. Using a common potting medium for both *P. ruthii* and *P. graminifolia* also allowed us to control for the influence of soil type on measured outcomes. The four pots containing seeds from each parent plant were randomly assigned to each of four growth chambers (model PGR15, Conviron Controlled Environments Limited, Winnipeg, Manitoba, Canada) such that each chamber contained one pot from each parent plant. All chambers were set initially to a 12-h photoperiod at constant 25°C, and pots were watered as needed to maintain moist soil during a 1-month germination period. We then thinned each pot to the single individual that exhibited the earliest third leaf development. We transplanted these individuals into separate 11-cm² × 9.5-cm-deep pots filled with the same potting medium to minimize the potential for plants to become root-bound (*n* reported in Appendix S2: Table S1).

Environmental treatments

To assess plasticity of *P. ruthii* and *P. graminifolia* in response to light, temperature, and water, we set four growth chambers to different conditions. Following the germination period, one chamber (i.e., the “ambient” chamber) was programmed to replicate field conditions during the *P. ruthii* growing season based on historical weather data, field measurements, and water management. We programmed the three other growth chambers to provide the same conditions but each with a contrasting level of a single condition (light, temperature, or water) to mimic how that abiotic factor could change as a result of climate change, land use, and management practices (USFWS, 2018). Environmental treatment details are provided in Appendix S1.

Growth, allocation, and photosynthesis measures

All individuals were grown for 4 months following treatment initiation during which time growth and photosynthetic data were collected. We rotated the positions of pots within each chamber weekly to control for spatial differences in microclimate. We reassigned treatment levels to each chamber monthly with all plants moved accordingly to minimize any chamber effects and alleviate pseudoreplication (Gibson, 2014). We measured

instantaneous rates of leaf-level photosynthesis (A ; $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) at 3 months after treatment initiation using a portable gas exchange system (6800XT, LI-COR, Inc., Lincoln, Nebraska, USA). At 4 months, we recorded plant height (in centimeters) and counted the numbers of leaves and buds/flowers of each individual. All individuals were then destructively harvested to quantify root length, shoot dry mass, root dry mass, total dry mass, specific leaf area, mass-based root-to-shoot ratio (RSR_{mass}), length-based root-to-shoot ratio ($\text{RSR}_{\text{length}}$), root mass fraction (RMF), and specific root length (SRL). Details of data collection are provided in Appendix S1.

Analyses

We analyzed the probability of flowering as a function of species, growth chamber treatment, and their interaction in a general linear mixed model framework with a binomial distribution with a logit link using Firth's (1993) bias-reduction method (R package *brglm*, version 0.7.1; see Kosmidis, 2020, Kosmidis & Firth, 2020). We incorporated source population as a fixed effect because this analytical framework does not accommodate random effects. We evaluated the significance of each fixed effect via likelihood ratio tests of models with and without that effect.

We used a two-way fixed-design analysis of variance (ANOVA) in SPSS (version 26; IBM Corp., Armonk, New York, USA) to test for the main effects and interaction of species and abiotic treatment (i.e., light, temperature, and water) on each measured trait. In these analyses, a significant interaction indicates that *P. ruthii* and *P. graminifolia* responded differently to a change in the environmental factor (i.e., that the species exhibited differences in plasticity). To explore population-level differences in plasticity within each species, we used a two-way mixed-design ANOVA to test for the interaction of population as a random factor and abiotic treatment as a fixed factor on each measured trait within each experiment. We tested for differences among species and populations within each abiotic treatment level with Games-Howell post hoc tests because the assumption of homogeneity of variances was not always met. To account for the numerous traits analyzed, we calculated and utilized corrected p values to control the false discovery rate (FDR) for each group of tests (Benjamini & Hochberg, 1995). Results of statistical tests were considered significant if FDR-corrected $p \leq 0.05$.

A relative distance plasticity index (RDPI; see Valladares et al., 2007) was used to calculate plasticity of traits to light, temperature, and soil moisture differences. The RDPI is based on the absolute phenotypic distances of genotypes across different environments and allows for statistical comparison of plasticity for species and populations

within species (Valladares et al., 2007). We used the index to calculate individual-level trait plasticity as:

$$\text{RDPI} = \frac{d_{ij \rightarrow i'j'}}{x_{i'j'} + x_{ij}}$$

where j and j' are two individuals of the same species (half to full siblings from the same parent), i and i' represent two different environments (i.e., ambient vs. reduced light, ambient vs. elevated temperature, and ambient vs. increased water in our experiment), $d_{ij \rightarrow i'j'}$ is the distance among trait values for the pair of individuals (with distance defined as the absolute value of the difference in trait values), and $x_{i'j'} + x_{ij}$ is the sum of the trait values (see Valladares et al., 2007). RDPI values range from 0 (no plasticity) to 1 (maximum plasticity); this standardized range allows for comparisons across traits.

To assess whether plasticity increases fitness, we conducted across-environment multivariate genotypic selection analysis (Stinchcombe et al., 2004; Van Kleunen & Fischer, 2001), using the *lmer* (linear mixed model) function of the R package *lme4* (version 1.1-21; Bates et al., 2015). To assess the effects of plasticity on fitness, we focused on traits for which we found significant evidence for plasticity (i.e., traits with significant effects of abiotic factor or abiotic factor by species interactions). We analyzed fitness as a function of mean trait values, plasticities (RDPI), species, and two-way interactions between mean traits and species and RDPI and species in separate models for each manipulated environmental condition (light, temperature, and water). We used total biomass as a fitness proxy in these regressions because it was measurable for all individuals included in our study and because there is a general positive association between vegetative size and greater reproductive output (Weiner et al., 2009). Prior to analysis, we calculated the average biomass across ambient and manipulated environmental conditions (e.g., ambient and reduced light) for each family, which we used as the response variable in our analyses. Significant effects of RDPI in a trait indicate selection for plasticity in both species if the slope is positive and selection against plasticity if the slope is negative. A significant interaction between species and RDPI suggests that the magnitude or directionality of selection differs across the two species. We used a Bonferroni-corrected $\alpha = 0.0167$ ($=0.05/3$) to assess significance and control for type I errors because we conducted three separate analyses of selection on plasticity. We visualized selection landscapes from these multiple regression models as partial residual plots using the *predictorEffects* function of the R package *effects* (version 4.2-0; Fox & Weisberg, 2018).

DNA extraction and microsatellite genotyping

DNA was extracted from leaf tissue collected from all *P. ruthii* and *P. graminifolia* individuals included in the growth chamber experiments prior to harvest. Individuals were genotyped using nine microsatellite loci (Boggess et al., 2014; Wadl et al., 2011) that amplified in all populations for both species and were polymorphic in at least one of the species (Appendix S1: Table S2). Polymerase chain reaction products were multiplexed, and fragment analysis was completed by the Georgia Genomics and Bioinformatics Core (University of Georgia, Athens, Georgia, USA). Details of genotyping protocols are described in Appendix S1.

Analysis of genetic diversity

A total of 170 *P. ruthii* and 147 *P. graminifolia* individuals amplified successfully and were included in the analysis. Initial review of alleles indicated that three of the *P. graminifolia* populations may include polyploids or a mix of ploidy as suggested by Semple and Bowers (1985), Weakley (2020), and Boggess et al. (2014). To account for a mix of ploidy, we followed recommendations from Meirmans et al. (2018) and Machado et al. (2021) and estimated three diversity indices: Shannon (1948), Simpson (1949), and Nei (1978), two of which are also used in ecology to quantify the species diversity of communities. Genetic diversity indices were calculated using the R package *Poppr* (version 4.0.3; Kamvar et al., 2014). To compare the genetic diversity of *P. ruthii* and *P. graminifolia*, we used a multivariate analysis of variance (MANOVA) that included all three diversity indices simultaneously with the `manova(f)` function in base R. To assess population structure and grouping of individuals in the study, we used a discriminant analysis of principal components (Jombart et al., 2010; Machado et al., 2021). This nonparametric approach combines principal component analysis, K-means clustering, and discriminant analysis to visualize population structure and can be applied to polyploid datasets (Meirmans et al., 2018).

RESULTS

Germination, survival, and flowering

Germination was highly successful for all populations except for the FL *P. graminifolia* population, which was eliminated from the experiment due to poor germination. In addition, 99.3% of *P. ruthii* individuals and 97.8% of *P. graminifolia* individuals used in our plasticity

experiment survived to harvest (Appendix S2: Table S1). Overall, <25% of plants flowered during the experiments (Appendix S2: Table S1), but the probability of flowering varied as a function of the interaction between treatment and species ($\chi^2 = 28.64$, $df = 3$, $p < 0.0001$). Rare *P. ruthii* had a significantly lower flowering probability than common *P. graminifolia* in elevated temperature ($z = 3.84$, $p = 0.0031$) and with increased water ($z = 3.19$, $p = 0.031$). In contrast, we found no evidence that the probability of flowering differed across species in ambient conditions ($z = 2.70$, $p = 0.13$) or when light was reduced ($z = 0.17$, $p = 1.00$; Appendix S2: Figure S1).

Growth, allocation, and photosynthesis trait values

In all three comparisons (i.e., ambient vs. altered light, temperature, and water), there were significant differences in most measured traits of *P. ruthii* and *P. graminifolia* across treatment levels (Appendix S2: Table S2). In general, *P. graminifolia* individuals were taller and had greater above- and belowground biomass than *P. ruthii*, as well as more leaves and longer roots when these traits differed between species (Appendix S2: Table S3). In contrast, the mean values of allocation traits and photosynthetic rate (hereafter: leaf *A*) were all greater in *P. ruthii* than in *P. graminifolia* when differences between species were significant (Appendix S2: Table S3).

Abiotic conditions had a significant effect on some of the measured traits in each experiment across species (Appendix S2: Table S2). When light was reduced relative to ambient conditions, plants generally produced fewer leaves and less root mass and had lower RSR_{length} , RMF, and leaf *A* (Appendix S2: Table S4). In contrast, increased temperature had an overall positive effect on plant height, number of leaves, and shoot mass (Appendix S2: Table S4). Under increased water, plants generally had longer roots, greater RSR_{length} and RMF, fewer leaves, and reduced leaf *A* than plants in ambient conditions (Appendix S2: Table S4).

Phenotypic plasticity

We found significant differences in phenotypic plasticity between *P. ruthii* and *P. graminifolia* for RSR_{length} and leaf *A* in response to light; plant height, number of leaves, and shoot mass in response to temperature; and number of leaves, root mass, RSR_{length} , and leaf *A* in response to water (Appendix S2: Table S2). These differences were context-dependent. In response to light, *P. ruthii* exhibited plasticity, while *P. graminifolia* did not (Figure 1). In contrast,

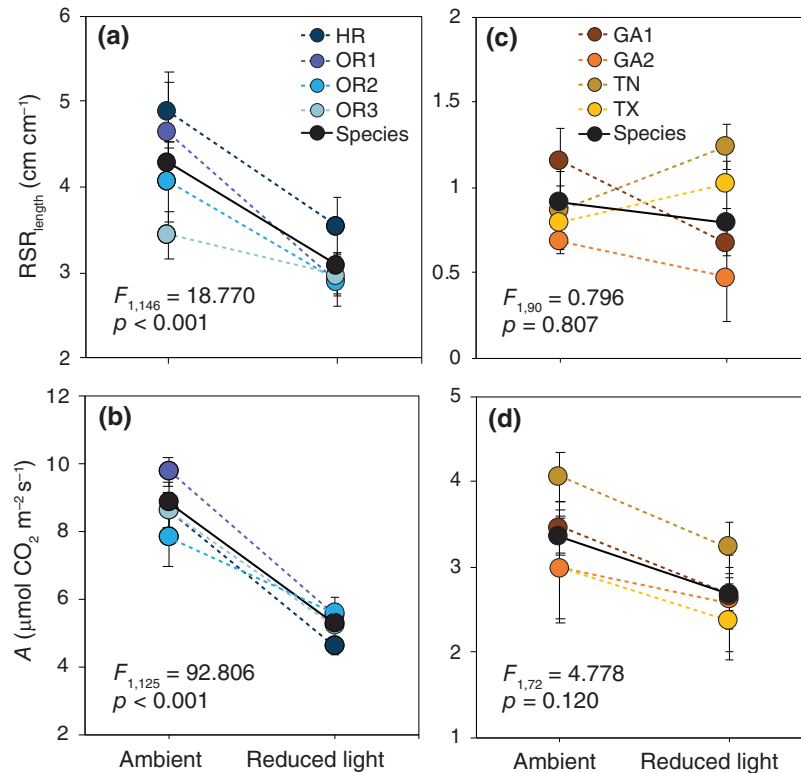


FIGURE 1 Reaction norms of the means of length-based root-shoot ratio (RSR_{length}) and leaf photosynthesis (A) of individuals of rare *Pityopsis ruthii* (a, b) and common *P. graminifolia* (c, d) grown in ambient conditions of *P. ruthii* habitat and with reduced light. Solid lines and symbols depict species-level means and norms; dashed lines and colored symbols depict population-level means and norms. Error bars represent ± 1 SE of the mean; p values denote the significance of differences in species means between abiotic treatment levels (i.e., species-level plasticity)

P. graminifolia exhibited plasticity in response to temperature, while *P. ruthii* did not (Figure 2). In response to water availability, *P. ruthii* exhibited plasticity of more traits than did *P. graminifolia* (Figure 3).

Despite observable population-level trends in both species (see Figures 1–3), significant differences in plasticity among populations were limited. Plasticity of two traits differed between populations of *P. ruthii*, while *P. graminifolia* populations exhibited no plasticity differences (Appendix S2: Table S5). Specifically, the plasticity of shoot mass in response to temperature of the OR1 population of *P. ruthii* differed from that of populations OR2 ($F_{1,66} = 7.148$, $p = 0.009$; Figure 2c) and HR ($F_{1,71} = 8.274$, $p = 0.005$; Figure 2c). Similarly, the plasticity of RMF in response to water of the OR1 population differed from that of populations OR2 ($F_{1,64} = 8.593$, $p = 0.005$) and HR ($F_{1,71} = 8.577$, $p = 0.005$; Appendix S2: Figure S2).

Adaptive nature of plasticity

Selection via biomass operated on trait plasticity under light and water manipulations, but not under temperature

manipulation (Appendix S2: Tables S6–S8 and Figures S3 and S4). We found significant species by plasticity interactions for four traits in response to light level. In two cases, these interactions signified that the magnitude of selection differed across species. Specifically, selection for adaptive plasticity in root mass was stronger in *P. graminifolia* than *P. ruthii* (Appendix S2: Figure S3b) and selection against plasticity (i.e., for trait canalization) in SRL was stronger in *P. graminifolia* than *P. ruthii* (Appendix S2: Figure S3d). For plasticity in RMF, the direction of selection differed across species, with selection favoring adaptive plasticity in *P. graminifolia* and reduced plasticity (canalization) in *P. ruthii* (Appendix S2: Figure S3c). Finally, selection acted against plasticity in a number of leaves of *P. graminifolia* but did not operate on plasticity of this trait in *P. ruthii* (Appendix S2: Figure S3a). Under variation in water level, selection favored adaptive plasticity in the number of leaves of *P. graminifolia* but did not operate on plasticity in this trait in *P. ruthii* (Appendix S2: Figure S4a). In contrast, selection acted similarly in both species for reduced plasticity (canalization) in root mass (Appendix S2: Figure S4b). Finally, we found divergent selection on plasticity in RSR_{length} across species, with selection for

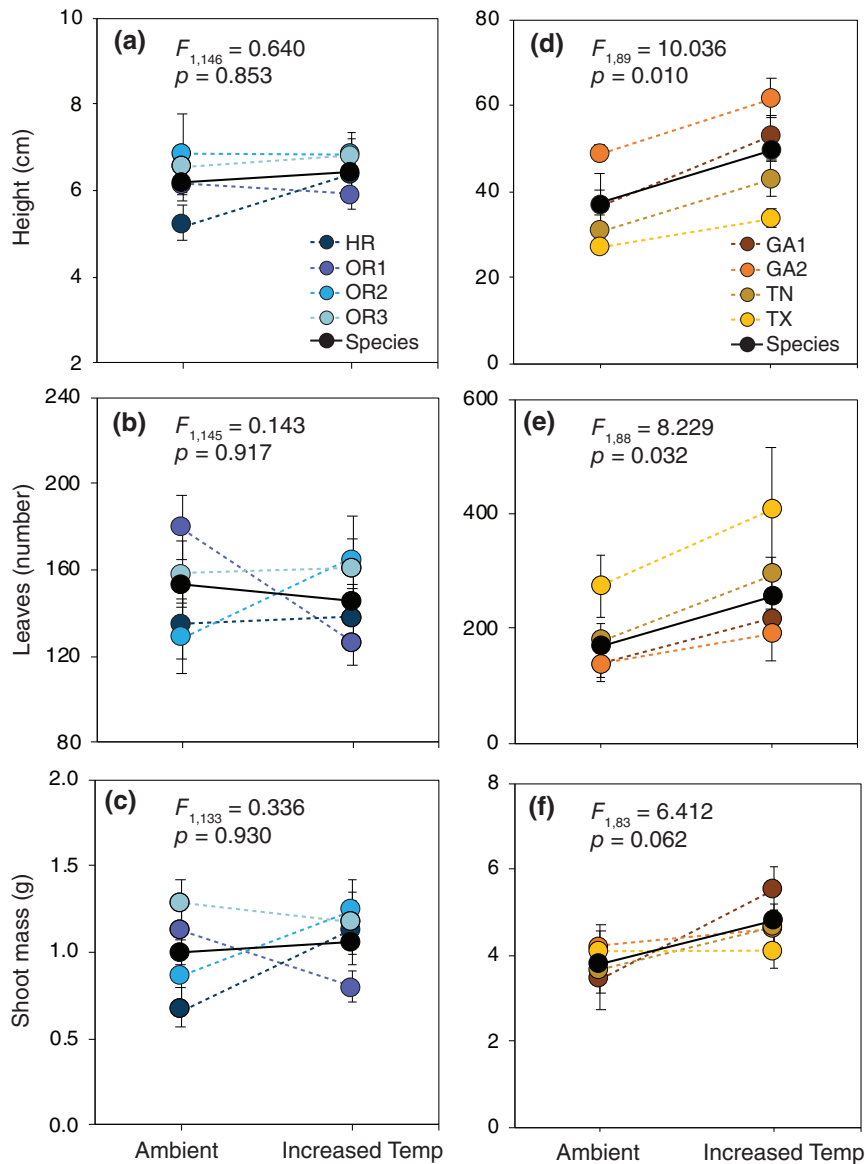


FIGURE 2 Reaction norms of the means of plant height, number of leaves, and shoot mass of individuals of rare *Pityopsis ruthii* (a, b, c) and common *P. graminifolia* (d, e, f) grown in ambient conditions of *P. ruthii* habitat and with increased temperature. Solid lines and symbols depict species-level means and norms; dashed lines and colored symbols depict population-level means and norms. Error bars represent ± 1 SE of the mean; p values denote the significance of differences in species means between abiotic treatment levels (i.e., species-level plasticity)

adaptive plasticity in *P. graminifolia* and for trait canalization in *P. ruthii* (Appendix S2: Figure S4c).

Genetic diversity

The average number of alleles per population at nine polymorphic loci of *P. graminifolia* (4.98 ± 0.23 , mean ± 1 SE) was about double that of *P. ruthii* (2.58 ± 0.33 ; $F_{1,6} = 34.8$, FDR-corrected $p = 0.001$) despite the greater sample size of *P. ruthii* (Appendix S2: Table S9). There was no significant difference in the Shannon or Simpson diversity estimates between the two species; however, Nei's diversity

index was greater in *P. graminifolia* than in *P. ruthii* (0.739 vs. 0.467, respectively; $F_{1,6} = 25.3$, FDR-corrected $p = 0.048$; Appendix S2: Table S10). Population clustering for *P. graminifolia* and *P. ruthii* populations was consistent with the distinct geographic locations of the populations sampled (Appendix S2: Figure S5).

DISCUSSION

Across taxa, species with small geographic distributions and narrow habitat specificity have greater extinction risks relative to species with broader distributions and

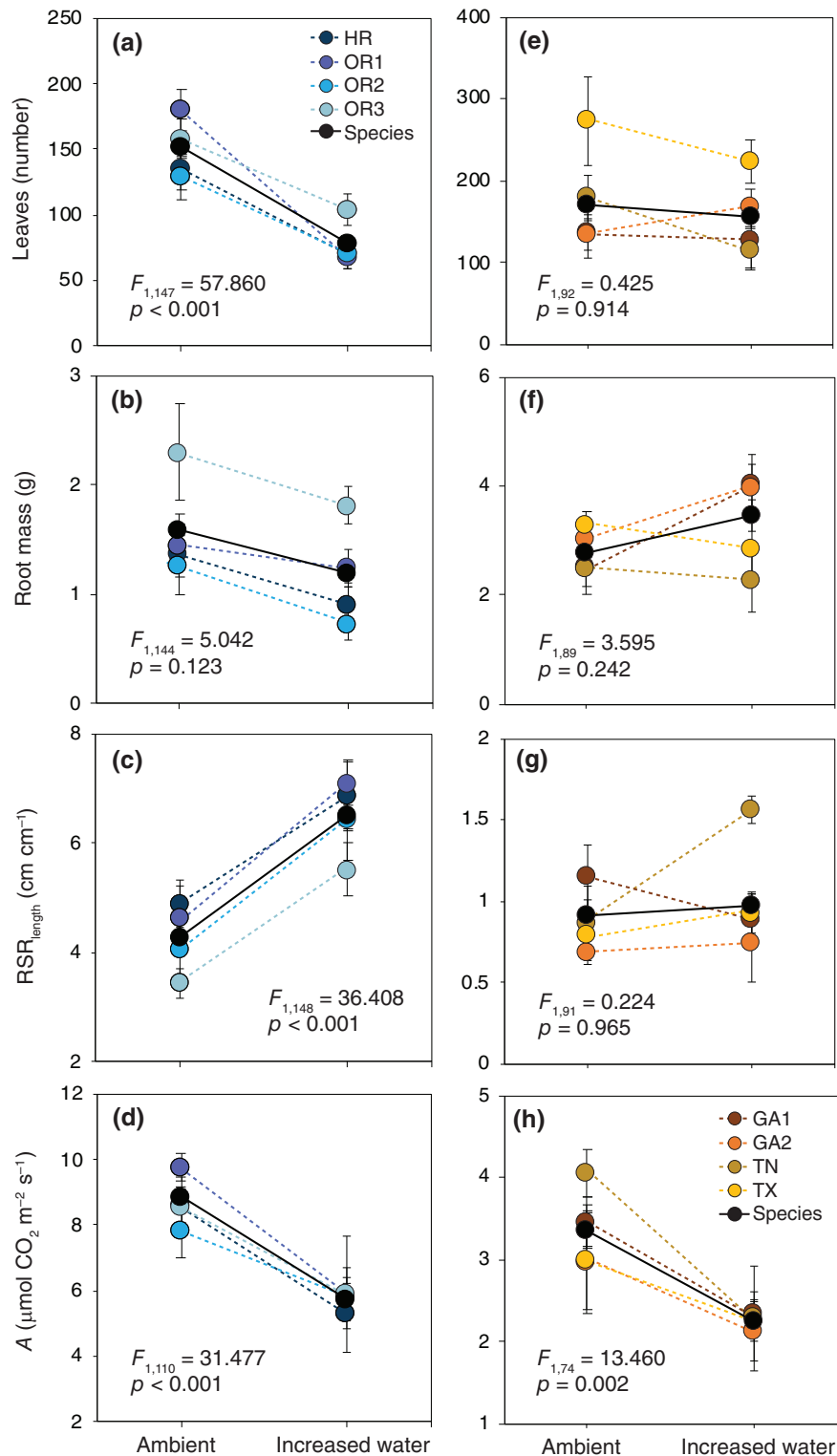


FIGURE 3 Reaction norms of the means of number of leaves, root mass, length-based root-shoot ratio (RSR_{length}), and leaf photosynthesis (A) of individuals of rare *Pityopsis ruthii* (a, b, c, d) and common *P. graminifolia* (e, f, g, h) grown in ambient conditions of *P. ruthii* habitat and with increased water availability. Solid lines and symbols depict species-level means and norms; dashed lines and colored symbols depict population-level means and norms. Error bars represent ± 1 SE of the mean; p values denote the significance of differences in species means between abiotic treatment levels (i.e., species-level plasticity)

ecological specificity (Chichorro et al., 2019; Harnik et al., 2012; Staude et al., 2020). Limited phenotypic plasticity could play an important role in constraining the current distributions and/or habitat breadths of species or could result from such constraints. Generalist species occurring across broad habitat types may be characterized by high plasticity relative to species with narrow habitat specificity (see review by Murray et al., 2002); however, our findings indicate that instead, plasticity could facilitate or result from specialization to habitats characterized by temporally dynamic environmental conditions. Specifically, we found that the rare endemic *P. ruthii* exhibited low plasticity in response to changes in temperature (Figure 2) but high plasticity in response to altered light (Figure 1) and water availability (Figure 3) relative to its widespread congener *P. graminifolia*. Although contrary to expected differences in rare/common species, these findings could help to explain the specific habitat restriction of *P. ruthii* to boulder crevices along two rivers with variable water flow regimes (Thomson & Schwartz, 2006) and the persistence of plants in locations ranging from sunny to fully shaded (Moore et al., 2016) despite early reports describing this species as performing best in high light environments (White, 1977).

Phenotypic plasticity could enable species to persist through rapid environmental change in the short term and could potentially afford time for adaptation to new conditions in the longer term (i.e., “plastic rescue”; Chevin et al., 2010; Snell-Rood et al., 2018). It is possible that the plasticity of *P. ruthii* in response to changes in light and water availability could buffer this rare species against changes in those abiotic conditions in the future, such as altered precipitation, river management, and surrounding land use. In contrast, the limited plasticity of *P. ruthii* in response to temperature could suggest that it may be less able than *P. graminifolia* to persist in the face of a warming climate. Plasticity also can be maladaptive, which is especially likely when it is elicited in response to environmental conditions that are novel, under which selection would not yet have occurred (Snell-Rood et al., 2018). But research on the adaptive nature of phenotypic plasticity in plant traits has been limited (Wei et al., 2020; but see Anderson et al., 2021; Baythavong et al., 2011; Baythavong & Stanton, 2010). The relatively high plasticity of *P. ruthii* in response to altered light and water availability in our study was associated with reductions in photosynthetic rate (which generally correlates with growth; Kruger & Volin, 2006; Figures 1b and 3d), leaf production (as a measure of growth; Figure 3a), and flowering (Appendix 2: Figure S1) in the directions of future change that we anticipated. These results suggest that *P. ruthii* may be less resilient to environmental change than its common congener, despite its plasticity.

Riparian plants often exhibit phenotypic plasticity of shoot and root traits in response to changes in water flow, especially flooding (Bailey-Serres & Colmer, 2014), yet few studies have tested whether such plasticity is adaptive (Wei et al., 2020). We found that *P. ruthii* exhibited flexibility in the allocation of above- and below-ground biomass that could support light and water acquisition in resource-limited conditions and to potentially strengthen mechanical anchoring in high-flow scenarios (Figures 1a and 3c). But selection operated only weakly on plasticity of belowground biomass allocation traits in *P. ruthii* in response to both light and water availability (Appendix S2: Figures S3 and S4) in comparison with *P. graminifolia*, suggesting that plasticity of these traits does not confer a strong fitness advantage and can be maladaptive in some scenarios. Theoretical work has suggested that plasticity reduces fitness when environmental stochasticity is high and unpredictable (Reed et al., 2010), and we propose that the dramatic effects of river management on *P. ruthii* habitat may have selected against plasticity in addition to the potential for plasticity to be maladaptive in response to novel conditions. We encourage future studies that evaluate the lifetime fitness consequences of phenotypic plasticity under realistic field conditions (Anderson et al., 2021; Baythavong et al., 2011; Baythavong & Stanton, 2010; Van Buskirk & Steiner, 2009).

Differences in management along the rivers where *P. ruthii* occurs can provide insight into the fitness consequences of changes in water availability historically and currently experienced by this species. To allow for both hydroelectric generation and recreational whitewater activities, *P. ruthii* populations along the Ocoee River experience more frequent changes in water flow than those along the HR, which are subject only to dammed conditions. Annual monitoring indicates that populations of *P. ruthii* along the Ocoee River generally have been increasing in size, while those along the HR have been experiencing declines in recent decades (Moore et al., 2016). These differences could arise through indirect impacts that differences in water flow may have on the encroachment of competing vegetation (Thomson & Schwartz, 2006; White, 1977). However, we suggest that the ability of *P. ruthii* to persist along the Ocoee River also may be influenced by its adaptation and/or an ability to adjust to short-term changes in water availability. Temperate and freshwater environments, like those in which *P. ruthii* occurs, are often characterized by highly dynamic conditions, but most research on phenotypic plasticity has focused on long-term environmental change rather than short-term dynamics (Burggren, 2018). Future research that includes a broader gradient of water availability and more complex aspects of water flow could help to further elucidate the unique habitat specificity of *P. ruthii* and its responses to environmental change.

The niche breadth hypothesis suggests that species distributions are influenced by niche limits (Cardillo et al., 2019; Gaston, 2000; Slatyer et al., 2013), such that geographically restricted rare species like *P. ruthii* may be constrained by their narrow niche breadths. Within the contexts of both light and water availability, our plasticity results suggest that the fundamental niche of *P. ruthii* could be larger than its current distribution, while the limited plasticity of *P. ruthii* in response to temperature could suggest that its current latitudinal and elevational extent may be constrained by a relatively low ability to acclimate to a wide range of temperatures (Figure 2). It has been proposed that the small range of *P. ruthii* along the Ocoee River and HR could represent a relic of a broader historical distribution when climate was generally cooler (Cruzan & Estill, 2001). However, factors such as the east–west orientation of these rivers, surrounding steep topography, and poor seed dispersal ability of *P. ruthii* likely also restrict its ability to migrate northward and/or to higher elevations (Cruzan & Estill, 2001). In addition, it has been long proposed that *P. ruthii* is constrained by its poor competitive ability relative to surrounding and encroaching vegetation (USFWS, 1992); however, the role of competition in restricting the realized niche of this species is supported by limited observation (Cruzan & Estill, 2001, Thomson & Schwartz, 2006, United States Forest Service, 2008; USFWS, 2018) and warrants empirical testing. Although the 2°C of warming in our experiment did not significantly influence growth of *P. ruthii* (Figure 2), further warming under climate change could affect this rare species. Here, we limited our investigations of plasticity to comparisons of responses in current versus near-future conditions, but future research focused on investigating plasticity in response to temperature could consider a wider range and number of treatment levels that could better capture phenotypic responses (see Arnold et al., 2019) and allow for a more robust assessment of acclimatory constraints. In addition, future multifactorial studies could generate robust predictions about the biological consequences of the simultaneous effects of warming and other abiotic environmental change factors along with biotic factors on *P. ruthii* and other rare species compared with common species.

Although limited variation in plasticity among populations was expected for *P. ruthii* given its small range and habitat specificity (see Darwin, 1859; Sides et al., 2014), we expected to find more differences among populations of *P. graminifolia* given its broader range and habitat associations. We suggest that the relatively high plasticity of *P. graminifolia* populations within the context of temperature (Figure 2) could have influenced its distribution across latitudes and that perhaps other

environmental conditions such as light and water availability could be more consistent among locations where this species is found. It has been suggested that plasticity could underlie the success of polyploids (Levin, 2002), which have been evidenced in *P. graminifolia* (Bogges et al., 2014; Semple & Bowers, 1985; Weakley, 2020) including some of the populations that we sampled. However, tests of this hypotheses have been inconclusive (Bretagnolle & Thompson, 2001; Hahn et al., 2012; Münzbergova, 2007; Petit et al., 1996; Petit & Thompson, 1997; Sánchez Vilas & Pannell, 2017) and any differences in ploidy between the *P. graminifolia* populations that we sampled were not associated with population-level differences in plasticity. Although we found lower genetic diversity in *P. ruthii* compared to its widespread congener as expected, we note that a previous survey of *P. ruthii* across its range found relatively high levels of genetic diversity compared with other plant species, including other rare and endemic species (Hatmaker et al., 2018). This finding, along with robust gene flow estimates (Hatmaker et al., 2018), plasticity in response to water availability, and clonal nature of *P. ruthii*, could help to explain its persistence in highly variable and stressful conditions along the two rivers within its limited range.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Boyd et al., 2021) are available from Dryad: <https://doi.org/10.5061/dryad.2v6wwpzm>.

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REFERENCES

- Anderson, J. T., M. I. Jameel, and M. A. Geber. 2021. “Selection Favors Adaptive Plasticity in a Long-Term Reciprocal Transplant Experiment.” *Evolution* 75(7): 1711–26.
- Arnold, P. A., L. E. B. Kruuk, and A. Nicotra. 2019. “How to Analyze Plant Phenotypic Plasticity in Response to a Changing Climate.” *New Phytologist* 222: 1235–41.
- Bailey-Serres, J., and T. D. Colmer. 2014. “Plant Tolerance of Flooding Stress—Recent Advances.” *Plant, Cell and Environment* 37: 2211–5.

- Balaguer, I., E. Martínez-Ferri, F. Valladares, F. Pérez-Corona, F. J. Baquédano, F. J. Castillo, and E. Manrique. 2001. "Population Divergence in the Plasticity of the Response of *Quercus coccifera* to the Light Environment." *Functional Ecology* 15: 124–35.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Baythavong, B. S., A. Agrawal, and M. A. McPeck. 2011. "Linking the Spatial Scale of Environmental Variation and the Evolution of Phenotypic Plasticity: Selection Favors Adaptive Plasticity in Fine-Grained Environments." *The American Naturalist* 178: 75–87.
- Baythavong, B. S., and M. L. Stanton. 2010. "Characterizing Selection on Phenotypic Plasticity in Response to Natural Environmental Heterogeneity." *Evolution* 64: 2904–20.
- Benjamini, Y., and Y. Hochberg. 1995. "Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing." *Journal of the Royal Statistical Society. Series B (Statistical Methodology)* 57: 289–300.
- Bevill, R. L., and S. M. Louda. 1999. "Comparisons of Related Rare and Common Species in the Study of Plant Rarity." *Conservation Biology* 13: 493–8.
- Bogges, S. L., P. A. Wadl, D. Hadziabdic, B. E. Scheffler, A. S. Windham, W. E. Klingeman, and R. N. Trigiano. 2014. "Characterization of 12 Polymorphic Microsatellite Loci of *Pityopsis graminifolia* var. *latifolia*." *Conservation Genetics Resources* 6: 1043–5.
- Boyd, J., Odell, J., Cruse-Sanders, J., Rogers, W., Anderson, J., Baskauf, C., Brzyski, J. 2021. "Phenotypic Plasticity and Genetic Diversity Elucidate Rarity and Vulnerability of an Endangered Riparian Plant." Dryad. Dataset. <https://doi.org/10.5061/dryad.2v6wwpzmz>.
- Bretagnolle, F., and J. D. Thompson. 2001. "Phenotypic Plasticity in Sympatric Diploid and Autotetraploid *Dactylis glomerata*." *International Journal of Plant Sciences* 162: 309–16.
- Burggren, W. 2018. "Developmental Phenotypic Plasticity Helps Bridge Stochastic Weather Events Associated with Climate Change." *Journal of Experimental Biology* 221: jeb161984.
- Capon, S. J., L. E. Chamber, R. Mac Nally, R. J. Naiman, P. Davies, N. Marshall, J. Pittock, et al. 2013. "Riparian Ecosystems in the 21st Century: Hotspots for Climate Change Adaptation?" *Ecosystems* 16: 359–81.
- Cardillo, M., R. Dinnage, and W. McAlister. 2019. "The Relationship between Environmental Niche Breadth and Geographic Range Size across Plant Species." *Journal of Biogeography* 46: 97–109.
- Chen, I.-C., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated with High Levels of Climate Warming." *Science* 333: 1024–6.
- Chevin, L.-M., R. Lande, and G. M. Mace. 2010. "Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory." *PLoS Biology* 8: e1000357.
- Chichorro, F., A. Juslén, and P. Cardoso. 2019. "A Review of the Relation between Species Traits and Extinction Risk." *Biological Conservation* 237: 220–9.
- Cleavitt, N. L. 2002. "Stress Tolerance of Rare and Common Moss Species in Relation to Their Occupied Environments and Asexual Dispersal Potential." *Journal of Ecology* 90: 785–95.
- Clewell, A. 1985. *Guide to the Vascular Plants of the Florida Panhandle*. Tallahassee, FL: Florida State University Press.
- Cole, C. T. 2003. "Genetic Variation in Rare and Common Plants." *Annual Review of Ecology, Evolution, and Systematics* 34: 213–37.
- Combs, J. K., A. M. Lambert, and S. H. Reichard. 2013. "Predispersal Seed Predation Is Higher in a Rare Species than Its Widespread Sympatric Congeners (*Astragalus*, Fabaceae)." *American Journal of Botany* 100: 2149–57.
- Crickenberger, S., and D. S. Wetthey. 2018. "Annual Temperature Variation as a Time Machine to Understand to Effects of Long-Term Climate Change on a Poleward Range Shift." *Global Change Biology* 24: 3804–19.
- Cruzan, M., and J. C. Estill. 2001. *Ecological Genetics of Pityopsis ruthii: Final Research Report II, Phylogeography*. Nashville, TN: Tennessee Department of Environment and Conservation, Division of Natural Heritage.
- Dangremond, E. M., I. C. Feller, and W. P. Sousa. 2015. "Environmental Tolerances of Rare and Common Mangroves along Light and Salinity Gradients." *Oecologia* 179: 1187–98.
- Darwin, C. R. 1859. *On the Origin of Species*. London: John Murray.
- Duncan, W. H., and M. B. Duncan. 1987. *Seaside Plants of the Gulf and Atlantic Coasts*. Washington, DC: Smithsonian Institution Press.
- Enquist, B. J., X. Feng, B. Boyle, B. Maitner, E. A. Newman, P. M. Jørgensen, P. R. Roehrdanz, et al. 2019. "The Commonness of Rarity: Global and Future Distribution of Rarity across Land Plants." *Science Advances* 5: eaaz0401.
- Farnsworth, E. J. 2006. "Plant Life History Traits of Rare Versus Frequent Plant Taxa of Sandplains: Implications for Research and Management Trials." *Biological Conservation* 136: 44–52.
- Firth, D. 1993. "Bias Reduction of Maximum Likelihood Estimates." *Biometrika* 80: 27–38.
- Fox, J., and S. Weisberg. 2018. "Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals." *Journal of Statistical Software* 87: 1–27.
- Gaston, K. J. 2000. "Global Patterns in Biodiversity." *Nature* 405: 220–7.
- Gibson, D. J. 2014. *Methods in Comparative Plant Ecology*. Oxford: Oxford University Press.
- Gitzendanner, M. A., and P. S. Soltis. 2000. "Patterns of Genetic Variation in Rare and Widespread Plant Congeners." *American Journal of Botany* 87: 783–92.
- Godoy, O., F. Valladares, and P. Castro-Diez. 2012. "The Relative Importance for Plant Invasiveness of Trait Means, and Their Plasticity and Integration in a Multivariate Framework." *New Phytologist* 195: 912–22.
- Godt, M. J., and W. J. L. Hamrick. 2001. "Genetic Diversity in Rare Southeastern Plants." *Natural Areas Journal* 21: 61–70.
- Hahn, M. A., M. van Kleunen, and H. Müller-Schärer. 2012. "Increased Phenotypic Plasticity to Climate May Have Boosted the Invasive Success of Polyploid *Centaurea stoebe*." *PLoS One* 7: e50284.
- Hamann, E., C. Pauli, Z. Joly-Lopez, S. C. Groen, J. S. Rests, N. C. Kane, M. D. Purugganan, and S. J. Franks. 2020. "Rapid Evolutionary Changes in Gene Expression in Response to Climate Fluctuations." *Molecular Ecology* 30: 193–206.
- Harnik, P. G., C. Simpson, and J. L. Payne. 2012. "Long-Term Differences in Extinction Risk among the Seven Forms of Rarity." *Proceedings of the Royal Society B* 279: 4969–76.

- Hatmaker, E. A., M. E. Staton, A. J. Dattilo, D. Hadziabic, T. A. Rinehart, E. E. Schilling, R. N. Trigiano, and P. A. Wadl. 2018. "Population Structure and Genetic Diversity within the Endangered Species *Pityopsis ruthii* (Asteraceae)." *Frontiers in Plant Science* 9: 943.
- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. "The Distributions of a Wide Range of Taxonomic Groups Are Expanding Polewards." *Global Change Biology* 12: 450–5.
- Iverson, L. R., M. W. Schwartz, and A. M. Prasad. 2004. "How Fast and Far Might Tree Species Migrate in the Eastern United States Due to Climate Change?" *Global Ecology and Biogeography* 13: 209–19.
- Jombart, T., S. Devillard, and F. Balloux. 2010. "Discriminant Analysis of Principal Components: A New Method for the Analysis of Genetically Structured Populations." *BMC Genetics* 11: 94.
- Jump, A. S., and J. Peñuelas. 2005. "Running to Stand Still: Adaptation and the Response of Plants to Rapid Climate Change." *Ecology Letters* 8: 1010–20.
- Kamvar, Z. N., J. F. Tabima, and N. J. Grünwald. 2014. "Poppr: An R Package for Genetic Analysis of Populations with Clonal, Partially Clonal, and/or Sexual Reproduction." *PeerJ* 2: e281.
- Kosmidis, I. 2020. *brglm: Bias Reduction in Binary-Response Generalized Linear Models. R Package Version 0.7.1*.
- Kosmidis, I., and D. Firth. 2020. "Jeffrey's Prior Penalty, Finiteness and Shrinkage in Binomial-Response Generalized Linear Models." *Biometrika* 108: 71–82.
- Kruger, E. L., and J. C. Volin. 2006. "Reexamining the Empirical Relation between Plant Growth and Leaf Photosynthesis." *Functional Plant Biology* 33: 421–9.
- Kunin, W. E., and K. Gaston. 1997. *The Biology of Rarity: Causes and Consequences of Rare-Common Differences*. New York: Springer.
- Leimu, R., and M. Fischer. 2008. "A Meta-Analysis of Local Adaptation in Plants." *PLoS One* 3: e4010.
- Levin, D. A. 2002. *The Role of Chromosomal Change in Plant Evolution*. Oxford: Oxford University Press.
- Machado, R. M., F. A. de Oliveira, F. de Matos Alves, A. P. de Souza, and E. R. Forni-Martins. 2021. "Population Genetics of Polyploid Complex *Psidium cattleianum* Sabine (Myrtaceae): Preliminary Analyses Based on New Species-Specific Microsatellite Loci and Extension to Other Species of the Genus." *Biochemical Genetics* 59: 219–34.
- Malhi, Y., J. Franklin, N. Seddon, M. Solan, M. G. Turner, C. B. Field, and N. Knowlton. 2020. "Climate Change and Ecosystems: Threats, Opportunities and Solutions." *Philosophical Transactions of the Royal Society B* 375: 20190104.
- May, R. M. 1988. "How Many Species Are There on Earth?" *Science* 241: 1441–9.
- Meirmans, P. G., S. Liu, and P. H. Tienderen. 2018. "The Analysis of Polyploid Genetic Data." *Journal of Heredity* 109: 283–96.
- Moore, P. A., P. A. Wadl, J. A. Skinner, R. N. Trigiano, and E. C. Bernard. 2016. "Current Knowledge, Threats, and Future Efforts to Sustain Populations of *Pityopsis ruthii* (Asteraceae), an Endangered Southern Appalachian Species." *Journal of the Torrey Botanical Society* 143: 117–34.
- Münzbergova, Z. 2007. "No Effect of Ploidy Level in Plant Response to Competition in a Common Garden Experiment." *Biological Journal of the Linnean Society* 92: 211–9.
- Murray, B. R., P. H. Thrall, M. Gill, and A. Nicotra. 2002. "How Plant Life-History and Ecological Trait Relate to Species Rarity and Commonness at Varying Spatial Scales." *Austral Ecology* 27: 291–310.
- Nature Serve. 2020. *Habitat-based plant element occurrence delimitation guidance*. Version 1.0 published October 2004, revised May 2020. Arlington, VA: NatureServe.
- Nei, M. 1978. "Estimation of Average Heterozygosity and Genetic Distance from a Small Number of Individuals." *Genetics* 89: 583–90.
- Nicotra, A. B., O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, et al. 2010. "Plant Phenotypic Plasticity in a Changing World." *Trends in Plant Science* 15: 684–92.
- Nicotra, A. B., and A. Davidson. 2010. "Adaptive Phenotypic Plasticity and Plant Water Use." *Functional Plant Biology* 37: 117–27.
- Osunkoya, O. O., and P. W. Swanborough. 2001. "Reproductive and Ecophysiological Attributes of the Rare *Gardenia actinocarpa* (Rubiaceae) Compared with its Common Co-Occurring Congener, *G. ovularis*." *Australian Journal of Botany* 49: 471–8.
- Parmesan, C. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37: 637–69.
- Perry, L. G., D. C. Andersen, L. V. Reynolds, M. Nelson, and P. B. Shafroth. 2012. "Vulnerability of Riparian Ecosystems to Elevated CO₂ and Climate Change in Arid and Semiarid Western North America." *Global Change Biology* 18: 821–42.
- Petit, C., and J. D. Thompson. 1997. "Variation in Phenotypic Response to Light Availability between Diploid and Tetraploid Populations of the Perennial Grass *Arrhenatherum elatius* from Open and Woodland Sites." *Journal of Ecology* 85: 657–67.
- Petit, C., J. D. Thompson, and F. Bretagnolle. 1996. "Phenotypic Plasticity in Relation to Ploidy Level and Corm Production in the Perennial Grass *Arrhenatherum elatius*." *Canadian Journal of Botany* 74: 1964–73.
- Pohlman, C. L., A. B. Nicotra, and B. R. Murray. 2005. "Geographic Range Size, Seedling Ecophysiology and Phenotypic Plasticity in Australian *Acacia* Species." *Journal of Biogeography* 32: 341–51.
- Rabinowitz, D. 1981. "Seven Forms of Rarity." In *The Biological Aspects of Rare Plant Conservation*, edited by H. Synge, 205–7. Hoboken, NJ: John Wiley & Sons Ltd.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. *Manual of the Vascular Flora of the Carolinas*. Chapel Hill, NC: The University of North Carolina Press.
- Reed, T. E., R. S. Waples, D. E. Schindler, J. J. Hard, and M. T. Kinnison. 2010. "Phenotypic Plasticity and Population Viability: The Importance of Environmental Predictability." *Proceedings of the Royal Society B* 277: 3391–400.
- Sánchez Vilas, J., and J. R. Pannell. 2017. "No Difference in Plasticity between Different Ploidy Levels in the Mediterranean Herb *Mercurialis annua*." *Scientific Reports* 7: 9848.
- Seebacher, F., C. R. White, and C. E. Franklin. 2015. "Physiological Plasticity Increases Resilience of Ecothermic Animals to Climate Change." *Nature Climate Change* 5: 61–6.
- Semple, J. C., and F. D. Bowers. 1985. "A Revision of the Goldenaster Genus *Pityopsis* Nutt. (Compositae: Astereae)." *University of Waterloo Biology Series* 28: 1–34.
- Shannon, C. E. 1948. "A Mathematical Theory of Communication." *Bell System Technical Journal* 37: 379–423.

- Sheth, S. N., M. W. Kulbaba, R. E. Pain, and R. G. Shaw. 2018. "Expression of Additive Genetic Variance for Fitness in a Population of Partridge Pea in Two Field Sites." *Evolution* 72: 2537–45.
- Sides, C. B., B. J. Enquist, J. J. Ebersole, M. N. Smith, A. N. Henderson, and L. L. Sloat. 2014. "Revisiting Darwin's Hypothesis: Does Greater Intraspecific Variability Increase Species' Ecological Breadth?" *American Journal of Botany* 101: 6–62.
- Simpson, E. H. 1949. "Measurement of Diversity." *Nature* 163: 88.
- Slatyer, R. A., M. Hirst, and J. P. Sexton. 2013. "Niche Breadth Predicts Geographical Range Size: A General Ecological Pattern." *Ecology Letters* 16: 1104–14.
- Snell-Rood, E., M. E. Kobiela, K. L. Sikkink, and A. M. Shephard. 2018. "Mechanisms of Plastic Rescue in Novel Environments." *Annual Review of Ecology, Evolution, and Systematics* 49: 331–54.
- Staude, I. R., D. M. Waller, M. Bernhardt-Römermann, A. D. Bjorkman, J. Bruney, P. De Frenne, R. Hédl, et al. 2020. "Replacements of Small- by Large-Ranged Species Scale up to Diversity Loss in Europe's Temperate Forest Biome." *Nature Ecology & Evolution* 4: 802–8.
- Stinchcombe, J. R., L. A. Dorn, and J. Schmitt. 2004. "Flowering Time Plasticity in *Arabidopsis thaliana*: A Reanalysis of Westerman & Lawrence (1970)." *Journal of Evolutionary Biology* 17: 197–207.
- Sultan, S. E. 2000. "Phenotypic Plasticity for Plant Development, Function and Life History." *Trends in Plant Science* 5: 537–42.
- Thomson, D. M., and M. W. Schwartz. 2006. "Using Population Count Data to Assess the Effects of Changing River Flow on an Endangered Riparian Plan." *Conservation Biology* 20: 1132–42.
- United States Fish and Wildlife Service. 1985. "Determination of Endangered Status for *Pityopsis ruthii* (Ruth's Golden Aster)." *Federal Register* 50: 29341–5.
- United States Fish and Wildlife Service. 1992. *Ruth's Golden Aster Recovery Plan*. Atlanta, GA: United States Fish and Wildlife Service, Southeast Region.
- United States Fish and Wildlife Service. 2018. *Ruth's Golden Aster (Pityopsis ruthii) 5-Year Review: Summary and Evaluation*. Cookeville, TN: U.S. Fish and Wildlife Service, Southeast Region, Tennessee Ecological Services Field Office.
- United States Forest Service. 2008. *Environmental Assessment: Experimental Removal of Competing Vegetation from a Population of Ruth's Golden Aster (Pityopsis ruthii) on the Hiwassee River*. Polk County, TN: United States Forest Service, Cherokee National Forest, Ocoee/Hiwassee Ranger District.
- Valladares, F., E. Gianoli, and J. M. Gómez. 2007. "Ecological Limits to Plant Phenotypic Plasticity." *New Phytologist* 176: 749–63.
- Valladares, F., S. J. Wright, E. Lasso, K. Kitajima, and R. W. Pearcy. 2000. "Plastic Phenotypic Response to Light of 16 Congeneric Shrubs from a Panamanian Rainforest." *Ecology* 81: 1925–36.
- Van Buskirk, J., and U. K. Steiner. 2009. "The Fitness Costs of Developmental Canalization and Plasticity." *Journal of Evolutionary Biology* 22: 852–60.
- Van Kleunen, M., and M. Fischer. 2001. "Adaptive Evolution of Plastic Foraging Responses in a Clonal Plant." *Ecology* 82: 3309–19.
- Wadl, P. A., A. J. Dattilo, B. E. Scheffler, and R. N. Trigiano. 2011. "Development of Microsatellite Loci for the Endangered Species *Pityopsis ruthii* (Asteraceae)." *American Journal of Botany*, 98, e342–5.
- Wadl, P. A., T. A. Rinehart, A. J. Dattilo, M. Pistrang, L. M. Vito, R. Milstead, and R. N. Trigiano. 2014. "Propagation for the Conservation of *Pityopsis ruthii*, an Endangered Species from the Southeastern United States." *HortScience* 49: 194–200.
- Weakley, A. S. 2020. *Flora of the Southeastern United States*. Chapel Hill, NC: University of North Carolina Herbarium, North Carolina Botanical Garden.
- Wei, G.-W., X.-S. Sun, Y.-H. Chen, F.-L. Luo, and F.-H. Yu. 2020. "Growth and Reproductive Responses of *Polygonum hydropiper* Populations to Elevations Difference Associated with Flooding." *Global Ecology and Conservation* 23: e01156.
- Weiner, J., L. G. Campbell, J. Pino, and T. Echarte. 2009. "The Allometry of Reproduction within Plant Populations." *Journal of Ecology*, 97, 1220–33.
- White, A. J. 1977. "An Autoecological Study of the Endangered Species, *Heterotheca ruthii* (Small) Harms." PhD thesis, University of Tennessee.
- Wunderlin, R. P. 1998. *Guide to the Vascular Plants of Florida*. Gainesville, FL: University Press of Florida.
- Xu, H., M. Detto, S. Fang, Y. Li, R. Zang, and S. Liu. 2015. "Habitat Hotspots of Common and Rare Tropical Species along Climatic and Edaphic Gradients." *Journal of Ecology* 103: 1325–33.

SUPPORTING INFORMATION

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