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RESEARCH ARTICLE

Divergent evolution of traits and plasticity across climate gradients in a widespread tree species

David Lerner[1,2] | Rebeca Gonzalez Rolfe[1] | Gili Greenbaum[2] | Tamir Klein[1]

[1]Weizmann Institute of Science, Rehovot, Israel

[2]Department of Ecology, Evolution & Behavior, The Hebrew University of Jerusalem, Jerusalem, Israel

Correspondence
David Lerner
Email: dlernerg@gmail.com

Tamir Klein
Email: tamir.klein@weizmann.ac.il

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Abstract

1. Species with large distributions that span significant environmental gradients have evolved complex mechanisms to adapt to different environments. This adaptation can be achieved both through the direct selection on traits that convey higher fitness under local environmental conditions, or through the evolution of phenotypic plasticity.
2. Under a common-garden experimental setup, we tested for the keystone African tree species *Acacia tortilis* how the interaction between direct selection on traits and evolution of plasticity has led to its widespread distribution to two contrasting environments: deserts and tropical savannas. In addition, we tested the predictability of evolution by comparing populations in opposing deserts of its distribution, the Sahara and Kalahari deserts.
3. We observed significant differences in how various phenotypes responded to the harsh desert environment compared with the more moderate tropical-savanna environment, with a stronger among-population differentiation expressed under desert conditions.
4. We found an isolation-by-environment signal mainly for phenotypic plasticity, with a strong association to precipitation gradients, suggesting that differentiation across the tropic-desert gradient occurs in this species primarily through selection on trait plasticity rather than trait means. Interestingly, the two desert-edge populations showed similar plastic responses, despite the large geographical distances between them, suggesting convergence in plasticity.
5. *Synthesis*. Taken together, our results suggest that phenotypic plasticity plays an important role in differentiation across the tropical-savanna to desert gradient in *Acacia tortilis*, with similar phenotypic responses observed between climatically comparable populations at opposing range edges.

KEYWORDS
Acacia tortilis, biogeography, phenotypic clines, phenotypic plasticity, quantitative evolution

David Lerner and Rebeca Gonzalez Rolfe equal contribution.

Gili Greenbaum and Tamir Klein equal contribution of last authors.

1 | INTRODUCTION

Species that are geographically widespread experience a broad range of environmental conditions (Endler, 1977; Hereford, 2009; Kawecki & Ebert, 2004). In many cases, environmental gradients throughout the geographic range generate directional selection pressures that lead to local adaptations, which can be reflected in the clinal phenotypic variation (Haldane, 1948; Holgate, 1964; Rellstab et al., 2015). A possible evolutionary role of plasticity is the reduction of the efficiency of adaptation by directional selection, since it may allow organisms to cope with environmental variability without the need for genetic modifications (Chevin et al., 2010; King & Hadfield, 2019; Sultan & Spencer, 2002). However, such environmental variability can also lead to adaptive evolution for varying levels of plasticity (Chevin & Lande, 2011; Cooper et al., 2022; Stotz et al., 2021; Usui et al., 2023). Therefore, adaptive plasticity and local adaptation may not be mutually exclusive (Stamp & Hadfield, 2020), and it is unclear how these two evolutionary processes interact in different settings and in different bioregions (Franks et al., 2014). One of the experimental setups best suited to disentangle the effects of directional selection and adaptive plasticity is common-garden experiments (de Villemereuil et al., 2016; Schwinning et al., 2022).

Evolutionary forces shape both the phenotypes and the plasticity of phenotypes, but the direction and manner in which phenotypes and their corresponding plasticity levels evolve usually differ for several reasons. First, different evolutionary pressures will select for trait means and trait plasticity, as they affect the individual's fitness differently (Chevin et al., 2010; Levins, 1968; Usui et al., 2023). While trait means are mainly shaped by directional selection, favouring optimal performance under prevailing environmental conditions, plasticity (the variance of a trait) is expected to be selected for in situations, such as predicable changing environment (Chevin & Lande, 2011; Tufto, 2015) or during range expansion (Brancalion et al., 2018; Carbonell et al., 2021; Lande, 2015; Swaegers et al., 2020). Second, because plasticity of a trait affects the evolutionary potential of the underlying traits (Ghalambor et al., 2015; West-Eberhard, 2003), complex interactions and feedbacks may be generated between plasticity and natural selection (Vinton et al., 2022). Finally, maintaining plasticity likely comes at some fitness cost to the organism (DeWitt et al., 1998; Ghalambor et al., 2007), which could limit its evolution. This is the case, for example, in stable environments where highly plastic individuals will be less fit than those that have low fitness because plasticity confers no benefit and endures a cost (DeWitt et al., 1998; Murren et al., 2015). Likewise, plasticity evolution could be limited in extreme environmental conditions since the cost for maladaptation could increase, leading to plasticity reducing fitness, and the relative cost of maintaining plasticity increases with respect to other energy and resource demands (Campbell-Staton et al., 2021; DeWitt et al., 1998). Such limitations to the evolution of plasticity can be observed when comparing populations at the core and edge of the species' range (Usui et al., 2023; Valladares et al., 2014). For example, at stable range edges, strong selective pressures may reduce the fitness of maladapted individuals, contributing to smaller population sizes and lower gene flow in edge populations (Angert et al., 2020), conditions that can further constrain the evolution and expression of plasticity relative to the core population (Chevin & Lande, 2011; Eriksson & Rafajlović, 2022; Sultan & Spencer, 2002; Valladares et al., 2014). Benign climatic conditions, such as those in tropical regions, can facilitate plasticity (Stotz et al., 2021) because lower abiotic stress may relax the costs of maintaining flexible responses. In contrast, stressful environments, such as arid desert conditions, can impose limits on plasticity by pushing organisms closer to their physiological limits (Stotz et al., 2021; Valladares et al., 2007; Voltas et al., 2018). In addition, greater climatic variability may select for increased plasticity (Lancaster & Humphreys, 2020). This raises the question of whether broad-scale drivers of plasticity differ between tropical and desert regions and, if so, whether they lead to an overall increase or decrease at global scales (Valladares et al., 2014). Thus, the interplay between environmental stability and variability determines whether plasticity evolves as a mechanism for persistence under stress or as a means of exploiting resource-rich conditions.

The emergence of broad-scale differentiating patterns between phenotypic plasticity and trait variance can have an effect on the realized niche of a single genotype, allowing performance across contrasting environments by shifting trait expression along the reaction norm. Plasticity can generate a generalist phenotype when environmental cues are reliable and costs are modest. Conversely, when plasticity is costly or unreliable, selection may favour canalized trait expression, yielding specialist genotypes with narrow reaction norms (Chevin et al., 2010; Hendry, 2015; Lande, 2015; van Tienderen, 1997). However, modelling and empirical data show that within-population variance can also influence the population niche breadth and stabilize performance across conditions by ensuring that different genotypes respond in complementary ways to environmental change. This diversity increases the likelihood that the combination of multiple genotypes will perform well across a wide range of environments, supporting generalist strategies at the population level even when mean plasticity is not elevated (Bolnick et al., 2003).

The higher plasticity observed in benign tropical environments (Stotz et al., 2021) negated previous assumptions that species in such environments are highly specialized with narrow niche breadths and constrained functional trait spaces (Pandit et al., 2009; Van Tienderen, 1991). This view aligns with mechanisms, such as 'tropical niche conservatism', a theory set to explain the high biodiversity of tropical regions (Klopfer & MacArthur, 1961; Wiens & Graham, 2005). However, other studies have suggested that tropical species may exhibit generalist tendencies, characterized by broader functional trait spaces and higher plasticity (Liu & El-Kassaby, 2019; Schoener, 1971). This generalist characteristic may result from environmental fluctuations in competition, precipitation or population size (Carbonell et al., 2021; Vázquez & Stevens, 2004), potentially supporting theories such as the 'niche expansion' and 'out-of-the-tropics' (Bolnick et al., 2007; Jablonski et al., 2006; Sjödin et al., 2018), since a

generalist strategy is considered advantageous for colonization of novel environments (Araújo et al., 2011). Consequently, it remains unclear whether tropical and extra-tropical regions generate distinct evolutionary strategies in terms of selection for fixed locally adaptive phenotypes versus trait plasticity. Addressing this question could provide critical insight into how biogeographical regions shape the adaptation process and the adaptive potential of species.

In plants, plasticity plays a particularly important role in fitness and survival, and specifically in perennial and woody species, as it allows them to cope with changes in their environment despite their sessile nature (Franks et al., 2014; Gratani, 2014; Schneider, 2022). In particular, plant species with wide-range distributions are of specific interest, because they tend to experience strong environmental gradients that result in significant phenotypic clines (Daday, 1965; Woods et al., 2012). In addition, similar environmental pressures can reoccur in multiple regions in the species' range, which can be useful for identification of specific selection pressures on traits and their corresponding trait plasticities. This is especially true for species with ranges that span both sides of the equator, where repeated evolutionary events can be studied in similar environmental conditions.

Acacia tortilis is a compelling model system for studying trait evolution and plasticity across broad environmental gradients. Beyond its role as a keystone species in many arid ecosystems (Beckmann et al., 2014; Suleiman et al., 2018; Uni et al., 2022; Winters et al., 2018), *A. tortilis* comprises a range of ecosystems, spanning both sides of the equator, from hot-arid deserts to mesic tropical savanna across Africa and the Middle East (Figure 1). This broad range allows the examination of how both the evolution of traits and trait plasticity contribute to its widespread success. In this study, we designed a common-garden experiment in which we grew representative *A. tortilis* individuals from two distinct biomes: *Deserts and Xeric Shrublands* and *Tropical and Subtropical Grasslands/Savannas/Shrublands* (Figure 1a). We used two common gardens designed to emulate tropical and desert environmental conditions. This experimental design, which involves the controlled environmental growth of populations from diverse geographical and environmental origins, provides valuable insights into how heritable traits and plasticity shape population responses to varying climate conditions (George et al., 2020; Gratani et al., 2003; Klein et al., 2013; Nicotra et al., 2010; Ramírez-Valiente & Cavender-Bares, 2017; Schwinning et al., 2022). Using this experimental setup we investigate several key questions: (i) Do extreme desert-like environments impose stronger or weaker selective pressures compared with the more benign tropical-like environment? (ii) Does spatial and environmental differences across

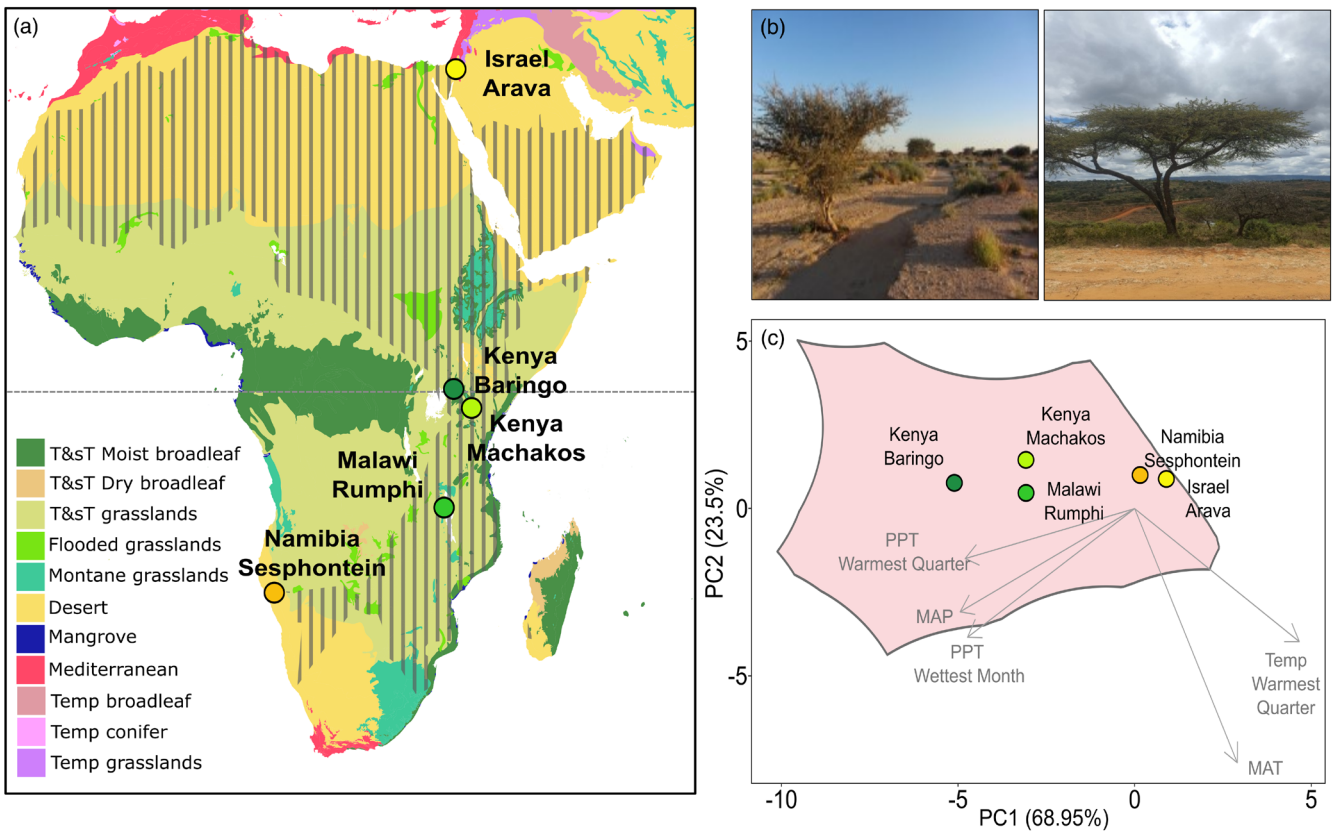

FIGURE 1 (a) Map of *A. tortilis* distribution (striped grey area), with the location of sampling sites. Biomes (WWF definitions) are marked by different colours. Equator is marked with a horizontal dotted line (b) Examples of *A. tortilis* trees used for seed collections in the Arava (Israel) and Machakos (Kenya) (left and right, respectively). (c) Biplot of the first two principal components from a PCA analysis of climatic variables of the species distribution. The polygon represents the climatic niche of the species, while the arrows represent the vectors of 10 climatic variables. The circles represent the populations studied.

the distribution correspond to divergence in trait expression or trait plasticity, consistent with divergent evolutionary strategies? (iii) Do similar environmental conditions at opposing range edges drive convergent evolution in traits and trait plasticity, despite differences in geographical and environmental contexts? Together, addressing these questions can allow us to disentangle the evolutionary mechanisms driving widespread species distributions, and the successful expansion of *A. tortilis* across contrasting environments and geographic scales.

2 | METHODS

2.1 | Experimental design

We sampled five populations of *A. tortilis* from both sides of the equator (Figure 1): Arava region in Israel (IA), Machakos region in Kenya (KM), Baringo region in Kenya (KB), Rumphi region in Malawi (RM) and Sesfontein region in Namibia (NS) (Table S1). We selected these populations to represent two contrasting biome groups, following WWF terrestrial biome classes (https://www.worldwildlife.org/): IA and NS are positioned in the 'Desert and Xeric Shurbland' biome, whereas KM, MR and KB are positioned within 'Tropical & Subtropical Grasslands/Savannas'. Notably, KB lies at the boundary with 'Tropical & Subtropical Moist Broadleaf Forests' (Figure 1a). To emphasize the distinction between the environments of these populations, we henceforth refer to these two bioclimatic groups as 'tropical-savanna' (KB, KM and MR) and 'desert' (IA and NS) populations.

Tropical-savanna and desert environments are diverse, and climatic conditions can vary significantly within them. We, therefore, examined the variability of climatic conditions among our five sites, and within and between the two groups. For this, we used climate data from WorldClim (Hijmans et al., 2005), and focused on identifying the climatic variables that most strongly characterize the differences between the two bioclimatic groups (Figures S1 and S2), subsequently used as the variables for the PCA representing the climatic niche of the species distribution (Figure 1c). We observed that variance in temperature (mainly mean annual temperature and temperature of the warmest quarter) and in precipitation (mainly annual precipitation and precipitation of the wettest quarter and month) best characterize the differences between the groups (Figure S1). However, variance within the bioclimatic groups was also observed, with higher precipitation of KB compared with KM and MR in the driest and coldest months, reflecting the proximity of KB to moist tropical forests (Figure 1a). Variability between the desert populations was also observed, particularly in the annual range of temperatures (Figure S1).

2.2 | Seed material

In each of the populations, seeds were collected from 5 to 10 trees (Table S3) that were located more than 20 meters apart from each other. This sampling distance was chosen to reduce the genetic relatedness between sampled trees, and we hereafter consider seeds from the same tree as half-sibs and seeds from different trees as unrelated.

The experimental design included two common-gardens with contrasting climates, where the conditions were set to emulate those of each of the natural environments: a hot and wet environment (henceforth *tropic-like*) in the controlled greenhouse, and a dry environment (henceforth *desert-like*) in a nethouse, in Rehovot, Israel (Table S2, Figures S3 and S4). The common gardens were simultaneously established in November 2022, and were maintained until August 2023 (10 months in total). Seedlings for both common gardens were grown in a nursery for 3 weeks for acclimation. Both common gardens had a full-block random design, with five blocks per common garden, where one repeat from each mother tree of all populations were represented in each block, allowing all half-sib trees to be present in each of the five blocks. This design enabled the nesting of individual trees, used as biological replicates, within each mother tree. Consequently, each mother tree represents the genetic variation in plasticity within its respective population, thereby facilitating the examination of genotype-by-environment ($G \times E$) interactions. In this setup, half-sib is the closest level to genetic replicate achievable, and therefore they are our best choice as proxy for genotypic values (Jose et al., 2025). We sampled five half-sib tree repeats per mother tree and 5–10 mother trees in each population, with a total of 200 trees in each common garden (Table S3).

2.3 | Trait measurements

We carried out a comprehensive analysis of multiple traits, encompassing leaf characteristics, morphology, physiology and growth (Table 1, Figure S5). All measurements were conducted on all individuals at the time of harvest (360 individuals, August 2023), with the exception of stem water potential, which was measured for two to four individuals per population in each treatment ($n = 28$). For further details, see Appendix Methods S1. Leaf area (LA), leaf dry mass (LDM) and specific LA were measured half-way through the experiment (March 2023) as well as at harvest (August 2023).

2.4 | Quantifying trait variability and plasticity

We assessed phenotypic differentiation at two levels: (1) each trait individually, and (2) composite phenotypes computed using a principal component analysis (PCA) of all the measured traits and their plasticity. Using individual trait and composite (PCA) analyses allowed us to capture both the unique variation in each trait and the broader patterns of phenotypic structure across multiple traits. The analysis was conducted separately for trait values and for plasticity.

TABLE 1 Summary of traits measured in the experiment. Further methodological details are provided in the Appendix.

Trait	Description	Calculation	Category
Leaf area (LA)	Area of a single leaf	Measured in cm	Leaf
Leaf dry mass (LDM)	Mass of dried leaf tissue	Oven-dried at 60°C, weighed in mg	Leaf
Specific leaf area (SLA)	Leaf area per unit dry mass	LA/LDM (cm/mg)	Leaf
Stomatal density (SD)	Number of stomata per area	Counted per mm	Leaf
$\delta^{13}C$	Carbon isotope ratio	Stable isotope analysis (‰)	Physiology
Photosynthetic efficiency (Fv/Fm)	Maximum quantum yield of PSII	LI-600 fluorometer, pre-dawn	Physiology
Stem water potential	Plant water status	Measured midday on terminal branches	Physiology
Longest shoot length	Vegetative growth	Measured length from base to tip (cm)	Growth
Basal diameter	Stem growth	Measured at base of stem (cm)	Growth
Above-ground biomass	Biomass allocation	Dry mass of shoots + leaves (g)	Growth
Below-ground biomass	Biomass allocation	Dry mass of roots (g)	Growth
Total biomass	Overall productivity	Above-ground + below-ground biomass (g)	Growth
Biomass ratio	Allocation balance	Below-ground/above-ground biomass	Morphology
Number of primary branches	Shoot architecture	Count of first-order branches	Morphology
Branches-to-stem ratio	Allocation balance	Length branches (cm)/length shoots (cm)	Morphology
Number of primary with secondary branches	Shoot architecture	Count of first-order and second-order branches	Morphology

2.4.1 | Trait-level analysis

Within gardens (trait values)

In order to assess the phenotypic differences between populations in each garden, we fitted a linear model for every trait in each garden.

$$y_{ijk} = \mu + p_j + g_{jk} + b + \epsilon_{ijk}, \quad (1)$$

where y_{ijk} is the trait value for individual i from mother tree k and population j, μ is the overall mean trait value, p_j represents the among-population random effect, g_{jk} is the random effect of the genotype (mother trees) nested within population, and b accounts for replicate (block) effects within each common garden. Residuals were assumed to follow a normal distribution, $\epsilon \sim \mathcal{N}(0, \sigma_\epsilon^2)$.

Quantitative genetic differentiation (Q_{ST}) for each trait was then calculated using the ratios between the within and between-population variances:

$$Q_{st} = \frac{\sigma_P^2}{\sigma_P^2 + 2\sigma_G^2}, \quad (2)$$

where σ_P^2 is the between-population genetic variance and σ_G^2 is the within-population genetic variance component (variance from mother trees) (McKay & Latta, 2002; Spitze, 1993). Confidence intervals (95%) were obtained by carrying out bootstrapping on the populations with 1000 replicates (resampling at the highest level, in our case populations, following best practices; O'Hara & Merilä, 2005).

Between gardens (trait plasticities)

Plasticity for each individual trait was estimated by calculating the coefficient of regression from a mixed model reaction norm between the two gardens, using the following equation:

$$y_{ijk} = \beta_0 + \beta_1 e_{ijk} + \left(p_j + p'_j e_{ijk}\right) + \left(g_{jk} + g'_{jk} e_{ijk}\right) + b + \epsilon, \quad (3)$$

where e_{ijk} is the dummy-coded fixed effects design variable indicating the environment (0 = desert-like, 1 = tropic-like) so that β_1 represents the plasticity response across the two environments, p_j and g_{jk} are the population and mother random effects, and b accounts for replicate and ϵ residuals as in Equation (1). We fitted the

random-coefficients with both population- and mother-specific intercepts and slopes (p' and g', respectively), as this allows the inclusion of genetic variation existing for plasticity (Jose et al., 2025). The mother-specific slope ($\beta_1 + p'_j e + g'_{jk} e$) is used as the genotype level plasticity. The random-slope variance components for among- and within-population variance (σ^2_P and σ^2_G, respectively) from Equation (3) were fitted into the model Equation (2) to obtain Q_{ST} for plasticity.

For LA, LDM and specific leaf area (SLA), we modelled temporal plasticity, that is, along a time axis (mid-experiment vs. harvest), by replacing the environment variable e_{ijk} with a dummy-coded time variable t_{ijk} to estimate time-based plasticity, denoted as ΔLA, ΔLDM and ΔSLA. Measuring the change in leaf functional traits throughout time can indicate plasticity in resource-strategy between a resource-acquisition and growth strategy and a resource-conservation and slower growth (Stotz et al., 2021; Wright & Meagher, 2003).

In order to obtain individual coefficients of plasticity per population to allow a regression model against climate of origin (Figure 5), we modified (Equation 3) by incorporating a fixed environment×population interaction (and maintaining a random mother-specific slopes, nested within population). The simple slope of environment within each population was taken as that population's coefficients (β) (with SE). We then regressed these coefficients on climate of origin using inverse-variance weights ($\frac{1}{SE^2}$).

2.4.2 | PCA-level analysis

Composite (PCA) traits were created, in addition to single-trait analyses, to summarize correlated traits onto orthogonal axes and to test divergence along multivariate phenotypes. We report PC loadings (Figure S6) which can be compared with single trait-level Q_{ST} (Figure 3) so that single-trait patterns remain explicit.

Composite trait PCA (within-gardens)

Within each garden we performed a PCA on centred and standardized mean trait values per individual. For each retained PC axis (selected using the knee break criterion), the PC score from mother tree k and population j (PC_{jk}), replaced y_{ijk} in model 1. The variance components from these PC models were converted to Q_{ST} values, and a composite value was generated by taking the variance-weighted average of the Q_{ST}, following the multi-trait F_{st} approach from (Duforet-Frebourg et al., 2016).

Composite plasticity PCA (between gardens)

For every trait, we first quantified plasticity at the mother-level in each population, by refitting the reaction-norm model given in Equation (3) separately for each mother within each population, so that random-effects term for population (p_j) is omitted. The slopes $\hat{\beta}_k$ obtained for each mother in each population were centred, scaled and subjected to PCA. The retained plasticity PC axes were then treated like traits and Q_{ST} was subsequently calculated as described above (replacement of y_{ijk} in model Equation (1) with PC_{jk}, and variance-weighted averaging across PCs).

2.4.3 | Pairwise association between genetic differentiation and climate

To examine whether quantitative genetic divergence is associated with climatic divergence among populations, we compared pairwise ΔQ_{ST} distances with both pairwise geographic and pairwise climatic distances (Figure 4). Pairwise contrast allows us to ask whether populations that differ most in climate also differ most in traits or in plasticity, by preserving the full gradient of phenotypic and environmental separation (10 population pairs from five populations) instead of collapsing the data in to a single, study-wide Q_{ST} value.

We formed 5×5 matrices of pairwise absolute differences between population-level (composite) Q_{ST} values (ΔQ_{ST}). Climatic distances were Euclidean distances on z-scored WorldClim BIO variables (30-arc-second resolution; (Hijmans et al., 2005)) and on climate PC axes (obtained from Figure 1c). Geographic distance was great-circle distance between source coordinates. Because pairs are non-independent, we related ΔQ_{ST} to climate and geography using (i) simple and partial Mantel tests (Figures S13 and S14) and (ii) multiple regression on distance matrices (MMRR) (Legendre et al., 1994) to obtain partial effects.

Although we did not measure genetic variance directly (i.e. through F_{ST}), analyses of clines in both trait means and trait plasticity provide a complimentary approach for detecting signals of adaptive evolution across species' climatic ranges (Akman et al., 2021; Cooper et al., 2022; Lázaro-Nogal et al., 2015). The simultaneous analysis of both climate and geography allows to distinguish patterns consistent with geographic or climatic processes (climate controlling geography and vice versa), to allow differentiating between effects of isolation-by-distance (IBD) and isolation-by-environment (IBE) (Wang, 2013). A positive climate effect (while holding geographic distance constant) indicates IBE, whereas the opposite indicates IBD (Wang, 2013). This distinction is crucial for interpreting whether divergence arises primarily from spatial separation and drift (IBD) or from selective filters imposed by the environment (IBE). However, genomic data (e.g. F_{ST}) would be required to confirm between genetic and phenotypic divergence or convergence.

With $n = 5$ populations (10 pairs), p-values are calculated given the finate unique label permutations (120). Mantel test was implemented in the *vegan* R package (v 2.6–4), and MMRR was implemented in the ecodist R package (v 2.1–3).

2.5 | Selection gradients of traits

In order to estimate selection gradients, we first calculated the BLUP (best linear unbiased predictors) breeding values for all

non-growth traits, based on the model described in Equation (1) (Lynch & Walsh, 1998). Phenotypic selection gradients were estimated as the coefficients of regression (β) from linear models, where the BLUP values were regressed against relative growth phenotypes (Table 1), serving as proxies for fitness. The relative growth phenotype was calculated as the log-transformed ratio of absolute fitness at each site to the mean fitness across all sites (Wright & Meagher, 2003). Breeding values were scaled to allow comparison between measurements (Lande & Arnold, 1983). Our rationale for including several growth measurements as proxies was to capture different axes of resource investment that may be relevant under contrasting environmental conditions. For example, variation in both above-ground and below-ground biomass components have been shown to be directly associated with seedling survival (Klein et al., 2011) and influence performance and survival in arid environments, specifically in *A. tortilis* (Uni et al., 2023). Nevertheless, growth-related traits may reflect multiple underlying processes, such as resource allocation and environmental stress responses. Therefore caution is warranted, as they do not always directly correlate with fitness (Laughlin et al., 2020).

Model selection and model averaging were conducted to include the strongest predictor variables in the final selection model, using an information-theoretic approach where models with AIC values within 2 units of the top model were averaged. Leaf dry mass was excluded due to its high covariance with LA, which caused multicollinearity issues. To ensure robustness, we also tested models using LA instead of LDM to evaluate the consistency of the results.

3 | RESULTS

3.1 | Trait and trait-plasticity differentiation across populations

By comparing trait variation across the two common gardens (Figure 2a), we found significant differences in phenotypic values among populations within each environment (PERMANOVA analyses: $R^2 = 0.371, F = 24.48, p < 0.001$ in the desert-like environment; $R^2 = 0.178, F = 10.18, p < 0.001$ in the tropic-like environment). Furthermore, the magnitude of variation differed markedly between environments. Specifically, we observed significantly greater within-population trait variation in the tropic-like garden than in the desert-like garden (Levene's test; $p < 0.01$ for both PC axes), and stronger among-population differentiation in the desert-like than in the tropic-like garden ($Q_{ST} = 0.50$, 95% CI 0.42–0.57 vs. $Q_{ST} = 0.25$, 95% CI 0.19–0.32, for desert and tropic-like environments, respectively), a pattern indicative of increased selective pressure in the desert-like environment. This was also reflected in clearer clustering by mother trees under desert-like conditions (Figure S12).

Overall plasticity differed among populations when considering the change in response between environments throughout all traits (Figure 2b). This pattern contrasts with trait expression, where some populations clustered closely (Figure 2a), but were far apart when accounting for plasticity space. For example, the three tropical-savanna populations expressed similar trait values (Figure 2a), yet showed distinct plasticity responses (Figure 2b). At the trait level, plastic responses were generally similar across populations, with

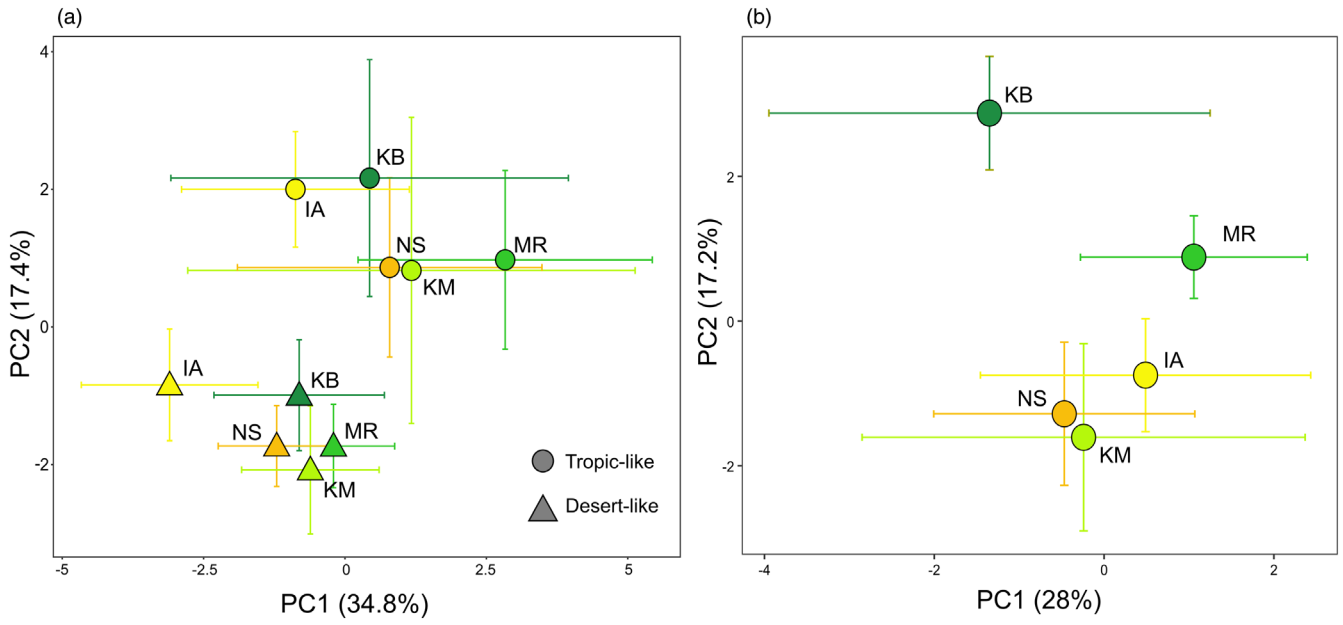

FIGURE 2 Principal component analysis of trait values for five *A. tortilis* populations (a) PC values for trait means in the tropic-like and desert-like gardens, across all individuals in each garden. (b) PC values for trait plasticity, obtained from the reaction-norm slopes between the individuals in the tropic-like and desert-like common gardens.

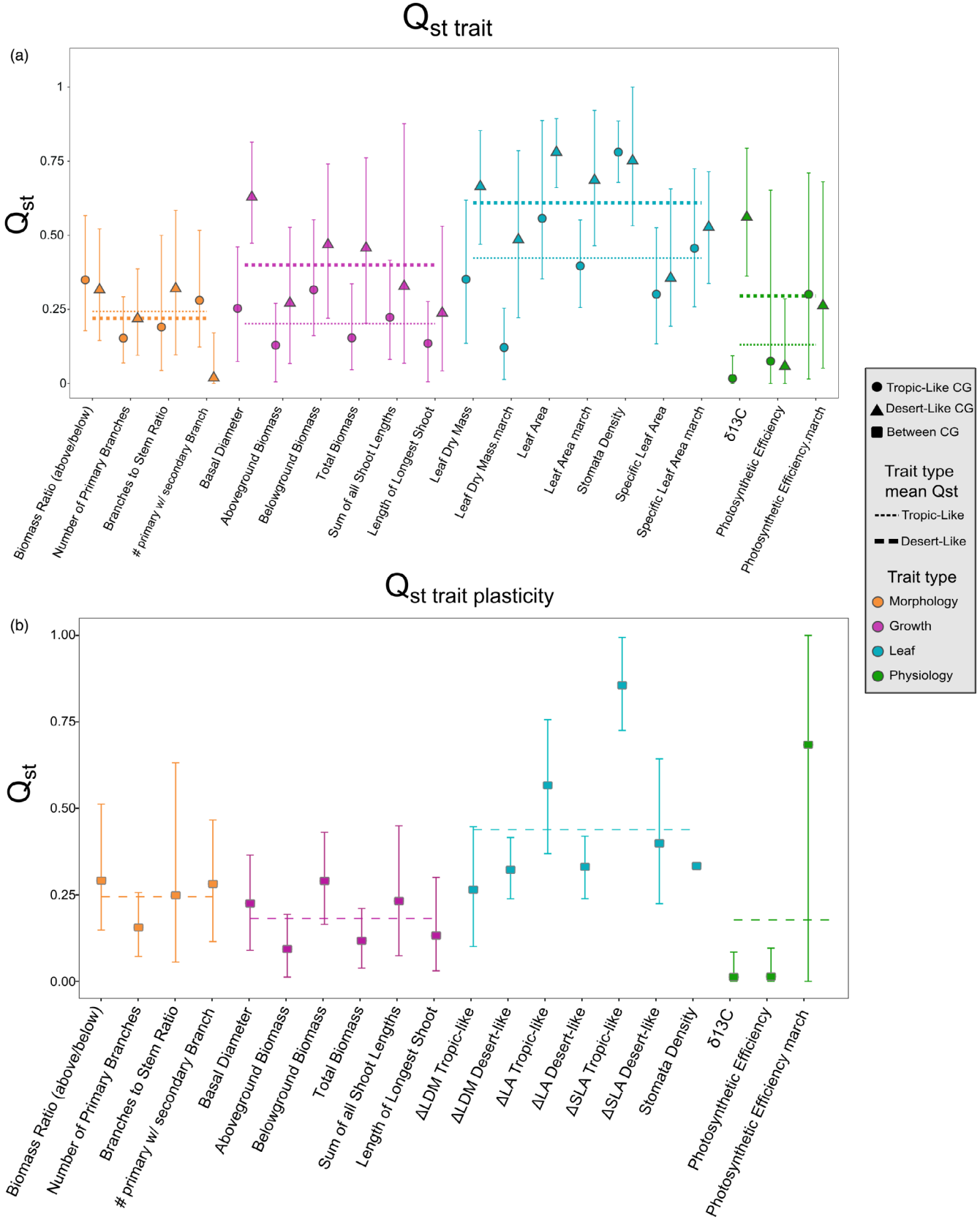

FIGURE 3 Trait and trait plasticity Q_{ST} distributions (variance among five *A. tortilis* populations) for each trait. Q_{ST} means and 95% confidence intervals for each phenotypic traits (a) measured in each of the conditions (tropic-like and desert-like) and traits plasticity (b) measured in each of the conditions (tropic-like and desert-like) across time and between conditions half-way into the experiment and at harvest. Traits and trait plasticity were measured at harvest (August), except for cases when it was measured half-way through the experiment (March), which in that case, is noted in the label. Temporal plasticity—a change in trait measure between March and August both the tropic-like and desert-like conditions—are labelled with a Δ sign. Dotted lines are group mean Q_{ST}, given their corresponding trait type groups.

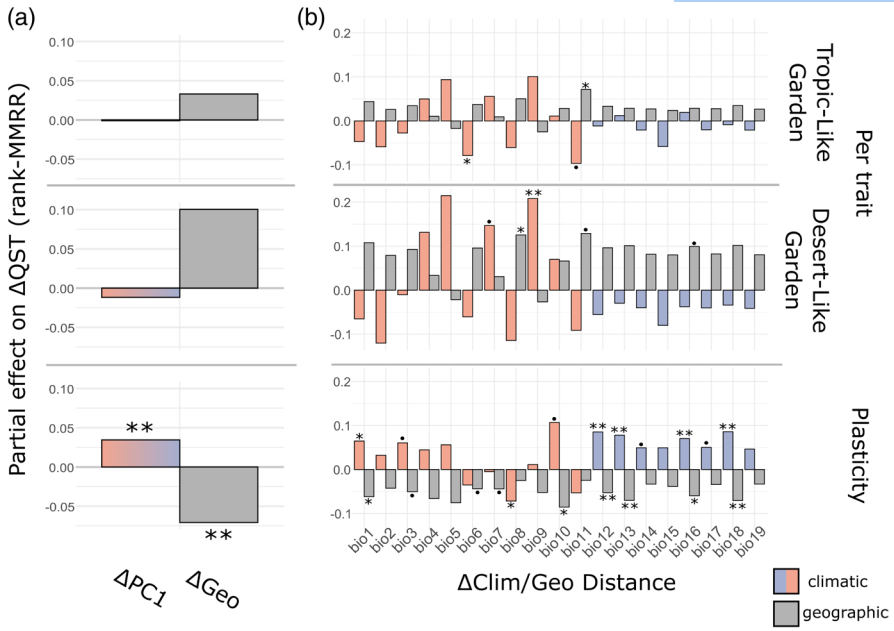

FIGURE 4 Partial effects of climatic and geographic distances on pairwise genetic differentiation among populations (ΔQ_{ST}) for trait means and plasticity (a, b) Bars are partial slopes from rank-MMRR (Spearman-type multiple regression on distance matrices) relating pairwise ΔQ_{ST} among populations ($n = 5 \rightarrow 10$ pairs) to two predictors included simultaneously: Pairwise climate distance (coloured) and pairwise geographic distance (grey). ΔQ_{ST} are obtained from the trait mean and trait-plasticity PC values (Figure 2). Positive slopes indicate that greater distances (climatic or geographic) are associated with higher ΔQ_{ST} (i.e. greater distance → stronger genetic divergence); negative slopes indicate the opposite (greater distance → stronger genetic convergence). (a) MMRR parial slopes for ΔPC1 (climate PCA axis 1; Figure 1c) and ΔGeo (geographic distance). (b) Partial slopes for individual WorldClim BIO variable. Shaded red and blue the 11 temperature and 8 precipitation variables, respectively. Asterisks denote permutation *p*-values (** < 0.05, * < 0.10, • < 0.15, 10,000 permutations).

significant plasticity occurring in the same traits and directions (Figure S9). Exceptions included temporal plasticity in LDM (observed only in KB in the tropic-like environment) and plasticity in total biomass and shoot length (observed only in MR). Most populations did not show significantly higher plasticity across trait groups (Figure S10), aside from differences between KM, KB and MR in leaf and morphological traits.

Within the tropic-like common garden and plasticity PCAs, among-population separation is primarily aligned with PC2 (Figure 2, Figure S6), while in the desert-like common garden, among-population differences are aligned with PC1, reflecting that the variance in the desert-like environment is largely explained by among-population differentiation, whereas in the tropic-like environment and trait plasticity, within-population variance is more prominent. This result was consistent with trait-specific Q_{ST}, whereby the traits with largest PC2 loadings for plasticity and for the tropic-like garden (e.g. SLA, LA and SD in Figure S6), also exhibited the highest Q_{ST} values (Figure 3). Likewise, traits with largest PC1 loadings in the desert-like garden exhibit the highest Q_{ST} values (Figure 3).

Because growth-related traits may primarily reflect environment-dependent performance rather than adaptive differences in broader trait responses, we repeated the analysis excluding these traits to test the robustness of the observed patterns. The results were qualitatively and quantitatively unchanged (Figure S7), indicating that the observed patterns are not driven by growth-related traits.

Lower differentiation was also observed at the individual level in the tropic-like common garden than in the desert-like common garden, with generally lower mean Q_{ST} values (Figure 3a). Mean Q_{ST} was higher in the desert-like garden for all trait groups except for morphology (Figure 3a). Several leaf and growth traits showed strong contrasts in among-population differentiation between environments, including basal diameter, which had a 2.5-fold higher Q_{ST} in the desert-like garden, and total biomass, which had a threefold higher Q_{ST} in the desert-like garden. Likewise, more traits showed elevated among-population differentiation in the desert-like garden, whereas the tropic-like garden tended to show relatively greater mother-tree differentiation (within-population), including for longest shoot length, total shoot sum, LDM, $\delta^{13}C$ and total biomass (Table S5, Figure S6).

Morphological traits showed low Q_{ST} values in both environments as well as in their plasticity (Figure 3). In leaf traits, on the contrary, we observed high Q_{ST} values in both the trait and trait plasticity (Figure 3), suggesting that these traits are functionally important in *A. tortilis* across its distribution.

3.2 | Clinal variation in trait and trait plasticity

To assess whether population differentiation is explained by climatic or geographic separation, we related pairwise Q_{ST} values (for trait means and plasticity) with geographic and climatic

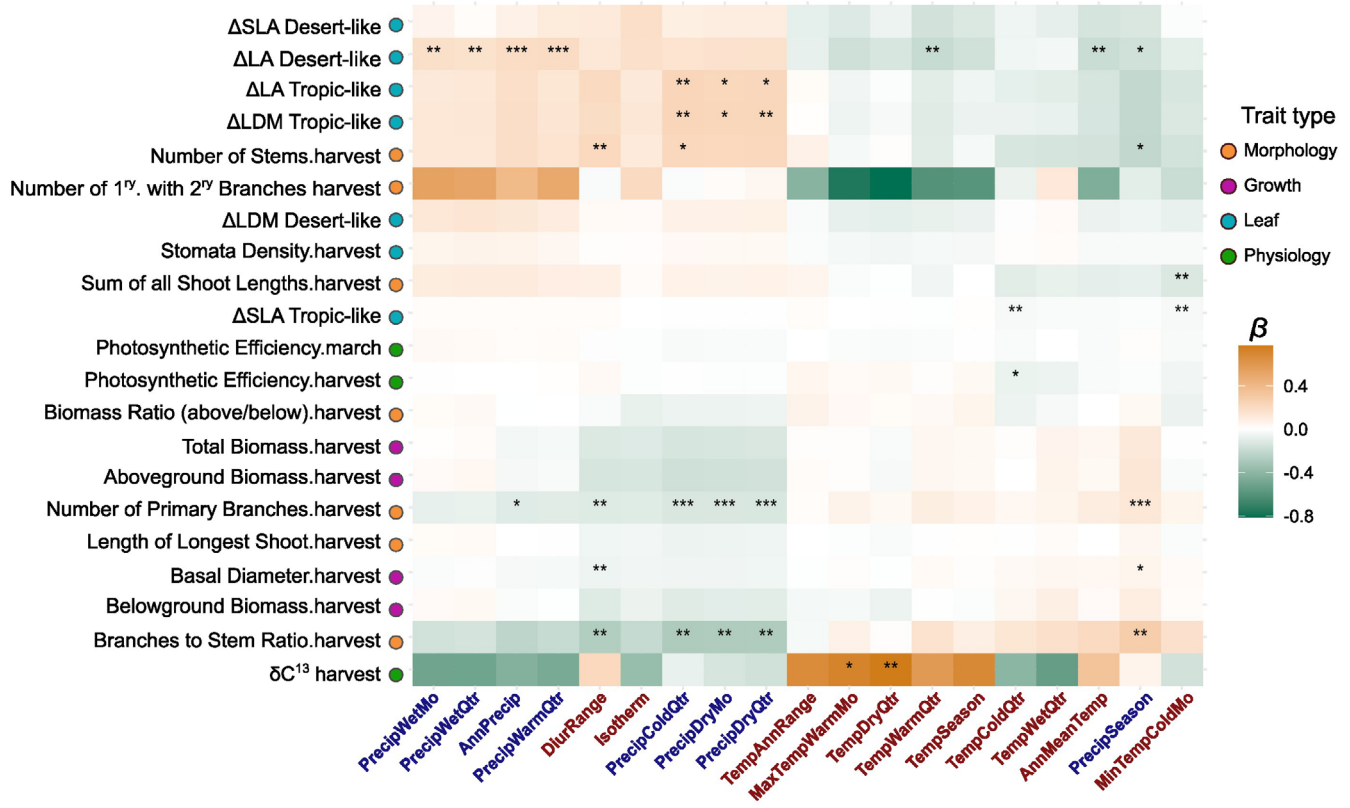

FIGURE 5 Plasticity clines for *A. tortilis populations*. Heatmap of standardized regression coefficients (β) for the prediction of plasticity traits through climatic variables. Asterisks indicate a significant association between trait plasticity and the climate variable. The heatmap rows and columns are clustered by the regression coefficients (β-values) Traits are colour coded depending on the trait type (as in Figure 3). The bioclimatic variables are colour coded red or blue for temperature or precipitation variables, respectively.

distance using rank-MMRR (Figure 4). We also tested whether divergence along a tropical-savanna to desert environmental gradient explained divergence using PC1 from Figure 1c as the climatic predictor.

Our results indicate that the tropical-savanna to desert environmental gradient only explains plasticity divergence (Figure 4a). In addition, geographic distance had a significantly negative effect on differentiation, with low ΔQ_{ST} between distant desert pairs and high ΔQ_{ST} between proximal tropical-savanna pairs. This suggests convergence in plasticity between distant populations and divergent plasticity between proximal populations. This pattern remained unchanged when growth-related traits were excluded (Figure S8), indicating that the climatic and spatial signal in plasticity divergence was not driven by performance-related traits.

The analysis of the effect of individual climatic variables on trait means and trait plasticity showed that precipitation-related variables have a positive partial effect on ΔQ_{ST} of plasticity (Figure 4). This indicates that, after controlling for geography, greater precipitation differences correspond to greater plasticity divergence. Likewise, we observed two temperature variables that influence garden-specific trends: minimum temperature of the coldest month having a negative association with ΔQ_{ST} in the tropic-like garden, while mean temperature of the driest quarter had a positive association in the desert-like garden (Figure 4b). In addition, there was a stronger association to geographic distance in the desert-like common garden than in the tropic-like common garden (Figure 4a). These results were broadly consistent with the trends obtained from partial mantel test results (Figure S14).

To further interpret the convergence and divergence in plasticity observed across the climatic gradient (Figure 4), we examined whether plastic responses were associated with climatic conditions at the population origin. This was done by performing a regression analysis of plastic responses against multiple climate variables (Figure 5). Traits that experienced strong and significant plasticity clines in response to their climate-of-origin were influenced by temperature and precipitation variables, but in opposing directions, with isothermality and diurnal range aligning with precipitation, and precipitation seasonality aligning with temperature (Figure 5). For example, we observed higher plasticity in leaf traits and in the sum of all shoots' length in wetter and cooler sites. Likewise, various traits, such as the morphological traits 'number of primary branches' and 'branches-to-stem ratio' showed higher plasticity in warmer and drier regions. The covariance of plastic response with different climatic variables further reflects the convergence in plasticity response among environmentally similar but geographically distant populations.

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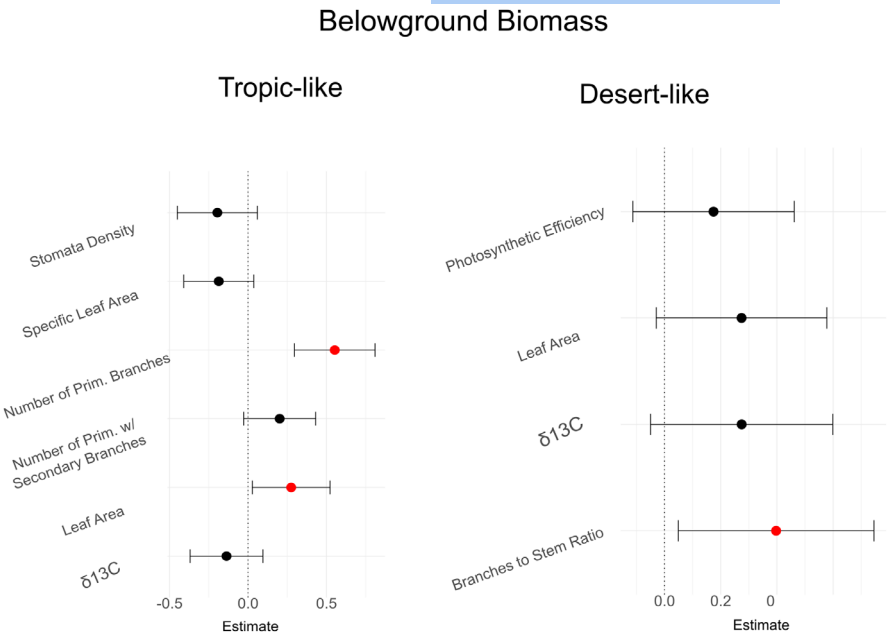

FIGURE 6 Selection gradients with below-ground biomass as fitness *proxy* across five *A. tortilis* populations. Forest plot of a model average from the highest predictors respect to fitness from a partial regression model (identified with a model selection). β values are shown for each predictor. Error bars represent 95% CI around the average effect. p-values < 0.05 are shown in red.

3.3 | Trait selection gradients

To further assess differences in selective pressures across environments, we quantified the strength and direction of natural selection acting on the measured traits throughout the range with a set of selection gradients, using growth traits as a proxy for fitness (Alía et al., 2024; Jiang et al., 2022). Significant positive and negative phenotypic selection gradients were observed in both the tropic-like and desert-like common gardens (Figure 6, Figures S15 and S16). However, the traits under selection differed markedly between environments with only LA and $\delta^{13}C$ appearing as predictors in both common gardens (Figure 6). In the tropic-like common garden, the direction of selection depended on the fitness proxy used: traits such as SLA and stomatal density were positively associated with above-ground biomass, while negatively associated with below-ground biomass (Figure S15). Surprisingly, a greater proportion of traits showed significant selection in the tropic-like environment, mainly leaf traits.

Although $\delta^{13}C$ was not significant in the final averaged models ($p = 0.46$), it was consistently included in models explaining below-ground biomass in both environments, indicating a potential role of water-use efficiency in root-related performance, albeit with contrasting effects across environments. Together, these results show that selective pressures differ markedly between the two environments, both in the traits under selection and in the direction of selection.

4 | DISCUSSION

Using a common-garden design in *A. tortilis*, a species spanning both sides of the equator, we identified contrasting patterns in divergence of traits values and trait plasticity. Trait divergence increased with geographic distance of the source populations, whereas plasticity divergence was better explained by the tropical-savanna to desert environmental gradient, particularly with precipitation. Across this climatic gradient, plasticity exhibited two distinct patterns: convergence among populations at opposing desert range edges, and high among-population variance within tropical-savanna populations, despite their geographic proximity, a pattern that may reflect population-level generalism (Araújo et al., 2011; Bolnick et al., 2003; Liang et al., 2020; Sjödin et al., 2018). In addition, we identified an environmentally driven modulation of phenotypic space across all populations, characterized by greater among-population divergence in the desert-like common garden, and higher within-population variance in the tropic-like environment. These findings suggest that repeated exposure to contrasting selective environments may have driven divergent evolutionary trajectories in this species, favouring canalization under harsher conditions and maintaining plasticity under more mesic tropical conditions.

4.1 | Selection on trait values versus trait plasticity

Our identification of phenotypic clines (Figure 4 and Figure 5) are indicative of adaptive evolution across *A. tortilis*' range. We show that plasticity divergence is more strongly explained by climate than by geography (Figure 4), supporting an IBE signal (i.e. the more different the environmental conditions, the more different are the levels of trait plasticity). The direct regressions of plasticity against climate variables (Figure 5) further highlight precipitation as the main driver in plasticity clines. In contrast, trait-mean divergence was shown to be better aligned with IBD (Figure 4) and weakly related to temperature variables. Together, these contrasting patterns indicate that plasticity and trait means are associated with different explanatory variables, supporting the view that plasticity

is not merely the by-product of a gene–environment interaction, but can itself act as a phenotype, subject to distinct evolutionary pressures, thus partly decoupled from its underlying trait (DeWitt & Scheiner, 2004; Schlichting, 2008).

Our findings indicate that, in *A. tortilis*, phenotypic traits are more strongly linked to temperature than to precipitation (Figure 4), consistent with previous findings showing that temperature is a key driver of plant phenotypes (Cooper et al., 2019; Moles et al., 2014) and a stronger predictor of species arrest at the geographic edges of their distributions (Lerner et al., 2023). The weak association observed in plants between trait values and precipitation is often attributed to broad climatic metrics that do not capture factors, such as soil and water availability (MacArthur, 1984; Vázquez & Stevens, 2004). However, the existence of plasticity clines associated with precipitation variables suggests that precipitation exerts selective pressure leading to among-population differentiation, an effect that could have been overlooked due to limited measurement of plasticity compared with trait values throughout studies (Vázquez & Stevens, 2004). Our results are, therefore, suggestive of a bias in detecting environment-trait associations rather than environment–plasticity associations due to the more complex experimental setup needed to measure plasticity compared with the measurement of trait values.

One of the main requirements for directional selection on plasticity is the presence of environmental heterogeneity, without which there is no fitness advantage for plasticity (Vinton et al., 2022). Although tropical and subtropical environments are often perceived as stable and benign, there can be high environmental heterogeneity, such as microclimate and edaphic contrasts. For example, spatial and temporal fluctuations in precipitation in tropical and subtropical climates can be much greater than those in temperate regions (MacArthur, 1984; Moles et al., 2014; Vázquez & Stevens, 2004). This can be seen, for example, between KB and KM despite their geographical proximity (Figure S1). This increased environmental heterogeneity in the tropics and subtropics, both spatially and temporally, can generate selective pressures that favour plastic responses, helping populations adapt to varying levels of water availability over time.

Higher plasticity has been shown to be associated with both mesic (Shemesh & Novoplansky, 2013) and xeric environments in plant species (Lázaro-Nogal et al., 2015). Our results point to the higher morphological plasticity in arid populations of *A. tortilis* (Figure 5) (Ward et al., 2012), which may be crucial for adapting to diverse micro-habitats obtained in desert regions, particularly during early life stages, such as seedling establishment and survival (Gibson, 2012; Stavi et al., 2015). Our results highlight strong differentiation in both trait means and plasticity of leaf traits, including SLA (Figure 3). While we did not compare these values directly to neutral genetic differentiation (F_{ST}), the trait-specific nature of the Q_{ST} patterns—with other traits (and trait groups) showing substantially lower values—suggests that selection, rather than drift alone, contributes to the observed among-population differentiation (Whitlock, 2008). In addition, a significant co-variation of leaf-trait plasticity with climate-of-source sites (Figure 5) imply an environment-specific component to divergence. While spatial variation in SLA is often attributed to plasticity (Sims & Pearcy, 1992), the high among-population differentiation observed (Figure 3) is in accordance with previous studies (Cornwell & Ackerly, 2009; Scheepens et al., 2010), indicating that genetic diversity, in addition to plasticity, shape leaf traits across environments.

4.2 | Ecological strategy contrast between tropical-savanna and desert regions

We observed substantial among-population variance in plasticity among tropical-savanna populations despite their close geographical proximity (Figure 1a), in contrast to the convergence in plasticity observed among the distant desert populations (Figure 2b and Figure 4a). This pattern implies greater genotypic variation in the tropical-savanna regions, consistent with population-level generalism (Bolnick et al., 2003). The persistence of these patterns after excluding growth-related traits further supports the interpretation of population-level generalism, indicating that our results are not driven by plasticity in performance traits, which may otherwise reflect ecological specialization (i.e. the outcome of plasticity rather than the mechanism Sultan, 2000). Thus, even in the absence of large shifts in mean plasticity at the individual level, a broadening of niche breadth at the regional scale can stabilize performance of the species across conditions (Araújo et al., 2011; Liang et al., 2020; Sjödin et al., 2018).

Second, we find a common-garden contrast in phenotypic expression, whereby the tropic-like garden had higher within-population variance and lower among-population differentiation, while the desert-like garden showed the opposite trend (Figure 2a, Figure S6, Table S5). We also observe a stronger IBD signature in the desert-like environment (Figure 4a). These results align with previous studies that identified a garden-dependent signal of selection (e.g. Akman et al., 2021; Cooper et al., 2022). Thus, the greater within-population variance within mesic heterogeneous conditions can increase the set of phenotypes on which selection can act upon, consistent with genetic accommodation and population-level generalism, (Chevin et al., 2013; Schlichting, 2008; West-Eberhard, 2003), adding understanding to the long-standing view of niche conservatism in tropical populations. In contrast, the reduced within-population phenotypic variation in the desert-like common garden can lead to strong directional selection and canalization over time under harsh conditions (Hoffmann & Hercus, 2000), driving the evolution of locally adapted specialists, a phenomenon previously reported (Santos-Del-Blanco et al., 2013; Uni et al., 2023; Voltas et al., 2018).

This highlights the role of plasticity, within-population variance and selective pressures in shaping adaptation strategies. Our results compare adaptation mechanisms between opposing environmental climates, but understanding the details of the evolutionary trajectories in different regions would require additional genetic analysis and finer spatial samplings.

4.3 | Resource acquisition trade-off between desert and tropical-savanna populations

The differential selection of traits between the desert-like and tropic-like common gardens (Figure 6) suggest a mechanistic trade-off between traits commonly associated with resource acquisition in the tropic-like environment and resource conservation in the desert-like environment, reflecting the contrasting environmental pressures in tropical-savanna and desert-like ecosystems. Resource conservation, often associated with reduced SLA (Stotz et al., 2021), is generally associated with greater stress tolerance due to thicker, denser leaves that reduce water loss (McKay et al., 2003). However, variation in SLA can arise from multiple processes, including abiotic stress, structural adjustments and allocation trade-offs, and should therefore be interpreted cautiously (Lázaro-Nogal et al., 2015; Stotz et al., 2022). In contrast, resource acquisition strategies, often linked to higher SLA values, allow for rapid growth under high resource availability, albeit cost of reduced stress tolerance, with greater plasticity in traits like biomass allocation (González-M et al., 2021). In our study, we observe positive selection for SLA in the tropic-like common garden when considering above-ground traits (e.g. above-ground biomass and height), which could highlight the importance of above-ground traits in regards to a resource acquisition strategy (Figure S16), in contrast with negative selection in the desert-like common garden. While these patterns are consistent with shifts in plant functional strategies across environments, they do not, on their own, demonstrate a specific resource acquisition strategy. Together, these results suggest that different growth-related traits should be viewed as components of ecological strategy rather than strict proxies for fitness, since their selective value depends on environmental context.

In addition, differences in hydraulic safety traits (e.g. $\delta^{13}C$, stomatal density) between the two environments reflected contrasting water-use strategies (González-M et al., 2021; Voltas et al., 2018). Positive selection of $\delta^{13}C$ in the desert-like common indicates selection of drought-tolerant phenotypes (Duforet-Frebourg et al., 2016), while negative selection in the tropic-like garden suggests a preference for high growth under high water availability. Furthermore, the negative selection for stomatal density exclusively in the tropic-like common garden likely reflects adjustments in gas exchange regulation and coordination with water availability. This pattern is consistent with a shift towards more acquisitive growth strategies, although it is unlikely to reflect direct resource allocation trade-offs with stomatal development.

5 | CONCLUSION AND IMPLICATIONS

Our study on *A. tortilis* highlights the potential for contrasting environments to generate differences in evolutionary pressures between traits and trait plasticities. In view of our results, we suggest two main evolutionary patterns that emerge between tropical-savanna and desert populations: (i) a distinction in phenotypic variance between the distinct clusters, suggestive of a generalist–specialist trade-off, with tropical-savanna showing a stronger generalist pattern and desert populations a stronger specialist pattern and (ii) a resource allocation trade-off, where tropical-savanna populations follow a resource acquisition strategy, while desert populations appear to adopt a resource-conservation strategy. Although this study focuses on a single species, our results highlight key evolutionary mechanisms, such as local adaptation and trade-offs that operate at large biogeographical scales. The strength of our experimental setup lies in its ability to identify these mechanisms at the intraspecies level, given the widespread and mirror-image distribution of the species *A. tortilis* across its range.

Future climate changes are bound to affect all global ecoregions (Costello et al., 2022). Tropical and subtropical regions, in particular, are predicted to experience intensified droughts and rising temperatures (Rong, 2015), leading to an amplification of selective pressures, such as increased aridity and heat stress. These changes are likely to drive shifts in species towards drought-tolerant phenotypes. Our study suggests that subtropical populations of the species *A. tortilis* possess sufficient phenotypic variance to withstand and adapt to such changes; however, a shift towards drought-tolerant phenotypes may come at a cost. Specifically, we demonstrate that increased selective pressures could reduce the phenotypic variance, given a reduction in genetic variance of these populations, likely driving smaller population sizes. We suggest that a reduction in variance and population size could diminish the proposed adaptive radiation potential and source-sink dynamic between tropical and extra-tropical populations. Such dynamic disruption could compromise the species' ability to maintain its broad geographic range, despite its potential adaptive capacity to increased aridity through phenotypic or genetic changes. These findings highlight the complex trade-offs that species face in responding to climate change and underscore the importance of conserving genetic diversity within vulnerable populations.

AUTHOR CONTRIBUTIONS

David Lerner conceived the idea and designed the experiment, with guidance from Tamir Klein and Gili Greenbaum. Rebeca Gonzalez Rolfe performed the greenhouse experiment with the help and guidance of David Lerner. David Lerner analysed the data and wrote the manuscript. David Lerner, Gili Greenbaum and Tamir Klein contributed critically to the drafts. All authors revised and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70374.

DATA AVAILABILITY STATEMENT

The raw data and analysis codes that support the findings of this study are openly available in Zenodo: https://doi.org/10.5281/zenodo.20161046 (Lerner et al., 2026).

ORCID

David Lerner https://orcid.org/0000-0001-9325-9924
Tamir Klein https://orcid.org/0000-0002-3882-8845

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SUPPORTING INFORMATION

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

Figure S1. Site-level climate profiles for the five provenance origins across WorldClim BIO variable.

Figure S2. Pairwise climatic distance along PC1 between-population origins, grouped by pair type.

Figure S3. Temperature in the common-garden treatments.

Figure S4. Relative humidity in the common-garden treatments.

Figure S5. Plasticity parameters utilized for quantifying plasticity.

Figure S6. Principal component analysis with loadings of trait values for five A. tortilis populations.

Figure S7. Principal component analysis of trait values for five A. tortilis populations without accounting for growth-related traits.

Figure S8. Partial effects of climatic and geographic distances on pairwise genetic differentiation among populations (ΔQST) for trait means and plasticity.

Figure S9. Plasticity of all populations for each trait.

Figure S10. Average (absolute) plasticity for each population throughout the four different trait groups.

Figure S11. Heatmap of the pairwise Qst differences between populations.

Figure S12. Pairwise Qst differences between mother trees.

Figure S13. Mantel correlations between pairwise genetic differentiation and climatic distance.

Figure S14. Partial Mantel correlations between pairwise genetic differentiation and climatic distance when correcting for geographic distance.

Figure S15. Selection gradients from individual regression models between the traits measured at harvest relative to different growth traits as tree fitness proxies.

Figure S16. Forest plot of a model average from the highest predictors of growth trait fitness proxies from a partial regression model (identified with a model selection).

Table S1. Seed collection.

Table S2. Treatment conditions for the common gardens.

Table S3. Number of seeds used.

Table S4. Table of plasticity parameter transformations.

Table S5. Variance explained and *p*-values for different random effects.

Data S1. Appendix.

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