

Phenotypic Selection Favors Missing Trait Combinations in Coexisting Annual Plants

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ABSTRACT: Trade-offs among traits are important for maintaining biodiversity, but the role of natural selection in their construction is not often known. It is possible that trade-offs reflect fundamental constraints, negative correlational selection, or directional selection operating on costly, redundant traits. In a Sonoran Desert community of winter annual plants, we have identified a trade-off between relative growth rate and water-use efficiency among species, such that species with high relative growth rate have low water-use efficiency and vice versa. We measured selection on water-use efficiency, relative growth rate, and underlying traits within populations of four species at two study sites with different average climates. Phenotypic trait correlations within species did not match the among-species trade-off. In fact, for two species with high water-use efficiency, individuals with high relative growth rate also had high water-use efficiency. All populations experienced positive directional selection for water-use efficiency and relative growth rate. Selection tended to be stronger on water-use efficiency at the warmer and drier site, and selection on relative growth rate tended to be stronger at the cooler and wetter site. Our results indicate that directional natural selection favors a phenotype not observed among species in the community, suggesting that the among-species trade-off could be due to pervasive genetic constraints, perhaps acting in concert with processes of community assembly.

Keywords: trade-offs, phenotypic selection analysis, Sonoran Desert, winter annual plants, relative growth rate, water-use efficiency.

Introduction

In evolutionary and community ecology, trade-offs among traits that influence fitness, both within and among species, are considered important for the maintenance of biodiversity (Tilman 1990; Chesson 2000; Agrawal et al. 2010). Trade-offs occur when traits favored in one environment are not favored in another or when the benefit of one trait

comes at the cost of allocating resources to a different trait (Grime 1977; Tilman 1994; Bonsall and Mangel 2004; Kneitel and Chase 2004). Documented negative trait correlations suggesting trade-offs (e.g., fig. 1) include offspring size versus number, growth rate versus shade tolerance, herbivory resistance versus tolerance, vegetative growth versus flowering time, competitive versus colonization abilities, and aboveground versus belowground biomass (Gleeson and Tilman 1990; Turnbull et al. 1999; Gilbert et al. 2006; Jia et al. 2011; Molina-Montenegro et al. 2012). Within species, trade-offs are thought to maintain genetic diversity when selection varies through space or time, leading to the success of different phenotypes in different environments (Futuyma and Moreno 1988; Fox et al. 1997). It is often assumed that some trait combinations, such as the production of many large offspring (e.g., as represented by individual X in fig. 1A), would be favored by natural selection yet are unobserved due to allocation of limited resources, laws of physics, or genetic constraints (Antonovics and van Tienderen 1991; Arnold 1992; Agrawal et al. 2010). However, certain trait combinations may not be favored by natural selection (e.g., few, small offspring; represented by individual Y in fig. 1A), and it is possible that other missing trait combinations (e.g., individual Z in fig. 1A) are missing for the same reason.

Trade-offs within species (fig. 1A) may result in trade-offs among species (fig. 1B) through macroevolutionary time, if genetic correlations within ancestral species influence the distribution of traits among descendant species (Schluter 1996; Agrawal et al. 2010). In this case, an among-species trade-off mirrors within-species trade-offs (e.g., species A in fig. 1C) and the upper “empty corner” of trait space in figure 1 likely reflects some fundamental constraint preventing the formation of certain phenotypes. However, an among-species trade-off is not necessarily an indication of within-species trade-offs (e.g., species B and C in fig. 1C). Some trait combinations may be unobserved

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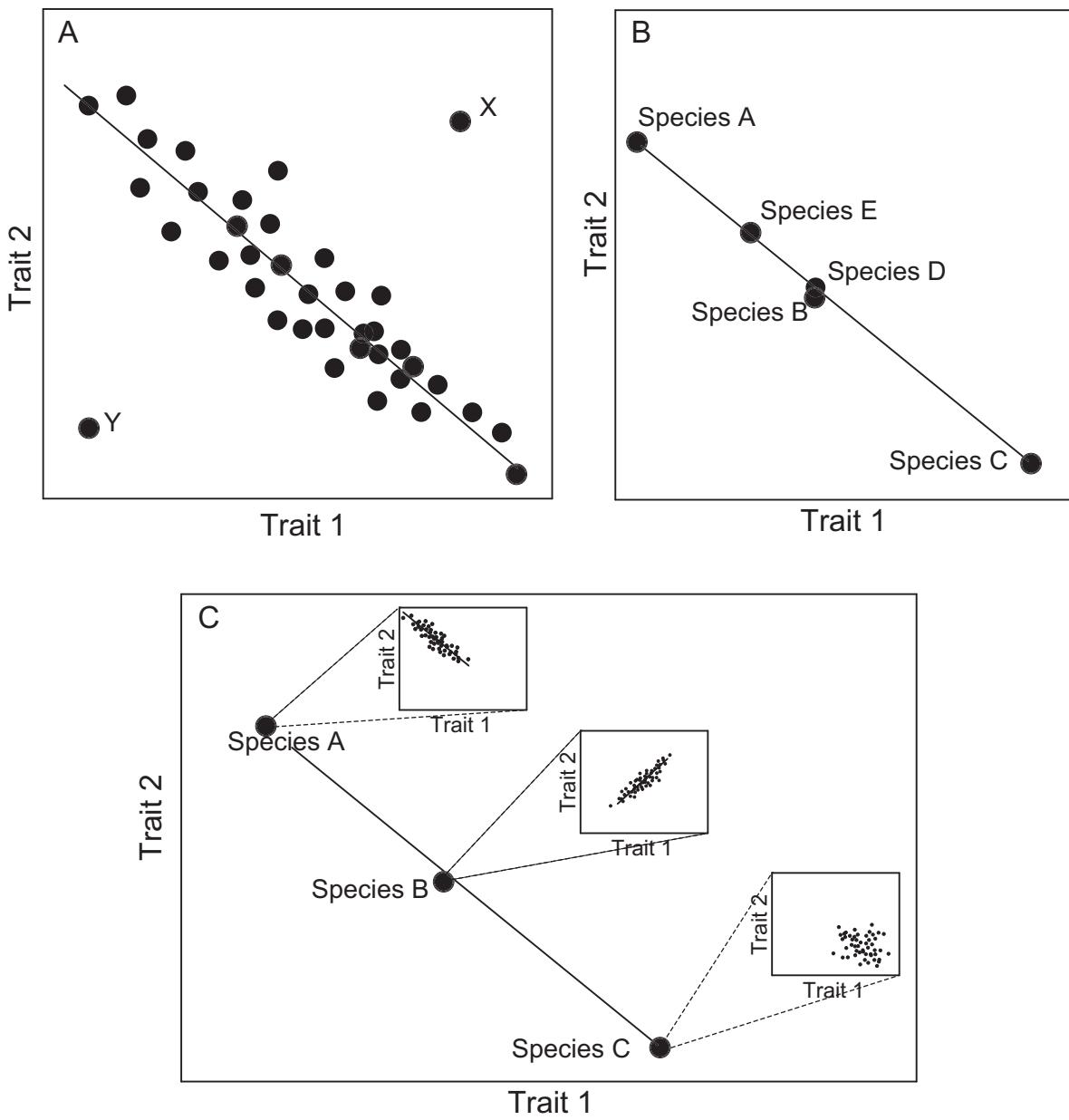


Figure 1: Conceptual diagram illustrating a trade-off between two traits. *A*, Filled circles represent individuals in the within-species trade-off. Most individuals exist along the trade-off axis, but X and Y occupy the “empty corners” of trait space. X has high values of both traits. This phenotype may be impossible to construct, but if it did exist, it would have high fitness. In contrast, Y represents an individual with low values of both traits, which is a trait combination unlikely to be found in nature because it would not be favored by selection. *B*, Filled circles represent species in a community. If a species with the same average trait value as species B dispersed to the community (species D), competition may act as a filter that would prevent establishment. Alternatively, selection via trait dispersion would result in successful establishment of individuals with trait values intermediate to species A and B (or to B and C), as in the example of species E. *C*, Insets depict individuals of each species. Although average trait values of the species exist along an among-species trade-off axis, that trade-off may or may not exist within species. Three possibilities for within-species trait combinations are illustrated, in no particular order. In species A, the among-species trade-off is reflected within species, perhaps suggesting some sort of fundamental constraint preventing the formation of alternative phenotypes. Within species B, individuals have trait combinations that are positively correlated. Within species C, there is no relationship between the two traits.

among species due to biogeographic contingencies or community-assembly processes. For example, species with certain trait combinations may be absent from the regional species pool (Gronroos and Heino 2012). During community assembly, competition could act as a filter that reduces the probability of persistence of a novel species into a community already occupied by a species with similar trait values (e.g., species D in fig. 1B; Shipley et al. 2006; Sonnier et al. 2012). Alternatively, competition could promote trait dispersion via selection to reduce niche overlap (e.g., species E in fig. 1B; Abrams 1990; Schlüter 2000). In the resulting community, species perform one ecological function well at the cost of performing another function, such that among-species trade-offs are thought to maintain local diversity through niche differentiation (Kneitel and Chase 2004). Invading species that have higher values of both traits associated with the trade-off may outcompete others and cause system instability (Molina-Montenegro et al. 2012). In this study, we measure natural selection on traits that trade off among species to determine whether phenotypic selection within species favors trait values in the empty corner of trait variation among species. If selection does favor empty corners and the trade-off exists within species, then the among-species trade-off may indeed represent within-species constraints.

One method of determining the strength and direction of selection on traits is phenotypic selection analysis, in which trait values of individuals are related to their fitness within natural populations (Arnold and Wade 1984; Dudley 1996; Arntz and Delph 2001; Donovan et al. 2009; Dudley et al. 2012). Since many traits are correlated, multiple regression and path analysis can be used to calculate the independent effect of each trait on fitness (Lande and Arnold 1983; Schemske and Horvitz 1988). One limitation of predicting potential evolutionary trajectories when studying selection in the field is that one cannot be certain whether measured trait values accurately reflect the genotype or to what extent traits reflect plastic responses to the environment (Arntz and Delph 2001; Caruso et al. 2006). Plant physiological traits, such as water-use efficiency and leaf nitrogen (N) content, vary with environment but are also heritable and respond to selection (Ackery et al. 2000; Geber and Griffen 2003; Culley et al. 2006; Agrawal et al. 2008). Although it would be ideal to measure the same genotype in multiple environments and directly measure plasticity (Via 1993; Agrawal et al. 2008), phenotypic selection studies conducted on the same species in more than one environment increase the range of observed trait variation and can enhance our understanding of the adaptive nature of traits and trade-offs (Dudley 1996; Donovan et al. 2009). For example, studies of selection on water-use efficiency have measured stronger selection in more arid environments, indicating that high

water-use efficiency may be adaptive in dry habitats (Dudley 1996; Saldana et al. 2007). Similarly, selection on early flowering is stronger at higher latitudes, suggesting that early flowering is an adaptation to cool habitats with short growing seasons (Munguía-Rosas et al. 2011). Previous studies of phenotypic selection on physiological traits have demonstrated relationships between trait values and fitness within single species, often across habitats (Saldana et al. 2007; Agrawal et al. 2008; Donovan et al. 2009). It is far less common to study selection across different environmental contexts on multiple species that broadly co-occur, despite the importance of such data for understanding community assembly and structure.

Our focus is on the strength of selection on functional traits within each of four species of co-occurring winter annual plants in two different environments of the Sonoran Desert. We focus on water-use efficiency, relative growth rate, and additional underlying traits contributing to these higher-order traits. Relative growth rate and water-use efficiency have previously been demonstrated to negatively covary among desert annual species, such that species with high relative growth rate have low water-use efficiency and vice versa (Angert et al. 2007; Huxman et al. 2008). Furthermore, the position of species along this putative trade-off axis has been linked to coexistence via the storage effect (Angert et al. 2009). Species with high relative growth rate are demographically variable and have greater-than-average fitness in years with large rain events, while species with high water-use efficiency are demographically buffered and have greater-than-average fitness in years with warm weather late in the growing season (Kimball et al. 2012). Here, at two sites characterized by different weather patterns, we examine patterns of trait variation and their relationship to fitness within species that occur at different points along the interspecific trade-off axis between relative growth rate and water-use efficiency. We address the following questions: (1) How do traits differ among species and between study sites with contrasting weather conditions? (2) Is there evidence of directional or stabilizing selection on traits relating to water-use efficiency and relative growth rate within species? (3) Does the strength of selection vary depending on the species and the site? (4) Does selection within species favor the high-relative-growth-rate/high-water-use-efficiency phenotype that is missing among species? We predict that species with higher relative growth rate will experience weaker selection on water-use efficiency and vice versa. We also predict that plants in drier environments will experience stronger selection on water-use efficiency than relative growth rate and that plants in wetter environments will experience stronger selection on relative growth rate. Our approach enables us to study selective pressures on the winter annual plant community, both within a site among species as well as between sites, which

is seldom done but is important for understanding links between functional biology, community ecology, and evolutionary ecology (Reich et al. 2003b).

Methods

Study System

Winter annual plants in the Sonoran Desert germinate with the arrival of winter rains, usually in December (Kimball et al. 2011). Continued growth and reproduction depend on the timing of subsequent rain events, but our long-term data set indicates that plants typically begin producing flowers in early February and that the winter growing season ends in April or May, when high temperatures cause annuals to complete reproduction and die (Kimball et al. 2011). We selected two sites in the Sonoran Desert with different climatic patterns. The cooler and wetter site is the University of Arizona's Desert Laboratory at Tumamoc Hill (32.17°N , 112.76°W ; hereafter referred to as site TH) in Tucson, Arizona. Site TH has a mixture of rocky and sandy soils, and the dominant perennial plants are creosote bush (*Larrea tridentata*) and bursage (*Ambrosia deltoidea*), with occasional saguaro (*Carnegiea gigantea*) and other cacti (*Opuntia* spp.). During the October–May growing season for winter annual plants, mean maximum temperature is 25°C , mean minimum temperature is 9.3°C , and mean total precipitation is 8.5 cm (averaged over the past 10 years using data from a nearby weather station). We selected Organ Pipe National Monument (32.17°N , 112.76°W ; hereafter referred to as site OP), south of Why, Arizona, as a warmer and drier contrast to site TH. Site OP is flat with sandy soils and scattered ocotillo (*Fouquieria splendens*) and saguaro (*C. gigantea*). Data from a nearby weather station in Ajo, Arizona (Coop ID 20080, 32.37°N , 112.87°W , elevation 537 m), indicate that the site has an average maximum winter temperature of 31°C (October through May, averaged over 10 years), average minimum temperature of 17°C , and mean total precipitation of ~ 7 cm. Although the mean total precipitation at site OP is not much lower than at site TH, the greater temperatures at site OP result in greater evaporative demand and potential for water stress than at site TH (Raddatz and Shaykewich 1998; Goyal 2004).

We selected four species occurring at different points along the continuum between relative growth rate and water-use efficiency that defines a major trade-off among species in our community (fig. 2). Moving in order from highest relative growth rate and lowest water-use efficiency

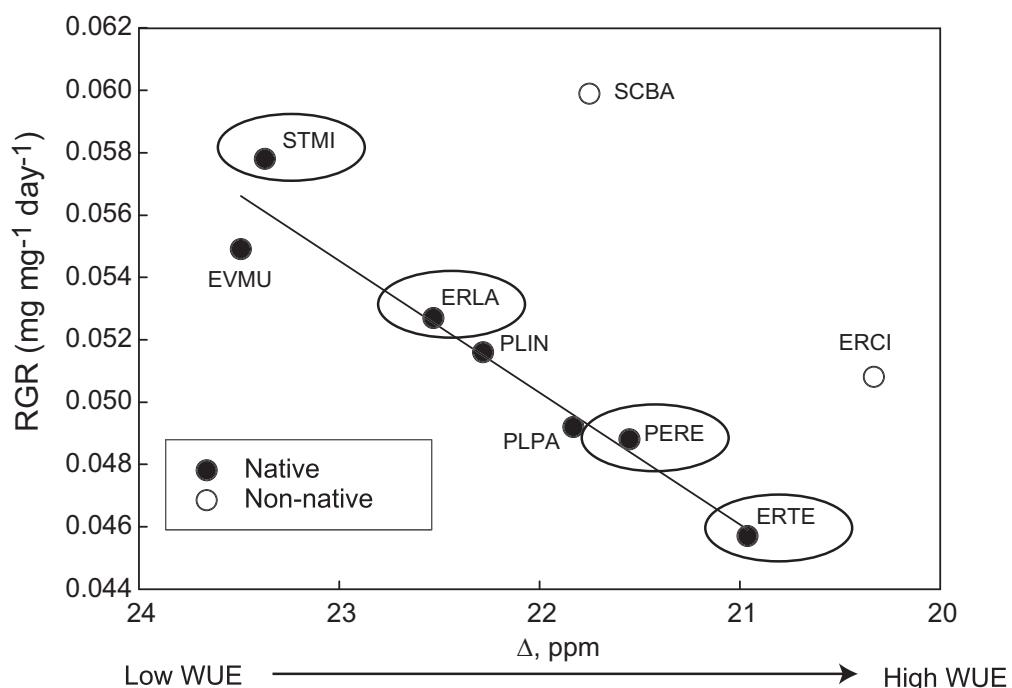


Figure 2: Trade-off between carbon isotope discrimination (Δ , which decreases with higher integrated water-use efficiency, WUE) and relative growth rate (RGR). Circles show the mean value for each species, with data from Angert et al. (2007). Species are abbreviated by their four-letter species codes: STMI = *Stylocline micropoides*, ERLA = *Eriophyllum lanosum*, PERE = *Pectocarya recurvata*, ERTE = *Erodium texanum*, EVMU = *Evax multicaulis*, PLIN = *Plantago insularis*, PLPA = *Plantago patagonica*, SCBA = *Schismus barbatus*, and ERCI = *Erodium cicutarium*. The four species included in this study are circled.

to lowest relative growth rate and highest water-use efficiency, the study species are *Stylocline micropoides* (Asteraceae), *Eriophyllum lanosum* (Asteraceae), *Pectocarya recurvata* (Boraginaceae), and *Erodium texanum* (Geraniaceae; fig. 2). The species *S. micropoides* and *E. lanosum* have previously been demonstrated to respond to large rain events with rapid leaf expansion, and *P. recurvata* and *E. texanum* are known to invest in light-harvesting processes that enable high photosynthetic rates at low temperatures (Angert et al. 2007, 2010; Huxman et al. 2008; Gremer et al. 2012). These particular species were selected both because they occupy different points along the trade-off axis and because they co-occurred in high local abundance at both sites during the year in which the study was conducted.

Traits Measured

We measured relative growth rate, integrated water-use efficiency, specific leaf area, root mass ratio, and leaf N content on more than 100 individuals from each of the four study species at each of the two study sites (see table A1 for sample sizes of each species-site combination; tables A1–A8 available online). Relative growth rate was measured nondestructively by counting leaves as the season progressed and estimating relative growth rate as the slope of log leaf number versus time with linear regression. Germination occurred after a mid-December storm in 2007. Individuals were marked following production of true leaves on January 29, 2008, at site OP and on January 30, 2008, at site TH and visited throughout the growing season to monitor development. Immediately prior to reproduction, on February 27, 2008, at site OP and on February 28, 2008, at site TH, leaves were counted again and plants were harvested and taken back to the lab, where they were divided into leaf, stem, root, and any reproductive material for separate dry-mass determinations. Leaves were scanned to determine leaf area and then dried, weighed, and sent to the University of Arizona's Environmental Isotope Laboratory for measures of percent N content and carbon (C) isotope ratios. Carbon isotope ratios were used to determine the degree of carbon isotope discrimination, Δ , which is a measure of integrated water-use efficiency over the lifetime of the leaf (Farquhar et al. 1989). Plants may reallocate nutrients and carbohydrates during reproduction (Edwards et al. 2012). Such reallocation of the time-integrated carbon signature represented by stable isotopes would make it difficult to use this variable for accurate measures of integrated water-use efficiency, so plants were harvested prior to reproduction. Specific leaf area was calculated as leaf area/dry mass of leaves. Root mass ratio was calculated as root dry mass/total dry mass.

At the end of the growing season, we returned to each

site to harvest a separate set of plants that had finished reproducing. We used these plants to determine whether biomass could be used as a proxy for seed production. Because biomass and seed production were highly linearly correlated (*E. lanosum*: $r = 0.973$, $P < .0001$, $N = 80$; *E. texanum*: $r = 0.957$, $P < .0001$, $N = 117$; *P. recurvata*: $r = 0.942$, $P < .0001$, $N = 121$; *S. micropoides*: $r = 0.808$, $P < .0001$, $N = 118$; table A2), we used total plant biomass as our measure of fitness.

Trait Variation among Species and Sites

To determine whether relative growth rate, specific leaf area, root mass ratio, leaf N content, and water-use efficiency differed depending on the species and site, we performed a MANOVA with species and site as fixed factors. Relative growth rate and root mass ratio were square-root transformed to improve normality. Separate canonical discriminant analyses were performed to determine which traits were responsible for the significant main effects of site and species in the MANOVA.

Patterns of Selection

To determine patterns of selection on traits for each species at each site, we performed multiple regressions for each species-site combination. Biomass, our measure of fitness, was transformed into relative fitness by dividing individual values by the population mean. To allow for comparisons among traits, we standardized trait values within each population by subtracting the mean and dividing by the standard deviation (Lande and Arnold 1983). We used linear regressions of relative fitness on each standardized trait to calculate selection differentials, S , indicating total selection for each trait, including direct selection on that trait in addition to indirect selection through correlated traits (Lande and Arnold 1983). We also calculated standardized linear selection gradients, β , with separate multiple regressions for each species and site. For this, relative fitness (relative biomass) was the dependent variable, and standardized traits (relative growth rate, specific leaf area, root mass ratio, leaf N content, and water-use efficiency) were the independent variables. The values for β provide estimates of direct selection, controlling for the effects of other traits that have been incorporated into the analyses (Lande and Arnold 1983). To estimate stabilizing, disruptive, and correlational selection, γ , the quadratic and two-way cross-product terms of the traits were included in a second model (Lande and Arnold 1983). Quadratic regression coefficients were doubled to estimate quadratic selection gradients (Lande and Arnold 1983; Stinchcombe et al. 2008). In order to determine whether selection gradients for each trait varied depending on species and site, we used

ANCOVA with site and species as categorical variables and traits as continuous variables (Heisler and Damuth 1987; Campbell et al. 1997; Aspi et al. 2003).

Some of the traits measured (specific leaf area, root mass ratio, and leaf N content) are known to influence relative growth rate and water-use efficiency (Evans 1989; Reich et al. 1995, 1998; Angert et al. 2007; Ignace and Huxman 2009). We performed path analyses on each species-site combination to examine the effects of underlying traits on relative growth rate and water-use efficiency and the effects of relative growth rate and water-use efficiency on fitness. Path analysis is commonly used in selection analyses to partition the effects of phenotypic traits on fitness into direct and indirect effects based on investigator predictions about the structure of the path diagram (Schemske and Horvitz 1988; Dudley 1996; Ritz and Kohler 2010). This approach contrasts with that of multiple regression, where all traits are assumed to have the potential to directly influence fitness. Hypothesized paths are based on knowledge of causal or correlative relationships between the traits. Our hypothesized path (fig. 3) allowed for root mass ratio, specific leaf area, and leaf N content to have direct effects on relative growth rate (Reich et al. 2003a; Wright et al. 2004). Root mass ratio and specific leaf area may also have indirect effects on relative growth rate through their hypothesized negative correlation (Tilman and Wedin 1991; Nagel et al. 2001). We did not include a direct relationship between specific leaf area and leaf N content, because this relationship is thought to be driven by leaf longevity (Grime 1977; Reich et al. 1992; Suding et al. 2003) and is therefore less important for annual plants. Our path diagram allows for both specific leaf area and leaf N content to affect water-use efficiency (Hamerlynck et al. 2004; Ignace and Huxman 2009). Relative growth rate and water-use efficiency have direct effects on fitness and indirect effects through their hypothesized negative correlation (Geber and Dawson 1997; Arntz and Delph 2001; Heschel and Riginos 2005; Angert et al. 2007). We present results from both multiple regression and path analysis because path analysis partitions the correlations among variables in the context of a specific hypothesis, which may be incorrect, and does not provide easily interpretable estimates of stabilizing or disruptive selection (Kingsolver and Schemske 1991; Scheiner et al. 2000; Ritz and Kohler 2010).

To visualize selection on relative growth rate and water-use efficiency, we used thin-plate spline regression (Ritz and Kohler 2010). This method provides an accurate view of the selection surface because it is flexible enough to allow for a variety of functions and uses local smoothing to reduce the influence of outliers (Schluter 1988). To prevent extrapolations based on few individuals with extreme trait values, graphs were constrained to include only

individuals with standardized trait values between -2 and $+2$.

Results

Trait Variation among Species and between Sites

Results from a two-way MANOVA indicated significant effects of study site, species, and interaction between site and species on the canonical variable summarizing the multivariate distribution of leaf relative growth rate, specific leaf area, root mass ratio, leaf N content, and integrated water-use efficiency ($P < .0001$ for interaction and main effects; table A3). The canonical discriminant analysis comparing species suggested that the effect of species was primarily due to differences in position along the trade-off axis between relative growth rate and water-use efficiency (table A4; fig. A1, available online). The first canonical discriminant function accounted for 66% of the trait variation at site OP and was strongly negatively correlated with water-use efficiency and positively correlated with relative growth rate. Similarly, at site TH, the first function accounted for 65% of the variation and was strongly negatively correlated with water-use efficiency; it was also positively correlated with a component of relative growth rate, specific leaf area. The first function differentiated *Stylocline* and *Eriophyllum*, which have low water-use efficiency and high relative growth rate or specific leaf area, from *Erodium* and *Pectocarya*, which have high water-use efficiency and low relative growth rate or specific leaf area. The second function accounted for 19% of the variation at site OP and 22% of the variation at site TH, differentiating individuals with high relative growth rate

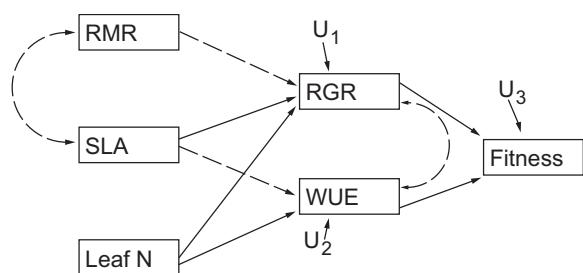


Figure 3: Path model of hypothesized relationships between measured traits and fitness. Residual variables U₁, U₂, and U₃ represent unmeasured factors that affect a given dependent variable. The diagram illustrates expected paths of causation for the effects of root mass ratio (RMR), specific leaf area (SLA), and leaf nitrogen content (leaf N) on relative growth rate (RGR) and water-use efficiency (WUE), and for the effects of RGR and WUE on fitness. Straight lines with single arrowheads indicate direct effects (path coefficients), and curved, dashed lines with double arrowheads indicate correlations. Dashed lines indicate negative relationships.

from those with low relative growth rate. For the canonical discriminant analysis comparing sites, there was only one canonical-discriminant function that captured all of the variation and indicated the importance of differences in relative growth rate and root mass ratio between sites ($P < .0005$; table A4). *Erodium texanum*, *Pectocarya recurvata*, and *Stylocline micropoides* had higher relative growth rate at site OP, while *Eriophyllum lanosum* had higher relative growth rate at site TH. The species *E. lanosum* and *S. micropoides* had higher root mass ratio at site OP, while *E. texanum* and *P. recurvata* had higher root mass ratio at site TH.

As expected, many of the measured traits were significantly correlated within populations. Contrary to the among-species pattern, relative growth rate and water-use efficiency were positively correlated within *E. texanum* at both study sites ($r = 0.55$ at site OP and 0.36 at site TH) and within *P. recurvata* at site TH ($r = 0.29$), indicating that individuals with high relative growth rate also tended to have high water-use efficiency (low Δ ; table A1). Relative growth rate was significantly negatively correlated with root mass ratio in all populations except for one species at each site (*P. recurvata* at site OP and *S. micropoides* at site TH) and positively correlated with leaf N for *E. texanum* and *P. recurvata*. Water-use efficiency was weakly negatively correlated with specific leaf area for *E. lanosum*, *P. recurvata*, and *S. micropoides*. Water-use efficiency was also negatively correlated with root mass ratio in most populations (table A1).

Patterns of Selection

All species experienced directional selection on all traits except specific leaf area, which was only related to fitness for *S. micropoides* and *E. lanosum* at site TH (see table A5 and fig. 4 for standardized linear selection gradients, β ; see table A6 and fig. 5 for standardized linear selection differentials, S ; data available from the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.c8c58>; Kimball et al. 2013). Selection gradients (β) estimate selection directly on the trait of interest, while selection differentials (S) estimate selection on a trait resulting from both direct and indirect selection on correlated traits (Lande and Arnold 1983). Selection gradients (β) and differentials (S) were very similar and always indicated selection in the same direction, suggesting that indirect effects of selection on correlated traits were small (Kingsolver et al. 2001).

Selection was positive on all traits except for specific leaf area in *S. micropoides* and *E. lanosum* and on root mass ratio in all species, which were under negative selection. Standardized selection gradients (β) for three of the four species (*E. lanosum*, *P. recurvata*, and *E. texanum*) indicated directional selection for water-use efficiency and

relative growth rate at both study sites (although selection on relative growth rate for *E. texanum* at site OP was only marginally significant, $P = .07$). *Stylocline micropoides* experienced positive selection on relative growth rate at both sites but did not experience significant selection on water-use efficiency (tables A5, A6; fig. 4). There was evidence for stabilizing selection (γ) on specific leaf area for *P. recurvata* at both sites (table A5). *Eriophyllum lanosum* and *E. texanum* experienced negative selection for root mass ratio at site OP, and *S. micropoides* showed negative selection for root mass ratio at both sites, while there was evidence of stabilizing selection on root mass ratio for *P. recurvata* at site OP. Three of the four species exhibited positive selection for leaf N at site OP.

Although fitness significantly increased with relative growth rate, integrated water-use efficiency (inverse of Δ), and leaf N and decreased with root mass ratio for all sites and species, results of the ANCOVA revealed that the strength of selection varied depending on the species and the site (table A7). For example, selection on root mass ratio was strongly negative at the warmer, drier site (site OP) but not at the more mesic site (site TH; table A7; fig. 4). Similarly, selection on root mass ratio was strongest in the species with higher relative growth rate, *S. micropoides*, and weakest in the species with higher water-use efficiency, *P. recurvata* (table A7; fig. 4). Selection on leaf N content and water-use efficiency were also stronger at site OP (table A7; fig. 4). Some differences in the strength of selection related to position of species along the trade-off axis between relative growth rate and water-use efficiency. Selection on water-use efficiency (inverse of Δ) depended on the species, with selection on water-use efficiency strongest in *E. texanum*, which has a high water-use efficiency, and weakest in *S. micropoides*, which has a high relative growth rate (table A7; fig. 4). Although the differences among species in strength of selection on specific leaf area were not statistically significant (nonsignificant specific leaf area \times species interaction; table A7), there was an interesting trend in which selection on specific leaf area tended to be negative in the two species with high relative growth rate and became slightly positive when moving along the trade-off axis toward species with high water-use efficiency (fig. 4).

The path analyses, which separate effects of traits on fitness into direct and indirect effects, indicated strong direct effects of relative growth rate and water-use efficiency on fitness for all species-site combinations except *S. micropoides* at site OP, in which the effect of water-use efficiency on fitness was smaller (fig. 6). The positive, indirect effect of leaf N content on fitness increased along the trade-off axis (weak in *S. micropoides* but strong in *E. texanum*) at both sites. At site TH, the strong indirect effect of leaf N content on fitness acted primarily through its effect on water-use

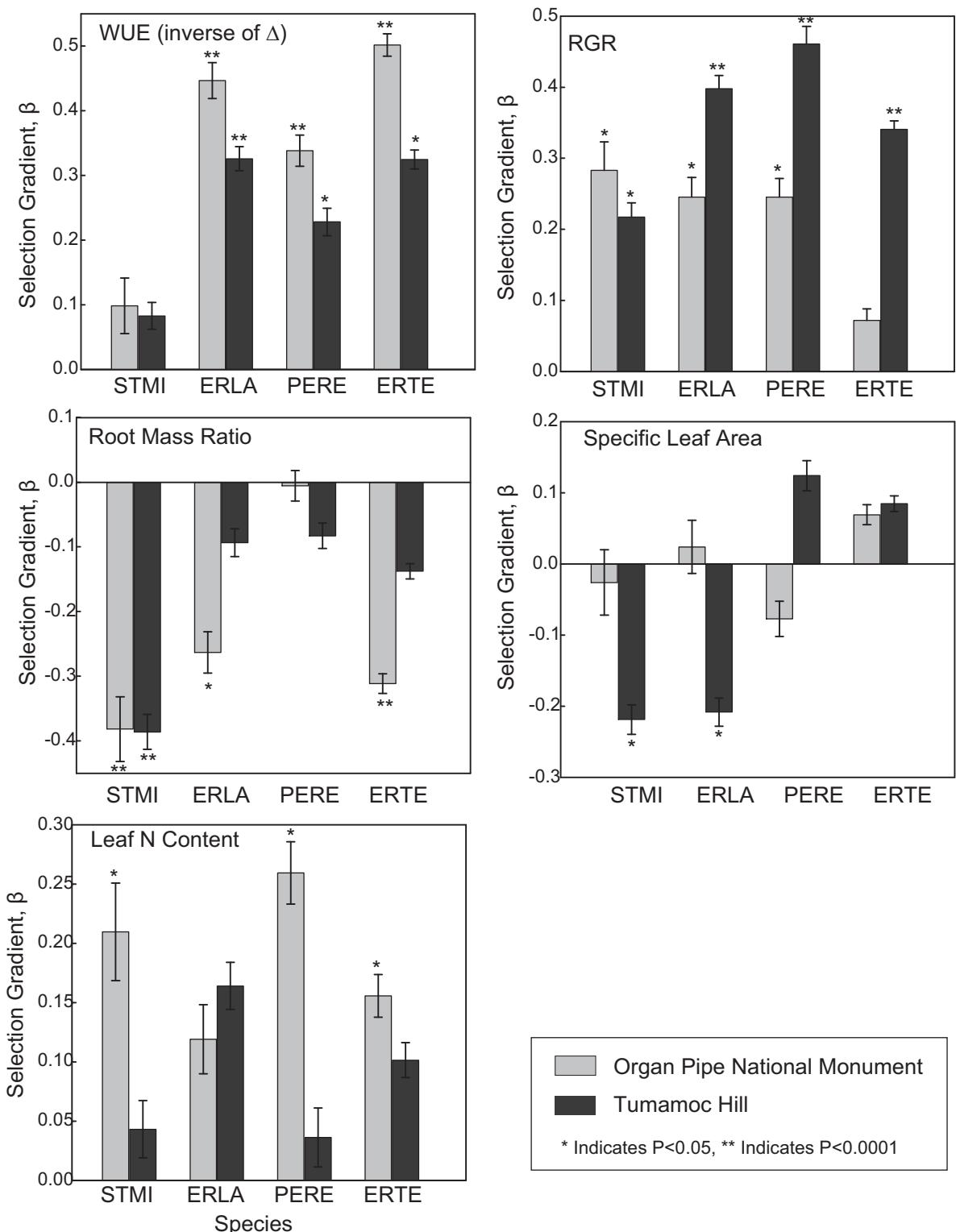


Figure 4: Standardized linear selection gradients (β) ± 1 standard error for the five traits measured on all four species at both study sites. Species are ordered on the X-axis from high relative growth rate (RGR) and low water-use efficiency (WUE) to low relative growth rate and high water-use efficiency. Species abbreviations are as in figure 2.

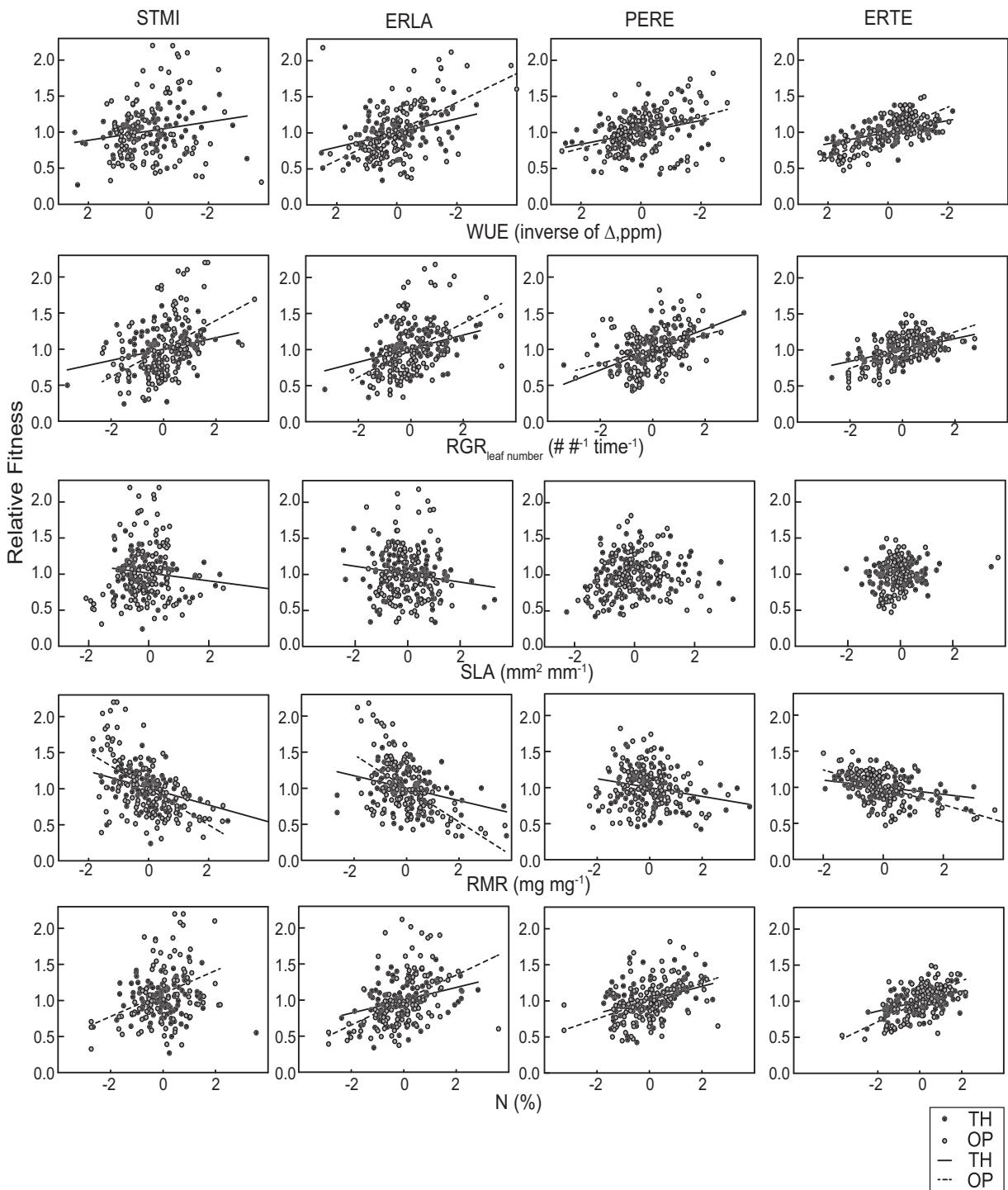


Figure 5: Relationship between standardized trait values and relative fitness for four species at Organ Pipe National Monument (site OP) and Tumamoc Hill (site TH) in Arizona. Traits are water-use efficiency (WUE, measured by Δ , where high Δ =low water-use efficiency), relative growth rate (RGR), specific leaf area (SLA), root mass ratio (RMR), and leaf nitrogen content (N). Regression lines were included to indicate significant selection differentials (S; table A6, available online). Species abbreviations are as in figure 2.

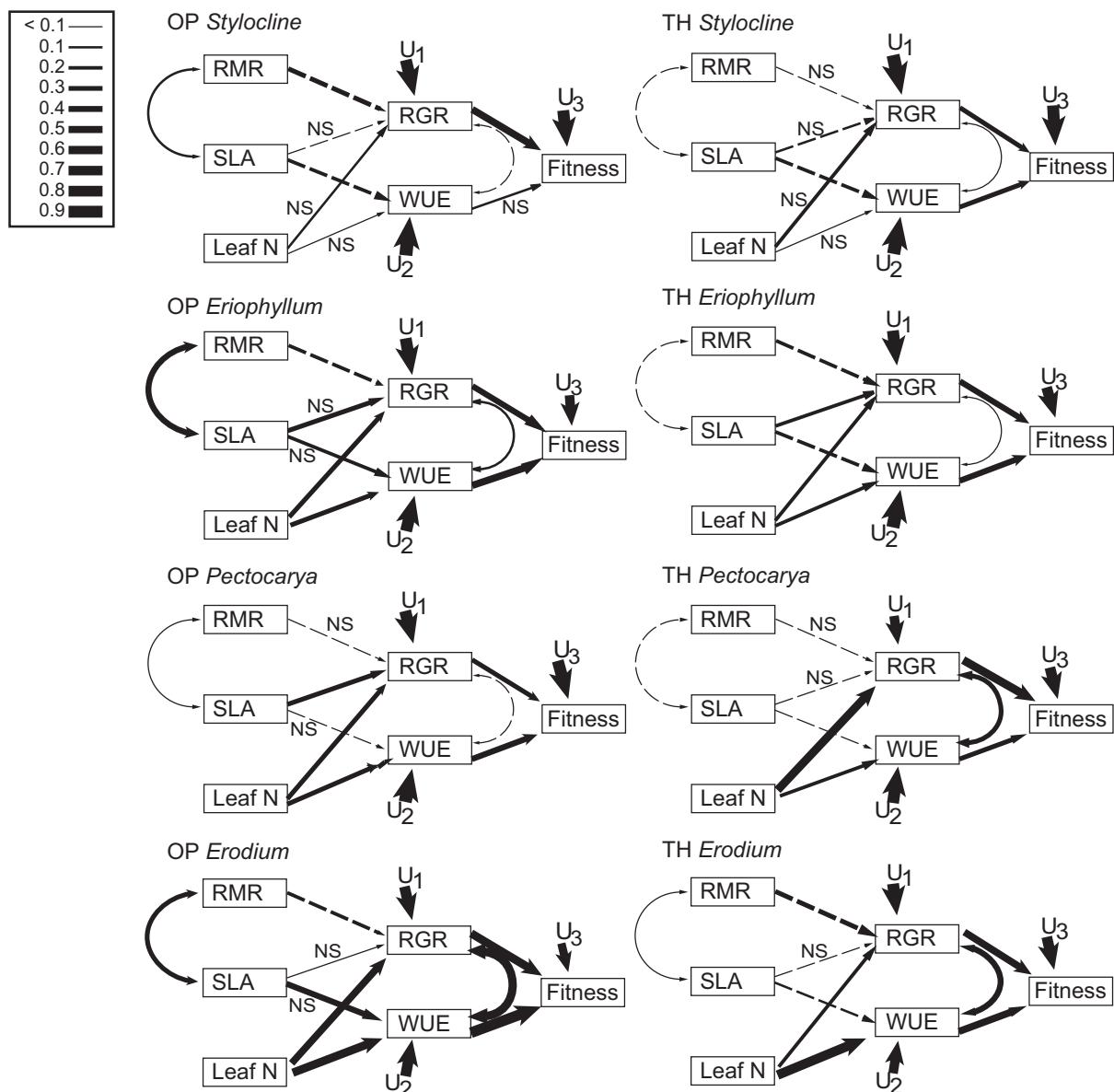


Figure 6: Path diagrams for *Stylocline micropoides*, *Eriophyllum lanosum*, *Pectocarya recurvata*, and *Erodium texanum* at Organ Pipe National Monument (site OP, left) and Tumamoc Hill (site TH, right) in Arizona. Positive effects are indicated by solid lines and negative effects by dashed lines. NS indicates nonsignificant effects. The legend (top left) gives the approximate magnitude of the coefficients indicated by the various line widths. See table A8, available online, for actual values and significance levels. Traits are as abbreviated in figure 3.

efficiency for *E. texanum* while acting primarily through its effect on relative growth rate for *P. recurvata*. Specific leaf area had a positive, indirect effect on fitness for *E. lanosum* and *P. recurvata* at site OP through its positive correlation with relative growth rate and for *E. lanosum* and *E. texanum* through its negative correlation with root mass ratio. The correlation between root mass ratio and specific leaf area was positive (mostly strongly positive) for all species at site OP, while it was negative or weak at site TH.

Thin-plate spline regressions allowed for a visual interpretation of the positive effects of high relative growth rate and high water-use efficiency on fitness for all species-site combinations (fig. 7). Conversely, individuals with low relative growth rate and low water-use efficiency tended to have the lowest fitness across species and sites. The fitness landscapes are generally steeper at site OP than at site TH for all species. Also, the fitness landscape for *E. lanosum* at site OP indicates the possibility for mild dis-

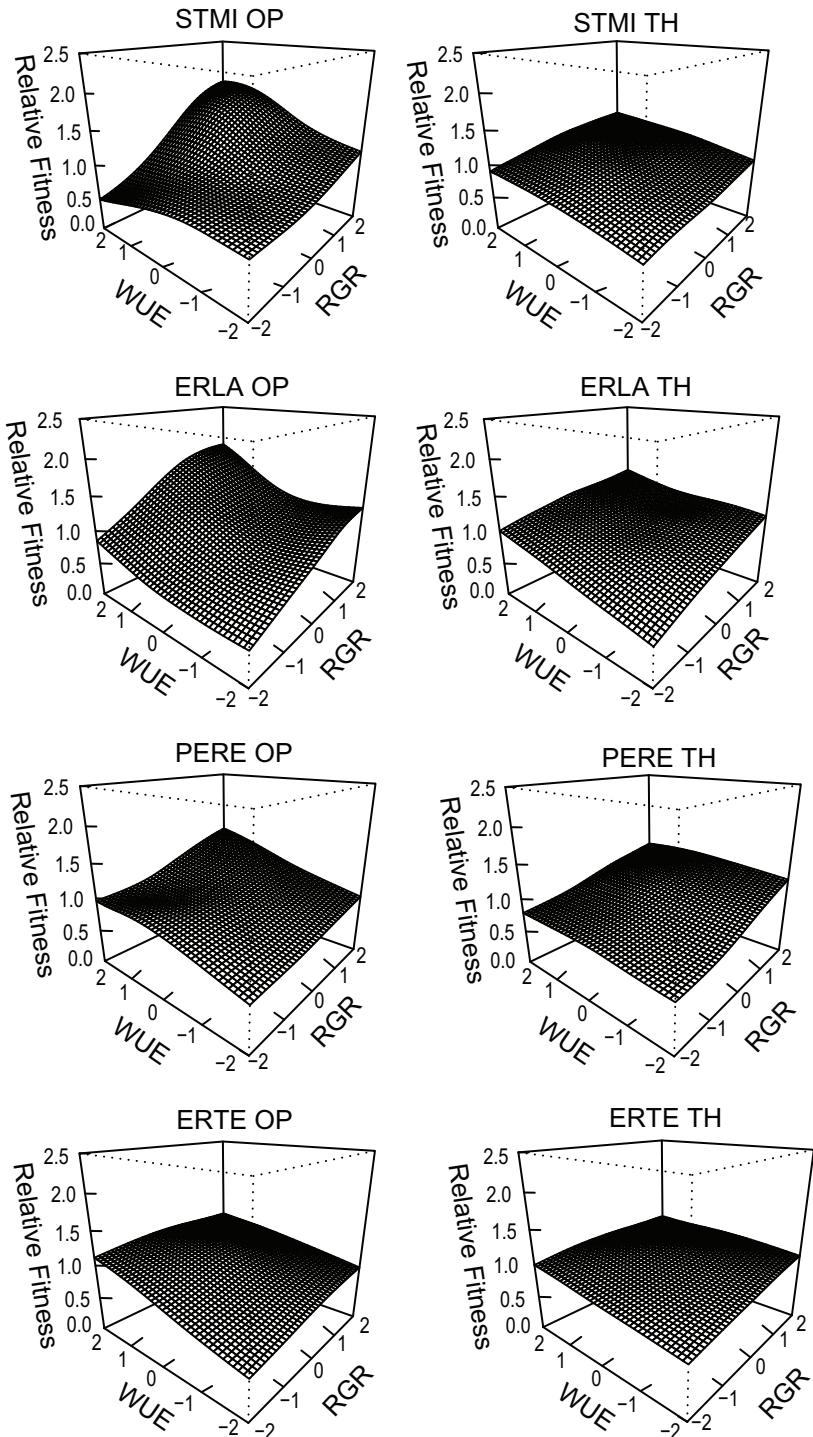


Figure 7: Relative fitness in relation to water-use efficiency (WUE) and relative growth rate (RGR) for *Stylocline micropoides* (STMI), *Eriophyllum lanosum* (ERLA), *Pectocarya recurvata* (PERE), and *Erodium texanum* (ERTE) at Organ Pipe National Monument (site OP, left) and Tumamoc Hill (site TH, right) in Arizona. Both traits are standardized. Selection surfaces resulted from thin-plate spline regression. Fitness was generally highest for individuals with high water-use efficiency and high relative growth rate.

ruptive selection, with a depression at intermediate water-use efficiency.

Discussion

Trade-offs are thought to be important at different scales, such that trade-offs that are present among individuals within a species may persist over evolutionary time and be reflected in trade-offs among species (Suding et al. 2003; Kneitel and Chase 2004; Agrawal et al. 2010). Transitivity of trade-offs across scales could indicate that fundamental constraints prevent the formation of certain trait combinations, with far-reaching consequences for both evolutionary ecology (e.g., the evolution of phenotypes) and community ecology (e.g., niche partitioning, community assembly, and the maintenance of biodiversity). The inference of genetic constraints on observable phenotypes assumes that patterns of phenotypic selection are at odds with available genetic variation (Antonovics and van Tienderen 1991), yet the adaptive value of trait combinations is often assumed rather than measured. Here, in two environments, we investigated phenotypic selection on relative growth rate and water-use efficiency (traits known to trade off among species in this system) within populations of four species that fall at different points along the trade-off axis. This enabled us to measure a range of trait variation within species and to determine whether certain trait combinations are favored by natural selection. Selection consistently favored a higher-relative-growth rate/higher-water-use-efficiency phenotype across species and environments, indicating that the absence of a species with this phenotype in the native community is not caused by the phenotype being unfavorable (fig. 7). This suggests that the important trade-off we observe among species, which influences population dynamics and facilitates species coexistence, could arise from pervasive constraints that operate within each species. It is also possible that the trade-off has been shaped by competition and species sorting to reduce niche overlap during community assembly.

Trait Differences among Species and Sites

Measurements of relative growth rate and water-use efficiency in this study correspond well with earlier measurements, although *Stylocline micropoides* had unusually low relative growth rate at site TH and *Eriophyllum lanosum* had unusually low relative growth rate at site OP (fig. A1; Angert et al. 2007; Huxman et al. 2008). Possibilities for why the relative growth rates of these two populations were lower than expected include the following: (1) some early growth occurred prior to our first leaf count, or growth leveled off prior to our last leaf count, so that we did not capture the period of maximum growth;

(2) our measurements of relative growth rate were less accurate because they were necessarily conducted with leaf counts rather than with whole-plant harvests; or (3) our measurements reflect real relative growth rates under these conditions, but relative growth rate is plastic, so species may shift rank order (Grime and Hunt 1975; Coleman et al. 1994; Hunt et al. 2002). Nonetheless, species' rankings along the trade-off axis between relative growth rate and water-use efficiency are largely consistent with our previous work in this system (Angert et al. 2007; Huxman et al. 2008).

Contrary to the among-species pattern, we found a positive correlation between relative growth rate and water-use efficiency within the two species with the highest water-use efficiency (*Erodium texanum* and *Pectocarya recurvata*; table A1). In these two species, leaf N content was correlated with both water-use efficiency and relative growth rate, suggesting that microhabitats with high soil N content may have enabled some individuals to achieve both high water-use efficiency and high relative growth rate, potentially masking an existing trade-off and artificially increasing estimates of selection on these traits (Stinchcombe et al. 2002; Agrawal et al. 2010). Positive correlations between water-use efficiency and leaf N content found in creosote shrubs growing in the Mojave Desert were attributed to high photosynthetic rates in habitats with increased resource availability (Hamerlynck et al. 2004). Leaf N content tends to be correlated with photosynthetic rate, which could enable individuals to have high relative growth rate and water-use efficiency, where the carbon accumulation portion of the water-for-carbon leaf exchange is maximized (Evans 1989; Reich et al. 1995). The path analyses illustrate that leaf N content had a direct, positive effect on relative growth rate and water-use efficiency in the species with the highest water-use efficiency, *E. texanum*, and that the effect decreased along the trade-off axis so that it was much less in the species with the lowest water-use efficiency, *S. micropoides* (fig. 6). This fits with our understanding that the species in our system with high water-use efficiency invest more in light-harvesting capacity, possibly due to greater investment in nitrogen-rich photosynthetic pigments and proteins (Huxman et al. 2008; Gremer et al. 2012).

Patterns of Selection across Species and Sites

We found positive directional selection for relative growth rate, water-use efficiency, and leaf N content (fig. 5), all traits that are important for acquisition and allocation of resources but whose relationship to fitness has rarely been quantified (Farris and Lechowicz 1990; Ackerly et al. 2000; Arntz and Delph 2001). Inferences made from the path analyses were similar but provided additional information

regarding how N may influence fitness, through either strong correlations with relative growth rate (in *Pectocarya* at site TH), strong correlations with water-use efficiency (in *Erodium* at site TH), or both (*Erodium* at site OP; fig. 6). Path analyses suggest specific leaf area may have influenced fitness on all species at site OP through its negative correlation with root mass ratio and, in *Eriophyllum* and *Pectocarya*, through its positive correlation with relative growth rate. Selection gradients did not indicate strong or consistent directional selection for specific leaf area (fig. 4). Slight negative selection on specific leaf area was also found in milkweed when estimated with phenotypic, but not genotypic, selection analysis (Agrawal et al. 2008). The difference between the phenotypic- and genotypic-selection estimates in that study may be due to high plasticity of specific leaf area and correlations with other traits included in that study, including leaf N content and C-to-N ratio (Agrawal et al. 2008).

One difficulty in studying selection on physiological traits is that many of the commonly measured traits, such as rates of carbon assimilation and water loss, vary greatly with age, development, time of day, and day of year. Water-use efficiency, in particular, exhibits genotypic differences as well as phenotypic plasticity, depending on environment (Heschel et al. 2002; Golluscio and Oesterheld 2007). For this reason, estimates of the fitness consequences of physiological traits that are integrated over a longer time span, such as the traits that we included in this study (integrated water-use efficiency calculated from measurements of carbon isotope discrimination during the life span of the leaf and relative growth rate from germination until reproduction), may be more accurate (Arntz and Delph 2001).

Relationships between traits and fitness varied depending on the site, which suggests that certain traits may be adaptations to specific environmental conditions (Dudley 1996; Donovan et al. 2009). Specifically, selection on water-use efficiency was stronger in the warmer, drier environment (site OP), which is consistent with other studies that measured selection on water-use efficiency in more than one environment and found stronger selection in drier environments (Evans 1989; Dudley 1996; Saldana et al. 2007). There was significant, positive selection for relative growth rate at site TH, the more mesic site, but selection on this trait was not as strong at site OP (fig. 4). Specific leaf area is frequently correlated with relative growth rate, in part because high specific leaf area confers increased surface area available for photosynthesis and decreased diffusional constraints for gas exchange (Atkin et al. 1996). We found that the relationship between specific leaf area and relative growth rate varied depending on species and site but was not particularly strong (fig. 6). However, there were significant positive correlations between specific leaf area and root mass ratio at site OP (the warmer and drier

site) and negative correlations between these two variables at site TH (fig. 6). In other words, individuals that invested more in roots were able to grow larger leaves in the drier environment but not in the more mesic environment. Selection on all traits was generally stronger in the warmer, drier environment at site OP than in the cooler, more mesic environment at site TH (figs. 4, 7).

Strength of selection varied depending on the position of species along the trade-off axis between relative growth rate and water-use efficiency. Selection on water-use efficiency tended to be higher in high-water-use-efficiency species than in low-water-use-efficiency species, and selection on root mass ratio was stronger in high-relative-growth-rate species with high values of root mass ratio. This suggests that environmental pressures were similar in the past and that current phenotypes reflect past selection, possibly on entire suites of traits (Reich et al. 2003a). The different patterns of selection may also indicate that competitive pressures favor character displacement, where evolution favors decreased niche overlap in coexisting species (Abrams 1990; Schlüter 2000). There may be multiple strategies for success in the same environment, such as selection for high relative growth rate in species that have suites of traits consistent with drought avoidance and selection for high water-use efficiency in drought-tolerant species (Arntz and Delph 2001). It is also important to note that the two species with high relative growth rate are both from the same family (Asteraceae), so they may have greater niche overlap due to phylogenetic relatedness.

Selection and Missing Trait Combinations

Missing trait combinations among species are often interpreted as evidence of functional constraints that operate within all species to prevent the construction of certain phenotypes (Grime 1977; Tilman 1982; Suding et al. 2003; Bonsall and Mangel 2004; Kneitel and Chase 2004). Among-species trade-offs need not arise due to pervasive phenotypic constraints but could also emerge from rules of community assembly and processes of sorting among species that specialize in distinct niches (Pianka 1980; Keddy 1992; Palmer et al. 1997; Tilman 1999). If a novel species invaded a community with very high values of both traits, then the community could be unstable and the invader would rapidly outcompete others (Aicher et al. 2011; Molina-Montenegro et al. 2012). Constraint-based and assembly-based explanations for trade-offs are not mutually exclusive. For example, competition could result in divergence along “genetic lines of least resistance” (Schlüter 1996). Regardless of the underlying cause, it is often assumed that high values of both traits in trade-offs (e.g., individual X in fig. 1A) are favored by natural selection, without corroborating estimates of the strength and di-

rection of selection. We have demonstrated that selection does favor a missing trait combination (high relative growth rate and high water-use efficiency) within species in this system (figs. 2, 7). The apparent inability of species to respond to this strong, directional selection suggests that the among-species trade-off might arise from a pervasive constraint, but quantitative genetic studies would be necessary to determine whether species experience fundamental constraints that prevent them from achieving both high relative growth rate and high water-use efficiency. Strong trade-offs between relative growth rate and water-use efficiency are expected because plants often achieve high water-use efficiency by closing their stomata to control transpirational water loss, resulting in reduced photosynthesis that can limit growth (Geber and Dawson 1990, 1997).

Quantitative genetic studies could also reveal whether heterogeneity of resource availability in the field causes phenotypic correlations to differ from underlying genetic correlations. Although we did not find evidence for the trade-off between relative growth rate and water-use efficiency within species, high values of both traits may occur, despite the existence of a trade-off, when individuals that occupy favorable microhabitats are able to increase resource allocation to both traits (Agrawal et al. 2010). This effect of habitat heterogeneity is related to one primary limitation of phenotypic selection analysis, that environmentally induced covariance between traits and fitness can make a trait appear to be under selection when in fact it is not (Rausher 1992; Stinchcombe et al. 2002). Genotypic selection analysis (using the average values of siblings) can result in very different estimates of the strength of selection but almost always results in the same qualitative assessment of selection (Stinchcombe et al. 2002; Agrawal et al. 2008). Thus, we suggest that water-use efficiency and relative growth rate are both under positive directional selection despite our use of phenotypic, rather than genotypic, selection analysis, but we do not yet know whether the trade-off exists due to fundamental constraints acting within species.

Phenotypic constraints can channel the direction of niche partitioning among interacting species as well as limit the spectrum of phenotypes that can be sorted during community assembly. Community assembly can result in empty corners, even in the absence of constraint, by minimizing niche overlap while complementing resource use, a process that reduces interspecific competition and results in a large dispersion of traits (Belyea and Lancaster 1999). Several lines of evidence suggest a role for community-assembly processes influencing the distribution of trait values among species in our system, either alone or in combination with intraspecific constraint. We know that the unique positions of species along the trade-off spectrum

are important in determining community structure and in promoting coexistence in this plant community (Angert et al. 2009; Venable and Kimball, forthcoming). Also, the competitive abilities of species vary depending on their position on the trade-off axis between relative growth rate and water-use efficiency and on environmental conditions (Gremer et al., forthcoming). Species with high water-use efficiency are more affected by competition in mesic conditions, while species with high relative growth rate are more affected by competition in xeric conditions. These findings suggest that niche partitioning contributes to the maintenance of diverse phenotypes along the trade-off spectrum. Finally, two nonnative species in this community have higher values of relative growth rate for their level of water-use efficiency than the native species, which places them near the empty corner of the native species' trait space (fig. 2). While this suggests that native species have been unable to build this phenotype, the nonnative species appear unlimited by the same fundamental constraint, which points to the importance of historical biogeography and contingency during community assembly.

Conclusions

Here we have demonstrated how natural selection acts on the traits that are known to be important in determining the population dynamics and community structure of winter annual plant species in the Sonoran Desert. All four species experienced selection on most traits in the same direction, confirming the importance of these traits to fitness in these habitats, while contrasting selection depending on habitat suggests that they are adaptations to particular environments. Variation in microhabitat quality may have masked trade-offs within species and/or inflated our estimates of the strength of selection through covariance between traits and fitness. Nonetheless, we have strong support that natural selection favors high values of both relative growth rate and water-use efficiency, a phenotypic combination that is unobserved among the native species in this community. This suggests that the among-species trade-off might arise due to fundamental phenotypic constraints operating within species, alone or in combination with processes operating among species during community assembly.

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Left, the Sonoran Desert winter annual community at the University of Arizona's Desert Laboratory at Tumamoc Hill in Tucson, Arizona (photograph by Kathy Gerst). *Right*, one of the study species, *Eriophyllum lanosum*, at Tumamoc Hill (photograph by Jonathan Horst).

