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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Species-specific trait–environment relationships among populations of widespread grass species

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Abstract

Intraspecific trait variation can be substantial and is driven by many factors. To develop predictive models of intraspecific trait variation, an understanding of the drivers of that variation is essential. At fairly broad scales, differences in the environment are expected to drive genetic variation in functional traits among populations. To isolate this genetic variability, we conducted a greenhouse common garden experiment using nine grass species native to the western United States. We assessed relationships between several root, leaf, and whole plant traits and a number of environmental conditions from the source population locations, including aspects of temperature, precipitation, vapor pressure deficit and soil moisture. We tested the hypotheses that (1) above- and belowground functional traits vary significantly within and among species, and (2) trait–environment relationships among populations of a species are consistent among species. First, we found that trait variation between species ranged from 13 to 77%, while trait variation within species ranged from 11 to nearly 39%. Traits related to overall plant size and growth rate exhibited the greatest intraspecific variation, and root traits the least variation. Second, while we found significant trait–environment relationships, they were highly variable among species. The magnitude of intraspecific trait variability found in this study indicates significant local adaptation with respect to specific trait–environment combinations, but that characterizing trait–environment relationships requires species-specific measurements and models.

Keywords Functional trait · Intraspecific trait variation · Trait–environment correlations · Poaceae · Belowground traits

Introduction

The goal of plant functional ecology is to make generalizable predictions across organizational and spatial scales (Adler et al. 2013). While these are not new objectives (Hiesey et al. 1942), they are persistent. To achieve the goals of functional plant ecology, Shipley et al. (2016) recently noted that several aspects need further refinement. One of these aspects is determining under what circumstances and at what scales to consider intraspecific trait variation (ITV, reviewed by Des Roches et al. 2018), and another is to better illustrate consistent trait-environment relationships with strong predictive power.

In a recent meta-analysis, ITV has been shown to account for on average a quarter of trait variation within communities and a third of trait variation among communities (Siefert et al. 2015). ITV tends to be most important up to a regional scale (Albert et al. 2011), beyond which factors such as species turnover begin to play a dominant role in trait variation (Siefert et al. 2015). At regional to smaller scales, ITV can vary substantially among traits and species. For example, though specific leaf area (SLA) and leaf dry matter content (LDMC) can have similar effects on leaf function (Pérez-Harguindeguy et al. 2013), SLA can be considerably more variable within species than LDMC (Violle et al. 2012; Garnier et al. 2001). ITV may also vary across species (Albert et al. 2010). For example, grasses demonstrated greater intraspecific variation compared to forbs in German meadows (Herz et al. 2017). In terms of community abundance, common species may have a smaller magnitude of ITV than rare species (Umaña et al. 2015). Additionally,

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ITV may be driven by different components of genetics of plasticity and acclimation, and can change rapidly in time (DeWitt et al. 1998; Hughes et al. 2008). However, much of the apparently species-specific variation in ITV among study systems may be attributable to a lack of comparability between environmental drivers of ITV among studies, as well as confounding effects of genetic and plastic variation (Al Hayek et al. 2015).

Clearly defining multiple aspects of environmental variation, including both climatic and edaphic factors, may help to improve our ability to predict variation in ITV at regional scales. Studies often show species-specific responses to environmental gradients (Albert et al. 2010; Siefert et al. 2014). While both climatic and edaphic factors prove to be important they still do not explain any majority of variation in functional traits. Wright et al. (2005) found that 18% of variation in their study of leaf traits was explained by climate. Similarly, between 8 and 18% of variation in fine root traits can be attributed to climate alone, whereas cation exchange capacity only explained up to 13% of total variation (Freschet et al. 2017), suggesting that both the aspects of climate and soil properties are important for characterizing relationships between ITV and the environment. In the field of functional ecology, root traits are often neglected, perhaps in part due to the challenges associated with harvesting, cleaning and measuring root systems, though deserve the attention given to aboveground functional traits (Laliberté 2017). Though the study of root traits is often neglected, ITV in roots has been shown to influence soil carbon dynamics and influence soil physical properties (Ali et al. 2017; De Deyn et al. 2008; Hu et al. 2013), warranting further examination.

Of the multiple sources that contribute to ITV, genetic responses are more likely to yield consistent predictive relationships to the environment (Chapin et al. 1993). In experiments done in common environments, which emphasize the genetic component of ITV–environment relationships, ITV still responds idiosyncratically across both traits and climate variables even within narrow taxonomic groups (Roybal and Butterfield 2018). Some climate variables, such as temperature, may exert influence on traits overall across species (Moles et al. 2014; Wright et al. 2017) as well as within species, making them better candidates for exploring trait–environment relationships across either traits or species further. Plants may also respond plastically to a variety of land use, biotic and abiotic factors, such as changes in soil properties (Andrade et al. 2014), elevation (Kichenin et al. 2013), grazing (Ryser and Urbas 2000), as well as mycorrhizal colonization (Weremijewicz and Seto 2016).

Understanding ITV and trait–climate relationships has important implications for the field of restoration ecology, specifically for identifying suitable seed sources for a range of environmental conditions (Bureau of Land Management Staff 2015). Both trait–climate relationships and ITV may also help to refine seed transfer zones for species commonly used in restoration projects (St. Clair et al. 2013). Characterizing trait–environment relationships will better ensure that plant materials in seed mixes display appropriate trait values for the climate of application. Characterization of trait–environment relationships will also help to establish suitability of plant materials for predicted climate (Butterfield et al. 2017). Similarly, better-developed understanding of ITV across regional scales can illustrate the potential adaptive capacity of restoration materials (Prober et al. 2015; Hufford and Mazer 2003).

In this study, we quantify ITV and trait–environment relationships among populations spanning the full regional climatic niche breadth of nine grass (Poaceae) species native to the Western United States. Plants were grown in a common environment, minimizing plastic responses to the environment. Our overarching objective was to determine whether species exhibit similar or different patterns of local adaptation across their distributions, based on trait–environment relationships among populations within species. First, we tested the hypothesis that trait values vary significantly both within and among species. Second, we tested the hypothesis that trait–environment relationships are consistent both among and within species. To address this thoroughly, we sought to incorporate multiple dimensions of the environment, including climatic and soil variables. Because precipitation is not always a reliable predictor of water availability to plants and subsequent variation in functional traits (Moles et al. 2014), we also included aspects of soil moisture and evapotranspiration as environmental predictors of trait variation.

Methods

We established a common garden experimental design, located within a research greenhouse on the Northern Arizona University campus in Flagstaff, Arizona. We selected nine grass species commonly used in restoration seed mixes on the Colorado Plateau and within the Great Basin deserts in the Southwestern United States: *Poa fendleriana, Poa secunda, Koeleria macrantha, Pseudoroegneria spicata, Leymus cinereus, Elymus elymoides, Aristida purpurea, Pleuraphis jamesii,* and *Bouteloua gracilis*. Ten accessions of each species were selected from the Germplasm Resources Information Network (USDA 1997), that most uniformly covered the climatic niche breadth of each species (Table S1). This selection process was based on coordinates for each accession obtained from the Seeds of Success program (Byrne and Olwell 2008). SOS protocol is to collect seeds from 30 randomly chosen individuals for outbreeding species, and 59 randomly chosen individuals for

self-fertilizing species (Brown and Marshall 1995, Bureau of Land Management Staff 2016). To account for the full niche breadth of the species, we performed a cluster analysis of six bioclimatic variables (see below). Climate data were accessed from WorldClim (Hijmans et al. 2005).

For each of the ten populations per species, we planted five seeds in each of ten pots. All populations of a single species were established in a single day, with species planting staggered over 3 weeks in May and June 2016. Greenhouse temperature was maintained at approximately 21 °C. Because of our desire to accurately study root functional traits, growth media were an important consideration for our study. Turf-ace (PROFILE Products LLC, Buffalo Grove, IL, USA) is a baked clay medium that proved to be easy to clean off roots which we used as a standard soil medium. Seeds were planted in a shallow well in the center of one-gallon pots and covered with a small layer of vermiculite to help prevent seeds being exposed during watering. We selected one-gallon pots to minimize the amount of growth media needed, and also seemed a sufficient volume for grasses grown over a single season. Initially, plants were misted twice a day to ensure that the seeds did not get pushed down in the pots. Once the seedlings developed two or three true leaves, the pots were thinned down to two seedlings. At this point, the pots received the manufacturer's recommended dose (~2.5 g per gallon of soil) of Osmocote Plus NPK and micronutrient fertilizer (Scotts, Marysville, OH, USA), and watering was reduced to one time a day with a standard garden wand. Once it was clear that both remaining seedlings were healthy, pots were thinned down to one individual. To standardize the environment within the greenhouse, pots were randomized between benches every 3 weeks throughout the course of their period of growth.

Trait measurements

Plants were harvested for measurement after approximately 12 weeks of growth in August, 2016. Harvesting began when roots were beginning to show from the bottom of the pots and some species were beginning to develop inflorescences. All functional traits were measured in accordance with Pérez-Harguindeguy et al. (2013). We measured height, specific leaf area (SLA), root dry matter content (RDMC) and specific root length (SRL) of coarse and fine roots. We define coarse roots as lignified with no root hairs, while fine as non-lignified with hairs. Roots were kept hydrated until scanning for SRL. RDMC was used as a proxy for root tissue density, according to Birouste et al. (2013). Above- and belowground biomass were determined and used to estimate root–shoot ratio (RSR), and relative growth rate, calculated as the natural log of final biomass divided by population mean seed mass (Pérez-Harguindeguy et al. 2013). Total biomass was the sum of above- and belowground biomass. LA and coarse root SRL were determined on a flatbed scanner (Epson Perfection V39, Epson America, Long Beach, CA, USA), whereas fine root SRL was estimated via WinRhizo software (Regent Instrument, Quebec, Canada).

Environmental variables of provenance populations

Using climate data of our source populations, we conducted principal components analysis (PCA) to select bioclimatic variables. The first six components had eigenvalues greater than one, and we selected the climate variables that loaded each of the axes most heavily. The six variables included mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality (the amount of temperature variation within a year), precipitation seasonality (the variation in monthly precipitation totals over the course of a year), mean diurnal temperature range (MDR) and precipitation of driest quarter (PDQ) as predictor variables (Hijmans et al. 2005). Using WorldClim actual vapor pressure values, we additionally calculated vapor pressure deficit (VPD, Walter et al. 2001). In addition to the orthogonal WorldClim variables, we wished to incorporate soil variables with particular relevant in dryland environments, such as aridity and soil moisture. Thus, we include VPD as a metric of aridity; specifically, it is the amount of moisture that needs to be added to the air to go from the actual vapor pressure to saturated vapor pressure. To incorporate aspects of soil moisture as a predictor, we ran the SOILWAT ecosystem water balance model, which has been validated in grasslands (Parton 1978). Model inputs included CONUS meteorological data (Livneh et al. 2013) and WISE soil property data (Batjes 2016). We selected variables indicating the degree of aridity, including the ratio of AET (actual evapotranspiration) to PET (potential evapotranspiration), and two variables reflecting soil dryness, specifically the average number of days the temperature exceeded 15 °C, and soil water potential was either below or above −3.9 kPa in the top 20 cm of soil (hereafter referred to as "warm dry soil" or "warm wet soil", respectively). From the SOILWAT model output, we selected the additional two dryness variables because they represented moisture in the top, biologically active soil layer, and a water potential threshold below which plants are unable to take up water. We performed a PCA on the remaining soil dryness variables, the result suggesting three heavily loaded axes, two representing the average number of days temperature exceeded 15 °C, and one with the average number of days temperature exceeded 25 °C. The distribution of our populations where temperature exceeded 25 °C was poor; so, this variable was eliminated.

Analysis

All analyses were performed using R (R core team, 2015). We addressed our first hypothesis in two ways. First, to test whether trait values varied among species and among populations within species, both interspecific and intraspecific differences were assessed using analysis of variance (ANOVA). Models were constructed with trait values as a response of population, which nested within species (using the code Trait value ~ Species | population). The purpose of this test was primarily descriptive, but speaks to the broader relevance of ITV compared to among-species variance. Second, we tested the intraspecific variance of each trait among species (trait value as a function of population, using the R code: Trait value ~ population). For each of these tests, we calculated effect size, the partial η^2, using the 'lsr' package in R (Navarro 2015), which is the sum of squares between groups divided by unexplained variation in *Y*, plus the variation explained by *X*. The advantage of the partial η^2 is the resulting effect size is comparable among species, despite their variation in environmental niche breadth.

To test our second hypothesis that trait–environment relationships are consistent among species, we evaluated relationships between environment and functional traits by two methods. First, we included all environmental variables in stepwise AIC model selection and all subsets regression, using the 'leaps' package in R for all subsets (Lumley and Miller 2017) to predict variation in population mean trait values across all species without including species identity. The objective of this analysis was to identify broad-scale trait–environment relationships to compare with species-specific relationships. We selected predictor variables that were included in at least seven models suggested by the all subsets regression method. Second, to assess how trait–environment relationships vary among populations within species, we estimated the Pearson correlation coefficient between the population mean trait value and population climate value.

Results

Common garden trait variation

In addressing our first hypothesis that trait values vary significantly both within and among species, we found that most traits exhibited significant ($p < 0.05$) variation with respect to both species and population nested within species (Table S2). Height exhibited the greatest variation among species (77%), followed by root–shoot ratio (69%), RGR (63%) and coarse and fine SRL (62% and 54%, respectively; Table 1). Root dry matter content of both coarse and fine roots varied only moderately among species (34% and 38%, respectively), and much less so SLA (13%). Relative growth rate exhibited the greatest variation among populations within species (38%), followed by height (30%), SLA (24%) and root–shoot ratio (22%). Coarse SRL and coarse RDMC varied moderately (20% and 17% respectively), and fine root traits varied the least among populations (14% for SRL, and 11% for RDMC). Specific leaf area was the only trait that exhibited greater variation within than among species, with 25% of variation explained by population.

Table 1 Portion of variation (partial η^2) explained by species and populations for each functional trait, including specific leaf area (SLA), specific root length (SRL), root dry matter content (RDMC), relative growth rate (RGR) and root–shoot ratio (RSR)

Trait	Source of variation	Partial η^2
Height	Species	0.774
	Population	0.305
c.SRL	Species	0.629
	Population	0.203
c.RDMC	Species	0.347
	Population	0.176
f.SRL	Species	0.548
	Population	0.140
f.RDMC	Species	0.389
	Population	0.110
SLA	Species	0.130
	Population	0.247
RGR	Species	0.630
	Population	0.386
RSR	Species	0.694
	Population	0.228

The prefixes f. and c. indicate fine and coarse roots, respectively

Analysis of variance among populations for each species individually revealed that traits relating to whole-plant size tended to have more variation explained by population than traits relating to specific tissues or allocation (Fig. 1). All species exhibited significant variation with respect to height and RGR, six of nine species for root–shoot ratio, SLA and coarse SRL, and four, three and two species for coarse RDMC, fine SRL and fine RDMC, respectively.

Trait–environment relationships

In addressing our second hypothesis that trait–environment relationships are consistent both among and within species, we found that all subsets regression was more restrictive than AIC in selecting predictor variables for each functional trait when trait–environment relationships were assessed across all populations regardless of species. The stepwise AIC selection method indicated that Mean Diurnal Range was a suitable predictor for all functional traits, followed by precipitation of driest quarter and MAT which were selected as a predictor for five of eight functional traits (Table 2). The

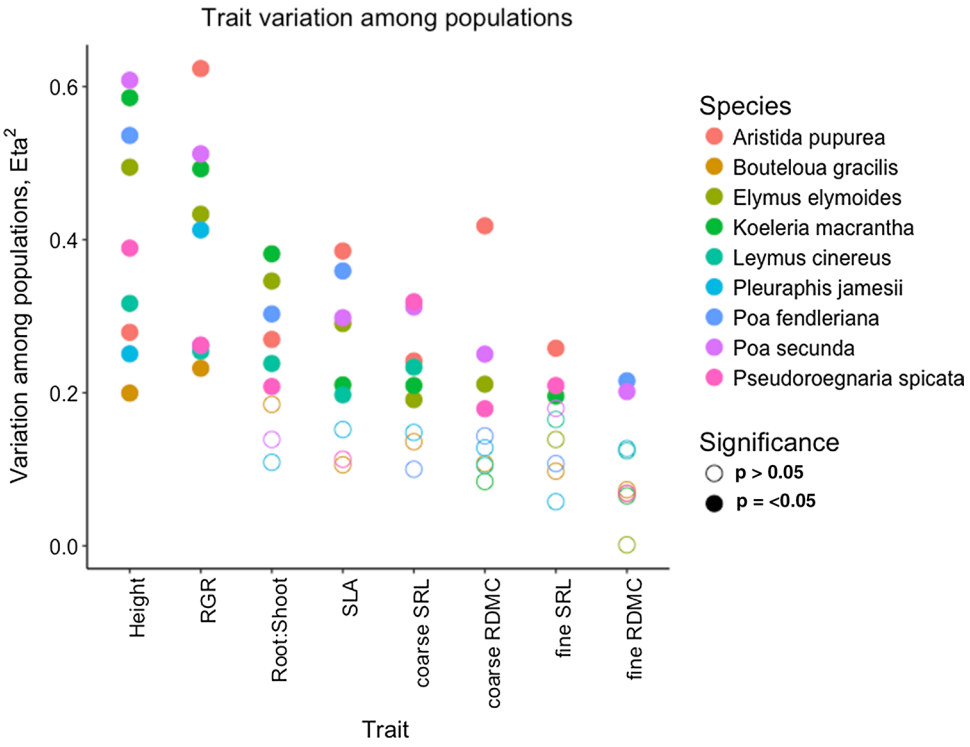

Fig. 1 Amount of variability explained by population for eight different traits. η^2 value is calculated as the sum of squares between groups divided by the total sum of squares. See Table 2 legend for trait abbreviations. Filled circles (1) indicate a significant trait variation among populations at $p \leq 0.05$; open circles (0) indicate a significant trait variation among populations at $p > 0.05$. Color version of this figure is available online

Table 2 Results of trait–climate model selection using both AIC and all subsets regression variable selection methods (AS)

	MAT		MDR		T. Seas		P. Seas		MAP		PDQ		Avg VPD		Warm-dry15		Warm-wet15		AET:PET	
	AIC	AS	AIC	AS	AIC	AS	AIC	AS	AIC	AS	AIC	AS	AIC	AS	AIC	AS	AIC	AS	AIC	AS
Height			X	X					X	X										
RGR	X	X	X	X			X	X			X	X	X				X			
RSR	X		X	X							X									X
SLA			X		X		X				X									
c.SRL	X	X	X	X																
c.RDMC	X		X		X		X						X	X	X	X			X	X
f.SRL	X	X	X	X	X						X	X			X				X	
f.RDMC			X				X				X		X	X	X	X	X		X	X

Functional trait abbreviations are coarse specific root length (c.SRL), coarse root dry matter content (c.RDMC), fine specific root length (f.SRL), fine root dry matter content (f.RDMC), specific leaf area (SLA), relative growth rate (RGR), and root to shoot ratio (RSR). Climate abbreviations are mean annual temperature (MAT), mean diurnal range (MDR), temperature seasonality (T. Seas), precipitation seasonality (P.Seas), mean annual precipitation (MAP), precipitation of driest quarter (PDQ), annual average vapor pressure deficit (Avg.VPD), average number of days the temperature exceeded 15 °C and soil water potential was below 3.9 kPa in the top 20 cm of soil (warmdry15), the average number of days the temperature exceeded 15 °C and soil water potential was above 3.9 kPa in the top 20 cm of soil (warmwet15), and the ratio of actual evapotranspiration to potential evapotranspiration (AET:PET)

climate variables selected using the all subsets regression method were a nested subset of those selected using AIC for all climate variables except for AET:PET. All climate variables were included in at least one model using the AIC selection, though MAP was a predictor for just one trait, height.

Intraspecific trait–climate relationships tended to be specific among species (Table 3), with both the strength and the directionality of the relationship varying. The mean of correlation coefficients taken across species for a single trait–environment, therefore, tended to be low. For example, the total correlation coefficient between relative growth rate and AET:PET was slightly negative at -0.0886, but obscured the relatively strong positive and negative relationships of individual species (*Pleuraphis jamesii* had a correlation coefficient of −0.743, and *Pseudoroegneria spicata* and

Table 3 Summary of relationship between eight intraspecific traits and ten environmental conditions, ratio of actual to potential evapotranspiration, precipitation of the driest quarter, the average number of days the temperature exceeded 15 °C and soil water potential was above 3.9 kPa in the top 20 cm of soil, average number of days the temperature exceeded 15 °C and soil water potential was below 3.9 kPa in the top 20 cm of soil, the ratio of actual to potential evapotranspiration, vapor pressure deficit, mean annual precipitation, mean annual temperature, and mean diurnal range

	Precipitation seasonality				Precipitation of driest quarter				Temperature seasonality				Warmwet15				Warmdry15			
	Total	−	NS	+	Total	−	NS	+	Total	−	NS	+	Total	−	NS	+	Total	−	NS	+
Height	0.17626	2	1	6	0.12802	2	4	3	−0.18	3	5	1	0.0352	2	4	3	0.2979	1	2	6
Relative growth rate	0.27072	0	4	5	−0.1388	3	4	2	0.0163	2	4	3	0.0595	3	3	3	−0.115	3	4	1
Root:shoot	−0.1597	4	2	3	0.10299	3	2	4	0.0711	4	2	3	−0.1701	5	0	3	−0.146	4	4	1
SLA	0.14918	2	2	5	−0.1036	5	2	2	−0.254	5	4	0	0.0809	2	4	3	0.2772	1	4	4
Coarse SRL	0.03815	3	3	3	−0.1899	4	4	1	0.057	2	5	2	0.1906	1	3	5	−0.164	5	3	1
Coarse RDMC	0.05051	3	3	3	0.051	2	3	4	0.0172	3	2	4	−0.0002	2	6	1	0.0655	4	1	4
Fine SRL	−0.004	4	1	4	−0.0186	2	3	4	−0.107	2	4	3	0.0915	3	4	2	−0.037	1	7	1
Fine RDMC	0.21231	2	1	6	−0.0916	4	3	2	0.025	2	4	3	−0.042	4	4	1	0.1088	4	1	4
	AET:PET				Vapor pressure deficit				Mean annual precipitation				Mean annual temperature				Mean diurnal range			
	Total	−	NS	+	Total	−	NS	+	Total	−	NS	+	Total	−	NS	+	Total	−	NS	+
Height	0.25919	1	4	4	0.08889	3	3	3	0.2069	3	1	5	0.1544	0	6	3	0.0372	3	1	5
Relative growth rate	−0.0886	3	4	2	0.03203	2	5	2	0.1388	1	3	5	0.1441	1	5	3	0.1311	2	3	4
Root:shoot	−0.0819	5	1	3	−0.2044	5	2	2	0.0867	3	1	5	−0.1846	4	2	3	0.0055	3	3	3
SLA	0.15728	2	3	4	−0.0589	3	4	2	−0.034	3	3	3	0.0259	3	3	3	0.0538	1	5	3
Coarse SRL	−0.2829	6	3	0	0.11964	2	2	5	−0.168	4	4	1	0.2108	1	3	5	0.0452	1	5	3
Coarse RDMC	0.22407	1	3	5	0.05684	2	5	2	0.1334	2	3	4	0.0844	2	3	4	0.0207	1	6	2
Fine SRL	0.00237	3	4	2	0.05281	2	4	3	−0.082	4	3	2	0.0458	3	3	3	−0.073	4	2	3
Fine RDMC	0.23604	2	1	6	0.02145	3	2	4	0.0816	2	4	3	0.0649	1	5	3	0.0594	2	4	3

The "total" column is the average correlation coefficient across all species for the given trait–environment relationship; −, + and NS indicates the number of positive, negative and non-significant relationships. See Table 2 legend for trait abbreviations

Koeleria macrantha both had correlation coefficients of 0.53, Table S3). Across all climate variables, precipitation seasonality had the most significant (positive and negative) relationships (55 out of 72) across traits, followed by MAP (50), AET:PET (49), precipitation of driest quarter (47). Warm wet soil and vapor pressure deficit had 45 out of 72 significant relationships, mean diurnal range and warm dry soil each had 43 significant relationships. MAT and temperature seasonality had the fewest significant relationships across traits (42 out of 72).

Discussion

Trait variation

All the traits we examined displayed more variation among species than among populations, with the exception of SLA. Variation within species ranged from approximately 11% (fine RDMC) to 39% (relative growth rate). These results fall within the range of other assessments of ITV in communities (Siefert et al. 2015), though the present results differ by reflecting solely genetic variation among populations spanning the full breadth of species distributions.

The amount of variation explained by population varies by functional trait. In general, functional traits related to plant size such as height, relative growth rate and root–shoot ratio were more explained by population, whereas organ-level traits, such as SLA and SRL displayed less intraspecific variation. Values of intraspecific variation were concurrent with the range published within the literature (generally around one quarter to one-third of total variation (Siefert et al. 2015; Albert et al. 2010).

When trait variation was evaluated at the species level, root traits showed less intraspecific variation compared to aboveground traits. We cannot conclude from our data that the overall smaller amount of inter- and intraspecific variation in roots indicates greater genetic plasticity; however, we believe that measuring root trait plasticity is an interesting avenue, given the diversity of soil environments and biotic conditions a single species may occupy in a relatively small

area. Roots must mediate interactions with neighbors (Valverde-Barrantes et al. 2013), respond to aboveground pressures such as herbivory and grazing (Smith et al. 2014), and respond to changes in soil gradients across relatively small spatial scales (Chen et al. 2013). Additionally, root traits have also been shown to respond plastically to mycorrhizal colonization (Weremijewicz and Seto 2016). Differences in the variation we were able to account for in our experiment between below and aboveground traits suggest that comparisons of trait plasticity between these two realms could also be a potentially interesting avenue of research.

Trait–environment relationships

Model selection indicated that some climate variables are promising for characterizing relationships between climate and functional traits, including mean diurnal temperature range and precipitation of driest quarter. Daily temperature variation has been shown to influence biogeochemical processes in drylands (van Gestel et al. 2011, 2016), which may offer a mechanism for its importance for predicting functional traits. However, the direct effects of mean diurnal range on trait dimensionality appear to be unstudied. In agreement with Moles et al. (2014) the least supported climate variable in model selection was mean annual precipitation, suggesting precipitation alone is a poor predictor of traits. Though environmental variables representing aspects of soil moisture were not commonly selected for models, all three soil moisture-related variables were selected as predictors for root traits. The strength of precipitation of the driest quarter as a predictor variable in the model selection outcome may help to illustrate the role that more extreme climatic conditions have on functional traits as extreme climate events such as severe drought might be more important in determining functional trait distributions rather than climate means (Weiher and Keddy 1995). In pairwise comparisons, 18 predictor variables did show highly significant correlations ($p > 0.001$, figure S4). However, this does not change our interpretation of the trait–environment models using a single predictor, and colinearity is addressed with the all subsets regression and AIC selection in models that have more than one predictor.

Even when factors that might interact with climate such as land use history, soil environment, and herbivory were eliminated in a common garden experimental setting, consistent patterns between climatic factors and functional traits within species did not emerge from our study. Responses to climate were unique to both traits and species. While we intentionally selected traits representing different axes, we would not necessarily expect correlated traits to display similar relationships to climate, as correlated traits may still be subject to different environmental filters (Sandel et al. 2016). The strength of predictions between the environment and trait outcomes may improve by incorporating information about soils. More detailed edaphic gradients including variables such as soil texture, pH, or cation exchange capacity may yield more and clearer patterns of trait variation (Jager et al. 2015; Pakeman 2013; Siefert et al. 2014; Simpson et al. 2016). Because we grew first generation seeds due to logistical constraints of the study, we also acknowledge that this study does not address the potential input of maternal effects due to different land use history, annual climatic conditions and localized habitat differences of the individual accessions.

Intraspecific trait variation among populations from field studies help to reinforce our findings from the greenhouse. While plants grown under favorable, resource-rich greenhouse conditions may display different values of both below- and aboveground traits from plants grown under natural conditions (Freschet et al. 2017; Schechter and Bruns 2013; Téllez and Møller 2006), we found that the variance of trait values between several of the species grown in the greenhouse and naturally in a field setting was essentially the same (Butterfield et al. 2017). Thus, results found under the conditions of greenhouse findings still inform our expectations of plants grown in natural settings. The focal specis of this study are commonly used in restoration of degraded rangelands across the Western US, making our findings highly relevant to the growing field of functional restoration (Wainwright et al. 2018). Functional restoration uses predictions of plant performance based on the environment in conjunction with the desired ecosystem effect of functional traits, such as enhancing soil stability or mitigating invasion risk (Funk et al. 2008; Jager et al. 2015), to help address specific restoration goals (Laughlin 2014).

A crucial opportunity for this field is using functional ecology to inform restoration decisions in the context of climate change, as plants become increasingly maladapted to their historical range (Harris et al. 2006; Havens et al. 2015). To this end, population-level differences prove to remain important (O'Neill et al. 2008). As the field of functional restoration continues to develop, understanding how the environment drives functional traits may make taking future climate into account easier when selecting either populations or species for restoration (Prober et al. 2015). Linking functional traits to environmental variation presents an opportunity to match trait values to climate, rather than a static location as in the "local is best" approach to restoration. If trait–environment relationships were consistent among species, seed source selection and trait–environment matching in a restoration context could be readily conducted using generalizable models across taxa. Our finding that trait–environment relationships differ among important restoration species indicates that species-specific models of adaptive responses of functional traits to environmental variation may need to be incorporated into seed selection and development.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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