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# Population and species neighbor identity impact trait–trait relationships and plant performance

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**Abstract**

Evaluating restoration practices such as admixture provenancing or mixing of multiple source populations for greater intraspecific variation in plant restorations helps to understand the utility of the practice in different scenarios. We do not know whether *any* population mixtures in admixture provenancing will deliver positive outcomes when interacting. To understand how population and species' identity influence plant performance and trait outcomes in mixtures, we assessed trait variation among populations of two forb species native to the Western United States (*Dieteria canescens* and *Heterotheca villosa*) following pairwise competition in pots with single-population monocultures, two-population mixtures, and two-species mixtures with *D. canescens* as a focal plant in a greenhouse common environment. Plants were harvested after 7 weeks and height, leaf count, root length, and root mass fraction (RMF) traits were measured, as well as whole plant biomass. We found two-population mixtures and single-population monocultures to have similar biomass while some two-species mixtures differed from respective single-population monocultures. Neighbor trait differences in shoot height and root length best predicted plant growth following interactions, while increasing neighbor trait differences resulted in positive growth outcomes for all but one trait by treatment interaction ($R^2 = 0.17$, $p < 0.001$). In this single case, plant growth decreased with increasing differences in RMF for the two-species mixture treatment, surprisingly. These findings show nuance in the outcomes of interactions within and between populations and species: they are highly dependent on population identity and traits measured, which are aspects that must be considered when evaluating restoration materials and strategies.

**KEYWORDS**

admixture provenancing, interactions, intraspecific variation, plasticity, trait hierarchy

## 1 | INTRODUCTION

Understanding aspects of plant–plant interactions at early life stages informs practical applications including how interactions promote or hinder plant restoration. Restoration practitioners often have the goal of creating communities or populations that are self-sustaining and persist over the long term (Society for Ecological

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Restoration, 2002), and approach this aim with many methods (e.g., De Vitis et al., 2022; Hallett et al., 2023). One restoration method is the mixing of multiple source populations, called admixture provenancing, for putatively greater intraspecific variation in plant restorations to improve both short- and long-term restoration outcomes (Breed et al., 2013; Bucharova et al., 2019). This appears to be a fruitful path for restoration practice because research demonstrates the benefits of increasing intraspecific variation on populations; this includes increases to plant survivorship, disease resistance, insect diversity, reductions to invasibility, community productivity, and the delivery of ecosystem benefits through mechanisms such as genetic and morphological diversity (Crawford & Rudgers, 2013; Kettenring et al., 2014; Su et al., 2023). However, positive effects of population mixtures depend on the sown genotypes, their competitive abilities, and whether the combination influences species interactions and diversity (sensu Chesson, 2000). Therefore, admixture provenancing approaches require further examination to understand their efficiency in delivering species diversity and ecosystem benefits.

One key knowledge gap for mixing populations is whether doing so changes the competitive dynamics of the interacting individuals when compared to both single-population monocultures and interspecific mixtures. This is important because species coexistence is predicated on intense intraspecific competition that results in self-limitation and weakened interspecific competition (Chesson, 2000). Self-limiting coexistence-promoting dynamics can be destabilized if population mixtures weaken intraspecific competition relative to single-population monocultures. Furthermore, self-limiting dynamics coupled with weaker interspecific competition compared to single-population monocultures help to promote species diversity (Adler et al., 2018; Chesson, 2000; HilleRisLambers et al., 2012) and researchers have advocated for incorporating the principle of self-limitation among populations into restoration goals (Des Roches et al., 2018; Hallett et al., 2023). Some studies have not shown the above-mentioned ecosystem benefits of mixing populations (Booth & Grime, 2003; Reiss & Drinkwater, 2018), and few studies, to our knowledge, have explicitly examined plant–plant trait interactions that influence intraspecific competition (Montazeaud et al., 2020). In fact, the resulting performance of mixed populations varies depending on the populations or genotypes in the mixture (Abbott & Stachowicz, 2016; Cope et al., 2021; Genung et al., 2012; Noto & Shurin, 2016). This indicates that we must evaluate the performance of different population mixes, and even preliminary evidence will help generate hypotheses for future research.

Varying performance outcomes between population mixtures make it unclear how to use admixture provenancing in restorations, but the picture can be made clearer by understanding what often leads to variability in plant interactions—functional trait variation. Specifically, trait values and trait differences between neighbors influence variation in competitive dynamics among and between populations and species (e.g., Foxx & Kramer, 2020; Leguizamón et al., 2011; Montazeaud et al., 2020). Plant–plant interactions can result in plasticity-induced trait variation by modifying the local availability of resources. How trait variation influences plant performance depends on whether greater trait differences between neighbors reduce competition (*limiting similarity*; Bennett et al., 2016; Fargione & Tilman, 2005) or intensify competition (*trait hierarchy*; Fort et al., 2014; Carmona et al., 2019). Most research on trait differences has been conducted at the species level (Feng & van Kleunen, 2016; Funk & Wolf, 2016; Kraft et al., 2014) and the limited empirical research on population mixtures reveals the importance of trait differences to competitive exclusion (Abbott & Stachowicz, 2016; Mahaut et al., 2023). We lack resolution on which traits and competitive relationships drive competitive outcomes, especially at an intraspecific level, which are needed to improve our understanding of how to prioritize morphological diversity within restored communities.

Traits can differ in how they influence plant survival, growth, reproduction (Violle et al., 2007), and competition, and root and shoot traits differ in their influences on plant performance under competition (Foxx & Fort, 2019; Kiaer et al., 2013). Additionally, different species will have different requirements for resources such as the difference between Fabaceae and Poaceae for nitrogen availability, and this is related to their traits and trait values (He et al., 2018). This also explains why competition between individuals of the same species differs from competition between two species. Moreover, the importance of the impact of trait differences on competition may change depending on the plant compartment considered: for example, neighbor shoot size differences often lead to intensified competition compared to neighbor root size differences (*size-symmetric and asymmetric competition*; Casper & Jackson, 1997; Del Río et al., 2014; but see Rajaniemi & Reynolds, 2004). Outlining trait targets that have the strongest influence on outcomes in intraspecific mixtures can support more rapid screening of populations under consideration for mixing.

In all, it is important to first know which traits vary the most among and within populations, which traits have the strongest (magnitude) influence on biomass, and lastly the directionality of those effects for growth outcomes. So here, we use a greenhouse study to

**TABLE 1** *Dieteria canescens* and *Heterotheca villosa* population source information. 'Accession' is the Seeds of Success voucher number.

| Species | Population code | Source | Accession | Latitude | Longitude | Elevation (m) | Level III ecoregion |
|---|---|---|---|---|---|---|---|
| *D. canescens* | DICA-A | Utah, USA | UT060-27 | 39.0273 | −109.2126 | 1338 | Colorado Plateau |
| | DICA-B | Utah, USA | UT080-193 | 40.0650 | −109.2907 | 1510 | Colorado Plateau |
| | DICA-C | New Mexico, USA | NM930N-90 | 36.2909 | −107.8842 | 2036 | New Mexico Plateau |
| *H. villosa* | HEVI-A | New Mexico, USA | NM930N-84 | 35.9654 | −107.0968 | 2123 | Colorado Plateau |
| | HEVI-B | Utah, USA | UT080-134 | 40.5149 | −109.7113 | 2491 | Colorado Plateau |
| | HEVI-C | Utah, USA | UT933-323 | 39.1169 | −111.2903 | 2504 | Wasatch Montane/Uinta Mountains |

*Note*: We present information on latitude, longitude, elevation, and the Level III ecoregion (Omernik, 1987) of each source population.

understand how population mixtures influence plant performance (measured as plant biomass) and whether traits differ in their influence on plant performance for three interaction treatments: single-population monocultures, two-population mixtures, and two-species mixtures. For plants growing in these treatments, we assessed variation in four traits: plant height, leaf count, root mass fraction (RMF), and root length. We used six populations: three from each of two restoration-relevant forb species (*Dieteria canescens* and *Heterotheca villosa*). Each species is native to the western United States where the practice to move and mix populations is increasing for restoration efforts (St. Clair et al., 2020; Wood et al., 2015). This system is ideal for study as both species co-occur and we previously documented both within- and among-population intraspecific variation in root and shoot traits for both species: the partitioning of this variation depended upon the trait measured (Zeldin et al., 2020). We ask (1a) Will two-population mixtures have differing competitive outcomes compared to single-population monocultures when evaluating plant biomass? (1b) Will two-species mixtures have differing competitive outcomes from single-population monocultures? (2) Will trait differences predict focal plant biomass and vary by trait and interaction treatment type? and (3) Will interaction type affect which traits best predict plant performance?

## 2 | METHODS

### 2.1 | Species and population information

We used two co-occurring perennial forbs native to the western United States from the Asteraceae family: *D. canescens* (Pursh) A. Gray (syn. *Machaeranthera canescens*) and *H. villosa* (Pursh) Shinners. These are priority species for use in large-scale restoration efforts in the Colorado Plateau (Wood et al., 2015; Zeldin et al., 2020). We used three populations each of *D. canescens* (DICA) and *H. villosa* (HEVI) from across eastern Utah and northwestern New Mexico, USA (Table 1), where seeds are currently moved and mixed for restoration (Wood et al., 2015). We sourced wild-collected seeds of both species from the Seeds of Success program, which uses standardized seed collection protocols to maximize genetic diversity represented in the collection (Haidet & Olwell, 2015).

### 2.2 | Propagation and design

We propagated and established plants in a greenhouse at the Chicago Botanic Garden (Glencoe, IL, USA). We planted one seed each into 2-cm cells in 200-cell trays with loam soil and watered them. Planting was carried out over 10 days in August 2018. Immediately after planting, we placed all trays in refrigerators at 3°C in the dark for 3 weeks to break dormancy. We then simultaneously moved the trays to a fog house to encourage emergence and establishment, maintaining moist soil at 18.3°C under ambient light for 4 weeks. Following establishment, we moved plants to experimental treatments in a greenhouse at 20°C/17.2°C day/night temperatures and 60% relative humidity. We moved seedlings from germination trays after watering them to keep soil intact and planted the seedlings between October 8, 2018 and October 16, 2018 into 5.1 cm × 5.1 cm × 10.2 cm pots (Stuewe & Sons, Tangent, OR, USA) with a 30% sand and 70% loam soil mixture, then immediately watered the seedlings. We simultaneously added two seedling neighbors to each pot. We organized pots into trays as blocks with 9 interaction treatments (see Section 2.3) randomly assigned to trays, with 305 pots. We allowed plants to interact for 7 weeks. We watered plants once every 4 days

and fertilized at weeks 1 and 4 using a solution containing 237 ppm nitrogen, phosphorus, and potassium. The greenhouse was sprayed weekly with MainSpring GNL insecticides (MainSpring, MD, USA) against aphids, mites, and thrips.

## 2.3 | Experimental treatments

*Dieteria canescens* served as the focal plant in the 18 pairwise competition treatments (Table S1). This included two types of intraspecific interactions: (i) single-population monocultures with two individuals of the same population for each of the three populations (three treatments); (ii) two-population mixtures with one individual from two different populations in each of three treatments (six treatments); and two-species mixtures, with each population of one species interacting with each population of the other species (nine treatments total). All treatments were replicated between seven and 20 pots and varied due to variation in germination success (305 total pots; Table S1).

## 2.4 | Data collection

Plants grew together for 7 weeks and both plants survived in more than 90% of our pots; we removed all pots where one or both plants died during the experiment from the analyses. At harvest, we watered each pot and separated the roots of the two interacting plants using hair conditioner (Alberto Vo5, Melrose Park, IL, USA) diluted in tap water to ease tangling, then rinsed with water. We lost little root material during root separation. Next, we photographed the plants while they were submerged in water, then removed the plants from water and measured plant height and length of the longest root with a ruler, then separated plants into aboveground and belowground parts before placing each part in separate envelopes. We then dried the plants in an herbarium drier at 35°C for 1 week. Plant samples were then kept at room temperature until processing 2 months later, when they were weighed to the nearest mg. Leaf count data were collected from plant images.

## 2.5 | Traits and calculations

We used full plant mass, root mass, leaf count, root length, and shoot height to make several trait calculations including RMF (root mass divided by total mass). The following variables were square root transformed to meet assumptions of normality: focal root length, focal root mass, focal shoot mass, and total mass; and we log-transformed focal plant height. We removed one focal RMF outlier value that fell beyond the medians of boxplots of the data.

We calculated the hierarchical or relative trait distances to test whether resulting trait differences predict focal plant biomass. We used the equations $t_a - t_b$, where $t_a$ is the trait of the focal plant and $t_b$ is the trait of the nonfocal neighbor plant (Fort et al., 2014, 2015; Kunstler et al., 2012). We made one calculation for each pot between plant neighbors on untransformed data for four trait distances: plant height difference, leaf count difference, RMF difference, and root length difference. Trait distances close to zero indicate the neighbor traits were similar, whereas nonzero values indicate trait differences between the focal and nonfocal plants.

## 2.6 | Analyses

All analyses were carried out in R (R Core Team, 2023, v4.3.2). We used focal plant biomass as an indicator of interaction outcomes. We first addressed Hypothesis 1a and 1b that two-population mixtures will have differing competitive outcomes from single-population monocultures when evaluating plant biomass. We used single-population monoculture groups as the reference, as species should compete more intensely with individuals of their own species than they do with individuals of different species for stable coexistence (Chesson, 2000), and deviations may positively or negatively influence the probability of coexistence. We calculated the standardized mean difference (SMD) and confidence intervals of total biomass of the two-population mixtures compared to single-population monocultures of the focal population. The SMD was calculated using the following equation:

$$\mathrm{SMD} = \frac{\bar{x_1} - \bar{x_2}}{S},$$

where $\bar{x_1}$ and $\bar{x_2}$ are the biomass means of two-population mixtures or two-species mixtures and single-population monocultures, respectively, and $S$ is the pooled standard deviation,

$$\sqrt{\left((n1_i - 1) * \mathrm{SD1}_i^2 + (n2_i - l) * \mathrm{SD2}_i^2\right)} / (n1_i + n2_i - 2),$$

where SD1 and SD2 are the standard deviations for the two-population and two-species mixtures and single-population monocultures, using the *escalc* function in the *metafor* package (Viechtbauer, 2010). The SMD denotes

the magnitude of difference between group means under comparison and addresses *how different* the groups are and in what direction. When the SMD is equal to zero, there is no difference between the means, and when the SMD is above zero, it indicates that the focal plant in two-population or two-species mixtures grew larger than in single-population monocultures, and SMD values below zero denote larger plants in the single-population monoculture compared to two-population and two-species mixtures. SMD values of 0.2 are generally considered small, 0.5 are medium, and 0.8 are large effects (Cohen, 1988). We calculated the 95% confidence intervals of the SMD using the cohen.d.ci function in the *psych* package (Revelle, 2022). Confidence intervals that do not overlap with zero indicate that the standardized mean values significantly differ by treatment groups of two-population and two-species mixtures compared to single-population monocultures (Faraone, 2008; Valentine et al., 2010).

Next, we address Hypothesis 2 and test whether trait differences will predict focal plant biomass, varying by trait and interaction treatment type. We first scaled neighbor trait difference variables to have means of zero and standard deviations of one (*z*-score scaling). We used one linear model with the maximal model containing the focal plant total biomass as the response variable and trait distance for neighbor interacting with interaction type (total $\text{biomass}_{\text{focal}} \sim \text{trait}$ difference * interaction type * trait type). We selected the best model using the *stepAIC* function in the *MASS* package (Venables & Ripley, 2002) which selects models with the lowest Akaike Information Criterion (AIC) value. We then addressed whether the relationships between focal plant total biomass and trait differences differ between treatment types. To do so, we performed a post hoc comparison test of slopes on four separate linear models with total mass as a response and interaction type as a predictor using the *pairs* and *lstrends* functions in the *emmeans* package (Lenth, 2022) for each trait.

Lastly, we addressed Hypothesis 3 and tested whether the trait that best predicts plant performance (shoot height difference, leaf count difference, RMF difference, and root length difference) will differ by interaction type. Following *z*-score scaling, we then used three multivariate linear regressions along interaction type with neighbor trait difference variables to evaluate how each trait difference variable influenced plant biomass using a multiple regression:

$$\text{Single} - \text{population monocultures}: \text{Total mass} = \beta_0 + \text{RMF} + \text{leaf count} + \text{root length} + \text{height}.$$

$$\text{Two} - \text{population mixtures}: \text{Total mass} = \beta_0 + \text{RMF} + \text{leaf count} + \text{root length} + \text{height}.$$

$$\text{Two} - \text{species mixtures}: \text{Total mass} = \beta_0 + \text{RMF} + \text{leaf count} + \text{root length} + \text{height}.$$

We estimated the relative importance of predictors (amount of variance explained, $R^2$) in the models using the Lindemann, Merenda, and Gold method and the Last method (determines each variables' contribution when included last) in the *calc.relimp* function in the *relaimpo* package (Grömping, 2006) to determine the influence each variable had on biomass following interactions. We then assessed multicollinearity using correlation plots and calculating the variance inflation factor with the *vif* function in the *car* package (Fox & Weisberg, 2019). Large variable inflation factor (VIF) values and high correlation indicate high correlation between variables and multicollinearity (Thompson et al., 2017) and convention dictating values greater than 10 indicating highly correlated variables.

## 3 | RESULTS

### 3.1 | Two-population and two-species mixture's influence on interaction outcomes

Plants demonstrated plastic responses to neighbor identity, and this was moderated by the plant's population identity (Figure S1). Population mixtures varied in whether the focal plant experienced more or less intense competition compared to the single-population monoculture (Figure 1). While two-population and single-population monocultures did not statistically differ in biomass response to interactions, DICA-B responded differently to competition from different HEVI populations (i.e., DICA-B vs. HEVI-B differed from DICA-B vs. HEVI-A; Figure 1). Three of these treatment comparisons had SMD confidence intervals that did not span zero, indicating a statistical difference between the means of the focal plant in two-species mixtures and single-population monocultures (two that led to lower biomass in the focal plant in two-species mixtures versus single-population monoculture: DICA-A vs. HEVI-B, DICA-B vs. HEVI-C, and one with higher biomass in the two-species mixtures: DICA-B vs. HEVI-B).

### 3.2 | Impacts of trait differences on focal plant biomass by interaction type

Greater trait differences resulted in larger focal plants for plant height, leaf count, and root length for two-population

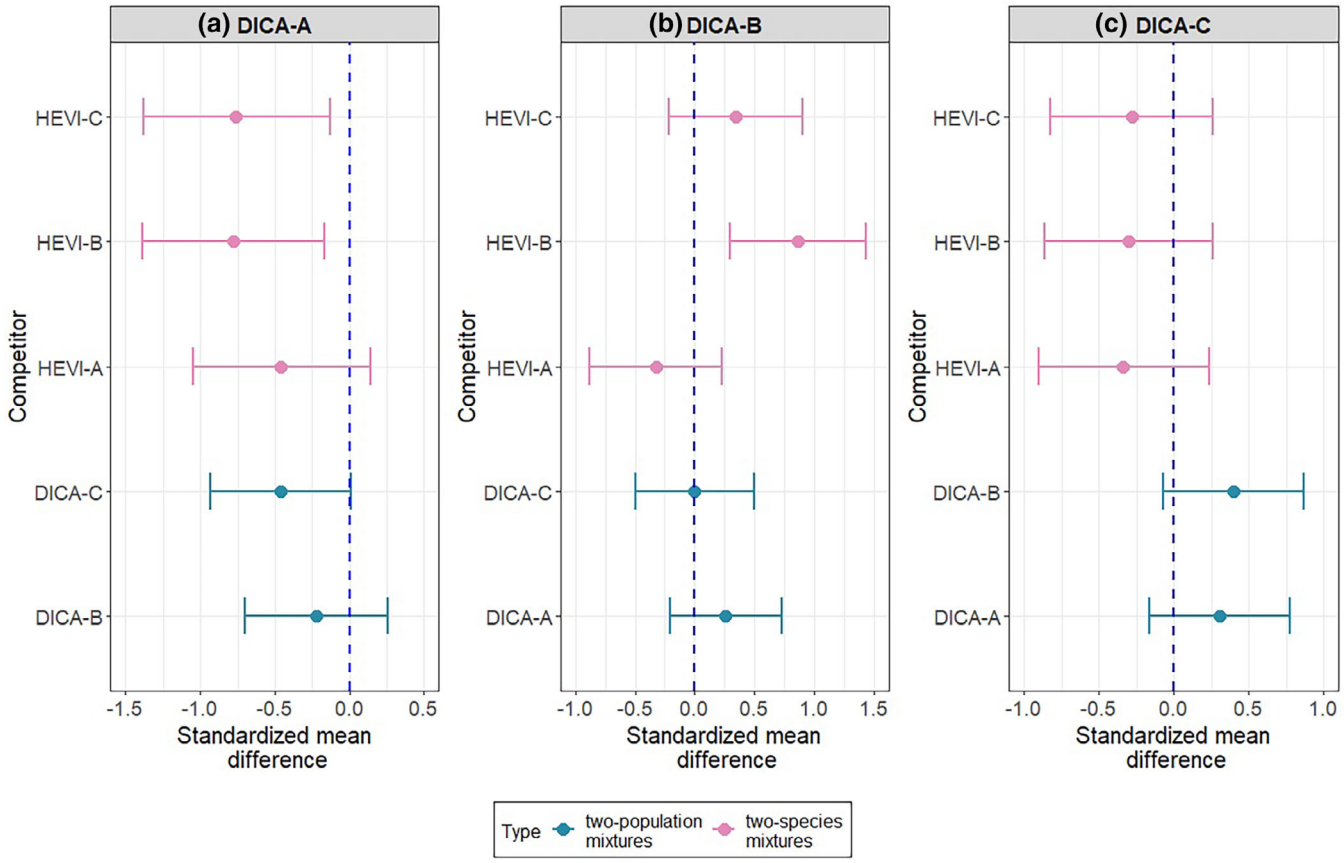



**FIGURE 1** *Dieteria canescens* (DICA) standardized mean difference (SMD) comparing between two-population or two-species mixtures (with *Heterotheca villosa*; HEVI) with the single-population monoculture treatments on focal whole plant mass (mg). The header population is the focal population A (a), B (b), and C (c), and names on the *y*-axis are the neighboring plants. Negative SMD values (left of dashed line) indicate that the focal plant was smaller when interacting with an individual from a different population or species compared to the single-population monoculture. Points are SMD values with 95% confidence intervals. The dashed line represents where the two neighbor values are equal.

and two-species mixtures and single-population monoculture treatments. Conversely, greater trait differences resulted in smaller focal plants for RMF among two-species mixture treatments (Figure 2). Variation in the relationship between focal plant total mass and all relative trait differences between neighbors was significantly explained by an interaction between interaction type and trait type ($R^2 = 0.17$, $F_{23,2387} = 21.24$, $p < 0.001$, AIC $= -433.03$). The steepness of the slopes representing the relationships varied (Table 2): the contrasts comparing the relationships between relative trait differences and plant mass differed significantly only when comparing RMF between interspecific mixtures and monocultures and between interspecific mixtures and population mixtures ($p < 0.001$; Table S2).

Whether differences in traits were important to focal plant mass varied by interaction type and trait. The combination of all the trait differences explained 32% of the variance of focal plant biomass for single-population monocultures ($R^2 = 0.32$, $F_{4,89} = 10.57$, $p < 0.001$), 42% for two-population mixtures ($R^2 = 0.42$, $F_{4,195} = 35.51$, $p < 0.001$ on 4 and 195 df), and 34% for two-species mixtures ($R^2 = 0.34$, $F_{4,264} = 34.46$, $p < 0.001$). When assessing the influence of individual trait differences by interaction types, trait differences have a consistent effect, but the traits that explain a larger amount of variation differ for the three interaction types. Shoot height differences between neighbors explained the most variation in focal plant biomass resulting from two-population mixtures; root length differences between neighbors explained most variation in focal plant biomass resulting from two-species mixtures; and RMF difference explained the most variation in biomass for two-population mixtures and had no effect on the two-species mixtures (Figure 3). Low VIF values and the absence of highly correlated predictor variables indicate the lack of collinearity (Figure S2).

## 4 | DISCUSSION

In this study, we show that the outcome of competitive interactions between plants can vary depending on the population identity of interspecific neighbors and weak

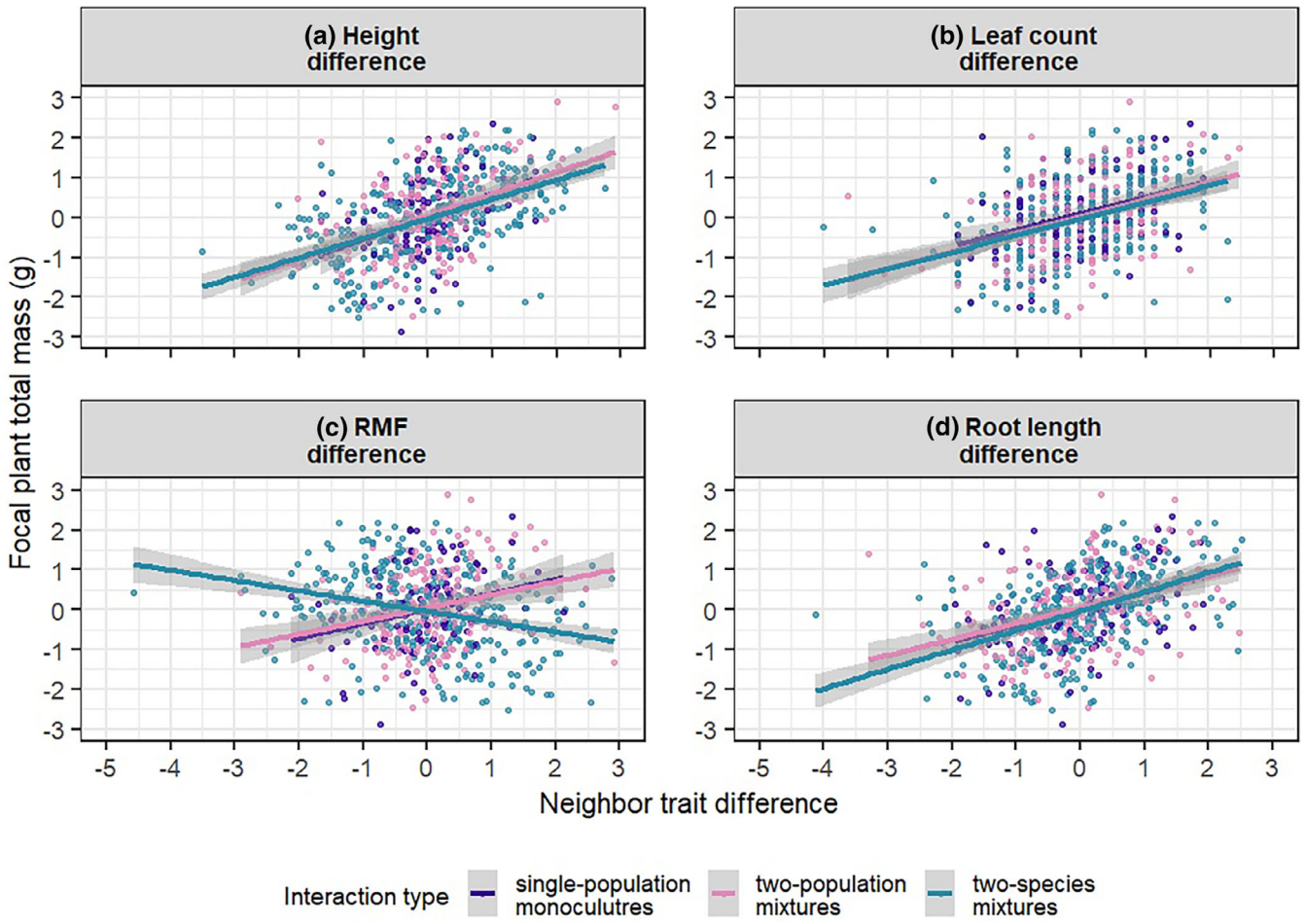



**FIGURE 2** Relationships between relative trait differences and scaled focal plant whole mass for *Dieteria canescens* (DICA) grown in single-population monocultures, two-population mixtures, or in two-species mixtures with *Heterotheca villosa* populations. For (a) neighbor shoot height difference (cm), (b) leaf count difference, (c) root mass fraction (RMF) differences, and (d) root length difference (cm) presented by interaction type. Fitted lines are from linear models, gray shading is the standard error of the fit, and points are raw values.

**TABLE 2** Correlation and equations of lines for the relationships between plant mass and trait differences (root length difference, shoot height difference, leaf count difference, and root mass fraction [RMF] difference) of the focal plant by interaction type.

| Interaction type | Trait difference | *r* | *p*-value | Intercept | Slope |
|---|---|---|---|---|---|
| Two-species mixtures | Height difference | 0.498 | <0.001 | −0.03 | 0.431 |
| Two-species mixtures | Leaf count difference | 0.419 | <0.001 | −0.04 | 0.391 |
| Two-species mixtures | RMF difference | −0.292 | <0.001 | −0.04 | −0.258 |
| Two-species mixtures | Root length difference | 0.488 | <0.001 | −0.04 | 0.485 |
| Two-population mixtures | Height difference | 0.472 | <0.001 | 0.04 | 0.546 |
| Two-population mixtures | Leaf count difference | 0.436 | <0.001 | 0.02 | 0.436 |
| Two-population mixtures | RMF difference | 0.293 | <0.001 | 0.05 | 0.330 |
| Two-population mixtures | Root length difference | 0.378 | <0.001 | 0.05 | 0.370 |
| Single-population monocultures | Height difference | 0.364 | <0.001 | 0.02 | 0.565 |
| Single-population monocultures | Leaf count difference | 0.378 | <0.001 | 0.09 | 0.408 |
| Single-population monocultures | RMF difference | 0.268 | 0.007 | 0.02 | 0.371 |
| Single-population monocultures | Root length difference | 0.390 | <0.001 | 0.02 | 0.415 |

*Note*: Correlation and equation parameters were calculated on raw values. RMF is calculated by root mass divided by total mass.

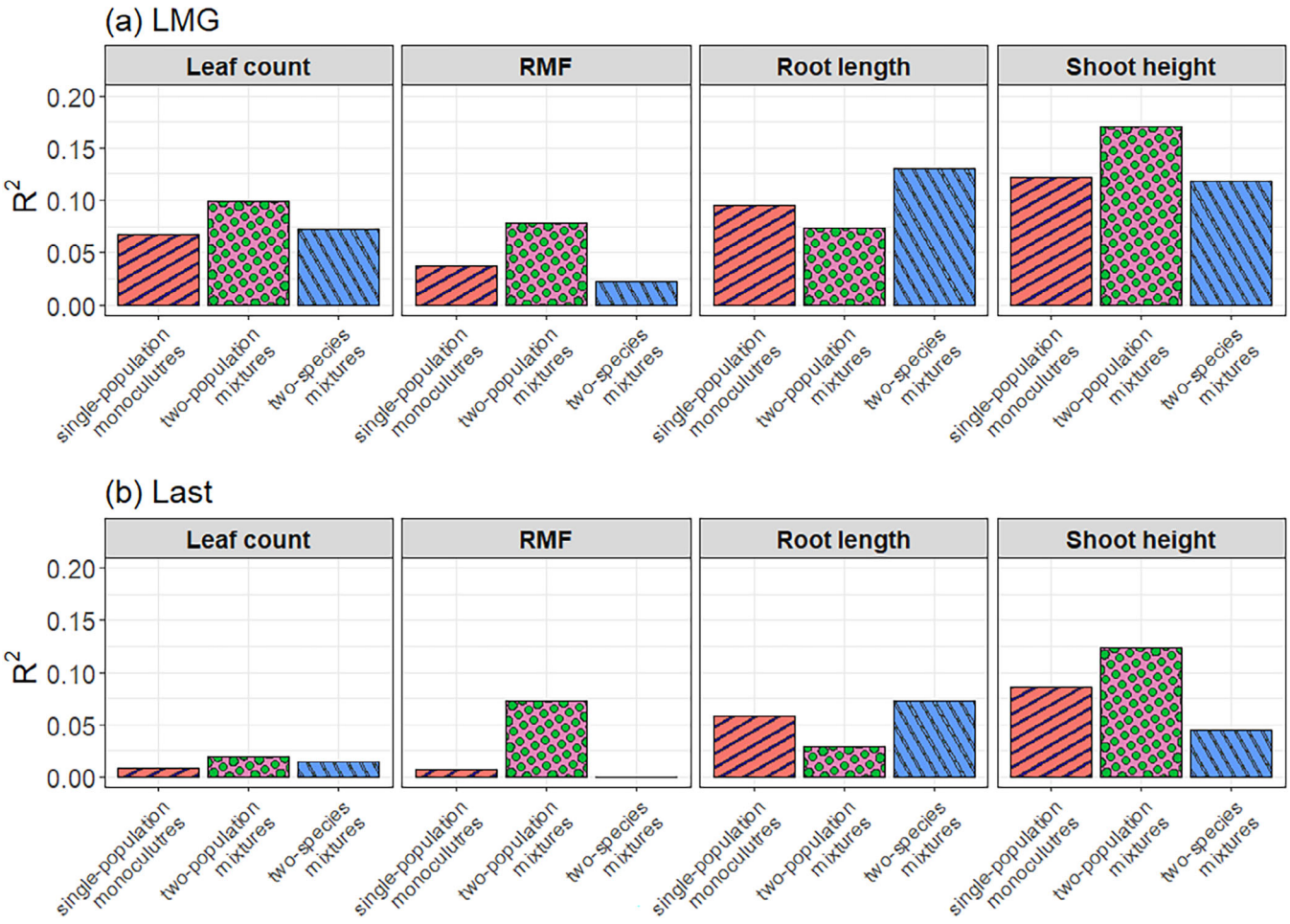



**FIGURE 3** Variable relative importance values, measured as average $R^2$, for the effect of neighbor trait differences on focal plant biomass (mg), based on four traits: leaf count, root mass fraction (RMF), root length, and shoot height. (a) Values calculated using the Lindemann, Merenda, and Gold (LMG) method. (b) Values calculated using the Last method for determining relative importance.

evidence that two-population mixtures result in performances that deviated from single-population monocultures. Importantly, we also show the difference in particular traits (e.g., RMF, root length, height, leaf count) varied in influence on focal plant biomass by interaction type (trait hierarchies vs. limiting similarity). These outcomes reflect that trait differences impact plant interactions depending on population identity and interaction types considered, with potential importance for species coexistence.

## 4.1 | Some two-population and two-species mixtures deviate from single-population monocultures

We found variability in whether focal plants were more suppressed when growing in single-population monocultures compared to two-population or two-species mixtures. Two-population and single-population monocultures did not differ in the imposed treatments and instead ranged nonsignificantly in general directions of more competitive or more facilitative (e.g., DICA-A two-population mixtures tended toward more suppressed than monocultures and DICA-C two-population mixtures trended toward less suppressed than monocultures). While we did not find evidence through biomass outcomes that two-population and single-population differ, our study was conducted in a greenhouse, and longer-term and field-based research will help elucidate if positions of the Modern coexistence theory hold true or whether competitive population mixtures would promote or hinder species coexistence (Chesson, 2000; HilleRisLambers et al., 2012; Mayfield & Levine, 2010), and thus influence restoration outcomes. Correspondingly, some two-species mixtures competed less intensely than in the single species monocultures (i.e., DICA-B vs. HEVI-B, DICA-B vs. HEVI-C), hinting at an ability to coexist and promote diversity in restoration settings. Coupled with our findings, evidence is mounting that positive intraspecific interactions can mitigate harm

from stressful environments; we need a nuanced perspective to understand factors influencing outcomes of intraspecific interactions (Reijers et al., 2019). However, ultimately, our methods lack treatments that examine how population mixtures influence interspecific interactions and exploring other coexistence mechanisms such as herbivory and time (Chesson, 2000); these are fruitful areas of future work.

## 4.2 | RMF trait differences follow a different pattern for two-species mixtures than intraspecific treatments

Another key result from this study was that, as trait distances were greater, the focal plant mass was greater between neighboring plants for height, leaf count, and root length. This was also evident for single-population monocultures and two-population mixtures for RMF, but two-species mixtures for RMF differences had opposing patterns. In this case, the focal plant mass was suppressed when the trait value of the neighboring plant was greater, suggesting variability in which trait differences result in trait hierarchies or limiting similarity (Kunstler et al., 2012). These surprising results could indicate limited coexistence of these neighbors and demonstrate that species mixtures, monocultures, and population mixtures must simultaneously be evaluated when exploring the relationship between traits and competitive outcomes. Furthermore, while aboveground traits like plant height and leaf count are important traits that influence light capture for photosynthesis (Perez-Harguindeguy et al., 2013; Westoby, 1998), one major undercurrent in trait-based ecology is that many empirical studies investigating the impacts of trait differences on interactions focus on aboveground traits (Carmona et al., 2019; Gross et al., 2015; Kraft et al., 2014). Our important findings on the differential influence of RMF by interaction type demonstrate that an aboveground trait approach only tells part of the story.

## 4.3 | Trait type with the greatest influence on focal plant biomass differed by interaction type

This is the first study, to our knowledge, to evaluate if single-population monocultures and multi-population mixtures differ in how neighbor trait difference influences plant performance. Interestingly, neighbor trait differences explained the most variation in biomass for two-population mixtures compared to single-population monocultures and explained the most variation in biomass for two-species mixtures for leaf count, RMF, and shoot height. One potential reason for neighbor differences explaining greater variability in two-population mixtures is that there may be more genetic similarities among individuals from the same population (single-population monoculture) compared to the cumulative genetic diversity with individuals from two different populations (two-population mixtures)—but, surprisingly, we see the opposing pattern of slightly more variability in single-population monocultures. We hypothesize that this increase in trait difference may better explain competitive interactions among plants from different populations of the same species than from different species because within the same species, trait values are more comparable, sharing similarities in physiology, phenology, and so forth. On the other hand, with interspecific interactions, some differences in resource acquisition strategies are not fully captured by the same traits—this is a phenomenon that could blur relationships. Furthermore, it appears that two-population mixtures are not equivalent to single-population monocultures in this system and that the influence of trait differences on focal plant biomass tends toward a different ecological strategy for two-species mixtures compared to single-population monocultures. Explicitly, trait differences have a greater influence on focal plant biomass response for two-population mixtures compared to single-population mixtures—but both interaction types result in the same trait distance-focal biomass patterns (Figure 2). Are these population mixtures a middle ground between being similar (monoculture) or markedly more different (species mixtures) that produce these outcomes? This requires more examination and research, specifically, to fully explore the conditions and mechanisms under which multipopulation mixtures deviate from single-population monocultures.

Neighbor differences in shoot height explained the most variation in the focal plant mass for two-population mixtures, and this signifies the cruciality of light competition between conspecifics in this system. Overall, when considering biomass effects due to neighbor trait differences, plants with taller shoots, more leaves, and longer roots were less impacted by competition and impacted neighbors more. This corroborates that size-related traits directly relate to competitive ability (Violle et al., 2009). Additionally, the implication of the importance of light is surprising for three reasons: (1) the importance of belowground resource capture in the arid environments from which these plants were sourced, (2) root competition is generally more intense than shoot competition, and (3) because the source arid environment is light-unlimited (Fowler, 1986; Schenk & Jackson, 2002). Unfortunately, we cannot explore trait–environment

relationships since we lack details on the maternal environment of these seeds requested from a repository.

Lastly, neighbor differences in root length explained the most variation in focal plant mass for two-species mixtures, and this indicates the importance of soil resources on competitive outcomes between species. These results are expected since root length in plant seedlings can help determine survivorship, particularly in dry environments (León et al., 2011), and this underscores the importance of root length to competition.

### 4.4 | Practical implications

We show that population selection for admixture provenancing in restoration (Bucharova et al., 2019) may influence interactions within and between species in restored plant communities, and this is the first study to explicitly evaluate population-level trait differences on interaction outcomes among multiple populations and species. Mixing multiple source populations for restoration may increase potential trait variation in restored populations; however, our results show that mixing different populations of the same species with another population may lead to different competitive outcomes based on population identity. This shows that the ability of an admixture provenancing approach to support establishment and long-term persistence of diverse plant communities will vary depending on the populations selected for mixing and the species matrix that they are planted into. Planting multiple populations that fail to establish wastes limited restoration resources and fails to meet restoration goals aimed at supporting within- and among-species diversity over the long term (SER, 2002). Testing and forecasting the effects of combining populations and species should be an informed process that considers both intraspecific and interspecific interactions and traits. Future work assessing population admixtures would need to quantify population growth, especially over time, to assess if stable coexistence is likely under population and species mixtures.

### 4.5 | Future work

Future research should assess how other species and populations interact with each other and how their traits influence coexistence over the long term. While trait assessments in controlled settings have direct applications to performance in the field (Schroeder-Georgi et al., 2016), future work should also assess underlying coexistence mechanisms in stressful field settings to remove issues of limited pot size and introduce other heterogeneous biotic and abiotic factors. Particularly, field studies where soil pathogens are present may substantially impact how competitive outcomes influence diversity (Wang et al., 2023). Unfortunately, outdoor experiments with multiple populations require greater space, logistics, and resources than outdoor experiments with one population representative of a species. It is also critical to assess variability in plastic responses to neighbors because plasticity can lead to different competitive outcomes between intraspecific neighbors that can affect stabilizing mechanisms (Foxx, 2021) critical to sustaining species diversity (Muthukrishnan et al., 2020; Pérez-Ramos et al., 2019; Turcotte & Levine, 2016). Our use of a low plant density is a limitation, and greater plant densities are more common in nature and can influence interaction outcomes. Lastly, more work assessing other traits is critical to identifying patterns in interaction outcomes with greater resolution, such as root architectural traits and other functional traits (Fort et al., 2015).

## 5 | CONCLUSIONS

Our results demonstrate that population identity and trait variation are crucial for understanding plant interactions in two key ways: (1) they provide evidence that intraspecific interactions from different populations structure competitive intensity that may be important to mechanisms for community establishment; and (2) species and population identity influence plant competitive ability and impact relationships between trait differences and competitive interactions, especially when biomass allocation is considered. In total, the functional traits of native plants used in restoration must be considered in restoration practice to better understand plant performance in restoration scenarios.

### AUTHOR CONTRIBUTIONS

AJF and AK designed the research. AJF performed the research, analyzed, and collected the data. AJF, AK, and FF interpreted the data; and AJF wrote the manuscript, and AK and FF revised the manuscript. All authors read and approved the final manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data are available from Mendeley Data at http://doi.org/10.17632/t7xbmj5jm5.1 and R code for testing the hypotheses of this study.

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## REFERENCES

Abbott, J. M., & Stachowicz, J. J. (2016). The relative importance of trait vs. genetic differentiation for the outcome of interactions among plant genotypes. *Ecology*, *97*, 84–94. https://doi.org/10.1890/15-0148.1

Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., Meiners, J. M., Tredennick, A. T., & Veblen, K. E. (2018). Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters*, *21*, 1319–1329. https://doi.org/10.1111/ele.13098

Bennett, J. A., Riibak, K., Tamme, R., Lewis, R. J., & Pärtel, M. (2016). The reciprocal relationship between competition and intraspecific trait variation. *Journal of Ecology*, *104*, 1410–1420. https://doi.org/10.1111/1365-2745.12614

Booth, R. E., & Grime, J. P. (2003). Effects of genetic impoverishment on plant community diversity. *Journal of Ecology*, *91*, 721–730.

Breed, M. F., Stead, M. G., Ottewell, K. M., Gardner, M. G., & Lowe, A. J. (2013). Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics*, *14*, 1–10. https://doi.org/10.1007/s10592-012-0425-z

Bucharova, A., Bossdorf, O., Hölzel, N., Kollmann, J., Prasse, R., & Durka, W. (2019). Mix and match: Regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. *Conservation Genetics*, *20*, 7–17. https://doi.org/10.1007/s10592-018-1067-6

Carmona, C. P., de Bello, F., Azcárate, F. M., Mason, N. W. H., & Peco, B. (2019). Trait hierarchies and intraspecific variability drive competitive interactions in Mediterranean annual plants. *Journal of Ecology*, *107*, 2078–2089. https://doi.org/10.1111/1365-2745.13248

Casper, B. B., & Jackson, R. B. (1997). Plant competition underground. *Annual Review of Ecology and Systematics*, *28*, 545–570.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Erlbaum.

Cope, O. L., Lindroth, R. L., Helm, A., Keefover-Ring, K., & Kruger, E. L. (2021). Trait plasticity and trade-offs shape intraspecific variation in competitive response in a foundation tree species. *New Phytologist*, *230*, 710–719. https://doi.org/10.1111/nph.17166

Crawford, K., & Rudgers, J. (2013). Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology*, *94*, 1025–1035.

De Vitis, M., Havens, K., Barak, R. S., Egerton-Warburton, L., Ernst, A., Evans, M., Fant, J., Foxx, A. J., Hadley, K., Jabcon, J., O'Shaughnessey, J., Ramakrishna, S., Sollenberger, D., Taddeo, S., Urbina Casanova, R., Lan, X., Woolridge, C., Zeldin, J., & Kramer, A. (2022). Why are some plant species missing from restorations? A diagnostic tool for temperate grassland ecosystems. *Frontiers in Conservation Science*, *3*, 1–25.

Del Río, M., Condés, S., & Pretzsch, H. (2014). Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. *Forest Ecology and Management*, *325*, 90–98. https://doi.org/10.1016/j.foreco.2014.03.047

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, *2*, 57–64. https://doi.org/10.1038/s41559-017-0402-5

Faraone, S. V. (2008). Interpreting estimates of treatment effects: Implications for managed care. *P & T: A Peer-Reviewed Journal for Formulary Management*, *33*, 700–711.

Fargione, J., & Tilman, D. (2005). Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia*, *143*, 598–606. https://doi.org/10.1007/s00442-005-0010-y

Feng, Y., & van Kleunen, M. (2016). Phylogenetic and functional mechanisms of direct and indirect interactions among alien and native plants. *Journal of Ecology*, *104*, 1136–1148. https://doi.org/10.1111/1365-2745.12577

Fort, F., Cruz, P., Catrice, O., Delbrut, A., Luzarreta, M., Stroia, C., & Jouany, C. (2015). Root functional trait syndromes and plasticity drive the ability of grassland Fabaceae to tolerate water and phosphorus shortage. *Environmental and Experimental Botany*, *110*, 62–72. https://doi.org/10.1016/j.envexpbot.2014.09.007

Fort, F., Cruz, P., & Jouany, C. (2014). Hierarchy of root functional trait values and plasticity drive early-stage competition for water and phosphorus among grasses. *Functional Ecology*, *28*, 1030–1040. https://doi.org/10.1111/1365-2435.12217

Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, *17*, 89–110. https://doi.org/10.1146/annurev.es.17.110186.000513

Fox, J., & Weisberg, S. (2019). *An {R} companion to applied regression*. Sage.

Foxx, A. (2021). Induced plasticity alters responses to conspecific interactions in seedlings of a perennial grass. *Scientific Reports*, *11*, 1–8. https://doi.org/10.17632/hhpnttctth.1

Foxx, A., & Fort, F. (2019). Root and shoot competition lead to contrasting competitive outcomes under water stress: A systematic

review and meta-analysis. *PLoS One*, *14*, 1–17. https://doi.org/10.1101/712208

Foxx, A. J., & Kramer, A. T. (2020). Variation in number of root tips influences survival in competition with an invasive grass. *Journal of Arid Environments*, *179*, 104189. https://doi.org/10.1016/j.jaridenv.2020.104189

Funk, J. L., & Wolf, A. A. (2016). Testing the trait-based community framework: Do functional traits predict competitive outcomes? *Ecology*, *97*, 2206–2211. https://doi.org/10.1002/ecy.1484

Genung, M. A., Bailey, J. K., & Schweitzer, J. A. (2012). Welcome to the neighbourhood: Interspecific genotype by genotype interactions in Solidago influence above- and belowground biomass and associated communities. *Ecology Letters*, *15*, 65–73. https://doi.org/10.1111/j.1461-0248.2011.01710.x

Grömping, U. (2006). Relative importance for linear regression in R: The package relaimpo. *Journal of Statistical Software*, *17*, 1–27.

Gross, N., Liancourt, P., Butters, R., Duncan, R. P., & Hulme, P. E. (2015). Functional equivalence, competitive hierarchy and facilitation determine species coexistence in highly invaded grasslands. *New Phytologist*, *206*, 175–186. https://doi.org/10.1111/nph.13168

Haidet, M., & Olwell, P. (2015). Seeds of success: A national seed banking program working to achieve long-term conservation goals. *Natural Areas Journal*, *35*, 165–173. https://doi.org/10.3375/043.035.0118

Hallett, L. M., Aoyama, L., Barabás, G., Gilbert, B., Larios, L., Shackelford, N., Werner, C. M., Godoy, O., Ladouceur, E. R., Lucero, J. E., Weiss-Lehman, C. P., Chase, J. M., Chu, C., Harpole, W. S., Mayfield, M. M., Faist, A. M., & Shoemaker, L. G. (2023). Restoration ecology through the lens of coexistence theory. *Trends in Ecology & Evolution*, *38*, 1085–1096.

He, D., Chen, Y., Zhao, K., et al. (2018). Intra- and interspecific trait variations reveal functional relationships between specific leaf area and soil niche within a subtropical forest. *Annals of Botany*, *121*, 1173–1182. https://doi.org/10.1093/aob/mcx2221

HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, *43*, 227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411

Kettenring, K. M., Mercer, K. L., Reinhardt Adams, C., & Hines, J. (2014). Application of genetic diversity-ecosystem function research to ecological restoration. *Journal of Applied Ecology*, *51*, 339–348. https://doi.org/10.1111/1365-2664.12202

Kiaer, L. P., Weisbach, A. N., & Weiner, J. (2013). Root and shoot competition: A meta-analysis. *Journal of Ecology*, *101*, 1298–1312. https://doi.org/10.1111/1365-2745.12129

Kraft, N. J. B., Crutsinger, G. M., Forrestel, E. J., & Emery, N. C. (2014). Functional trait differences and the outcome of community assembly: An experimental test with vernal pool annual plants. *Oikos*, *123*, 1391–1399. https://doi.org/10.1111/oik.01311

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., Kattge, J., & Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. *Ecology Letters*, *15*, 831–840. https://doi.org/10.1111/j.1461-0248.2012.01803.x

Leguizamón, E., Yanniccari, M., Guiamet, J., & Acciaresi, H. (2011). Growth, gas exchange and competitive ability of *Sorghum halepense* populations under different soil water availability. *Canadian Journal of Plant Science*, *91*, 1011–1025. https://doi.org/10.4141/cjps10202

Lenth, R. (2022). *emmeans: Estimated marginal means, aka least-squares means*. https://CRAN.R-project.org/package=emmeans

León, M. F., Squeo, F. A., Gutiérrez, J. R., & Holmgren, M. (2011). Rapid root extension during water pulses enhances establishment of shrub seedlings in the Atacama Desert. *Journal of Vegetation Science*, *22*, 120–129. https://doi.org/10.1111/j.1654-1103.2010.01224.x

Mahaut, L., Violle, C., Shihan, A., Pélissier, R., Morel, J. B., de Tombeur, F., Rahajaharilaza, K., Fabre, D., Luquet, D., Hartley, S., Thorne, S. J., Ballini, E., & Fort, F. (2023). Beyond trait distances: Functional distinctiveness captures the outcome of plant competition. *Functional Ecology*, *37*, 2399–2412. https://doi.org/10.1111/1365-2435.14397

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, *13*, 1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

Montazeaud, G., Violle, C., Roumet, P., Rocher, A., Ecarnot, M., Compan, F., Maillet, G., Fort, F., & Fréville, H. (2020). Multifaceted functional diversity for multifaceted crop yield: Towards ecological assembly rules for varietal mixtures. *Journal of Applied Ecology*, *57*, 2285–2295. https://doi.org/10.1111/1365-2664.13735

Muthukrishnan, R., Sullivan, L. L., Shaw, A. K., & Forester, J. D. (2020). Trait plasticity alters the range of possible coexistence conditions in a competition–colonisation trade-off. *Ecology Letters*, *23*, 791–799. https://doi.org/10.1111/ele.13477

Noto, A. E., & Shurin, J. B. (2016). Population variation affects interactions between two California salt marsh plant species more than precipitation. *Oecologia*, *180*, 499–506. https://doi.org/10.1007/s00442-015-3473-5

Omernik, J. M. (1987). Ecoregions of the conterminous United States. *Annals of the Association of American Geographers*, *77*, 118–125. https://doi.org/10.1111/j.1467-8306.1987.tb00149.x

Perez-Harguindeguy, N., Diaz, S., Garnier, E., et al. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234.

Pérez-Ramos, I. M., Matías, L., Gómez-Aparicio, L., & Godoy, Ó. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, *10*, 1–11. https://doi.org/10.1038/s41467-019-10453-0

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rajaniemi, T. K., & Reynolds, H. L. (2004). Root foraging for patchy resources in eight herbaceous plant species. *Oecologia*, *141*, 519–525. https://doi.org/10.1007/s00442-004-

Reijers, V. C., van den Akker, M., Cruijsen, P. M. J. M., Lamers, L. P. M., & van der Heide, T. (2019). Intraspecific facilitation explains the persistence of Phragmites australis in

modified coastal wetlands. *Ecosphere*, *10*(8), e02842. https://doi.org/10.1002/ecs2.2842

Reiss, E. R., & Drinkwater, L. E. (2018). Cultivar mixtures: A meta-analysis of the effect of intraspecific diversity on crop yield. *Ecological Applications*, *28*, 62–77. https://doi.org/10.1002/eap.1629

Revelle, W. (2022). *psych: Procedures for psychological, psychometric, and personality research*. CRAN. R package version 2.4.12. https://CRAN.R-project.org/package=psych

Schenk, H. J., & Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, *90*, 480–494. https://doi.org/10.1046/j.1365-2745.2002.00682.x

Schroeder-Georgi, T., Wirth, C., Nadrowski, K., Meyer, S. T., Mommer, L., & Weigelt, A. (2016). From pots to plots: Hierarchical trait-based prediction of plant performance in a mesic grassland. *Journal of Ecology*, *104*, 206–218. https://doi.org/10.1111/1365-2745.12489

Society for Ecological Restoration. (2002). *SER international primer on ecological restoration*. Society for Ecological Restoration International.

St. Clair, A. B., Dunwiddie, P. W., Fant, J. B., Kaye, T. N., & Kramer, A. T. (2020). Mixing source populations increases genetic diversity of restored rare plant populations. *Restoration Ecology*, *28*(3), 583–593. https://doi.org/10.1111/rec.13131

Su, Y., Yu, R. P., Xu, H. S., Sun, J.-H., Zhao, J.-H., Zhang, W.-P., Yang, H., Surigaoge, S., Callaway, R. M., & Li, L. (2023). Crop cultivar mixtures stabilize productivity, partly via facilitation, when conditions are less benign. *Field Crops Research*, *302*, 109046. https://doi.org/10.1016/j.fcr.2023.109046

Thompson, C. G., Kim, R. S., Aloe, A. M., & Becker, B. J. (2017). Extracting the variance inflation factor and other multicollinearity diagnostics from typical regression results. *Basic and Applied Social Psychology*, *39*, 81–90. https://doi.org/10.1080/01973533.2016.1277529

Turcotte, M. M., & Levine, J. M. (2016). Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution*, *31*, 803–813. https://doi.org/10.1016/j.tree.2016.07.013

Valentine, J. C., Pigott, T. D., & Rothstein, H. R. (2010). How many studies do you need? *Journal of Educational and Behavioral Statistics*, *35*, 215–247. https://doi.org/10.3102/1076998609346961

Venables, W., & Ripley, B. (2002). *Modern applied statistics with S* (4th ed.). Springer.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*, 1–44.

Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., Blanchard, A., & Navas, M. L. (2009). Competition, traits and resource depletion in plant communities. *Oecologia*, *160*, 747–755. https://doi.org/10.1007/s00442-009-1333-x

Violle, C., Lecoeur, J., & Navas, M. L. (2007). How relevant are instantaneous measurements for assessing resource depletion under plant cover? A test on light and soil water availability in 18 herbaceous communities. *Functional Ecology*, *21*, 185–190. https://doi.org/10.1111/j.1365-2435.2006.01241.x

Wang, G., Burrill, H. M., Podzikowski, L. Y., Eppinga, M. B., Zhang, F., Zhang, J., Schultz, P. A., & Bever, J. D. (2023). Dilution of specialist pathogens drives productivity benefits from diversity in plant mixtures. *Nature Communications*, *14*, 8417. https://doi.org/10.1038/s41467-023-44253-4

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227. https://doi.org/10.1023/A:1004327224729

Wood, T. E., Doherty, K., & Padgett, W. (2015). Development of native plant materials for restoration and rehabilitation of Colorado Plateau ecosystems. *Natural Areas Journal*, *35*, 134–150. https://doi.org/10.3375/043.035.0117

Zeldin, J., Lichtenberger, T. M., Foxx, A. J., Webb Williams, E., & Kramer, A. T. (2020). Intraspecific functional trait structure of restoration-relevant species: Implications for restoration seed sourcing. *Journal of Applied Ecology*, *57*, 864–874. https://doi.org/10.1111/1365-2664.13603

## SUPPORTING INFORMATION

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

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