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How predictable are evolutionary responses to environment? Comparing trait-environment relationships among three species of Asteraceae forbs in the Great Basin

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ABSTRACT

Restoring native forbs in the Great Basin Desert is an important part of regenerating a healthy landscape that benefits wildlife, plant communities, and humans. Despite their importance and contribution to plant diversity, forbs have been understudied relative to grasses and shrubs. To begin bridging this knowledge gap, we examined three Asteraceae species (*Chaenactis douglasii, Dieteria canescens, Erigeron pumilus*) collected from a wide geographic area and grown in common garden experiments, asking how variable these species and populations are, how their traits were associated with environment of origin, and how two of the three species responded to water addition in direct-seeding environments. We also asked if trait-environment relationships were similar among these three species. As expected, we found that populations were extremely variable, and that much of this variation was significantly different among populations, with some variation explained by the ecoregion where populations were gathered. All three species had at least one trait strongly correlated with an environmental variable, sometimes in similar ways. For example, we found a consistent relationship where plants from higher elevation locations flowered earlier across all species, as well as a relationship with plant height and mean annual temperature, with taller plants sourced from warmer areas. Across species, the strongest trait-environment relationships we found were found for plant height, flowering phenology, and flower production, though there was variation in which environmental variables were most correlated with these responses. Our results suggest that approaches that generalize across species, even closely related ones, may not be adequate when determining whether a potential seed-source is well-matched to a target restoration site. Instead, our results support the idea that species-specific seed zones (areas where seeds can be moved without loss of performance) should be developed to help make this decision. Additionally, we found that environmental variables such as mean annual temperature and elevation were highly associated with traits that are typically considered important in restoration, i.e. phenology, number of inflorescences, and plant size. Therefore, before species-specific seed zones are available, we may be able to use these environmental factors as proxies to help us better match seed sources to target restoration sites. Finally, we also found that at least one species (*C. douglasii*) emerged from seed more readily when it was sourced from a drier origin, in both ambient and water addition conditions. Although more research needs to be done in this area, this suggests that seeds sourced from drier locations may be better suited for restoration projects that are being direct-seeded.

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INTRODUCTION

Biodiversity has long been recognized as an important factor in ecosystem health. It is linked to increased community resilience, invasion resistance, and recovery after disturbance (Maron and Marler 2007; Tilman et al. 2001). Additionally, increased biodiversity is known to influence ecosystem function and stability (van der Plas 2019). Even a species that has relatively low abundance and biomass can play a pivotal role in ecosystems (Narango, Tallamy, and Shropshire 2020; Paine 1969), and understudied species may perform functions we have yet to discover. Human-caused declines in biodiversity have become increasingly rapid since the mid-twentieth century (Cafaro, Hansson, and Götmark 2022; Millenium Ecosystem Assessment 2005) and are expected to continue or accelerate on both local and global scales (Venter et al. 2016; Millenium Ecosystem Assessment 2005), with potentially devastating consequences for plants, wildlife, pollinators, and humans.

Plant community restoration is an essential part of maintaining biodiversity in our natural systems, and has the potential to slow or reverse biodiversity declines (Hughes et al. 2018; Bullock et al. 2011). Despite restoration being important and widely attempted, projects are not always successful (Shackelford et al. 2021). This is especially true in dryland systems globally (Shackelford et al. 2021), including the shrub steppe ecosystem of the Great Basin, USA (Pilliod, Welty, and Toevs 2017; Arkle et al. 2014; Knutson et al. 2014) where our project is focused. In this region, increasing disturbance pressure from wildfires, drought, and invasive species has led to the degradation and loss of important plant communities and range contraction (Davies et al. 2011). Steppe ecosystems dominated by big sagebrush (*Artemisia tridentata* Nutt.) previously occupied over 62 million hectares in the western United States and southwestern Canada (Miller and Eddleman 2001; Burkhardt and Tisdale 1969). Today, however, this ecosystem occupies only 56% of its historical range and is becoming increasingly fragmented (Schroeder et al. 2004; Knick et al. 2003). As a result, more than 350 species of plants and animals associated with sagebrush ecosystems have been labeled as species of conservation concern (Connelly et al. 2000), with major research efforts conducted for some species, such as the Greater sage-grouse (*Centrocercus urophasianus* Bonaparte [Phasianidae]), and big sagebrush (*Artemisia tridentata* Nutt.) (Chambers et al. 2017). However, not all species or functional groups are well studied in the Great Basin (Dumroese et al. 2015).

All plants are important in ecosystems, but some plants, like forbs, are more species-rich and less studied than other lifeforms (Bråthen, Pugnaire, and Bardgett 2021; Jones et al. 2018). While forbs make up roughly 50% of taxa in the Great Basin, only 30% of local adaptation experiments have focused on this functional group (Baughman et al. 2019a). Forbs are also an important part of ecosystem services in this region. For example, research done on the Greater sage-grouse following its proposed listing under the endangered species act suggests that a diverse mixture of plants is an essential component of greater sage-grouse habitat, and that they require many different forb genera to support their complex diet through seasonal and ontogeny changes (Luna, Mousseaux, and Dumroese 2018; Dumroese et al. 2015). To-date, habitat restoration for Greater sage-grouse is believed to have been less successful due to lack of forb recovery at post-fire restoration sites (Dumroese et al. 2015). In addition to Greater sage-grouse, forbs are a major food source for other native fauna such as pronghorn, elk, rodents, and insects including pollinators (Hagen, Connelly, and Schroeder 2007; Aldridge and Brigham 2002). Forbs can also can play an important role in post-disturbance succession and provide competition with invasive plants (Gucker and Shaw 2018b; LaForgia et al. 2018). For all of these reasons, including forbs in restoration projects can be an important way to increase diversity and function in disturbed systems.

Beyond considerations of species diversity in restoration projects, it is also important to consider the populations that restoration species are sourced from. Population-based phenotypic and genetic differentiation is common when a species lives across a range of environments due to evolutionary processes such as natural selection and genetic drift, which can affect survival and reproduction in restored populations (Ackerly et al. 2000; Loveless and Hamrick 1984). For example, if there is heritable variation in fitness-related traits within populations, natural selection can act on these populations differently based on their local conditions, and habitat-correlated intraspecific variation can arise. Through this process, populations may evolve strategies that give them higher fitness in their local conditions. This is known as local adaptation (Kawecki and Ebert 2004; Linhardt and Grant 1996; Langlet 1971; Hiesey, Clausen, and Keck 1942). Considering the many environmental gradients existing in the Great Basin, we would expect to see population differentiation associated with environmental variation. Indeed, phenotypic trait differences in plant size, leaf morphology, and phenology are commonly associated with environmental factors, including temperature, soil conditions, precipitation and elevation (Balazs et al. 2020; Baughman et al. 2019a; Dilts 2015; Hereford 2009; Parkhurst and Loucks 1972).

Non-reciprocal common garden experiments are one way to measure intraspecific variation which is then used to infer local adaptation. In this type of experiment, plants collected from multiple populations are grown together in a single location to control for environmental effects, which allows for direct comparison of traits among populations (Hiesey, Clausen, and Keck 1942). If traits are expressed differently in this common environment, we can infer that these differences are likely due to underlying genetic variation rather than being responses to conditions of the growth environment (Endler 1986). Further, by correlating mean trait values of source populations with information from each population's environment-of-origin, we can identify whether there is a relationship between traits and source environment (Kilkenny 2015). While these types of trait-environment analyses do not measure local adaptation directly, like a reciprocal transplant experiment would (i.e., planting each population in home and non-local sites and observing whether local populations outperform others), strong trait-environment correlations does suggest that local adaptation has occurred (Endler 1986). This is important for ecological restoration, as local populations frequently have higher fitness than non-local ones (Baughman et al. 2019).

Although an effective way to infer trait-environment correlations, common garden experiments are notorious for the amount of work they require to establish and maintain, as well as the amount of work needed to find and sample a large number of populations from a broad range of sites. Because of these constraints, most common gardens tend to study relatively few populations. For example, in forb common gardens of the Great Basin, an average of 10 populations were measured (Baughman et al. 2019). A higher number of populations, especially when sampled across a gradient of source-environments, increases model accuracy and allows inferences that local adaptation has occurred to be made with greater confidence (Endler 1986).

Because of the challenges of establishing so many collections in common gardens, it is common practice to establish plants from transplants, rather than seeds (Bucharova et al. 2017; Kawecki and Ebert 2004). While this is often necessary to have full representation of sampled populations in a garden, there are questions about how this process may mask adaptations at the seed germination and early seedling stages, which often take place in controlled greenhouse settings for common garden experiments, rather than in field sites.

For this reason, I also included a direct-seeding experiment for two of our three species in order to quantify emergence differences among populations.

The study presented here contains the most populations studied to-date for each of the species examined, and represents some of the largest forb common gardens, in terms of numbers of populations included, that we are aware of anywhere in the world. This project includes 98 populations of *Dieteria canescens*, 86 populations of *Chaenactis douglasii,* and 39 populations of *Erigeron pumilus*. These populations also represent a gradient of source-population environments over a large geographic area, spanning six states, 11 level III ecoregions, over two degrees of latitude and almost 11 degrees of longitude, or roughly 1,200km north to south and 1000km east to west.

Our overall goal was to measure intraspecific variation and local adaptation in order to inform restoration practices. Using our large number of populations from a wide geographic range, we are asking the following specific questions

1. How variable are these species and populations in survival, phenotype, phenology, and environment of origin?
2. How does intraspecific variation in multiple forb species relate to the environmental conditions of a population's home range?
    a. Are the same traits strongly correlated with environmental variables for all three species, and are trait-environment relationships consistent?
    b. Are all species equally adapted to their environments?
3. How do results from a transplanted common garden compare with direct-seeded plants?

a. Can these species establish directly from seed in a dry site?

b. How does water availability affect emergence and survival, and is this affected by the mean annual precipitation at the collection site?

We expected to find trait-environment correlations in all three species studied. Given findings in the literature (Baughman et al. 2019a), we expected size and phenology traits to be most strongly correlated with environmental factors such as temperature and precipitation. Because there is evidence to support a wide range of responses, we are unsure if the trait-environment associations would have the same strength or direction for each of our study species, which often co-occur. Communities such as those where our study species are found are typically made up of interacting species which have both similar and different characteristics, with abiotic characteristics acting as a first filter selecting for similar characteristics, and biotic interactions potentially leading to differences. For example, niche differentiation is frequently observed amongst interacting species (Meilhac et al. 2020; Zuppinger-Dingley et al. 2014). Alternately, if environmental variables apply strong selection pressure, the same characteristics can be adaptive for multiple species and result in convergent, rather than divergent evolution toward the same suite of traits in multiple species (Agneray 2022). Finally, phylogenetic conservatism, wherein closely related species maintain shared ancestral traits (Davies et al. 2013), may result in similar trait-environment relationships in closely related species, such as plants in the same family (Andersson 1990). All of our study species are in the same plant family, and occupy roughly similar habitats. Thus, it's possible that we will see similar trait/environment correlations among these species, which could potentially be employed to estimate patterns of local adaptation in other Asteraceae forbs. Alternatively, if trait/environment relationships are different even for these related species, we should question how well previously defined groups can be applied to restoration applications. For example, the concept of functional groups, provisional seed zones (discrete categories of climatically similar areas where seeds are often believed to be mostly able to be transplanted), and level III ecoregions, may all be more or less helpful than previously thought when it comes to estimating the outcomes restoration projects.

Finally, for our direct seeding experiment, we expected that seeds originating from drier locations would germinate, emerge, and survive more readily at dry ambient conditions when compared with seeds sourced from wetter origins. Since the expected ambient conditions at our experiment site were equivalent to the driest site of populations that were sampled, we expected very few populations to emerge without the aid of supplemental watering treatments.

MATERIALS AND METHODS

Study species

Three native forb species were examined in this study. They include *Dieteria canescens* (Pursh) Nutt., *Chaenactis douglasii* (Hook.) Hook. & Arn., and *Erigeron pumilus* Nutt (Figure 1). Each of these species are widely found throughout the Great Basin with broad geographic ranges that span diverse environmental conditions, and they sometimes co-occur. They have also been recognized by Great Basin land managers and scientists as good candidates for restoration because they have known value to wildlife, are early-successional plants that produce a lot of seed, are easy to identify for seed collectors, and have been more widely researched than other Great Basin forb species (Gucker and Shaw 2021; 2018a; 2018b). Additional attributes that make them valuable contributors to a landscape, whether natural or restored, are discussed for each species below.

Chaenactis douglasii is a biennial or short-lived perennial forb that supports at least 19 species of native bees (Gucker and Shaw 2018a; Cane, Love, and Swoboda 2012). Additionally, it has lower levels of seed dormancy when compared to other forbs (Gucker and Shaw 2018a), which may mean more predictable emergence when planted for restoration. This plant may be especially valuable in the context of increasing wildfires: *C. douglasii* has been observed in early post-fire communities, so it may be a valuable bee resource in the first post-fire year (Cane, Love, and Swoboda 2012). Plants used for seed collections for this study were often found near moderately disturbed landscapes, such as near hiking trails.

Dieteria canescens is an annual to short-lived perennial and acts as a valuable food source for Greater sage-grouse, elk, pronghorn, rodents, and multiple bee and butterfly species (Gucker and Shaw 2018b). It is one of the few late-summer flowers in the Great Basin, flowering as late as October or November (Tilley 2015; Morgan 2006). This may make it a valuable food source for pollinators later in the season after many other flowering plants have senesced. It has also been observed surviving alongside highly invasive plants including cheatgrass (*Bromus tectorum*) and knapweed (*Centaurea sp.*) (Tilley 2015). During seed collection for this study, *D. canescens* was often found in highly disturbed environments such as along dirt roads and ORV routes, on steep and loose slopes, and in actively grazed pasturelands.

Finally, *E. pumilus* is a clonal perennial forb that has been observed increasing its density in grazed areas (Gucker and Shaw 2021; Maron et al. 2021; McLean, Lord, and Green 1971). It is also known to be a valuable food source for native fauna including pronghorn, Greater sage grouse, 10 bumblebee species, and other pollinators (Gucker and Shaw 2021; Luna et al. 2018; Dumroese et al. 2016; Koch, Strange, and Williams 2012). While gathering seed for the populations used in this study, *E. pumilus* was often found in low-lying areas near ephemeral springs and along dry washes.

Seed collection and common garden set-up

Seeds were collected from populations across Idaho, Oregon, Washington, Utah, and California by the USDA Forest Service Rocky Mountain Research Station (USFS RMRS) in Boise, ID, with additional help from the USDI Bureau of Land Management Plant Conservation Great Basin Ecoregional Programs, and the Great Basin Native Plant Project (Figure 2). Seed collection locations were discovered via historic herbarium collections and field visits to potential habitat, opportunistically collecting from populations that met the following criteria: to be included in this experiment, populations had to consist of 100 or more plants within 1.6 km^2 that were 16km or more away from the next nearest collected population, criteria designed to minimize impact on small populations and to maximize genetic diversity within our sample. Seeds from a total of 98 populations *D. canescens,* 86 populations of *C. douglasii*, and 39 populations of *E. pumilus* were included in this study, collected over a two year time period (2018-2019) from 11 different ecoregions (Table 1). Seeds from each population were grown by USFS RMRS in a greenhouse in Moscow, ID (46.724 °N, 117.005°W) in Ray Leach “Cone-tainers” filled with a 45% peat/ 55% vermiculite mix. They were irrigated at 75% field capacity and fertilized using a 25-100ppm nitrogen solution. After growing in the greenhouse for roughly six months, they were transplanted as plugs into a common garden located in Reno, NV, at the University of Nevada, Reno Agricultural Experiment Station. This common garden, located at 39.5398 °N, 119.805°W, is equivalent to one of the driest locations where populations were gathered. The 30-year normal for annual precipitation at the Reno garden is 222.7mm, while the median annual precipitation for all populations gathered was 366 mm, with a minimum of 199 mm and a maximum of 992 mm (PRISM Climate Group 2022).

Prior to planting, the site of the common garden was plowed multiple times and then watered to soften the ground. This was necessary as the soils at this location were deposited as Truckee River outwash sediments with a high silicate clay content (Ramelli et al. 2010; Bell and Garside 1987), which is prone to solidifying when not saturated. Additionally, the soil at this site has been compacted by a history of heavy machinery use, and, even after these softening treatments, a diamond-tipped auger was required to dig holes for transplants. The common garden was then covered in landscape fabric to decrease weed pressure and punctured by a grid of 15cm-wide holes for transplants. Each hole was placed 1 m apart from the next in its row and 0.8 m apart from the next column. *C. douglasii* and *D. canescens* were transplanted in October of 2019, while *E. pumilus* was transplanted in November 2020. Plants were installed using a randomized block design, with 1 plant from each population within each block. There were 8 blocks of *C. douglasii*, 8 blocks of *D. canescens*, and 13 blocks of *E. pumilus*. Placement of each population was randomized within a block and weeding was done as needed to reduce the effects of competition. Blocks did not affect the vast majority of responses, so they were not included in final analyses.

Trait measurements

Multiple phenotypic trait measurements (Supplement 1 & 2) were conducted biweekly until the first plant bolted, after which monitoring of many traits was completed on a weekly basis. A subset of traits was measured during each monitoring session, including phenophase (Supplement 1), flower presence, and seed presence. These measures were later used to derive discrete phenology-related traits such as day of first flower. Plant size, leaf vapor pressure deficit (VPD), and color measurements were taken once at the onset of a prespecified phenophase (Supplement 2). Color data was collected by visually matching swatches in a Munsell Plant Tissue Color book (Munsell 2012) to living leaves on each plant. These values were then transformed and split into 3 cartesian color coordinates using the methods described in Ruck and Brown (Ruck and Brown 2015). Size measurements included multiple measures of width and height. Leaf VPD was approximated by measuring leaf temperature, ambient temperature, and relative humidity using an Extech RH401 digital psychrometer and infrared thermometer. Leaf area was measured for leaves collected at a pre-specified phenophase, scanned in using a scanner by the Boise USFS RMRS, and analyzed using the Regent Instrument Inc.'s WinFOLIA leaf area and morphology software (Regent Instruments Inc. 2022). Seed mass was measured by bagging a single senescing inflorescence with a muslin bag and collecting it two to three weeks later. These were then sent to the Boise USFS RMRS, where the seeds were separated from chaff and inviable seed, had their mass weighed, and then counted. Average seed mass was determined by the total weight of viable seed mass/number of seeds. Only size and phenology measurements were taken for *E. pumilus*, due to time constraints during the second year of monitoring common gardens.

Environmental data

We used data from multiple sources to gather an array of environmental traits for each collection location that we hypothesized could be associated with forb traits, based on findings from previous literature and field observations (Baughmanet al. 2019a; Dilts et al. 2015). These included both climatic and other environmental variables for each population origin. Climatic variables for original collection locations were extracted from PRSIM's 30-year normals from 1991-2020 (PRISM Climate Group), and included mean annual precipitation, annual minimum temperature, and annual maximum temperature. Elevation, slope and aspect were also extracted for each population using the elevatr package (Hollister et al. 2021). Latitude, longitude, soil available water capacity (AWC), slope, aspect, monthly precipitation, and monthly mean temperature were used to model and extract additional environmental variables (Redmond 2022) including monthly actual evapotranspiration (AET). We used these variables to derive additional environmental traits that have previously been shown to be relevant in plant distributions in arid environments, including monsoonality and annual climate water deficit (CWD) (Dilts et al. 2015).

Soil characteristics including percent clay, percent sand, percent organic, and particle size were extracted from the soil survey geographic database (SSURGO) in R using the soilDB package (Beaudette et al. 2022). Lithology types of underlying bedrock were extracted from the state geologic map compilation (SGMC) geodatabase of the conterminous United States (Horton, San Juan, and Stoeser 2017) using ArcGIS. The lithology types were then categorized by whether soil weathered from each bedrock type is considered “normal”. Normal, or zonal, soils have a relatively balanced set of minerals and nutrients that provide the basic components a plant needs to survive (Kruckeberg 2002). These normal, or zonal, soils are often more influenced by climatic and vegetal pressures than the chemical makeup of their parent lithology (Kruckeberg 2002). Azonal or non-normal soils, on the other hand, are highly influenced by parent bedrock and tend to have limited or missing mineral and nutrient components necessary for plants to thrive. At sites where lithology values extracted from the SGMC were too vague to make an assessment of normality (i.e. sedimentary or volcanic), we consulted various state-level geologic maps with more detail than what is displayed in the SGMC map (Rowley et al. 2017; Henry et al. 2016; 2004).

Finally, we noted which ecoregion each population was collected from, using the level III ecoregions of the continental United States (U.S. Environmental Protection Agency 2013; Table 1). Ecoregions were created to encompass areas where ecosystems are considered similar based on analysis of biotic and abiotic factors. Many factors, such as geology, landforms, soils, vegetation, climate, land use, wildlife, and hydrology, were collated to create and maintain the classification of these regions (Omernik and Griffith 2014; Omernik 2004; 1995). There are four levels of ecoregions, with Level III being the most commonly used in federal and state ecological and restoration projects in the Great Basin Desert. These are often used to identify source seed, sometimes in conjunction with provisional seed zones based on climate variables (Kramer, Larkin and Fant 2015; Bower, St. Clair, and Erickson 2014).

Direct-Seeded Common Garden

An additional common garden experiment was set up using a subset of the populations from the transplanted common garden for two species with abundant seed availability to assess how early life-history traits, such as seedling emergence and survival, were affected by environment-of-origin and water availability. Ten populations of *C. douglasii* and *D. canescens* were selected via a stratified random process from all of the available population seed collections. The aim of this selection process was to choose populations from a wide array of locations and climatic conditions, focusing on the PRISM 30-year climate normal models from 1991- 2020. I created a principal component analysis (PCA) of seasonal average precipitation and minimum and maximum temperature for all populations collected of each species. I chose populations that were the farthest from (0,0) in each quadrant and then used a random number generator to choose an additional population from each quadrant. In the quadrant with the highest number of populations, I randomly selected another population to bring the total number of populations up to 10 for each species. *E. pumilus* was not included in this experiment because seeds were not available.

Seeds were sown directly into the ground at the UNR Valley Road Field station in December 2019, adjacent to the transplanted garden. Each population was planted in 30 randomly located plots across a 9x100m grid. Six seeds were planted at each plot in a fixed pattern 1 cm apart for a total of 180 seeds per population. Each plot was 0.4m from the next to decrease the effects of competition and each row was 0.8m apart to allow for working space. This direct-seeded garden was weeded on a biweekly basis to decrease confounding effects from interspecific competition.

I applied three watering treatments to determine whether there was an association between seedling emergence and water availability. These watering treatments were applied randomly to 10 seeded plots per species. Water addition was based on the 30-year normal seasonal precipitation of all the populations that were gathered for the transplanted common garden (Supplement 3). Originally, we considered varying watering treatments for each species, but values were similar enough that I combined collection locations of all species to create one target in order to simplify the watering treatments. Watering was adjusted on a seasonal basis in an effort to match this region's typical climate (Table 2, Supplement 4). We created watering targets for each treatment, but our final values deviated slightly because we didn't water on weeks with natural precipitation (Table 2). The three treatments included:

1. Ambient: Reno NV, where this germination garden was established, was comparable to one of the driest seed collection locations amongst all populations. A nearby weather station recorded actual precipitation levels at this location. On average, the site receives a total of 15.9cm of precipitation over the course of the experimental timeframe (December 1st

2019-June 30th 2020), but it was an exceptionally dry year and only received 7.1cm of precipitation over the course of the experiment (Table 2, Supplement 3).

2. Mean precipitation for all populations: I added water periodically throughout the season to approximate the mean precipitation level for all populations gathered. The target precipitation value for the entire experiment (December 1st 2019 - June 30th 2020) was 26.9cm, and 22.6cm of water was actually applied, including natural precipitation.

3. 1.75x mean of all populations: This bracket encompassed a precipitation regime that was greater than or equal to the mean value for the majority of populations and represents a relatively wet collection location, with a target of 51.0 cm from December 1st- June 30th. 46.9cm of water was actually added to this treatment group, including natural precipitation.

Watering was done using a battery-operated sprayer cart with a constant flow, adding the equivalent of approximately 12cm of precipitation during each application. We did not add water when the soil was saturated or during natural precipitation events. Treatment 1 received additional water amount 1-2 times a week while treatment 2 received water 2-3 times per week depending on ambient precipitation (Supplement 5). I monitored this garden every 2 weeks starting on January 28th and recorded when seedlings emerged and whether they continued to survive. I recorded the date of emergence and death.

ANALYSIS

Data were analyzed using R statistical software (v4.0.2; R Core Team 2020), using packages listed below. Significance was assessed with a $P < 0.05$ criteria.

Trait Selection

After trait data were recorded and processed, we found that many traits were correlated with one another. In order to maintain statistical independence, we chose traits that are biologically important and have previously been shown to be likely candidates for association with environmental variables in other species. We also ensured that no traits were highly correlated with one another. Through this selection process, we reduced our traits to nine variables that were minimally correlated (correlation coefficient of 0.5 or lower) for all study species, focusing on traits that could be compared across multiple species (Table 3). For all three species, the traits used in analyses included date of first flower (F.flw), number of inflorescences (n.Flw), plant height, and survival to production of mature seed*.* Additionally, seed mass, leaf area (LfA), leaf vapor pressure deficit (VPD), and two color (lightness, Col.Sat) variables were used for *D. canescens,* and *C. douglasii* (Table 3).

We analyzed whether populations and ecoregions differed in the above traits using general linear models with populations nested within ecoregion as fixed effects and each trait as a response variable (stats pkg; R Core Team 2020). Analysis of variance was then done on these linear models to determine whether responses were significantly different among ecoregions and populations (stats pkg; R Core Team 2020). We also visualized relationships among traits for each species using principal components analysis (PCA), and correlations between biologically important characteristics using Pearson correlation coefficients (corrplot; Wei and Simko 2021).

Environmental Variable Selection

After reducing our list of plant traits, we used the randomForest package (Liaw and Wiener 2002) to determine which environmental variables had the most importance in predicting our list of traits for each species. We did this by calculating the percentage increase in mean square error for each environmental variable and recording the three most important environmental variables for each trait on a per-species basis. We then further reduced environmental variables by eliminating environmental variables that were strongly correlated with other important environmental variables (0.7 or higher). This resulted in a total of nine environmental traits: Longitude, latitude, mean annual temperature (MAT), mean annual precipitation (MAP), elevation, slope, % sand (sand), % organic (organic), and lithology normalcy (LNorm) (Table 4, Supplement 6).

Trait-Environment Correlations and Model Selection

We assessed trait-environment correlations in two ways. First, we calculated Pearson correlation coefficients for each pair of plant traits and environmental variables (Supplement 6, Supplement 7). This allowed us to directly compare the strength and direction of trait-environment relationships among our three species, without possible complications from collinearity.

We then performed model selection using generalized linear models with scaled environmental variables as fixed effects to determine which environmental variables best predicted model fit for each plant trait and species. This was done by first manually determining which data transformation or distribution resulted in the best looking q-q plot and most normal residuals on a per-trait basis without being over dispersed (Table 5; Hartig 2021). Then, we used MASS model selection in R (Venables and Ripley 2002) to find the set of environmental variables that resulted in the lowest AIC value. We additionally removed some variables for each species (elevation was removed for *D. canescens* and *E. pumilus*, MAT was removed for *C. douglasii*) due to high variance inflation factors (VIF), and thus results provide a slightly different perspective than simple pairwise correlations. We removed longitude, elevation, and organic matter for survival models in *E. pumilus*, due to high VIF in that model. Various distributions and transformations were used to get well-fitting models (Table 5) based on good fit assessment using the DHARMa package in R (Hartig 2021). Best model fit for each response trait was determined using AIC values from models including single environmental predictor variables, multiple additive environmental variables and predictor variables multiplied together using the MASS package (Venables and Ripley 2002). We present only the best-fitting models in the main text (Table 6), but additional models with comparable AIC values (within 2 of the best) are listed in Supplement 8.

Direct-Seeded Common Garden

Of the two species that were direct seeded, only *C. douglasii* had sufficient seedlings emerge for statistical analysis. Specifically, *C. douglasii* had 151 seeds emerged from 104 plots, while for *D. canescens, only* 33 seeds emerged in 28 plots. Emergence was analyzed on a per-seed basis, while survival to 13 days (n13, a point at which many of the seedlings had died) was analyzed for each plot, noting whether any plant was alive within our 6-seed arrays. Logistic regression and analysis of variance (R Core Team 2020) were used with our binary emergence and n13 responses to ask whether watering treatments and climate-of-origin interacted with one another and if treatments or populations were significantly different from one another. This model included MAP at the site of origin, watering treatment, and their interaction with either emergence or n13 as a response variable.

RESULTS

Question 1a: Trait variation among species, populations, and ecoregions

Survival

Although over 80% of plants in the transplanted common garden survived to produce seed, survival was unequal among populations and species (Table 6, Table 7, Figure 3). Overall, *E. pumilus* had the highest average survival (83%), with the greatest range of population survival rates. Of *E. pumilus*' 23 populations, one had 0% survival and 12 had 100% survival. *D. canescens* had the next highest average survival (79%), and the lowest variation, with all populations having at least 25% survival. Of the 108 *D. canescens* populations, 22 populations had 100% survival. *Chaenactis douglasii* had the lowest average survival (24%). Of the 71 populations, 14 had 0% survival, and zero had 100% survival. There was also a significant difference in survival among ecoregions for both *D. canescens* and *E. pumilus* (Figure 3, Table 8). Interestingly, although *E. pumilus* had significant survival differences among populations, ecoregions did not differ (Table 8C).

Flowering phenology and inflorescence number

Erigeron pumilus was the first species to flower, with dates ranging from Apr 26 – May 15 for all populations (Table 7, Figure 3). *Chaenactis douglasii* flowered next, with the first population flowering May 3rd and all populations flowering by the end of May (Table 7, Figure 3) *D. canescens* had the latest and most variable date of first flowers. Specifically, the first population flowered in mid-May and flower initiation continued for 3 months until mid-August.

The number of inflorescences was variable for all species across all populations, though there were some differences in whether ecoregions, populations, or both were significantly different (Table 7, Table 8, Figure 3). *Dieteria canescens* had the greatest variation, with nearly exponential increase in inflorescence number within multiple ecoregions once populations were sorted by value (Figure 3). Number of inflorescences was significantly different among populations and ecoregions for *D. canescens* (Table 8B), but there were no significant differences for either factor in *C. douglasii* (Table 8A). *Erigeron pumilus* had significant inflorescence differences among ecoregions, but not among populations (Table 8C).

Height

Plant height was highly variable among all three species (Table 7, Table 8, Figure 3). *Dieteria canescens* had more variation among populations (138% difference between shortest and tallest) than the other two species (*E. pumilus* 100%, *C. douglasii* 84%). *Dieteria canescens* also had some populations with exceptionally large plants that originated primarily from places where there was likely higher than average water stress (hot, dry, or sandy; see trait-environment correlations below). *Erigeron pumilus* heights varied in a continuous manner, except for one population, from the Bruneau-Jarbidge wilderness in SW Idaho, which had plants that were notably taller than the rest (Figure 3). The average height of plants for this population was 171mm, while the average height of all the other populations was 95.8mm with a standard deviation of 28mm. This site also had the lowest elevation and was the sandiest out of all the sampled *E. pumilus* populations. Height differences were significant among populations and ecoregions for all three species (Table 8).

Other traits

Five additional traits were measured for *D. canescens* and *C. douglasii*, but not *E. pumilus*: two color metrics (col.sat and lightness), seed weight, leaf area and LfVPD. Of these traits, seed weight (Figure 3) and leaf area (Supplement 9) exhibited significant differences among populations for both species (Table 8). There was no significant difference among populations or ecoregions for LfVPD in either species. Color variables also had few differences exhibited for populations or ecoregions; the only factor that was significantly different for color metrics was for *C. douglasii,* which varied among ecoregions (Table 8, Supplement 10).

Trait correlations

Principal components revealed differences in trait correlations among species (Figure 4). For example, shorter *C. douglasii* plants flowered earlier and had smaller seeds and smaller leaves (Figure 4). In *D. canescens*, on the other hand, taller plants tended to flower later and have smaller seeds and smaller leaves, but the relationship was weak (Figure 4). For *E. pumilus*, we measured fewer traits, but taller plants tended to have more flowers.

Question 1b: Environmental variation among species' collection sites

By design, there was considerable overlap in environmental variables across all collection sites for each species, however *D. canescens* had the widest range of conditions at collection sites (Figure 5, Table 9). On average, *D. canescens* originated from lower elevation sites, while *E. pumilus* came from the highest elevation sites, and *C. douglasii's* average elevation was intermediate. *Dieteria canescens* had the widest range in elevation, with collection sites from much lower than the other two species (~220m elevation) in

Washington state. Species were all collected from sites with a similar range of MAT, although *E. pumilus*' populations were found in slightly cooler locations. *Erigeron pumilus* and *D. canescens* were collected from drier sites on average, while *C. douglasii* was collected from wetter sites. *Chaenactis douglasii's* sites also had less variable MAP than those of *D. canescens* and *E. pumilus* (Figure 5, Table 9).

Question 2: Trait-environment correlations

In our pairwise analysis, all species had multiple phenotypic traits correlated with at least one environmental variable (Figure 6). While there were differences in trait-environment correlations among species, there were also some similarities. For example, there was a positive relationship between mean annual temperature and plant height for all three species, with taller plants sourced from warmer areas (Figure 6). There was also a consistent negative relationship between elevation and the date of first flower for all three species, with lower elevation sources flowering earlier than higher ones. Across all three species, the strongest trait-environment relationships were found for plant height, flowering phenology, and flower production, though there was variation in which environmental variables were most correlated with these responses. Similarly, some environmental variations were strongly correlated with traits across all three species, including elevation, MAP, latitude, longitude, and to a lesser degree, MAT and slope.

There were some relationships between traits and soil properties exhibited in all species as well (Figure 6). For example, *C. douglasii* had several small but significant relationships between height, leaf area, and flower number with soil components such as sand and organic; plants from sandier sites tended to flower earlier and have smaller leaves. *Dieteria canescens* also had a few traits (i.e. plant height, leaf area) significantly correlated with sand, with sandier origins correlating with smaller leaves and taller plants.

Additionally, seed weight was strongly correlated with slope for both *D. canescens* and *C. douglasii*, with larger seeds on steeper slopes. Plant height in *E. pumilus* was also significantly correlated with organic, with taller plants more likely to be present in places with less organic matter.

In addition to these pairwise tests, we also ran multiple regression models separately for each species, which included between 5 and 8 environmental variables, depending on the variance inflation factor (VIF), correlation structure, and available traits for each species. On average, model fit was poor for traits of *C. douglasii* (r2= 0.04-0.22), *D. canescens* traits had variable model fit (r2= 0-0.56), and *E. pumilus* traits had a smaller number of response variables but model fit was highest, relative to the other species (r2= 0.19-0.43) (Table 6).

Mirroring the strength of relationships in the pairwise correlations, the most predictive models found for all three species were for plant height (r2=0.22 for *C. douglasii*, 0.56 for *D. canescens*, and 0.37 for *E. pumilus*; Table 6). Similar combinations of environmental variables contributed to models of plant height across all species, with some variation. For example, MAT was the strongest predictor variable for *C. douglasii*'s height, with taller plants in annually hotter conditions, although LNorm and sand also had effects. The height of *D canescens*, on the other hand, was most strongly related to elevation (taller plants at higher elevations) with longitude and Lnorm also mattering to a smaller extent. In *E. pumilus*, LNorm and elevation were the strongest predictors for height, with latitude also contributing to the model. Per this model, taller *E. pumilus* plants were from higher elevation locations with normal lithography.

For other traits, such as seed weight, there was almost no overlap between our two species in which environmental variables served as the best predictor. For example, seed weight in *C. douglasii* was related to longitude and MAT, while slope and LNorm had the strongest relationship for *D. canescens*.

While there were strong correlations between plant height and n.flw in *D. canescens* (0.73 pearson corr coefficient), the model fit varied significantly, with plant height having a poorer fit (r2=0.26) than n.flw (r2=0.56). In *E. pumilus*, there was also a correlation between plant height and n.flw (0.68), but model fits were comparatively predictive (r2=0.37 and 0.33 respectively), with larger plants originating farther north and having with more inflorescences present. Number of inflorescences and plant height also had a similar total contribution from elevation in *E. pumilus*, although in the opposite direction. Specifically, plants tended to have fewer flowers at higher elevations, but were then often taller. Even though their models had similar fits and some similarities, plant height and number of inflorescences of *E. pumilus* also had differences in predictive variables; number of inflorescences was predicted by MAP and organic, while plant height was predicted by LNorm and sand.

Question 3: How do results from a transplanted common garden compare with direct-seeded plants?

Establishment from seed and survival

Overall, emergence was low for the 10 randomly selected populations seeded directly into the ground of *D. canescens* and *C. douglasii*. This was generally true across all populations and watering treatments. 1.8% total seeds emerged for *D. canescens*, and 8.1% of *C. douglasii* seeds emerged as seedlings. Of the 33 *D. canescens* seeds that emerged, 11 of them survived up to or past 13 days (a point at which many seedlings died). Of the 151 *C. douglasii* seeds that emerged, 90 of them survived to 13 days. Thus, I will only be discussing *C. douglasii*, since it was the only species that had sufficient emergence for analyses.

Effects of water availability and precipitation at environment-of-origin

There was no significant interaction between MAP and treatment, but there were significant main effects of both of these factors. Overall, populations of *C. douglasii* originating from locations with lower annual precipitation had higher emergence ($p<0.0001$, $F= 23.612$, $df=1/1800$) and greater early survival ($p=0.028$, $F= 5.72$, $df=1/18$) relative to populations originating from sites with higher annual precipitation (Figure 7). There was also a significant effect of water addition on both emergence ($p<0.0001$, $F= 30.16$, $df=2/18$) and survival ($p<0.0001$, $F= 13.440$, $df=2/1800$). Though the interaction was not significant, this relationship was qualitatively stronger in treatments where water was added to the plot, as opposed to the dry ambient treatment, where emergence was below 30% for all populations.

DISCUSSION

Effectively regenerating landscapes in the Great Basin Desert in a way that benefits wildlife, plant communities, and people requires understanding an essential part of the landscape: forbs (J. Maron and Marler 2007; Tilman et al. 2001; 1997). Despite their importance and contribution to diversity, they have been understudied in the Great Basin relative to grasses and shrubs, and thus the biology of many forbs is not well understood (Siebert and Dreber 2019; LaForgia et al. 2018). We grew three Asteraceae species (*C. douglasii, D. canescens, E. pumilus*) collected from a wide geographic range in common garden experiments to ask how variable these populations are, how their traits were associated with environment of origin, and how two of three species responded to direct seeding and water addition. We also asked if trait-environment relationships were similar among these three species.

We found that each species had highly variable populations that were often differentiated among the various ecoregions from which they were originally collected. While we found a few similarities between the species (i.e. higher elevation populations flowering later, among other similarities), there were also many differences. The strongest trait-environment relationships we found for all species were for plant height, flowering phenology, and flower production, but the environmental variables with which they were associated generally differed depending on the species. However, we also found some generalities across species in the environmental variables that were most correlated with potentially adaptive traits. Specifically, we observed that MAT and elevation were both highly correlated and predictive of traits that are often considered important in restoration, such as phenology, number of inflorescences, and plant size. Therefore, before species-specific seed zones are available for each of the species we studied, it may be possible to use these factors as proxies to help us better match seed sources to target restoration sites.

Many common garden studies use transplants, rather than direct seeding, due to the desire to have high survivorship and representation of all populations sampled so researches can measure later life history traits (Bucharova et al. 2017; Kawecki and Ebert 2004). However, earlier life history traits, such as seed germination, also contribute to the long-term persistence of plant populations. Here, we tried direct seeding two of our three species in a separate experiment, to determine if patterns of local adaptation were also apparent in seed germination and seedling performance. One species (*D. canescens*) had extremely low seed germination, even in water addition plots, so analyses were not possible. The other species *(C. douglasii*) was more likely to emerge when planted from seed that originated from a drier environment, but due to relatively low germination rates, we were unable to determine whether other potential relationships exist between germination and environmental variables. More research needs to be done in this area, especially because our seeding experiment was conducted in an exceptionally dry year, but this finding suggests that seeds sourced from drier locations may be better at emerging from seed.

This study was one of the largest common gardens for plants in the Great Basin, both in terms of the number of populations included and the range of collection environments. Of 72 Great Basin common garden experiments where similar environmental variables were available, only 19 had a wider range of either elevation, MAP, or MAT in comparison to this study. Only five of these were forb species, all of which had fewer populations represented, n=3-67 (Baughman et al. 2019b; Bushman, Bhattarai, and Johnson 2010). Given our large sample size, it is notable that we found many strikingly similar patterns to even smaller studies, which we describe in more detail below.

Variation in trait expression among our populations was high, with significant differences between populations and ecoregions for each species and for almost all traits measured. This is consistent with past studies, which have found overwhelming evidence that among-population variation exists across many plant species (Balazs et al. 2020; Hereford 2009). This is especially true in the Great Basin Desert, where 92.2% of relevant experiments completed between 1994 and 2015 found among-populations variation (Baughman 2019a). Here, we found that size and phenology (specifically, plant height and date of first flower) showed the greatest variation between the populations surveyed for all three species examined (Table 8), which is consistent with differences in these characteristics in other studies (Baughman 2019a).

Interestingly, *D. canescens* had more variation in almost every trait measured when compared with *E. pumilus* and *C. douglasii*. We hypothesize that this could be related to two factors. First, this was the species with the most seed collections and the widest geographic area sampled. Perhaps because of this breadth of sampling, more variation was captured. Second, *D. canescens* has been subdivided into 10 distinct varieties, some with dramatically different growth forms (Cronquist et al. 1994). This taxonomic variation suggests that genetic differentiation could be affecting phenotypic differentiation, and some of the variation we observed in *D. canescens* could be explained by these classifications. A future analysis comparing the taxonomic boundaries and geographic overlap with the populations considered here could be instructive.

Much of the intraspecific trait variation we observed was associated with environment variables, which is a signature of local adaptation. Again, this is consistent with past studies, with 81.4% of experiments in the Great Basin Desert testing trait-environment-associations found similar patterns (Tumber-Dávila et al. 2022, Baughman 2019a). We found that traits such as date of first flower, inflorescence number, and plant height in all three species were highly correlated with longitude, latitude, MAT, MAP, and elevation. These traits and environmental conditions are commonly reported as being associated with one another: in the Great Basin Desert, 75% of local adaptation experiments reported that latitude was associated with variation in at least one plant trait, 50% of studies reported that MAP was associated with traits (Baughman 2019a).

The model fits for the trait regression equations varied greatly among species. While many relationships were significant overall, we were surprised by how little trait variation environmental variables predicted for *C. douglasii* in particular (Table 6). Compared to previous studies done on various grass species, with R^2 values ranging from 0.42 – 0.66 on trait-environment models and single-trait correlations ranging from 0.02-0.36 (Johnson et al. 2017;2012), the R^2 of our *C. douglasii* models ranged from 0.04-0.22 with correlation coefficients from 0.01-0.35 (Supplement 6). Although the range of our correlation coefficients were comparable, the amount of variance in phenotypic traits was not well accounted for with the environmental variables used. We hypothesize there are a few complicating factors that could be contributing to this discrepancy. One of these factors is the available resolution of environmental variables, which can obscure micro-climatic and other local-level variation. This may be particularly important for forbs, which often exist in patchy, rather than contiguous, distributions. Climatic variables such as MAT and MAP were derived from rasters with approximately $800m^2$ units. While this level of coarseness is unlikely to greatly affect MAT, which was strongly correlated with many traits, it may mask important variation in water availability that would generally be indicated by MAP, which had less of an effect than we expected. We suspect that some of this discrepancy is due to the fact that water availability is not always directly related to MAP in the Great Basin Desert, and that localized hydrological dynamics may be having a greater effect on intraspecific variation on finer scales. For example, although our *E. pumilus* populations were, on average, collected from locations with lower MAP than the other two species, I observed that many of the *E. pumilus* populations found during the seed-collection phase were present in lowland areas in the landscape or near ephemeral streams and dry washes. In this instance, although MAP indicated that these populations were sourced from relatively dry locations, it seems likely that there was significantly more water available to *E. pumilus* populations where they were actually growing. Population locations were also recorded as a single point, as opposed to a polygon or range of points from which the seed collections were made. We hypothesize that we may find a water-availability-metric that better predicts trait variation than MAP if population source-polygons were combined with additional, and more detailed, hydrological data.

Alternately, it could be that forbs are under different selection pressures than the grasses and shrubs that have been studied in the Great Basin, and the prevalence of particular trait-environment associations found in previous studies may not be representative of those found in forbs. For example, forbs are palatable to a wider array of herbivores than grasses and many shrubs (Dumroese et al. 2015). This could mean that there are strong selective pressures acting on species and populations outside of the environmental variables that are generally measured. This could be the case with the leaf color traits measured in this study, which varied among populations but were not associated with any environmental variables. Previous work has shown that while leaf color may be associated with physiological function (Qi et al. 2022; Majer et al. 2010), it can also be affected by other interactions such as herbivory and how well a plant matches its surrounding substrate (Cheng et al. 2018; Niu, Sun, and Stevens 2018; Strauss and Ivalú Cacho 2013). We suggest that more work should be done on biological interactions, herbivory in particular, that may be affecting trait evolution in potential restoration forb species, to better understand how these interactions might affect seed source selection.

Many associations between traits and environmental variables were consistent across all three species. For example, plant height was similarly correlated with longitude, MAT, and elevation for all three species. This is consistent with how often each of these environmental factors has been associated with plant traits in the Great Basin Desert (55% of studies with longitude and elevation, 60% of studies with MAT). Other studies have found that taller plants in dryland grasses are associated with less rainfall (Holthuijzen and Veblen 2015), and that plant height across many taxa and environments is predicted by precipitation, longitude, and MAT, with woody plants being shorter in dry environments, and the height of herbaceous plants not being related to aridity (Tumber-Dávila et al. 2022). Plant height has also historically been recognized as an important trait reflecting the trade-offs between competition and stress tolerance in other dryland systems and is often associated with environmental variables (75% of studies), especially MAT and MAP (Balazs et al. 2020; Baughman et al. 2019a).

There were also differences between species. For example, seed weight was associated with multiple environmental variables in *C. douglasii*, but only slope predicted seed weight in *D. canescens* and none of our environmental variables were associated with seed weight for *E. pumilus*. These similarities and differences are interesting in the context of how closely related these species are. The effect of phylogenetic distance on local adaptation has been tested in other systems, and results of its importance vary across experiments and lifeforms (Melero et al. 2022; Butaitė, Kramer, and Kümmerli 2021; Desnoues et al. 2017). All three species studied here are in the same subfamily (Asteroideae), with *D. canescens* and *E. pumilus* in the same tribe (Astereae). This makes *D. canescens* and *E. pumilus* more phylogenetically similar to each other than to *C. douglasii* (Chaenactideae tribe in the Heliantheae complex). Despite *D. canescens* and *E. pumilus* being more closely related, there was no evidence that their expression of local adaptation was more similar to each other than to *C. douglasii*. More work would need to be done in additional forb species to make an accurate assessment of phylogenetic signals in local adaptation. With this small subset of species, however, outcomes suggest that phylogenetic distance is not a determinant in how similar or dissimilar local adaptation is expressed in the Asteraceae family of forbs.

Each of the forbs studied here had a unique set of characteristics that could be used to guide decisions about which species and seed-sources to plant in potential restoration sites. For example, during a single season, we observed plants from multiple populations of *D. canescens* grow from transplants into adult plants with large canopies that produced thousands of seeds (Figure 1). Populations with these characteristics may help in specific restoration cases, such as when large areas of ground have been disturbed and a restoration island approach is being employed (de Bell, Graham, and White 2020; Hulvey et al. 2017), or when nurse plants are desired to hold soil and provide shade (Madrigal-González et al. 2020). *Dieteria canescens'* large size and fast-growing form could make it competitive with *B. tectorum*, as has been observed for other annual forbs (Ott et al. 2019), and we suggest someone try these experiments. However, we had difficulties establishing *D. canescens* from seed in an outdoor setting, which means they may be more suitable for smaller-scale restoration projects where transplanting is an option. Alternatively, treating seeds to break dormancy may be helpful to encourage success, although past literature is mixed on this point. *Dieteria canescens* is considered mostly non-dormant (Gucker and Shaw 2018b), with some studies suggesting that short periods of cold stratification improve germination rates (Pendleton and Pendleton 2014), while others suggest that cold stratification increases germination dramatically (Kramer and Foxx 2016).

Erigeron pumilus, on the other hand, seems to be the only true perennial studied in this experiment. Although we don't know how well it establishes from seed in a natural setting, survival between the first and second year of the common garden was much higher than either *C. douglasii* or *D. canescens*. Additionally, many individual *E. pumilus* plants in Reno began to put out new flowers late in the fall, after going dormant in the summer. Our partners at Boise USFS RMRS, who monitored an additional 7 common gardens containing *E. pumilus* at the same time, corroborated that this was unusual, and that the Reno garden was the only location where this was a common occurrence. Although more studies need to be done to determine what may be causing this potential expression of trait plasticity, a late-season food source for pollinators in dry sites may provide valuable refugia in a landscape where there are few species that flower so late in the season.

Lastly, a valuable characteristic of *C. douglasii* in our experimental sites was that it established readily from seed. While it can be biennial, no populations resprouted during its second year in our common garden. This ability to establish from seed is still valuable in a post-fire setting, where quick establishment of native plants may help stave off a cheatgrass monoculture (Agneray 2022; Blank et al. 2020; Ott et al. 2019). Additionally, we observed that *C. douglasii* may be more sensitive to external pressures than the other two forb species that we grow. During its time in the common garden, we observed many *C. douglasii* plants wilting and dying, after appearing healthy, and while surrounded by healthy plants. Although the exact cause of this wilting was never discovered, it may have been due to an unseasonably dry year, a heavy aphid infestation, or an unknown disease. Regardless, many *C. douglasii* began to wilt and die while *D. canescens*, only 1.5 m away, did not. This may indicate sensitivity to stressors outside of environmental variables and could explain why our models fits and correlation coefficients were low for this species.

Take-aways for application

Considering all of our results, there are several take-aways from these analyses that may be useful for restoration application. First, we found that D. canescens and E. pumilus populations were better at surviving to produce seed when compared to C. douglasii. This suggests that seed-sourcing may be less important for D. canescens and E. pumilus, while population choice is likely to be extremely important for the survival of C. douglasii in a restoration setting. D. canescens may be more suitable for transplant restoration than for direct seeding, but with transplants, it is a very reliable flower producer and makes copious seeds. On the other hand, C. douglasii emerged and survived more readily when it was grown from seed than D. canescens, again with differences among populations. This suggests that C. douglasii may establish better when direct seeding is used, but it may not be as long-lived, and again, population choice may be important. Since increased emergence and survival in early life stages is an especially desirable trait in arid-climate restoration projects that rely on direct-seeding in areas where resources are limited, these traits found in populations from drier environments-of-origin may be a valuable tool in increasing restoration efficacy. Although dry conditions are likely to lead to seedling death, irrespective of environment of origin, our results demonstrate that seeds sourced from drier environments are more likely to germinate in a variety of moisture conditions, and could potentially persist if spring conditions provided appropriate moisture for survival. Finally, while we found some common trait-environment relationships among these species, we did find species-specific patterns in important characteristics, such as seed weight, which had different drivers for each species. Our study confirms the importance of doing species-specific collections, studies, and descriptions to determine optimal seed sources for each species.

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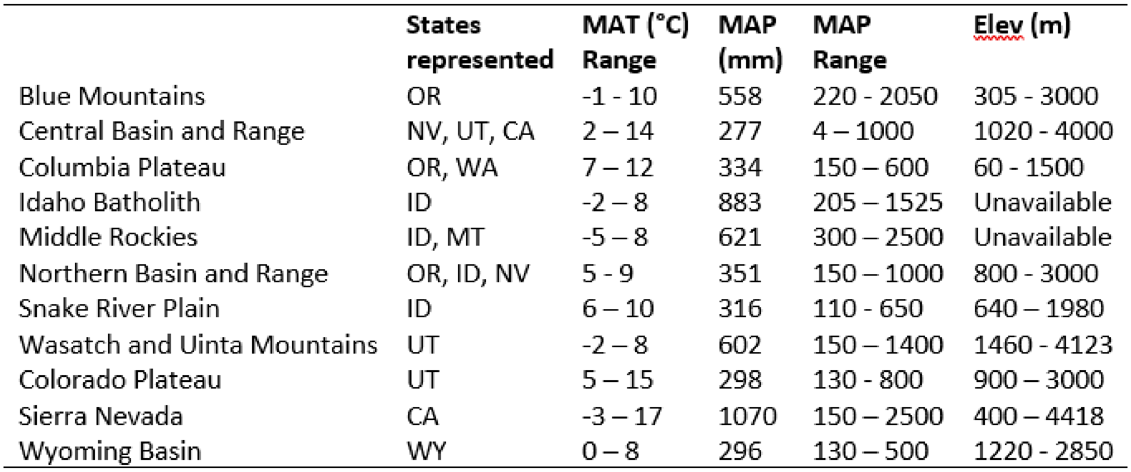
TABLES

Table 1: A list of Omernik Level III ecoregions where populations were gathered and a summary of some environmental variables that typify each ecoregion (United States Environmental Protection Agency 2013).



	States represented	MAT (°C) Range	MAP (mm)	MAP Range	Elev (m)
Blue Mountains	OR	-1 - 10	558	220 - 2050	305 - 3000
Central Basin and Range	NV, UT, CA	2 – 14	277	4 – 1000	1020 - 4000
Columbia Plateau	OR, WA	7 – 12	334	150 – 600	60 - 1500
Idaho Batholith	ID	-2 – 8	883	205 – 1525	Unavailable
Middle Rockies	ID, MT	-5 – 8	621	300 – 2500	Unavailable
Northern Basin and Range	OR, ID, NV	5 - 9	351	150 – 1000	800 - 3000
Snake River Plain	ID	6 – 10	316	110 - 650	640 – 1980
Wasatch and Uinta Mountains	UT	-2 – 8	602	150 – 1400	1460 - 4123
Colorado Plateau	UT	5 – 15	298	130 - 800	900 – 3000
Sierra Nevada	CA	-3 – 17	1070	150 – 2500	400 – 4418
Wyoming Basin	WY	0 – 8	296	130 – 500	1220 - 2850

Table 2: Target and actual amounts of precipitation applied for each watering treatment in the direct-seed common garden. The expected amount of precipitation for the ambient treatment was derived from PRISM's monthly 30-year norms for Reno, NV, where the experiment was located. The target amounts for treatments 1 and 2 was determined by mean MAP of all populations and 1.75xmean MAP respectively. Actual values are a combination of actual precipitation (measured by a nearby weather station) and an approximation of the water added in treatments 1 and 2.

	Ambient Precipitation (cm)		Treatment 1 Precipitation (cm)		Treatment 2 Precipitation (cm)	
	Expected	**Actual**	**Target**	**Actual**	**Target**	**Actual**
Winter (Dec 1-Feb 29)	8.70	4.80	10.10	10.92	18.57	21.3
Spring (Mar 1-May 31)	5.80	2.18	10.52	9.07	20.1	18.24
Summer (Jun 1-30)	1.40	0.33	6.27	2.63	11.3	7.22
Totals	15.9	7.31	26.89	22.62	50.97	46.76

Table 3: Reduced set of traits and their abbreviations used in analyses. All traits were measured for *D. canescens* and *C. douglasii*, with a subset used for *E. pumilus* analyses. Traits measured in all three species marked with *.

*Survival	Did the plant survive until it was able to produce mature seeds?
*F.Flw	First Flower; The date when a flower with reproductive structures first appeared
*n.Flw	Number of inflorescences; how many reproductively-active flowers were present on a single plant during the time of counting, which was when the first senesced inflorescence was observed.
*Plant Ht	Plant Height; a linear measurement perpendicular to the ground starting from the bottom of the plant and going to the tallest part (mm)
Col.Sat	(Sine of the hue, or color, of a leaf) x (how saturated that color was)
Light-ness	The value, or lightness, of a leaf
Seed weight	The average mass (g) of a single viable seed
LfVPD	Leaf Vapor Pressure Deficit (kPa). The difference between the amount of moisture in the air vs. the amount of moisture in the leaf. A higher VPD indicates that there is a greater difference between the vapor pressures of the air and leaf, which indicates that a plant may transpire more.

Table 4: Reduced set of environmental variables used in analyses. Most variables were used for all three species except elevation (which was used exclusively for *E. pumilus*) and annual mean temperature (which was not used for *E. pumilus*) due to slightly different correlation structure among collection sites for each species.

Longitude	The geographical angular distance east or west on the earth's surface for each population.
Latitude	The geographical angular distance north or south on the earth's surface for each population.
MAT	Mean Annual temperature (°C), extracted from PRISM's 30- year climate normals 1991-2020.
MAP	Annual accumulation of precipitation (mm), extracted from PRISM's 30- year climate normals 1991-2020.
Elevation	Height above sea level (m)
Slope	How many degrees the collection site deviated from horizontal.
Sand	% sand present in soil estimated by SSURGO. Mineral particles 0.05mm to 2.0mm in equivalent diameter as a weight percentage of the less than 2 mm fraction.
Organic	% organic materials present in the soil estimated by SSURGO. The amount by weight of decomposed plant and animal residue expressed as a weight percentage of the less than 2 mm soil material.
Lith	The most general description of the major lithologic components of the geologic unit at the population's origin. Extracted from The State Geologic Map Compilation (SGMC) geodatabase of the conterminous United States.
LNorm	Whether or not the geology underlying at a collection site is considered 'normal.' Lithologies are considered normal if that bedrock type typically weathers into components that provide plants with all basic and necessary nutrient requirements.

Table 5: Data transformations and distributions (listed as transformation-distribution) used to achieve well-fitting models. Trait abbreviations are shown in Table 1.

Trait	***C. douglasii***	***D. canescens***	***E. pumilus***
Survival	none-binomial	none-binomial	none-binomial
F.Flw	log-gaussian	log- gaussian	sqrt- gaussian
n.Flw	none-negative binomial	none-negative binomial	none-negative binomial
Plant Ht	none-gaussian	none-Gamma inverse	none-Gamma inverse
color.sat	none-gaussian	none-gaussian	NA
lightness	none- gaussian	log- gaussian	NA
Seed weight	none- gaussian	none- gaussian	NA
LfVPD	log-gaussian	log- gaussian	NA
Lf Area	log-gaussian	sqrt- gaussian	NA

Table 6: Best Models predicting relationships between environmental variables and traits for 3 Asteraceae traits Significance for each environmental variable is listed in the second column using the following notation: ‘$p<0.1$, *$p<0.05$, **$p<0.01$, ***$p<0.001$. R^2 indicates model fit, and scaled coefficients show the strength and direction of each relationship.

A: *C. douglasii*

Trait	**Environmental variables in best model**	**R^2**	**Coefficient List**
Survival	Longitude* + Latitude* + MAT’+ slope** + per.sand’ + per.organic	0.04	0.26 Longitude, 0.27 Latitude, -0.2 Ann tmean, 0.31 slope, 0.22 sand, -0.18 organic
F.Flw	Latitude** + MAT* + per.sand*	0.10	0.02 Latitude, 0.01 MAT, 0.01 sand
n.Flw	Latitude** + MAT’ + MAP + sand’ + Lnorm***	0.14	0.26 Latitude,0 .15 MAT, -0.17 ppt, -0.15 sand, 0.73 LNorm
Plant Ht	Latitude’ + MAT*** + MAP + per.sand** + Lnorm*	0.22	14.96 Latitude, 27.50 MAT, -14.37 ppt, -18.72 sand, 39.39 Lnorm
color.sat	Longitude* + per.sand’	0.09	0.14 Longitude, .01 sand
lightness	Latitude	0.07	-0.279 Latitude
Seed weight	Longitude *+ MAT* + Lnorm’	0.15	-1.0e04 Longitude, 9.4e05 MAT, 1.9e04 Lnorm
LfVPD	Longitude’ + MAP + per.organic	0.06	-0.10 Longitude, -0.12 MAP, 0.09 organic
Lf Area	MAT** + per.sand*	0.06	0.085 MAT, -0.08 per.sand

B. *D. canescens*

Trait	**Environmental variables in best model**	**R²**	**Coefficient List**
Survival	Latitude** + MAP*	0.02	0.29 Latitude, 0.19 MAP
F.Flw	Longitude*** + Elev*** + MAP*** + per.organic + LNorm1**	0.52	0.03 Longitude, -0.12 elev, 0.03 ppt, -0.01 organic, 0.03 Lnorm
n.Flw	Longitude*** + Latitude ***+ elev** + slope*** + Lnorm*	0.26	0.25 Longitude, 0.55 Latitude, -0.23 elev, -0.19 slope, 0.23 Lnorm
Plant Ht	Longitude*** + Latitude* + MAP** + elev*** + sand*** + Lnorm*	0.56	-1.5e-04 Longitude, 1.1e-04 Latitude, -1.2e-04 ppt , 8.9e-04 elev, 8.6e-05 sand, -1.3e-04 Lnorm
color.sat	elev	0.001	-0.03 elev
lightness	slope	0.01	0.03 slope
Seed weight	Longitude' + elev' + slope** + Lnorm*	0.19	-4.4e-05 Longitude, 6.2e-05 elev, 5.6e-05 slope, -9.8e-05 LNorm
LfVPD	Longitude + slope' + LNorm1.	0.01	-0.02 Longitude, 0.03 slope, 0.06 Lnorm
Lf Area	Longitude***+ elev*** + MAP**	0.13	-0.07 Longitude, 0.13 elev, 0.05 MAP

C. *E. pumilus*

Trait	**Environmental variables in best model**	**R²**	**Coefficient List**
Survival*	MAP*** + slope + LNorm**	0.43	-8.95 MAP, 2.70 slope, -3.99 LNorm
F.Flw	MAP*** + elev*** + sand	0.19	1.06 MAP, 1.11 elev, 1.04 sand
n.Flw	Latitude** + MAP*** + elev*** + organic***	0.33	0.44 Latitude, 0.86 ppt, -0.36 elev, -0.49 org

*VIF was extremely high for environmental factors in this binary model, so results came from a different set of environmental variables than every other trait. We omitted Longitude, elev, and organic variables to create this model. Variables included in this model were Latitude, MAP, slope, %sand and LNorm

Table 7: Mean (standard deviation) and range of a subset of traits among populations and species. % Survival is the percent of plants that survived to make seed, plant height is the height of the perpendicular line from the ground to the tallest part of the plant, F.Flw was the first day of the year that flowers had mature stamens and/or pistils which were then converted into dates, and the # Inf was the number of inflorescences that that had mature stamens and/or pistils at the point when the first senesced inflorescence was observed. CHDO= *C. douglasii*, DICA= *D. canescens*, ERPU= *E. pumilus*

	% Survival Mean	**% Survival Range**	**F.Flw: Mean (# days, date)**	**F.Flw: Range**	**# Inf: Mean**	**# Inf: Range**	**Plant height (cm): Mean**	**Plant height (cm): Range**
CHDO	51 (32)	0-100	134 (7) May 13th	123-151 May 2nd-May 30th	70 (47)	1-228	305 (62)	180-440
DICA	79 (17)	25-100	175(24) Jun 23rd	137-230 May 16th-Aug 17th	36 (49)	1-174	390 (155)	153-834
ERPU	83 (30)	0-100	125 (6) May 5th	116-136 Apr 26th-May16th	27 (21)	1-98	96 (28)	57-171

Table 8: Results of analysis of variance comparing traits among populations nested within ecoregions for traits of A) *C. douglasii*, B) *D. canescens*, and C) *E. pumilus*. Values reported are from ANOVA tests, and include numerator (n) and denominator (d) of degrees of freedom (df), test statistics (F), and significance (p). Bolded p-values indicate a significance <0.05.

A) *C. douglasii*		df_n	df_d	F	p
Survival	Ecoregion	7	479	1.90	0.151
	Population	50	479	1.28	**0.047**
First Flower	Ecoregion	7	186	5.83	**<0.001**
	Population	50	186	2.14	**<0.001**
No. of Inflorescences	Ecoregion	7	88	1.45	0.195
	Population	49	88	1.21	0.216
Plant Height	Ecoregion	7	94	3.16	**.004**
	Population	50	94	2.52	**<0.001**
Color-saturation	Ecoregion	6	37	4.44	**0.002**
	Population	36	37	1.11	0.381
Lightness	Ecoregion	7	41	3.86	**0.003**
	Population	37	41	1.70	0.050
Seed Weight	Ecoregion	7	44	1.12	0.368
	Population	40	44	2.44	**0.002**
Leaf VPD	Ecoregion	7	52	0.28	0.960
	Population	42	52	0.95	0.559
Leaf Area	Ecoregion	7	172	1.14	0.338
	Population	50	172	2.10	**<0.001**

B) *D. canescens*		df_n	df_d	F	p
Survival	Ecoregion	9	881	2.45	**0.011**
	Population	98	881	1.38	**<0.001**
First Flower	Ecoregion	9	593	202.5	**<0.001**
	Population	98	593	13.24	**<0.001**
No. of Inflorescences	Ecoregion	9	562	17.28	**<0.001**
	Population	98	562	2.46	**<0.001**
Plant Height	Ecoregion	9	589	172.9	**<0.001**
	Population	98	589	11.79	**<0.001**
Color-saturation	Ecoregion	9	165	1.02	0.429
	Population	97	165	1.03	0.429
Lightness	Ecoregion	9	165	1.06	0.395
	Population	97	165	0.93	0.652
Seed Weight	Ecoregion	9	40	2.69	**0.015**
	Population	67	40	2.35	**0.002**
Leaf VPD	Ecoregion	9	598	1.28	0.241
	Population	98	598	1.8	0.981
Leaf Area	Ecoregion	9	544	7.20	**<0.001**
	Population	98	544	2.13	**<0.001**

C) E. pumilus		df_n	df_d	F	p
Survival	Ecoregion	7	236	17.26	**<0.001**
	Population	14	236	2.31	**0.005**
First Flower	Ecoregion	7	237	7.35	**<0.001**
	Population	14	237	2.40	**0.003**
No. of Inflorescences	Ecoregion	7	285	23.28	**<0.001**
	Population	15	285	2.25	0.061
Plant Height	Ecoregion	7	237	20.19	**<0.001**
	Population	14	237	9.41	**<0.001**

Table 9: Mean (standard deviation) and range of select environmental variables at collection sites among populations and species, with temperature and precipitation variables derived from PRISM's 30-year climate normal (1991-2020). CHDO= *C. douglasii*, DICA= *D. canescens*, ERPU= *E. pumilus.*

	MAT (° C)	**MAT (° C) Range**	**MAP (mm)**	**MAP Range**	**Elev (masl)**	**Elev Range**
CHDO	7.4 (1.9)	1.5-10.9	449.0 (156.6)	252.3-829.4	1754.2(494.1)	828.7-2767.9
DICA	7.4 (2.4)	2.45-11.45	411.5 (169.1)	201.2-992.3	1728.2 (553.2)	218.5-2878.7
ERPU	6.3 (2.0)	2.9-10.5	405.8 (175.4)	198.8-931.0	1857.3 (494.9)	950.1-2938.6

FIGURES

Figure 1: Photos of each study species, *Chaenactis douglasii* (A), *Dieteria canescens* (B), and *Erigeron pumilus* (C), as well as a photo of the Reno common garden (D).

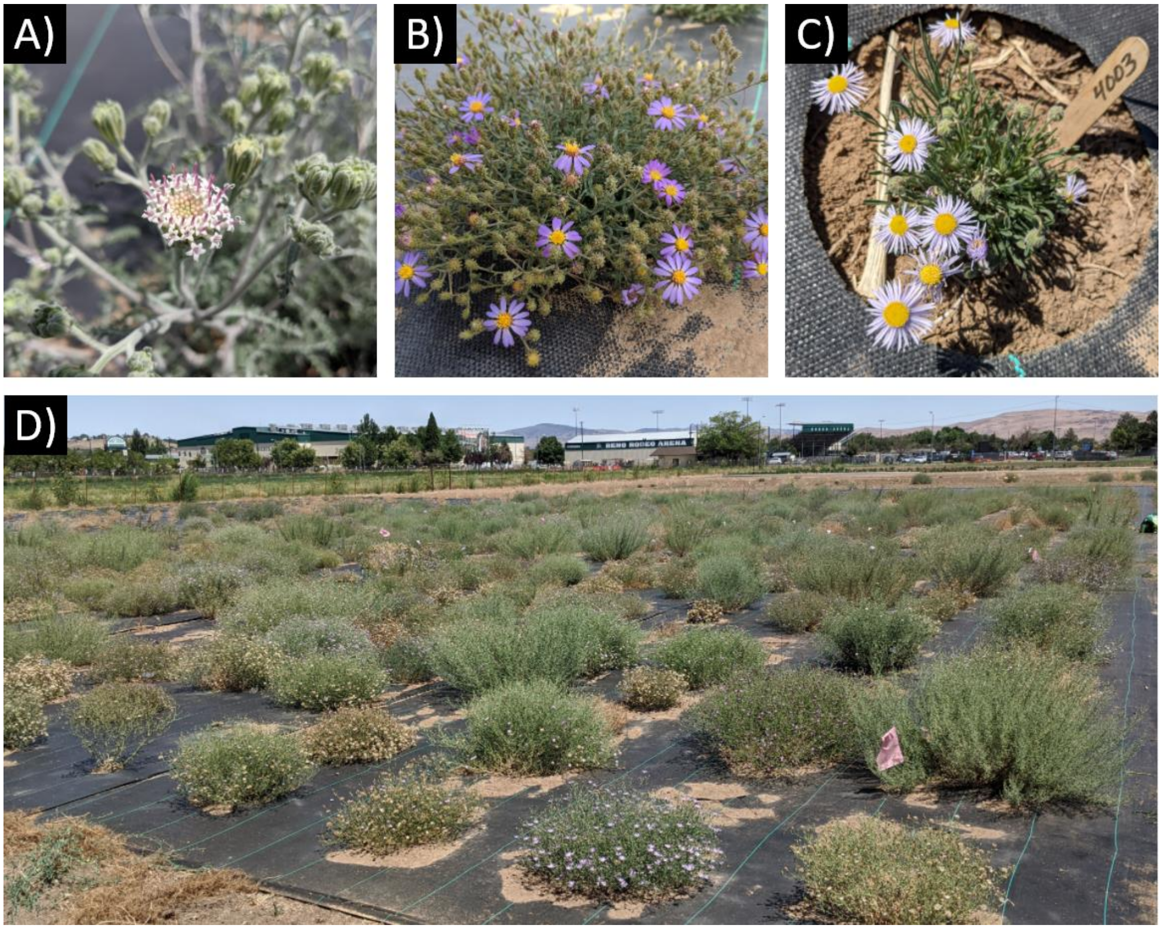


Figure 2: Map of all populations collected by the US Forest Service and used in the Reno common garden. The Great Basin floristic province is outlined in orange dashes, collection locations for *Chaenactis douglasii* are shown in white diamonds, *Dieteria canescens* are shown in purple pentagons, and *Erigeron pumilus* are shown in green circles, with US state boundaries in black.

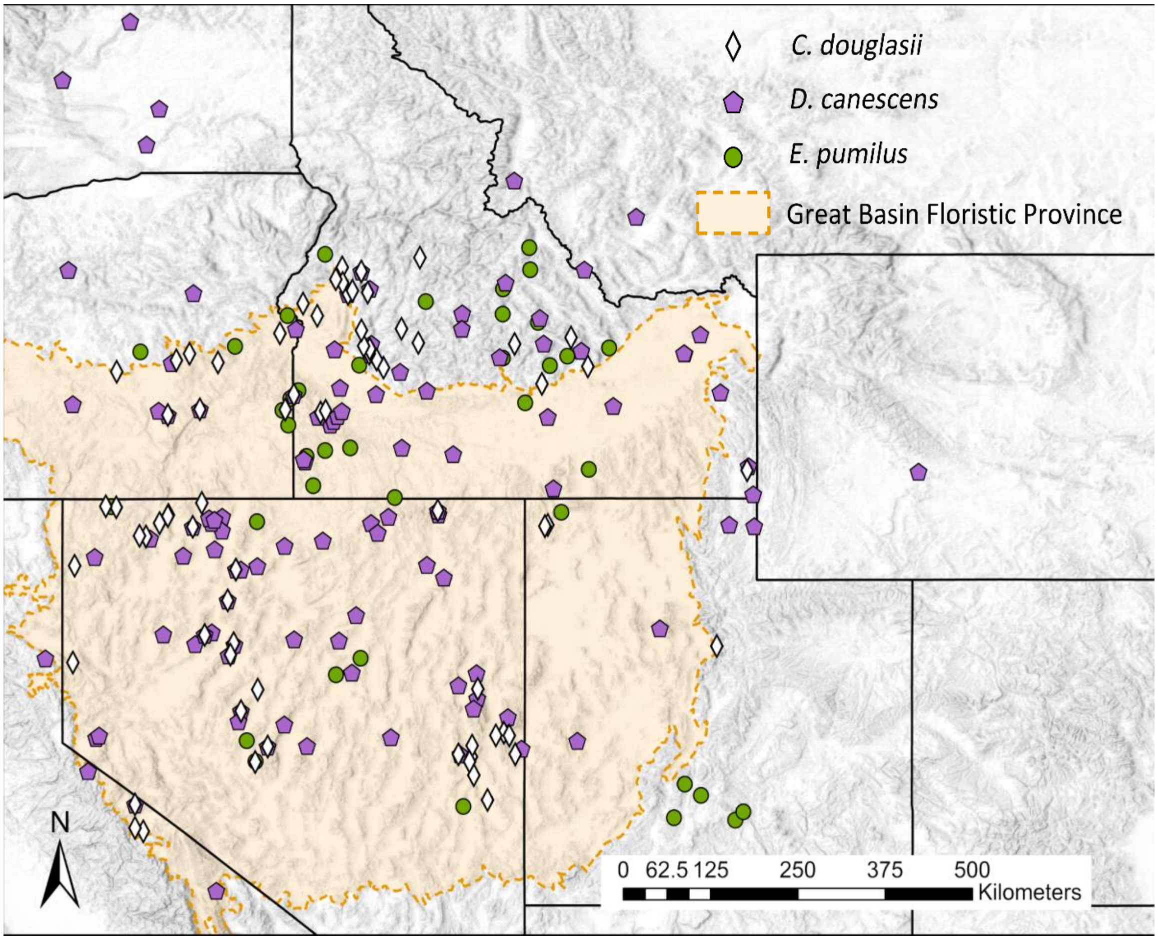
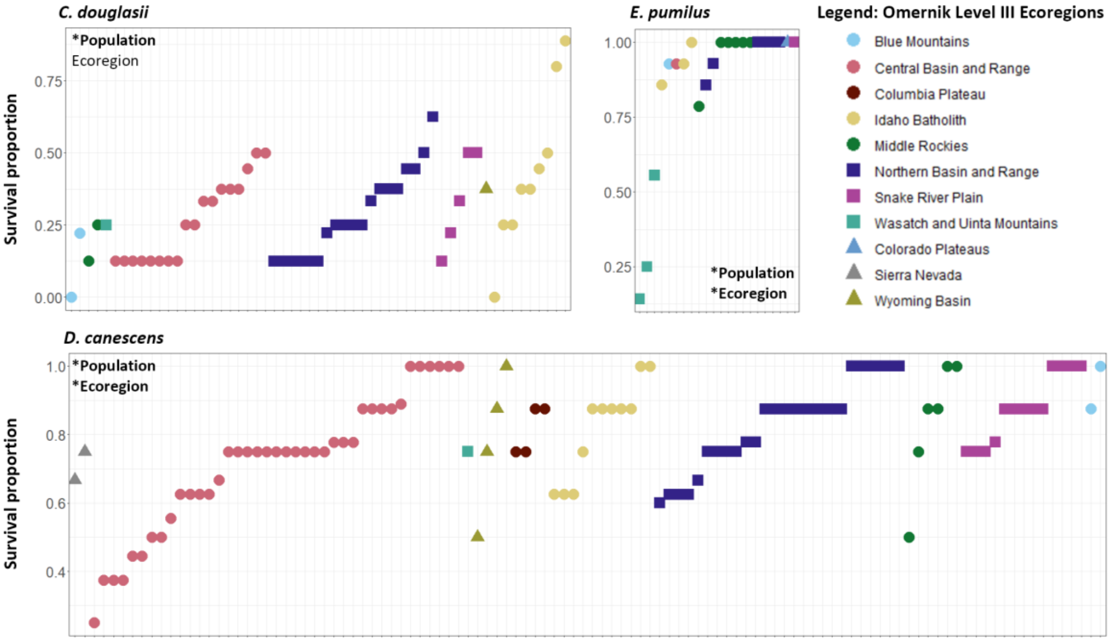
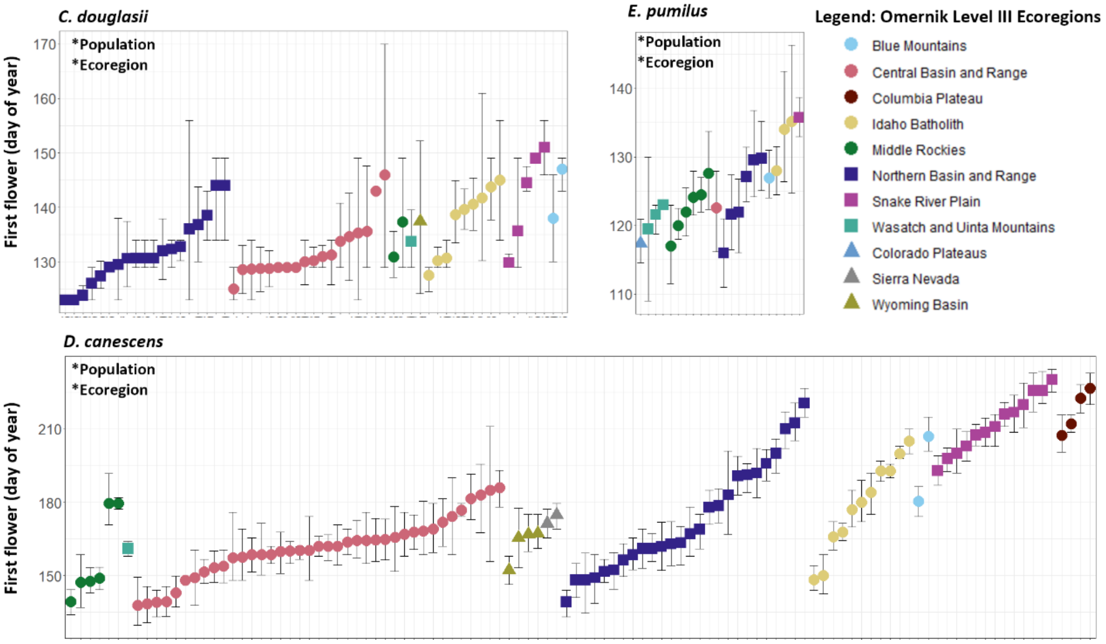


Figure 3: Mean trait measures (with 95% confidence interval) for each population arranged by Omernik level III ecoregions for *Erigeron pumilus, Dieteria canescens*, and *Chaenactis douglasii.* If variation was significant among populations and/or ecoregions (Table 1), the corresponding factor is bolded and marked with an asterisk. Traits shown include survival (A), first flower (B), plant height (C), and seed weight (D). Each point represents a population, but population names (x-axis) are omitted for legibility; See Supplement 9 for all trait graphs with populations listed.

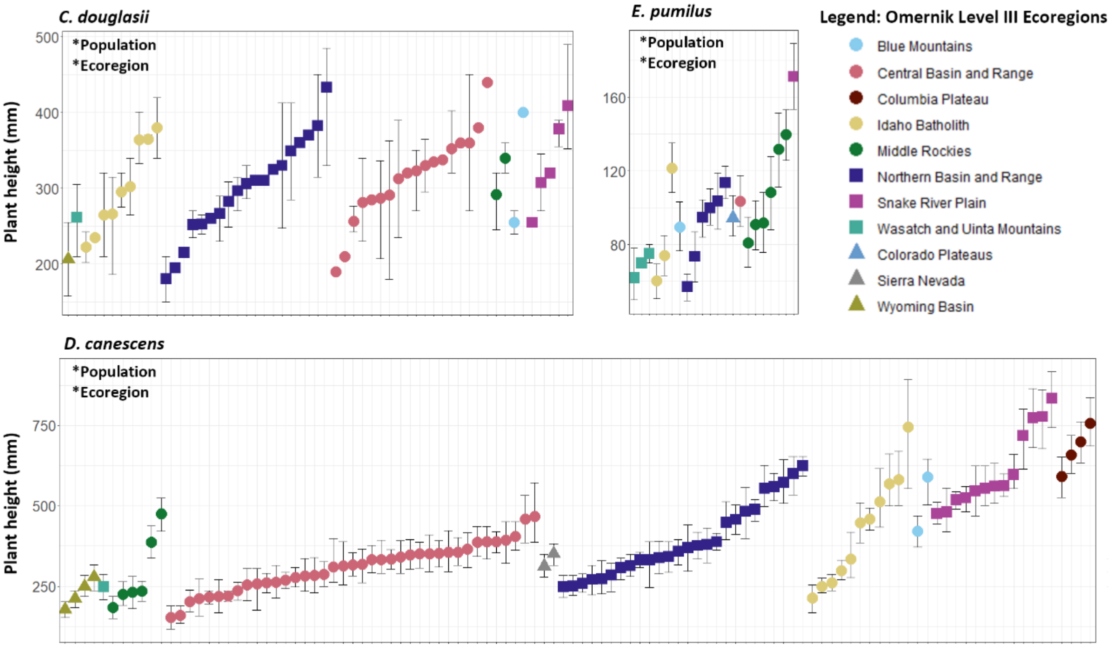
A) Survival



B) First Flower



C) Plant Height



D) Average Seed Weight

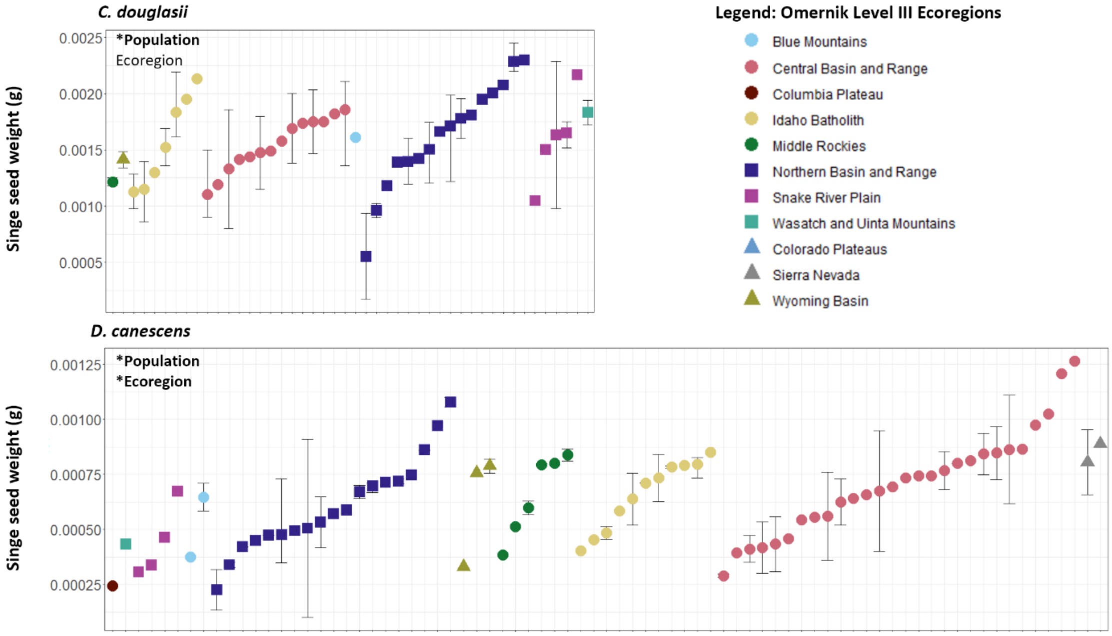
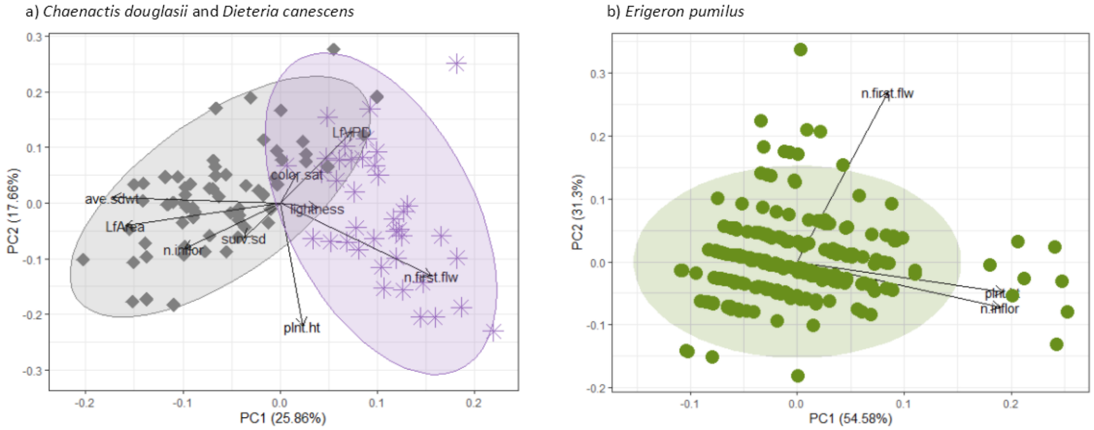


Figure 4: Trait PCA a) for *C. douglasii* and *D. canescens*, and b) for *E. pumilus*. *Erigeron pumilus* is not graphed with *C. douglasii* and *D. canescens* to account for the fewer number of traits measured.



	% Explained Variance
PC1	25.86
PC2	17.66
PC3	12.35
PC4	11.3
PC5	10.53

Loadings for the first 3 principal components

Traits	PC1	PC2	PC3
n.first.flw	0.50	-0.42	0.04
surv.sd	-0.12	-0.20	-0.08
n.inflor	-0.32	-0.26	-0.38
plnt.ht	0.08	-0.71	-0.13
color.sat	0.05	0.17	-0.80
lightness	0.12	-0.03	-0.41
ave.sdwt	-0.55	0.03	-0.06
LfVPD	0.24	0.41	-0.12
LfArea	-0.51	-0.13	0.10

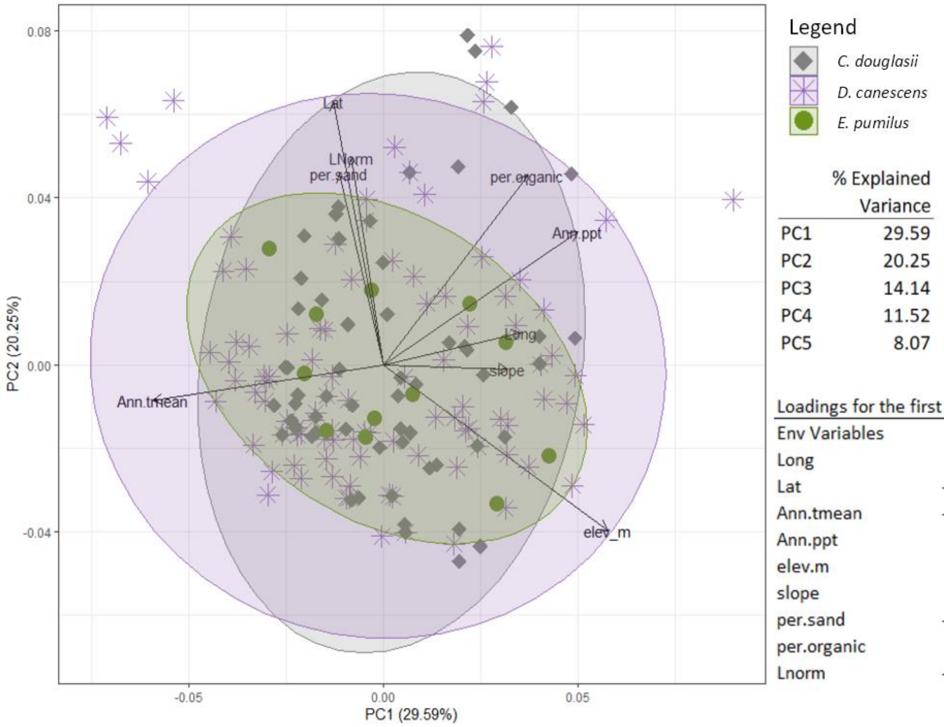
Legend
◆ *C. douglasii*
✳ *D. canescens*
● *E. pumilus*

	% Explained Variance
PC1	54.58
PC2	31.30
PC3	14.12

Loadings for the first 3 principal components

Traits	PC1	PC2	PC3
n.first.flw	0.30	0.95	0.06
n.inflor	0.67	0.26	0.70
plnt.ht	0.68	-0.17	-0.71

Figure 5: PCA for environmental variation among all three species, *C. douglasii*, *D. canescens*, *and E. pumilus*.



	% Explained Variance
PC1	29.59
PC2	20.25
PC3	14.14
PC4	11.52
PC5	8.07

Loadings for the first 3 principal components

Env Variables	PC1	PC2	PC3
Long	0.31	0.07	-0.28
Lat	-0.11	0.55	-0.46
Ann.tmean	-0.51	-0.07	0.18
Ann.ppt	0.43	0.28	-0.02
elev.m	0.50	-0.34	0.17
slope	0.28	-0.01	0.50
per.sand	-0.10	0.40	0.44
per.organic	0.32	0.39	-0.04
Lnorm	-0.07	0.43	0.46

Figure 6: Trait x environment correlation coefficients for each environmental variable and forb species tested (CHDO= C*. douglasii*, DICA= *D. canescens*, ERPU=*E. pumilus*). More saturated colors indicate higher correlation, orange squares indicate negative correlations, and blue signifies positive correlations. Significance values are indicated for each correlation coefficient using the following notation: *p<0.05, **p<0.01, ***p<0.001. If no significance indication is listed, the correlation is considered insignificant at p>0.05.

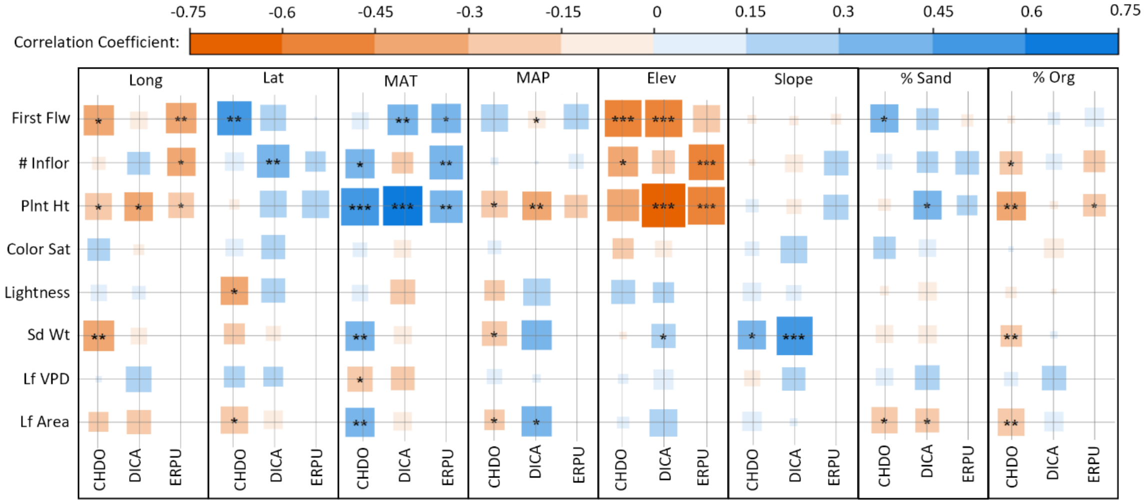


Figure 7: % Emergence of *Chaenactis douglasii* observed for each population and watering treatment, arranged from wettest environment-of-origin to driest. Treatment 0: dry ambient treatment; Treatment 1: water added equal to mean precipitation of all populations from transplanted common garden; Treatment 2: water added equal to 1.75*mean precipitation of all populations from transplanted common garden.

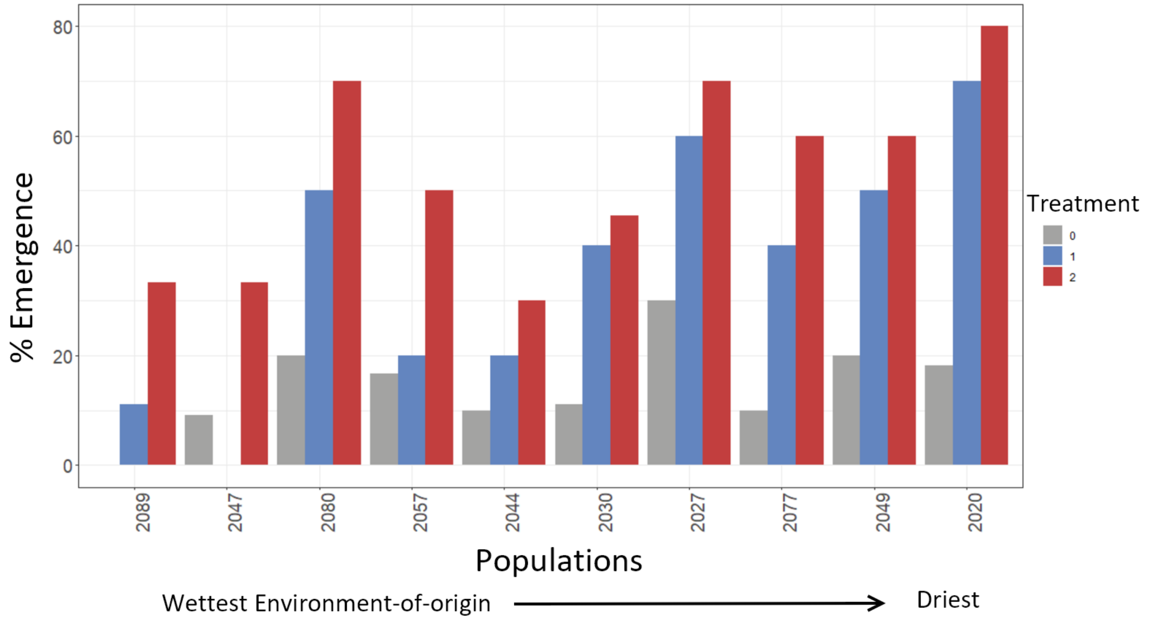
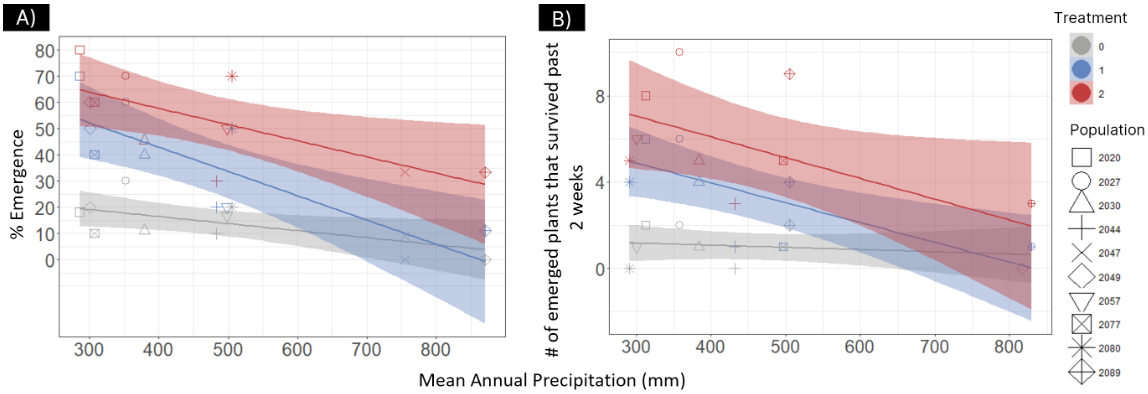


Figure 8: Relationship between mean annual precipitation at the source population and a) % emergence and b) number of emerged plants that survived after two weeks. Trend lines were derived using linear models and cones represent 95% confidence intervals. Results are shown for all three watering treatments (0 ambient, 2 the highest watering treatment), but effects were consistent across all treatments.



SUPPLEMENTAL MATERIAL

Supplement 1: Description of each phenology phase that was recorded. During each visit, the phenology phase that was recorded was the highest one presenting on each plant, regardless of what phase the majority of the plant was exhibiting.

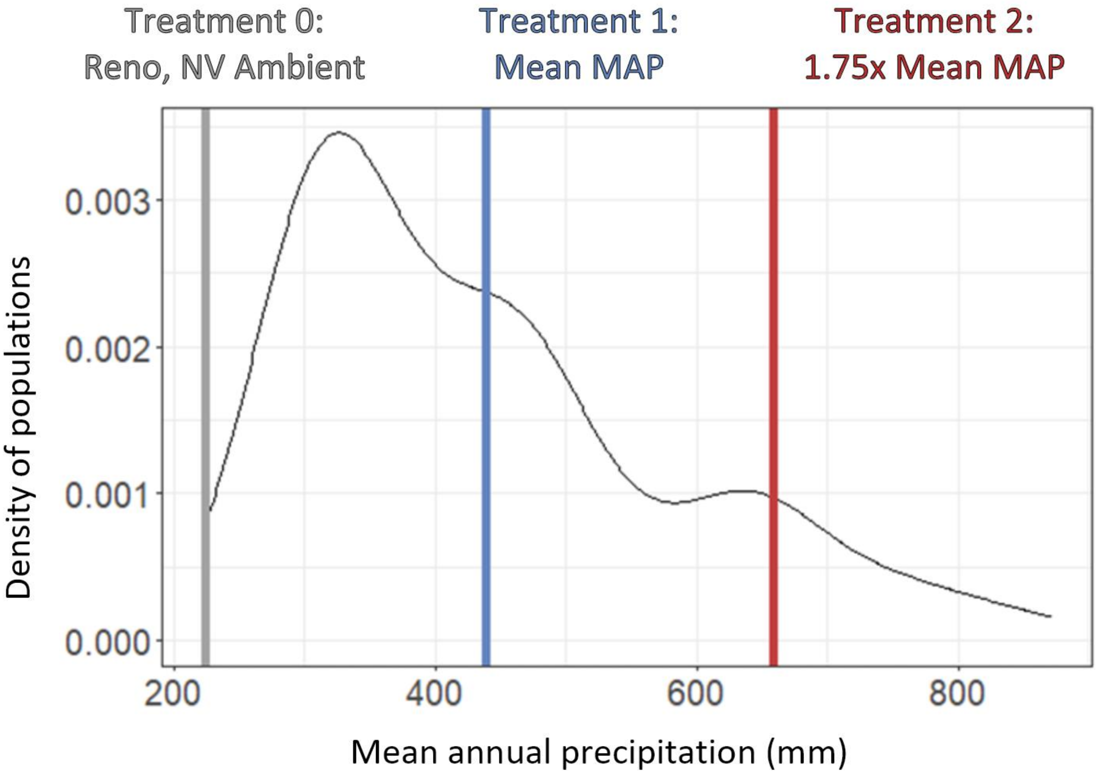
Phenology Phase (PP)	Description
0	No plants or plant material present
1	A seedling is present. Leaves that are present are small and not fully developed
2	Leaves are present and fully developed
2.5	New leaves are growing on a plant that otherwise appears dead
3	A plant is obviously bolting but buds are not yet present
3.5	Buds are present on at least 1 terminus of the plant
4	Buds are beginning to open. Showy flower parts may be present, but no pistils or stamens have yet emerged.
5	A flower is reproductively active. Pistils and/or stamens are visible.
6	Flower is senescing. Pistils/stamens no longer visible and showy petals may be curling back
7	Mature seeds are present
8	All seeds on a single inflorescence have distributed.
9	All seeds on the entire plant have distributed and/or there is biomass still present but it does not appear to be alive/active.

Supplement 2: Detailed description of traits and relative schedule for when various traits were measured on each individual in the garden.

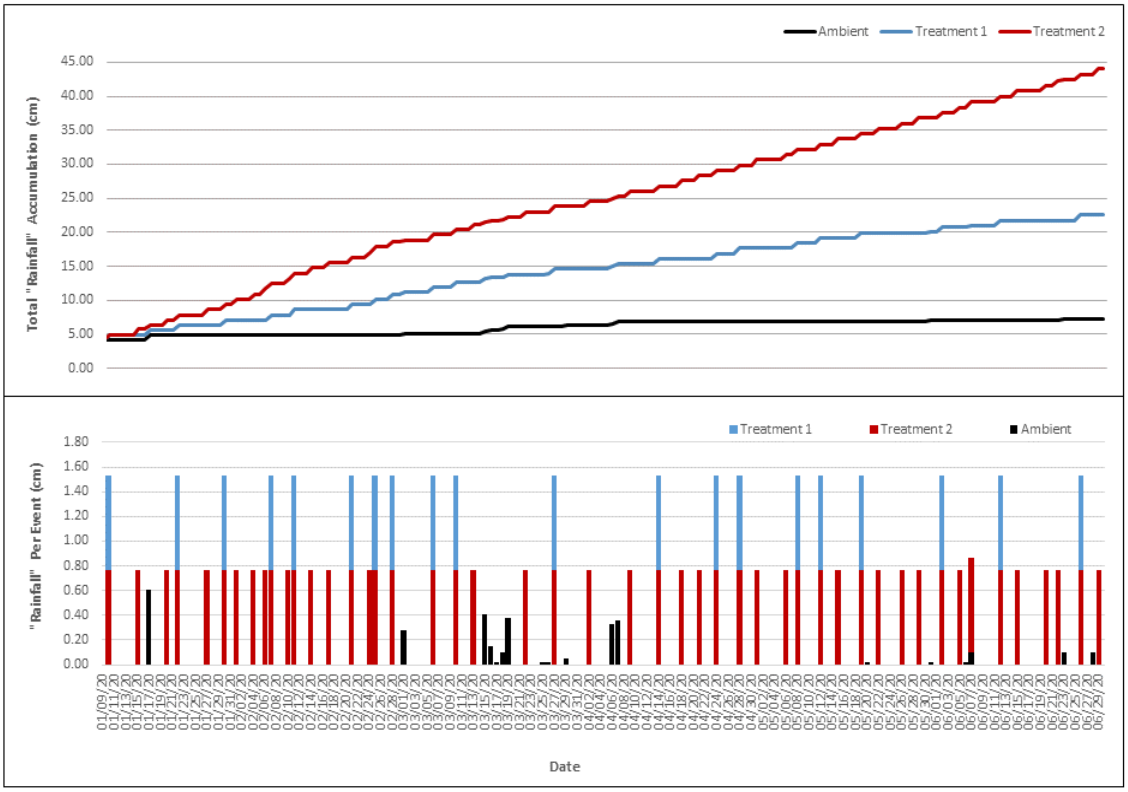
Trait	**Description & when measured**
Number of surviving neighbors	Count (0-8) how many neighbors each plant has in any phenology phase other than 0 or 9. To be done each visit (weekly or biweekly depending on current phenology phase).
Flowers still present?	During each visit, determine (Yes or No) if there are still flowers present in phenology phase 5 (reproductively active).
Diameter of basal rosette leaves	To be measured once after an individual first exhibits phenology phase 3 (bolting) or higher.
Leaf size and shape	Collect leaves once after an individual first exhibits phenology phase 3 (bolting) or higher.
Gland density/ pubescence	Collect leaves once after an individual first exhibits phenology phase 3 (bolting) or higher.
Number of inflorescences per plant	Count the number of flowers that are in phenology phase 5 (reproductively-active flowers). Do this count once after an individual has reached phenology phase 6 (flower senescing).
Plant height (stem length)	Follow stem from the ground to the highest terminus of the plant. Measure once after an individual has reached phenology phase 6 (flower senescing).
Plant height (linear)	Measure the total height of a plant as a straight perpendicular line between the ground and the highest point of the plant. Measure once after an individual has reached phenology phase 6 (flower senescing).
Crown width	Measure the linear width of a plant between its outermost termini at whatever height exhibits the plant's widest dimension. Measure once after an individual has reached phenology phase 6 (flower senescing).
Number of seeds per inflorescence	Bag an inflorescence using a muslin bag after an individual exhibits phenology phase 6. Collect bag after phenology phase 8 to count seeds. 2 repetitions to be done per garden, in randomly chosen blocks 3 & 6. Count number of seeds.

Seed weight	Bag an inflorescence using a muslin bag after an individual exhibits phenology phase 6. Collect bag after phenology phase 8 to count seeds. 2 repetitions to be done per garden, in randomly chosen blocks 3 & 6. Weigh a subset of seeds.
Water-use efficiency measures	Measure ambient temperature, leaf temperature and on the sunny side of tha plant once using a digital psychrometer and infrared thermometer

Supplement 3: A density curve showing the distribution of precipitation values for all populations relative to the amount of water applied in each treatment. Treatment 0 (shown in gray) is ambient precipitation at Reno, NV. Treatment 1 (shown in blue) is the mean precipitation value across all populations. Treatment 2 (shown in red) is 1.75x mean. These treatments were originally calculated using seasonal values but have been displayed here as annual values.



Supplement 4: The actual precipitation and water added to the direct-seeded garden. Ambient precipitation (shown in black) was the rain and snowfall that occurred naturally and counted as our ambient treatment. Treatment 1 (shown in blue) was supplemented with water added using a watering cart, with the goal of achieving the mean precipitation value across all collection sites. Treatment 2 (in red) was also supplemented with water with the goal of achieving 1.75x mean precipitation.

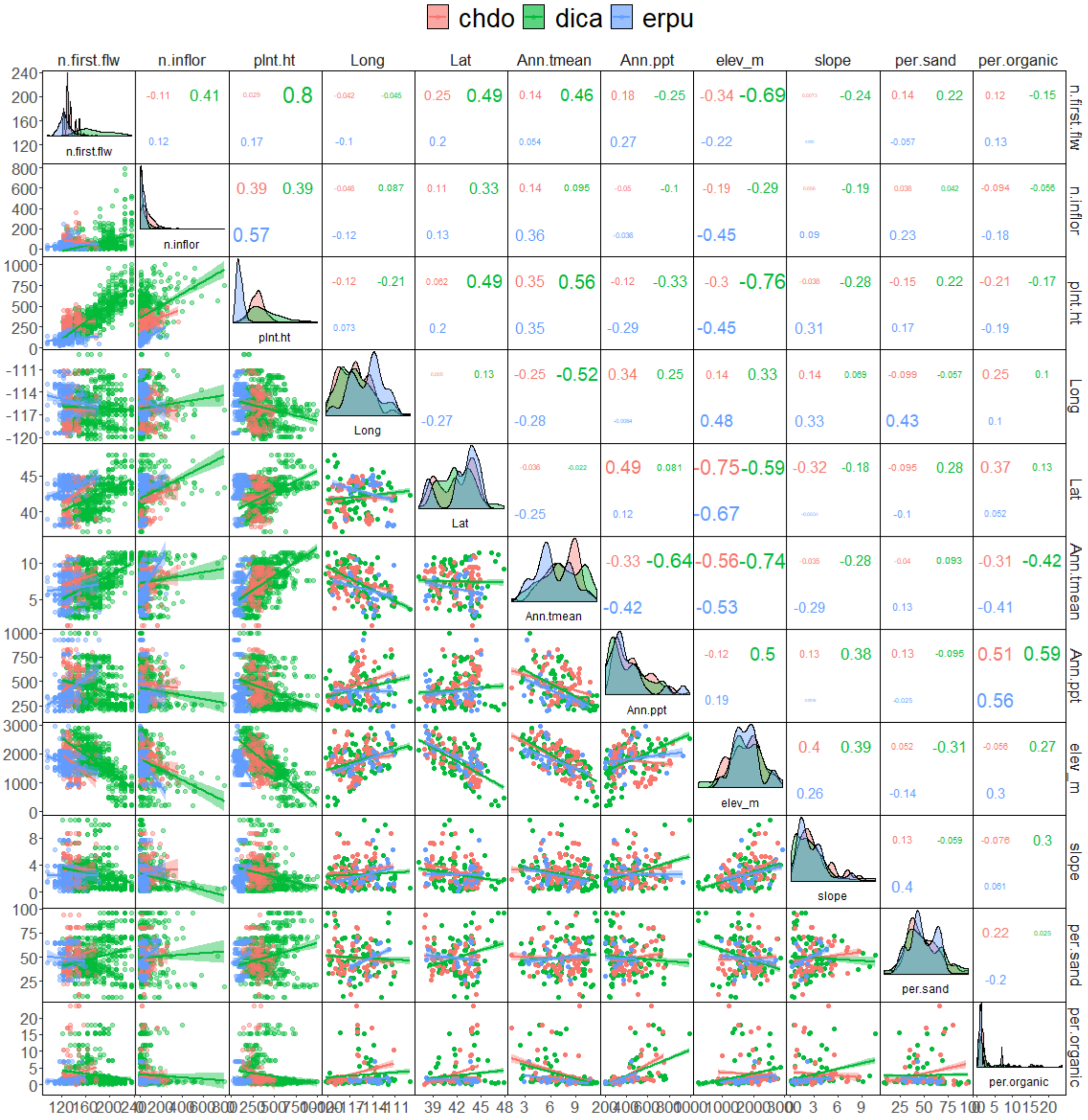


Supplement 5: Supplemental Methods - Watering treatments

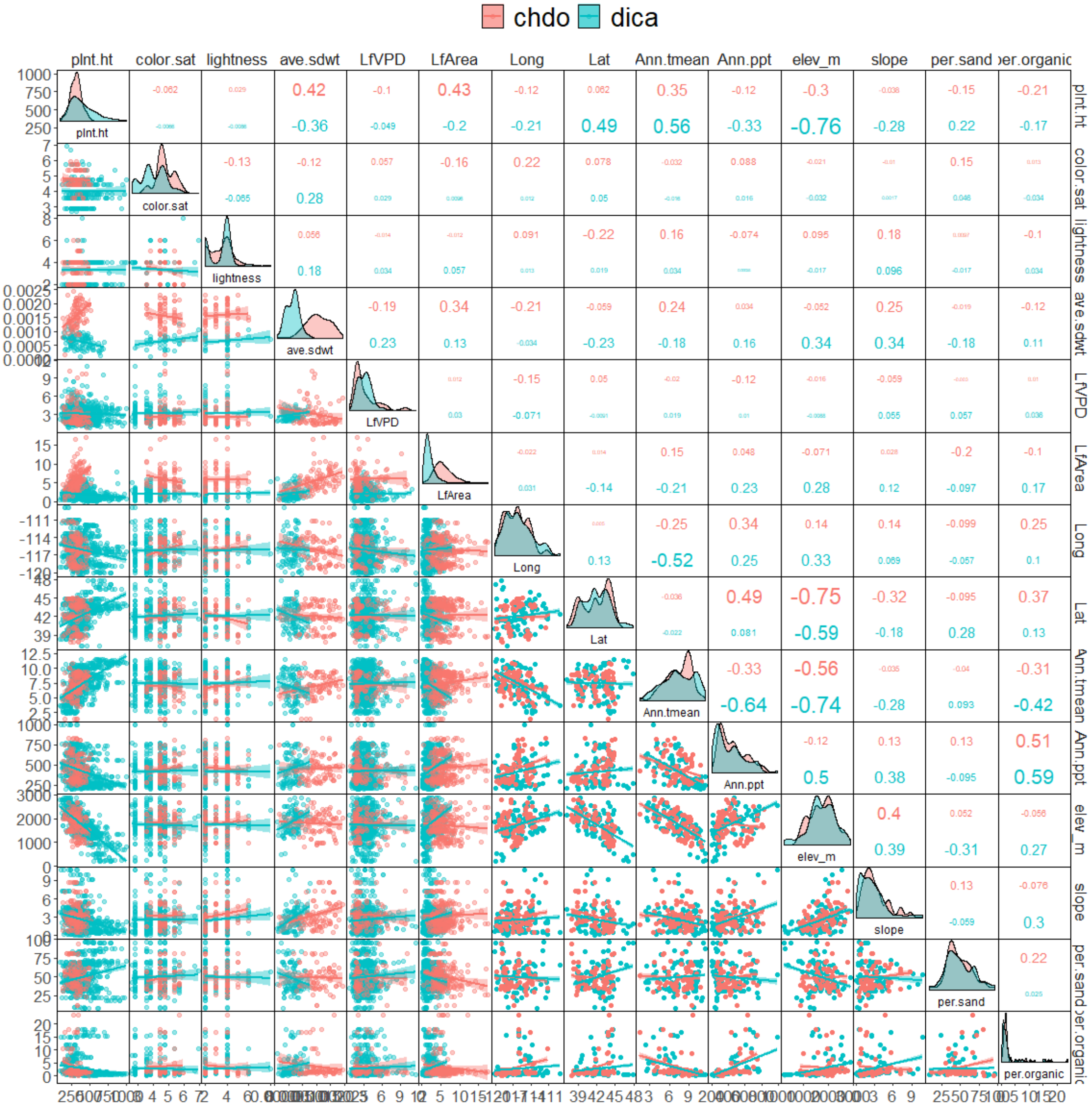
Through experimentation, I found watering for longer than 3 seconds caused significant run-off. In an attempt to maximize water absorption into soil, I chose to use a 3-second interval to standardize the output of water I would apply to each seed-site. I then calculated the rainfall amount using the area sprayed and the volume of water output during my chosen 3-second interval. Each row was watered twice every time I visited the garden to maximize water absorption into the soil while decreasing the number of visits needed to hit my target water amounts. In total, 120ml (which converts to 80mm of precipitation) is applied to each seed-site every time I water. I then planned the number of visits that would be needed to hit my target precipitation amounts and watered 2-3 times each week depending on ambient precipitation. A new density curve with different target precipitation amounts was created starting March 1st to reflect lower spring precipitation levels, as well as on June 1st to reflect summer precipitation levels. I continued my watering treatments until the end of June 2020, when there was a significant decline in expected precipitation across all population locations.

Supplement 6: Data structure and correlation coefficients and relationships between plant traits and environmental variables and the data structure for each variable, separated into two figures whether the traits were collected for all three species (a), or just *D. canescens* (dica) and *C. douglasii* (chdo) (b). erpu=*E. pumilus.*

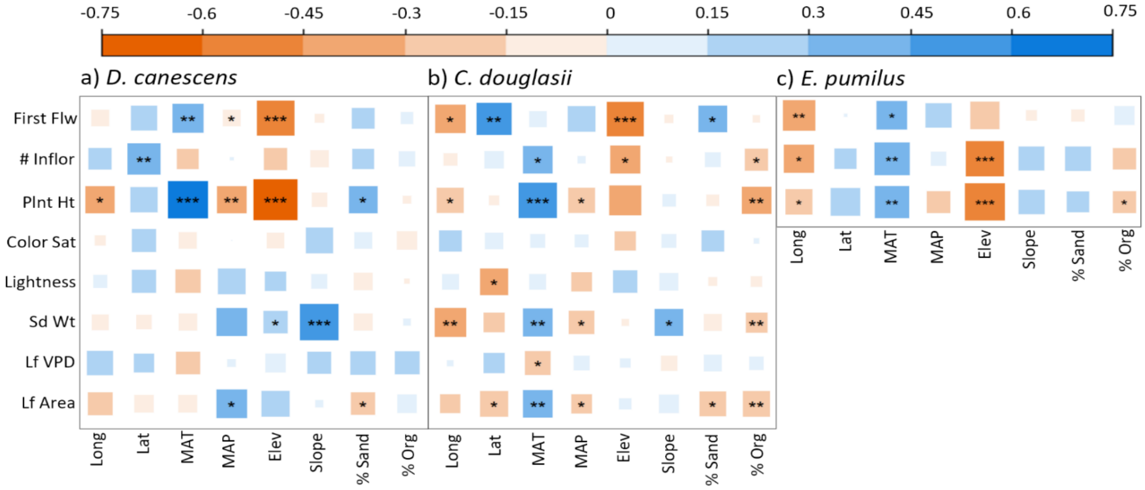
a) data from traits that were collected from all 3 species.



b) data from traits collected for just *D. canescens* (dica) and *C. douglasii* (chdo), plus plant height for easy comparison with the previous figure.



Supplement 7: Trait x environment correlation coefficients for each species, a) *Dieteria canescens*, b) *Chaenactus douglasii*, and c) *Erigeron pumilus*. More saturated colors indicate higher correlation, orange squares indicate negative correlations, and blue signifies positive correlations. Significance values are indicated for each correlation coefficient using the following notation:*p<0.05, **p<0.01, ***p<0.001. If no significance indication is listed, the correlation is considered insignificant at p>0.05



Supplement 8: AIC table from model selection step with models that were comparable to the best-fitting model. This includes all models within 2 AIC of the best model for each species. DICA= *D. canescens,* CHDO= *C. douglasii*, ERPU= *E. pumilus.*

a)DICA

Trait	**AIC**	**Input**
Seed weight	-1807.03	Start:ALL
	-1814.13	Best: Longitude, elev, slop, LNorm1
	-1812.53	Longitude + elev_m + slope + per.organic + LNorm
Survival Sd	830.64	Start
	821.16	Best:Latitude + MAP
	821.76	Latitude + MAP + slope
	823.1	Latitude + MAP + slope + per.sand
n.inflor	5762.04	Start
	5759.81	Best: Longitude + Latitude + elev_m + slope + Lnorm
	5760.31	Longitude + Latitude + elev_m + slope + per.organic + LNorm
	5760.68	Longitude + Latitude + elev_m + slope + per.sand + per.organic + Lnorm
plnt.ht	7723.69	Start
	7720.63	Best: Longitude + Latitude + MAP + elev_m + per.sand + Lnorm
	7721.82	Longitude + Latitude + MAP + elev_m + per.sand + per.organic + Lnorm
color.sat	624.44	Start
	614.3	Best: elev_m
	613.67	LNorm
	615.23	per.organic + LNorm
	615.76	MAP + per.organic + LNorm
light	188.55	Start

	179.05	Best: slope
	179.41	slope + LNorm
	180.39	MAP + slope + LNorm
LfA	606.13	Start
	599.37	Best: Longitude + elev_m + MAP
	600.26	Longitude + elev_m + MAP + per.organic
	601.11	Longitude + elev_m + MAP + per.organic + LNorm
LfVPD	725.71	Start
	716.18	Best: Longitude + slope + LNorm, family
	717.95	Longitude + elev_m + slope + LNorm
n.first.flw	-1059.63	Start
	-1062.5	Best: Longitude + elev_m + MAP + per.organic + Lnorm
	-1062.28	Longitude + elev_m + MAP + slope + per.organic + LNORm
	-1061.38	Longitude + elev_m + MAP + slope + per.sand + per.organic + Lnorm

b)CHDO

Trait	**AIC**	**Input**
Seed weight	-1225	Start
	-1230.65	Best: Longitude + MAT + Lnorm
	-1230.58	Longitude + MAT + slope + LNorm
	-1229.75	Longitude + MAT + slope + per.sand + LNorm
	-1228.81	Longitude + MAT + slope + per.sand + per.organic + Lnorm
Survival Sd	531.78	Start
	527.79	Best:Longitude + Latitude + MAT + slope + per.sand + per.organic
	529.78	Longitude + Latitude + MAT + MAP + slope + per.sand + per.organic
n.Inflor	1211.01	Start
	1208.1	Best: Latitude + MAT + MAP + per.sand + LNorm
	1208.16	Longitude + Latitude + MAT + MAP + per.sand + LNorm
plnt.ht	1387.22	Start
	1382.45	Best: Latitude + MAT + MAP + per.sand + Lnorm
	1383.71	Latitude + MAT + MAP + per.sand + per.organic + Lnorm
color.sat	133.31	Start
	124.18	Best: Longitude+ per.sand
	125.55	Longitude + per.sand + per.organic
	126.17	Longitude + Latitude + per.sand + per.organic
light	230.74	Start
	218.25	Best:Latitude
	219.3	Latitude + slope
LfA	285.97	Start
	277.67	Best :MAT + per.sand

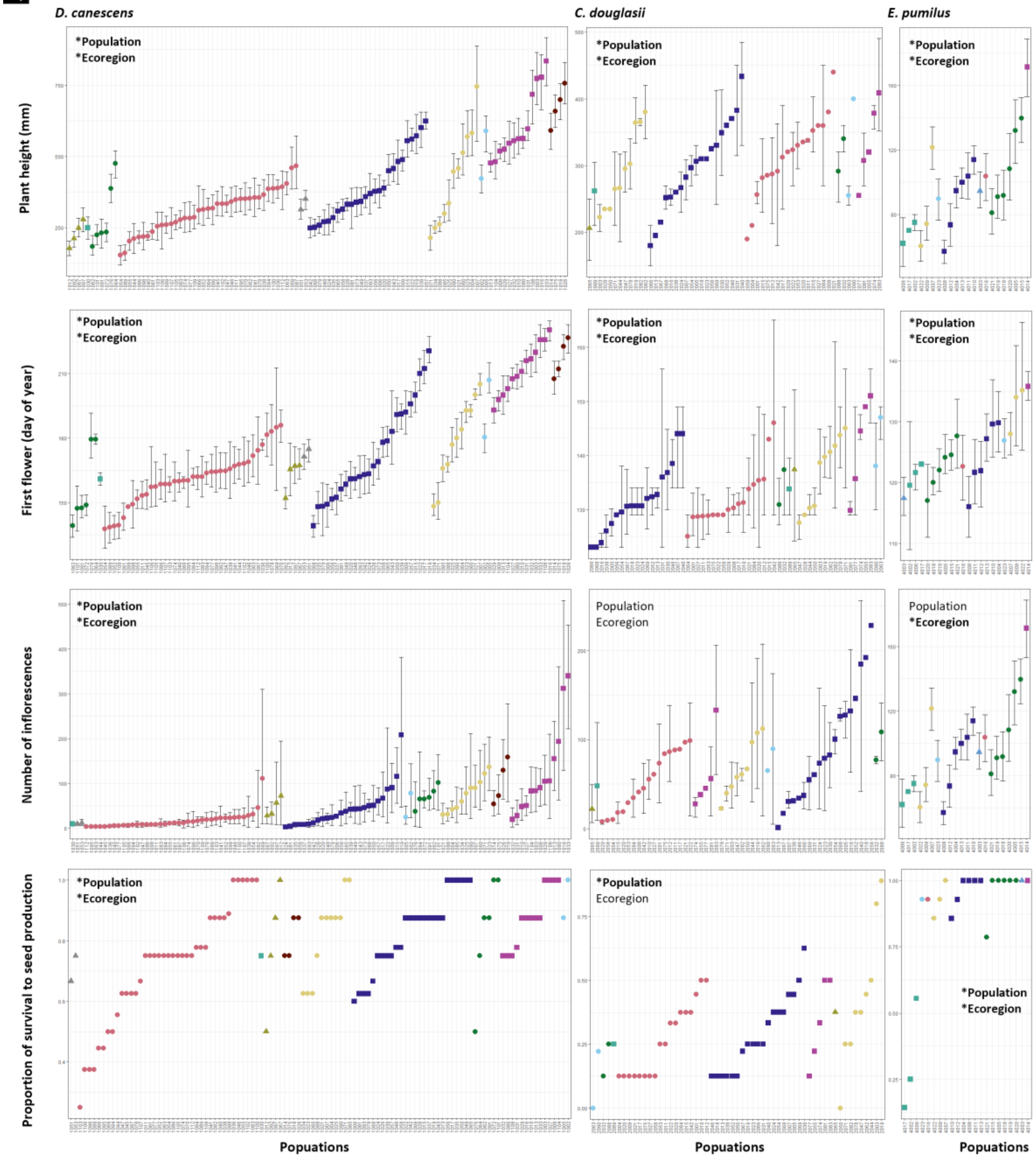
	279.12	MAT + MAP + per.sand + per.organic
	278.13	MAT + MAP + per.sand
LfVPD	152.73	Start
	145.52	Best: Longitude + MAP + per.organic
	146.19	Longitude + Latitude + MAP + per.organic
	147.29	Longitude + Latitude + MAP + per.organic + LNorm
FFlw	-554.87	Start

c)ERPU

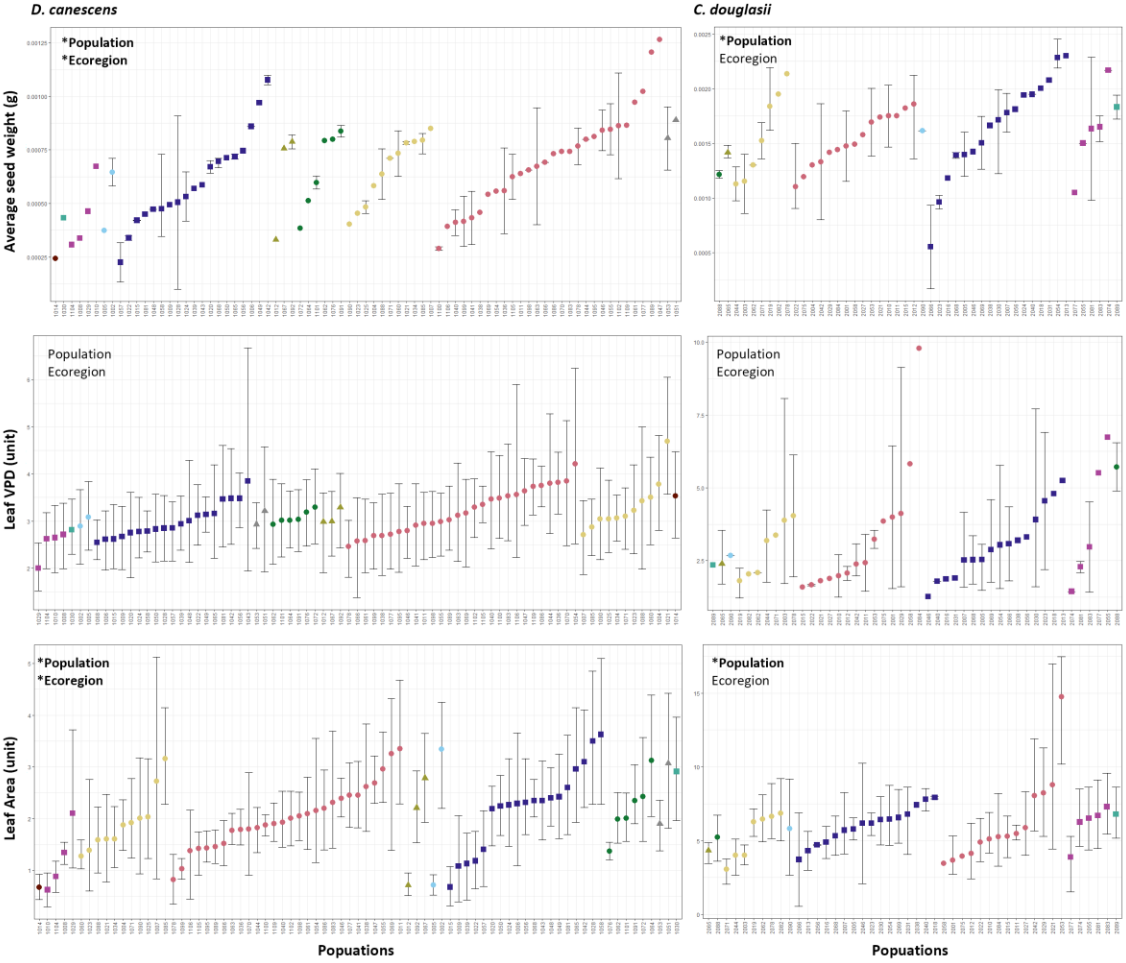
Surv.sd	68.88	Start
	67.271	Best: MAP + slope + Lnorm
	68.26	MAP + slope + per.sand + LNorm
n.inflor	1217.73	Start
	1212.6	Best: Latitude + MAP + elev_m + per.organic
	1210.55	Latitude + MAP + elev_m + per.organic
	1212.02	Latitude + MAP + elev_m + per.organic + LNorm
	1213.74	Latitude + MAP + elev_m + per.sand + per.organic + Lnorm
plnt.ht	1369.21	Start
	1362.1	Best: Latitude + elev_m + per.sand + LNorm,
	1363.45	Longitude + Latitude + elev_m + per.sand + LNorm
FFlw	154.11	Start
	146.28	Best: MAP + elev_m + per.sand
	147.18	MAP + elev_m + per.sand + LNorm

Supplement 9: Mean trait measures (with 95% confidence interval) for each population arranged by Omernik level III ecoregions for *Erigeron pumilus, Dieteria canescens*, and *Chaenactis douglasii* (A), or just *C. douglasii* and *D. canescens* (B). If variation was significant among populations and/or ecoregions (Table 8), the corresponding factor is bolded and marked with an asterisk.

A)



B)


D. canescens
C. douglasii
*Population
*Ecoregion
Average seed weight (g)
0.00025
0.00050
0.00075
0.00100
0.00125
*Population
Ecoregion
0.0005
0.0010
0.0015
0.0020
0.0025
Population
Ecoregion
Leaf VPD (unit)
2
3
4
5
6
Population
Ecoregion
2.5
5.0
7.5
10.0
*Population
*Ecoregion
Leaf Area (unit)
1
2
3
4
5
*Population
Ecoregion
0
5
10
15
Popuations
Popuations

Supplement 10: Color graphs for *C. douglasii* (A), and *D. canescens* (B), arranged by level III ecoregions. C. *douglasii*, which had significant differences among ecoregions (Table 1), has an additional graph with 95% confidence envelopes drawn around color variables, and ecoregion labels at the mean point of each ecoregion color.