Directional selection shifts trait distributions of planted species in dryland restoration

Kathleen R. Balazs¹,² | Seth M. Munson³ | Caroline A. Havrilla³,⁴ | Bradley J. Butterfield¹,²

¹Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA
²Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA
³Southwest Biological Science Center, US Geological Survey, Flagstaff, AZ, USA
⁴Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO, USA

Correspondence
Kathleen R. Balazs
Email: kathleen.balazs@gmail.com

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Abstract
1. The match between species trait values and local abiotic filters can restrict community membership. An often-implicit assumption of this relationship is that abiotic filters select for a single locally optimal strategy, though difficulty in isolating effects of the abiotic environment from those of dispersal limitation and biotic interactions has resulted in few empirical tests of this assumption. Similar constraints have made it difficult to assess whether the type and intensity of abiotic filters shift along gradients of environmental harshness, as predicted by the stress-dominance hypothesis.

2. We planted 9,216 plants of 29 perennial grass and forb species that had a range of functional trait values and were assigned to a warm, intermediate or cool temperature tolerance pool across eight sites on the Colorado Plateau. We compared the distributions of traits of surviving individuals to null distributions to evaluate whether there were shifts in trait means and variation. Borrowing from phenotypic selection concepts in evolutionary biology, we assessed support for stabilizing, directional and disruptive abiotic filtering of trait distributions and whether these types of filtering varied with initial species pool.

3. Functional composition was significantly different from null distributions for nearly all traits at all sites, with trait variation more restricted in harsher abiotic conditions, supporting the stress-dominance hypothesis. Contrary to expectations, we primarily found evidence for directional selection, which increased in frequency in warm species pools while disruptive selection was found more often in cool and intermediate species pools.

4. Synthesis. This study provides a controlled experimental approach to test the effect of the abiotic environment on plant trait filtering. We found that opportunistic strategies allowing for rapid water acquisition during favourable periods improved survival at warmer sites. Species with these strategies may be expected to benefit from increasing aridity and may be selected for active management efforts. More generally, the prevalence of directional selection may have important implications for dynamic vegetation models that rely on trait distributions for translating environmental variation into ecosystem processes.

Keywords
community assembly, directional selection, dryland, environmental filtering, functional diversity, restoration, stress-dominance hypothesis
Numerous processes shape the distribution of biodiversity. One of the most frequently invoked is environmental filtering (Butterfield, 2015; Cingolani et al., 2007; Cornwell et al., 2006; Craven et al., 2018; de Bello et al., 2013a; Le Bagousse-Pinguet et al., 2017; Lebrija-trejos et al., 2010; Li et al., 2018; Maire et al., 2012; Swenson et al., 2012), which is the effect of abiotic factors on the sorting of species into local communities based on their functional trait values (Keddy, 1992). Isolating filtering effects is complicated, however, due to potentially similar signatures of abiotic, biotic and dispersal processes on the distribution of functional traits within and among communities (Buitenhuis & Callaway, 2013; Cadotte & Tucker, 2017; Kraft et al., 2015; Mayfield & Levine, 2010; Nash et al., 2003). Distinctions between these filtering mechanisms are well-defined in theory (Funk et al., 2008), but in practice the ability to isolate the effect of each filter in existing plant communities is very difficult (but see Fraajje et al., 2015). Experiments that manipulate filters are crucial for understanding their individual effects, and for predicting how communities may respond to shifts in abiotic conditions in the future.

One consequence of the challenge in differentiating among filtering mechanisms is that we can rarely quantify the degree to which the abiotic environment produces stabilizing, directional or disruptive selection on the local species pool. These terms, borrowed from evolutionary biology, have been used recently in the field of community ecology (Ackerly, 2003; Loranger et al., 2018; Muscarella & Uriarte, 2016; Rolhauser et al., 2019; Rolhauser & Pucheta, 2017) to represent shifts in functional trait distributions in the context of environmental filtering. These different forms of selection can have implications for the long-term growth, survival and reproduction of members of the community as they experience environmental changes. Stabilizing selection, also referred to as optimizing selection (sensu Travis, 1989), results in a unimodal trait distribution centring on ‘optimal’ trait values for a given set of conditions (Figure 1). It is often assumed that unimodal patterns of trait distribution dominate in natural communities, though it has been shown that functional diversity is better accounted for when trait distributions are explicitly tested for rather than assumed (Laughlin et al., 2015). Trait distributions shaped by directional and disruptive selection move distributions from central towards extreme trait values. Disruptive selection can occur when there are highly distinct trait strategies that are viable in a single locale—this phenomenon is often discussed in the context of niche partitioning where coexistence is maintained by temporal or spatial separation in resource uptake (Rolhauser et al., 2019). Directional selection is not commonly discussed in the context of plant communities, though some evidence suggests it can be caused by successional changes in a community (Houssard & Escarré, 1991; Mori et al., 2017) or the pressures of environmental ‘mismatch’ (Ackerly, 2003; Enquist et al., 2017; Kooyers, 2015; Tielbörger et al., 2014). The structure of existing trait distributions is likely maintained by biotic interactions in a community; however, the extent to which abiotic factors alone can produce these different patterns of trait abundance is unknown. Identifying the influence of the abiotic environment on trait distributions, and determining whether such effects are consistent or highly variable across multiple traits and environments is an important step towards more predictable trait-based models of community assembly (Funk et al., 2016).

Stabilizing, directional and disruptive selection can be detected by investigating mean trait values and trait variation found within a plant community (Loranger et al., 2018). While inspecting the shape of trait distributions is often approached with the four moments of distribution (Enquist et al., 2015; Gross et al., 2017), additional investigation of skewness and kurtosis is often redundant with these measures of mean and variation (Loranger et al., 2018). While other elements of functional diversity can be estimated using indices such as functional richness, evenness and divergence (Carmona et al., 2016), mean trait values and trait variation are good predictors of environmental selection (Denelle et al., 2019). Using theoretical trait distributions, we show that significant restriction in variation but no change in mean values reflects stabilizing selection; restriction in variation and significant shift in mean values reflect directional selection; greater variation but no change in trait means reflects disruptive selection; and greater variation along with a significant shift in mean values reflect a combination of directional and disruptive selection (Figure 1).

Since most observational studies cannot separate the effects of biotic and abiotic factors, it is a challenge to address hypotheses about the relative contribution of each filtering process. The stress-dominance hypothesis (Coyle et al., 2014; Swenson & Enquist, 2007) predicts that environmental (abiotic) filtering will play a greater role in structuring communities in more stressful environments, while competition (biotic filtering) is more important when there is lower abiotic stress. According to the stress-dominance hypothesis, we might expect increasing stabilizing selection in more severe environments (Rolhauser & Pucheta, 2017; Weiher & Keddy, 1995a) where trait variation is restricted due to abiotic filtering on traits critical for stress tolerance resulting in convergence on optimal trait values (Coyle et al., 2014). The ‘favourability hypothesis’ (Swenson et al., 2012; Wieczynski et al., 2019) also predicts a similar phenomenon where environmental filtering is stronger when conditions for growth are less favourable. Most studies within arid regions focus on biotic interactions such as facilitation (Berdugo et al., 2019); however, there is little investigation of how individual plants respond to abiotic conditions. Aridity gradients related to soil moisture and/or atmospheric demand represent strong environmental variation across space and time. Within arid systems, the abiotic environment represents a particularly strong filter due to the overwhelming role of physical processes on plant-available soil moisture in water-limited environments (Goldberg & Novoplansky, 1997). While there is variation by region, the hotter, drier conditions forecasted for many global drylands (Bradford et al., 2020; Koutouris, 2019) make it increasingly important to develop predictive models of trait-based community assembly in dryland regions. Drylands occupy 47% of the globe and often experience a disproportionate amount of environmental stress.
of anthropogenic disturbance (Koutroulis, 2019) which further increases abiotic stress. These dryland areas are therefore an excellent and important study system to test the stress-dominance hypothesis and to investigate how abiotic factors shape trait distributions.

Ecological restoration experiments provide an opportunity to isolate the signature of environmental filters on community assembly, and reciprocally a knowledge of trait-based environmental filtering can better inform restoration practice (Balazs et al., 2020). The need for restoration is brought on by fire, overgrazing, invasive species and other anthropogenic disturbances (e.g. mining, recreation) that often erase the signature of the previous community, both in terms of seed sources (dispersal filters) and biotic feedbacks (biotic filters). The early stages of restoration experiments, in which the unfiltered species pool is known and initial plant densities are low, therefore provide an opportunity to identify a nearly pure abiotic filter in determining the subsequent composition of new plant communities. Quantifying the impacts of these environmental filters on trait distributions is not only of theoretical interest, but may also reflect an increasingly common context for assisted migration into disturbed environments (Butterfield et al., 2017).

In this study, we conducted a dryland restoration experiment replicated across a climatic gradient ('RestoreNet'; Havrilla et al., 2020) to identify the outcomes of abiotic filtering on community assembly, with an experimentally controlled dispersal filter and minimal biotic filter. In contrast to most observational studies of environmental filtering that compare species and traits along an abiotic gradient such as elevation (Alexander et al., 2011; Read et al., 2014), aridity (Dwyer & Laughlin, 2017; Nunes et al., 2017), light (Lusk & Laughlin, 2017) or multiple gradients (de Bello et al., 2013b; Le Bagousse-Pinguet et al., 2017; Menezes et al., 2020), to a regional species pool, our study compares traits of surviving species to those that were planted in an early stage of restoration with minimal biotic interaction. The unfiltered species pools in our study are defined by 16 species that were planted at each site based on temperature tolerances, thus the initial pool of available species influences the outcome of filtering. Our objectives were to first test the hypothesis that non-random patterns of functional composition are present in the experimental communities, meaning that environmental filtering is indeed occurring. Second, we investigated the hypothesis that these non-random patterns vary as a function of species pool, trait or their interaction, meaning that shifts in trait means and variances could be predicted by trait or by the initial unfiltered pool of planted species and its suitability for local conditions.

We explored the alternative outcomes of stabilizing, directional and disruptive selection found within restored communities. Previous observational studies in similar environments have found overall more restrictive assembly filters in both very cold and very hot dryland environments (Butterfield & Munson, 2016), and drylands with primarily cool-season rather than warm-season precipitation regimes (Butterfield, 2015). Thus, we predicted that stabilizing selection would be more common and intense at sites with the most stressful conditions (within the warm species pool), and directional or disruptive selection would occur more frequently at sites with favourable conditions (within cool and/or intermediate species pools).

2 | MATERIALS AND METHODS

2.1 | Species pool and trait screening

We tested the filtering of plant functional traits using a grassland restoration experiment on the Colorado Plateau, a high-elevation semi-arid region in the western United States. Twenty-nine species of perennial grasses and forbs native to the region were selected...
based on their prevalence in seed mixes used in restoration actions carried out by the Bureau of Land Management and US Forest Service on the Colorado Plateau and adjacent ecoregions (https://wri.utah.gov/wri).

Ten replicates of each species were grown for a destructive trait screening at the Research Greenhouse at Northern Arizona University in the summer of 2017. Plants were grown to vegetative maturity in 3.79-L pots with a fired clay growing medium (Turface® Pro League®) that facilitated oxygenation of the root systems of these arid-adapted plants while also permitting complete removal of the medium for root system analysis. Each plant was harvested prior to flowering to collect plant trait data (Table 1). Height data were collected prior to harvesting plants. Five fully developed leaves were then taken from each plant and immediately weighed, scanned on a flatbed scanner at 300 dpi and dried to calculate SLA and leaf dry matter content (LDMC). Roots were cleaned and samples of tap roots (forbs only), lignified coarse roots and absorptive fine roots (non-lignified with root hairs) were collected. Three coarse root samples from each plant were weighed, then scanned with a flatbed scanner to calculate root length and then dried to obtain specific root length (SRL) and root dry matter content (RDMC). The fine root samples were weighed, then scanned submerged in water using the WinRHIZO™ scanner bed software for analysis of root length and finally dried to obtain SRL and RDMC. Above-ground biomass was separated from below-ground biomass and dried separately to calculate root-to-shoot ratio.

2.2 | Experimental design

The field experiment was conducted at eight restoration sites located on the Colorado Plateau (Figure S1; Table 2) that are a part of a broader RestoreNet study (Havrilla et al., 2020). RestoreNet systematically tests multiple restoration techniques using standardized protocols across drylands of the southwestern United States and is coordinated by the Restoration Assessment and Monitoring Program for the Southwest (https://usgs.gov/sbrc/ramps). Restoration sites were selected within common potential vegetation zones across the region where overgrazing or other disturbances have reduced perennial vegetation. The sites have a range in mean annual temperature of 8.8–16.5°C, mean annual precipitation of 206–491 mm and 32%–45% of yearly precipitation comes in the summer (July–September) monsoon season (Table 2). Initial perennial vegetation cover was low at all sites, though non-native weeds were common. All standing vegetation was removed prior to the establishment of the experiment.

Plants used in the experiment were grown in the Northern Arizona University Research Greenhouse in 3.8 × 14 cm ‘cone-tainers’ (Stuewe and Sons). Plants received 30 ppm of 20-20-20 Miracle-Gro® Water Soluble Plant Food after true leaves emerged twice weekly for approximately 4 weeks, and the fertilizer was flushed out prior to hardening. Plants were hardened for approximately 2 weeks outside the research greenhouse before planting at field sites. The 29 experimental species were classified into three different pools of 16 species, with some overlap of species between pools, each based on their estimated heat tolerances, referred to as cool, intermediate and warm species pools (Table 3). Heat tolerances were estimated by extracting species occurrence records from GBIF via the gbif function in the R package dismo [Hijmans et al., 2015, Available from: https://www.gbif.org [12 March 2018]] and quantifying the 95th percentile of species mean annual temperature distributions after removing outliers (Butterfield & Munson, 2016), therefore all species had a MAT95 limit above the site MAT. Each species pool contains a mix of perennial grasses and forbs. All species pools intentionally share some species in common to allow for comparisons of shared species across sites; there are three species that all pools share, while cool and intermediate share an additional

| Functional traits (units) | Abbreviation | Measurement | Ecological significance |
|---------------------------|--------------|-------------|------------------------|
| Height (cm) | Height | Perpendicular height of photosynthetic material | Competition for light, resistance to exposure |
| Root-to-shoot ratio | Root:shoot | Ratio of below-ground biomass to above-ground biomass | Investment in above- or below-ground growth and storage |
| Specific leaf area (mm²/ mg) | SLA | Area of fresh leaf in square millimetres divided by the weight of the dried leaf tissue | Investment in photosynthetic tissue—maximize growth rate or conserve energy |
| Leaf dry matter content (mg/g) | LDMC | Weight of dried leaf tissue (mg), divided by the weight of fresh leaf tissue (g) | Amount of structural components in leaves, resistance to herbivory |
| Coarse root specific root length (m/g) | SRLc | Length of root (m) divided by the weight of dried root tissue (g) | Investment in exploratory roots versus conserving energy (conductive roots) |
| Coarse root dry matter content (mg/g) | RDMCc | Weight of dried root tissue (mg) divided by the weight of fresh root tissue (g) | Proxy for root tissue density (conductive roots) |
| Fine root specific root length (m/g) | SRLf | Length of root (m) divided by the weight of dried root tissue (g) | Investment in exploratory roots versus conserving energy (absorptive roots) |
| Fine root dry matter content (mg/g) | RDM Cf | Weight of dried root tissue (mg) divided by the weight of fresh root tissue (g) | Proxy for root tissue density (absorptive roots) |
Multivariate analysis of variance revealed that the species pools did not differ in their average trait values (see Appendix S1); however, we retain the initial unfiltered ‘species pool’ as a factor that may influence the outcome of our study to account for any differences in the variance or range.

### Table 2

| Site                  | Ecoregion level IV                    | Soil Texture  | Lat   | Long  | Elevation (m) | Mean Annual Temp (°C) | Total Annual Precip. (mm) | Monsoon Precip. (% of annual) |
|-----------------------|---------------------------------------|---------------|-------|-------|---------------|------------------------|---------------------------|-------------------------------|
| La Sal                | Semi-arid benchlands and canyonlands  | Sandy Loam    | 38.29 | −109.07 | 2,233         | 8.9                    | 394                       | 32                            |
| Babbitt PJ            | Conifer woodlands and savannas        | Clay          | 35.6  | −111.94 | 1,983         | 9.6                    | 490                       | 38                            |
| Canyonlands           | Semi-arid benchlands and canyonlands  | Sandy Loam    | 38.07 | −109.57 | 1,655         | 11.3                   | 280                       | 32                            |
| Flying M              | Conifer woodlands and savannas        | Loam          | 34.84 | −111.11 | 1,873         | 10.8                   | 366                       | 44                            |
| Bar T Bar             | Semi-arid tablelands                  | Sandy Loam    | 34.89 | −110.06 | 1,783         | 11.2                   | 320                       | 44                            |
| Petrified Forest      | NE AZ Shrub-Grasslands                | Sandy Clay    | 34.91 | −109.81 | 1,645         | 12.9                   | 229                       | 45                            |
| Spider Web            | NE AZ Shrub-Grasslands                | Sandy Loam    | 35.64 | −111.48 | 1,586         | 13.6                   | 206                       | 44                            |
| Montezuma Well        | Lower Mogollon Transition             | Sandy Loam    | 34.65 | −111.76 | 1,140         | 16.5                   | 373                       | 40                            |

### Table 3

| Cool species pool     | Intermediate species pool            | Warm species pool  |
|-----------------------|--------------------------------------|--------------------|
| **Species**           | **Growth form** | **MAT 95** | **Species** | **Growth form** | **MAT 95** | **Species** | **Growth form** | **MAT 95** | **Species** | **Growth form** | **MAT 95** |
| Pseudoroegneria spicata | Grass | 11.4 | Linum lewisii | Forb | 13.3 | Achillea millefolium | Forb | 15.5 |
| Hedysarum boreale     | Forb | 11.7 | Heliomeris multiflora | Forb | 13.7 | Dalea candida | Forb | 15.7 |
| Elymus trachycalis    | Grass | 5.9 | Bromus marginatus | Grass | 14.2 | Bouteloua gracilis | Grass | 15.9 |
| Elymus wawawaiensis   | Grass | 12.0 | Pascopyrum smithii | Grass | 14.2 | Poa secunda | Grass | 16.7 |
| Leymus cinereus       | Grass | 12.1 | Pleuraphis jamiess | Grass | 15.1 | Sporobolus cryptandrus | Grass | 16.9 |
| Hesperostipa comata   | Grass | 12.2 | Elymus elymoides | Grass | 15.5 | Machaenthera tanacetifolia | Forb | 17.0 |
| Sphaeralcea grossularifolia | Forb | 12.7 | Achillea millefolium | Forb | 15.5 | Bouteloua eriopoda | Grass | 17.1 |
| Linum lewisii         | Forb | 13.3 | Dalea candida | Forb | 15.7 | Krascheninnikovia lanata | Forb | 17.4 |
| Heliomeris multiflora | Forb | 13.7 | Bouteloua gracilis | Grass | 15.9 | Penstemon palmeri | Forb | 18.1 |
| Bromus marginatus     | Grass | 14.2 | Poa secunda | Grass | 16.7 | Achnatherum hynemoides | Grass | 18.3 |
| Pascopyrum smithii    | Grass | 14.2 | Sporobolus cryptandrus | Grass | 16.9 | Bouteloua curtipendula | Grass | 18.7 |
| Pleuraphis jamiess    | Grass | 15.1 | Machaenthera tanacetifolia | Forb | 17.0 | Asclepias tuberosa | Forb | 19.4 |
| Elymus elymoides      | Grass | 15.5 | Bouteloua eriopoda | Grass | 17.1 | Aristida purpurea | Grass | 21.1 |
| Achillea millefolium  | Forb | 15.5 | Krascheninnikovia lanata | Forb | 17.4 | Baileya multiradiata | Forb | 21.4 |
| Dalea candida         | Forb | 15.7 | Penstemon palmeri | Forb | 18.1 | Hilaria mutica | Grass | 21.5 |
| Bouteloua gracilis   | Grass | 15.9 | Achnatherum hynemoides | Grass | 18.3 | Senna covesi | Forb | 21.7 |

Six species and intermediate and warm share an additional seven.
A single species pool was assigned to each site based on the similarity between the temperature of that site and the average heat tolerances of each pool. Each site consisted of 36 plots, including 16 monocultures, and 16 polycultures. A total of 9,216 individuals were planted across all eight sites. Each species was planted in one monoculture (single species) plot per site, and four different polyculture (multispecies) plots. In polyculture plots, there were nine individuals each of four species. Species were assigned to polycultures using an algorithm that ensured each species co-occurred with every other species in at least one polyculture, which also ensured that no two polycultures had the same four species combination. This design was intended to explore the effects of species interactions at a later stage of restoration; however, at this early stage of restoration, plants were small enough to negate species interactions. Within each 2 × 2 m plot, 36 plants were spaced 30.5 cm apart in a grid 23.8 cm from the edge of the plot. Prior to planting, a soil auger was used to dig a ~15-cm deep hole, into which ~0.24 L of water was poured before transplanting. After transplanting, each plant immediately received an additional ~0.71 L of water and plots were covered with white weed cloth, with holes cut for each plant, which served to retain soil moisture and to inhibit weeds in the first season of growth.

Survival and growth of each individual plant were monitored each month throughout the 2018 and 2019 growing seasons to capture differences among species and treatments. An individual was judged to have survived if it had new leaf tissue at any point throughout the growing season which was also confirmed by having an increase in height and/or width from one time point to another. For the duration of this study, there was a large amount of climatic variability; most notably, there was a high variability in monsoon precipitation between sites in 2018 with 24%–50% of precipitation falling during the monsoon season, and below average monsoon precipitation in 2019 (6%–24%), while the range for an average year is 32%–45%.

2.3 Data analysis

To test for environmental filtering, null models were employed to determine whether the trait distributions of surviving plants were different than expected by chance based on the original planted community. Specifically, the number of surviving individuals at each site was randomly drawn from the original pool of individuals (72 individuals of 16 species) without replacement 999 times. Since each species pool (cool, intermediate and warm) had a different set of species planted and each site had a different number of surviving plants, this null permutation modelling was done separately for each site. Functional composition indices, coefficient of variation (CoV) and community-weighted mean (CWM), were then calculated from those randomly drawn communities and compared to the observed surviving community. The standardized effect size (SES) of observed relative to the mean of the null distribution was then calculated as SES = (Mobserved − Mnull)/SDnull. Since null values were normally distributed, we considered SES > |1.96| to be significantly different than expected.

Coefficient of variation was selected as a measure of the variability of the trait values within a community. CoV for a given trait may increase (SES > 1.96) or decrease (SES < −1.96) in an experimental community, thus this metric can be used to test whether stressful abiotic conditions result in lower trait variability than more moderate environments. Community-weighted mean was selected as a measure of ‘optimal’ trait values in a community, and was calculated as the average trait value of all individuals in a community; traits are weighted proportionally to species abundance (survival) in a community. Trait values may be higher than expected (SES > 1.96) or lower than expected (SES < −1.96) reflecting community-level directional shifts.

To test the hypothesis that filtering produces non-random patterns of functional trait composition, we calculated the proportion of SES values greater than |1.96| for CoV and CWM.

Then, after determination that non-random patterns were present, we investigated the hypothesis that these non-random patterns vary as a function of species pool, trait or their interaction by employing linear mixed-effects models using the ‘lmer’ function in the lme4 package with site as a random factor. We used the lmerTest package to obtain Type III Analysis of Variance Table with Satterthwaite’s method and the MuMln package to obtain R² marginal and conditional values.

Because climate variation among sites was partially independent of species pool, we investigated whether climate variables improved any of the statistical models used to test H2. We extracted daily interpolated climate variables covering the duration of the study related to precipitation, temperature and humidity (precipitation, mean and maximum temperatures, mean dew point temperature and vapour pressure deficit) at 4-km resolution from PRISM (prism.oregonstate.edu). We found that the addition of these local climate variables did not improve model fit as evidenced by higher AIC values in models containing climate variables (Tables S1 and S2).

Finally, we assigned a type of selection (stabilizing, directional or disruptive) for each trait and site using the sign and magnitude of standardized effect sizes for CoV and CWM. Stabilizing selection occurred in communities with significant restriction in variation but no change in CWM; directional selection occurred in communities with restriction in variation and significant shift in CWM; and disruptive selection occurred when there was greater variation but no change in CWM. The applicability of CoV and CWM to testing the alternative assembly outcomes was confirmed with application to several idealized trait distributions (Figure 1). We acknowledge that a range of distributions that are intermediate between these idealized distributions can be produced within a similar selection category, but these categories based on CWM and CoV help to simplify the interpretation of a complex set of processes.

3 RESULTS

The average total survival of restoration plantings ranged from 41% to 89%, with cool and intermediate temperature sites generally
performing better than warm sites (Table S3). Overall, grass species performed better than forb species across all sites with notable exceptions such as *Linum lewisii*. A t-test showed no significant differences (p = 0.86) in mean survival rates between monocultures (0.74) and polycultures (0.73), therefore the 72 individuals per species at each site were pooled to estimate species-level survival rates.

### 3.1 H1. Trait-based environmental filtering is occurring

Non-random trait distributions were prevalent for both functional composition indices, supporting the hypothesis of trait-based environmental filtering. The CoV was significantly different than expected from random chance in 75% of cases (49/64 sesCoV > |1.96|) with 27 cases resulting in higher CoV that expected and 22 lower than expected. Community-weighted mean was different than expected from random chance in 81% of cases (52/64 sesCWM > |1.96|). These results indicate that abiotic filtering influences trait variation and mean trait values in structuring the survival of restoration plantings even when species are selected to match species temperature tolerances.

### 3.2 H2. Environmental filtering varies as a function of species pool, trait or their interaction

We expected that non-random patterns in trait distributions would depend on the initial unfiltered species pools that were planted as well as individual functional traits of those plants. A large absolute value for sesCoV would illustrate that variation within the surviving plants was highly different from that of the planted community, helping to identify where trait variation can be targeted to improve restoration outcomes. A large absolute value for sesCWM would identify where mean trait values of the species used in restoration can be adjusted in the future restoration efforts. We found that trait and species pool did significantly interact to influence both sesCoV and sesCWM (Table 4). Within trait, the greatest differences in sesCoV and sesCWM occurred with coarse RDMC, with a reduction in variation and shift towards lower coarse RDMC across species pools. Additionally, the warm species pool had greater differences in sesCoV and sesCWM than cool and intermediate species pools. These results identify that mean trait values in the warm species pool as well as variation and mean coarse RDMC are important to target when selecting species for restoration.

Investigating the interaction between trait and species pool further revealed instances where trait values could be adjusted to match the local environment. For instance, SLA had greater restriction in variation than expected based on initial planting at sites within warm species pools and lower restriction in variation than expected at sites within cool and intermediate species pools (Table S4; Figure 2A). We see in Figure 2A that variation in other traits also appears to be moderately influenced by species pool with a similar trend for lower variation found within the warmer species pools for height and SRLc. For sesCWM, a Tukey’s HSD test showed a significant shift towards higher SLA values for the cool species pool and lower SLA values for the warm species pool, and CWM for SRLc of surviving individuals was lower than expected in the warm and intermediate pools, higher than expected in the cool pool (Table S5; Figure 2B). We also see similar trends in other traits from Figure 2B, such as height (higher in the cool species pool and lower in the other pools) and root-to-shoot ratio (lower ratio at sites within warm species pools). These results indicate where the pooled trait values of species used in restoration can be better tailored to improve survival.

We expected to see greater stabilizing selection at sites with more stressful, water-limiting conditions. The patterns of selection for traits included stabilizing, directional and disruptive selection (Figure 3). There were 21 instances (33%) of directional selection and eight (13%) instances of disruptive selection; these instances were counted when a site that received a species pool matched theoretical distributions. Directional selection occurred most at sites that received a warm species pool with 13 instances, and there were six instances at sites that received a cool species pool and two at sites that received an intermediate species pool. Disruptive selection occurred equally within cool and intermediate species pool (four instances within each pool), but not within warm species pools. Only one instance of stabilizing selection was found (for SRL within one site that received a cool species pool). There were 15 instances (23%) of a selection pattern that is a combination of disruptive and directional where sesCoV > 1.96 and sesCWM > |1.96|. Finally, there were 19 instances of no selection occurring (30%).

### 4 DISCUSSION

Our experiment sought to better understand community assembly by isolating the abiotic filter acting on trait distributions of planted perennial grass and forb species. Two growing seasons after planting...
across Colorado Plateau sites, these small plants experienced a relatively low biotic filter at this early stage of restoration since planting densities were low and there was no difference in survival between monocultures and polycultures. While each site differed in overall survival, the variation and relative abundance of traits in surviving species reflected the abiotic environmental filter acting upon survival within a site. Indeed, environmental filtering significantly altered all eight above- and below-ground traits of surviving individuals away from null distributions. Results supported the stress-dominance hypothesis as there were greater reductions in trait variance and stronger shifts in CWMs for sites that had the warmest and driest conditions, meaning that filtering was more intense in these stressful environments. Contrary to expectations, however, we found that the type of environmental filtering in these arid conditions could predominantly be associated with directional, not stabilizing, selection as we had hypothesized.

The greater intensity of environmental filtering found in the warmest environments supported the stress-dominance hypothesis, but also emphasized the importance of gradient length and environmental context. For many years, there has been a discussion on the relative impact of environmental filtering in stressful environments versus competition in productive environments (Cornwell & Ackerly, 2009; Grime, 1977; May et al., 2013; Weiher & Keddy, 1995); however, the gradient upon which this idea is tested can influence the outcome. For example, Swenson & Enquist (2007) tested this hypothesis on a global scale and found trait convergence in cold (temperate) regions, and high trait variation in warm (tropical) regions. In contrast, Lhotsky et al. (2016) found higher trait convergence in arid environments on
traits related to resource use versus regeneration in a grassland to wetland gradient within Hungary. Similarly, May et al. (2013) found an increase in trait convergence with greater aridity in a transition from desert to Mediterranean environments in Israel. In all these studies, there is a clear transition from biome to biome, whereas our study entirely occurred within a dryland region. Though we have a relatively short gradient compared to a global study or a cross-biome study, this scale allowed us to determine how climate influences functional trait composition on species otherwise adapted to a similar biome. While we did find there was a significant shift in functional composition in surviving species, we did not see convergence on similar trait values consistent with stabilizing selection. Our findings suggest that the most successful species locally may often have more extreme trait values than the rest of the species pool. In other words, perhaps stabilizing selection would have been found if there had been a broader range of trait values present in our species pools that extended beyond species selected to match heat tolerances.

Contrary to theoretical expectations (Weiher & Keddy, 1995a), stabilizing selection generated by abiotic filtering alone was very rare (a single example in the cool species pool), while directional and disruptive selection were predominant. We found greater disruptive selection at cool and intermediate sites, consistent with the expectation that trait composition is less restricted when conditions are favourable. There is a debate in the literature about whether trait divergence in a community is the result of limiting similarity from competition (Grime, 2006; MacArthur & Levins, 1967), or environmental heterogeneity in space or time (Cavender-Bares et al., 2009; Lhotsky et al., 2016; Weiher & Keddy, 1995b), or other frequency-dependent interactions. In this study, environmental heterogeneity is restricted to temporal or soil moisture availability at depth; however, an alternative explanation is that there is lower restriction of trait variability in favourable conditions. One instance that aligns with this explanation is the pattern of higher CoV found in root-to-shoot ratio at one of the intermediate sites, Flying M Ranch (Table S4). This site received the highest precipitation during the study period, so it could be that species with deeper roots are accessing soil moisture at depth and other species are taking advantage of surface soil moisture. This conclusion tends to agree with the literature that more soil resources allow for higher trait divergence (Bernard-Verdier et al., 2012; Wang et al., 2018). At the Canyonlands Research Center (CRC) site, there were three instances of disruptive selection. Even though this site is in the cool species pool, it differs from other sites in that pool during the years that the study took place since it received low precipitation, close to the levels found at the warmest sites. This site also had the highest weed cover in 2019. It could be that the high rate of disruptive selection occurring here is due to the differing trait strategies needed to survive in cool areas with low precipitation and higher weed cover (such as more competitive strategies vs. stress tolerating). In addition to eight cases of disruptive selection, we also found that the combination of directional–disruptive selection was somewhat common (occurring in 18 instances, more commonly within cool and intermediate species pools). This combination indicates that there may be a broad range of viable trait strategies, but that one end of the trait distribution is favoured. Alternatively, the signal for the selection mode may have been clearer if a broader range of trait values was applied.

While we predicted that sites with harsher abiotic conditions such as those found at the warmer sites would produce patterns of
stabilizing selection, we found that these warmer sites most often produced patterns of directional selection. The intensity of heat and aridity at all sites was likely exacerbated by the high heat absorption of bare ground, often found at this early stage of restoration. The effect of aridity is often buffered by existing vegetation (Berdugo et al., 2018; Michalet, 2006), therefore an experiment conducted during early plant establishment can reveal the true abiotic filter in these arid environments, demonstrating that restoration in highly disturbed environments has an even greater barrier to overcome than can be demonstrated in observational studies of existing communities. A further examination of the individual traits driving these alternative selection outcomes helps solidify the argument that support for the stress-dominance hypothesis is found in the prevalence of directional selection in harsher environments and prevalence of disruptive selection in less harsh environments. Within the harsh conditions at a restoration site, it may be that the optimum trait values that will be successful in these conditions are at the edge of the trait distribution of species that are present in an older, established community. This relates to the ‘trait gradient boundary effect’ (Denelle et al., 2019), that suggests that the limitation of available trait values in a community often drives patterns related to environmental filtering such as directional selection. When selecting for species in restoration, most practitioners use a species temperature tolerances or reference communities to select species that should be adapted to local environmental conditions, but our results illustrate that this approach does not always result in survival in the early stage of restoration. Indeed, directional selection was similarly found in a restoration experiment in the Great Basin (higher survival of plants with smaller stature even though local species were used; Kulpa & Leger, 2013). The high prevalence of directional selection on species used in restoration indicates that trait-based approaches identify areas where we can improve the selection of species applied to improve restoration success.

The traits relevant for success varied among species pools, with a particularly complex combination of above- and below-ground strategies resulting in success in the warmest species pool. Successful trait strategies in harsher environments are consistent with opportunistic uptake of limited precipitation pulses, while there was greater variation in viable strategies in more favourable conditions. High LDMC was consistently successful across all environments, likely due to its relevance for stress tolerance in the dry conditions of barren soil in these arid ecosystems (Pierce et al., 2013). However, in the warmest species pool, high SLA was beneficial. While high SLA (low leaf mass per area) is generally associated with wetter conditions (Wright et al., 2004), in our study, this result likely reflects the drought avoidance strategy of cool-season species such as Poa secunda that are dormant during the summer. This mechanism may also explain the observation (non-significant) that absorptive (fine) roots with high SRL performed better in the warm pool, whereas the opposite was true in the cool pool. Both the SLA and SRL patterns suggest an opportunistic resource uptake strategy in these environments where soil moisture comes in seasonal or subseasonal pulses similar to what was found by Rolhauser and Pucheta (2017).

The success of lower RDMC found at all sites may seem counter-intuitive; however, this pronounced decrease in RDMC allows for flexibility in the root system consistent with the need for opportunistic quick growing roots (Birouste et al., 2014). Lastly, coarse roots showed the opposite SRL pattern of fine roots in the warm species pool, indicating that extensive root system diversification may couple extensive absorptive root area with a short hydraulic path length of conductive roots. These patterns emphasize the truly multifaceted nature of roots (Kramer-Walter et al., 2016)—uptake, conduction, storage, stability—and their importance in determining environmental filtering in dryland ecosystems. While we found that the nature of environmental filtering does not follow the standard assumption of stabilizing selection, we do see that trait selection towards strategies that aid in opportunistic resource acquisition is more prevalent in harsh (arid, warm) environments. Additionally, this study only includes data from 2 years of monitoring after planting, the first of which was anomalously wet and the second received below average monsoon precipitation. Therefore, our results may not reflect species responses to average climatic conditions and continued monitoring, or experimental replication may reveal different patterns.

The findings of this study can be used to improve vegetation management through a better understanding of the environmental filters controlling plant performance. Selecting plants for restoration that match trait values to local environmental conditions should enhance restoration outcomes (Balazs et al., 2020), though additional understanding of the traits that influence biotic interactions should also be included (Funk et al., 2008). Continuing to follow the current experiment as plants get larger and begin to interact with one another may shed light on this issue. Regardless, the trait-based approach presented here can help managers to select seed sources based on their trait values without conducting extensive species-by-species trials. A greater understanding of species trait responses, rather than using existing species occurrence, can improve restoration efforts, especially in topographically diverse regions such as the southwestern United States that can be difficult to model (Butler et al., 2017). These trait-environment models may become increasingly relevant as climate conditions may preclude restoration of sites to historical conditions. As extreme climate events become more common, we are seeing that these extremes can additionally shift functional composition away from historical values (Griffin-Nolan et al., 2019). Restoration practitioners may need to consider assisted migration and other ‘pre- Restoration’ strategies (Butterfield et al., 2017) to match species to climate projections for their sites in the future and using species with traits that may benefit survival in disturbed environments (Ferguson & Nowak, 2012). Our study suggests certain trait values such as high LDMC and low RDMC may be beneficial broadly for restoration treatments on the Colorado Plateau; however, there are many opportunities to select species with better suited traits to match site conditions (e.g. higher SRL at our warm, dry sites). The ability to predict the outcome of seeding and transplanting efforts is highly valuable to the field of restoration.
ecology, especially as land managers and other restoration practitioners plan for a warmer future.

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CONFLICT OF INTEREST
None of the authors of this article have a conflict of interest.

AUTHORS’ CONTRIBUTIONS
K.R.B. led the writing of the manuscript, performed fieldwork, laboratory work and analyses; B.J.B. developed the project idea and conceptual framework along with K.R.B. and S.M.M., and contributed to data analyses and writing; C.A.H. contributed to writing and editing. All authors substantially contributed to manuscript drafts and correspondence.

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DATA AVAILABILITY STATEMENT
Associated data are available on the TRY Plant Trait Database at https://doi.org/10.17871/TRY.54 and Dryad Digital Repository at https://doi.org/10.5061/dryad.z8w9ghdxj [Balazs et al., 2021].

ORCID
Kathleen R. Balazs https://orcid.org/0000-0001-7198-3890
Seth M. Munson https://orcid.org/0000-0002-2736-6374
Caroline A. Havrilla https://orcid.org/0000-0003-3913-0980
Bradley J. Butterfield https://orcid.org/0000-0003-0974-9811

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