TRAIT-BASED APPROACHES TO DRYLAND RESTORATION

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ABSTRACT

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Land degradation leads to the loss of ecosystem functioning such as primary productivity, invasive plant suppression, and erosion mitigation. Attempts to restore degraded drylands are often met with failure due to harsh barriers to plant establishment. Trait-based approaches can improve the outcome of restoration treatments, especially in challenging areas to restore such as drylands. Each of the chapters in my dissertation address trait-based approaches to dryland restoration: chapters 2 and 3 are focused on improving the survival of restoration seeding and planting treatments by matching plant traits to environmental conditions and chapter 4 addresses the issue of rebuilding ecosystem functioning through restoration. Chapter 2 involves an analysis of a long-term restoration outcomes database for the Colorado Plateau. I found that matching trait values to environmental conditions improved restoration outcome. More specifically, temperature seasonality along with seed mass and plant height best predicted seeding success. Most restoration of large areas is done with seeding, however the experiment in chapter 3 and 4 jump-started the establishment of restoration species by growing them out in the greenhouse and transplanting them into the field through an experiment so I could investigate additional questions such as the impact of the restored community on ecosystem processes. From this restoration planting experiment, I had two main questions: how does plant functional composition influence survival in restoration? And, once established, how does a restored community influence ecosystem functioning? First, I found that the species with greatest survival had multiple trait strategies including drought tolerance and drought escape. A combination of slow-growing drought tolerant leaves and fast-growing, drought escaping roots promoted survival across sites. Additionally, in chapter 4, I found that recovery of aboveground primary productivity supported the recovery of other ecosystem functions including weed suppression and erosion mitigation. There were certain trait strategies such as drought tolerant yet acquisitive leaves and roots that lead to greater aboveground productivity. These results can aid land managers in selecting the species with appropriate traits to use in restoration that can establish given the conditions of a site, and that have a positive impact on rebuilding ecosystem functions of concern. These trait-based approaches are a powerful tool for drylands that are difficult to restore but cover nearly half the earth's terrestrial surface.

TABLE OF CONTENTS

List of Tables

The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Bell curve trait distributions do not ring true: Directional environmental selection is common and amplified by aridity

Restoration of primary productivity in drylands supports weed suppression and erosion mitigation

List of Figures

The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Bell curve trait distributions do not ring true: Directional environmental selection is common and amplified by aridity

Restoration of primary productivity in drylands supports weed suppression and erosion mitigation

1. Introduction

Drylands currently comprise 47% the terrestrial surface of the world and are forecasted to increase in area as global temperatures rise (Koutroulis 2019). Drylands are very sensitive to disturbance and climate change due to low soil fertility and existing vegetation cover (Huang 2016). Severe degradation has already likely occurred in a 1/5 of global drylands (Maestre 2016). Changes in community composition and plant cover can lead to the loss of vital ecosystem functions such as primary productivity, weed suppression, and erosion mitigation. Restoration can reverse this degradation by rebuilding these vital ecosystem functions.

Trait-based ecological restoration is a promising route to recovering ecosystem functioning in disturbed drylands. Functional traits, such as seed mass or height, are a meaningful way to assign a value to plants to allow for comparisons between species or populations. rather than characterizing a plant by species identity or grouping plants into categories such as grass versus shrub (Grime 1977, Westoby 1998, McGill 2006, Violle 2007). Typically, these measurements provide a numerical value, though some traits are inherently categorical, such as photosynthetic pathway. These traits are meaningful because they reflect tradeoffs in allocation to plant components that impact growth, reproduction, and survival. Generally, information can be drawn from plant trait values to understand how much a plant has invested in each of its components. If a single leaf, for example, is long-lived and has many structural components to make it tougher and more able to regulate water loss versus a fast-growing leaf that may not live as long, but will give a quick return on investment. This slow-fast framework (Reich 2014) is useful for understanding what plant traits mean for a plant and I will be referring back to this framework throughout my dissertation.

In order to restore a degraded dryland, there are numerous barriers to overcome; these barriers “filter” out trait values that are unsuitable for a given condition. The environmental filtering metaphor is useful in understanding the barriers to plant establishment in restoration (Funk et al. 2008). One barrier to establishment is the lack of seeds in the soil or being dispersed from existing vegetation, this can be overcome in restoration by adding seeds. Another barrier to establishment is the physical environment at a restoration site including climate and other abiotic factors. The abiotic filter is the one I will primarily address in my dissertation because it is a very strong filter in degraded drylands, and it can be overcome by including plants that are appropriate for a site’s environmental conditions. The abiotic filters are very strong in a disturbed site. When there is a high prevalence of bare ground, there are additional challenges to overcome for the survival of restoration species. Reference communities nearby are inherently different from disturbed sites, therefore they may not always include species that are suited for restoration. It is necessary to take into consideration the increased strength of environmental filtering when in consideration of the species used for restoration at a highly disturbed site. The final barrier to establishment includes the biotic interactions. In a disturbed restoration site, this often includes weedy species, therefore the selection of species for restoration that can outcompete weeds can be one way overcome this barrier. Even if a new plant community can overcome these filters to survive at a restoration site, the next question is whether this restored community will bring back vital ecosystem functions.

Species diversity can improve ecosystem functions such as plant productivity, but we know that it is functional diversity within a community that drives this outcome (Díaz and Cabido 2001). The hypothesis of niche complementarity (Tilman 1997) postulates that greater diversity leads to more efficient resource uptake resulting in higher productivity. Additionally, diversity can have a positive impact on many ecosystem functions for example, soil stability (Gould et al 2016). However, it's not just diversity that can impact ecosystem functions, the traits of dominant species in a community can tell an essential part of the story (mass ratio hypothesis – Grime 1998). If the dominant species in a community have more biomass, this will impact productivity and therefore diversity will not play as large of a role and may even negatively impact productivity. One way to estimate the impact of dominant species is by using an index such as community-weighted mean is a way of averaging the trait values in a community based on species abundance.

The dominant trait values (mass ratio hypothesis) and trait diversity (niche complementarity hypothesis) in a community both tell part of the story of how the community impacts ecosystem processes. Diaz et al. (2007) propose a framework for including both community-weighted trait values and functional diversity in the analysis of biodiversity-ecosystem functioning assessments where abiotic factors and idiosyncratic species effects are also taken into consideration. In the early stages of restoration in degraded drylands getting any plants to establish starts to have an impact on ecosystem function. This is one reason why it can be useful to include the amount of restored biomass into these assessments. The way that trait composition impacts ecosystem functioning may change over time as a community shifts through successional stages. The "vegetation quantity hypothesis" (Lohbeck et al 2015) addresses this concept by incorporating biomass into the Diaz framework for biodiversity-ecosystem functioning studies. This relates to the idea that primary productivity is a supporting service that contributes to all other ecosystem services (Garland et al 2020). Even though increased primary productivity is itself a goal of many restoration projects, it also plays a role in mediating the impact of plant functional composition on other ecosystem functions.

My first research chapter is titled: The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes. This chapter of my dissertation covers an analysis of the Colorado Plateau Restoration Outcomes Database, which is a large database of restoration treatments compiled by the Chicago Botanic Garden funded in part by the Colorado Plateau Native Plant Program including 15 years and 150 sites where seeding treatments occurred. These data come from several agencies, primarily the Utah watershed restoration initiative. Looking into the outcomes of these different seeding treatments, I asked which plant traits influenced restoration success and which trait strategies worked best in different environments. In order to address these research questions, I obtained plant trait and climate data. Functional trait data were obtained from the TRY initiative which is a database of plant trait data from around the world). I asked whether restoration success could be predicted by plant traits, climate, or an interaction between the two. An interaction between trait and environment means that trait values can be matched to site conditions in order to improve the outcome of restoration treatments.

Land managers around the globe apply tens of millions of dollars of seed annually to degraded ecosystems in the hopes of restoring structure and function (Woodworth 2006; Malakoff 2012, Kimball 2015). The National Native Seed Strategy in the US has taken to using the phrase “The right seed, in the right place, at the right time” (Plant Conservation Alliance 2015). In this chapter, I test the idea of applying “The right trait in the right place at the right time”. In other words, I assess the application of functional trait-based approaches to restoration, using 15 years of restoration data from a dryland region (the Colorado Plateau, U.S.) to determine how plant traits interact with the environment to predict restoration success.

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The previous chapter involved an investigation into large-scale trends in restoration success across the Colorado Plateau. In order to hone in on more specific traits that could not be obtained for such a large scale, my second research chapter investigates similar questions with a more controlled approach that gave higher-resolution data to compare the number of individuals that survived versus what was planted along with plants that were previously screened for both above and belowground trait values. My second research chapter is titled: Bell curve trait distributions do not ring true: Directional environmental selection is common and amplified by aridity. This chapter additionally investigates how to improve restoration efforts by selecting species with trait distributions that are suited for the harsh abiotic conditions in dryland restoration sites.

I planted 29 species of perennial grasses and forbs that are commonly used in restoration in the Colorado Plateau region. I planted 9,216 perennial grasses and forbs across eight dryland sites varying in climate across the Colorado Plateau, a high-elevation dryland region. My field sites within Arizona and Utah are a subset of the RestoreNet experiment, which is a network of restoration sites maintained by the USGS Restoration Assessment and Monitoring Program for the Southwest. These sites are in degraded areas that have low native perennial vegetation cover, and some have problems with invasive non-native species. All sites have the potential to be restored to perennial grasslands, shrublands, and woodlands and differ in mean annual temperature, so they are categorized as cool, intermediate, and warm. Before planting, I did a greenhouse trait screening in which I grew replicates of each species and measured trait values to understand more about the trait strategies of these species.

For the greenhouse trait screening, 10 individuals of each species were grown in Northern Arizona University research greenhouse in 2017-2018 for baseline trait measurements. I harvested plants prior to flowering to obtain the entire above- and below-ground biomass and extracted additional measurements for the calculation of plant traits. I measured several important plant traits related to stature, leaves, and roots. Though grown in different conditions, traits from greenhouse-grown plants are useful to inform field-based studies. Greenhouse studies are helpful for collecting root systems that would otherwise be extremely difficult in natural conditions. Additionally, destructive aboveground and belowground measurements are not possible for a long-term study such as RestoreNet.

After sites were planted, I monitored survival and growth of each plant, the second research chapter discusses the survival up until the end of the 2019 growing season which was between 40 and 89% based on the site. But how do plant traits influence these differences in survival? Initial planting densities were low enough to eliminate any biotic interactions, therefore abiotic conditions were isolated in acting on plant survival. I investigated the shape of trait abundance distributions caused by abiotic filtering, employing terms from evolutionary biology, namely stabilizing, directional, and destabilizing selection. Additionally, I tested the stress-dominance hypothesis which predicts that environmental filtering will play a greater role in structuring communities in more stressful environments. According to the stress-dominance hypothesis (Coyle et al. 2014, Rolhauser et al. 2017), stabilizing selection is expected at sites with harsher conditions due to greater restriction on trait variation resulting in convergence on optimal trait values, thus I predicted that stabilizing selection would occur at sites that received our warm species pool (warm sites, with water-limiting conditions).

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My first and second research chapters address how to improve survival and establishment of native plants in restoration, but what impact does the restored plant community then have on ecosystem functioning? This is what my third research chapter addresses with an additional analysis of the RestoreNet experiment. Using restored plant biomass and additional site assessments of weed cover and soil processes, I asked how plant traits influence ecosystem functions that managers care about, specifically productivity, weed suppression, and erosion mitigation. I investigated how community composition including dominant trait values (mass ratio hypothesis) and trait diversity (niche complementarity hypothesis) influence these ecosystem functions, however I also include restored biomass in the assessment of weed suppression and soil processes related to erosion mitigation (vegetation quantity hypothesis).

Plant functional composition impacts ecosystem services such as primary productivity, erosion mitigation, and weed suppression, but those effects are contingent upon the ability to restore plant biomass. Specifically, functional composition is likely to have a greater impact when the amount of biomass is high. Recovering native plant biomass in drylands can be especially challenging, therefore investigating the role of functional composition contributing to the restoration of aboveground biomass is one step towards meeting restoration goals in drylands. The next step is investigating the role of restored biomass in mediating the impact of functional composition on indicators of ecosystem function such as weed suppression and soil processes related to erosion control.

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2. The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes.

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Running Head: Trait-based restoration

Abstract

The challenges of restoration in dryland ecosystems are growing due to a rise in anthropogenic disturbance and increasing aridity. Plant functional traits are often used to predict plant performance and can offer a window into potential outcomes of restoration efforts across environmental gradients. We analyzed a database including 15 years of seeding outcomes across 150 sites on the Colorado Plateau, a cold desert ecoregion in the western United States, and analyzed the independent and interactive effects of functional traits (seed mass, height, and specific leaf area) and local biologically-relevant climate variables on seeding success. We predicted that the best models would include an interaction between plant traits and climate, indicating a need to match the right trait value to the right climate conditions to maximize seeding success. Indeed, we found that both plant height and seed size significantly interacted with temperature seasonality, with larger seeds and taller plants performing better in more seasonal environments. We also determined that these trait-environment patterns are not influenced by whether a species is native or non-native. Our results inform the selection of seed mixes for restoring areas with specific climatic conditions, while also demonstrating the strong influence of temperature seasonality on seeding success in the Colorado Plateau region.

Key Words: restoration, plant functional traits, climate suitability, dryland, height, seed mass, temperature seasonality

Introduction

Sustainable management of dryland ecosystems faces many challenges such as overgrazing, urban development, wildfire, invasive species introduction, and other anthropogenic disturbances (Schwinning et al. 2008). Land managers seeking to recover plant and ecosystem properties following these disturbances must also overcome drought, extreme temperature fluctuations, and limited resources when undertaking restoration projects (e.g. Wilson et al. 2018, Bainbridge 2012, Kildisheva et al. 2016). Guidelines for restoration-relevant research and land management actions have emerged internationally to ensure the right seed is sown in the right place at the right time to improve restoration outcomes (Hawke 1989, Oldfield and Olwell 2015, Mcdonald et al. 2016). Understanding how seed mixes interact with site-level environmental conditions to determine restoration success should enhance management outcomes (Kimball et al. 2015, Copeland et al. 2017).

Functional traits are standardized, quantifiable characteristics of plants that reflect fundamental constraints and trade-offs in relation to the environment that determine growth, survival and reproduction (Lavorel and Garnier 2002). Using functional traits rather than other forms of classification, such as species or lifeform, has improved our ability to predict ecological dynamics such as plant survival and productivity and their impacts on ecosystem services (Funk et al. 2016). Restoration practitioners and land managers are recognizing the potential for functional traits to identify general trends in restoration outcomes across treatment sites (Kardol and Wardle 2010, Clark et al. 2012, Laughlin 2014). The effect of traits on restoration success also depends in part on the environmental context of a restoration site. Optimal functional strategies have been shown to shift from ruderal to competitive through succession during restoration of resource-rich grasslands of Britain (Pywell et al. 2003), whereas the stressors of the Great Basin desert in North America favored a different strategy – traits related to stress-avoidance rather than rapid resource acquisition (Kulpa and Leger 2013). Trade-offs between traits related to resource-conservation and rapid resource acquisition facilitate predictions of environmental context for which different plant strategies are successful.

Seed mass, plant height and specific leaf area are three commonly measured traits that represent biophysically independent aspects of plant form and function (Westoby 1998, Moles 2018). Seed mass represents the regeneration niche and reflects a plant’s strategy for reproduction and colonization. Small seeds have been shown to persist longer in the seed bank awaiting optimal conditions for germination (Venable 2018). In contrast, large seeds have more energy stores to help seedlings persist in resource-limited conditions (Tilman and Downing 1994). Regeneration traits (e.g. seed size) have been identified as important determinants of seeding success in the degraded conditions of restoration sites (Larson et al. 2015). Plant height reflects the trade-off between competition and stress tolerance; tall plants are better competitors for light in productive environments, while shorter plants may more insulated against desiccating wind and heat (Grime 1977), however woody shrubs in arid systems have been shown to be more stress tolerant than shorter species due to a more extensive root system often associated with taller plants (D'Odorico and Porporato 2006). Specific leaf area (SLA) is the ratio of leaf area to dry mass, and represents a trade-off between competition and resource-use efficiency; high SLA leaves tend to be less resource-use efficient, but their high photosynthetic potential can allow them to be competitively superior in resource-rich environments (Wright et al. 2004, Reich 2014). Each of these functional traits can respond independently to abiotic and biotic factors at a site to determine plant establishment success.

Synthesis of restoration outcomes is facilitated by large-scale experiments and regional-scale meta-analyses (Gerla et al. 2012, Kimball et al. 2015, 2017). Integrating functional trait information into such syntheses can reveal generalizable patterns across sites and species that are not detectable from individual projects. While a trait-based approach is already being used in some regions to select optimal species for restoration (Pywell et al. 2003, Hérault et al. 2005, Fischer et al. 2013), a lack of trait data can limit such approaches in other regions. Intentionally incorporating functional trait measurements into the design of restoration treatments may help to create a comparable, unifying framework for assessment of restoration success across environmental gradients.

In this study, we investigated how plant functional traits and environmental conditions influenced seeding outcomes, using restoration monitoring data across a dryland region. We hypothesized that traits matched to suitable climate conditions can explain more of the variability influencing seeding success than just traits or climate on their own (i.e., traits and environmental conditions interact to determine seeding success). We tested this hypothesis by determining whether statistical models that included interactions between climate and traits out-performed models based on either type of variable alone. Specifically, we expected that species with more stress-tolerant, conservative plant functional strategies (large seeds, short height, and low SLA) would be more successful in extreme environmental conditions.

Methods

Study System: The Colorado Plateau is a dryland ecoregion in the western United States, comprising much of Utah, northern Arizona, western Colorado and northwestern New Mexico. The dominant disturbance necessitating restoration activities in the region is wildfire, though intensive grazing and invasive species motivate many restoration activities as well (Copeland et al. 2017). Data from the Utah Watershed Restoration Initiative (WRI), the USGS Land Treatment Digital Library (LTDL), as well as additional data from projects occurring within the Bureau of Land Management and the National Park Service were used to develop the Colorado Plateau Restoration Outcomes Database (for description see Appendix S1, and see Appendix S1: Table S1 for site locations and climate). This database only includes projects for which information on seed mix used in restoration was available. The database includes seeding treatment as well as pre- and post-treatment monitoring results from 1999-2014 at 194 sites across primarily Utah and western Colorado, and northern Arizona, with 417 unique species seeded. The dataset was reduced to 150 sites (Figure 1) and 88 species that could be evaluated for seeding success, this represented approximately 68% of species seeded per site. Seeding success could only be evaluated where the species seeded were not present in monitoring data from the seeded site prior to the species being seeded. Seeding success was evaluated as presence of the seeded species at the site in at least one post-seeding monitoring effort due to the inclusion of both annual and perennial species. Species that were not present at the site prior to seeding and were never recorded in post-treatment monitoring efforts were recorded as unsuccessful.

Local climate variables for each restoration site were extracted from PRISM at a 4 kilometer resolution and converted into nineteen biologically-relevant (BIOCLIM) variables using the dismo package in R (Hijmans et al. 2005). We extracted climate variables for a two-year window including year of treatment and post treatment, as most sites (148/150) had at least 2 years of monitoring data and available climate data. See Appendix 1: Table 1 for these values in our study sites.

Functional Trait Data

Functional trait data were obtained primarily from the TRY database (Kattge et al. 2011). The traits used in this study were seed dry mass (mg), plant height (m), and specific leaf area (mm2 mg-1). Data from the TRY database is collected by different researchers around the world in many different experimental contexts, therefore we weighted measurements by the number of individuals per dataset when there was more than one source of data for that species. We used data from TRY (see Appendix S2 for a reference of TRY contributors to this dataset) to calculate weighted species-level trait mean values when available and supplemented sparingly with additional measurements of natural communities and mature greenhouse-grown plants (see Appendix S3: Table S1 for trait source and Appendix S4 for methods).

Analyses

Generalized linear mixed models with a log-link function were used to analyze variation in seeding success (yes/no – species present after treatment or not). We used a principal component analysis to select six independent climate variables to use in our models: annual mean temperature, annual precipitation, precipitation seasonality (coefficient of variation=ratio of standard deviation of monthly precipitation to annual mean), temperature seasonality (std dev of mean monthly temperature), isothermality (100*mean diurnal range/temperature annual range), and precipitation of warmest quarter. We found no significant correlations between trait values used in our models (SLA-Seed Mass: r = 0.15, P = 0.26, SLA-Height: r = -0.18, P =0.15, Height-Seed Mass: r =0.16, P=0.18). We tested our hypothesis – that interactions between traits and climate would represent the most parsimonious models – separately for each functional trait by including its independent effect, then the effect of each climate variable, and finally the interaction between that trait and each of the six climate variables. Site was included as a random factor to account for variation in seed mix and site characteristics. We used Akaike Information Criterion (AIC) to select the best model for each functional trait, where lower AIC values indicate a more parsimonious model. Models with a ΔAIC of 2 or less were considered to be comparably parsimonious. Isothermality, temperature seasonality, specific leaf area, seed mass, and plant height were natural log transformed to conform to normality. All analyses were performed in R version 3.6.1.

Overall seeding success was 35.3%, however we found that non-native species were 11% more successful (166/389) than native species (277/866). To aid in interpretation, we also performed analysis of variance between native and non-native species for each functional trait. Non-native species often have traits related to higher growth rate that allow them to establish better than native species (Weber et al. 2010). Functional differences between native and non-native species could therefore explain differences in seeding outcomes, although differences could simply be because there were over twice as many native species used and there is not enough data from non-native species to compare.

Results

For seed mass, the model with the lowest AIC value included the interaction between seed mass and temperature seasonality (Table 1), outperforming the main effects of trait and environment. As demonstrated by this interaction, establishment of smaller seeded species was slightly improved by low temperature seasonality conditions, whereas establishment of larger seeded species was strongly improved by high temperature seasonality conditions (Figure 2a). There was no significant difference between the seed mass of native and non-native seeded species ($P = 0.1$, Appendix S5: Figure S1A).

For plant height, the best model included the interaction between plant height and temperature seasonality (Table 1). Establishment of shorter plants was slightly improved by low temperature seasonality conditions, while establishment of taller plants was greatly improved by high temperature seasonality conditions (Figure 2b). There was no significant difference in height among native and non-native seeded species ($P = 0.17$; Appendix S5: Figure S1B).

For the subset of data used to model the effect of SLA, the most parsimonious model did not contain an interaction nor was SLA significant, but temperature seasonality on its own was highly significant in predicting restoration seeding success (Table 1). The model containing precipitation seasonality without any interaction had ΔAIC of 1 so we considered this model equally parsimonious. Establishment of restoration species was improved by high temperature seasonality and high precipitation seasonality (Table 1). Non-native species had significantly higher SLA than native species ($t = 4.9$, $P = 0.001$, Appendix S5: Figure S1C).

Discussion

This study analyzed restoration seeding outcome for 88 species across 150 sites and 15 years on the Colorado Plateau. We found significant interactions between climate and functional traits in determining seeding success. More specifically we identified a single climate variable, temperature seasonality, that consistently influenced restoration success depending on all three traits we analyzed. In the cold, high desert region where these restoration treatments occurred, high temperature seasonality is associated with valley bottoms experiencing high summer temperatures and cold winter inversions (Appendix S6: Figure S1; correlation with elevation $r = -0.52$, $P < 0.001$). While we expected precipitation variables that more directly influence water availability to play a more important role, our results instead suggest that growing season length and temperature extremes may be more relevant for predicting plant strategies. This result aligns with previous work demonstrating that temperature is a stronger driver of community assembly across our study region (Butterfield et al. 2016b).

The interactive effects of seed mass and climate on seeding success suggest that species with larger seed are more successfully established in seasonally extreme environments. This is consistent with the idea that the greater energy reserves and conservative functional strategies associated with seedlings of larger seeded species are better suited to stressful environments (Baker 1972, Leishman et al. 2000). Extreme heat has also been related to higher metabolic costs, which larger seeds have a greater ability to overcome (Murray et al. 2004).

Increasing plant height reflects more exposure to fluctuating temperatures and desiccating winds. We found that tall species had greater seeding success at sites with greater temperature seasonality, while the success of shorter species was not influenced by temperature seasonality. Shrubs had greater height than herbaceous species in our database ($t = -1.95$, $P = 0.076$), and the interaction between height and temperature seasonality fits with other dryland studies in which larger and deeper root systems of taller, woody species buffer them from extreme heat (Padilla and Pugnaire 2007). Woody species may be able to take greater advantage of the fluctuation in temperature since their deeper roots allow them to persist when and where extreme temperatures inhibit growth of shallower-rooted species.

The lack of a significant effect of SLA, either alone or interacting with climate, was surprising given its typically strong ties to multiple aspects of resource use and acquisition (Reich 2014). Global studies of restoration have found that high SLA is important for colonizing highly competitive areas (Fischer et al. 2013, Zirbel et al. 2017). SLA may therefore play a larger role in dryland systems during later stages of succession when plant densities become high enough to result in competition. Different traits can be associated with habitat filtering versus competitive interactions in the same system (Maire et al. 2012). Long-term monitoring may be necessary to reveal the roles that different traits play in the multiple stages of ecosystem restoration in dryland environments.

Indeed, the ability to draw conclusions from a large-scale synthesis relies on comparable reporting and monitoring across projects over sufficient time periods. The measure of restoration success is limited in our study to evaluation of species presence pre- and post-treatment; however additional measures of seeding success such as species abundance or cover would also improve our understanding of how climate-trait interactions affect restoration outcomes (Copeland et al. 2018). Other factors such as site preparation, timing of treatment, soil type, and seeding/planting technique (Kimball et al. 2015, Copeland et al. 2017) likely interact with functional traits as well, and exploring these trait-environment interactions could greatly improve predictions and prescriptions for restoration outcomes across many systems.

Summary and Management Implications

Drylands face severe threats due to growing land-use disturbances, which increases the need to find successful restoration strategies in these regions (Moreno García et al. 2014). For the Colorado Plateau, our results suggest that temperature seasonality is the most influential climate variable by which we can tailor species to include in restoration projects; we find that larger seeded, taller species are best to include in areas with high temperature seasonality, while small-seeded, shorter species are better to include in areas with lower temperature seasonality. At the scale of an individual restoration project, the inclusion of species with traits that match the local environment may boost restoration success in areas where success has so far been limited. At a regional scale, identifying relevant plant traits in determining restoration success helps to prioritize plant materials production to make appropriate species available to practitioners. Working across these scales will be necessary to develop native plant materials markets that provide locally-optimal resources across a broad range of environments and restoration goals (Camhi et al. 2019).

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Literature Cited

Bainbridge, D. A. 2012. A guide for desert and dryland restoration: new hope for arid lands. Island Press.

Baker, H. 1972. Seed Weight in Relation to Environmental Conditions in California. Ecology 53:997–1010.

Butterfield, B. J., J. B. Bradford, S. M. Munson, and J. R. Gremer. 2017. Aridity increases below-ground niche breadth in grass communities. Plant Ecology 218.

Butterfield, B. J., A. L. Camhi, R. L. Rubin, and C. R. Schwalm. 2016a. Tradeoffs and Compatibilities Among Ecosystem Services : Biological , Physical and Economic Drivers of Multifunctionality. Page Ecosystem Services: From Biodiversity to Society Part 2. First edition. Elsevier Ltd.

Butterfield, B. J., S. M. Copeland, S. M. Munson, C. M. Roybal, and T. E. Wood. 2016b. Prestoration: Using species in restoration that will persist now and into the future. Restoration Ecology 25:155–163.

Camhi, A. L., C. Perrings, B. J. Butterfield, and T. E. Wood. 2019. Market-based opportunities for expanding native seed resources for restoration: A case study on the Colorado Plateau. Journal of Environmental Management 252.

Clark, D. L., M. Wilson, R. Roberts, P. W. Dunwiddie, A. Stanley, and T. N. Kaye. 2012. Plant traits - a tool for restoration? Applied Vegetation Science 15:449–458.

Copeland, S. M., S. M. Munson, D. S. Pilliod, J. L. Welty, J. B. Bradford, and B. J. Butterfield. 2017. Long-term trends in restoration and associated land treatments in the southwestern United States. Restoration Ecology:1–12.

Copeland, S. M., S. M. Munson, D. S. Pilliod, J. L. Welty, J. B. Bradford, and B. J. Butterfield. 2018. Long-term trends in restoration and associated land treatments in the southwestern United States. Restoration Ecology.

D'Odorico, P., and A. Porporato. 2006. Dryland Ecohydrology. Springer.

Fischer, L. K., M. Von Der Lippe, and I. Kowarik. 2013. Urban grassland restoration: which plant traits make desired species successful colonizers? Applied Vegetation Science 16:272–285.

Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C. Laughlin, A. E. Sutton-Grier, L. Williams, and J. Wright. 2016. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological Reviews.

Gerla, P. J., M. W. Cornett, J. D. Ekstein, and M. A. Ahlering. 2012. Talking big: Lessons learned from a 9000 hectare restoration in the northern tallgrass prairie. Sustainability 4:3066–3087.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American naturalist:1169–1194.

Hawke, B. 1989. Speech by the Prime Minister: Launch of Staement on the Environment.

Hérault, B., O. Honnay, and D. Thoen. 2005. Evaluation of the ecological restoration potential of plant communities in Norway spruce plantations using a life-trait based approach. Journal of Applied Ecology 42:536–545.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Kardol, P., and D. A. Wardle. 2010. How understanding aboveground-belowground linkages can assist restoration ecology. Trends in Ecology and Evolution 25:670–679.

Kattge, J., S. Diaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M. Westoby, P. B. Reich, and I. J. Wright. 2011. TRY–a global database of plant traits. Global Change Biology 17:2905–2935.

Kildisheva, O. A., T. E. Erickson, D. J. Merritt, and K. W. Dixon. 2016. Setting the scene for dryland recovery: an overview and key findings from a workshop targeting seed-based restoration. Restoration Ecology 24.

Kimball, S., M. E. Lulow, K. R. Balazs, and T. E. Huxman. 2017. Predicting drought tolerance from slope aspect preference in restored plant communities. Ecology and Evolution 7:3123–3131.

Kimball, S., M. Lulow, Q. Sorenson, K. Balazs, Y.-C. Fang, S. J. Davis, M. O'Connell, and T. E. Huxman. 2015. Cost-effective ecological restoration. Restoration Ecology 23.

Kramer, A. T., S. Still, and N. Talkington. (n.d.). Colorado Plateau Restoration Outcomes Database.

Kulpa, S. M., and E. A. Leger. 2013. Strong natural selection during plant restoration favors an unexpected suite of plant traits. Evolutionary Applications 6:510–523.

Laughlin, D. C. 2014. Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecology Letters 17:771–784.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556.

Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The Evolutionary Ecology of Seed Size. Pages 31–57 Seeds: The Ecology of Regeneration in Plant Communities.

Maire, V., N. Gross, L. Börger, R. Proulx, C. Wirth, L. da S. Pontes, J. F. Soussana, and F. Louault. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. New Phytologist 196:497–509.

Mcdonald, T., G. D. Gann, J. Jonson, and K. W. Dixon. 2016. International Standards for the Practice of Ecological Restoration - Including Principles and Key Concepts. Washington D.C.

Moles, A. T. 2018. Being John Harper: Using evolutionary ideas to improve understanding of global patterns in plant traits. Journal of Ecology 106:1–18.

Moreno García, C. A., J. Schellberg, F. Ewert, K. Brüser, P. Canales-Prati, A. Linstädter, R. J. Oomen, J. C. Ruppert, and S. B. Perelman. 2014. Response of community-aggregated plant functional traits along grazing gradients: Insights from African semi-arid grasslands. Applied Vegetation Science 17:470–481.

Murray, B. R., A. H. D. Brown, C. R. Dickman, and M. S. Crowther. 2004. Geographical gradients in seed mass in relation to climate. Journal of Biogeography 31:379–388.

Oldfield, S., and P. Olwell. 2015. The Right Seed in the Right Place at the Right Time. BioScience 65:955–956.

Padilla, F. M., and F. I. Pugnaire. 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology 21:489–495.

Plant Conservation Alliance. 2015. National Seed Strategy for Rehabilitation and Restoration.

Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40:65–77.

Reich, P. B. 2014. The world-wide ‘fast–slow’plant economics spectrum: a traits manifesto. Journal of Ecology 102:275–301.

Schwinning, S., J. Belnap, D. R. Bowling, and J. R. Ehleringer. 2008. Sensitivity of the Colorado Plateau to change: Climate, ecosystems, and society. Ecology and Society 13.

Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature 367:363–365.

Venable, D. L. 2018. Size-Number Trade-Offs and the Variation of Seed Size with Plant Resource Status Author (s): D . Lawrence Venable Source : The American Naturalist , Vol . 140 , No . 2 (Aug ., 1992), pp . 287-304 Published by : The University of Chicago Press for The 140:287–304.

Weber, E., M. Fischer, and M. van Kleunen. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology letters 13:235–45.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213–227.

Wilson, S. D., D. R. Schlaepfer, J. B. Bradford, W. K. Lauenroth, M. C. Duniway, S. A. Hall, K. Jamiyansharav, G. Jia, A. Lkhagva, and S. M. Munson. 2018. Functional Group, Biomass, and Climate Change Effects on Ecological Drought in Semiarid Grasslands. Journal of Geophysical Research: Biogeosciences 123:1072–1085.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, and M. Diemer. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Zirbel, C. R., T. Bassett, E. Grman, and L. A. Brudvig. 2017. Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. Journal of Applied Ecology:1070–1079.

Tables and Figures

	Seed Mass (ln), n=1199				Height (ln), n=1154				SLA (ln), n=1087			
	Wald Type II Chi Squared, df=1		AIC	ΔAIC	Wald Type II Chi Squared, df=1		AIC	ΔAIC	Wald Type II Chi Squared, df=1		AIC	ΔAIC
	X2	p			X2	p			X2	p		
Trait	10.23	0.001	1486.5	8.7	6.39	0.011	1443.2	9.9	0.30	0.59	1378.8	4.5
Temperature Seasonality (ln)	4.48	0.034	1492.6	14.8	4.72	0.03	1445.0	11.7	4.98	0.03	**1374.3**	**0.0**
Trait	9.53	0.002			6.04	0.01			0.22	0.64		
Temperature Seasonality (ln)	4.48	0.034			4.33	0.04			4.89	0.03		
Trait:Temperature Seasonality (ln)	8.02	0.005	**1477.8**	**0.0**	9.23	0.00	**1433.3**	**0.0**	0.92	0.34	1377.2	2.9
Annual Mean Temperature	1.36	0.244	1495.5	17.7	0.68	0.41	1448.8	15.5	0.39	0.53	1378.7	4.4
Trait	9.71	0.002			5.89	0.02			0.22	0.64		
Annual Mean Temperature	0.99	0.319			0.55	0.46			0.32	0.57		
Trait:Annual Mean Temperature	2.02	0.155	1487.5	9.7	7.45	0.01	1439.0	5.7	2.94	0.09	1379.5	5.2
Total Annual Precipitation	0.09	0.763	1496.8	19.0	0.08	0.77	1449.4	16.1	0.17	0.68	1378.9	4.6
Trait	10.02	0.002			6.09	0.01			0.31	0.58		
Total Annual Precipitation	0.15	0.698			0.08	0.77			0.18	0.67		
Trait:Total Annual Precipitation	3.35	0.067	1487.0	9.2	7.05	0.01	1439.9	6.6	0.13	0.72	1382.5	8.2
Precipitation Seasonality	5.12	0.024	1491.8	14.0	4.25	0.04	1445.3	12.0	3.77	0.05	**1375.3**	**1.0**
Trait	9.26	0.002			6.23	0.01			0.39	0.53		
Precipitation Seasonality	4.42	0.036			4.09	0.04			3.85	0.05		
Trait:Precipitation Seasonality	2.50	0.114	1483.7	5.9	0.00	0.98	1443.1	9.8	0.68	0.41	1378.3	4.0
Precipitation of Warmest Quarter	1.48	0.224	1495.4	17.6	1.19	0.28	1448.3	15.0	1.29	0.26	1377.8	3.5
Trait	9.78	0.002			6.26	0.01			0.23	0.63		

Precipitation of Warmest Quarter	1.23	0.268			1.06	0.30			1.15	0.28		
Trait:Precipitation of Warmest Quarter	3.22	0.073	1486.1	8.3	0.40	0.53	1445.7	12.4	3.99	0.05	1377.6	3.3
Isothermality (ln)	0.60	0.437	1496.3	18.5	0.48	0.49	1449.0	15.7	0.29	0.59	1378.8	4.5
Trait	10.19	0.001			6.24	0.01			0.25	0.61		
Isothermality (ln)	0.57	0.450			0.37	0.54			0.25	0.62		
Trait:Isothermality (ln)	0.01	0.914	1489.9	12.1	1.49	0.22	1445.3	12.0	0.11	0.75	1382.4	8.1

Table 1. Predictive models of plant establishment. Analysis of deviance for main effects using Wald Type II denotes model significance. Akaike information criterion (AIC) is the criterion used to determine model parsimony. ΔAIC of 2 or less are considered equal. GLMM results are in Appendix S7: Table S1

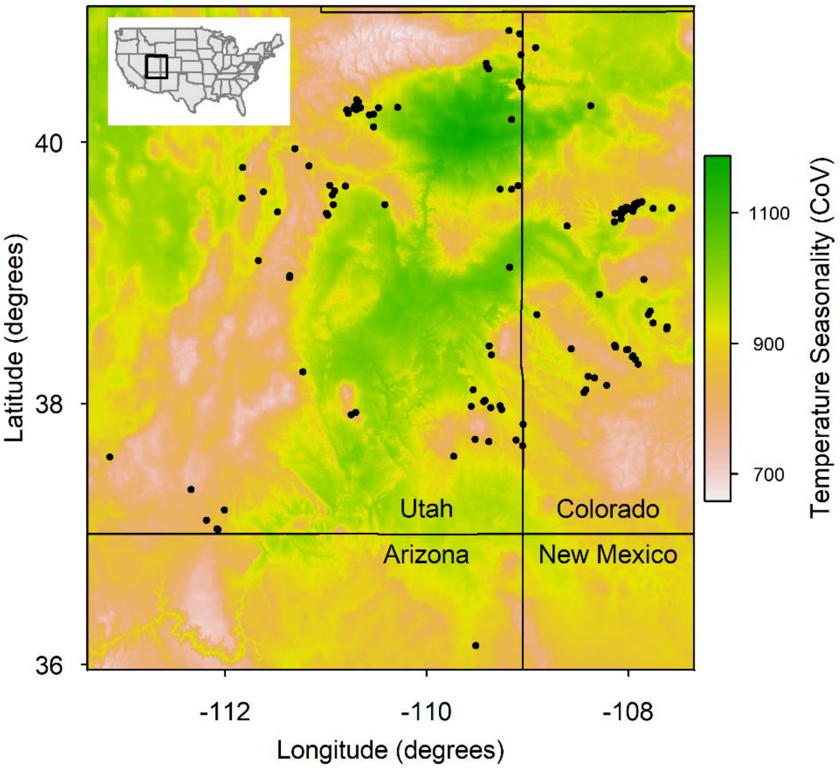

Figure 1. Map of sites included in analyses. Black dots represent location of restoration treatments. Background color represents average temperature seasonality for the region.

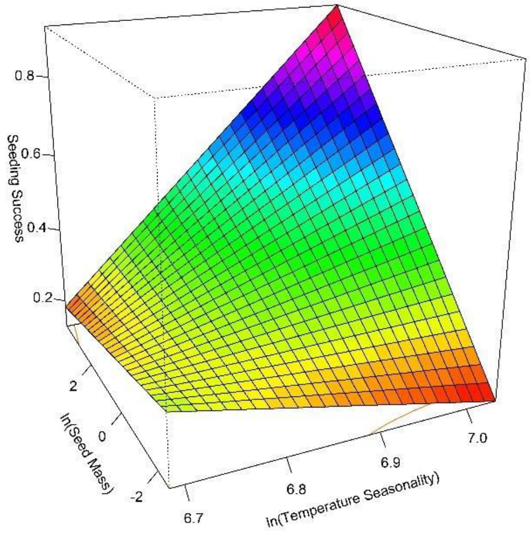

Figure 2a.

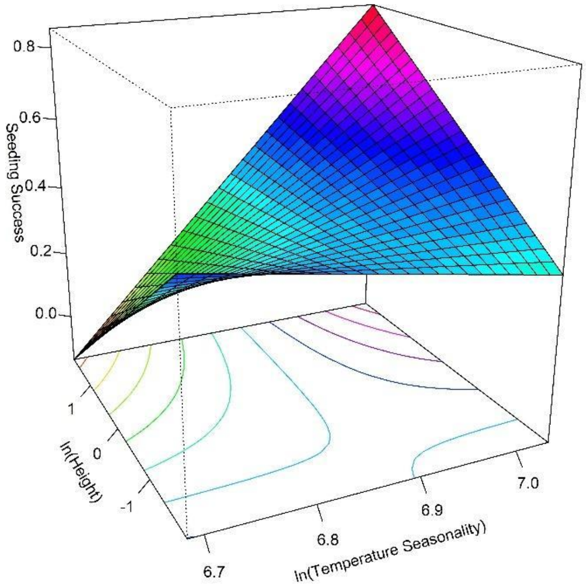

Figure 2b.

Figure 2. Fitted model of seeding success as a function of (a) seed mass and temperature seasonality, and (b) plant height and temperature seasonality. Contour lines and color gradient show proportion of success at trait/climate combination. Sample sizes are $n = 1198$ in (a) and $n = 1153$ in (b). All variables are ln transformed.

3. Bell curve trait distributions do not ring true: Directional environmental selection is common and amplified by aridity.

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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 create unimodal trait distributions centered around a 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 perennial grass and forb species that had a range of functional trait values and were assigned to either warm, intermediate, or cool temperature tolerance pools 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 destabilizing 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 destabilizing 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 favorable 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.

Key Words: environmental filtering, dryland, stress dominance hypothesis, functional diversity, community assembly, directional selection, restoration

Introduction

Numerous processes shape the distribution of biodiversity. One of the most frequently invoked is environmental filtering (Butterfield, 2015; Cingolani, Cabido, Gurvich, Renison, & Díaz, 2007; Cornwell, Schwilk, & Ackerly, 2006; Craven, Hall, Berlyn, Ashton, & van Breugel, 2018; de Bello et al., 2013a; Le Bagousse-Pinguet et al., 2017; Lebrija-trejos, Pérez-garcía, Meave, Bongers, & Poorter, 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 (Butterfield & Callaway, 2013; Cadotte & Tucker, 2017; Kraft et al., 2015; Mayfield & Levine, 2010). Distinctions between these filtering mechanisms are well-defined in theory (Funk, Cleland, Suding, & Zavaleta, 2008), but in practice the ability to isolate the effect of a single filter in existing plant communities is very difficult (but see Fraaije, ter Braak, Verduyn, Verhoeven, & Soons, 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 destabilizing 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, Munoz, Shipley, & Violle, 2018; Muscarella & Uriarte, 2016; Rolhauser, Nordenstahl, Aguiar, & Pucheta, 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 centering on "optimal" trait values for a given set of conditions (Fig. 1). Stabilizing selection is typically assumed in studies of community assembly, though other patterns are often present in natural communities (Laughlin et al., 2015). Trait distributions shaped by directional and destabilizing selection move distributions from central toward extreme trait values and are often discussed in the context of competition, niche partitioning, and environmental heterogeneity (Rolhauser et al., 2019), however, the extent to which abiotic factors alone can produce these patterns distributions of trait abundance is unknown. Without biotic interactions, stabilizing selection could break down, resulting in highly skewed or multi-modal trait distributions. 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 toward more predictable trait-based models of community assembly (Funk et al., 2016).

Since most observational studies cannot separate the effects of competition and abiotic stressors, this is a challenge for addressing the stress-dominance hypothesis (Coyle et al., 2014; Swenson & Enquist, 2007) which predicts that environmental filtering will play a greater role in structuring communities in more stressful environments, while competition 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). Aridity gradients represent important variation in an environmental filter, namely soil moisture and/or atmospheric demand, that may vary in their intensity and nature across space and time. Furthermore, it has been argued that the abiotic environment represents a particularly strong filter in water-limited environments as compared to more mesic biomes due to the overwhelming role of physical processes, rather than biotic uptake, on plant-available soil moisture (Goldberg

& Novoplansky, 1997). While there is variation by region, the hotter, drier conditions forecasted for many global drylands (Bradford, Schlaepfer, Lauenroth, & Palmquist, 2020; Koutroulis, 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 anthropogenic disturbance (Koutroulis, 2019) which further increases abiotic stress. These dryland areas are therefore an excellent and important study system in which 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 propagule pressure 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, Copeland, Munson, Roybal, & Wood, 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, Moorhead, Swenson, Bailey, & Sanders, 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 a restoration context with minimal biotic interaction. Our objectives were to first test the hypothesis that non-random patterns of functional composition are present in the experimental communities. Second, we investigated the hypothesis that the magnitude of these non-random patterns varies as a function of species pool, trait, or their interaction. Finally, we tested the hypothesis that the direction of these non-random patterns varies as a function of species pool, trait, or their interaction.

We explored the alternative outcomes of stabilizing, directional, and destabilizing 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 in those environmental conditions with stressors limiting viable trait values at either extreme, and directional selection would occur more frequently when there was selective pressure limiting trait values at one extreme.

Methods

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 U.S. Bureau of Land Management and 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-liter 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 specific leaf area (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, 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^{TM} scanner bed software for analysis of root length and finally dried to obtain SRL and RDMC. Aboveground biomass was separated from belowground biomass and dried separately to calculate root-to-shoot ratio.

Experimental Design

The field experiment was conducted at eight restoration sites located on the Colorado Plateau (Fig. 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 US and is coordinated by the Restoration Assessment and Monitoring Program for the Southwest (https://usgs.gov/sbsc/ramps). Sites were selected to represent common potential vegetation types across the region, but that have been degraded by overgrazing or other disturbances that have reduced perennial vegetation. The sites have a range in mean annual temperature of 8.8-16.5 °C, mean annual precipitation of 206-491mm, 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 establishment of the experiment.

Plants used in the experiment were grown in the Northern Arizona University Research Greenhouse in 3.8 x 14 cm "cone-tainers" (Stuewe and Sons, Tangent, Oregon, USA). Plants received 30 ppm of 20-20-20 liquid fertilizer after true leaves emerged twice weekly for approximately 4 weeks, and the fertilizer was flushed out prior to hardening. Plants were hardened for approximately two weeks outside the research greenhouse before planting at field sites. The 29 experimental species were classified into three different pools of 16 species 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, Phillips, Leathwick, & Elith, 2015, BIF.org (2018), GBIF Home Page. 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). All species pools share some species in common, and all contain a mix of perennial grasses and forbs. Multivariate analysis of variance revealed that the species pools did not differ in their average trait values (See Appendix S1).

Species pools were 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 4 control plots, 16 monocultures, and 16 polycultures. A total of 9,216 individuals were planted across all 8 sites. Each species was planted in one monoculture (single species) plot per site, and four different polyculture (multi-species) 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. Within each 2x2 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. All four of the control plots at each site received the weed cloth, but two control plots also received transplants of dead container plants that had been treated with herbicide to control for the impact of digging and transplanting cones containing potting soil and the same amount of water was applied.

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 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%.

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, warm) had a different set of species planted and each site had a different number of surviving plants, this null permutation modeling 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 $SES=(M_{\text{observed}}-M_{\text{null}})/SD_{\text{null}}$. Since null distributions followed a standard bell curve, we considered SES > |1.96|, when significant at $P < 0.01$, to be significantly different than expected.

Coefficient of variation (CoV) 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 (CWM) was selected as a measure of ‘optimal’ trait values in a community. Community-weighted mean (CWM) 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. Two-way analysis of variance on |sesCoV| and |sesCWM| was used to further investigate whether the magnitude of non-random patterns varied as a function of species pool, trait, or their interaction.

To determine whether directional selection (when present) resulted in consistent or variable selection for particular trait values across sites, a two-way analysis of variance was performed on sesCWM (not its absolute value) with species pool, trait, and their interaction as predictors.

To test the hypothesis that functional diversity is restricted more in severe environments we used two-way analysis of variance on sesCoV to determine whether the direction varied as a factor of species pool, trait, or their interaction.

Finally, we assigned a type of selection (stabilizing, directional, or destabilizing) 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 destabilizing 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 (Fig. 1).

Results

Average total survival of restoration plantings ranged from 41-89%, with cool and intermediate temperature sites generally performing better than warm sites (Table S1). 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.

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 coefficient of variation was significantly different than expected from random chance in 75% of cases (48/64 sesCoV >|1.96|). Community-weighted mean was different than expected from random chance in 81% of cases (52/64 sesCWM >|1.96|).

H2. The strength of environmental filtering varies as a function of species pool, trait, or their interaction.

Only the main effect of trait significantly influenced the standard effect size of the trait coefficient of variation (|sesCoV|) (Table 4), such that coarse RDMC had higher |sesCoV| compared to all other traits (Fig. 2, A). Both trait and species pool independently influenced the standard effect size of the trait community weighted mean (|sesCWM|), but their interaction did not (Table 4). The |sesCWM| of coarse RDMC was greater than most traits, with |sesCWM| of

SLA and fine SRL in the middle (Fig. 2B) and the warm species pool had higher |sesCWM| than cool and intermediate species pools (Fig. 2C). For both |sesCoV| and |sesCWM| all traits except fine RDMC were significantly different than expected from a random draw of species trait values.

H3. The direction of environmental filtering varies as a function of species pool, trait, or their interaction.

Trait and species pool significantly interacted to influence both sesCoV and sesCWM (Table 3). While this interaction was significant, a Tukey's HSD test revealed that there was still overlap in sesCoV of traits for different species pools, thus there were no significant differences in trait values among species pool for any trait (Table S2, Fig. 3A). However, comparing the observed values relative to a null expectation (i.e., if values exceed a standardized effect size of |1.96|), there is lower CoV of height, SLA, and SRLc of the surviving individuals than expected in the warmer species pool, and greater sesCoV values of SLA for the intermediate and cool species pool, and of height and SRLc for the intermediate species pool. Additionally, CoV for LDMC, RDMCf, and root to shoot ratio of surviving individuals was greater than expected in the cool, intermediate, and warm pools, respectively, and not different than expected for the other pools. Finally, for SRLf, CoV of trait values for surviving individuals was lower than expected in the cool pool, higher in the intermediate pool, and not different than expected for the warm pool. In total, CoV was significantly different from expected for 6 traits in the warm pool, 6 in the intermediate pool, and 4 in the cool pool. For sesCWM, a Tukey's HSD test showed a significant increase in SLA from the cool species pool to the warm species pool, but no significant differences for all other traits (Table S3, Fig. 3B). Again, by comparing observed to expected values, CWM for SRLc of surviving individuals was lower than expected in the warm and intermediate pools, higher than expected in the cool pool, while height was greater than expected in the cool pool, and lower than expected in the other pools. Also, CWM of SRLf of surviving individuals were greater than expected in the warm pool, lower than expected in intermediate pool, and not different than expected for cool pool. Additionally, RDMCf and root to shoot ratio were lower than expected in the warm species pool and not different in the other species pools. In total, CWM was significantly different from expected for 8 traits in the warm pool, 5 in the intermediate pool, and 6 in the cool pool.

We expected to see greater stabilizing selection at sites with more stressful, water-limiting conditions. Patterns of selection for traits included stabilizing, directional, and destabilizing selection (Fig. 4). There were 21 instances (33%) of directional selection and eight (13%) instances of destabilizing selection; these instances were counted when a site within a species pool matched the theoretical distributions in Fig. 1. Directional selection occurred most at sites in the warm species pool with 13 instances and there were six instances at sites within cool species pool, and two at sites within intermediate species pool. Destabilizing selection occurred equally within cool and intermediate species pool, but not at within warm species pools. Only one instance of stabilizing selection was found (for SRL within one site in cool species pool). There were 15 instances (23%) of a selection pattern that is a combination of destabilizing and directional where sesCoV >1.96 and sesCWM >|1.96|. Finally, there were 19 instances of no selection occurring (30%).

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 species experienced a negligible biotic filter as evidenced by 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. The magnitude of environmental filtering across sites supported the stress-dominance hypothesis, as filtering was more intense in the warmest, driest conditions (Fig. 2). Contrary to expectations, however, we found that the type of environmental filtering in these harsh conditions could predominantly be associated with directional, not stabilizing selection as we had hypothesized. 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 favorable conditions.

The greater intensity of environmental filtering found in the warmest environments supports the stress-dominance hypothesis, but also emphasizes the importance of gradient length and environmental context. For many years there has been discussion of the relative impact of environmental filtering in stressful environments versus competition in productive environments (Cornwell & Ackerly, 2009; Grime, 1977; May, Giladi, Ristow, Ziv, & Jeltsch, 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 toward the cold (temperate), and high variation at the warm end (tropical). 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 allows us to determine how climate influences functional trait composition on species otherwise adapted to a similar biome. Most of our findings are related to the relative intensity of stressors which all our sites experience such as heat and aridity. While we did find there was a significant shift in functional composition in surviving species, we did not see the convergence on similar trait values found with stabilizing selection.

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 destabilizing selection were predominant. We found greater destabilizing selection at cool and intermediate sites, consistent with the expectation that trait composition is less restricted when conditions are favorable. There is 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, Kozak, Fine, & Kembel, 2009; Lhotsky et al., 2016; Weiher & Keddy, 1995b). In the present study environmental heterogeneity is restricted to temporal or rooting-depth, however an alternative explanation is that there is lower restriction of trait variability in favorable 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 S2). 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 destabilizing 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 destabilizing 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 versus stress tolerating. Destabilizing selection was found in 8 cases, but the most common type of selection was directional.

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, Soliveres, Kéfi, & Maestre, 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 destabilizing selection in less harsh environments.

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. 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, Brusa, Vagge, & Cerabolini, 2013). However, in the warmest species pool, high SLA was beneficial. While this may seem contradictory with the LDMC and height results, as high SLA (low leaf mass per area) is generally associated with wetter conditions (Wright et al., 2004), in our study, this result likely reflects phenological differences among species, including early season species such as *Poa secunda* take advantage of cool season moisture then going 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 sub-seasonal pulses similar to what was found by Rolhauser et al 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, Zamora-Ledezma, Bossard, Pérez-Ramos, & Roumet, 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.

Some caveats to this study include a limitation on the range of trait values tested, for example, the pool of species planted did not include particularly tall species since we were working with grassland species. Additionally, the plants used in this study came from readily available cultivars, which have traits that may differ significantly from wild populations and provide merit to conducting trait- instead of species-level analyses. This study only includes data from two 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. Additionally, we could not disentangle the effect of warm species pool from warm site, as the two covaried.

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, Cleland, Suding, & Zavaleta, 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. These trait-environment models may become increasingly relevant as climate conditions may preclude restoration of sites to historical conditions. Rather, restoration practitioners may need to consider assisted migration and other “prestoration” 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,

& Advisor, 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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Author Contributions

KB lead the writing of the manuscript, performed fieldwork, lab work, and analyses. BB developed the project idea and conceptual framework along with KB and SM and contributed to data analyses and writing. CH contributed to writing and editing. All authors substantially contributed to manuscript drafts and correspondence.

References

Ackerly, D. D. (2003). Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments. *International Journal of Plant Sciences*, *164,* S164–S184.

Alexander, J. M., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipel, T., … Walsh,

N. (2011). Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(2), 656–661. doi:10.1073/pnas.1013136108

Balazs, K. R., Kramer, A. T., Munson, S. M., Talkington, N., Still, S., & Butterfield, B. J. (2020). The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes. *Ecological Applications*, *0*(0), 1–7. doi:10.1002/eap.2110

Berdugo, M., Soliveres, S., Kéfi, S., & Maestre, F. T. (2018). *The interplay between facilitation and habitat type drives spatial vegetation patterns in global drylands*. *Ecography*. doi:10.1111/ecog.03795

Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*. doi:10.1111/1365-2745.12003

Birouste, M., Zamora-Ledezma, E., Bossard, C., Pérez-Ramos, I. M., & Roumet, C. (2014). Measurement of fine root tissue density: A comparison of three methods reveals the potential of root dry matter content. *Plant and Soil*, *374*(1–2), 299–313. doi:10.1007/s11104-013-1874-y

Bradford, J. B., Schlaepfer, D. R., Lauenroth, W. K., & Palmquist, K. A. (2020). Robust ecological drought projections for drylands in the 21st century. *Global Change Biology*, (February), 1–14. doi:10.1111/gcb.15075

Butterfield, B. J. (2015). Environmental filtering increases in intensity at both ends of climatic gradients, though driven by different factors, across woody vegetation types of the southwest USA. *Oikos*, *124*(10), 1374–1382. doi:10.1111/oik.02311

Butterfield, B. J., & Callaway, R. M. (2013). A functional comparative approach to facilitation and its context dependence. *Functional Ecology*, *27*(4), 907–917. doi:10.1111/1365-2435.12019

Butterfield, B. J., Copeland, S. M., Munson, S. M., Roybal, C. M., & Wood, T. E. (2017). Prestoration: using species in restoration that will persist now and into the future. *Restoration Ecology*. doi:10.1111/rec.12381

Butterfield, B. J., & Munson, S. M. (2016). Temperature is better than precipitation as a predictor of plant community assembly across a dryland region. *Journal of Vegetation Science, 27*(5), 938–947. doi:10.1111/jvs.12440

Cadotte, M. W., & Tucker, C. M. (2017). Should Environmental Filtering be Abandoned? *Trends in Ecology and Evolution*, *32*(6), 429–437. doi:10.1016/j.tree.2017.03.004

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*(7), 693–715. doi:10.1111/j.1461-0248.2009.01314.x

Cingolani, A. M., Cabido, M., Gurvich, D. E., Renison, D., & Díaz, S. (2007). Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits? *Journal of Vegetation Science*, *18*(6), 911–920. doi:10.1111/j.1654-1103.2007.tb02607.x

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological*

Monographs, *79*(1), 109–126.

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A Trait-Based Test for Habitat Filtering : Convex Hull Volume. *Ecology*, *87*(6), 1465–1471. doi:10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Coyle, J. R., Halliday, F. W., Lopez, B. E., Palmquist, K. A., Wilfahrt, P. A., & Hurlbert, A. H. (2014). Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in Eastern North American tree communities. *Ecography*, *37*(9), 814–826. doi:10.1111/ecog.00473

Craven, D., Hall, J. S., Berlyn, G. P., Ashton, M. S., & van Breugel, M. (2018). Environmental filtering limits functional diversity during succession in a seasonally wet tropical secondary forest. *Journal of Vegetation Science*, *29*(3), 511–520. doi:10.1111/jvs.12632

de Bello, F., Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F., & Thuiller, W. (2013a). Hierarchical effects of environmental filters on the functional structure of plant communities: A case study in the French Alps. *Ecography*. doi:10.1111/j.1600-0587.2012.07438.x

de Bello, F., Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F., & Thuiller, W. (2013b). Hierarchical effects of environmental filters on the functional structure of plant communities: A case study in the French Alps. *Ecography*, *36*(3), 393–402. doi:10.1111/j.1600-0587.2012.07438.x

Dwyer, J. M., & Laughlin, D. C. (2017). Constraints on trait combinations explain climatic drivers of biodiversity: the importance of trait covariance in community assembly. *Ecology Letters*, 872–882. doi:10.1111/ele.12781

Ferguson, S. D., Nowak, R., & Advisor, T. (2012). Investigations of physiological and competitive relationships of Elymus species related to establishment in the Great Basin, USA.

Fraaije, R. G. A., ter Braak, C. J. F., Verduyn, B., Verhoeven, J. T. A., & Soons, M. B. (2015). Dispersal versus environmental filtering in a dynamic system: Drivers of vegetation patterns and diversity along stream riparian gradients. *Journal of Ecology*, *103*(6), 1634–1646. doi:10.1111/1365-2745.12460

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution*, *23*(12), 695–703. doi:10.1016/j.tree.2008.07.013

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., … Wright, J. (2016). Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews*.

Goldberg, D., & Novoplansky, A. (1997). On the Relative Importance of Competition in Unproductive Environments. *Journal of Ecology*, *85*(4), 409–418.

Grime, J. P. (1977). Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist*, *111*(982), 1169–1194.

Grime, J. Philip. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*. doi:10.1111/j.1654-1103.2006.tb02444.x

Grime, Jo P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, 1169–1194.

Havrilla, C. A., Munson, S. M., McCormick, M. L., Laushman, K. M., Balazs, K. R., & Butterfield, B. J. (2020). RestoreNet: An emerging restoration network reveals controls on seeding success across dryland ecosystems. *Journal of Applied Ecology*, (June), 1–12. doi:10.1111/1365-2664.13715

Hijmans, R., Phillips, S., Leathwick, J., & Elith, J. (2015). dismo: Species distribution modeling. (R package). Retrieved from https://cran.r-project.org/package=dismo

Joseph Travis. (1989). The role of optimizing selection in natural populations. *Annual Review of Ecology and Systematics*, *20*(279–96).

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, *3*(2), 157–164.

Koutroulis, A. G. (2019). Dryland changes under different levels of global warming. *Science of the Total Environment*, *655*, 482–511. doi:10.1016/j.scitotenv.2018.11.215

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 592–599. doi:10.1111/1365-2435.12345

Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., & Laughlin, D. C. (2016). Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, *104*(5), 1299–1310. doi:10.1111/1365-2745.12562

Laughlin, D. C., Joshi, C., Richardson, S. J., Peltzer, D. A., Mason, N. W. H., & Wardle, D. A. (2015). Quantifying multimodal trait distributions improves trait-based predictions of species abundances and functional diversity. *Journal of Vegetation Science*, *26*(1), 46–57. doi:10.1111/jvs.12219

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F. T., Maire, V., de Bello, F., Fonseca, C. R., … Liancourt, P. (2017). Testing the environmental filtering concept in global drylands. *Journal of Ecology*, *105*(4), 1058–1069. doi:10.1111/1365-2745.12735

Lebrija-trejos, E., Pérez-garcía, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system Published by : Ecological Society of America Functional traits and environmental drive community filtering in a species-rich tropical system assembly. *Ecology*, *91*(2), 386–398. doi:10.1890/08-1449.1

Lhotsky, B., Kovács, B., Ónodi, G., Csecserits, A., Rédei, T., Lengyel, A., … Botta-Dukát, Z. (2016). Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *Journal of Ecology*, *104*(2), 507–517. doi:10.1111/1365-2745.12532

Li, Y., Shipley, B., Price, J. N., Dantas, V. de L., Tamme, R., Westoby, M., … Batalha, M. A. (2018). Habitat filtering determines the functional niche occupancy of plant communities worldwide. *Journal of Ecology*, *106*(3), 1001–1009. doi:10.1111/1365-2745.12802

Loranger, J., Munoz, F., Shipley, B., & Violle, C. (2018). What makes trait–abundance relationships when both environmental filtering and stochastic neutral dynamics are at play? *Oikos*, *127*(12), 1735–1745. doi:10.1111/oik.05398

Lusk, C. H., & Laughlin, D. C. (2017). Regeneration patterns, environmental filtering and tree species coexistence in a temperate forest. *New Phytologist*, *213*(2), 657–668. doi:10.1111/nph.14168

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 377–385.

Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., … Louault, F. (2012). Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist*, *196*(2), 497–509. doi:10.1111/j.1469-8137.2012.04287.x

May, F., Giladi, I., Ristow, M., Ziv, Y., & Jeltsch, F. (2013). Plant functional traits and community assembly along interacting gradients of productivity and fragmentation. *Perspectives in Plant Ecology, Evolution and Systematics*, *15*(6), 304–318. doi:10.1016/j.ppees.2013.08.002

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

Menezes, B. S., Martins, F. R., Carvalho, E. C. D., Souza, B. C., Silveira, A. P., Loiola, M. I. B., & Araújo, F. S. (2020). Assembly rules in a resource gradient: Competition and abiotic filtering determine the structuring of plant communities in stressful environments. *PLoS ONE*, *15*(3), 1–19. doi:10.1371/journal.pone.0230097

Michalet, R. (2006). Is facilitation in arid environments the result of direct or complex interactions? *New Phytologist*, *169*(1), 3–6. doi:10.1111/j.1468-8137.2006.01617.x

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827). doi:10.1098/rspb.2015.2434

Nunes, A., Köbel, M., Pinho, P., Matos, P., Bello, F. de, Correia, O., & Branquinho, C. (2017). Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. *Agricultural and Forest Meteorology*, *239*, 176–184. doi:10.1016/j.agrformet.2017.03.007

Pierce, S., Brusa, G., Vagge, I., & Cerabolini, B. E. L. (2013). Allocating CSR plant functional types: The use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology*, *27*(4), 1002–1010. doi:10.1111/1365-2435.12095

Read, Q. D., Moorhead, L. C., Swenson, N. G., Bailey, J. K., & Sanders, N. J. (2014). Convergent effects of elevation on functional leaf traits within and among species. *Functional Ecology*. doi:10.1111/1365-2435.12162

Rolhauser, A. G., Nordenstahl, M., Aguiar, M. R., & Pucheta, E. (2019). Community-level natural selection modes: A quadratic framework to link multiple functional traits with competitive ability. *Journal of Ecology*, *107*(3), 1457–1468. doi:10.1111/1365-2745.13094

Rolhauser, A. G., & Pucheta, E. (2017). Directional, stabilizing, and disruptive trait selection as alternative mechanisms for plant community assembly. *Ecology*, *98*(3), 668–677. doi:10.1002/ecy.1713

Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, *94*(3), 451–459. doi:10.3732/ajb.94.3.451

Swenson, N. G., Enquist, B. J., Pither, J., Kerkhoff, A. J., Boyle, B., Weiser, M. D., … Nolting, K. M. (2012). The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography*, *21*(8), 798–808. doi:10.1111/j.1466-8238.2011.00727.x

Wang, R., Wang, Q., Liu, C., Kou, L., Zhao, N., Xu, Z., … He, N. (2018). Changes in trait and phylogenetic diversity of leaves and absorptive roots from tropical to boreal forests. *Plant and Soil*, *432*(1–2), 389–401. doi:10.1007/s11104-018-3816-1

Weiher, E., & Keddy, P. A. (1995a). Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. *Oikos*, *74*(1), 159–164.

Weiher, E., & Keddy, P. A. (1995b). The Assembly of Experimental Wetland Plant Communities. *Oikos*, *73*(3), 323–335.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. doi:10.1038/nature02403

Tables

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 belowground biomass to aboveground biomass	investment in above or belowground growth and storage
Specific Leaf Area (mm2/mg)	SLA	area of fresh leaf in square millimeters 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 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 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 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 weight of dried root tissue (g)	investment in exploratory roots versus conserving energy (absorptive roots)
Fine Root Dry Matter Content (mg/g)	RDMCf	weight of dried root tissue (mg) divided by weight of fresh root tissue (g)	proxy for root tissue density (absorptive roots)

Table 1. *Functional traits used in study and descriptions of how they were measured and their ecological significance.*

Site	**Ecoregion level IV**	**Soil Texture**	**Lat**	**Long**	**Elevation (m)**	**Mean Annual Temp (°C)**	**Total Annual Precip. (mm)**	**Monsoon Precip. (% of annual)**
La Sal	Semiarid benchlands and canyonlands	Sandy Loam	38.29	-109.07	2233	8.9	394	32
Babbitt PJ	Conifer woodlands and savannahs	Clay	35.6	-111.94	1983	9.6	490	38
Canyonlands	Semiarid benchlands and canyonlands	Sandy Loam	38.07	-109.57	1655	11.3	280	32
Flying M	Conifer woodlands and savannahs	Loam	34.84	-111.11	1873	10.8	366	44
Bar T Bar	Semiarid tablelands	Sandy Loam	34.89	-111.06	1783	11.2	320	44
Petrified Forest	NE AZ Shrub-Grasslands	Sandy Clay Loam	34.91	-109.81	1645	12.9	229	45

Spider Web	NE AZ Shrub-Grasslands	Sandy Loam	35.64	-111.48	1586	13.6	206	44
Montezuma Well	Lower Mogollon Transition	Sandy Loam	34.65	-111.76	1140	16.5	373	40

Table 2. *Site characteristics, existing plant community, soil texture, location, elevation, and climate variables calculated from PRISM 30-year averages (1990-2019). Color-coded by species pool (blue – cool, yellow – intermediate, red – warm).*

cool species pool		
species	growth form	MAT 95
Pseudoroegneria spicata	grass	11.4
Hedysarum boreale	forb	11.7
Elymus trachycaulis	grass	5.9
Elymus wawawaiensis	grass	12.0
Leymus cinereus	grass	12.1
Hesperostipa comata	grass	12.2
Sphaeralcea grossulariifolia	forb	12.7

intermediate species pool		
species	growth form	MAT 95
Linum lewisii	forb	13.3
Heliomeris multiflora	forb	13.7
Bromus marginatus	grass	14.2
Pascopyrum smithii	grass	14.2
Pleuraphis jamesii	grass	15.1
Elymus elymoides	grass	15.5
Achillea millefolium	forb	15.5

warm species pool		
species	growth form	MAT 95
Achillea millefolium	forb	15.5
Dalea candida	forb	15.7
Bouteloua gracilis	grass	15.9
Poa secunda	grass	16.7
Sporobolus cryptandrus	grass	16.9
Machaeranthera tanacetifolia	forb	17.0
Bouteloua eriopoda	grass	17.1

Linum lewisii	forb	13.3
Heliomeris multiflora	forb	13.7
Bromus marginatus	grass	14.2
Pascopyrum smithii	grass	14.2
Pleuraphis jamesii	grass	15.1
Elymus elymoides	grass	15.5
Achillea millefolium	forb	15.5
Dalea candida	forb	15.7
Bouteloua gracilis	grass	15.9

Dalea candida	forb	15.7
Bouteloua gracilis	grass	15.9
Poa secunda	grass	16.7
Sporobolus cryptandrus	grass	16.9
Machaeranthera tanacetifolia	forb	17.0
Bouteloua eriopoda	grass	17.1
Krascheninnikovia lanata	forb	17.4
Penstemon palmeri	forb	18.1
Achnatherum hymenoides	grass	18.3

Krascheninnikovia lanata	forb	17.4
Penstemon palmeri	forb	18.1
Achnatherum hymenoides	grass	18.3
Bouteloua curtipendula	grass	18.7
Asclepias tuberosa	forb	19.4
Aristida purpurea	grass	21.1
Baileya multiradiata	forb	21.4
Hilaria mutica	grass	21.5
Senna covesii	forb	21.7

Table 3. *Species p*ools. Each site has 16 species with unique species in blue and red, and shared species between cool and intermediate in green, cool, intermediate, and warm in yellow, and intermediate and warm in orange. MAT95 values represent 95th percentile of species mean annual temperature distributions after removing outlier

Magnitude

Model	Predictor	df	SS	MS	F	p
abs(sesCoV) ~ pool*trait	pool	2	63.1	31.6	2.2	0.123
	trait	7	1060.2	151.5	10.6	<0.001
	pool:trait	14	225.7	16.1	1.1	0.363
abs(sesCWM) ~ pool*trait	pool	2	147.2	73.6	7.3	0.002
	trait	7	382.9	54.7	5.4	<0.001
	pool:trait	14	193.7	13.8	1.4	0.209

Direction

Model	Predictor	df	SS	MS	F	p
sesCoV ~ pool*trait	pool	2	311.2	155.6	5.7	0.007
	trait	7	1701.8	243.1	8.9	<0.001
	pool:trait	14	790.7	56.5	2.1	0.038
sesCWM ~ pool*trait	pool	2	59.3	29.7	1.6	0.207
	trait	7	1537.7	219.7	12.2	<0.001
	pool:trait	14	727.2	52.0	2.9	0.004

Table 4. *ANOVA results for magnitude and direction of SES Coefficient of Variation (CoV) and Community-weighted Mean (CWM).*

Figures

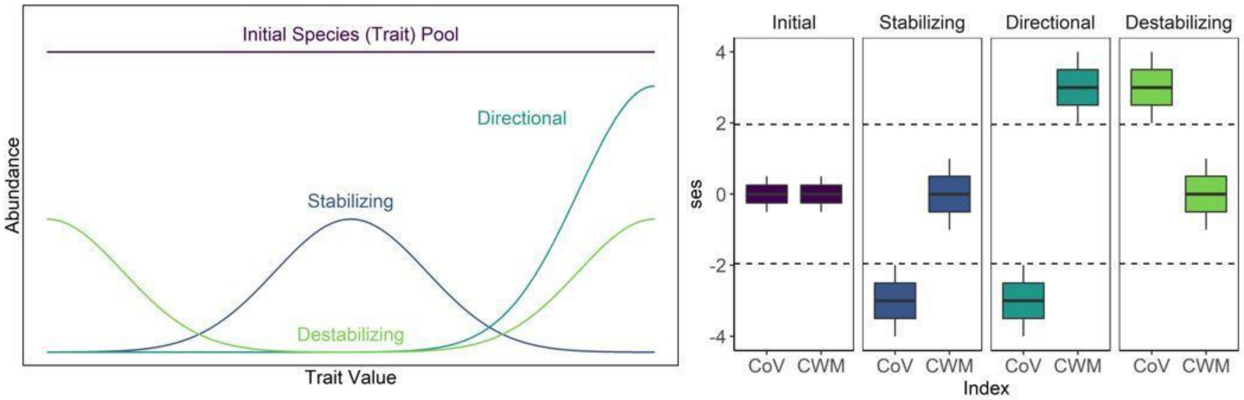

Figure 1. *Conceptual diagram of theoretical selection types.* To investigate the patterns of trait abundance, SES of functional composition indices CoV and CWM was used on hypothetical communities displaying stabilizing (n-shaped), directional, or destabilizing (u-shaped) selection. Stabilizing selection within a community reflects a lower CoV than expected (less than -1.96) and CWM is unchanged, directional selection reflects lower CoV than expected and CWM is significantly different from null expectation, while destabilizing selection reflects greater sesCoV than expected and sesCWM is unchanged. Each hypothetical distribution contains the same area under the curve representing the number of surviving individuals in a community.

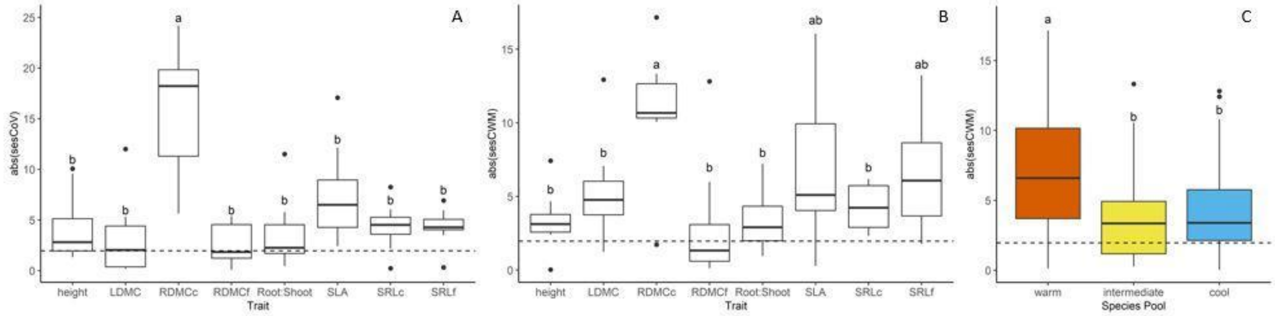

Figure 2. *Results from Tukey's Honest Significant Difference Test for magnitude of a) Coefficient of Variation (CoV), b) and Community-weighted Mean (CWM), and c) species pool. X-axis label for traits matches abbreviation found in Table 1.*

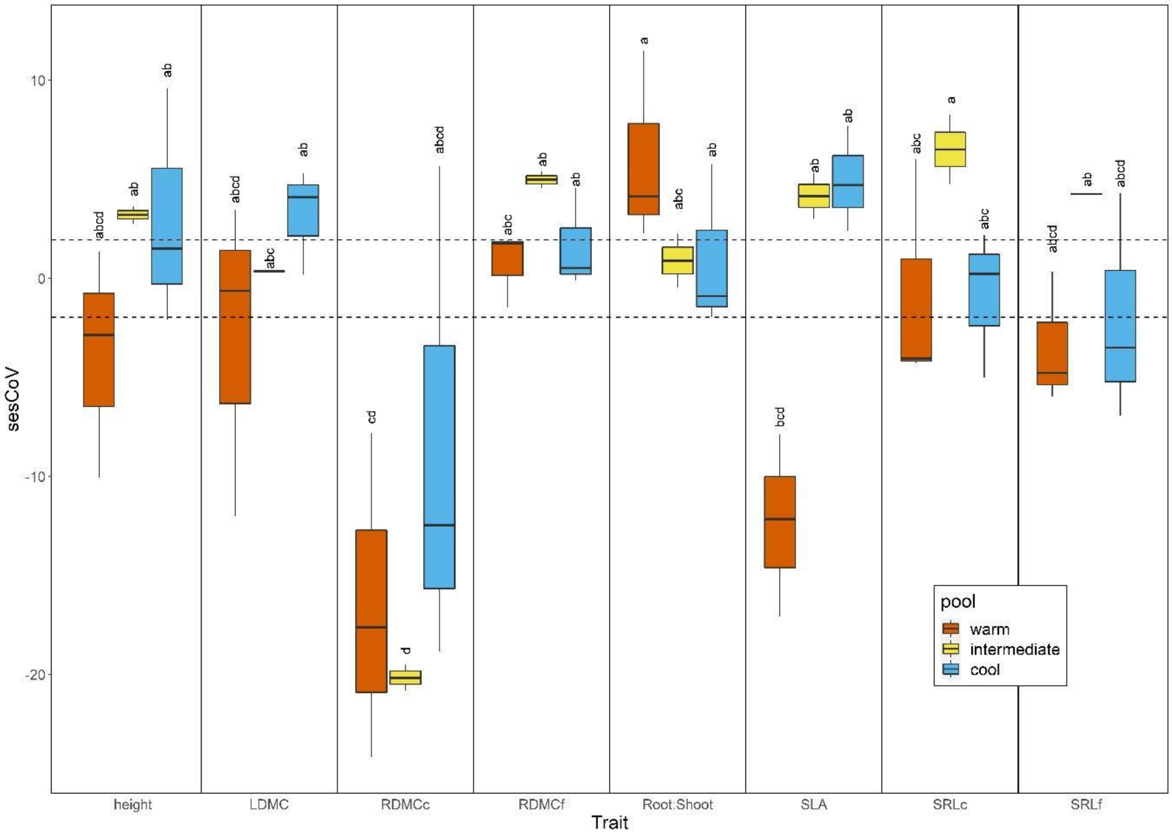

Figure 3A. Standardized effect size (SES) values for coefficient of variation (CoV) in warm, intermediate, and cool species pools. Points beyond dashed lines represent a significantly different SES greater than 1.96 or less than -1.96. Different letters represent significant differences among interactions between traits and species pools as determined by a Tukey's Honest Significant Difference Test.

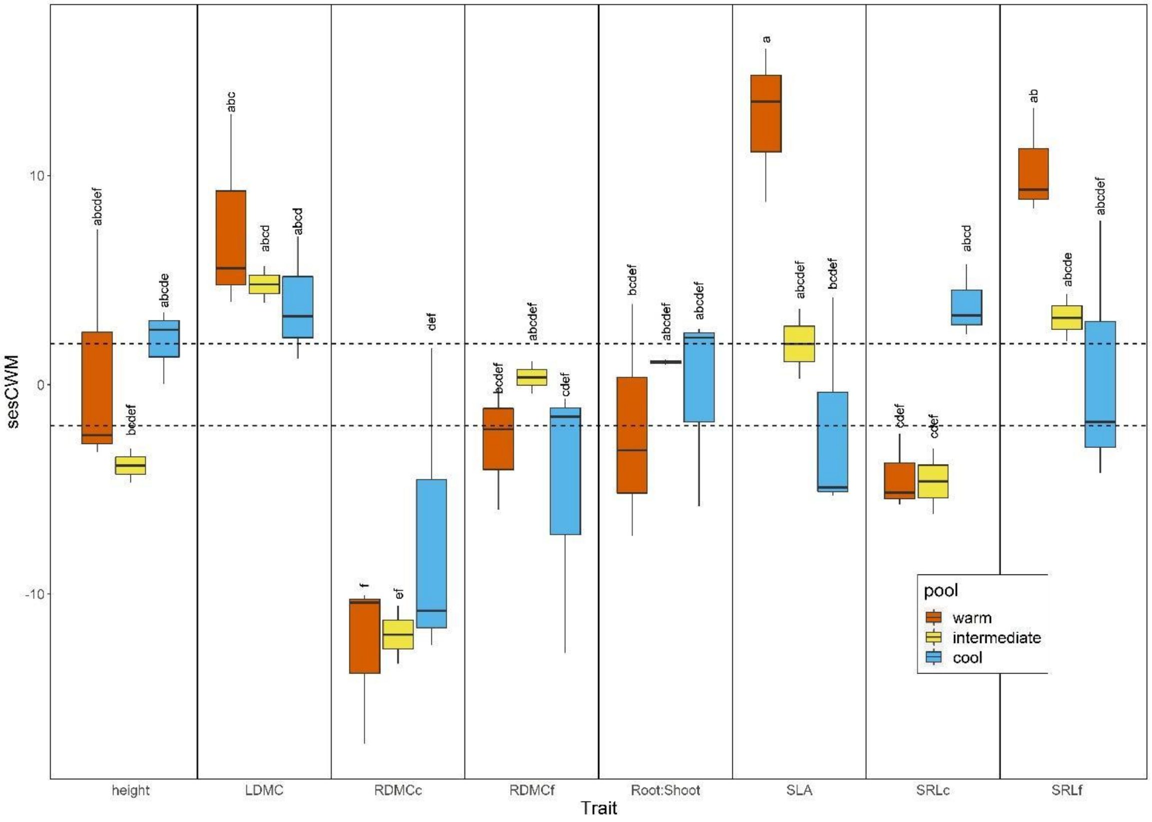

Figure 3B. Standardized effect size (SES) values for *community weighted mean (CWM)* in warm, intermediate, and cool species pools. Points beyond dashed lines represent a significantly different SES greater than 1.96 or less than -1.96. Different letters represent significant differences among interactions between traits and species pools as determined by a Tukey's Honest Significant Difference Test.

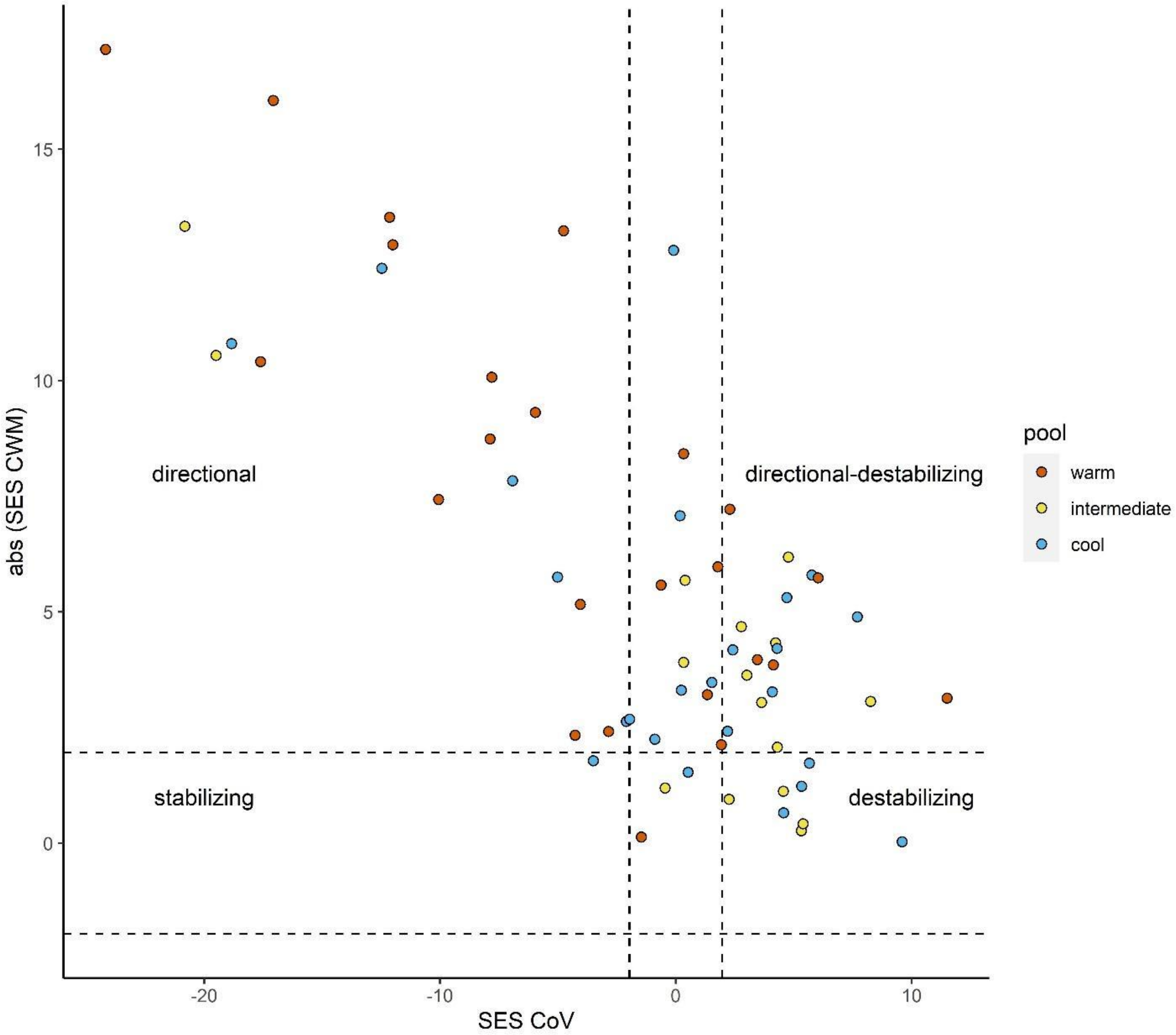

Figure 4. *Selection types across experimental communities.* Standardized effect size (SES) values for coefficient of variation (CoV) and absolute values of SES for community weighted mean (CWM). Dashed lines represent SES of 1.96 or -1.96, points beyond this line are significantly different than expected.

4. Restoration of primary productivity in drylands supports weed suppression and erosion mitigation

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Abstract

1. Drylands, which account for nearly half the world's terrestrial surface, are losing vital ecosystem services such as primary productivity, invasive plant suppression, and erosion mitigation. By restoring native plant communities, we can rebuild these services to mitigate future stressors. However, research is lacking in the context of restoration concerning the impact of species on rebuilding ecosystem processes including biomass accumulation and soil stabilization. Plant functional trait-based approaches have the potential to improve species selection to accomplish these objectives where success has been limited.
2. Abiotic factors and functional composition of plant communities each contribute to ecosystem functioning. However, in highly disturbed dryland sites where restoration is needed, the amount of restored aboveground biomass may determine the impact of

functional composition. While primary productivity is a targeted ecosystem service, it additionally supports the existence of other regulating services; The impact of functional composition is likely low when little vegetation is present but will likely have a greater influence as the amount of vegetation increases.

3. To elucidate the impacts of restored species on ecosystem functions of concern, we planted perennial grass and forb species across a network of degraded dryland sites. After two growing seasons, we measured indicators of ecosystem services including primary productivity, weed suppression, and erosion mitigation. Using linear models, we determined how abiotic site conditions, dominant trait values, functional diversity, and species identity contributed to ecosystem functioning.
4. We found that abiotic conditions predicted all measured indicators of ecosystem function, but dominant trait values and species identity explained additional variation for nearly all indicators, while functional diversity did not explain additional variation at this early stage of restoration. We show that a combination of drought tolerant and acquisitive trait strategies is important to ensure greater restored biomass. Additionally, our results support the idea that primary productivity is a supporting ecosystem service in that interactive effects of biomass and community-weighted trait values in the restored communities determine weed suppression, and indicators of erosion mitigation.
5. Synthesis: This study provides a controlled experimental approach to test the effect of plant functional composition on ecosystem properties in drylands recovering from disturbance. We have shown that the incorporation of trait-based approaches can aid

in species selection in active management efforts to target and rebuild ecosystem functions.

Key Words: dryland, restoration, biodiversity-ecosystem functioning, biomass, productivity, community-weighted mean, weed suppression, infiltration, soil stability

Introduction

Drylands (arid and semi-arid ecosystems) are home to 39% of the global human population, and face the loss of key ecosystem functions and services due to disturbance (Koutroulis, 2019; Sala & Paruelo, 1997). Many human impacts reduce soil stability in drylands, spread weedy species, and reduce native plant biomass, making these landscapes more prone to wind and water erosion (Blanco-Canqui & Lal, 2010; Munson, Belnap, & Okin, 2011). This loss of key ecosystem services can accelerate degradation and drive increased risk of extreme fires, dust storms, and flooding which have costly socioeconomic effects. The goal of many restoration efforts is to rebuild ecosystem function to return vital services of erosion mitigation and weed suppression (Kollmann et al., 2016).

Restoring plant biomass in drylands can be especially challenging since these areas have strong barriers to plant survival; however, trait-based restoration research can improve the ability to select species for restoration that match environmental conditions (Balazs et al., 2020). The establishment of a productive restored plant community is influenced by abiotic factors and the functional traits of the plants used. While plant functional traits impact numerous ecosystem services such as erosion control and weed suppression, primary productivity is a vital ecosystem service that supports all other ecosystem services (Garland et al., 2020). As aboveground productivity is restored, plant functional composition is likely to have a greater impact on weed suppression and erosion mitigation. Thus, in order to restore plant communities to provide these ecosystem services, we need to investigate the role of plant traits in contributing to the restoration of aboveground productivity and investigate the role of restored productivity in mediating the impact of plant traits on weed suppression and erosion mitigation (Fig 1).

Abiotic factors such as precipitation, temperature, and humidity play an important role in mediating biodiversity-ecosystem functioning across landscapes (Díaz et al., 2007). Especially in drylands, factors that mediate soil moisture and atmospheric water demand will control plant activity as well as plant adaptations to prevent water loss (citation). Soil moisture can often predict variability in plant cover, for example a lower amount of soil moisture resulted in a reduction in perennial grass cover on the Colorado Plateau (Gremer, Bradford, Munson, & Duniway, 2015). Climate variables that influence soil moisture, such as vapor pressure deficit and dewpoint temperature, likely influence ecosystem function (Kimball, Running, & Nemani, 1997, Liu et al., 2020; Seager et al., 2015). In addition to mediating productivity in vulnerable systems, these climate factors can also directly influence soil physical processes, for example high temperatures and low precipitation can reduce soil aggregate stability (Sanchis, Torri, Borselli, & Peosen, 2009). While these abiotic factors greatly impact ecosystem functioning, plant community composition often explains additional variation, necessitating the application of a stepwise framework to understand the role of plant species and traits (such as that outlined in Díaz et al.,2007).

Within the limits of abiotic constraints, the functional composition of plant communities often plays a large role in predicting ecosystem functions (Díaz et al., 2007). According to Grime’s mass-ratio hypothesis, the traits of the most abundant species in a community will have the greatest impact on ecosystem functions (Grime, 1998). Community-weighted mean (CWM) trait value is a functional composition index used to weight trait values by species abundance in a community that can be used to predict community impact on ecosystem processes (Díaz et al., 2007; Violle et al., 2007). Community-weighted mean leaf traits often predict plant productivity, for example, higher CWM leaf nitrogen resulted in greater aboveground biomass in a subalpine grassland (Díaz et al., 2007). Belowground traits can also predict ecosystem functioning, for example, greater CWM root density can lead to higher soil stability (Ali, Reineking, & Münkemüller, 2017; Erktan et al., 2016).

While CWM trait values typically have a large impact on ecosystem functioning, the next steps are evaluating the contributions of functional diversity and idiosyncratic species to the explanation of additional variation in ecosystem functioning (Díaz et al., 2007). Diversity is often targeted to improve ecosystem function and, indeed, positive correlations between diversity and ecosystem functioning have been demonstrated in many established communities (Cardinale et al., 2012). The positive effects of diversity are often linked to niche complementarity, reflecting the optimization of diverse functional strategies for resource acquisition (Díaz & Cabido, 2001). Functional diversity often is important in high productivity environments where productivity can be maximized in some communities by increasing species diversity (Tilman, 1997). There is also evidence that root trait diversity and individual species have been linked to the improvement of soil physical attributes such as aggregate stability in high productivity environments (Ali et al., 2017; Gould et al., 2016). In addition to diversity, idiosyncratic effects of individual species or groups, such as legumes fixing nitrogen, may additionally explain variation in ecosystem processes that is not always captured by measured functional traits (Lawton, 1994, Clark et al. 2012). Growing species in monocultures and mixtures can help elucidate the contribution of individual species versus complementarity effects. Identifying the specific aspects of functional diversity that influence particular ecosystem processes, rather than general metrics of taxonomic diversity, can help develop targeted species mixes for local restoration objectives.

Many previous trait-based studies have been conducted in well-established plant communities in high productivity environments, where nuanced effects of trait diversity have time to develop. Early successional communities and communities reestablishing through active restoration are instances where establishment of biomass may play a more critical role in re-establishing other ecosystem functions. For example, biodiversity–ecosystem function relationships changed through succession in the Arctic, where diversity became a more important driver of soil carbon stocks later in successional stage (Mori, Osono, Cornelissen, Craine, & Uchida, 2017). Additionally, soil aggregate stability has been shown to increase through succession, linked to greater diversity and shoot biomass (Erktan et al., 2016). The amount of vegetation changes through time in these scenarios. Thus the role of biomass is an important factor to consider when looking into the impact of functional composition on ecosystem properties. Building on similar observations, "the vegetation quantity hypothesis" was first outlined and tested in restoration of tropical forests in Mexico where biomass was found to be a stronger predictor of ecosystem functioning during early succession than functional diversity or CWM trait values (Lohbeck et al., 2015). In another test of the vegetation quantity hypothesis, restoration of biomass was found to be important for targeting ecosystem multifunctionality in a semi-arid region of Brazil (Teixeira, Oliveira, Krah, Kollmann, & Ganade, 2020). We argue that this hypothesis is important for any type of low productivity and early successional community, including dryland restoration sites where establishment of biomass will have a strong impact on ecosystem processes. Therefore, the addition of the vegetation quantity hypothesis to the classic Díaz et al., 2007 framework may be applied to assessments of biodiversity-ecosystem functioning relationships in dryland restoration. This framework can help improve the restoration of native biomass in dryland communities and help to understand the role of restored plant biomass in regulating the effects of functional composition on dryland ecosystem processes.

Relevant trait-based restoration experiments are particularly lacking in drylands, despite an urgent need to improve restoration prescriptions for rebuilding ecosystem functions and the added difficulty of overcoming barriers to plant establishment in areas with high temperatures and/or low water availability. Our outplanting experiment occurred at eight sites within a dryland network of restoration sites (RestoreNet - Havrilla et al., 2020) on the Colorado Plateau in the United States where we installed a large array of native perennial grass and forb species with known functional trait values in 2018. Our networked study provides a controlled experimental approach to determine the effect of plant functional composition on the improvement of ecosystem processes in disturbed drylands. Outplanting species across a network of distributed sites allowed us to investigate the contribution of environmental variation to driving the rate of ecosystem recovery. We monitored restored biomass, weed cover, and soil processes that characterize function and stability, including soil penetration resistance, aggregate stability, shear strength, and water infiltration. We used these data in stepwise linear models to investigate 1) whether productivity, as indicated here by restored biomass, is explained by abiotic factors and/or functional composition and, 2) how abiotic factors, restored biomass, and functional composition interact to predict regulating services including weed suppression and erosion mitigation (fig. 1). Application of these results can aid land managers in trait-based species selection for restoration of native plant communities to rebuild vital ecosystem services.

Methods

Study Sites

Our study occurred at a subset of eight RestoreNet sites located on the Colorado Plateau in the southwestern United States (Havrilla et al., 2020, Balazs et al. In Revision; https://usgs.gov/sbsc/ramps). The Colorado Plateau is a high-elevation semi-arid region. Our field sites experience a range in mean annual temperature of 8.8-16.5 °C and mean annual precipitation of 206-491mm (Balazs et. al unpublished). Approximately 32-45% of yearly precipitation comes in the summer (July-September) during the North American Monsoon season. All sites have a history of disturbance, therefore there was minimal perennial vegetation with extensive bare ground and non-native annual species cover prior to installation of the experiment. For the duration of this study, we extracted daily interpolated climate variables related to precipitation, temperature, and humidity (precipitation, mean, minimum, and maximum temperatures, mean dewpoint temperature, and minimum and maximum vapor pressure deficit) at 4km resolution from PRISM (prism.oregonstate.edu) (Table 1).

RestoreNet Biodiversity-Ecosystem Functioning Experiment

We installed an experimental planting treatment in 2018 to assess biodiversity-ecosystem functioning effects of the restored communities. Twenty-nine perennial grass and forb species native to the Colorado Plateau, selected based on their prevalence in restoration efforts in the region (https://wri.utah.gov/wri/), were planted into monocultures and polycultures, with a subset of 16 species used at each site that were suited for the temperature at each site (see appendix S# for planting details). Survivorship of individual outplants was monitored and previously reported in Balazs et al. (In Revision). In each site there were 36 plots, including four control, 16 monoculture, and 16 polyculture treatments. Control plots received the same disturbance from digging that planted plots received and the mono versus polyculture treatments isolated the impact of diversity versus individual species. Within each 2x2 m plot there were 36 plants, resulting in a total of 9,216 individuals planted across all eight sites. Each species was present in one monoculture plot and in four polyculture plots which contained nine individuals of four species (Fig. S1). Species were assigned to polyculture plots using an algorithm that ensured each species co-occurred with every other species from that site in at least one polyculture, which also ensured that no two polycultures had the same four-species combination. Plants were spaced 30.5 cm apart in a grid 23.8 cm from the edge of the plot, producing interspaces with four surrounding plants that were used for many of the sub-plot soil measurements. These interspaces were left bare and were undisturbed throughout the experiment until the final sub-plot soil measurements were collected at the end of the 2020 growing season. Both plot and sub-plot level measurements were used to measure indicators of ecosystem function.

Functional Trait Measurements

The twenty-nine species used in this experiment were grown in the greenhouse during 2017 and 2018 for destructive trait-screening. Ten replicates of each species were grown to vegetative maturity in 3.79-liter pots with a fired clay growing medium (Turface® Pro League®) at the Research Greenhouse at Northern Arizona University. This growing medium was chosen to facilitate complete removal of the root systems for analysis. To measure specific leaf area (SLA) and leaf dry matter content (LDMC), five fully developed leaves were taken from each plant and immediately weighed, scanned on a flatbed scanner at 300 dpi, and oven dried. The remainder of the aboveground biomass was additionally dried and used to calculate root to shoot ratio. Roots were then washed to remove growing medium and separated to retrieve samples of lignified coarse roots, and absorptive fine roots (non-lignified with root hairs). Three coarse root samples from each plant were weighed, scanned with a flatbed scanner to calculate root length, then dried to obtain specific root length (SRL) and root dry matter content (RDMC). The fine root samples were weighed, then submerged in water and scanned using the WinRHIZO^{TM} scanner bed software for analysis of root length and finally dried to obtain SRL and RDMC. Leaf area and root length were calculated with WinRHIZO^{TM} image analysis software. The remainder of the belowground biomass was dried and used to calculate root to shoot ratio. See table 2 for detailed description of each trait and its ecological significance. All traits used in our analyses were found to be independent of one another (Balazs et al., In Revision).

Ecosystem Function Measurements

Aboveground Biomass: Plant size was monitored multiple times per growing season from installation until the end of the 2020 growing season. Height and two perpendicular canopy widths were measured on active photosynthetic tissue of living plants (flowering stalks excluded). To prevent destructive harvesting during the ongoing experiment, aboveground biomass was interpolated based on allometric equations for each individual across monitoring dates using plant height from time of monitoring and leaf dry matter content for that species. Height and LDMC were selected as the best predictors of biomass from competing models using traits of greenhouse individuals of the same species and seed source (see table S1). To account for the impact of aboveground biomass through time, while giving more weight to later measurements, time-weighted biomass of a community was calculated as $M_{comm} = \Sigma \frac{(\frac{Mi \times Ti}{T})}{ni}$ where M_{comm} represents the time-integrated biomass of a community, M_i represents the biomass of a plant community (either at the plot level or four-plant interspace level) at the time of measurement, T_i represents the days since planting that this measurement was taken, T represents the total number of days the experiment occurred at a site prior to final measurement, and ni represents the number of times this was monitored at a given site. T and ni allow biomass to be comparable across sites since there was variation in the planting dates and the number of times sites were monitored. Analyses based on samples from interspaces between plants used the functional composition (biomass-weighted) of the 4 surrounding plants for each interspace. While aboveground biomass is the way we assess primary productivity in this study, this measurement was also used to assess the influence of vegetation quantity on other ecosystem processes.

Weed Suppression: To assess how well the restored plant communities suppressed unintended plant species, percent cover of unplanted species per plot was estimated across monitoring dates using visual canopy cover estimates that were calibrated with cover estimation guides (CDFW-CNPS Protocol), and additionally checked against plot photos. It is important to note that our weed cover estimation did not account for weed biomass and that landscape fabric, used to help establish outplants, generally promoted weed growth in the first season. Time-weighted weed cover was calculated using the same method as time-weighted biomass so that cover was weighted by days since planting.

Soil Processes: Soil processes were measured once at the end of the 2020 growing season (2 years of cumulative plant growth) in pre-selected interspaces between four neighboring plants in a plot. Adjustments to interspace sampling location were made if pre-selected interspace had substantial crevices or interspace was otherwise obscured by woody stems or rocks. Water infiltration was measured using the Bottleless Single Ring Infiltration Method (Herrick et al. 2005). Two interspaces per plot were assessed for water infiltration rate (I8, I18, refer to fig.1). Soil aggregate stability was measured to estimate resistance to water and wind erosion. These measurements were done using the Jornada Experimental Range Kit to determine soil stability class (https://jornada.nmsu.edu/files/SoilAggStabKit.pdf)(Herrick et al., 2001). Soil stability was assessed for two interspaces in each plot (I12, I14, refer to fig.1) at two -depths: surface and 25mm subsurface. Soil surface resistance was measured with a pocket penetrometer, (Whalley, To, Kay, & Whitmore, 2007). Two interspaces were assessed for resistance to penetration (I12, I14, refer to fig.1). To assess how restored communities impacted soil cohesion and stability, soil shear strength was measured with a E285 Pocket Vane Shear Tester (https://www.globalgilson.com/pocket-shear-vane-set). Shear strength was assessed in two interspaces in each plot (I3, I23, refer to fig.1).

Preliminary analyses showed that there was a difference in all of the measured indicators of ecosystem functioning: restored biomass, weed cover, and sub-plot soil measurements (Table S2). This analysis was a two-way analysis of variance including site and treatment. Treatment consisted of planted versus control plots, or alternatively plots with low restored biomass (under one gram) versus plots with higher restored biomass. These differences suggest that further analysis of the treatment effect on these measured indicators is justified and that within site variation is outweighed by treatment effects.

Data Analysis

To assess the impact of our restored plant communities on the supporting service of primary productivity, and the regulating services of weed suppression and erosion mitigation, we used aboveground biomass, weed cover and the described soil processes as indicators. Following Diaz et al. 2007, we adhered to a set of steps to assess the hierarchical influence of abiotic and plant functional composition on these indicators. We additionally incorporated the hypothesis that primary productivity is a supporting ecosystem service by including aboveground biomass as an interaction term for the remainder of the measured indicators. Functional composition indices including community-weighted mean (CWM) of each individual trait, and multi-trait indices (Villeger 2008) including functional richness (FRic), functional evenness, (FEve), and functional divergence (FDiv) were calculated with the FD package in R (dbFD function) for each plant community (either for a plot including surviving members of 36 planted individuals or for an interspace including four neighboring individuals, depending on the analysis). Plant communities were-abundance weighted using biomass for each species. CWM trait values were calculated for specific leaf area (SLA), leaf dry matter content (LDMC), leaf CN, root-to-shoot ratio, specific root length (SRL), and root dry matter content (RDMC) for both fine (absorptive) and coarse (conductive) roots separately using greenhouse trait measurements. Time-weighted CWM, FRic, FEve, and FDiv were calculated the same way as biomass. All analyses were done in R version 3.6.3.

We first tested the impact of abiotic factors on restored biomass, using linear models with the following model formula for each abiotic factor: Indicator ~ climate factor. The unit of replication in these models were plot-level restored biomass, plot-level weed cover, or interspace-level soil property measurements. Akaike Information Criterion (AIC) was used to determine which model was the most parsimonious; models with a delta AIC of less than 2 were considered equally parsimonious as the model with the lowest AIC value. This method of AIC selection was applied to the following steps, residuals from the most parsimonious model from each step were used to determine whether further biotic factors explained additional variation.

Residuals from the most parsimonious abiotic variable model(s) were then used in the next step to determine whether additional variation was explained by CWM trait values. To test the impact of community-weighted mean (CWM) trait values on restored biomass, the following model formula was applied for each trait: $\text{Residuals}_{\text{abiotic}}$ ~ CWM trait. For the remaining indicators of weed cover and soil processes (water infiltration rate, surface and subsurface soil stability, surface resistance to penetration, and shear strength), models were structured as: $\text{Residuals}_{\text{abiotic}}$ ~ Biomass * CWM trait.

Residuals from the most parsimonious CWM model(s) were then used in the next step to investigate whether additional variation was explained by functional diversity. The following formula was applied for each functional diversity (FD) index: $\text{Residuals}_{\text{CWM}}$ ~ FD index (biomass), $\text{Residuals}_{\text{CWM}}$ ~ biomass * FD index (remaining indicators). Residuals from the most parsimonious FD model(s) were then used in the final step to determine whether additional variation was explained by idiosyncratic species effects: $\text{Residuals}_{\text{FD}}$ ~ individual species (biomass).

Results

Abiotic factors explained variation for all tested indicators of ecosystem function, though subsurface aggregate stability and resistance to penetration (r-squared: 0.03-0.08) were not as well explained by climate as biomass, weed cover, surface aggregate stability, and shear strength (r-squared:0.14 - 0.41; Table 2). Community-weighted mean trait values further explained variation for all indicators other than subsurface stability. While a large amount of variation in biomass could be attributed to CWM traits (r-squared 0.41), relatively less variation was explained by CWM traits for the other indicators (r-squared values were under 0.10). Functional diversity indices did not explain any additional variation, but species identity did predict additional variation for most indicators (with r-squared values of less than 0.05), except for surface stability and surface resistance to penetration.

Step 1. Abiotic Factors

Aboveground biomass was positively correlated with precipitation and negatively correlated with temperature and vapor pressure deficit (table 3a). Greater maximum vapor pressure deficit was associated with increased weed cover, all precipitation and temperature were also positively correlated with weed cover, though these models were not as parsimonious (table 3b). Infiltration rate was positively correlated with precipitation (table 3c). Increased surface and subsurface aggregate stability were associated with higher temperature (table 3d,e). Surface resistance to penetration was positively correlated with vapor pressure deficit, while precipitation was negatively correlated, though the model with minimum vapor pressure deficit was the most parsimonious (table 3f). Soil shear strength was negatively correlated with precipitation, while all other climate factors besides mean dewpoint temp were positively correlated with shear strength, though these models were not as parsimonious (table 3g).

Step 2. Biomass x Community-Weighted Mean Trait Values

After abiotic factors were taken into account, all CWM trait values were correlated with aboveground biomass, however CWM leaf carbon to nitrogen ratio was the best predictor with a positive correlation to biomass. (table 4, fig.2, fig S2). Weed cover was further explained by an interaction between biomass and CWM leaf dry matter content, with lower weed cover associated with a combination of greater biomass and higher CWM leaf dry matter content (table5a, fig. 3, fig S3). For infiltration rate, an interaction between biomass and CWM fine root specific root length best predicted additional variation, with the highest infiltration occurring with a combination of high biomass and high CWM fine root specific root length, or low biomass and low CWM fine root specific root length. (table5b, fig.4). Additional variation in soil stability was explained by an interaction between biomass and CWM of two traits: fine root dry matter content and leaf carbon to nitrogen ratio (table5c). Surface stability was highest with a combination of low CWM fine root dry matter content and higher aboveground biomass (fig. 5). A combination of higher CWM leaf carbon to nitrogen ratio and greater aboveground biomass also was associated with higher surface stability. However, there was no impact of functional composition on subsurface stability (table 5d). For surface resistance to penetration, further variation was explained by an interaction between biomass and CWM fine root dry matter content where a combination of greater aboveground biomass and higher CWM fine root dry matter content was associated with the greatest resistance (table5e, fig. 6). Shear strength was further explained by an interaction between biomass and CWM leaf carbon to nitrogen ratio, with the greatest shear strength associated with a combination of higher aboveground biomass, and higher leaf carbon to nitrogen ratio (table5f, fig 7).

Step 3. Biomass x Functional Diversity

After biomass and CWM trait values were taken into account, no additional variation was explained by functional richness (FRic), functional evenness, (FEve), or functional divergence (FDiv) (table S3, S4a-f).

Step 4. Idiosyncratic Species Effects

After abiotic factors and functional composition were taken into account, additional variation for most indicators of ecosystem function was explained by unique contributions of species. The presence of *Elymus wawawaiensis* best explained additional variation for plot level biomass even after the interaction between biomass and CWM leaf carbon to nitrogen ratio was taken into account. Seven other grasses including *Achnatherum hymenoides, Hesperostipa comata, Leymus cinereus, and Pascopyrum smithii* were also associated with greater biomass, while three forbs: *Dalea candida*, *Hedysarum boreale*, and *Sphaeralcea grossulariifolia*, were associated with lower plot level biomass (table S5a). The presence of *Heliomeris multiflora*, *Dalea candida*, and *Penstemon palmeri* was associated with increased weed cover, while *Poa secunda* was associated with decreased weed cover (table S5b). Presence of *Hedysarum boreale* was positively associated with higher infiltration, while presence of *Poa secunda* was associated with lower infiltration rate (table S5c). Additionally, the presence of *Aristida purpurea* was associated with higher infiltration rate. While there were no effects of species on surface stability, for subsurface stability the presence of *Achillea millefolium* and *Heliomeris multiflora* were associated with greater subsurface stability (table S5e). Species identity did not further explain any additional variation in surface resistance to penetration. The presence of *Pascopyrum smithii* was associated with reduced shear strength (table S5g).

Discussion

Across our network of restoration plantings, we found that functional composition and idiosyncratic species, but not functional diversity, explained variation seen in ecosystem functions after abiotic factors were considered. Results support the idea that productivity is a supporting service; restored biomass mediated the impact of community-weighted mean trait values on weed suppression and indicators of erosion control, supporting both the vegetation quantity hypothesis and the mass-ratio hypothesis. Functional diversity, however, did not explain much additional variation beyond what was explained by other factors. Our results provide a basis for using a trait-based approach to prescribe restoration treatments for improving ecosystem functions of concern, the selection of community-weighted mean trait values for the species used in restoration treatments can have an impact on rebuilding vital ecosystem functions of concern including primary productivity and erosion mitigation.

Improving primary productivity is a goal of many restoration projects. In drylands, this can be very difficult due to low plant establishment and limiting resources. However, we found that functional composition and species identity predicted aboveground productivity after abiotic factors were considered. The strongest predictor was CWM leaf carbon to nitrogen ratio, though it was predicted by all other traits despite trait independence from one another. These relationships reveal that there are several different strategies for plants to accumulate biomass in water-limited environments, some are related to slower growth and others faster (Reich, 2014). High values of leaf carbon to nitrogen ratio, leaf dry matter content, and root dry matter content are drought tolerant strategies (Kooyers, 2015), yet other high values such as specific leaf area, root to shoot ratio, and specific root length are acquisitive strategies. These biomass results did not necessarily align with survival; for example, many species with low carbon to nitrogen ratios established successfully (such as *Poa secunda* - Balazs et al. unpublished), but their biomass was lower. Restoring for survival versus restoring for primary productivity can involve a trade-off of different approaches, though a combination of drought-tolerant and quicker growing drought escapers contributes both to survival and biomass production. Restoring with biomass in mind is essential for improving ecosystem function in low productivity environments. These results support the vegetation quantity hypothesis and reiterate the need to include biomass as a component in predicting other ecosystem processes.

Restoration of aboveground plant productivity was important for mediating the impact of functional composition on weed suppression and indicators of erosion mitigation (infiltration rate, surface stability, shear strength, and resistance to penetration) after abiotic factors were accounted for. In this study we found that restored aboveground growth inhibited weed growth, but the interaction between aboveground biomass and CWM leaf dry matter content further predicted how restoration efforts can be used to combat weedy species. Additionally, just after three growing seasons, we saw improvements of infiltration, surface stability, shear strength, and resistance to penetration, demonstrating that restoration of aboveground productivity aids in restoring crucial ecosystem processes involved in erosion control. While sites with greater precipitation had faster infiltration rates, plants with greater investment in fine exploratory roots also promoted infiltration when there was a high amount of restored biomass. Restored biomass had a strong effect on surface stability and resistance to penetration, though we found opposing effects of root dry matter content on these soil processes. The interactions between restored biomass and CWM trait value demonstrate that traits typically have a low impact on ecosystem functioning when biomass is low, and their impact is not only amplified but also dependent on the amount of restored biomass. These interactions support the vegetation quantity hypothesis since functional composition only matters when restored biomass is higher.

Though we did not explicitly investigate multifunctionality, results from our study indicate that there are combinations of functional traits that improve both primary productivity and weed suppression. Additionally, since restored biomass mediated the impact of functional composition on soil processes involved in erosion control, improving multiple ecosystem services may be possible with these results. For example, higher leaf carbon to nitrogen ratio promoted greater biomass and also greater soil shear strength, additionally a combination of greater biomass and higher fine root dry matter content promoted increased soil stability and resistance to penetration. Primary productivity is a supporting service, and just by restoring for greater biomass, other ecosystem functions should improve, creating win-win scenarios. This relates to previous findings that increased productivity also increased biological control (Iverson et al., 2014). There is a limit to how many ecosystem functions a community can provide and it is important to study the relationships/tradeoffs in ecosystem services (Bennett, Peterson, & Gordon, 2009). High diversity is not always the answer, some research shows that low levels of diversity can sometimes better support multiple ecosystem services (Storkey et al., 2015). Indeed, our research shows that dominant traits can have a larger control than diversity on many ecosystem services. However, in drylands, landscape-scale diversity can be used to promote multiple ecosystem services as patches that maximize specific functions.

The early stages of a restoration project can be likened to an early successional community. The species that establish first are not always the ones that will persist through time, though they play an important role in altering ecosystem processes and mitigating the impacts of degradation. Increasing weed suppression, infiltration rate and soil stability will promote further colonization; the later successional stage may be where trait diversity plays a larger role. However, in the early stages of restoration these impacts will be diminished if there is not enough restored biomass. It is worth noting that 2018, the year the study was initiated, had above average growing season precipitation across most study sites, which had a positive effect on biomass and increased the strength of traits in influencing ecosystem functions. Nonetheless, improving the ability to restore biomass can be done by selecting species with optimal trait values. While drylands are the focus of this paper, other low productivity environments may also benefit from this assessment. In high productivity environments, the impact of restored biomass may still play a role, but diversity is often more important (Gould et al., 2016). Since the importance of these drivers may change through succession, functional diversity in a seed mix may contribute to additional improvements in functioning later on down the line.

Summary and Management Implications:

After two growing seasons, the restored communities at RestoreNet sites were already improving ecosystem function. The networked experiment allowed us to tease apart the influence of abiotic and biotic factors on indicators of ecosystem functioning. Drought tolerant, yet acquisitive strategies improved biomass production. Community-weighted mean trait values had the greatest impact on weed suppression and soil stability under greater restored biomass, indicating that selecting species for improved biomass production will also improve weed suppression and erosion control. Water infiltration was improved by quick growing, acquisitive roots, and thus inclusion in restoration efforts of species with this strategy may increase soil moisture, thereby making it easier for other species to establish. These results were found at an early stage of restoration suggesting that the effects of functional composition will continue to increase as the community further develops through succession and recruitment. Prioritization of ecosystem functions in restoration will help land managers select which species to use to meet their goals. The trait-based approach presented here improves restoration success in drylands, not only for improving primary production of native plant communities, but also for the rebuilding of weed suppression and erosion mitigation.

References

Ali, H. E., Reineking, B., & Münkemüller, T. (2017). Effects of plant functional traits on soil stability : intraspecific variability matters. *Plant and Soil*, (February). doi:10.1007/s11104-016-3036-5

Balazs, K. R., Kramer, A. T., Munson, S. M., Talkington, N., Still, S., & Butterfield, B. J. (2020). The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes. *Ecological Applications*, *0*(0), 1–7. doi:10.1002/eap.2110

Bennett, E. M., Peterson, G. D., & Gordon, L. J. (2009). Understanding relationships among multiple ecosystem services. *Ecology Letters*, *12*(12), 1394–1404. doi:10.1111/j.1461-0248.2009.01387.x

Blanco-Canqui, H., & Lal, R. (2010). *Principles of soil conservation and management*. *Principles of Soil Conservation and Management*. doi:10.1007/978-1-4020-8709-7

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *489*(7415), 326–326. doi:10.1038/nature11373

Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, *16*(11), 646–655.

doi:10.1016/S0169-5347(01)02283-2

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, *104*(52), 20684–20689. doi:10.1073/pnas.0704716104

Erktan, A., Cécillon, L., Graf, F., Roumet, C., Legout, C., & Rey, F. (2016). Increase in soil aggregate stability along a Mediterranean successional gradient in severely eroded gully bed ecosystems: combined effects of soil, root traits and plant community characteristics. *Plant and Soil*, *398*(1–2), 121–137. doi:10.1007/s11104-015-2647-6

Garland, G., Banerjee, S., Edlinger, A., Miranda Oliveira, E., Herzog, C., Wittwer, R., … van der Heijden, M. G. A. (2020). A closer look at the functions behind ecosystem multifunctionality: A review. *Journal of Ecology*, (April), 1–14. doi:10.1111/1365-2745.13511

Gould, I. J., Quinton, J. N., Weigelt, A., De Deyn, G. B., Bardgett, R. D., & Seabloom, E. (2016). Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecology Letters*, *19*(9), 1140–1149. doi:10.1111/ele.12652

Gremer, J. R., Bradford, J. B., Munson, S. M., & Duniway, M. C. (2015). Desert grassland responses to climate and soil moisture suggest divergent vulnerabilities across the southwestern United States. *Global Change Biology*, *21*(11), 4049–4062. doi:10.1111/gcb.13043

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*(6), 902–910. doi:10.1046/j.1365-2745.1998.00306.x

Havrilla, C. A., Munson, S. M., McCormick, M. L., Laushman, K. M., Balazs, K. R., & Butterfield, B. J. (2020). RestoreNet: An emerging restoration network reveals controls on seeding success across dryland ecosystems. *Journal of Applied Ecology*, (June), 1–12. doi:10.1111/1365-2664.13715

Iverson, A. L., Marín, L. E., Ennis, K. K., Gonthier, D. J., Connor-Barrie, B. T., Remfert, J. L., … Perfecto, I. (2014). Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. *Journal of Applied Ecology*, *51*(6), 1593–1602. doi:10.1111/1365-2664.12334

Kimball, J. S., Running, S. W., & Nemani, R. (1997). An improved method for estimating surface humidity from daily minimum temperature. *Agricultural and Forest Meteorology*, *85*(1–2), 87–98. doi:10.1016/S0168-1923(96)02366-0

Kollmann, J., Meyer, S. T., Bateman, R., Conradi, T., Gossner, M. M., de Souza Mendonï¿½a, M., … Weisser, W. W. (2016). Integrating ecosystem functions into restoration ecology—recent advances and future directions. *Restoration Ecology*, *24*(6), 722–730. doi:10.1111/rec.12422

Kooyers, N. J. (2015). The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Science*, *234*, 155–162. doi:10.1016/j.plantsci.2015.02.012

Koutroulis, A. G. (2019). Dryland changes under different levels of global warming. *Science of the Total Environment*, *655*, 482–511. doi:10.1016/j.scitotenv.2018.11.215

Lawton, J. H. (1994). What Do Species Do in Ecosystems? *Oikos*, *71*(3), 367–374.

Lehman, C. L., & Tilman, D. (2000). Biodiversity, Stability, and Productivity in Competitive

Communities. *The American Naturalist, 156*(5), 534–552. doi:10.1086/303402

Liu, L., Gudmundsson, L., Hauser, M., Qin, D., Li, S., & Seneviratne, S. I. (2020). Soil moisture dominates dryness stress on ecosystem production globally. *Nature Communications*, *11*(1), 1–9. doi:10.1038/s41467-020-18631-1

Lohbeck, M., Poorter, L., Martínez-ramos, M., Bongers, F., Lohbeck, M., Poorter, L., … Bongers, F. (2015). Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology*, *96*(5), 1242–1252.

Mori, A. S., Osono, T., Cornelissen, J. H. C., Craine, J., & Uchida, M. (2017). Biodiversity–ecosystem function relationships change through primary succession. *Oikos*, *126*(11), 1637–1649. doi:10.1111/oik.04345

Munson, S. M., Belnap, J., & Okin, G. S. (2011). Responses of wind erosion to climate-induced vegetation changes on the Colorado Plateau. *Proceedings of the National Academy of Sciences*, *108*(10), 3854–3859. doi:10.1073/pnas.1014947108

Reich, P. B. (2014). The world-wide 'fast–slow'plant economics spectrum: a traits manifesto. *Journal of Ecology*, *102*(2), 275–301.

Sala, O. E., & Paruelo, J. M. (1997). Ecosystem services in grasslands. *Nature's Services: Societal Dependence on Natural Ecosystems*, 237–251.

Sanchis, M. P. S., Torri, D., Borselli, L., & Peosen, J. (2009). Climate effects on erodibility. *Earth Surface Processes and Landforms*, *34*(March), 613–628. doi:10.1002/esp

Seager, R., Hooks, A., Williams, A. P., Cook, B., Nakamura, J., & Henderson, N. (2015). Climatology, variability, and trends in the U.S. Vapor pressure deficit, an important fire-related meteorological quantity. *Journal of Applied Meteorology and Climatology*, *54*(6), 1121–1141. doi:10.1175/JAMC-D-14-0321.1

Storkey, J., Döring, T., Baddeley, J., Collins, R., Roderick, S., Jones, H., & Watson, C. (2015). Engineering a plant community to deliver multiple ecosystem services. *Ecological Applications*, *25*(4), 1034–1043. doi:10.1890/14-1605.1

Teixeira, L. H., Oliveira, B. F., Krah, F. S., Kollmann, J., & Ganade, G. (2020). Linking plant traits to multiple soil functions in semi-arid ecosystems. *Journal of Arid Environments*, *172*(October 2019), 104040. doi:10.1016/j.jaridenv.2019.104040

Tilman, D. (1997). Biodiversity and ecosystem functioning. *Nature's Services: Societal Dependence On Natural Ecosystems*. doi:Export Date 19 June 2013

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892.

Figures

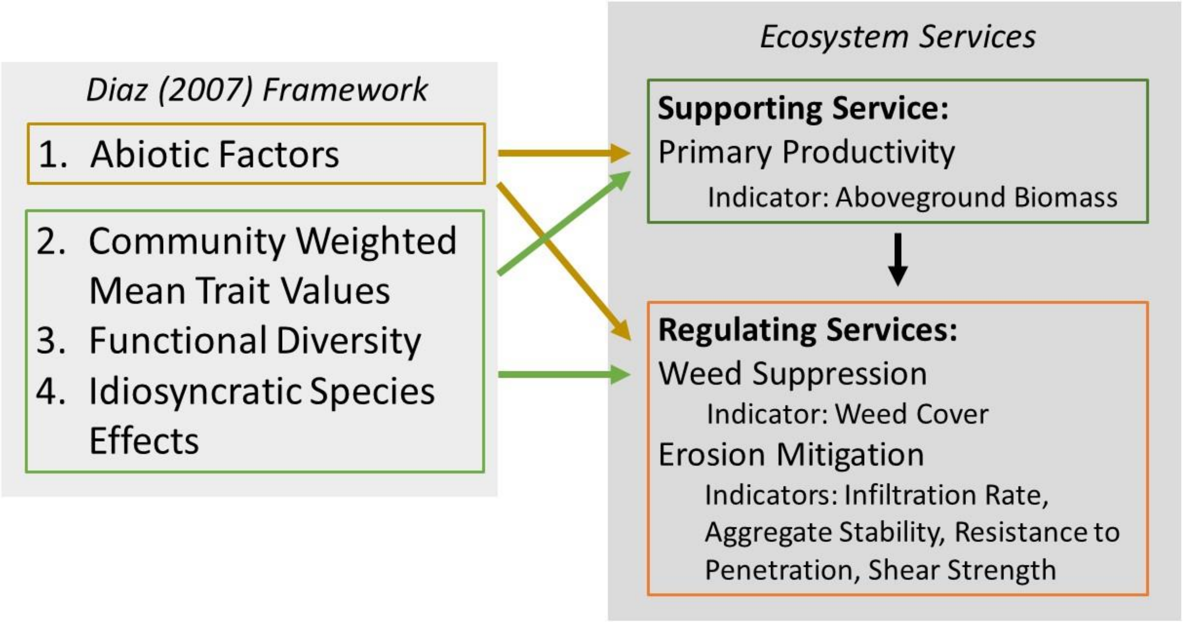

Figure 1. Conceptual diagram of the steps investigating the impact of abiotic factors and plant functional composition on rebuilding ecosystem services in restoration.

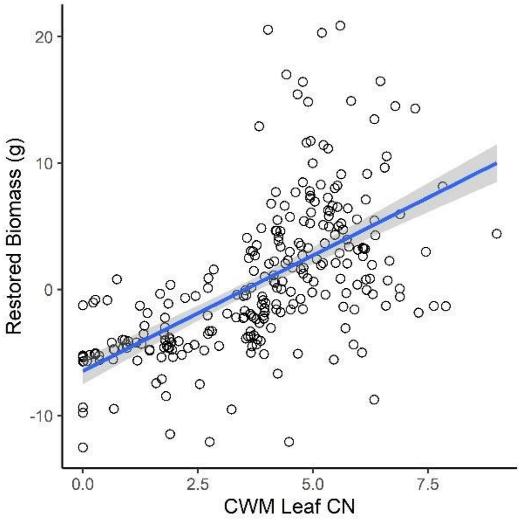

Figure 2. Restored plot-level aboveground biomass as a function of CWM leaf carbon to nitrogen ratio (CN). This analysis was done at the plot level, sample size = 288.

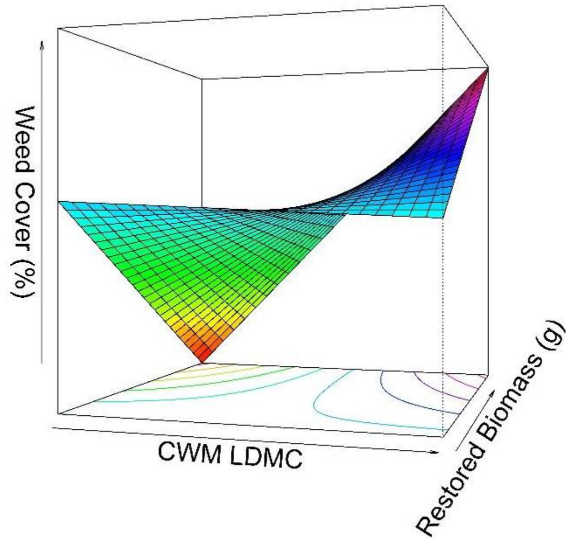

Figure 3. Fitted models of weed cover as a function of biomass x CWM leaf dry matter content (LDMC). Contour lines and color gradient show weed cover at various combinations of restored biomass and CWM trait values. This analysis was done at the plot level, sample size = 288.

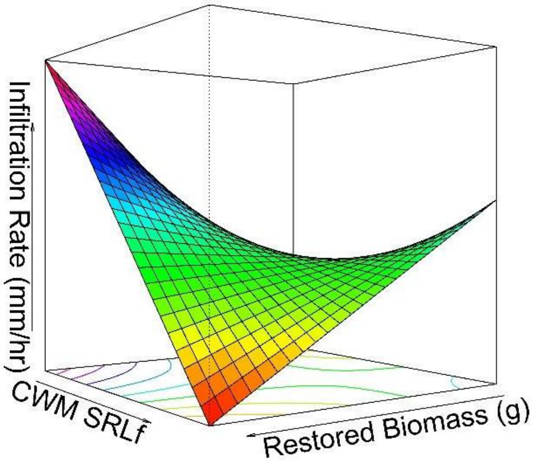

Figure 4. Fitted model of infiltration rate as a function of biomass x CWM specific root length (SRL). Contour lines and color gradient show infiltration rate at various combinations of restored biomass and CWM trait values. This analysis was done on two interspaces per plot, sample size = 562.

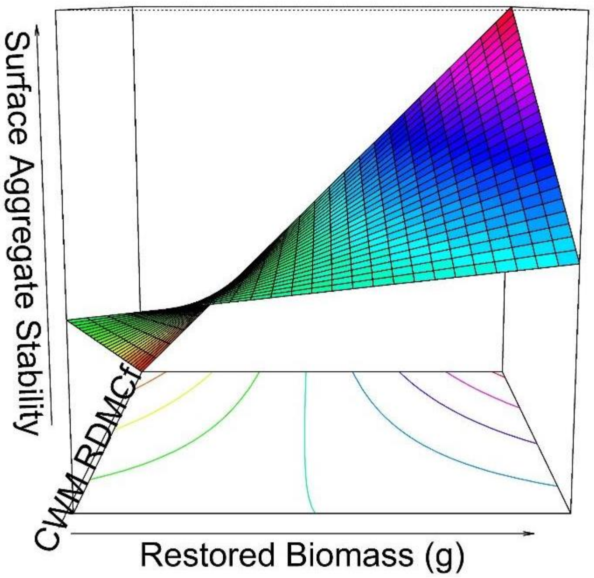

Figure 5. Fitted model of surface aggregate stability as a function of biomass x CWM fine root dry matter content (RDMCf). Contour lines and color gradient show infiltration rate at various combinations of restored biomass and CWM trait values. This analysis was done on two interspaces per plot, sample size = 576.

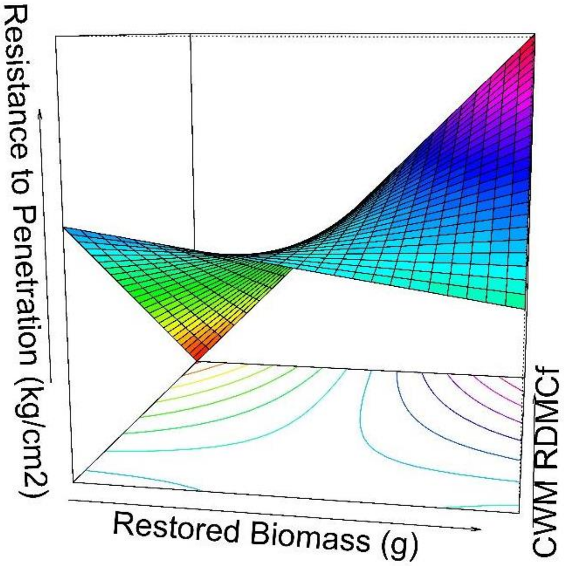

Figure 6. Fitted model of soil resistance to penetration as a function of biomass x CWM fine root dry matter content (RDMCf). Contour lines and color gradient show infiltration rate at various combinations of restored biomass and CWM trait values. This analysis was done on two interspaces per plot, sample size = 576.

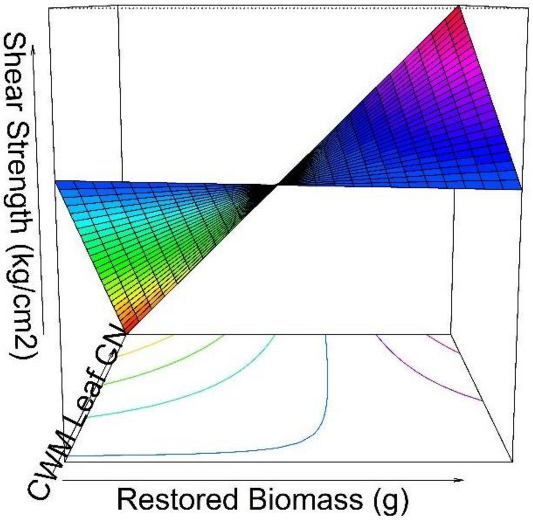

Figure 7. Fitted model of soil shear strength as a function of biomass x CWM leaf carbon to nitrogen ratio (CN). Contour lines and color gradient show infiltration rate at various combinations of restored biomass and CWM trait values. This analysis was done on two interspaces per plot, sample size = 576.

Tables:

Site	Lat	Long	Elevation (m)	Soil Texture	Total Precipitation (mm)	Average Minimum Temp. (°C)	Average Mean Temp. (°C)	Average Dewpoint Temp. (°C)	Average Maximum Temp. (°C)	Average Minimum Vapor Pressure Deficit (hPa)	Average Maximum Vapor Pressure Deficit (hPa)
La Sal	38.3	-109.07	2233	Sandy Loam	799.0	3.3	9.8	16.3	-4.3	4.1	17.9
Babbitt PJ	35.6	-111.94	1983	Clay	1094.7	2.4	10.9	19.4	-2.6	2.4	20.8
Canyonlands	38.1	-109.57	1655	Sandy Loam	586.7	5.2	12.2	19.1	-2.8	4.9	22.6
Flying M	34.8	-111.11	1873	Loam	737.6	4.2	12.2	20.1	-0.4	2.8	21.2
Bar T Bar	34.9	-111.06	1783	Sandy Loam	621.4	4.7	12.7	20.6	-0.5	3.2	22.2
Petrified Forest	34.9	-109.81	1645	Sandy Clay Loam	594.1	5.5	14.1	22.6	-0.5	3.8	26.4
Spider Web	35.6	-111.48	1586	Sandy Loam	507.4	7.4	14.9	22.4	-0.7	5.2	26.0
Montezuma Well	34.7	-111.76	1140	Sandy Loam	868.3	8.7	17.5	26.4	1.6	4.7	32.4

Table 1. Sites and abiotic factors including soil texture, elevation, and climate variables averaged (summed for precipitation) from daily interpolated values from 4km resolution (prism.oregonstate.edu).

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 belowground biomass to aboveground biomass	investment in above or belowground growth and storage
Specific Leaf Area (mm2/mg)	SLA	area of fresh leaf in square millimeters 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 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 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 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 weight of dried root tissue (g)	investment in exploratory roots versus conserving energy (absorptive roots)
Fine Root Dry Matter Content (mg/g)	RDMCf	weight of dried root tissue (mg) divided by weight of fresh root tissue (g)	proxy for root tissue density (absorptive roots)

Table 2. Functional traits used in study and descriptions of how they were measured and their ecological significance.

		a. Biomass (n=288)					b. Weed Cover (n=288)					c. Infiltration Rate (n=562)				
		t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC
	~1 (null model)	16.3	<0.001	0.00	-83.5	71.2	15.9	<0.001	0.00	-56.9	149.9	33.3	<0.001	0.00	-75.3	48.5
Abiotic Factors	precipitation (mm)	7.3	<0.001	0.16	-130.2	24.5	4.7	<0.001	0.07	-76.6	130.2	**7.3**	**<0.001**	**0.09**	**-123.8**	**0.0**
	minimum temperature (°C)	-8.2	<0.001	0.19	-141.9	12.9	11.1	<0.001	0.30	-158.8	48.0	0.7	0.52	0.00	-73.7	50.1
	mean temperature (°C)	-8.9	<0.001	0.22	-151.6	3.2	12.7	<0.001	0.36	-183.9	22.9	1.0	0.30	0.00	-74.4	49.5
	maximum temperature (°C)	-8.7	<0.001	0.21	-149.0	5.8	12.6	<0.001	0.36	-182.5	24.3	1.2	0.22	0.00	-74.8	49.0
	mean dewpoint temperature (°C)	**-9.1**	**<0.001**	**0.23**	**-154.7**	**0.0**	10.4	<0.001	0.27	-146.7	60.1	1.1	0.26	0.00	-74.6	49.2
	minimum vapor pressure deficit (hPa)	-3.4	<0.001	0.04	-93.2	61.6	4.0	<0.001	0.05	-70.2	136.6	1.0	0.31	0.00	-74.3	49.5
	maximum vapor pressure deficit (hPa)	-7.9	<0.001	0.18	-138.7	16.0	**14.1**	**<0.001**	**0.41**	**-206.8**	**0.0**	1.5	0.13	0.00	-75.6	48.2

		d. Surface Stability (n=576)					e. Subsurface Stability (n=576)					f. Penetration Resistance (n=576)				
		t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC
	~1 (null model)	21.4	<0.001	0.00	338.9	84.6	18.97	<0.001	0.00	285.96	43.72	15.7	<0.001	0.00	-628.4	13.0
Abiotic Factors	precipitation (mm)	0.2	0.85	0.00	340.9	86.6	-1.67	0.10	0.01	285.18	42.94	-2.6	0.01	0.01	-633.2	8.1
	minimum temperature (°C)	**9.7**	**<0.001**	**0.14**	**254.3**	**0.0**	**6.89**	**<0.001**	**0.08**	**242.24**	**0.00**	1.4	0.18	0.00	-628.2	13.1
	mean temperature (°C)	8.3	<0.001	0.11	275.5	21.2	6.25	<0.001	0.06	249.99	7.75	0.8	0.42	0.00	-627.0	14.3
	maximum temperature (°C)	6.9	<0.001	0.08	295.3	41.0	5.43	<0.001	0.05	259.13	16.89	0.4	0.69	0.00	-626.5	14.8
	mean dewpoint temperature (°C)	6.4	<0.001	0.07	300.6	46.3	5.24	<0.001	0.05	261.06	18.82	-1.7	0.08	0.01	-629.4	11.9
	minimum vapor pressure deficit (hPa)	7.1	<0.001	0.08	292.4	38.1	4.54	<0.001	0.04	267.67	25.43	**3.9**	**0.00**	**0.03**	**-641.4**	**0.0**
	maximum vapor pressure deficit (hPa)	**8.6**	<0.001	0.11	271.4	17.0	6.36	<0.001	0.07	248.69	6.45	2.3	0.03	0.01	-631.5	9.9

		g. Shear Strength (n=576)				
		t	p	R^2	AIC	ΔAIC
	~1 (null model)	44.5	<0.001	0.00	-137.4	131.8
Abiotic Factors	precipitation (mm)	**-12.3**	**<0.001**	**0.21**	**-269.3**	**0.0**
	minimum temperature (°C)	7.6	<0.001	0.09	-190.0	79.3

	mean temperature (°C)	4.5	<0.001	0.03	-155.5	113.8
	maximum temperature (°C)	2.3	0.02	0.01	-140.6	128.7
	mean dewpoint temperature (°C)	1.0	0.32	0.00	-136.4	132.9
	minimum vapor pressure deficit (hPa)	11.9	<0.001	0.20	-262.7	6.5
	maximum vapor pressure deficit (hPa)	4.9	<0.001	0.04	-159.5	109.8

Table 3. Results from step 1. Ecosystem Service Indicator ~ Abiotic Factor. Akaike Information Criterion (AIC) was used to determine which model was the most parsimonious; models with a delta AIC of less than 2 were considered equally parsimonious as the model with the lowest AIC value.

		Biomass (n=288)				
		t	p	R^2	AIC	ΔAIC
	~1 (null model)	0.0	1.00	0.00	-156.7	151.8
Community-weighted Trait Values	LDMC	13.7	<0.001	0.40	-299.3	9.2
	SLA	12.5	<0.001	0.35	-279.7	28.9
	Leaf CN	**14.2**	**<0.001**	**0.41**	**-308.6**	**0.0**
	Root:Shoot	9.6	<0.001	0.24	-234.5	74.0

	coarse RDMC	11.8	<0.001	0.33	-269.1	39.4
	fine RDMC	11.0	<0.001	0.30	-255.7	52.9
	coarse SRL	11.4	<0.001	0.31	-261.9	46.6
	fine SRL	11.1	<0.001	0.30	-257.4	51.2

Table 4. Results from step 2. Biomass ~ CWM trait. Akaike Information Criterion (AIC) was used to determine which model was the most parsimonious; models with a delta AIC of less than 2 were considered equally parsimonious as the model with the lowest AIC value.

		a. Weed Cover (n=288)					b. Infiltration Rate (n=562)					c. Surface Stability (n=576)				
		t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC
	~1 (null model)	0.0	1.00	0.00	-208.8	7.5	0.0	1.00	0.00	-125.8	4.4	0.0	1.00	0.00	252.3	12.7
	biomass	1.2	0.06	0.01	-210.5	5.8	-1.2	0.22	0.00	-125.3	4.9	3.0	0.00	0.02	245.4	5.8
Community-weighted Trait Values	LDMC	1.8	0.08	0.01	-209.9	6.4	-0.2	0.83	0.00	-123.9	6.4	3.1	0.00	0.02	244.8	5.1
	biomass	-2.5	0.01				1.1	0.28				-0.6	0.55			
	LDMC	-0.6	0.55				1.8	0.07				0.7	0.49			
	biomass x LDMC	**3.1**	**0.00**	**0.05**	**-216.3**	**0.0**	-2.0	0.05	0.01	-126.4	3.8	1.2	0.24	0.02	246.5	6.9
	SLA	1.6	0.11	0.01	-209.4	6.9	0.3	0.80	0.00	-123.9	6.3	3.3	0.00	0.02	243.7	4.1
	biomass	-1.5	0.15				-0.4	0.68				0.0	0.97			
	SLA	-0.7	0.49				2.2	0.03				1.1	0.26			
	biomass x SLA	2.4	0.02	0.03	-212.3	4.0	-1.1	0.29	0.01	-126.0	4.2	0.5	0.64	0.02	247.1	7.4

Leaf CN	2.1	0.04	0.02	-211.0	5.3	0.1	0.89	0.00	-123.9	6.4	**3.6**	**0.00**	**0.02**	**241.2**	**1.6**
biomass	-2.3	0.02				0.3	0.75				-1.9	0.06			
Leaf CN	0.0	0.96				2.0	0.05				1.3	0.19			
biomass x Leaf CN	**2.7**	**0.01**	**0.04**	**-214.9**	**1.4**	-1.3	0.20	0.01	-125.8	4.5	**2.2**	**0.03**	**0.03**	**240.2**	**0.6**
Root:Shoot	1.1	0.25	0.01	-208.1	8.2	0.7	0.50	0.00	-124.3	5.9	2.4	0.02	0.01	248.3	8.7
biomass	-0.8	0.45				-1.3	0.20				1.2	0.23			
Root:Shoot	-1.0	0.31				1.6	0.11				0.5	0.59			
biomass x Root:Shoot	1.7	0.09	0.02	-209.4	6.9	0.2	0.86	0.01	-125.3	4.9	-0.3	0.78	0.02	249.1	9.5
coarse RDMC	2.1	0.03	0.02	-211.4	4.9	0.0	0.99	0.00	-123.8	6.4	3.3	0.00	0.02	243.7	4.0
biomass	-1.7	0.09				0.3	0.73				-1.2	0.25			
coarse RDMC	0.0	0.98				1.6	0.11				0.4	0.68			
biomass x coarse RDMC	2.2	0.03	0.03	-212.7	3.6	-1.2	0.23	0.01	-124.1	6.2	1.8	0.07	0.03	243.6	3.9
fine RDMC	1.5	0.13	0.01	-209.1	7.2	0.1	0.95	0.00	-123.8	6.4	**3.8**	**0.00**	**0.03**	**239.6**	**0.0**
biomass	-1.6	0.11				0.1	0.94				-1.5	0.13			
fine RDMC	-0.8	0.40				1.6	0.12				1.1	0.28			
biomass x fine RDMC	2.3	0.02	0.03	-212.0	4.3	-1.0	0.34	0.01	-123.8	6.5	**1.9**	**0.06**	**0.03**	**239.9**	**0.3**
coarse SRL	2.0	0.05	0.01	-210.7	5.6	0.0	0.99	0.00	-123.8	6.4	3.3	0.00	0.02	243.3	3.7
biomass	-1.3	0.21				0.4	0.67				0.4	0.69			
coarse SRL	-0.1	0.91				2.0	0.04				1.4	0.17			
biomass x coarse SRL	2.0	0.05	0.03	-211.4	4.9	-1.8	0.07	0.01	-126.4	3.8	0.1	0.96	0.02	246.8	7.2
fine SRL	1.2	0.22	0.01	-208.3	8.0	1.2	0.22	0.00	-125.3	4.9	2.9	0.00	0.02	245.8	6.2
biomass	-0.4	0.66				-1.5	0.14				0.7	0.49			
fine SRL	-0.9	0.37				2.5	0.01				0.8	0.41			
biomass x fine SRL	1.4	0.16	0.02	-208.5	7.8	**-0.2**	**0.85**	**0.02**	**-130.3**	**0.0**	0.1	0.94	0.02	248.2	8.6

		d. Subsurface Stability (n=576)					e. Penetration Resistance (n=576)					f. Shear Strength (n=576)				
		t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC
	~1 (null model)	0.0	1.0	0.0	240.2	0.8	**0.0**	**1.00**	**0.00**	**-643.4**	**27.3**	0.0	1.00	0.00	-271.3	41.0
	biomass	1.0	0.3	0.0	241.3	1.9	**-0.9**	**0.40**	**0.00**	**-642.1**	**28.6**	-0.1	0.91	0.00	-269.3	43.0
Community-weighted Trait Values	LDMC	1.4	0.2	0.0	240.3	0.9	**-0.9**	**0.37**	**0.00**	**-642.2**	**28.5**	0.9	0.39	0.00	-270.0	42.3
	biomass	-1.2	0.2				-4.5	<0.001				-6.3	<0.001			
	LDMC	0.5	0.6				-2.2	0.03				-0.9	0.36			
	biomass x LDMC	1.2	0.2	0.0	242.7	3.3	5.0	<0.001	0.04	-662.4	8.3	6.4	<0.001	0.07	-307.4	4.9
	SLA	1.6	0.1	0.0	239.8	0.4	-1.1	0.28	0.00	-642.6	28.1	1.2	0.25	0.00	-270.6	41.7
	biomass	-1.7	0.1				-3.0	0.00				-5.9	<0.001			
	SLA	0.5	0.6				-2.2	0.03				-0.5	0.62			
	biomass x SLA	1.8	0.1	0.0	240.5	1.1	**3.8**	**0.00**	**0.03**	**-653.1**	**17.6**	6.1	<0.001	0.07	-304.9	7.3
	Leaf CN	1.3	0.2	0.0	240.5	1.1	**-1.3**	**0.20**	**0.00**	**-643.0**	**27.7**	0.7	0.48	0.00	-269.8	42.5
	biomass	-0.8	0.4				-4.6	<0.001				-6.7	<0.001			
	Leaf CN	0.6	0.6				-2.5	0.01				-0.6	0.55			
	biomass x Leaf CN	0.9	0.4	0.0	243.8	4.3	5.3	<0.001	0.05	-666.6	4.1	6.8	<0.001	**0.08**	**-312.3**	**0.0**
	Root:Shoot	0.7	0.5	0.0	241.8	2.4	**-0.9**	**0.38**	**0.00**	**-642.2**	**28.5**	0.4	0.71	0.00	-269.4	42.9
	biomass	0.0	1.0				-3.3	0.00				-4.6	0.00			
	Root:Shoot	-0.3	0.7				-2.4	0.02				-2.0	0.05			
	biomass x Root:Shoot	0.5	0.6	0.0	245.0	5.6	3.8	0.00	0.03	-652.5	18.2	5.0	<0.001	0.04	-290.4	21.9
	coarse RDMC	1.1	0.3	0.0	241.1	1.6	-1.4	0.15	0.00	-643.4	27.3	0.5	0.63	0.00	-269.5	42.8
	biomass	-0.6	0.5				-4.1	<0.001				-5.2	0.00			
	coarse RDMC	0.0	1.0				-3.6	0.00				-2.1	0.03			
	biomass x coarse RDMC	0.9	0.4	0.0	244.3	4.8	4.8	0.00	0.04	-662.0	8.7	5.5	<0.001	0.05	-295.3	17.0

	fine RDMC	1.5	0.1	0.0	240.1	0.6	-0.8	0.42	0.00	-642.0	28.6	0.5	0.65	0.00	-269.5	42.8
	biomass	-1.5	0.1				-5.3	<0.001				-5.7	<0.001			
	fine RDMC	0.1	0.9				-3.2	0.00				-2.4	0.02			
	biomass x fine RDMC	1.6	0.1	0.0	241.4	2.0	**5.8**	**<0.001**	**0.06**	**-670.7**	**0.0**	6.1	<0.001	0.06	-301.9	10.4
	coarse SRL	1.1	0.3	0.0	240.9	1.5	-1.0	0.32	0.00	-642.4	28.3	0.8	0.45	0.00	-269.8	42.4
	biomass	-0.4	0.7				-3.4	0.00				-5.5	<0.001			
	coarse SRL	0.2	0.8				-2.5	0.01				-1.4	0.17			
	biomass x coarse SRL	0.7	0.5	0.0	244.5	5.0	**4.2**	**0.00**	**0.03**	**-655.6**	**15.1**	6.0	<0.001	0.06	-302.1	10.1
	fine SRL	**1.7**	**0.1**	**0.0**	**239.4**	**0.0**	**-0.4**	**0.66**	**0.00**	**-641.6**	**29.1**	0.2	0.84	0.00	-269.3	43.0
	biomass	-0.5	0.6				-4.4	0.00				-4.4	<0.001			
	fine SRL	0.9	0.4				-2.7	0.01				-2.5	0.01			
	biomass x fine SRL	0.4	0.7	0.0	243.1	3.7	4.9	**0.00**	0.04	-662.2	8.5	5.1	<0.001	0.04	-290.7	21.6

Table 5. Results from step 2. Indicator of ecosystem function ~ Biomass * CWM trait. Akaike Information Criterion (AIC) was used to determine which model was the most parsimonious; models with a delta AIC of less than 2 were considered equivalently parsimonious as the model with the lowest AIC value.

5. Discussion of Results and Conclusions

Throughout my dissertation research I sought to improve restoration outcomes in disturbed drylands. Investigating the restoration outcomes from fifteen years of seeding efforts on the Colorado Plateau I found that overall seeding success rates are about 35% across the region and as low as 0% for some areas within the database, however the right combination of trait value and environment can result in up to 80% success. The main finding from my first research chapter was that temperature seasonality interacted with two traits to predict restoration seeding outcome: seed mass and plant height. Both outcomes are related to the stress of high temperature seasonality: large seeds - have more nutrients stored for developing embryo and tend to be more successful in resource-limited environments, and tall plants in this case consist of shrubs that have deeper root systems which allow them to persist through harsh conditions. These results provide restoration practitioners with a way to tailor their seed mix to local environmental conditions to greatly improve restoration success. Land managers on the Colorado Plateau can use this information to select species to include in restoration treatments such as: large-seeded, taller species in areas with higher temperature seasonality and small-seeded, shorter species in areas with lower temperature seasonality. This framework can be applied elsewhere in regions where restoration success is limited and can additionally be applied to find populations of species that are best suited for the local environment.

My restoration planting experiment at RestoreNet sites on the Colorado Plateau was a continuation of research on improving restoration outcome. Functional composition of plant communities impacts critical ecosystem functions, however, to determine which species will survive in changing environments we need to understand how the abiotic environment filters out potential species. Observational studies alone cannot separate the effects of competition and abiotic stressors, thus experimental plantings are essential to address this issue. In contrast to my first research chapter, a controlled number of individuals were planted at each site within this experiment, additionally all species had previously been screened for comprehensive trait values. This allowed me to estimate the functional composition of the surviving restored communities across sites and ask how certain trait values were being filtered out and how the functional composition of the restored communities impacted ecosystem function.

Investigating the survival results from the RestoreNet experiment I asked which plant traits influenced survival and whether drought response strategies were involved in influencing survival. There was below average monsoon precipitation in 2019 meaning that drought response strategies could be very important for survival. There are many strategies to deal with drought, such as escape, avoidance, and tolerance. Drought escape typically involves quick growing plants that undergo their life cycle before drought occurs, or alternatively remain dormant until conditions improve; this strategy is typically associated with “fast” traits. Drought avoidance tends to be associated with deeply rooted species that can access water during drought. Drought tolerant plants, however, reduce the amount of water loss that occurs during drought with highly regulated tissues; this strategy is typically associated with “slow” traits. There can be combinations of “fast” and “slow components within an individual plant.

In my second research chapter, I found many significant shifts in functional composition within surviving members of the planted communities relative to random mortality, however these shifts predominately reflected directional selection in our warmer species pools rather than stabilizing selection. I found unsurprisingly that higher leaf dry matter content (a drought-tolerating strategy) was important for survival across all species pool, but surprisingly that high specific leaf area (an acquisitive strategy) was important for survival at warm species pools and that lower root dry matter content was beneficial in all species pools. I determined that these strategies allowed for rapid, opportunistic water acquisition during favorable periods, such as quick growing leaves and roots. These results shed light on the strength of the abiotic filter, alone, in determining functional composition of a planted community as well as its role in directional selection of functional trait values. Additionally, our findings are relevant to restoration practitioners who face enormous ecological barriers to overcome when restoring ecosystem structure and function; using trait-based models to improve species selection for restoration projects can greatly improve success, especially in harsh environments such as global drylands.

Chapter 4. Aboveground biomass was promoted by multiple trait strategies: slower-growing, drought-tolerant strategy, and faster-growing, acquisitive strategy. Even though each of these traits are independent of one another, determining that they all relate to restored biomass shows that many combinations of fast- and slow- trait strategies contribute to increasing restored biomass. I also measured several soil processes related to erosion mitigation such as water infiltration rate which is important because higher soil infiltration capacity reduces the volume of surface run-off and consequently soil erosion. Greater plant biomass and longer, more exploratory roots improved infiltration rate. This makes sense because longer roots create more channels and pores that enable diffusion of water further into the soil. These results do support the idea that primary productivity is a supporting ecosystem service that contributes to other ecosystem services. One of the takeaway messages is that no single plant can improve all these functions, but perhaps patches within a landscape can achieve multiple goals. A combination of plant strategies could accomplish this improvement for multiple ecosystem functions, however land managers may prioritize certain functions over others.

All three of my research chapters utilize slightly different trait-based approaches to improve dryland restoration. My first two research chapters address the survival of species in restoration and the third addresses the impact that a restored community has on ecosystem functioning. A unifying theme throughout each of these chapters is dryland restoration sites have very strong abiotic filters including low water availability, bare ground and degraded soil that make them extremely challenging to restore. However, another unifying theme is that the outcome of restoration can be improved by selecting species with appropriate traits that will help achieve restoration goals. The cost of restoration treatments can be reduced by understanding that certain traits will promote success in different restoration contexts or at different stages following disturbance. Whether success is measured by survival or the improvement of ecosystem services such a primary productivity, weed suppression, or erosion mitigation, this success can be achieved by applying the results from trait-based experiments. Applying results from my first research chapter: taller plants with greater seed should be included at sites with high temperature seasonality. Applying results from my second research chapter: species with a combination of slow growing leaves and fast-growing roots should be included in highly disturbed, drought prone environments. And finally, applying results from my third research chapter: species with a combination of slower growing above and belowground components improve ecosystem functions of concern in drylands.

Further work could build on this research to test for optimal combinations of species to improve multiple ecosystem functions at the same time. Additionally, further research could explore how trait diversity and redundancy could contribute to the maintenance of ecosystem functioning after restoration to ensure that further disturbances do not cause the loss of function.

Appendices

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The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Ecological Applications, 2020

Appendix S1. Colorado Plateau Restoration Outcomes Database Methods

The Colorado Plateau Restoration Outcomes Database (CPROD) assimilated seeding and monitoring data from multiple sources for habitat restoration projects occurring on the Colorado Plateau within the last 15 years. Our goal was to investigate how native plant materials used in a restoration perform over the short- and long-term. We targeted restoration projects that included a revegetation component occurring post-wildfire and/or post-disturbance (for example, following oil and gas pad decommissioning or pipeline installation). Wildlife habitat improvement projects (vegetation thinning, pinyon-juniper removal), prescribed burns, invasive plant treatment, soil stabilization projects, and transplanting projects were also included.

Our primary online data sources were the Utah Watershed Restoration Initiative (WRI) database for restoration activities occurring in Utah and the USGS's Land Treatment Digital Library database (LTDL), which contains information on restorations carried out by the Bureau of Land Management across the west. In addition, we also obtained data through direct communication with the National Park Service and Bureau of Land Management. Botanists were contacted from the following national parks in the Colorado Plateau: Grand Canyon, Zion, Arches, Canyonlands, Capitol Reef, Canyon de Chelly to solicit seeding and monitoring data. In an effort to fill in gaps in the LTDL database, to include more recent projects, and to try and obtain additional monitoring data, BLM field offices in the Colorado Plateau were solicited directly in Fall/Winter 2015/16. The following field offices provided seeding and monitoring data for habitat restoration projects: Uncompahgre, Grand Junction, Colorado River Valley, Tres Rios, White River, Little Snake, San Luis Valley (Colorado), Moab, Monticello, Price (Utah).

Project centroids, size, ecological site description, date of treatment/s, and the specific treatment/s associated with the project (for example, prescribed burn and aerial seeding) were entered into the CPROD database along with information about the commercial source, cultivar type, and price of each species seeded or planted for each of the revegetation treatments associated with the project, as available. We also recorded all available pre-treatment and post-treatment monitoring data associated with each project with the goal of determining which revegetated species and seed sources were considered "successful" (i.e. they showed up in post-treatment monitoring).

Additional description of the database and contact information at https://sites.northwestern.edu/kramerlab/restoration_ecology/.

Data limitations:

There were limitations to this approach in that there was no way to determine revegetation success if natural populations of the species seeded were present at the site before treatment occurred. Also, for many projects, monitoring occurred on a project-level basis and it was impossible to separate out monitoring results by treatment. For example, if a project site was both aerially and drill seeded, there was no way to tell which method was most effective at reestablishing native cover. Another limitation to CPROD was the lack of consistent monitoring methods between data sources to allow for direct comparisons between projects, and even within a single source (such as the BLM), monitoring methods often differed between field offices. Seed mix lists recorded for each treatment were not always the final list of what was seeded, and could actually be a proposed list, depending on what data was available. However, for many projects completed after 2008, seed tags were kept, which were a reliable source for determining which species and cultivars were seeded and the amount of seed used.

Table S1. Site Locations and Climate Variables

Study Name	ID	latitude	longitude	Annual Mean Temperature	Isothermality	Temperature Seasonality	Total Annual Precipitation	Precipitation Seasonality	Precipitation of Warmest Quarter	Elevation (meters)
12 Mile Dixie	1	39.09467	-111.67	8.15	33.73	907.21	386.57	53.20	65.15	1879.63
Allen Smith Reseed	7	40.22253	-110.776	7.41	35.71	930.01	327.23	64.69	66.27	2009.83
Alton-Millcreek 2	10	37.33951	-112.335	8.75	41.58	855.72	317.69	89.08	55.65	2005.26
Bell Draw Dixie	17	37.98133	-109.272	9.26	35.09	889.77	405.35	87.76	106.74	2107.56
Black Ridge Fuel Reduction	24	38.37281	-109.355	9.95	32.00	972.07	322.72	47.86	82.76	2040.43
Black Ridge Roller Chop 2	753	38.68007	-107.798	10.10	36.93	909.92	346.00	43.62	96.28	2223.56
Blacktail Chaining	25	40.26568	-110.656	7.15	34.65	962.82	314.51	63.96	64.37	2044.31
Blacktail Chaining	26	40.26568	-110.656	7.15	34.65	962.82	314.51	63.96	64.37	2044.31
Box Canyon Sage Grouse	28	38.97867	-111.358	5.69	32.46	831.92	306.31	45.99	55.57	2560.13
Brotherson Chaining	32	40.26795	-110.287	7.04	31.39	1077.29	209.53	58.85	50.77	1915.49
Brown's Field	36	40.83176	-109.077	8.30	36.72	927.44	270.32	68.27	67.46	1710.24
Brush Creek Dixie	39	40.56323	-109.386	7.78	30.70	1066.19	253.72	54.36	53.32	1756.21
Buckskin 1	43	37.03837	-112.079	11.35	37.34	884.19	274.32	98.02	74.26	1921.75
Buckskin 2	44	37.03424	-112.069	11.18	37.37	837.22	352.11	97.21	74.18	1942.2
Buckskin 2	46	37.03424	-112.069	11.35	37.34	884.19	274.32	98.02	74.26	1942.2

Bull Hill Mechanical Treatment	610	38.6798	-108.905	10.20	36.83	908.18	324.62	78.71	97.20	2220.1
Burn Canyon Fire	830	38.10459	-108.418	9.26	37.68	886.53	367.17	70.30	72.95	2148.8
Burn Canyon Fire	831	38.10459	-108.418	9.26	37.68	886.53	367.17	70.30	72.95	2148.8
Burn Canyon Fire	832	38.08278	-108.439	8.70	38.29	872.73	381.60	67.26	73.21	2185.16
Burn Canyon Fire	833	38.08278	-108.439	8.70	38.29	872.73	381.60	67.26	73.21	2185.16
Buster Flats Fire-PJ	816	40.72666	-108.919	7.92	34.55	981.62	279.29	52.02	56.94	1948.67
Buster Flats Fire-Sage	822	40.72666	-108.919	7.92	34.55	981.62	279.29	52.02	56.94	1948.67
Campbell Fire	757	38.41877	-108.566	9.67	35.60	866.73	429.86	67.01	122.80	2222.64
Canyon de Chelly Experimental Reveg	562	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Canyon de Chelly Experimental Reveg	563	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Canyon de Chelly Experimental Reveg	564	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Canyon de Chelly Experimental Reveg	565	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Canyon de Chelly Experimental Reveg	566	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Canyon de Chelly Experimental Reveg	567	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Canyon de Chelly Experimental Reveg	568	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Canyon de Chelly Experimental Reveg	569	36.1458	-109.51	11.12	37.40	928.51	222.61	70.36	62.29	1701.87
Cedar Point Fire 2006	267	37.71955	-109.11	10.06	38.17	915.48	362.26	90.21	76.26	2050.17
Chew Dixie	54	40.46302	-109.084	6.98	29.50	992.63	354.61	83.25	68.84	2341.06
Columbia WUI Hazardous Fuels Treatment 2009	280	39.52247	-110.414	10.41	31.13	936.18	357.20	82.02	72.89	1802.21
Consumer Bench	56	39.62867	-110.913	8.60	34.09	917.11	344.73	75.76	76.73	1872.07
Craig Draw Fire	759	38.13905	-108.214	8.23	39.55	805.19	424.91	71.94	136.60	2280.36
Cushman Mesa Hydoaxe 1	755	38.44595	-108.132	8.70	34.56	852.25	418.52	62.17	134.02	2293.07
Cushman Mesa Rollerchop	787	38.43	-108.123	7.97	36.28	833.70	464.95	58.48	140.58	2340.1
Dave Wood Hydroaxe 1	763	38.33603	-107.925	8.45	37.79	914.04	292.81	61.32	64.72	2221.46
Dave Wood Hydroaxe 2	770	38.35614	-107.958	8.84	37.40	825.50	311.46	56.26	64.10	2233.07

Deadman Greenstrip	68	40.17629	-109.155	10.01	31.64	991.99	268.01	70.63	59.38	1764.59
Deadman Greenstrip	69	40.17629	-109.155	8.63	29.73	1136.32	217.69	51.18	42.39	1764.59
Devil Canyon Fuels Reduction and Vegetation Restoration	597	37.70842	-109.38	9.52	34.06	901.91	340.96	80.62	95.06	2053.04
DOE 1-M-29	618	39.49291	-108.014	8.98	34.00	929.62	386.77	41.43	76.03	1740.69
DOE 1-W-20	619	39.50396	-108.019	9.48	35.40	958.40	339.08	54.68	83.57	1908.14
DOE 1-W-20	620	39.50396	-108.019	9.51	34.40	999.25	359.33	61.64	69.69	1908.14
DOE 2-W-29	633	39.49792	-108.016	9.51	34.40	999.25	359.33	61.64	69.69	1788.17
DOE RM 2-8	634	39.53744	-107.905	7.94	30.14	890.57	442.34	41.53	77.68	1808.96
Dominguez Fire	761	38.83407	-108.285	10.84	32.71	985.69	248.04	52.65	74.15	1635.12
Dove Creek Fire 2006	298	37.67656	-109.047	9.92	37.38	906.48	383.45	89.52	77.77	2012.45
Dugout (Hart Draw)	75	38.10401	-109.537	11.25	33.57	900.87	340.30	84.85	84.94	1997.28
East Santaquin Chaining	78	40.25029	-110.698	6.98	35.11	951.67	325.97	62.44	66.54	2104.4
East Santaquin Chaining	79	40.25029	-110.698	6.98	35.11	951.67	325.97	62.44	66.54	2104.4
Five Mile Mountain Sagebrush Restoration 2006	309	37.18363	-112.007	11.94	37.05	890.59	247.05	83.40	44.16	1629.1
Five Mile Mountain Sagebrush Restoration 2007	313	37.10418	-112.183	10.63	41.65	891.19	208.98	77.88	45.05	1744.06
Fountain Green Dixie and Plateau	83	39.62245	-111.618	7.09	36.95	954.82	307.28	54.29	45.81	1779.94
Fruitland Fire	752	38.70749	-107.781	10.52	38.14	854.37	335.76	56.91	109.56	2017.55
Fruitland Fire	788	38.70749	-107.781	10.52	38.14	854.37	335.76	56.91	109.56	2017.55
Garvey Hazardous Fuels Treatment	612	39.35995	-108.606	9.30	32.81	945.91	418.10	73.80	76.66	2033.72
GGU 12-28	701	39.49788	-107.566	8.06	34.56	961.12	370.66	45.38	53.67	1889.56
GGU 13-28	702	39.49435	-107.566	8.06	34.56	961.12	370.66	45.38	53.67	1888.28
GM 11-36	635	39.48619	-108.065	8.33	30.55	931.93	387.88	36.74	63.78	1733.79
GM 42-11	639	39.45378	-108.072	9.69	35.13	1000.96	348.35	50.75	63.74	1671.38
Golden Stairs Chaining	85	40.32624	-110.693	7.04	36.59	855.90	368.33	66.99	71.88	2056.75
Grammer Fire	762	38.19619	-108.335	8.61	37.46	899.44	323.25	53.38	100.57	2124.37
Grey Wolf Chaining	89	40.24918	-110.791	6.79	36.49	851.56	380.83	62.73	70.74	2077.62
GV 8-14	645	39.44344	-108.07	9.50	35.27	960.42	355.85	42.72	67.80	1585.33

Hart Draw Flat 1	93	38.02307	-109.418	9.82	36.97	866.65	381.21	88.85	92.74	1936.04
Hart Draw Flat 2	94	38.01979	-109.425	9.37	35.25	837.86	445.36	93.52	104.33	1930.99
Harts Windmill	95	38.01376	-109.434	9.37	35.25	837.86	445.36	93.52	104.33	1922.11
Howerton's	103	39.4674	-111.478	7.59	36.61	873.87	475.94	56.09	58.73	1855.83
HWY 90 Hydroaxe 1	760	38.41025	-108.016	9.19	36.73	834.36	316.15	57.63	67.22	2144.18
HWY 90 Hydroaxe 2	756	38.41261	-108.004	9.19	36.73	834.36	316.15	57.63	67.22	2100.07
HWY 90 Hydroaxe 3	821	38.41261	-108.004	9.19	36.73	834.36	316.15	57.63	67.22	2100.07
Indian Springs Bullhog	105	39.64131	-109.155	8.88	32.69	971.89	374.52	87.53	88.71	2246.21
Indian Springs Bullhog 2	106	39.66787	-109.091	7.14	32.00	948.12	499.11	50.63	114.75	2332.35
Jensen Aerator 1	751	38.61781	-107.752	7.79	36.11	868.57	467.55	54.79	71.83	2459.03
Johnson Creek	109	37.72587	-109.518	9.76	34.30	921.45	394.62	75.14	76.31	2130.82
L26NW	687	39.49435	-107.751	9.27	36.27	969.06	328.52	56.69	93.35	1933.05
Levan Spray and Drill	110	39.57351	-111.832	9.05	34.32	1009.18	341.51	56.04	51.80	1668.43
Little Baullie Mesa Fuels Reduction Project 2009-PJ	334	37.59613	-109.73	10.70	34.40	930.84	358.75	76.04	77.68	1962.06
Little Baullie Mesa Fuels Reduction Project 2009-Sage	820	37.59613	-109.73	10.70	34.40	930.84	358.75	76.04	77.68	1962.06
Little Donkey	111	40.58215	-109.403	8.66	33.23	951.65	276.23	76.28	47.46	1752.03
Lower Horesefly Rollerchop 1	779	38.30064	-107.902	7.23	38.84	850.55	419.14	53.35	88.26	2348.26
Mailbox Park Rollerchop 2	783	38.20707	-108.396	9.73	37.00	867.33	364.08	62.70	74.90	2018.28
McCook Ridge Plateau Exclosure North	119	39.64193	-109.269	8.45	33.18	949.59	330.24	45.63	74.16	2020.76
McCook Ridge Plateau Exclosure Outside	120	39.64124	-109.269	8.45	33.18	949.59	330.24	45.63	74.16	2023.4
McCook Ridge Plateau Exclosure South	121	39.64151	-109.27	8.45	33.18	949.59	330.24	45.63	74.16	2018.88
McGruder Fire	758	38.95126	-107.844	7.56	35.14	838.35	519.85	60.05	96.98	2232.27
Mill Fork Chaining	122	39.9516	-111.305	7.39	34.47	970.22	498.05	63.77	57.84	1894.21
Mohrland Roller Chopper 1	124	39.458	-110.993	6.80	32.38	903.68	297.79	53.60	52.89	2129.44
Mohrland Roller Chopper 2	127	39.44296	-110.979	7.71	32.37	952.87	266.56	58.35	44.96	2052.82
MV 15-8	647	39.45765	-108.129	9.57	31.82	933.92	438.32	73.95	107.08	1858.82
MV 45-10	651	39.45709	-108.093	10.13	36.68	907.47	431.16	61.08	108.48	1788.94

North Hills Bullhog	139	37.59006	-113.144	9.73	37.15	868.50	305.97	55.92	60.39	1938.83
North Little Donkey	144	40.60749	-109.406	8.03	33.37	904.57	312.02	67.41	57.66	1830.51
North Spring	145	39.52229	-110.925	8.75	34.28	984.57	264.83	81.36	62.81	1895.06
NR 314-2	652	39.54501	-107.861	8.72	32.81	967.75	430.38	60.98	98.87	1789.95
PA 11-28	654	39.50158	-108.012	9.51	34.40	999.25	359.33	61.64	69.69	1819.01
PA 11-33	656	39.48611	-108.011	9.62	34.68	950.98	415.70	67.48	95.20	1608.61
PA 13-28	660	39.49027	-108.012	9.48	35.40	958.40	339.08	54.68	83.57	1716.55
PA 23-26	663	39.49442	-107.967	9.20	34.72	942.87	359.03	40.90	72.03	1715.29
PA 33-28	664	39.49409	-108	8.92	32.80	968.35	449.54	60.23	98.74	1673.9
PA 334-31	665	39.47538	-108.039	9.94	35.94	983.32	338.73	43.01	68.88	1595.62
PA 42-31	668	39.48229	-108.033	7.97	29.90	919.59	447.97	44.20	102.40	1638.75
PA 42-31	669	39.48229	-108.033	7.97	29.90	919.59	447.97	44.20	102.40	1638.75
Pack Creek	147	38.44014	-109.377	10.60	32.54	987.44	315.75	54.65	77.80	1804.38
Peter's Canyon	148	37.9674	-109.361	8.15	34.78	922.39	382.03	75.73	75.71	2129.51
Pinyon Hills Hydroaxe 1	786	38.36437	-107.952	8.88	37.90	864.08	309.98	56.04	58.40	2182.9
Poison Spring Ridge Roller Chop 1 Middle	781	38.58146	-107.613	7.27	36.73	858.47	517.47	54.74	73.19	2498.46
Poison Spring Ridge Roller Chop 1 North	780	38.58761	-107.611	7.27	36.73	858.47	517.47	54.74	73.19	2433.15
Poison Spring Ridge Roller Chop 1 South	782	38.57157	-107.617	7.27	36.73	858.47	517.47	54.74	73.19	2585.72
Quaking Aspen Spring	158	37.93047	-110.702	8.90	33.45	870.36	456.59	63.17	72.89	2098.73
Rabbit Gulch Chaining	162	40.21559	-110.526	8.04	33.71	1017.81	237.92	73.35	57.08	1782.02
Rabbit Gulch Interseed	163	40.2121	-110.566	7.13	32.09	1050.52	238.40	62.58	47.53	1856.38
RMV 39-16	699	39.52798	-107.901	7.94	30.14	890.57	442.34	41.53	77.68	1732.79
Ruple Cabin	167	40.67026	-109.063	6.93	32.74	893.27	350.75	62.61	66.69	2124.94
RWF 12-19	676	39.51007	-107.938	9.84	35.40	963.07	388.14	69.02	91.59	1765.98
RWF 12-9	677	39.53896	-107.904	7.94	30.14	890.57	442.34	41.53	77.68	1815.16
RWF 13-19	678	39.50709	-107.937	10.10	37.49	988.19	284.84	57.91	76.94	1744.86
RWF 21-18	679	39.52877	-107.935	7.69	30.44	913.35	461.93	46.61	100.12	1874.92
RWF 22-18	680	39.52701	-107.932	8.34	31.71	924.49	386.93	53.36	86.18	1844.44

RWF 32-10	682	39.54097	-107.868	9.32	34.52	997.73	342.65	63.52	72.08	1769.22
RWF 324-9	684	39.53426	-107.899	7.94	30.14	890.57	442.34	41.53	77.68	1770.29
Santaquin Chaining	169	40.27605	-110.714	6.58	35.68	851.69	398.77	70.79	80.17	2090.46
Santaquin Chaining	170	40.27605	-110.714	6.58	35.68	851.69	398.77	70.79	80.17	2090.46
Santaquin Greasewood	172	40.26068	-110.722	6.81	35.58	855.90	369.37	72.30	73.28	2074.58
Scenic Drive Reveg	465	38.24149	-111.226	10.56	34.37	924.06	223.93	92.40	100.75	1744.71
Scenic Drive Reveg	466	38.24149	-111.226	10.72	32.70	958.96	257.66	104.00	86.77	1744.71
Scenic Drive Reveg	467	38.24149	-111.226	10.56	34.37	924.06	223.93	92.40	100.75	1744.71
Scofield Dixie	174	39.81911	-111.167	4.13	35.32	867.18	457.21	53.01	67.26	2389.53
SG 41-26	685	39.41229	-108.07	9.99	35.53	1005.07	356.35	43.56	81.17	1591.68
Shay Mesa Bullhog	184	37.97768	-109.558	8.35	31.12	883.42	389.02	67.35	73.73	2129.75
Sidhill Spring	185	37.91478	-110.748	8.24	34.66	860.59	473.41	62.62	75.85	2361.6
SITLA Dixie	187	37.95192	-109.255	8.64	36.84	907.49	394.53	87.88	101.68	2074.24
SK Holdings Wildlife Project	823	39.39102	-108.136	10.26	34.66	1026.71	382.89	66.83	77.96	1557.07
Skitzy Chaining	190	40.11834	-110.525	7.57	34.63	874.12	327.05	60.46	68.00	2090.55
Stateline North	195	37.83986	-109.043	9.10	37.67	919.09	336.78	90.80	82.19	2036.62
Toliver Creek Bullhog	199	40.85531	-109.181	NA	NA	NA	NA	NA	NA	1845.46
Two Bar-Black Tail Chaining	203	40.30873	-110.674	6.44	32.79	965.53	304.06	65.65	50.45	2153.83
Two Bar-Sand Wash Chaining	206	40.26622	-110.479	7.27	31.03	1089.49	207.67	63.66	45.09	1881.75
Upper Porphyry	212	39.59813	-110.936	8.50	33.81	900.49	338.63	76.52	67.20	1928.72
W 37-1	686	39.47186	-107.953	8.96	34.60	949.30	393.11	44.17	100.50	1684.55
West Coal Creek Bullhog	213	39.66492	-110.804	8.79	31.09	1035.19	274.28	71.32	47.58	1971.92
West Stuntz	215	40.42524	-109.059	6.46	29.66	982.86	398.21	83.35	80.22	2390.93
Westwater II Fire Emergency Stabilization 2006	419	39.04209	-109.175	12.61	36.23	1025.57	262.22	88.28	58.53	1391.93
Wildcat Canyon Pinyon-Juniper Removal	219	39.66925	-110.961	7.21	33.75	989.57	310.12	65.09	58.22	2016.19
Wildcat Disking	217	38.96505	-111.361	5.76	33.81	800.82	398.73	54.92	80.87	2590.23
Willow Creek Dixie (Willow Creek Plateau)	222	39.80693	-111.824	9.48	33.05	965.48	400.31	54.58	42.40	1638.95

Wolf Fire Rehabilitation 2012	423	40.2814	-108.37	8.10	29.84	1008.18	412.43	63.71	89.99	1957.27

Supporting Information

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The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Ecological Applications, 2020

Appendix S2. TRY data contributors

Adler, P. B., D. G. Milchunas, W. K. Lauenroth, O. E. Sala, and I. C. Burke. 2004. Functional traits of graminoids in semi-arid steppes: A test of grazing histories. Journal of Applied Ecology 41:653–663.

Blonder, B., V. Buzzard, I. Simova, L. Sloat, B. Boyle, R. Lipson, B. Aguilar-Beaucage, A. Andrade, B. Barber, C. Barnes, D. Bushey, P. Cartagena, M. Chaney, K. Contreras, M. Cox, M. Cueto, C. Curtis, M. Fisher, L. Furst, J. Gallegos, R. Hall, A. Hauschild, A. Jerez, N. Jones, A. Klucas, A. Kono, M. Lamb, J. D. R. Matthai, C. Mcintyre, J. Mckenna, N. Mosier, M. Navabi, A. Ochoa, L. Pace, R. Plassmann, R. Richter, B. Russakoff, H. S. Aubyn, R. Stagg, M. Sterner, E. Stewart, T. T. Thompson, J. Thornton, P. J. Trujillo, T. J. Volpe, and B. J. Enquist. 2012. The leaf-area shrinkage effect can bias paleoclimate and ecology research. American Journal of Botany 99:1756–1763.

Blonder, B., C. Violle, L. P. Bentley, and B. J. Enquist. 2011. Venation networks and the origin of the leaf economics spectrum. Ecology Letters 14:91–100.

Butterfield, B. J., and J. M. Briggs. 2011. Regeneration niche differentiates functional strategies of desert woody plant species. Oecologia 165:477–487.

Campetella, G., Z. Botta-Dukát, C. Wellstein, R. Canullo, S. Gatto, S. Chelli, L. Mucina, and S. Bartha. 2011. Patterns of plant trait-environment relationships along a forest succession chronosequence. Agriculture, Ecosystems and Environment 145:38–48.

Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87:109–122.

Cerabolini, B. E. L., G. Brusa, R. M. Ceriani, R. de Andreis, A. Luzzaro, and S. Pierce. 2010. Can CSR classification be generally applied outside Britain? Plant Ecology 210:253–261.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Chen, Y., W. Han, L. Tang, Z. Tang, and J. Fang. 2013. Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. Ecography 36:178–184.

Choat, B., S. Jansen, T. J. Brodribb, H. Cochard, S. Delzon, R. Bhaskar, S. J. Bucci, T. S. Feild, S. M. Gleason, U. G. Hacke, A. L. Jacobsen, F. Lens, H. Maherali, J. Martínez-Vilalta, S. Mayr, M. Mencuccini, P. J. Mitchell, A. Nardini, J. Pittermann, R. B. Pratt, J. S. Sperry, M. Westoby, I. J. Wright, and A. E. Zanne. 2012. Global convergence in the vulnerability of forests to drought. Nature 491:752–755.

Cornwell, W. K., J. H. C. Cornelissen, K. Amatangelo, E. Dorrepaal, V. T. Eviner, O. Godoy, S. E. Hobbie, B. Hoorens, H. Kurokawa, N. Pérez-Harguindeguy, H. M. Quested, L. S. Santiago, D. A. Wardle, I. J. Wright, R. Aerts, S. D. Allison, P. Van Bodegom, V. Brovkin, A. Chatain, T. V. Callaghan, S. Díaz, E. Garnier, D. E. Gurvich, E. Kazakou, J. A. Klein, J. Read, P. B. Reich, N. A. Soudzilovskaia, M. V. Vaieretti, and M. Westoby. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters.

Dainese, M., and L. Bragazza. 2012. Plant traits across different habitats of the Italian Alps: A comparative analysis between native and alien species. Alpine Botany 122:11–21.

Everwand, G., E. L. Fry, T. Eggers, and P. Manning. 2014. Seasonal Variation in the Capacity for Plant Trait Measures to Predict Grassland Carbon and Water Fluxes. Ecosystems 17:1095–1108.

Fitter, A. H., and H. J. Peat. 1994. The Ecological Flora Database. Journal of Ecology 82:415–425.

Flowers, T. J., H. K. Galal, and L. Bromham. 2010. Evolution of halophytes: Multiple origins of salt tolerance in land plants. Functional Plant Biology 37:604–612.

Fonseca, C. R., J. M. C. Overton, B. Collins, and M. Westoby. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. Journal of Ecology 88:964–977.

Freschet, G. T., J. H. C. Cornelissen, R. S. P. van Logtestijn, and R. Aerts. 2010. Evidence of the “plant economics spectrum” in a subarctic flora. Journal of Ecology 98:362–373.

Fry, E. L., S. A. Power, and P. Manning. 2014. Trait-based classification and manipulation of plant functional groups for biodiversity-ecosystem function experiments. Journal of Vegetation Science 25:248–261.

Gachet, S., E. Véla, and T. Tatoni. 2005. BASECO: A floristic and ecological database of Mediterranean French flora. Biodiversity and Conservation 14:1023–1034.

Gallagher, R. V., and M. R. Leishman. 2012. A global analysis of trait variation and evolution in climbing plants. Journal of Biogeography 39:1757–1771.

Gallagher, R. V., M. R. Leishman, and A. T. Moles. 2011. Traits and ecological strategies of Australian tropical and temperate climbing plants. Journal of Biogeography 38:828–839.

Garnier, E., S. Lavorel, P. Ansquer, H. Castro, P. Cruz, J. Dolezal, O. Eriksson, C. Fortunel, H. Freitas, C. Golodets, K. Grigulis, C. Jouany, E. Kazakou, J. Kigel, M. Kleyer, V. Lehsten, J. Lepš, T. Meier, R. Pakeman, M. Papadimitriou, V. P. Papanastasis, H. Quested, F. Quétier, M. Robson, C. Roumet, G. Rusch, C. Skarpe, M. Sternberg, J. P. Theau, A. Thébault, D. Vile, and M. P. Zarovali. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. Annals of Botany 99:967–985.

Green, W. 2009. USDA PLANTS Compilation, version 1, 09-02-02.

Guy, A. L., J. M. Mischkolz, and E. G. Lamb. 2013. Limited effects of simulated acidic deposition on seedling survivorship and root morphology of endemic plant taxa of the Athabasca Sand Dunes in well-watered greenhouse trials. Botany 91:176–181.

Han, W., Y. Chen, F. J. Zhao, L. Tang, R. Jiang, and F. Zhang. 2012. Floral, climatic and soil pH controls on leaf ash content in China’s terrestrial plants. Global Ecology and Biogeography 21:376–382.

Han, W., J. Fang, D. Guo, and Y. Zhang. 2005. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. New Phytologist 168:377–385.

Hickler, T. 1999. Plant functional types and community characteristics along environmental gradients on Öland’s Great Alvar (Sweden). University of Lund, Sweden.

Hill, M. O., C. D. Preston, and D. B. Roy. 2004. PLANTATT - Attributes of British and Irish Plants: Status, Size, Life history, Geography and Habitats. Centre for Ecology and Hydrology:73.

Kapralov, M. V., J. A. C. Smith, and D. A. Filatov. 2012. Rubisco Evolution in C4 Eudicots: An Analysis of Amaranthaceae Sensu Lato. PLoS ONE 7.

Kattge, J., W. Knorr, T. Raddatz, and C. Wirth. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. Global Change Biology 15:976–991.

Kazakou, E., D. Vile, B. Shipley, C. Gallet, and E. Garnier. 2006. Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. Functional Ecology 20:21–30.

Kerkhoff, A. J., W. F. Fagan, J. J. Elser, and B. J. Enquist. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. The American naturalist 168.

Kew, R. B. G. 2008. Seed information database (SID). Version 7.1.

Kirkup, D., P. Malcolm, G. Christian, and A. Paton. 2005. Towards a digital African Flora. Taxon 54:457–466.

Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. Van Groenendael, L. Klimeš, J. Klimešová, S. Klotz, G. M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J. G. Hodgson, A. K. Jackel, I. Kühn, D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase: A database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266–1274.

Kühn, I., W. Durka, and S. Klotz. 2004. BiolFlor: A New Plant-Trait Database as a Tool for Plant Invasion Ecology. Diversity and Distributions 10:363–365.

Louault, F., V. D. Pillar, J. Aufrère, E. Garnier, and J. F. Soussana. 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. Journal of Vegetation Science 16:151–160.

Manning, P., K. Houston, and T. Evans. 2009. Shifts in seed size across experimental nitrogen enrichment and plant density gradients. Basic and Applied Ecology 10:300–308.

Medlyn, B. E., F. W. Badeck, D. G. G. De Pury, C. V. M. Barton, M. Broadmeadow, R. Ceulemans, P. De Angelis, M. Forstreuter, M. E. Jach, S. Kellomäki, E. Laitat, M. Marek, S. Philippot, A. Rey, J. Strassemeyer, K. Laitinen, R. Liozon, B. Portier, P. Roberntz, K. Wang, and P. G. Jarvis. 1999. Effects of elevated [CO2] on photosynthesis in European forest species: A meta-analysis of model parameters. Plant, Cell and Environment 22:1475–1495.

Mencuccini, M. 2003. The ecological significance of long-distance water transport: Short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant, Cell and Environment 26:163–182.

Meziane, D., and B. Shipley. 1999. Interacting determinants of specific leaf area in 22 herbaceous species: Effects of irradiance and nutrient availability. Plant, Cell and Environment 22:447–459.

Milla, R., and P. B. Reich. 2011. Multi-trait interactions, not phylogeny, fine-tune leaf size reduction with increasing altitude. Annals of Botany 107:455–465.

Moretti, M., and C. Legg. 2009. Combining plant and animal traits to assess community functional responses to disturbance. Ecography 32:299–309.

Ogaya, R., and J. Peñuelas. 2003. Comparative field study of Quercus ilex and Phillyrea latifolia: Photosynthetic response to experimental drought conditions. Environmental and Experimental Botany 50:137–148.

Ordoñez, J. C., P. M. Van Bodegom, J. P. M. Witte, R. P. Bartholomeus, J. R. Van Hal, and R. Aerts. 2010. Plant strategies in relation to resource supply in mesic to wet environments: Does theory mirror nature? American Naturalist 175:225–239.

Paula, S., M. Arianoutsou, D. Kazanis, Ç. Tavsanoglu, F. Lloret, C. Buhk, F. Ojeda, B. Luna, J. M. Moreno, A. Rodrigo, J. M. Espelta, S. Palacio, B. Fernández-Santos, P. M. Fernandes, and J. G. Pausas. 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90:1420.

Peco, B., I. De Pablos, J. Traba, and C. Levassor. 2005. The effect of grazing abandonment on species composition and functional traits: The case of dehesa grasslands. Basic and Applied Ecology 6:175–183.

Pierce, S., G. Brusa, I. Vagge, and B. E. L. Cerabolini. 2013. Allocating CSR plant functional types: The use of leaf economics and size traits to classify woody and herbaceous vascular plants. Functional Ecology 27:1002–1010.

Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, R. Villar, U. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA):a meta-analysis. New Phytologist 182:565–588.

Prentice, I. C., T. Meng, H. Wang, S. P. Harrison, J. Ni, and G. Wang. 2011. Evidence of a universal scaling relationship for leaf CO2 drawdown along an aridity gradient. New Phytologist 190:169–180.

Preston, K. A., W. K. Cornwell, and J. L. Denoyer. 2006. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. New Phytologist.

Price, C. A., and B. J. Enquist. 2007. Scaling mass and morphology in leaves: An extension of the wbe model. Ecology 88:1132–1141.

Reich, P. B., J. Oleksyn, and I. J. Wright. 2009. Leaf phosphorus influences the photosynthesis-nitrogen relation: A cross-biome analysis of 314 species. Oecologia 160:207–212.

Reich, P. B., M. G. Tjoelker, K. S. Pregitzer, I. J. Wright, J. Oleksyn, and J. L. Machado. 2008. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. Ecology Letters 11:793–801.

Sandel, B., J. D. Corbin, and M. Krupa. 2011. Using plant functional traits to guide restoration: A case study in California coastal grassland. Ecosphere 2:1–16.

Scherer-Lorenzen, M., E. D. Schulze, A. Don, J. Schumacher, and E. Weller. 2007. Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). Perspectives in Plant Ecology, Evolution and Systematics 9:53–70.

Schweingruber, F., and W. Landolt. 2005. The xylem database (updated). Birmensdorf, Switzerland: Swiss Federal Research Institute, WSL.

Sheremet’ev S.N. 2005. Herbs on the soil moisture gradient (water relations and the structural-functional organization). KMK Moscow.

Shipley, B. 1989. The Use of Above-Ground Maximum Relative Growth Rate as an Accurate Predictor of Whole-Plant Maximum Relative Growth Rate. Functional Ecology 3:771–775.

Shipley, B. 1995. Structured Interspecific Determinants of Specific Leaf Area in 34 Species of Herbaceous Angiosperms. Functional Ecology 9:312–319.

Shipley, B. 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: Relationship with daily irradiance. Functional Ecology 16:682–689.

Shipley, B., and M. Parent. 1991. Germination Responses of 64 Wetland Species in Relation to Seed Size, Minimum Time to Reproduction and Seedling Relative Growth Rate. Functional Ecology 5:111.

Shipley, B., and M. J. Lechowicz. 2000. The functional co-ordination of leaf morphology, nitrogen concentration, and gas exchange in40 wetland species. Écoscience 7:183–194.

Shipley, B., and T.-T. Vu. 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. New Phytologist:359–364.

Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. Journal of Ecology 100:652–661.

Van Bodegom, P. M., B. K. Sorrell, A. Oosthoek, C. Bakker, and R. Aerts. 2008. Separating the effects of partial submergence and soil oxygen demand on plant physiology. Ecology 89:193–204.

Vergutz, L., S. Manzoni, A. Porporato, R. Novais, and R. Jackson. 2012. A global database of carbon and nutrient concentrations of green and senesced leaves. ORNL DAAC.

Vile, D. 2005. Significations fonctionnelle et ecologique des traits des especes vegetales: exemple dans une succession post-cultural mediterraneenne et generalisations.

White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani. 2000. Parameterization and Sensitivity Analysis of the BIOME–BGC Terrestrial Ecosystem Model: Net Primary Production Controls. Earth Interactions 4:1–85.

Willis, C. G., M. Halina, C. Lehman, P. B. Reich, A. Keen, S. McCarthy, and J. Cavender-Bares. 2010. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. Ecography 33:565–577.

Wirth, C., and J. W. Lichstein. 2009. The Imprint of Species Turnover on Old-Growth Forest Carbon Balances – Insights From a Trait-Based Model of Forest Dynamics. Pages 81–113 Old-Growth Forests.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, Ü. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Authors: Kathleen R. Balazs, Andrea T. Kramer, Seth M. Munson, Nora Talkington, Shannon Still, and Bradley J. Butterfield

The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Ecological Applications, 2020

Appendix S3. Plant functional trait sources. For each species, n indicates how many times it occurs in the analysis dataset. Data sources: TRY – TRY initiative, BB1 – Butterfield et al 2017, BB2 – Butterfield additional data submitted to TRY, KB – Balazs additional data submitted to TRY. (Data from BB2 and KB can be found at [https://www.try-db.org/TryWeb/Data.php#54, DOI: 10.17871/TRY.54](https://www.try-db.org/TryWeb/Data.php#54))

Table S1

Species	**nativity**	**n**	**Seed Mass**	**Height**	**SLA**
Achillea millefolium	native	29	TRY	TRY	TRY
Achnatherum hymenoides	native	48	TRY, BB1	TRY	BB1
Agropyron cristatum	non-native	34	TRY	TRY	TRY
Agropyron fragile	non-native	28	TRY	TRY	KB
Aristida purpurea	native	8	TRY, BB1	TRY	BB1
Artemisia frigida	native	1	TRY	TRY	TRY
Artemisia ludoviciana	native	1	TRY	TRY	TRY
Artemisia nova	native	1	TRY	TRY	NA
Artemisia tridentata	native	20	NA	NA	NA
Astragalus cicer	non-native	15	TRY	TRY	TRY
Atriplex canescens	native	59	TRY	TRY	TRY
Atriplex confertifolia	native	9	TRY	TRY	BB2
Bahia dissecta	native	4	NA	TRY	NA
Balsamorhiza sagittata	native	1	TRY	TRY	TRY
Bassia prostrata	non-native	19	KB	TRY	KB
Bouteloua curtipendula	native	2	TRY	TRY	TRY
Bouteloua gracilis	native	17	TRY, BB1	TRY	TRY, BB1
Bromus marginatus	native	1	TRY	TRY	KB
Cercocarpus montanus	native	4	TRY	TRY	BB2
Cleome serrulata	native	9	TRY	TRY	KB
Coreopsis tinctoria	native	4	TRY	TRY	NA
Cryptantha flava	native	4	NA	TRY	NA

Dactylis glomerata	non-native	24	KB	TRY	TRY
Distichlis spicata	native	8	TRY	TRY	NA
Elymus elymoides	native	28	TRY, BB1	TRY	BB1
Elymus hoffmannii	non-native	3	NA	NA	NA
Elymus lanceolatus	native	37	KB	NA	NA
Elymus trachycaulus	native	43	TRY	TRY	TRY
Elymus wawawaiensis	native	24	KB	KB	KB
Ephedra viridis	native	2	TRY	TRY	NA
Ericameria nauseosa	native	3	TRY	TRY	BB2
Eriogonum umbellatum	native	10	TRY	TRY	TRY
Fallugia paradoxa	native	2	TRY	TRY	BB2
Festuca arizonica	native	1	TRY, BB1	TRY	BB1
Festuca ovina	non-native	2	TRY	TRY	TRY
Gaillardia pulchella	native	4	TRY	TRY	NA
Gaillardia spathulata	native	2	TRY	NA	NA
Hedysarum boreale	native	2	TRY	TRY	KB
Helianthus annuus	native	26	KB	TRY	TRY
Heliomeris multiflora	native	2	KB	KB	TRY
Hesperostipa comata	native	27	TRY, BB1	TRY	BB1
Heterotheca villosa	native	2	TRY	TRY	TRY
Hymenoxys richardsonii	native	2	TRY	NA	NA
Koeleria macrantha	native	2	NA	TRY	TRY
Krascheninnikovia lanata	native	10	TRY	TRY	KB
Lactuca serriola	non-native	1	TRY	TRY	TRY
Leymus cinereus	native	11	TRY	TRY	KB
Leymus salinus	native	2	TRY	TRY	NA
Linum lewisii	native	3	TRY	TRY	TRY
Linum perenne	non-native	41	TRY	TRY	TRY
Machaeranthera tanacetifolia	native	4	TRY	TRY	KB
Medicago sativa	non-native	54	TRY	TRY	TRY
Melilotus officinalis	non-native	6	TRY	TRY	TRY
Monarda citriodora	native	4	TRY	NA	NA
Nassella viridula	native	3	TRY	TRY	KB

Oenothera elata	native	8	TRY	TRY	NA
Oenothera pallida	native	8	TRY	TRY	NA
Onobrychis viciifolia	non-native	37	TRY	TRY	TRY
Osmorhiza occidentalis	native	1	TRY	TRY	TRY
Pascopyrum smithii	native	67	TRY	TRY	TRY
Penstemon palmeri	native	30	TRY	TRY	KB
Penstemon strictus	native	23	TRY	TRY	BB2
Penstemon utahensis	native	1	NA	NA	NA
Phacelia crenulata	native	4	TRY	NA	NA
Pleuraphis jamesii	native	7	TRY, BB1	TRY	BB1
Poa fendleriana	native	3	TRY	TRY	BB1
Poa secunda	native	52	TRY	TRY	KB
Psathyrostachys juncea	non-native	33	TRY	TRY	KB
Pseudoroegneria spicata	native	47	TRY	TRY	TRY
Psilosthrophe sparsiflora	native	2	NA	NA	NA
Purshia stansburiana	native	2	TRY	TRY	BB2
Purshia tridentata	native	22	TRY	TRY	TRY
Sanguisorba minor	non-native	62	TRY	TRY	TRY
Sphaeralcea coccinea	native	13	TRY	TRY	TRY
Sphaeralcea grossulariifolia	native	1	TRY	TRY	KB
Sphaeralcea munroana	native	2	TRY	TRY	NA
Sphaeralcea parvifolia	native	2	TRY	NA	NA
Sporobolus airoides	native	14	TRY	TRY	NA
Sporobolus cryptandrus	native	47	TRY, BB1	TRY	TRY, BB1
Stanleya pinnata	native	2	TRY	TRY	NA
Thinopyrum intermedium	non-native	19	TRY	TRY	KB
Thinopyrum ponticum	non-native	3	TRY	TRY	KB
Trifolium fragiferum	non-native	1	TRY	TRY	TRY
Triticum aestivum	non-native	2	TRY	TRY	TRY
Verbesina encelioides	native	4	TRY	TRY	NA
Vicia americana	native	4	TRY	TRY	TRY
Vulpia octoflora	native	4	TRY	NA	NA

Yucca harrimaniae	native	1	NA	NA	NA
Summary statistics for all species in this study:			**Seed Mass (g)**	**Height (m)**	**SLA (mm2 mg-1)**
mean			4.30	0.90	14.90
min			0.10	0.10	2.70
max			48.30	5.30	41.80
sd			7.50	0.80	7.50

Supporting Information

Authors: Kathleen R. Balazs, Andrea T. Kramer, Seth M. Munson, Nora Talkington, Shannon Still, and Bradley J. Butterfield

The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Ecological Applications, 2020

Appendix S4. Supplementary trait measurement methods

Seed mass data were available for almost all species in the dataset (74/88). We obtained commercially grown seed of an additional 6 species, estimating seed masses from an average weight of 100 dry seeds per species to bring this number up to 80/88 (seed weighing methods: Cornelissen et al. 2003, Prez-Harguindeguy et al. 2013). Plant height data were available for 74/88 species. Values for specific leaf area (SLA) were the least available (28/88), so we supplemented these values with additional measurements of species (Butterfield, data submitted to TRY - https://www.try-db.org/TryWeb/Data.php#54, DOI: 10.17871/TRY.54) to bring this number up to 40/88.

We further supplemented the trait data with values from a greenhouse trait screening that included 40 species from our seeding dataset (Balazs, data submitted to TRY - https://www.try-db.org/TryWeb/Data.php#54, DOI: 10.17871/TRY.54). Because greenhouse-grown plants are known to differ systematically from natural populations in their trait values (Poorter et al., 2016), we assessed differences in SLA and height between species for which we had TRY and greenhouse data. Based on paired t-tests, greenhouse plants had on average 8.53 mm^2 mg^{-1} greater SLA (t = -4.66, df = 21, P <0.001) than plants from the TRY dataset (which itself may be a combination of natural and greenhouse populations), and 0.48 m shorter (t = 8.44, df = 34, P <0.001). Thus, for the sake of comparability, we subtracted 8.53 from the SLA values and added 0.48 to the height values of the greenhouse data. The differences in SLA are very comparable to those between greenhouse-grown and natural populations of perennial grasses from a regional study (Roybal & Butterfield, 2019), so we are confident in the adjustment used here. The addition of this trait data brought our coverage of SLA up to 62/88 species and height up to 76/88. See Appendix S4 for a summary of species for which values of different traits were available. All trait variables in our dataset are uncorrelated: seed mass and height (Pearson's $r = 0.16$), SLA and seed mass ($r = 0.15$), SLA and height ($r = -0.18$).

Literature Cited

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., … Heijden, M. G. A. Van Der. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335–380.

Poorter, H., Fiorani, F., Pieruschka, R., Wojciechowski, T., van der Putten, W. H., Kleyer, M., … Postma, J. (2016). Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytologist*, *212*(4), 838–855. doi:10.1111/nph.14243

Prez-Harguindeguy, N., Daz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., … Gurvich, D. E. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234.

Roybal, C. M., & Butterfield, B. J. (2019). Species-specific trait–environment relationships among populations of widespread grass species. *Oecologia*, *189*(4), 1017–1026. doi:10.1007/s00442-019-04372-6

Authors: Kathleen R. Balazs, Andrea T. Kramer, Seth M. Munson, Nora Talkington, Shannon Still, and Bradley J. Butterfield

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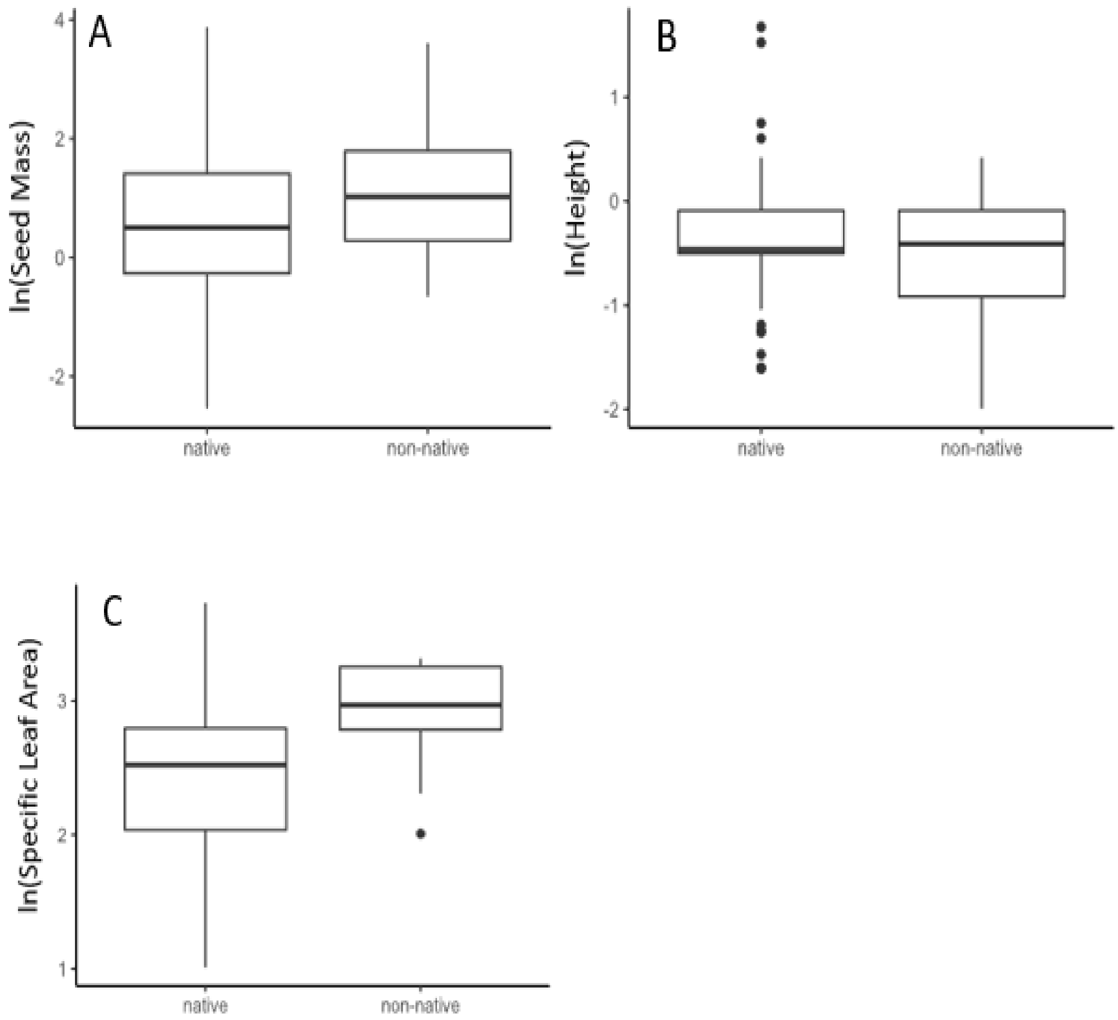
Ecological Applications, 2020

Appendix S5. Comparison of Trait Values between Native and Non-Native Seeded Species

Figure S1


A
ln(Seed Mass)
4
2
0
-2
native
non-native
B
ln(Height)
1
0
-1
-2
native
non-native
C
ln(Specific Leaf Area)
3
2
1
native
non-native

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The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Ecological Applications, 2020

Appendix S6.

Fig S1 The relationship between temperature seasonality and elevation (r = -0.52, P < 0.001)

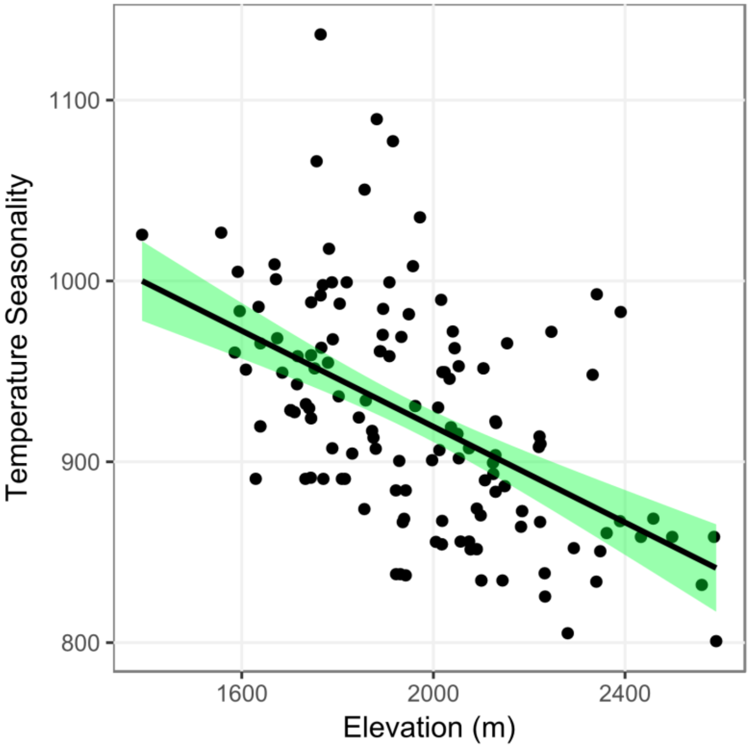
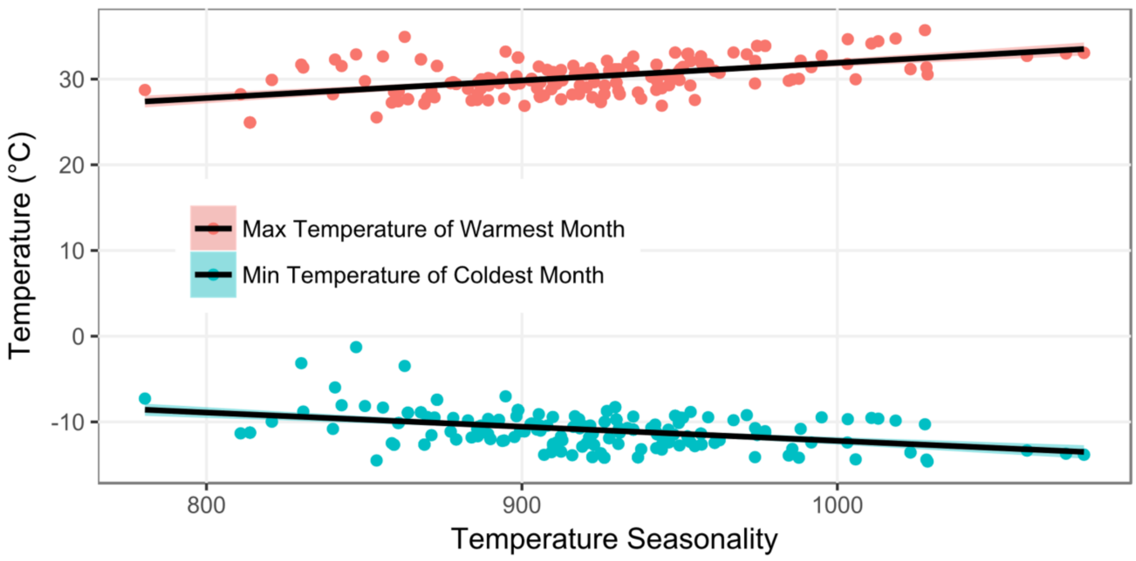


Fig S2 The relationship between temperature seasonality and seasonal extremes. Temperature seasonality and maximum temperature of warmest month: r=0.51 , p<0.01. Temperature seasonality and minimum temperature of warmest month: r=-0.42 , p<0.01.



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The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes

Ecological Applications, 2020

Appendix S7.

Table S1. Additional statistics to Table 1 in main article. Results from generalized linear mixed models for each trait testing for main effects and interactive effects with climate variables. Marginal (R2m) and conditional (R2c) r-squared values indicate the proportion of variation in each model explained by fixed and random effects.

	Seed Mass (ln), n=1199				Height (ln), n=1154				SLA (ln), n=1087			
	z	SE	R2m	R2c	z	SE	R2m	R2c	z	SE	R2m	R2c
Trait	3.20	0.36	0.012	0.220	-2.53	0.41	0.007	0.203	0.55	0.32	0.000	0.195
Temperature Seasonality (ln)	2.12	0.55	0.011	0.202	2.17	0.54	0.012	0.189	2.23	0.54	0.013	0.188
Trait	-1.26	0.86			-3.79	0.99			1.07	0.74		
Temperature Seasonality (ln)	-1.52	1.20			-1.51	1.06			1.90	1.12		
Trait:Temperature Seasonality (ln)	2.83	2.02	0.032	0.227	3.04	2.29	0.031	0.215	-0.96	1.69	0.014	0.189
Annual Mean Temperature	-1.17	0.66	0.005	0.209	-0.83	0.65	0.002	0.196	-0.62	0.65	0.001	0.196

Trait	-0.45	1.25			-3.34	1.35			1.78	1.13		
Annual Mean Temperature	-1.73	1.35			-2.65	1.14			1.19	1.30		
Trait:Annual Mean Temperature	1.42	2.11	0.022	0.229	2.73	2.34	0.017	0.214	-1.71	1.93	0.005	0.200
Total Annual Precipitation	-0.30	0.47	0.000	0.209	-0.29	0.46	0.000	0.196	-0.41	0.46	0.001	0.195
Trait	3.18	0.72			1.09	0.83			-0.06	0.70		
Total Annual Precipitation	1.34	0.89			1.99	0.79			-0.52	0.90		
Trait:Total Annual Precipitation	-1.83	1.40	0.016	0.226	-2.66	1.63	0.016	0.212	0.35	1.33	0.001	0.195
Precipitation Seasonality	2.26	0.50	0.014	0.211	2.06	0.49	0.011	0.198	1.94	0.49	0.010	0.197
Trait	2.68	0.90			-1.03	0.97			1.02	0.73		
Precipitation Seasonality	2.33	1.16			1.10	0.93			1.68	1.02		
Trait:Precipitation Seasonality	-1.58	1.91	0.029	0.222	-0.03	1.98	0.018	0.205	-0.82	1.52	0.012	0.198
Precipitation of Warmest Quarter	-1.22	0.56	0.004	0.209	-1.09	0.55	0.003	0.196	-1.13	0.55	0.004	0.194
Trait	3.16	0.70			-0.75	0.79			1.97	0.64		
Precipitation of Warmest Quarter	0.96	1.08			-0.03	1.01			1.18	1.08		
Trait:Precipitation of Warmest Quarter	-1.79	1.79	0.019	0.220	-0.63	2.12	0.011	0.204	-2.00	1.70	0.009	0.200
Isothermality (ln)	-0.78	0.53	0.002	0.207	-0.69	0.52	0.001	0.194	-0.54	0.52	0.001	0.194
Trait	1.13	0.94			0.18	1.08			-0.11	0.84		
Isothermality (ln)	-0.46	1.09			0.69	0.96			-0.53	1.07		
Trait:Isothermality (ln)	0.11	1.76	0.015	0.218	-1.22	2.05	0.010	0.203	0.32	1.58	0.001	0.193

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Bell curve trait distributions do not ring true: Directional environmental selection is common and amplified by aridity

Cool Species Pool			
	Babbitt PJ	La Sal	CRC
species	**survival**		
Achillea millefolium	96%	100%	100%
Bouteloua gracilis	100%	100%	100%
Bromus marginatus	89%	100%	100%
Dalea candida	89%	71%	85%
Elymus elymoides	90%	94%	99%
Elymus trachycaulis	79%	100%	100%
Elymus wawawaiensis	100%	100%	93%
Hedysarum boreale	100%	29%	69%
Heliomeris multiflora	29%	99%	99%
Hesperostipa comata	100%	90%	31%
Leymus cinereus	94%	94%	99%
Linum lewisii	86%	99%	100%
Pascopyrum smithii	100%	64%	100%
Pleuraphis jamesii	100%	14%	15%
Pseudoroegneria spicata	96%	57%	83%
Sphaeralcea grossulariifolia	32%	10%	82%

Intermediate Species Pool		
	Flying M	Bar T Bar
species	**survival**	
Achillea millefolium	99%	93%
Achnatherum hymenoides	100%	97%
Bouteloua eriopoda	99%	99%
Bouteloua gracilis	100%	97%
Bromus marginatus	100%	90%
Dalea candida	69%	90%
Elymus elymoides	100%	88%
Heliomeris multiflora	81%	74%
Krascheninnikovia lanata	88%	78%
Linum lewisii	89%	89%
Machaeranthera tanacetifolia	14%	3%
Pascopyrum smithii	100%	92%
Penstemon palmeri	92%	97%
Pleuraphis jamesii	100%	93%
Poa secunda	100%	83%
Sporobolus cryptandrus	100%	97%

Warm Species Pool			
	Montezuma Well	Petrified Forest	Spider Web
species	**survival**		
Achillea millefolium	100%	93%	14%
Achnatherum hymenoides	94%	85%	53%
Aristida purpurea	94%	8%	69%
Asclepias tuberosa	6%	0%	10%
Baileya multiradiata	97%	0%	24%
Bouteloua curtipendula	100%	10%	50%
Bouteloua eriopoda	99%	8%	92%
Bouteloua gracilis	99%	76%	99%
Dalea candida	86%	11%	24%
Hilaria mutica	94%	81%	65%
Krascheninnikovia lanata	81%	82%	11%
Machaeranthera tanacetifolia	17%	11%	0%
Penstemon palmeri	97%	6%	1%
Poa secunda	93%	90%	100%
Senna covesii	1%	0%	0%
Sporobolus cryptandrus	97%	93%	93%

Average	**86%**	**76%**	**85%**	***Average***	**89%**	**85%**	***Average***	**78%**	**41%**	**44%**

Table S1. Summary of survival broken down by species per site.

site	Babbitt PJ, n=994					Flying M, n=1029				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	42.86	43.41	0.26	-2.10	0.025	36.47	35.55	0.25	3.64	<0.001
Specific Leaf Area	24.53	23.52	0.13	7.70	<0.001	25.95	25.58	0.12	3.01	0.001
Leaf Dry Matter Content	23.92	23.88	0.21	0.18	0.440	23.02	22.94	0.20	0.39	0.379
Root:Shoot	28.73	29.01	0.14	-1.97	0.023	45.80	45.14	0.29	2.25	0.003
Specific Root Length (coarse)	32.62	32.57	0.19	0.24	0.422	36.93	36.08	0.18	4.77	<0.001
Specific Root Length (fine)	34.65	33.38	0.30	4.29	<0.001	37.10	36.14	0.23	4.22	<0.001
Root Dry Matter Content (coarse)	29.61	28.34	0.22	5.66	<0.001	25.06	28.17	0.15	-20.83	0.001
Root Dry Matter Content (fine)	18.45	18.38	0.15	0.52	0.289	26.49	25.37	0.21	5.40	<0.001

site	Bar T Bar, n=979					Petrified Forest, n=471				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	36.40	35.56	0.30	2.77	0.002	29.65	31.27	0.56	-2.85	0.007
Specific Leaf Area	26.32	25.58	0.14	5.32	<0.001	21.28	25.58	0.55	-7.88	0.001
Leaf Dry Matter Content	23.05	22.97	0.23	0.33	0.374	28.67	29.20	0.83	-0.63	0.250
Root:Shoot	44.97	45.13	0.36	-0.46	0.313	53.03	42.60	0.91	11.50	<0.001
Specific Root Length (coarse)	37.85	36.06	0.22	8.25	<0.001	43.07	45.66	0.61	-4.28	0.001
Specific Root Length (fine)	37.38	36.15	0.28	4.30	<0.001	42.71	46.85	0.87	-4.77	0.001
Root Dry Matter Content (coarse)	24.60	28.18	0.18	-19.50	0.001	27.23	32.26	0.64	-7.81	0.001
Root Dry Matter Content (fine)	26.47	25.36	0.24	4.55	<0.001	27.62	26.23	0.73	1.93	0.031

site	Montezuma Well, n=904					Spider Web, n=507				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	31.61	31.27	0.26	1.33	0.080	25.61	31.24	0.56	-10.06	0.001
Specific Leaf Area	22.58	25.57	0.25	-12.14	0.001	16.39	25.60	0.54	-17.07	0.001
Leaf Dry Matter Content	30.45	29.19	0.37	3.46	<0.001	19.88	29.15	0.77	-12.00	0.001
Root:Shoot	43.51	42.64	0.38	2.29	0.007	46.30	42.60	0.90	4.13	<0.001
Specific Root Length (coarse)	44.54	45.66	0.28	-4.05	0.001	49.16	45.66	0.58	6.03	<0.001
Specific Root Length (fine)	44.62	46.84	0.37	-5.96	0.001	47.17	46.89	0.84	0.33	0.386
Root Dry Matter Content (coarse)	25.17	32.24	0.29	-24.18	0.001	21.44	32.27	0.62	-17.61	0.001
Root Dry Matter Content (fine)	26.77	26.22	0.31	1.78	0.034	25.20	26.20	0.68	-1.47	0.071

site	Canyonlands, n=975					La Sal, n=879				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	46.22	43.40	0.29	9.59	<0.001	43.99	43.43	0.37	1.52	0.062
Specific Leaf Area	24.20	23.53	0.14	4.71	<0.001	23.95	23.52	0.18	2.42	0.004
Leaf Dry Matter Content	25.13	23.88	0.24	5.33	<0.001	25.07	23.89	0.29	4.09	<0.001
Root:Shoot	28.89	29.02	0.15	-0.89	0.187	30.16	29.01	0.20	5.77	<0.001
Specific Root Length (coarse)	33.03	32.57	0.21	2.19	0.011	31.22	32.57	0.27	-5.02	0.001
Specific Root Length (fine)	31.14	33.39	0.32	-6.93	0.001	31.95	33.39	0.41	-3.50	0.001
Root Dry Matter Content (coarse)	23.99	28.33	0.23	-18.85	0.001	24.23	28.33	0.33	-12.47	0.001
Root Dry Matter Content (fine)	19.11	18.39	0.16	4.57	<0.001	18.36	18.38	0.20	-0.10	0.450

Table S2. H1 results for Coefficient of Variation (CoV). For each site, “n” indicates the number of individuals that survived planting. Values were calculated from greenhouse trait measurements for each species.

site	Babbitt PJ, n=994					Flying M, n=1029				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	23.61	23.30	0.12	2.63	0.005	19.71	19.94	0.07	-3.04	0.003
Specific Leaf Area	22.64	22.95	0.06	-4.89	0.001	22.27	22.06	0.06	3.64	0.001
Leaf Dry Matter Content	23.10	22.66	0.06	7.08	<0.001	23.30	22.99	0.05	5.68	<0.001
Root:Shoot	0.48	0.47	0.00	2.68	0.003	0.44	0.43	0.00	0.95	0.172
Specific Root Length (coarse)	26.91	26.56	0.10	3.31	<0.001	26.67	27.31	0.10	-6.19	0.001
Specific Root Length (fine)	322.22	327.56	1.27	-4.21	0.001	313.64	308.92	1.09	4.33	<0.001
Root Dry Matter Content (coarse)	11.24	11.18	0.04	1.73	0.043	12.48	12.98	0.04	-13.33	0.001
Root Dry Matter Content (fine)	5.22	5.24	0.01	-1.53	0.069	5.52	5.53	0.01	-0.42	0.348

site	Bar T Bar, n=979					Petrified Forest, n=471				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	19.52	19.93	0.09	-4.68	0.001	17.49	17.96	0.19	-2.42	0.012
Specific Leaf Area	22.08	22.06	0.07	0.27	0.599	22.74	21.04	0.19	8.74	<0.001
Leaf Dry Matter Content	23.25	22.99	0.07	3.91	<0.001	25.69	24.33	0.24	5.58	<0.001
Root:Shoot	0.44	0.43	0.00	1.19	0.122	0.45	0.47	0.01	-3.13	0.001
Specific Root Length (coarse)	26.94	27.30	0.12	-3.06	0.002	26.03	27.03	0.43	-2.34	0.008
Specific Root Length (fine)	311.59	308.80	1.34	2.08	0.016	312.71	256.06	4.28	13.24	<0.001
Root Dry Matter Content (coarse)	12.51	12.97	0.04	-10.55	0.001	12.31	13.91	0.16	-10.07	0.001
Root Dry Matter Content (fine)	5.55	5.53	0.02	1.12	0.123	5.53	5.65	0.05	-2.13	0.011

site	Montezuma Well, n=904					Spider Web, n=507				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	17.67	17.95	0.09	-3.21	0.001	19.35	17.96	0.19	7.43	<0.001
Specific Leaf Area	22.18	21.04	0.08	13.53	<0.001	23.93	21.03	0.18	16.06	<0.001
Leaf Dry Matter Content	24.78	24.33	0.11	3.97	<0.001	27.40	24.34	0.24	12.93	<0.001

Root:Shoot	0.45	0.47	0.00	-7.22	0.001	0.50	0.47	0.01	3.85	0.001
Specific Root Length (coarse)	26.04	27.03	0.19	-5.16	0.001	24.65	27.02	0.41	-5.74	0.001
Specific Root Length (fine)	273.69	256.03	1.90	9.31	<0.001	289.93	255.78	4.06	8.42	<0.001
Root Dry Matter Content (coarse)	12.71	13.91	0.07	-17.16	0.001	12.32	13.91	0.15	-10.41	0.001
Root Dry Matter Content (fine)	5.51	5.65	0.02	-5.98	0.001	5.64	5.65	0.05	-0.13	0.442

site	Canyonlands, n=975					La Sal, n=879				
trait	observed	null mean	null sd	SES	P	observed	null mean	null sd	SES	P
Height	23.30	23.30	0.13	0.03	0.520	23.85	23.30	0.16	3.47	<0.001
Specific Leaf Area	22.58	22.94	0.07	-5.31	0.001	23.32	22.95	0.09	4.18	<0.001
Leaf Dry Matter Content	22.75	22.66	0.07	1.23	0.104	22.94	22.66	0.09	3.27	<0.001
Root:Shoot	0.47	0.47	0.00	2.25	0.014	0.46	0.47	0.00	-5.80	0.001
Specific Root Length (coarse)	26.84	26.56	0.11	2.42	0.007	27.40	26.56	0.15	5.75	<0.001
Specific Root Length (fine)	338.25	327.59	1.36	7.83	<0.001	324.50	327.56	1.72	-1.78	0.037
Root Dry Matter Content (coarse)	10.76	11.18	0.04	-10.80	0.001	10.55	11.18	0.05	-12.42	0.001
Root Dry Matter Content (fine)	5.23	5.24	0.01	-0.66	0.261	5.03	5.24	0.02	-12.81	0.001

Table S3. H1 results for Community-weighted mean (CWM). For each site, “n” indicates the number of individuals that survived planting. Values were calculated from greenhouse trait measurements for each species.

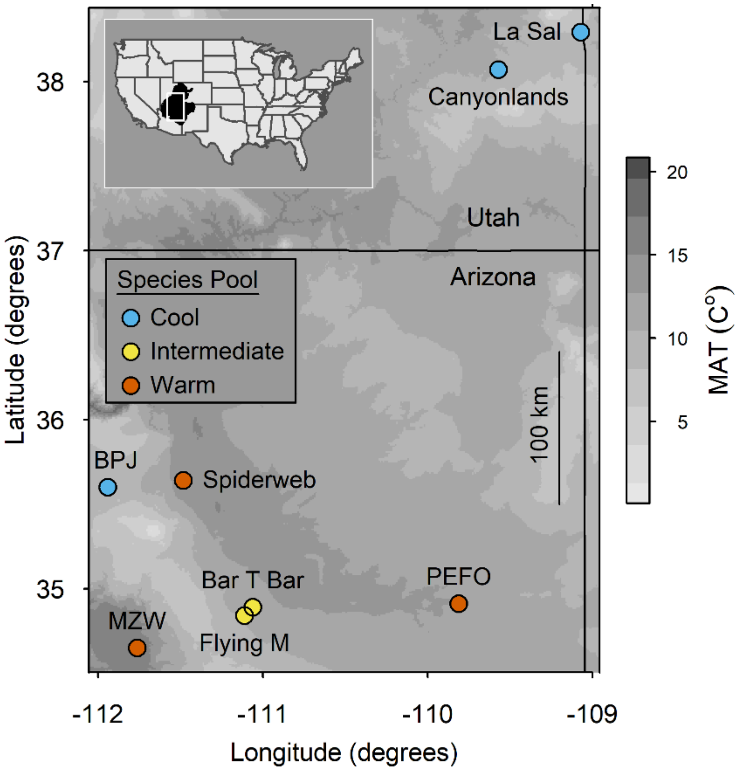
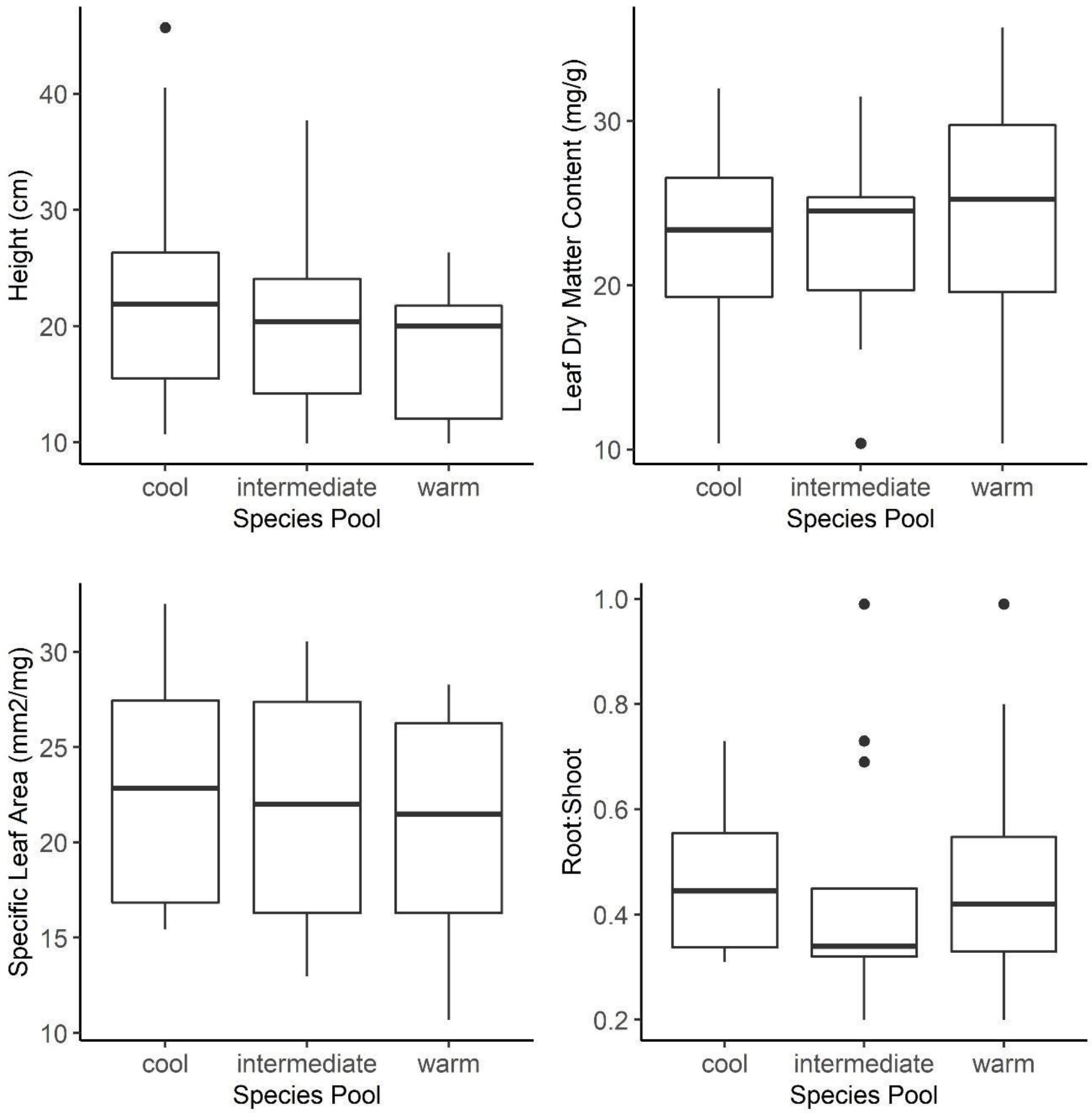
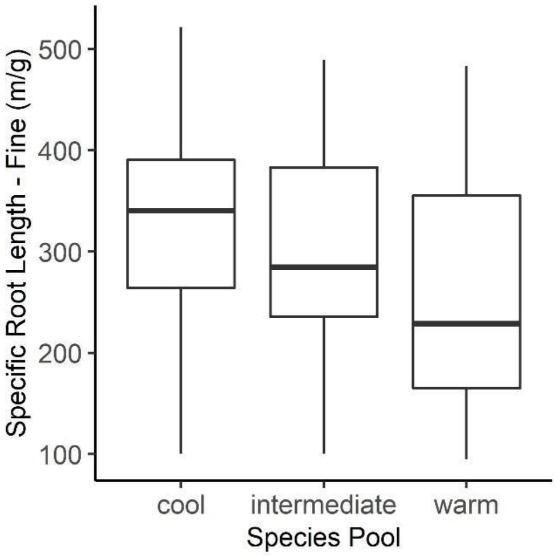
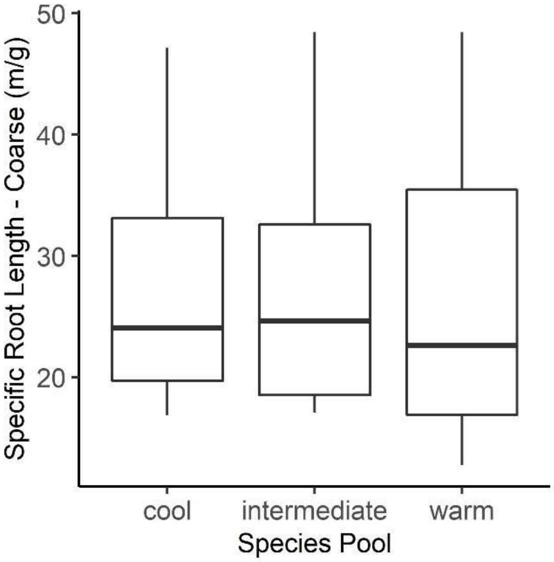


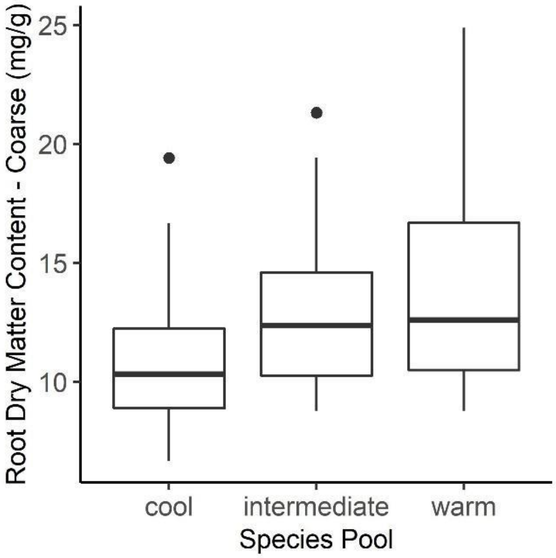
Figure S1. Map of sites within the Colorado Plateau (colored black on United States inset). Background is Mean Annual Temperature.

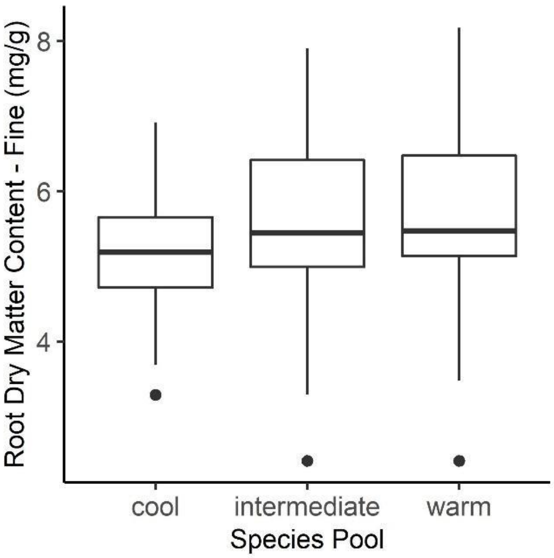
Appendix S1. Boxplots showing results from multivariate analysis of variance for trait differences in species pools, no significant differences found.




Specific Root Length - Fine (m/g)
500
400
300
200
100
cool
intermediate
warm
Species Pool


Specific Root Length - Coarse (m/g)
50
40
30
20
cool
intermediate
warm
Species Pool


Root Dry Matter Content - Coarse (mg/g)
25
20
15
10
cool
intermediate
warm
Species Pool


Root Dry Matter Content - Fine (mg/g)
8
6
4
cool
intermediate
warm
Species Pool

Authors: Kathleen R. Balazs, Seth M. Munson, Bradley J. Butterfield

Restoration of primary productivity in drylands supports weed suppression and erosion mitigation

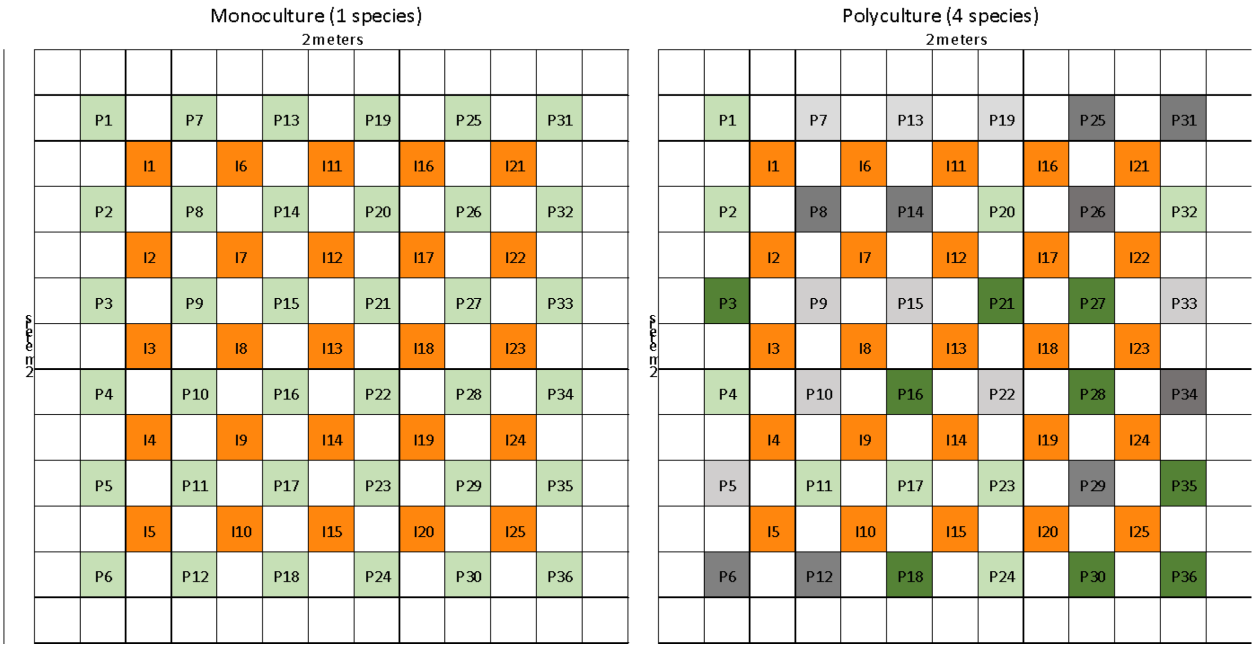


Figure S1. Plot layout. P1-P36 represent planted individuals, I1-I25 represent interspaces where soil measurements were collected.

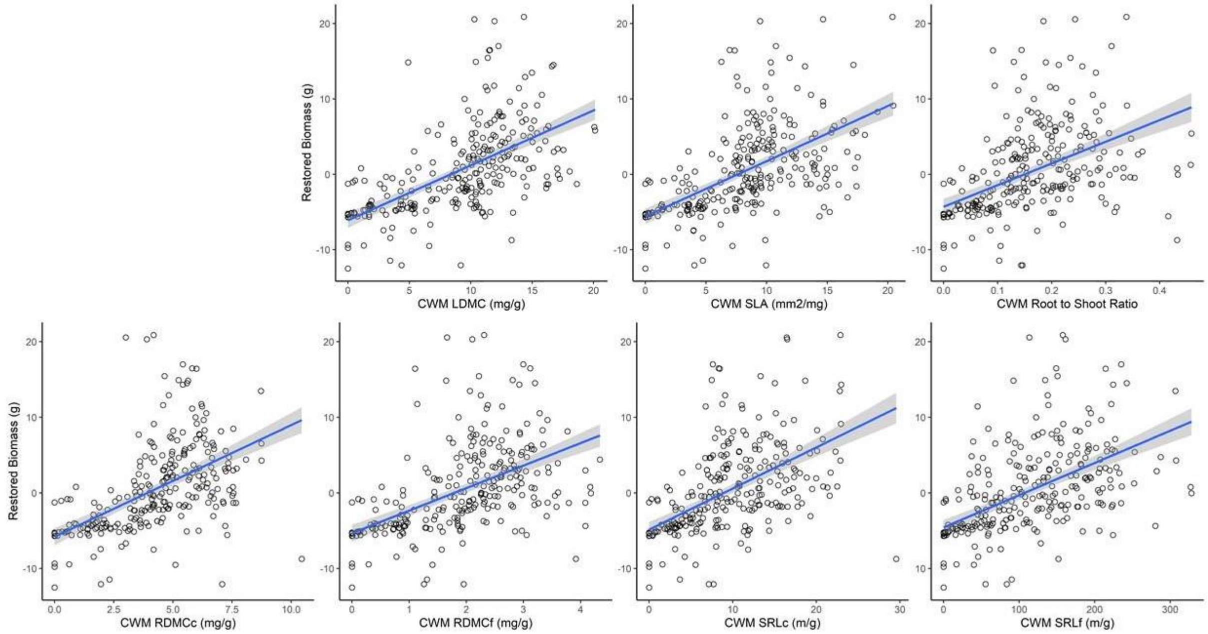


Figure S2. Restored plot-level aboveground biomass as a function of CWM trait values. Sample size = 288.

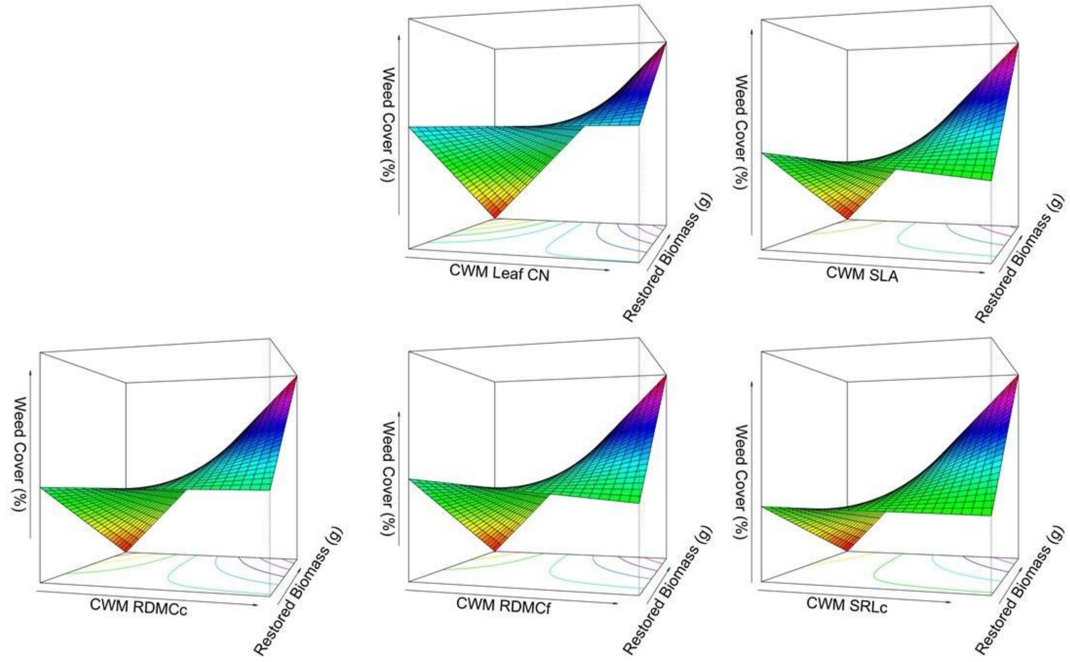


Figure S3. Fitted models of weed cover as a function of biomass x CWM trait values. Contour lines and color gradient show weed cover at various combinations of restored biomass and CWM trait values. Sample size = 288.

type	model (forced 0 intercept)	Rsq	df
grass	AGB_g ~ 0 + height_cm + LDMC	0.773	160
forbs	Total_Biomass ~ 0 + height_cm + LDMC	0.7718	99
forbs	Total_Biomass ~ 0 + height_cm + SLA	0.7695	99
grass	AGB_g ~ 0 + height_cm	0.767	163
grass	AGB_g ~ 0 + height_cm + SLA	0.766	162
forbs	Total_Biomass~ 0 + height_cm	0.763	100
grass	AGB_g ~ 0 + ellipsoid	0.763	163
grass	AGB_g ~ 0 + pyramid	0.763	163
grass	AGB_g ~ 0 + cone	0.763	163
grass	Total_Biomass ~ 0 + height_cm + LDMC	0.760	160
forbs	AGB_g ~ 0 + height_cm + LDMC	0.7598	99
forbs	AGB_g ~ 0 + height_cm + SLA	0.7597	99
all	AGB_g ~ 0 + height_cm + LDMC	0.755	261
forbs	AGB_g ~ 0 + height_cm	0.753	100
grass	Total_Biomass ~ 0 + height_cm + SLA	0.749	162
all	Total_Biomass ~ 0 + height_cm + LDMC	0.749	261
all	AGB_g ~ 0 + height_cm + SLA	0.748	263
grass	Total_Biomass~ 0 + height_cm	0.747	163
all	AGB_g ~ 0 + height_cm	0.745	264
all	Total_Biomass ~ 0 + height_cm + SLA	0.740	263
all	Total_Biomass~ 0 + height_cm	0.732	264
grass	Total_Biomass ~ 0 + ellipsoid	0.727	163
grass	AGB_g ~ 0 + LDMC	0.691	161
all	AGB_g ~ 0 + LDMC	0.676	262
forbs	AGB_g ~ 0 + LDMC	0.6489	99
all	AGB_g ~ 0 + w_w	0.648	264
all	AGB_g ~ 0 + ellipsoid	0.583	264

all	AGB_g ~ 0 + pyramid	0.583	264
all	AGB_g ~ 0 + cone	0.583	264
forbs	AGB_g ~ 0 + ellipsoid	0.555	100
forbs	AGB_g ~ 0 + pyramid	0.5551	100
forbs	AGB_g ~ 0 + cone	0.5551	100
all	Total_Biomass ~ 0 + ellipsoid	0.555	264
forbs	Total_Biomass ~ 0 + ellipsoid	0.554	100

Table S1. Models predicting biomass from traits of greenhouse grown individuals. Competing models included height, two perpendicular width measurements, volume, or leaf dry matter content (LDMC) in predicting aboveground biomass (AGB) or total biomass.

model	SS	df	MS	F	p-value
restored biomass ~ treatment + site					
control vs. planted	1671	1	1670	67	<0.001
site	5232	7	748	30	<0.001
weed cover ~ treatment + site					
control vs. planted	523	1	523	22	<0.001
site	47264	7	6752	283	<0.001
surface stability ~ treatment + site					
control vs. planted	7	1	7	5	0.0318
site	660	7	94	63	<0.001
infiltration ~ treatment + site					
bare/low biomass versus established	32210	1	32210	12	<0.001
site	1061062	7	151580	55	<0.001
subsurface stability ~ treatment + site					
bare/low biomass versus established	10	1	10	6	0.0154
site	377	7	54	31	<0.001
subsurface stability ~ treatment + site					
bare/low biomass versus established	2	1	2	42	<0.001
site	79	7	11	197	<0.001
subsurface stability ~ treatment + site					
bare/low biomass versus established	3	1	3	5	0.0254
site	346	7	49	76	<0.001

Table S2. Two-way analysis of variance for treatment and site effects on indicators of ecosystem functioning. There is significant difference between treatments (control or low biomass plots versus higher biomass planted plots).

		Biomass (n=288)				
	residuals~FD	t	p	R^2	AIC	ΔAIC
Functional Diversity Indices	~1 (null model)	0.0	1.00	0.00	-310.6	1.3
	FRic	-1.5	1.28	0.01	-310.9	1.0
	FEve	-1.4	0.18	0.01	-310.4	1.5
	FDiv	-1.8	0.07	0.01	-311.9	0.0

Table S3. Results from step 3. Biomass ~ FD index. Akaike Information Criterion (AIC) was used to determine which model was the most parsimonious; models with a delta AIC of less than 2 were considered equally parsimonious as the model with the lowest AIC value.

		a. Weed Cover (n=288)					b. Infiltration Rate (n=562)					c. Surface Stability (n=576)				
	residuals~FD	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC
Functional Diversity Indices	~1 (null model)	**0.0**	**1.00**	**0.00**	**-222.3**	**0.0**	**0.0**	**1.00**	**0.00**	**-127.3**	**1.1**	**0.0**	**1.00**	**0.00**	**231.0**	**0.0**
	biomass	0.0	1.00	0.00	-220.3	2.0	0.0	1.00	0.00	-125.3	3.1	0.0	1.00	0.00	233.0	2.0
	FRic	0.5	0.59	0.00	-220.6	1.7	1.8	0.08	0.01	-128.4	0.0	-1.2	0.23	0.00	231.5	0.5
	biomass	-0.3	0.75				-0.4	0.71				0.2	0.84			
	FRic	-0.2	0.85				0.4	0.68				-1.2	0.24			
	biomass x FRic	0.5	0.64	0.00	-216.8	5.5	0.4	0.73	0.01	-124.7	3.8	0.8	0.45	0.00	234.8	3.8
	FEve	0.1	0.89	0.00	-220.3	2.0	1.5	0.13	0.00	-127.7	0.7	-1.1	0.25	0.00	231.6	0.7
	biomass	-0.3	0.76				-0.4	0.68				0.3	0.75			
	FEve	-0.6	0.58				0.5	0.63				-0.9	0.34			
	biomass x FEve	0.7	0.49	0.00	-216.8	5.5	0.1	0.96	0.01	-123.9	4.5	0.5	0.60	0.00	235.2	4.2

FDiv	0.7	0.48	0.00	-220.8	1.5	1.5	0.14	0.00	-127.6	0.8	-1.2	0.22	0.00	231.4	0.4
biomass	-0.5	0.64				-0.4	0.66				0.4	0.71			
FDiv	-0.1	0.90				0.3	0.77				-0.9	0.35			
biomass x FDiv	0.5	0.60	0.00	-217.2	5.1	0.3	0.79	0.00	-123.8	4.6	0.5	0.64	0.00	234.9	4.0

Functional Diversity Indices

	d. Subsurface Stability (n=576)					e. Penetration Resistance (n=576)					f. Shear Strength (n=576)				
residuals~FD	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC
~1 (null model)	**0.0**	**1.00**	**0.00**	**240.2**	**0.0**	**0.0**	**1.00**	**0.00**	**-676.7**	**1.9**	**0.0**	**1.00**	**0.00**	**-318.3**	**0.0**
biomass	1.0	0.33	0.00	241.3	1.1	0.0	1.00	0.00	-674.7	3.9	**0.0**	**1.00**	**0.00**	**-316.3**	**2.0**
FRic	-0.7	0.46	0.00	241.7	1.5	**-2.0**	**0.05**	**0.01**	**-678.6**	**0.0**	**0.3**	**0.78**	**0.00**	**-316.3**	**1.9**
biomass	1.3	0.21				0.6	0.53				-0.2	0.83			
FRic	-0.1	0.90				-0.6	0.55				-0.8	0.45			
biomass x FRic	-0.3	0.77	0.00	244.1	3.8	-0.2	0.85	0.01	-675.0	3.6	0.9	0.37	0.00	-313.2	5.1
FEve	-0.8	0.42	0.00	241.6	1.3	**-1.6**	**0.10**	**0.01**	**-677.4**	**1.2**	**-0.5**	**0.59**	**0.00**	**-316.5**	**1.7**
biomass	1.2	0.22				0.6	0.55				-0.1	0.94			
FEve	-0.9	0.35				-0.7	0.47				-1.6	0.12			
biomass x FEve	0.5	0.61	0.01	243.5	3.2	0.1	0.94	0.01	-673.8	4.8	1.5	0.15	0.00	-314.7	3.6
FDiv	-0.7	0.47	0.00	241.7	1.5	**-1.9**	**0.06**	**0.01**	**-678.2**	**0.4**	**-0.3**	**0.75**	**0.00**	**-316.4**	**1.9**
biomass	1.2	0.23				0.7	0.47				-0.2	0.88			
FDiv	-0.8	0.41				-0.8	0.45				-1.5	0.15			
biomass x FDiv	0.4	0.68	0.00	243.8	3.5	0.0	1.00	0.01	-674.7	3.9	1.4	0.15	0.00	-314.4	3.8

Table S4. Results from step 3. Indicator of ecosystem function ~ Biomass * FD index. Akaike Information Criterion (AIC) was used to determine which model was the most parsimonious; models with a delta AIC of less than 2 were considered equivalently parsimonious as the model with the lowest AIC value.

	a. Biomass (n=288)					b. Weed Cover (n=288)					c. Infiltration Rate (n=562)					d. Surface Stability (n=576)				
	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC
~1 (null model)	0.00	1.00	0.00	-313.9	41.22	0.00	1.00	0.00	-222.3	2.82	0.00	1.00	0.00	-127.3	6.49	0.00	1.00	0.00	231.0	0.91
Achnatherum hymenoides	4.06	<0.001	0.05	-328.0	27.10	-0.22	0.83	0.00	-220.4	4.77	-0.82	0.41	0.00	-126.0	7.82	1.65	0.10	0.01	230.2	0.19
Achillea millefolium	0.72	0.47	0.00	-312.4	42.70	1.58	0.12	0.01	-222.8	2.30	1.36	0.18	0.00	-127.2	6.64	0.70	0.49	0.00	232.5	2.42
Aristida purpurea	0.73	0.47	0.00	-312.4	42.69	1.19	0.23	0.01	-221.7	3.38	2.29	0.02	0.01	-130.6	3.26	-1.71	0.09	0.01	230.0	0.00
Asclepias tuberosa	0.50	0.62	0.00	-312.1	42.97	1.20	0.23	0.01	-221.7	3.38	1.25	0.21	0.00	-126.9	6.93	1.32	0.19	0.00	231.2	1.16
Baileya multiradiata	3.34	<0.001	0.04	-322.9	32.22	0.24	0.81	0.00	-220.4	4.76	-0.34	0.74	0.00	-125.4	8.38	1.13	0.26	0.00	231.7	1.63
Bouteloua curtipendula	2.04	0.04	0.01	-316.0	39.05	0.67	0.50	0.00	-220.8	4.36	-0.52	0.60	0.00	-125.6	8.22	0.41	0.68	0.00	232.8	2.74
Bouteloua eripoda	0.55	0.58	0.00	-312.2	42.92	0.10	0.92	0.00	-220.3	4.80	0.25	0.81	0.00	-125.4	8.43	-0.29	0.77	0.00	232.9	2.83
Bouteloua gracilis	-0.45	0.66	0.00	-312.1	43.02	0.22	0.83	0.00	-220.3	4.77	0.04	0.97	0.00	-125.3	8.49	0.05	0.96	0.00	233.0	2.91
Bromus marginatus	0.87	0.39	0.00	-312.6	42.47	0.67	0.50	0.00	-220.8	4.36	-0.52	0.60	0.00	-125.6	8.22	1.17	0.24	0.00	231.6	1.54
Dalea candida	-3.44	<0.001	0.04	-323.6	31.52	1.80	0.07	0.01	-223.6	1.57	0.72	0.47	0.00	-125.9	7.97	0.29	0.77	0.00	232.9	2.83
Elymus elymoides	1.62	0.11	0.01	-314.5	40.58	-0.09	0.93	0.00	-220.3	4.81	1.08	0.28	0.00	-126.5	7.32	-1.13	0.26	0.00	231.7	1.64
Elymus trachycaulus	0.70	0.48	0.00	-312.4	42.73	-0.52	0.60	0.00	-220.6	4.54	0.96	0.34	0.00	-126.3	7.56	0.68	0.50	0.00	232.5	2.45
Elymus wawawaiensis	**6.81**	<0.001	**0.14**	**-355.1**	**0.00**	-0.40	0.69	0.00	-220.5	4.65	-0.10	0.92	0.00	-125.3	8.48	-0.54	0.59	0.00	232.7	2.62
Hedysarum boreale	-2.40	0.02	0.02	-317.6	37.47	0.27	0.79	0.00	-220.4	4.74	**2.92**	**0.00**	**0.02**	**-133.8**	**0.00**	0.20	0.84	0.00	232.9	2.87

Hesperostipa comata	2.79	0.01	0.03	-319.6	35.51	-0.99	0.32	0.00	-221.3	3.83	-0.71	0.48	0.00	-125.8	7.98	-0.06	0.95	0.00	233.0	2.91
Heliomeris multiflora	-0.95	0.34	0.00	-312.8	42.31	**2.20**	**0.03**	**0.02**	**-225.1**	**0.00**	-0.67	0.51	0.00	-125.8	8.05	0.42	0.67	0.00	232.8	2.73
Krascheninnikovia lanata	1.61	0.11	0.01	-314.5	40.62	1.34	0.18	0.01	-222.1	3.03	-1.63	0.11	0.01	-128.0	5.84	1.03	0.31	0.00	231.9	1.86
Leymus cinereus	3.59	<0.001	0.04	-324.6	30.50	-0.59	0.56	0.00	-220.6	4.47	-0.73	0.47	0.00	-125.9	7.95	-0.63	0.53	0.00	232.6	2.51
Linum lewisii	0.57	0.57	0.00	-312.2	42.89	0.93	0.36	0.00	-221.2	3.95	1.74	0.08	0.01	-128.4	5.47	-0.09	0.93	0.00	233.0	2.91
Machaeranthera tanacetifolia	0.25	0.80	0.00	-311.9	43.16	0.63	0.53	0.00	-220.7	4.41	-1.52	0.13	0.00	-127.6	6.19	0.36	0.72	0.00	232.8	2.79
Pascopyrum smithii	2.50	0.01	0.02	-318.1	37.00	-1.04	0.30	0.00	-221.4	3.72	0.45	0.66	0.00	-125.5	8.29	-0.58	0.57	0.00	232.6	2.58
Penstemon palmeri	0.36	0.72	0.00	-312.0	43.09	1.75	0.08	0.01	-223.4	1.75	-0.23	0.82	0.00	-125.4	8.44	1.49	0.14	0.00	230.7	0.69
Pleuraphis jamesii	1.81	0.07	0.01	-315.2	39.94	0.25	0.81	0.00	-220.4	4.75	-1.49	0.14	0.00	-127.6	6.27	0.22	0.83	0.00	232.9	2.87
Pleuraphis mutica	-0.59	0.55	0.00	-312.2	42.87	1.11	0.27	0.00	-221.5	3.57	0.14	0.89	0.00	-125.4	8.47	-0.22	0.83	0.00	232.9	2.87
Poa secunda	0.58	0.59	0.00	-312.2	42.92	-1.75	0.08	0.01	-223.4	1.76	**-2.66**	**0.01**	**0.01**	**-132.4**	**1.46**	-1.16	0.25	0.00	231.6	1.57
Pseudoroegneria spicata	2.67	0.01	0.02	-318.9	36.15	-1.10	0.27	0.00	-221.5	3.61	1.41	0.16	0.00	-127.3	6.51	-0.83	0.41	0.00	232.3	2.22
Senna covesii	0.62	0.53	0.00	-312.3	42.83	0.66	0.51	0.00	-220.7	4.38	-0.04	0.97	0.00	-125.3	8.49	-1.00	0.32	0.00	232.0	1.92
Sporobolus cryptandrus	0.98	0.33	0.00	-312.8	42.25	-0.20	0.84	0.00	-220.3	4.77	-0.96	0.34	0.00	-126.3	7.57	-0.85	0.40	0.00	232.2	2.19
Sphaeralcea grossulariifolia	-3.16	0.00	0.03	-321.8	33.33	0.09	0.93	0.00	-220.3	4.81	1.17	0.24	0.00	-126.7	7.13	0.31	0.76	0.00	232.9	2.82
	e. Subsurface Stability (n=576)					f. Penetration Resistance (n=576)					g. Shear Strength (n=576)									
	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC	t	p	R^2	AIC	ΔAIC					

~1 (null model)	0.00	1.00	0.00	240.2	6.85	0.00	1.00	0.00	-676.7	0.91	0.00	1.00	0.00	-318.3	15.29
Achnatherum hymenoides	0.71	0.48	0.00	241.7	8.34	0.87	0.39	0.00	-675.4	2.15	-0.55	0.58	0.00	-316.6	16.99
Achillea millefolium	**2.98**	**0.00**	**0.02**	**233.4**	**0.00**	1.20	0.23	0.00	-676.1	1.47	2.76	0.00	0.01	-323.9	9.70
Aristida purpurea	-1.92	0.06	0.01	238.6	5.16	-0.37	0.71	0.00	-674.8	2.77	0.63	0.53	0.00	-316.7	16.89
Asclepias tuberosa	1.63	0.11	0.01	239.6	6.20	-0.91	0.37	0.00	-675.5	2.08	1.71	0.09	0.01	-319.2	14.38
Baileya multiradiata	-0.29	0.78	0.00	242.2	8.76	-0.31	0.76	0.00	-674.8	2.81	1.07	0.29	0.00	-317.4	16.14
Bouteloua curtipendula	0.30	0.77	0.00	242.2	8.76	-0.31	0.76	0.00	-674.8	2.81	1.98	0.05	0.01	-320.2	13.36
Bouteloua eripoda	-0.30	0.77	0.00	242.2	8.76	-0.91	0.36	0.00	-675.5	2.08	-1.02	0.31	0.00	-317.3	16.25
Bouteloua gracilis	0.40	0.69	0.00	242.1	8.69	-0.49	0.63	0.00	-674.9	2.67	0.31	0.76	0.00	-316.4	17.20
Bromus marginatus	-0.29	0.77	0.00	242.2	8.76	-1.01	0.32	0.00	-675.7	1.89	1.07	0.28	0.00	-317.4	16.13
Dalea candida	-0.90	0.37	0.00	241.4	8.03	0.85	0.40	0.00	-675.4	2.19	0.45	0.66	0.00	-316.5	17.09
Elymus elymoides	-0.52	0.61	0.00	242.0	8.58	1.13	0.26	0.00	-676.0	1.62	-0.20	0.84	0.00	-316.3	17.25
Elymus trachycaulus	-0.10	0.92	0.00	242.2	8.84	0.42	0.67	0.00	-674.9	2.73	-0.12	0.90	0.00	-316.3	17.28
Elymus wawawaiensis	0.47	0.64	0.00	242.0	8.63	0.06	0.95	0.00	-674.7	2.90	0.98	0.33	0.00	-317.2	16.34
Hedysarum boreale	-1.54	0.12	0.00	239.9	6.47	-0.74	0.46	0.00	-675.2	2.36	-1.28	0.20	0.00	-317.9	15.64
Hesperostipa comata	1.59	0.11	0.00	239.7	6.32	0.81	0.42	0.00	-675.3	2.24	2.03	0.04	0.01	-320.4	13.18

Heliomeris multiflora	1.97	0.05	0.01	238.3	4.95	1.70	0.09	0.01	-677.6	0.00	1.09	0.28	0.00	-317.5	16.10
Krascheninnikovia lanata	0.24	0.81	0.00	242.2	8.79	0.96	0.34	0.00	-675.6	1.98	-0.29	0.77	0.00	-316.3	17.21
Leymus cinereus	-0.16	0.88	0.00	242.2	8.82	0.37	0.71	0.00	-674.8	2.77	-0.51	0.61	0.00	-316.5	17.03
Linum lewisii	-0.02	0.98	0.00	242.2	8.85	-0.04	0.97	0.00	-674.7	2.90	0.07	0.95	0.00	-316.3	17.29
Machaeranthera tanacetifolia	-0.84	0.40	0.00	241.5	8.15	1.33	0.19	0.00	-676.4	1.15	2.49	0.01	0.01	-322.4	11.11
Pascopyrum smithii	-0.50	0.62	0.00	242.0	8.60	-1.66	0.10	0.01	-677.4	0.15	**-4.18**	**<0.001**	**0.03**	**-333.6**	**0.00**
Penstemon palmeri	0.80	0.42	0.00	241.6	8.20	-0.71	0.48	0.00	-675.2	2.40	0.46	0.64	0.00	-316.5	17.08
Pleuraphis jamesii	-0.59	0.56	0.00	241.9	8.50	-0.84	0.40	0.00	-675.4	2.20	-1.39	0.17	0.00	-318.2	15.35
Pleuraphis mutica	-0.80	0.42	0.00	241.6	8.20	0.87	0.39	0.00	-675.4	2.15	1.69	0.09	0.01	-319.1	14.45
Poa secunda	0.00	1.00	0.00	242.2	8.85	0.24	0.81	0.00	-674.7	2.85	-0.40	0.69	0.00	-316.4	17.13
Pseudoroegneria spicata	-0.10	0.93	0.00	242.2	8.84	-1.07	0.28	0.00	-675.8	1.75	-0.29	0.77	0.00	-316.3	17.20
Senna covesii	0.39	0.70	0.00	242.1	8.70	0.07	0.94	0.00	-674.7	2.90	2.57	0.01	0.01	-322.9	10.69
Sporobolus cryptandrus	0.23	0.82	0.00	242.2	8.80	-0.74	0.46	0.00	-675.2	2.36	-0.62	0.54	0.00	-316.6	16.91
Sphaeralcea grossulariifolia	0.02	0.99	0.00	242.2	8.85	-0.12	0.90	0.00	-674.7	2.89	**0.18**	**0.86**	0.00	-316.3	17.26

Table S5. Results from step 4. Ecosystem Service Indicator ~ Species. Akaike Information Criterion (AIC) was used to determine which model was the most parsimonious; models with a delta AIC of less than 2 were considered equally parsimonious as the model with the lowest AIC value.