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RESEARCH ARTICLE

Seed transfer models applied to commercial germplasms reveal trait divergence from wildland populations of a restoration grass species

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Abstract

Introduction: Due to the prevalence of local adaptation in plants, the provenance of seed sources can impact plant community restoration outcomes. Yet programs developing commercial germplasm releases often overlook local adaptation as a development criterion, leading to the selection of traits that may not support restoration success. In many cases, commercial germplasms are more available than plant materials developed explicitly considering spatial adaptation patterns.

Objectives: This study aims to demonstrate how seed transfer models can calibrate restoration guidance for commercially available germplasms of bottlebrush squirreltail (*Elymus elymoides*) in the Western United States. The goal is to assess the alignment of these germplasms with spatial adaptation patterns predicted by seed transfer models.

Methods: We applied seed transfer models, derived from a common garden study of wildland seed sources, to evaluate six commercially available germplasms of bottlebrush squirreltail grown alongside the wildland sources. These models predicted trait expression in relation to the climate of origin. Predicted traits were compared with actual traits to find divergence that could be due to evolutionary shifts during germplasm development.

Results: Our analysis revealed that distances between actual and predicted trait values were generally greater for commercial germplasms than for wildland populations, indicating evolutionary changes during the germplasm collection and development processes.

Conclusions: Even when germplasm is developed under controlled standards, significant divergence from expected traits can occur. This emphasizes the need for assessing the degree to which seed transfer guidance frameworks developed for wildland populations can be used to guide seed transfer of commercial germplasms.

Implications for Practice: Restoration practitioners should carefully consider how commercially available germplasms might perform in local environments. The methods presented here provide a way to assess whether seed transfer models developed for wildland populations can be used to guide seed transfer of commercial germplasms. These methods can also be used to map areas where a seed transfer model is likely to be most accurate for a given germplasm. As demonstrated, these methods can reveal different degrees of alignment among different commercially available germplasms. This approach can guide the appropriate use of commercial germplasms in restoration projects, improving the chances of success in restoration efforts.

Key words: commercial germplasm releases, *Elymus elymoides*, local adaptation, plant material development, provenance, restoration seed sourcing

Introduction

The provenance of seed sources, particularly the climate of origin, can affect the success of plant community restoration, due to the likelihood that source populations are adapted to local site conditions where they have evolved through relevant time periods (Baughman et al. 2019). Given the potential importance of local adaptation to successful restoration, germplasm provenance is seen by the international restoration community as key to restoration success (Breed et al. 2018). However, strict local provenancing (hereafter "seed sourcing"), with selection of seed sources limited to a small area near a restoration site, may lead to difficulties in procuring sufficient seed for restoration needs if local populations have low reproductive output (Broadhurst et al. 2008). Use of strictly local populations may also be detrimental to restoration success if local populations

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have experienced loss of adaptive alleles through genetic drift, express deleterious alleles due to inbreeding, or do not harbor enough genetic diversity to respond to novel selection pressures that may arise from seed transfer itself or from changing environmental conditions (Montalvo et al. 1997; Havens et al. 2015).

Seed transfer zones are developed from transfer functions (regression models or algorithmic equivalents) that model climate–trait relationships across a plant species' range and are mapped as either a set of bounded regions (fixed-boundary seed zones) or as climate suitability gradients matching source locations or restoration sites (floating- or focal-point seed zones) (Kilkenny 2015). Seed zones relax the need for strict local seed sourcing by defining larger regions within which seed sourcing and use are likely to be successful (Havens et al. 2015; Bucharova et al. 2019). To that end, there are concerted regional and international efforts to develop seed zones for native "workhorse" restoration species (Erickson 2008; Johnson et al. 2010; Durka et al. 2017) and to develop generalized seed zones for use in cases where genetic information is lacking (Bower et al. 2014; De Vitis et al. 2017; Richardson et al. 2024). Governmental agencies are also adopting policies and strategies that encourage or require the use of seed zones in restoration seed sourcing (Prasse et al. 2010; PCA 2015; NASEM 2023) and the use of appropriate seed transfer guidance frameworks has been called for in international standards for restoration seed trade and use (Pedrini & Dixon 2020). While seed zones can guide the use of seed sources developed and/or procured within these frameworks, it is less clear how plant materials developed outside of seed transfer guidance frameworks might fit into seed sourcing decisions, especially when these sources have been altered through deliberate or inadvertent selection and/or breeding in an agronomic setting.

Plant material development programs that produce and release commercially available germplasms have not always been concerned with local adaptation as a development criterion (Jones 2019), and sometimes select, either by favoring sources with desired phenotypes or by selection within germplasm lines, for traits negatively correlated with population persistence in natural environments (Leger & Baughman 2015; Blumenthal et al. 2021). Additionally, inadvertent selection or genetic drift may occur over multiple generations in agronomic or nursery production and result in trait shifts that lead to maladaptation at restoration sites (Espeland et al. 2017; Pizza et al. 2021). Nevertheless, the scale of seed needs in many global regions is large and increasing (Cross et al. 2020), often far exceeding amounts that can be supplied through wildland seed collections alone (Ladouceur et al. 2018). Meeting global restoration targets may require pragmatic approaches that leverage existing resources (Zinnen et al. 2021). Due to economies of scale in seed production, commercial germplasms are often the most readily available seed for restoration projects (Chivers et al. 2016; Ladouceur et al. 2018; Zinnen et al. 2021). Therefore, it is important to define areas where commercial germplasms are most likely to be useful by incorporating them into seed transfer guidance frameworks, where applicable (Erickson & Halford 2020). Evaluating the applicability of a seed transfer guidance framework for commercial germplasms is, in our view, an important first step, which can be accomplished by examining whether the commercial germplasms' climate–trait patterns are sufficiently aligned with those captured by the framework.

Regions with well-developed restoration seed markets can offer instructive examples of this type of incorporation. The Intermountain Region of the western United States contains some of the most imperiled ecosystems in the United States (Noss et al. 1995; Chambers & Wisdom 2009), due to a long history of overgrazing (Morris & Rowe 2014), exotic annual grass and forb invasions (Pilliod et al. 2017a), and increasingly frequent wildfires (Balch et al. 2013). This has led federal and state land management agencies to conduct post-wildfire seedings at massive scales, seeding over 50,000 ha in 15 different years between 1985 and 2014, with five of those years reaching or exceeding 250,000 ha of seeding (Pilliod et al. 2017b). Due to the scale of post-wildfire seeding and other restoration activities in the Intermountain Region, a substantial restoration seed market has developed (Monsen & Shaw 2001; Jones 2019). Recent strategies and assessments in the region have called for more collection, production, and use of locally and regionally sourced seed directed by seed transfer guidance frameworks (e.g. NNSP 2020) but non-market locally and regionally sourced seed supplies remain well below needed levels (NASEM 2023). There have been several attempts to place commercial germplasms into seed transfer guidance frameworks in the Intermountain Region (e.g. the Native Plant Seed Mapping Toolkit, https://www.usgs.gov/apps/seed-toolkit/) but so far, these attempts have mostly used climate of origin to predict locations where commercial germplasms might be most effective (e.g. Doherty et al. 2017) and, to our knowledge, none have explicitly incorporated data on adaptive trait variation in commercial germplasms. Because of the scale of restoration needs and practice, a well-developed restoration seed market, and concerted, but still nascent, attempts at developing seed transfer guidance frameworks that include commercial germplasms, examples from the Intermountain Region can provide important lessons for other global regions at various stages of restoration seed market and seed transfer guidance framework development.

Here we consider whether a seed transfer model developed for wildland populations of bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), a native "workhorse" restoration species in the Intermountain Region, can be applied to a set of currently available commercial germplasms. To address this question, we examine the degree to which this seed transfer model accurately predicts traits of commercial germplasms at the locations where they were originally sourced, relative to the corresponding accuracy of predictions based on wildland populations. We also demonstrate how predictive accuracy can be mapped to show the distribution of model applicability within an area of interest. These analyses allow us to assess whether (or to what degree, or where) these models reliably provide seed transfer guidance for commercial germplasms, based on whether trait expression patterns of these commercial germplasms diverge from what would be expected for the geographic locations and climates of their original collection sites.

Methods

Study Species

Bottlebrush squirreltail is a cool-season, short-lived, self-pollinating, perennial bunchgrass native to semiarid regions of western North America (Jones 1998). It is considered a "workhorse" species in native plant community restoration (Erickson 2008) and is one of the most commonly seeded bunchgrasses in the Intermountain Region (Jones 2019). It can colonize disturbed sites (Simmons & Rickard 2002), is relatively fire-tolerant (Ellsworth & Kauffman 2010) and is a potential competitor with the invasive grasses Medusahead (*Taeniatherum caput-medusae* [L.] Nevski) and Cheatgrass (*Bromus tectorum* L.) (McGlone et al. 2012; Sheley & James 2014). Trait variation at the population level has been shown to be associated with source environments (Blumenthal et al. 2021) and is potentially important in restoration outcomes (Leger et al. 2021).

Seed Transfer Model Development

Seed transfer models for bottlebrush squirreltail were developed following methods presented in Kilkenny et al. (2026). Broadly, we took trait measurements from plants representing 98 wildland populations grown at three common garden sites (Fig. 1), converted trait values into axes of trait variation using principal component (PC) analysis, then modeled the relationship between each significant PC axis and climate variation at population source locations using random forest modeling. Trait measurements were also taken from plants representing six commercial germplasms (Table 1) grown concurrently alongside the wildland populations at the common gardens, but these measurements were not used for developing the seed transfer models. The commercial germplasms, like the wildland populations, originated from an area spanning eight states and 11 U.S. Environmental Protection Agency (EPA) Level III Ecoregions (Omernik & Griffith 2014) which served as an area for mapping model predictions (Fig. 1).

Specifically, seed from the 98 wildland populations was collected between 2007 and 2010 by the authors in partnership with volunteers from multiple institutions (see Acknowledgments), while seed of the commercial germplasms was obtained directly from their developers at the USDA-ARS Forage and Range Laboratory in Logan, Utah or from the USDA-ARS National Plant Germplasm System repository at Pullman, Washington. Plants of both wildland populations and commercial germplasms were grown in a greenhouse for 18–41 weeks, depending on when germination occurred, before being transplanted to common gardens in fall 2011. Twelve individuals from each wildland population and commercial germplasm were planted across six blocks (two individuals per block) at each garden, for a total of 1248 plants per garden (3744 across the entire study). Phenology was monitored at least weekly during the growing season and every other day during significant phenological transitions (Table S1). Growth, reproductive and morphological traits were measured at the end of the growing season before senescence occurred (late July or August, depending on the site) (Table S1). Traits measured in 2013, after a season of growth and acclimatization in 2012, were used to build seed transfer models. Nine traits were included: aboveground dry biomass, plant height, leaf length, leaf width, leaf ratio (length/width), heading date, seed maturation date, number of inflorescences, and survival (from 2012 to 2013).

Each of the nine traits expressed at each of the three common gardens (with the exception of leaf ratio at Reno, which had low population-level variance and was removed from the dataset), was treated as a separate trait column of the input matrix for PC analysis using the *ade4* package in R (Dray & Dufour 2007; R Core Team 2016). Six PCs were retained for subsequent modeling based on a Monte Carlo significance test of the sums of eigenvalues (Dray & Dufour 2007; Dray 2008). Random forest models were built using the *randomForest* package in R (Liaw & Wiener 2002; R Core Team 2016) with PC axes as response variables and 30-year (1981–2010) normals for 23 climate variables (Table S2) at population source locations as predictor variables for each model. Values of climate variables at population source locations were obtained from the Climate of Western North America (ClimateWNA) computer application (Wang et al. 2016).

Random forest models for the six PC axes were projected geographically onto the mapping region through spatial predictions with the *raster* R package (Hijmans 2015; R Core Team 2016). Spatial predictions were applied to a 0.057 × 0.057 decimal degree (ca. 6 km × 6 km) grid of climate variables from ClimateWNA (Wang et al. 2016) for the mapping area in the Intermountain Region. The combined spatial predictions of the six PC axes served as the transfer function for a focal-point seed zone model capable of predicting climate suitability of seed sourced from any chosen location within the area. For a designated source location grid cell (focal point), the predicted climate suitability of each remaining grid cell (non-focal point) was calculated as the multivariate Euclidean distance connecting predicted positions of focal and non-focal cells in predicted multidimensional PC space. As explained in the following section, this framework also provided the basis for calculating the accuracy of climate suitability predictions.

Trait Space Comparisons Between Actual and Predicted Values

The multidimensional trait space defined by PC axes provided a framework for comparing actual trait values with those predicted by the transfer function. Since PC axes are orthogonal, that is, uncorrelated, and scaled by the amount of variation they capture, Euclidean distance is a suitable measure for quantifying distances between points with known positions relative to the axes (Teng et al. 2020). Our method thus entailed identifying actual and predicted positions on PC axes and calculating the Euclidean distance between them for each wildland population and commercial germplasm. Actual positions of wildland populations were pulled directly from the output of the PC analysis (i.e. the *li* table generated by *dudi.pca* in R package *ade4*; Dray & Dufour 2007). In the case of commercial germplasms, which were not included in the PC analysis, actual positions were inferred based on measured trait values (i.e. using the *suprow* function in *ade4*; Dray & Dufour 2007). Predicted

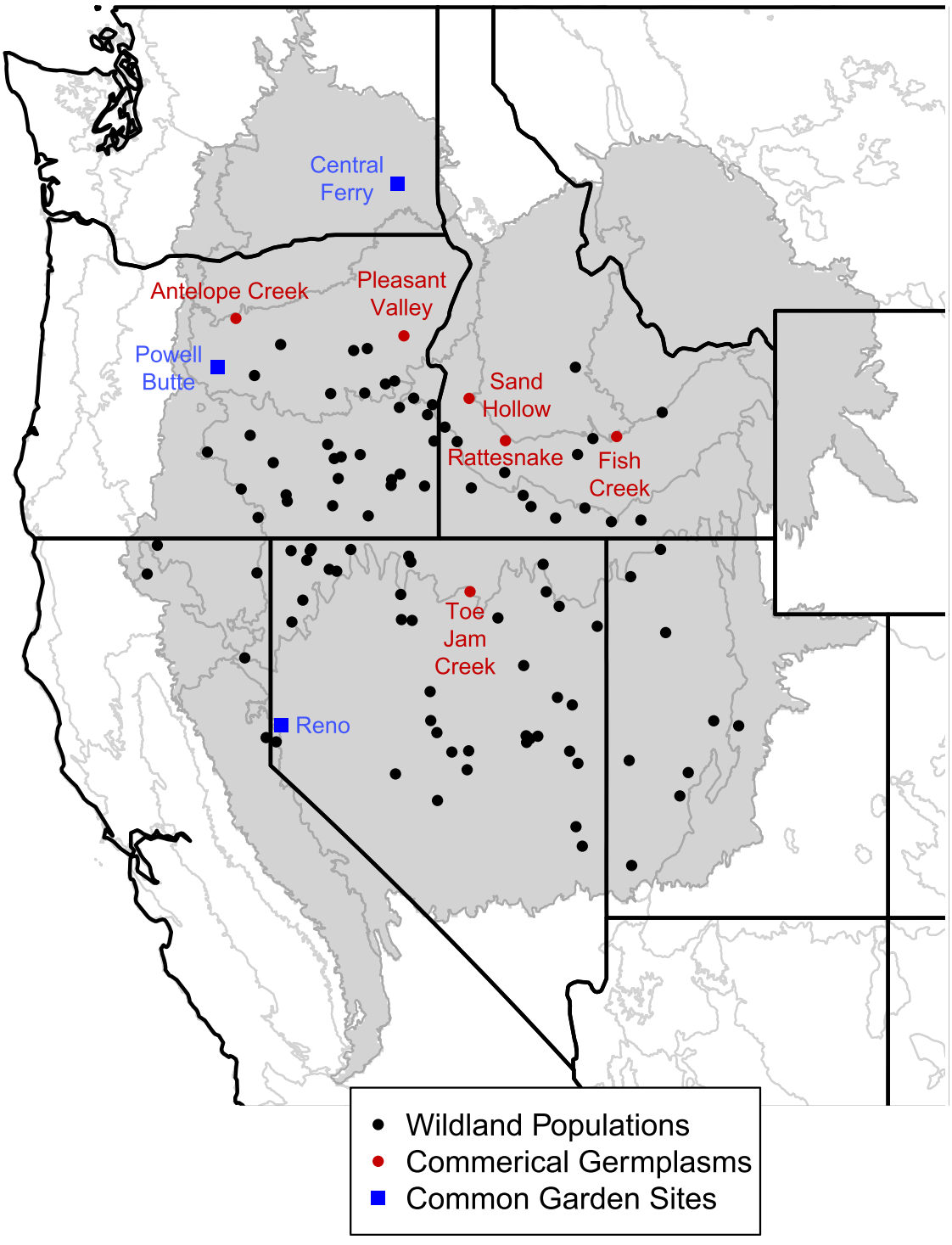

Figure 1. Source locations of wildland populations and commercial germplasms, and locations of common garden sites, in a mapping region spanning (shaded) eight states and 11 U.S. Environmental Protection Agency (EPA) Level III Ecoregions (Omernik & Griffith 2014).

positions were obtained by applying the transfer function for values of climate variables at the source location of each wildland population and commercial germplasm. For wildland populations, the same climate variable values were used for both building the transfer function and applying it predictively, such that distances between actual and predicted positions give an indication of the error or inaccuracy of the transfer function as a predictive model. For commercial germplasms, while the input

Table 1. Bottlebrush and big squirreltail (*Elymus elymoides* and *E. multisetus*) commercial germplasms grown alongside wildland populations at common gardens.

		Collection source location					
Germplasm	*Taxon*	*County, State*	*Elevation (m)*	*Lat., Long. (dd)*	*Collection year*	*Release year*	*Citation*
Antelope Creek	*E. elymoides* ssp. "C"	Wasco, Oregon	1111	44.9, −120.6	2003	2009	Jones et al. (2014)
Fish Creek	*E. elymoides* ssp. *elymoides*	Blaine, Idaho	1450	43.343, −113.863	1995	2003	Jones et al. (2004a)
Pleasant Valley	*E. elymoides* ssp. "C"	Baker, Oregon	1166	44.67, −117.62	2002	2010	Jones et al. (2014)
Rattlesnake	*E. elymoides* ssp. *elymoides*	Elmore, Idaho	1169	43.289, −115.836	1995	2007	Jones (2010)
Sand Hollow	*E. multisetus* (originally identified as *E. elymoides*)	Gem, Idaho	830	43.846, −116.464	1984	1996	Jones et al. (1998)
Toe Jam Creek	*E. elymoides* ssp. *californicus*	Elko, Nevada	1829	41.299, −116.464	1986 or before	2003	Jones et al. (2004b)

was different than what had been used to build the model, the null expectation was that distance values would fall within the same range as the wildland populations. To test the effect of this approach on commercial germplasm distance values, we examined results of supplementary analyses that (1) excluded wildland populations from the PC analysis, one at a time, in addition to commercial germplasms, and (2) included commercial germplasms in addition to all wildland populations in the PC analysis and subsequent modeling procedure (Supplement S1).

Predicted trait values were estimated from predicted positions on the PC axes by reversing the transformation from traits to PCs. First, the PC row coordinates matrix was multiplied by the column normed scores matrix (i.e. li % × % c1, where li and c1 are matrices returned by *dudi.pca* in *ade4*; Dray & Dufour 2007). The scaling step of the PC analysis was then reversed by multiplying each matrix cell value by the standard deviation of its corresponding trait, followed by the reversal of the centering step by adding on trait mean values (i.e. using *cent* and *norm* tables returned by *dudi.pca* in *ade4*; Dray & Dufour 2007).

Climate suitability maps were created for each commercial germplasm by applying transfer functions across grid cells within a set of focal ecoregions in the western United States. Climate normals were extracted for each grid cell using ClimateWNA (Wang et al. 2016), as in the case of source locations, so that PC axis positions could be predicted for the populations that presumably occur in unsampled cells. Predicted climate suitability for a given commercial germplasm in a given cell was quantified as the multidimensional Euclidean distance between the predicted position at the commercial germplasm's source location and the corresponding position predicted for the cell, where shorter distances indicate greater suitability. This procedure can be described as a focal point transfer model (Parker & van Niejenhuis 1996) applied using commercial germplasm source locations as focal points. For contrast, we also estimated and mapped climate suitability based on actual trait values of the commercial germplasms, which involved replacing predicted PC positions at a commercial germplasm's source location with positions directly inferred from measured traits (see preceding paragraphs of this section). Climate suitability based on actual traits did not involve a focal point and thus did not necessarily reveal any specific cell location having maximal suitability. The cell-by-cell absolute difference between actual and predicted values was mapped for each commercial germplasm to show how the contrast was distributed spatially.

Results

We found that the distance between actual and predicted positions in trait space was higher for commercial germplasms than for wildland populations in most cases (Fig. 2). Four of the six commercial germplasms (Sand Hollow, Pleasant Valley, Rattleshake, Toe Jam Creek) were outliers in comparison to the wildland populations, and the other two commercial germplasms (Fish Creek, Antelope Creek) were marginal outliers at the edge of boxplot whiskers (third quartile plus 1.5 times interquartile range) (Fig. 2). These patterns were driven by some traits more than others in ways that varied among commercial germplasms (Fig. 3). For example, actual values of biomass, plant height, inflorescence number, heading date, and seed maturation date were noticeably higher than predicted values for Pleasant Valley while Rattleshake and Toe Jam Creek had noticeably lower actual leaf width and higher actual leaf length and leaf-width ratio than predicted (Fig. 3).

Discrepancies between actual versus predicted suitability were also evident when climatic suitability models were projected onto geographic space via the transfer function (Fig. 4). Predicted suitability based on similarity to climates at locations where material for commercial germplasms was originally collected (Fig. S1) differed from suitability calculated from actual trait values of each germplasm (Fig. S2). Commercial germplasms with higher divergence in trait space (e.g. Sand Hollow and Pleasant Valley) displayed large areas of high difference between actual and predicted climatic

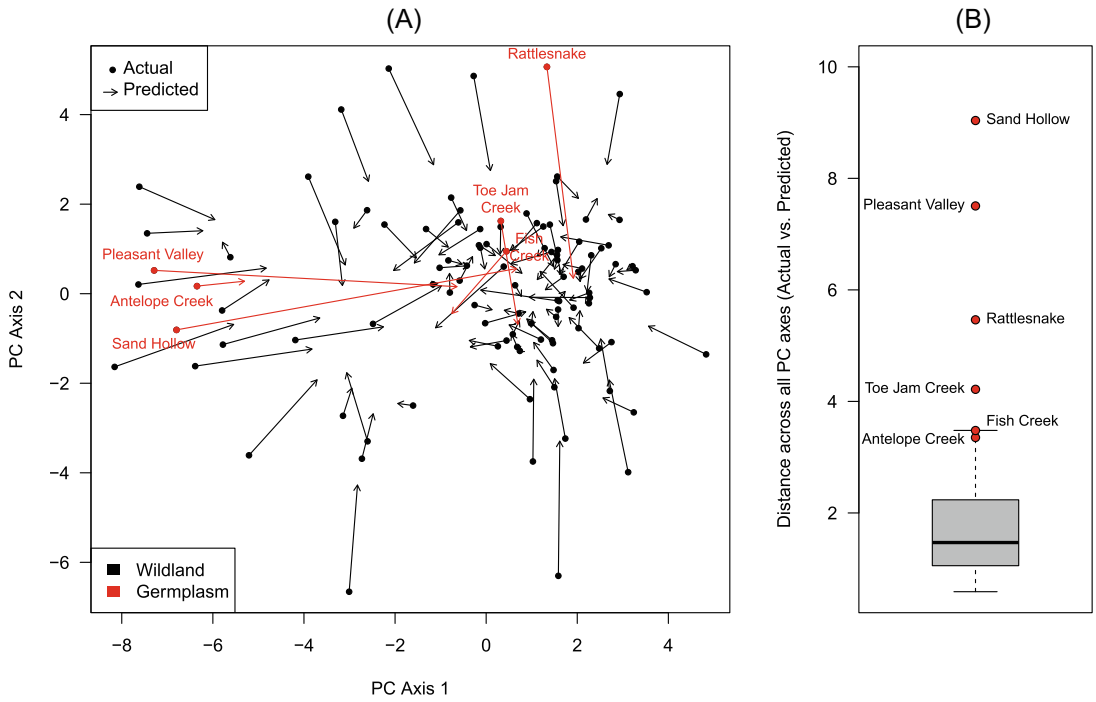

Figure 2. Distance in multidimensional trait space between actual trait values (averages of measurements in common gardens) and predicted values at source locations (calculated via a transfer function) for wildland populations and commercial germplasms of squirreltail (*Elymus elymoides* and *E. multisetus*) from the Intermountain Region of the western United States. The multivariate trait space is defined by principal component (PC) axes that represent variation among seven traits (see figure) at three common garden sites. PCs and their associated transfer function were built using data from wildland populations only (all *E. elymoides*) and germplasms were subsequently projected onto the PC axes. (A) Ordination of PC axes 1 and 2, showing distances as arrows from actual to predicted positions along these axes, with germplasms colored and labeled in red. (B) Boxplot of multidimensional Euclidean distances across all PC axes, showing points for each germplasm. All but one of the germplasms, but none of the wildland populations, were outliers.

suitability, and these differences tended to be greater at lower elevations where the climate is hotter and drier (Fig. 4). Models based on measured trait values indicated that Pleasant Valley and Sand Hollow had low suitability values across much of the Intermountain Region; Antelope Creek and Rattlesnake generally had moderate suitability; and Toe Jam Creek and Fish Creek had relatively high suitability across much of the region (Fig. S2).

Supplementary analyses showed that the high distance values of the commercial germplasms can be partially attributed to the fact that the commercial germplasms were excluded from the original analyses upon which the seed transfer models were built (Supplement S1). Populations excluded from the original modeling procedure were more likely to be outliers when subsequently projected onto the models, as shown not only for commercial germplasms, but also for wildland populations excluded one at a time (Supplement S1). Conversely, when the commercial germplasms were included alongside all wildland populations in developing the models, the discrepancy between actual and predicted positions in trait space was lower (Supplement S1). However, these alternative approaches still confirmed that the commercial germplasms tended to be outliers relative to the wildland populations (Supplement S1).

Discussion

The observed divergence in trait space between wildland populations and commercial germplasms of bottlebrush squirreltail suggests that selection or genetic drift has occurred, either intentionally or inadvertently, during the collection and development process. The Sand Hollow germplasm has since been identified as big squirreltail (*Elymus multisetus* M.E. Jones) (USDA-NRCS 2022), which likely explains its trait discrepancies—we decided to report our Sand Hollow germplasm results because bottlebrush and big squirreltail are highly related (Larson et al. 2003), interbreed within significant portions of the western United States (Wilson 1963), and are often used interchangeably in restoration seedings by federal and state agencies. Because we obtained the commercial germplasms from stock seed repositories or the developers themselves, the generations tested were equivalent to the initial releases to commercial growers; meaning that observed trait divergence likely occurred during the seed collection and plant material development process and is not indicative of what might occur after release and during the commercial production of later generations. Additionally, all the commercial germplasms evaluated here are certified as selected class, natural track, pre-variety germplasms, which means that they were developed from one to several wildland collected source populations

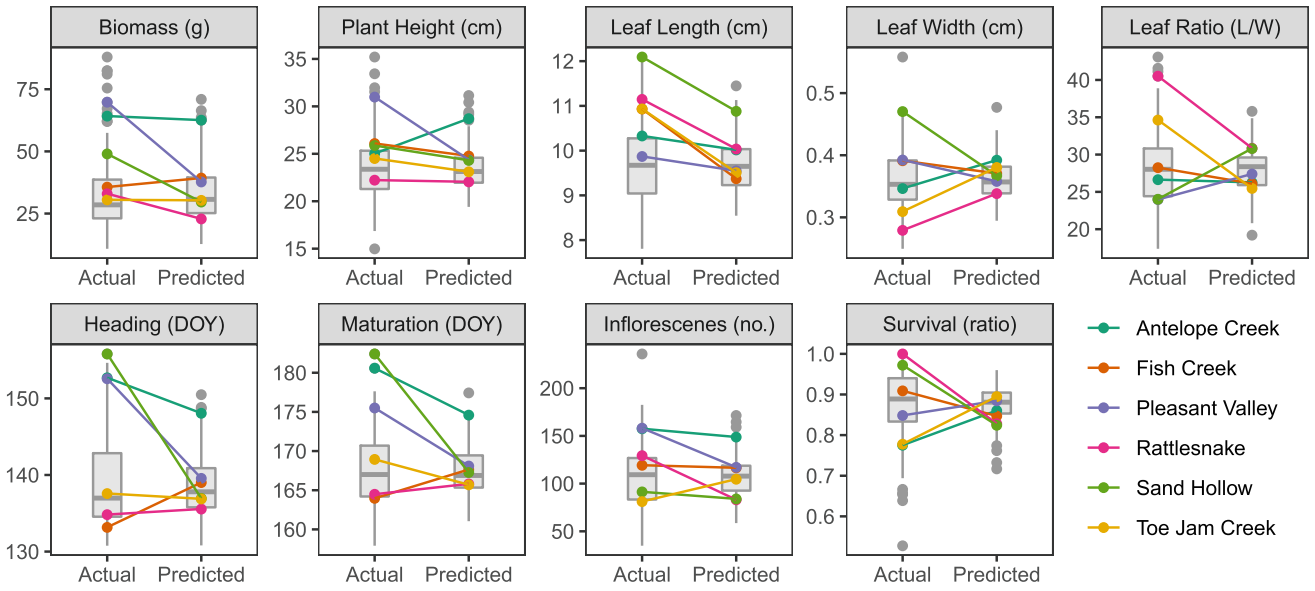

Figure 3. Actual trait values (averages of measurements in three common gardens) compared to predicted values at source locations (calculated via a transfer function) for wildland populations and germplasms of squirreltail (*Elymus elymoides* and *E. multisetus*) from the Intermountain Region of the western United States. The transfer function was built from principal components of traits using data from wildland populations only (all *E. elymoides*) and was subsequently applied to germplasms. Boxplots show distributions for all populations, overlain by colored points indicating germplasms (gray points are wildland populations' outliers), with lines connecting actual and predicted germplasm trait values.

and put through minimal development processes with no intentional artificial selection within germlines (Houck 2009). While inadvertent within-germline selection or genetic drift during plant material development is one potential explanation for this difference (Espeland et al. 2017), plant material developers in the Intermountain Region usually take measures to avoid this issue in natural track germplasms, including the use of large initial seed collections to avert genetic bottlenecks (Lippitt et al. 1994; Monsen & Shaw 2001), as well as iterating through a minimal number of generations (usually one or two), which may not be rapid enough for evolutionary change (Nagel et al. 2019), before releasing seed to commercial growers (e.g. Jones 2010).

Another potential, and more likely, explanation for these patterns may derive from seed collectors and plant material developers initially seeking and later selecting source populations with certain observable desired characteristics. This would mean that, while no artificial selection was performed within germlines, selection could still occur across a suite of seed sources, both during wildland collecting, where desired phenotypes are likely to be sought, and during the development process, where multiple germplasms are usually evaluated in comparison to one another and then chosen based on trait expression patterns (e.g. Jones et al. 2003). Indeed, Intermountain Region plant material developers have generally sought, selected, and released germplasms with greater biomass and seed set, which support forage production and commercial seed production but may not be optimal traits for supporting fitness in the wild (Kulpa & Leger 2013; Leger & Baughman 2015). For example, in environments that are hotter and drier, there are trade-offs between bottlebrush squirreltail growth traits and traits that tend to increase long-term survival, such as drought resistance (Blumenthal et al. 2021), which may help explain why we found greater divergence of commercial germplasms from suitability expectations in more arid regions. It is also possible that some of the commercial germplasms display trait divergence because they originated in microhabitats with conditions that are unrepresentative of climates at their source locations. For example, several of the commercial germplasms were likely collected near waterways (Antelope Creek, Fish Creek, and Toe Jam Creek), where water tables and moisture availability may have been elevated relative to surrounding landscapes. In a case like this, plants in moister microhabitats might display characteristics that fit collectors' desired search images, such as large size, and also appear to persist in conditions that are drier than what they actually experience.

Regardless of specific causes, the potential for generating mismatches between traits and climates of use should be considered by new and existing plant material development and restoration programs seeking to incorporate commercial germplasms into seed transfer guidance frameworks, especially since seed needs in many regions are likely to only be met through commercial seed production and as a greater emphasis on artificial selection in restoration plant materials is being advocated as a response to global change (e.g. Chivers et al. 2016; Jones et al. 2022; Torres et al. 2023). This study found that commercial germplasms representative of early generations and developed using strict standards still displayed divergence between expected and actual trait values. This could mean that commonly used procedures for minimizing evolution during the plant material development process (e.g. large initial seed collections, large development populations, and few development

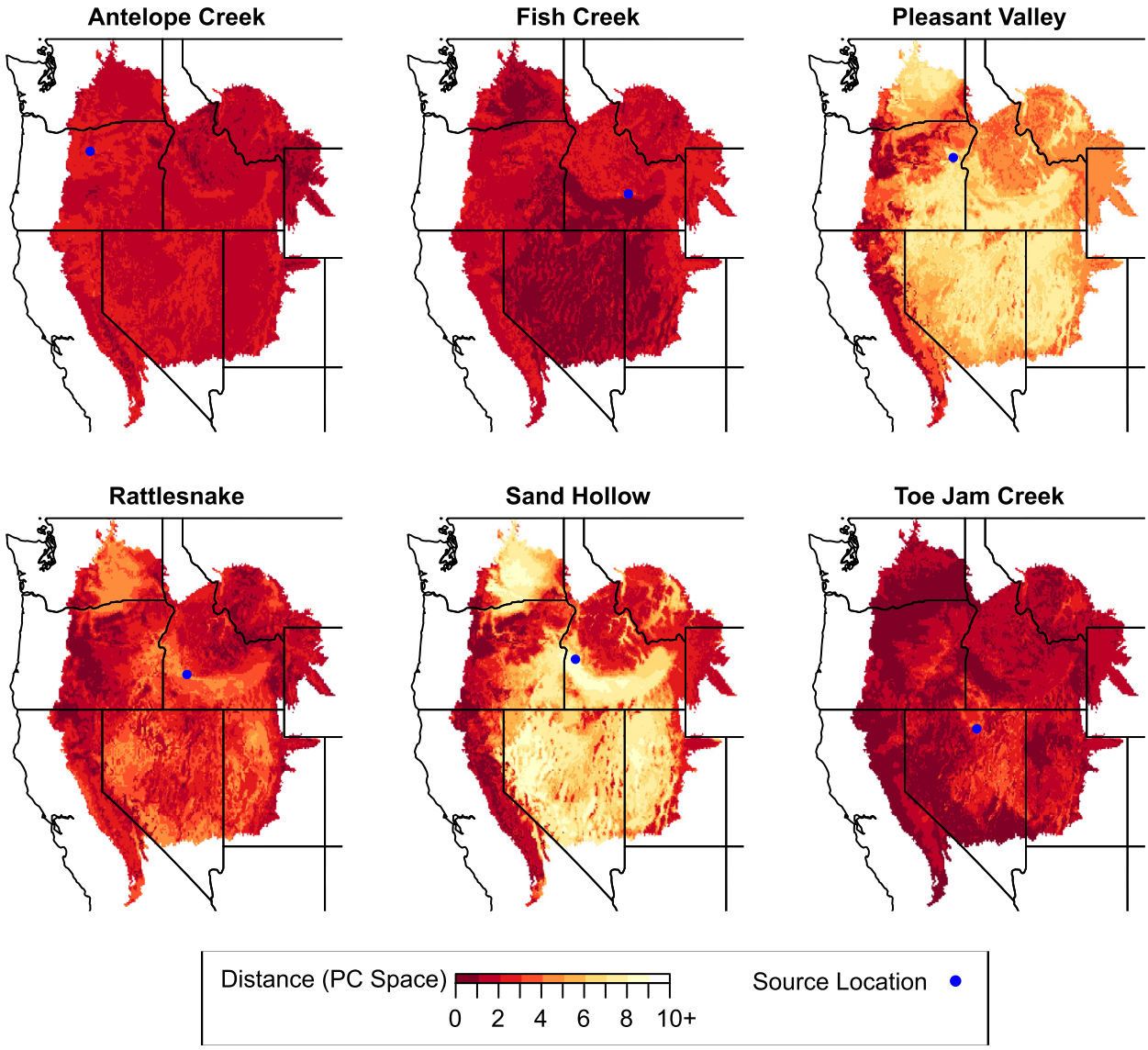

Figure 4. Maps depicting, for six germplasms of squirreltail (*Elymus elymoides* and *E. multisetus*), the degree to which modeled climate suitability differs when based on predicted trait values at source locations (see Fig. S1) versus actual trait values of these germplasms measured in common gardens (see Fig. S2). Units are Euclidean distances across six significant PC axes, with larger values indicating greater absolute difference between modeled climate suitability for predicted versus actual traits. Mapped values were generated using a transfer function that quantifies relationships between principal components (PCs) of trait variation and climate variables in focal ecoregions of the Intermountain Region of the western United States. PCs and their associated transfer function were developed using data from wildland populations only (all *E. elymoides*) and subsequently applied to germplasms.

generations) are not as effective as believed in minimizing trait divergence from wildland populations. More importantly, our findings demonstrate that choosing among seed sources, during collection and/or development, is a form of artificial selection that can have both intended and unintended effects on trait expression in commercial germplasms. These are likely to be greater issues for germplasms that have undergone less strict development processes and have been in seed production for more generations, since phenotypic and genotypic shifts can happen at any point throughout these processes and are increasingly likely to occur as development and production generations progress further from initial seed collections (Espeland et al. 2017).

The possibility of trait divergence during plant material development and seed production also highlights the need for procedures, such as ours, that measure and classify trait divergence between wild populations and commercial germplasms. Despite the importance of this issue to ecological restoration practice (see Leger et al. 2024), it is still extremely understudied and there are no consensus measurement protocols available to restoration practitioners (Conrady et al. 2023). Study

approaches have generally focused on divergence after many generations (e.g. Pizza et al. 2021) or across multiple species (e.g. Nagel et al. 2019; Conrady et al. 2023) but have usually compared commercial germplasms to a small number of wildland populations. While this can be an effective way to measure divergence, especially when comparing across generations within the same source lineage, it cannot resolve how typical a given trait combination might be within a larger species context. One of the strengths of our approach is that it uses the range of trait variation within wild populations as a basis for evaluating trait divergence in commercial germplasms. This contextual research approach may be particularly useful in cases where it is not possible to compare later germplasm generations to the original sources, which was the case here and is likely to be a common situation in many regions with active restoration seed markets. At the same time, we recognize that implementation of this approach is not easy, given the need for extensive sampling of wild populations, followed by detailed trait measurements of wild and germplasm plants that ideally should be grown concurrently in a common environment. Determining which traits to measure also requires attention, as some traits may be more relevant than others in the restoration context. In our study, logistic constraints prevented us from measuring potentially important traits in dryland plants, such as root characteristics and stomatal conductance.

While the commercial germplasms studied here are generally unrepresentative of the locations where they were initially collected, they still display trait combinations that are within the range of variation of wildland populations. By using a trait-based approach to transfer function modeling, in contrast to using source climate alone, we were able to place potentially divergent commercial germplasms into a seed transfer guidance framework. To our knowledge, this is a novel use of a methodology that could be replicated in other restoration settings. In this case, three of the six commercial germplasms (Fish Creek, Rattlesnake, and Toe Jam Creek) appear to maintain moderate to high utility in many areas across the Intermountain Region, while the other three (Sand Hollow, Pleasant Valley, and Antelope Creek) match more restricted areas—information that could help regional land managers and restoration practitioners make source-selection decisions. It should be noted that our accuracy in predicting new suitability distributions for the commercial germplasms rests on the assumption that these germplasms are adapted to a similar range of environments, broad or narrow, as wildland populations. Plant material developers in the Intermountain Region often argue that commercial germplasms are more broadly adapted than most wildland collected sources (Jones 2019), in which case our methods may underestimate their suitability; though there is evidence against broad adaptation in these germplasms (e.g. Kulpa & Leger 2013). Nevertheless, this assumption is not fundamental to our methodology and information on adaptive range can be incorporated by assessing germplasms across a series of environments.

When adequate data exists, generally from common garden or greenhouse studies, the methods presented here can be used in any context where the provenance of seed sources is important to restoration outcomes and where plant germplasms that have been developed outside of a seed transfer guidance framework are being considered for use. These methods are particularly relevant for germplasms that have been deliberately manipulated or inadvertently changed from their original sources through collection, development and cultivation practices. Given the environments from which they originated, such germplasms may turn out to be significant trait outliers, and in such cases, the guidance provided by seed transfer models may not be applicable. Alternatively, there may be areas within a region where seed transfer guidance for a germplasm is sufficiently applicable to warrant its use. The methods we have presented provide tools to assess germplasms in these ways. We note that these methods could be integrated with existing transfer function-based tools (e.g. St. Clair et al. 2022) to help restoration practitioners consider and compare a wider array of plant material sources, allowing for greater flexibility in restoration seed sourcing.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Testing the effect of exclusion versus inclusion of populations in seed transfer modeling building process.
Figure S1. Maps showing modeled climate suitability for six germplasms of squirreltail (*Elymus elymoides* and *E. multisetus*) based on predicted trait values at their source locations.
Figure S2. Maps showing modeled climate suitability for six germplasms of squirreltail (*Elymus elymoides* and *E. multisetus*) based on actual trait values measured in common gardens.
Table S1. Traits measured on *Elymus elymoides* plants grown at common garden sites.
Table S2. Climate variables (30-year normals, 1981–2010) used for modeling and mapping genetic trait variation of bottlebrush squirreltail (*Elymus elymoides*).

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