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STRATEGIC ISSUES ARTICLE

Assessment of population genetics and climatic variability can refine climate-informed seed transfer guidelines

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Restoration guidelines increasingly recognize the importance of genetic attributes in translocating native plant materials (NPMs). However, when species-specific genetic information is unavailable, seed transfer guidelines use climate-informed seed transfer zones (CSTZs) as an approximation. While CSTZs may improve how NPMs are developed and/or matched to restoration sites, they overlook genetic factors that can diminish restoration success and/or deteriorate natural patterns of genetic diversity and environmental factors that may introduce unexpected variation. Here, we analyze molecular data and geographic patterns of environmental variability across the western United States and demonstrate how they can refine CSTZs. Using genetic data available for 13 relevant plant species, we found that the probability of mixing genetically differentiated individuals (i.e. from different evolutionary lineages, or populations) was approximately 8% when considering locations separated by 50 km and reached nearly 80% by 500 km, which are distances relevant to ecoregionally constrained CSTZs. Furthermore, climate analyses revealed that geographically proximate locations are likely to maintain environmental similarity, regardless of CSTZ or ecoregion assignment. These results suggest constraining CSTZ-informed seed transfer decisions by distance may mitigate the opportunity for negative genetic outcomes. Furthermore, environmental variability and/or specificity of NPMs (depending upon the restoration strategy) should be achieved by sourcing NPMs from geographically proximate locations to avoid introducing excessive genetic differentiation. Our results highlight the utility of combining molecular genetic data with other genetic inferences (i.e. of adaptation) to determine how best to transfer seed across restoration species' ranges and develop new restoration materials.

Key words: genetic differentiation, native plant materials, population structure, restoration guidelines, seed transfer zones, western United States

Implications for Practice

- While climate-informed seed transfer zones (CSTZs) promote restoration, their use may lead to unintended consequences when guiding seed transfer or native plant material development.
- Patterns of genetic differentiation are highly variable in the topographically and environmentally heterogeneous western United States and the probability of mixing populations (i.e. genetically differentiated units that may affect restoration outcomes) increases rapidly with distance.
- Environmental variation is spatially autocorrelated such that geographically proximate locations, even across CSTZ or ecoregion boundaries, can be more similar than geographically distant locations within the same ecoregionally constrained CSTZ.
- Seed transfer and plant materials development strategies utilizing CSTZs would benefit from minimizing distance between sources to decrease the probability that genetically differentiated individuals are mixed and to avoid/understand unintended environmental variation.

Introduction

As restoration needs for natural landscapes increase due to more frequent and/or larger disturbances, the establishment of invasive species, and impacts resulting from climate change (Suding 2011; Winkler et al. 2018; see also UN Decade on Ecosystem Restoration, www.unenvironment.org), considerable time and resources are being invested to guide the development and deployment of native plant materials (NPMs) for priority

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restoration species. While there are species for which knowledge of genetic differentiation and adaptation are available to inform restoration practices (e.g. St. Clair et al. 2013; Durka et al. 2017; Shryock et al. 2017; Massatti et al. 2018), a lack of these data for many restoration species requires that practitioners and managers rely upon climatological data as a proxy. In particular, climate-informed seed transfer zones (CSTZs; e.g. Bower et al. 2014; Doherty et al. 2017; Shryock et al. 2018) are guiding large-scale restoration efforts across public lands in the western United States (Chambers et al. 2017; Edwards et al. 2019) because they provide clear, straightforward seed transfer guidance and are easily integrated into development strategies for new NPMs (Bucharova et al. 2019). While CSTZs provide opportunities to improve restoration decision-making and implementation, caution must be taken to mitigate inadvertent problems they could facilitate resulting from unaccounted genetic and environmental variability within their boundaries.

CSTZs are delineations of geographic space based on climatic similarity, for example cold and warm season temperature means and mean annual precipitation (Bower et al. 2014). They are utilized in restoration under the well-demonstrated principle that plants show adaptive responses across climatic gradients (Hereford 2009). In other words, CSTZs help decision makers account for local adaptation with the hope that seed transfer informed by their boundaries increases restoration success. To further increase their efficacy, CSTZs are typically grouped into larger hierarchical units (e.g. by the level III ecoregions for North America, Omernik 1987) that delineate areas with approximately similar environmental characteristics. For example, CSTZs bounded by level III ecoregions of the western United States have been shown to approximate inferred adaptation resolved from common garden studies (Bower et al. 2014; Kramer et al. 2015). Despite geographic constraints, CSTZs can still span hundreds of kilometers (e.g. Prasse et al. 2010; Crow et al. 2018; Shryock et al. 2018), which may provide opportunities for environmental (e.g. moisture availability due to soil characteristics) and genetic (e.g. reduced gene flow) factors to decrease their effectiveness—these factors would be pronounced in topographically and environmentally heterogeneous landscapes such as the western United States (e.g. Baughman et al. 2019).

Range-wide patterns of genetic differentiation within species, in addition to adaptive similarity as inferred through CSTZs or other methods (e.g. empirical seed transfer zones, see Kilkenny 2015), are important to consider when developing seed transfer guidelines. Hereafter, our use of genetic terms (aside from adaptation) concerns neutral genetic variation identified using molecular techniques. This is in contrast to adaptive genetic variation, which is commonly (though not exclusively) inferred by looking at how plant phenotypes vary in response to environmental gradients (e.g. Kilkenny 2015). Neutral genetic variation is necessary for discerning relationships within and among species, patterns of genetic diversity and differentiation, and evolutionary processes like gene flow and population size dynamics (Hartl & Clark 2006). These patterns and processes cannot be assessed by looking at plant phenotypes, yet they have the capacity to influence restoration outcomes. For example, the probability of genetic incompatibilities between individuals (or groups of individuals that share a common evolutionary history, also known as populations) that may affect reproductive capacity increases as the time since the last effective gene flow occurred increases (e.g. approximately 500 generations sensu Frankham et al. 2011, see also McKay et al. 2005). This amount of separation (or significantly more) is common in topographically heterogeneous landscapes affected by Pleistocene glaciations (Massatti et al. 2018; Massatti & Knowles 2020). Our use of the term "population" throughout the text refers to units within a species composed of all individuals across geographic space (which can cover small or large areas) that have a common history and shared recent gene flow. In other words, populations represent species' patterns of genetic differentiation that formed as their distributions shifted, expanded, shrank, split into isolated units, and/or merged together in response to climatic fluctuations or other historical events. Genetic patterns among species are often unique due to processes ranging from chance to species-specific interactions with their environments based on life history characteristics (Papadopoulou & Knowles 2016), and they do not necessarily coincide with CSTZs (e.g. Listl et al. 2017, 2018; Massatti et al. 2018; Massatti & Knowles 2020).

Another instance where minimizing the genetic distance (i.e. differentiation) between NPMs and local conspecifics at a restoration site may support successful restoration outcomes is when genetic identity affects community-level processes (Whitham et al. 2006; Vandegehuchte et al. 2012; Bucharova et al. 2016). While the mechanisms underlying the interactions among local genotypes of a restoration species and other species in the community are likely numerous, it is reasonable to hypothesize that genetically similar NPMs may promote those interactions, irrespective of inferred adaptive similarity (especially when adaptive similarity is estimated using only a few climatic gradients). However, regardless of how genetic differentiation may improve restoration outcomes, species' natural patterns of genetic variation are increasingly recognized as important resources, as is evidenced by the interest in protecting genetic diversity within the wild relatives of agronomically important species (Hoban et al. 2013).

Environmental variation across heterogeneous landscapes also complicates the application of CSTZs to restoration. For example, the physiographic history of western North America resulted in a complex geographic mosaic of substrates, which CSTZs ignore outside of what is captured by ecoregional delineations. In dryland ecosystems like those across much of interior western North America, the availability of soil moisture for plants is an important factor that determines survival within or failure of seeding treatments (Kildisheva et al. 2016; Shriver et al. 2018) and represents a potentially highly selective gradient (Sthultz et al. 2009; Smith et al. 2016). Patterns of plant-available soil moisture are influenced by interactions among temperature, precipitation, and edaphic conditions, notably soil texture and depth (Noy-Meir 1973; Sperry & Hacke 2002). If a goal of CSTZs is to maximize the inference of local adaptation to a specific suite of environmental conditions, then defining

CSTZs by climate alone may miss important environmental patterns and potentially underestimate the magnitude of geographic variation.

Here, we synthesize available genetic and environmental data across the western United States to demonstrate how genetic and environmental variability is implicit within CSTZs, even when constrained by ecoregional boundaries. Specifically, we assess how geographic distance correlates with genetic differentiation across western North America in common, lower-elevation species of restoration interest and report a probabilistic framework that indicates the likelihood that different populations will be sampled as geographic distance increases. Furthermore, we characterize environmental variability in multiple widespread CSTZs across three large ecoregions and demonstrate how environmental dissimilarity between locations increases as a function of distance. As a result, we develop region-specific knowledge that can be used to refine CSTZs such that NPMs can be used and/or developed more accurately with respect to their targeted environmental adaptations to further improve restoration outcomes. Similar analyses can be applied wherever there is interest in using CSTZs and may be especially informative in areas characterized by high topographic and environmental heterogeneity.

Methods

Quantifying Patterns of Genetic Differentiation Across Western North America

To assess how genetic differentiation varies across space, we identified genetic studies on graminoids, forbs, and shrubs distributed across interior western North America. Tree species were not included due to their large dispersal distances and lack of use in restoration treatments across the lower elevations of the interior West. To conduct a comprehensive literature search, we used a variety of search terms in Google Scholar related to population genetics, phylogeography, STRUCTURE analyses (i.e. Pritchard et al. 2000), and the geography of western North America and identified 13 studies that: (1) focused on regionally common, lower-elevation species; (2) included multiple individuals from a sampling location and conducted STRUCTURE genetic analyses; and (3) reported geographic locations (Table 1). We used an estimation of population structure (i.e. from STRUCTURE analyses) as our measure for genetic differentiation because it correlates well with genetic distance, parallels intraspecific genetic lineages, and typically reflects the processes that affected species during and after the last glacial period (Avise 2000); as such, population structure approximates levels of genetic differentiation that have the capacity to influence restoration outcomes, such as when populations have not exchanged gene flow for extended periods of time (Frankham et al. 2011). The units identified by the STRUCTURE algorithm (i.e. *K* values) are what we call populations throughout the text. For each species, we generated a table that included a unique pair of sampling locations, the geographic distance between the locations (km), and a binary value indicating whether the locations were included in the same population (0) or different populations (1). We used R 3.3.2 (R Core Team 2017) to visualize the distribution of geographic distances within each category (0 and 1). Next, for each species, we binned sampling location pairs by 50 km increments. Within each bin, we calculated the proportion of sampling location pairs that contained different populations, which was graphed against distance; the conversion of pairwise data points per 50 km increment to one relative value controlled for the different empirical sample sizes across the studies (Table 1). Scripts and data generated during this study are available from the USGS ScienceBase-Catalog (Massatti & Shriver 2020).

Quantifying Environmental Variability Across Western North America

An implicit assumption when developing CSTZs is that accounting for the average climate regime will allow locations within CSTZs to be environmentally interchangeable and spatially independent. We tested this idea using semivariograms. Variograms are a well-established approach in spatial statistics to quantify spatial autocorrelation and how differences among locations (semivariance; i.e. ½ variance) change as a function of distance from a given point (Legendre 1993). If locations that are nearby are more similar than those further away, then variance will increase as a function of distance. In contrast, if locations are completely spatially independent (i.e. no spatial autocorrelation), then variance will show no relationship to distance. We implement these ideas within the framework of three geographically widespread, adjacent CSTZs in the Central Basin and Range, Northern Basin and Range, and Snake River Plain ecoregions (Omernik 1987), including the 15–20°F/6–12°C/m precipitation, 20–25°F/6–12°C/m precipitation, and 20–25°F/12–30°C/m precipitation CSTZ (hereafter referred to as the cool–dry, warm–dry, and warm–wet zones, respectively; Bower et al. 2014). As these CSTZs group areas of similar climate, we may predict that environmental variance will increase when assessing locations across two adjacent CSTZs compared to locations within the same CSTZ. Alternatively, geographically proximate locations may be classified into different CSTZs but share many topo-edaphic environmental similarities compared to geographically distant locations in the same CSTZs. Using 7 km gridded mean annual temperature and precipitation (1915–2015) from the Livneh dataset (Livneh et al. 2013) and simulated 7 km soil water availability (SWA) derived from SoilWat2 (Schlaepfer & Murphy 2018), we developed semivariograms using all climate grid point pairs within two CSTZs (warm–dry and warm–wet) and across all grid point pairs of adjacent CSTZs for two comparisons (i.e. warm–dry/warm–wet and warm–dry/cool–dry). Comparisons are binned by 20 km intervals to represent variance estimates. Variograms were calculated using the “variogram” function in the “gstat” package in R.

Results

Genetic Variability

Species varied in the number of populations (i.e. their inferred *K* values) estimated across their western North American

Table 1. Plant species across interior western North America with molecular data appropriate for this study. Elevation range and distance range refer to the minimum and maximum values among sampling locations.

Taxon	*Growth Habit*	*No. of Sampling Locations*	K *Value*	*Elevation Range (m)*	*Distance Range (km)*	*Citation*
Pseudoroegneria spicata	Graminoid	210	4	141–2,547	1–1,267	Massatti et al. (2018)
Hilaria jamesii	Graminoid	34	3	1,015–2,249	14–1,230	Massatti & Knowles (2020)
Sporobolus cryptandrus	Graminoid	23	3	1,382–2,097	26–704	Massatti unpublished
Astragalus filipes	Forb	65	5	270–2,578	2–1,322	Bushman et al. (2010)
Dalea ornata	Forb	22	3	110–1,163	11–542	Bhattarai et al. (2010)
Dalea sericea	Forb	20	2	1,326–2,036	10–575	Bhattarai et al. (2011)
Lepidium papilliferum	Forb	21	2	757–1,635	1–222	Larson et al. (2010)
Lotus utahensis	Forb	14	3	1,800–2,780	20–297	Stettler et al. (2017)
Penstemon deustus	Forb	8	7	1,368–2,649	4–474	Kramer et al. (2011)
Penstemon pachyphyllus	Forb	10	4	1,119–2,560	5–342	Kramer et al. (2011)
Penstemon rostiflorus	Forb	10	3	1,632–2,768	5–596	Kramer et al. (2011)
Sphaeralcea parvifolia	Forb	14	3	1,197–2,150	3–582	Sriladda et al. (2012)
Coleogyne ramosissima	Shrub	14	2	1,132–1,684	23–785	Richardson & Meyer (2012)

distributions (Table 1). Across species, population identity was shared between sampling locations separated by large distances, but the converse was also true, where population identity was mismatched between sampling locations separated by small distances (Fig. 1). When considering the change in population identity across space, the probability of sampling a different population was ca. 8% (95% CI 3–13%) at 50 km (Fig. 2). The 95% CI reached 100% probability of sampling two populations starting at a distance of 600 km (mean 82%, 95% CI 58–100%; Fig. 2). Beyond 600 km, average probabilities and their 95% CIs remained uniformly high. Considering distances which are applicable to CSTZs within or across ecoregions (e.g. 100–500 km), the mean probability of sampling different populations was positively correlated with distance and ranged from 40 to 80%.

Our approach characterizing genetic differentiation across western North America assumes that the reported populations (Table 1) are meaningful units that should be accounted for when considering seed transfer. While populations are the result of historical factors that affected evolutionary processes through

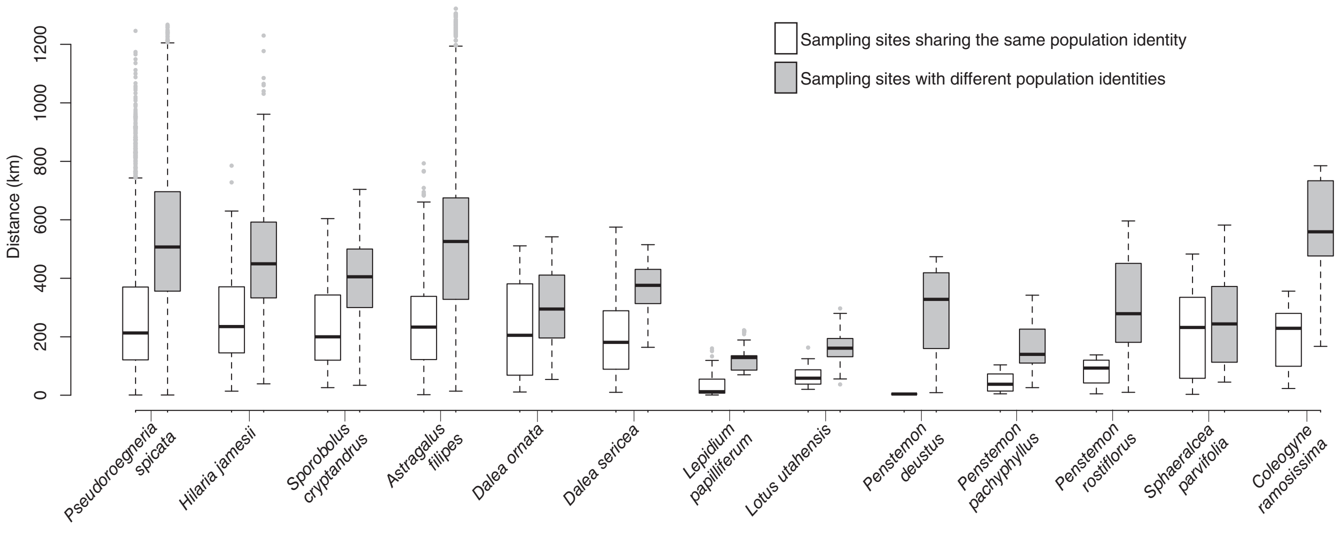

Figure 1. Species-specific paired box-and-whisker plots, with the first showing the distribution of distances (km) for all of the sampling location pairs belonging to the same population and the second showing the distribution of distances for all of the location pairs belonging to different populations. Box-and-whisker plots depict the median, first and third quantiles, standard deviation, and total range across sampling location pairs.

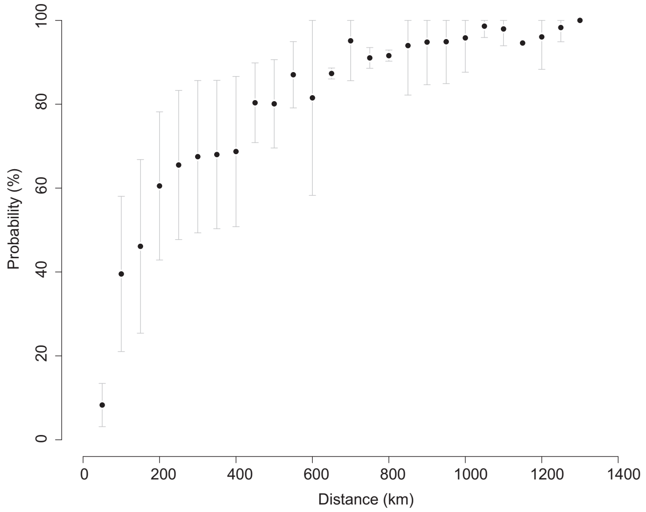

Figure 2. Probability of sampling different populations as geographic distance between sampling locations increases. Each point represents an average probability when considering all species together, with gray lines representing the ±95% CI.

time, they may have less applicability to contemporary population dynamics (e.g. contemporary gene flow). More likely, in some instances they are important, while in others they are not. For example, Massatti et al. (2018) estimated migration rates between adjacent population pairs of bluebunch wheatgrass (*Pseudoroegneria spicata*) and resolved (relatively) high per generation migration rates between one pair of adjacent populations and rates close to zero between all other comparisons. Parallel results were reported for James' galleta grass (*Hilaria jamesii*) across the Colorado Plateau (Massatti & Knowles 2020). In such circumstances, it may be determined that exchanging plant materials between the two populations with higher migration rates poses fewer risks, which would reduce the total number of comparisons. However, determining contemporary migration rates at which populations become demographically linked, and therefore that may be treated as one unit, is not straightforward and requires further study (Palsbøll et al. 2007).

Life history characteristics are important to consider when discussing geographic patterns of genetic variation, as there are well-known relationships between pollen and seed dispersal vectors and rates of gene flow (Reisch & Bernhardt-Römermann 2014). For example, wind and long-distance pollen dispersers like hawkmoths (Skogen et al. 2016) tend to increase the distances over which genetic differentiation is observed, while other insect pollination may result in reduced gene flow and finer-scale differentiation (Kramer et al. 2011). The species used in analyses herein are representative of a range of life history characteristics (Table 1; Fig. 1), though our choice of species was based on availability and not an equal representation of different life history strategies. When estimating how life history characteristics affect genetic differentiation across western North America, a conservative strategy may be to assume that species with higher predicted dispersibility display distance relationships closer to the lower 95% CI in Figure 2, while

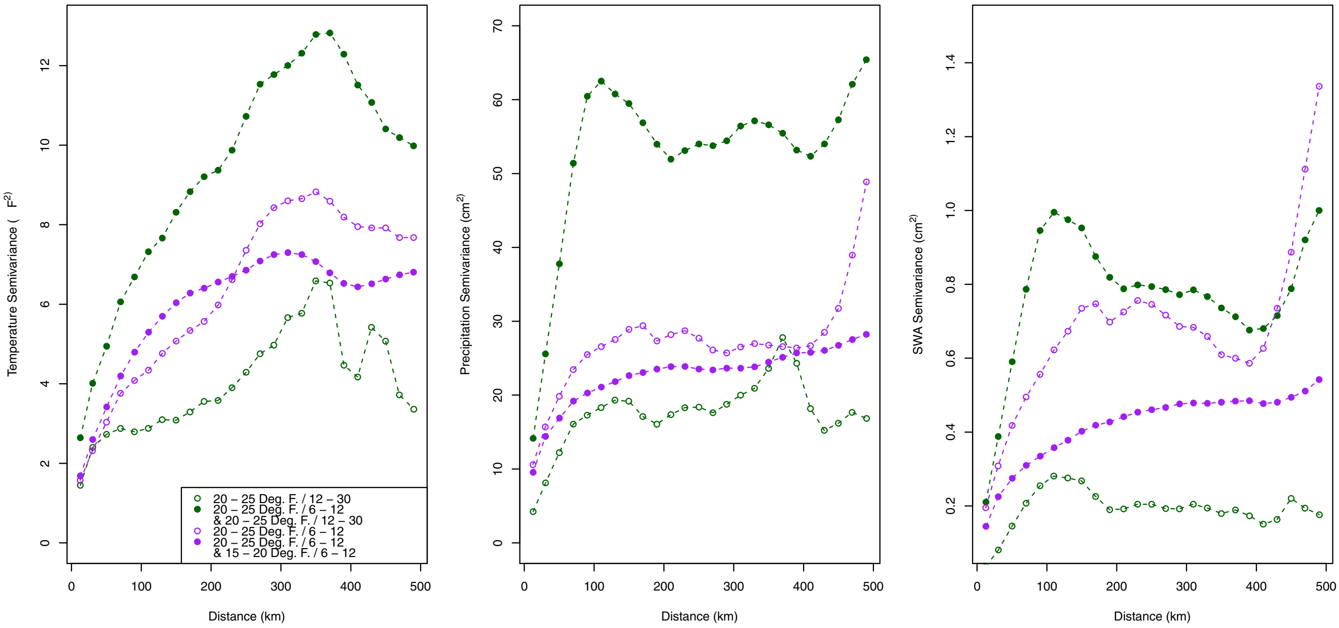

Figure 3. Semivariograms of mean annual temperature, precipitation, and soil water availability (SWA) as a function of distance. Symbols represent either a single CSTZ (unfilled circles) or the combination of two adjacent CSTZs (filled circles); analyses include comparisons between all target CSTZ grid cells within the Central Basin and range, Northern Basin and range, and Snake River Plain ecoregions. Each point is an estimate of semivariance across comparisons within a 20 km bin. The number of locations within CSTZs was positively correlated with zone size and included: 858 points for warm-wet; 1,913 points for warm-dry; 5,135 points for cool-dry. Variability in semivariance estimates at large distances is influenced by small sample sizes.

species with lower dispersibility fall along the higher end of the 95% CI. When considering species with high effective gene flow, our results remain similar—the probability of sampling multiple populations remains high at small geographic distances (e.g. Massatti et al. 2018), likely due to the effect of complex topography, environmental heterogeneity, and Pleistocene glacial cycles.

Climatic Variability

Semivariograms indicate that nearby locations are more likely to share similar environmental conditions than distant locations, regardless of CSTZ classification. Differences (i.e. semivariance) in temperature, precipitation, and SWA all increased with distance between grid cell locations in both within-CSTZ and across-CSTZ comparisons regardless of ecoregion identity (Fig. 3). However, the magnitude of increases varied based on the specific CSTZ being considered. Temperature showed the most consistent response among CSTZs, with semivariance increasing rapidly with distance before stabilizing around approximately 5–10°F at 300 km. There was little difference in the increase in temperature variation with distance between the single-zone warm–dry analysis and the dual-zone warm–dry and cool–dry comparison (purple in Fig. 3). In contrast, the single-zone warm–wet analysis showed the smallest overall variation among comparisons, but temperature semivariance was considerably higher in the dual-zone warm–dry and warm–wet comparison (green in Fig. 3). Precipitation and SWA showed similar overall patterns within and across CSTZs; notably semivariance increases with distance in most cases, including with SWA, which has important implications for restoration seeding success and may be a strongly selective environmental gradient (Sthultz et al. 2009). Given the large grid cells (i.e. 7 km) that average over local heterogeneity, our estimates of spatial dependence are likely underestimated. Nonetheless, these results suggest that consideration of how environmental conditions change as a function of distance is relevant to restoration outcomes because nearby locations in an adjacent CSTZ may be more environmentally similar than distant locations from the same CSTZ. In other words, maximizing the estimation of adaptiveness of an NPM to a restoration site would benefit from considering the distance to the site and not just the identity of the CSTZ.

Discussion

Integrating Genetic and Climate Variability Into Seed Transfer and Native Plant Materials Development

Our analyses demonstrate that geographic distance from any given location within a CSTZ is positively correlated with increasing genetic and environmental variability. Furthermore, environmental variability increases even when CSTZs are constrained by ecoregions due to the distance over which some CSTZs are mapped and the heterogeneity of the western North American landscape. Moreover, geographically proximate locations from adjacent CSTZs, even across ecoregions, can be more genetically and environmentally similar than geographically distant locations from the same CSTZ. These results can provide valuable guidance to restoration professionals trying to make informed decisions regarding seed transfer. For example, the likelihood of a population mismatch increases rapidly with distance from a restoration site such that, by about 200 km, it is more likely that an NPM will represent a different population that experiences divergent environmental conditions. As such, placing a distance constraint on seed transfer decisions would help mitigate the unintended consequences of mixing genetically differentiated individuals that can decrease restoration success; the distance constraint can be tailored to the amount of risk that managers or practitioners are willing to assume.

Note that selecting an NPM representing high levels of environmental variation or specific environmental conditions not yet represented at the restoration site (i.e. future climates) may be part of the restoration treatment design. In these cases, it is important that practitioners understand how environmental variability corresponds to increasing distance so that NPM selection can be accurate with respect to the intended goals. However, regardless of what environmental representation is targeted in NPMs for a restoration site, our results suggest that prioritizing geographically proximate seed sources would be beneficial (either within or across CSTZs or ecoregions), given the positive correlation between genetic differentiation and distance. Also note that genetic diversity within a restoration site is necessary to avoid negative genetic consequences like inbreeding depression, but that genetic diversity can be achieved without mixing different populations (e.g. by sourcing genetically diverse NPMs belonging to the same population—Massatti et al. 2018; Kaulfuß & Reisch 2019). Identifying the importance of geographic distance highlights the utility of focal point seed zones, which tend to be more highly correlated with distance from a restoration site compared to CSTZs (Ukrainetz et al. 2011; Richardson & Chaney 2018).

Managers and practitioners rarely have the opportunity to choose among multiple NPMs for a given restoration species, especially from the same CSTZ compared to the restoration site. More likely, our results may be useful for informing the development of new regionally and genetically appropriate NPMs. There are a variety of NPM development strategies, including, for example, developing cultivars (Chivers et al. 2016), using strictly local materials, or increasingly popular composite techniques that mix seeds across stratified environmental or geographic space (see Bucharova et al. 2019 and references therein for a comprehensive discussion). While it is not within the purview of this article to support one strategy over another, our results suggest that composite NPM development strategies that aggregate seeds from locations across large geographic areas would increase the likelihood of population mismatches, as well as increase the environmental variability that an NPM represents. Bucharova et al. (2019) suggest regional admixture provenancing as a strategy to mitigate the risks of mixing genetically differentiated sources while maintaining genetic diversity and adaptive potential; while not providing any specific guidance on how to delineate regions, those that they provide as examples (i.e. ecoregions, Miller et al. 2011; climatic zones, Bower et al. 2014; genecology, St. Clair et al. 2013; or a combination of strategies, Gibson & Nelson 2017) would result in the mixing of highly genetically differentiated individuals (i.e. populations) when considering western North America due to the region's topographic and environmental heterogeneity and history during the Pleistocene. For example, three populations were resolved in the Central Basin and Range ecoregion for bluebunch wheatgrass (Massatti et al. 2018), and even if practitioners use the best available information to source seeds for generating a new NPM under a regional admixture protocol (i.e. trait-based empirical seed transfer zones, St. Clair et al. 2013), the probability of mixing individuals from different bluebunch wheatgrass populations is high because the species' empirical seed transfer zones currently rely upon ecoregional delineations. This example highlights the utility of molecular genetic data in developing restoration guidelines, as they provide information that has the capacity to influence restoration outcomes yet cannot be otherwise ascertained.

Future Directions: Restoration Based on the Unit of a Population

CSTZs are used when species-specific, trait-based genetic information is unavailable. Fortunately, more species-specific data, especially involving molecular analyses, are being generated as restoration science progresses (e.g. Breed et al. 2019). When molecular data are available, using population boundaries (i.e. the units of genetic differentiation used in the analyses herein) as the framework for deploying restoration materials, instead of an ecoregion or other arbitrary boundary, would help minimize the mixing of highly genetically differentiated individuals. For example, following geographic population delineations of bluebunch wheatgrass (Massatti et al. 2018) instead of ecoregions would not only ensure that genetically differentiated individuals are not mixed from, for example, the Central Basin and Range ecoregion (see above), but they would simplify seed transfer/NPM sourcing decisions because the species has fewer populations than the number of ecoregions it is distributed across; such guidelines are in development. If significant environmental heterogeneity exists within the population boundaries of a restoration species, practitioners would still best be served by developing multiple NPMs to maximize local adaptation—development may be directed by using population-constrained CSTZs, focal point seed zones, or molecular data (e.g. Massatti & Knowles 2020), but ideally should be based on field-based trials such as reciprocal transplants or common gardens (e.g. Kilkenny 2015).

Utilizing populations is not new for managers of biological resources. Within the conservation field, they are recognized as management units (Moritz 1994; Palsbøll et al. 2007) and used to prioritize recovery efforts for sensitive species. Creating management units takes the additional step of elucidating contemporary migration among populations, which can be estimated using an appropriate molecular dataset and methods (Wilson & Rannala 2003). Even though restoration species are common across the landscape, managing them in the framework of management units would protect natural patterns of genetic variation, the benefits of which are increasingly being identified and discussed (Hughes et al. 2008; Sgrò et al. 2011; Hoban et al. 2013). The mitigation of negative consequences due to mixing highly genetically differentiated individuals would automatically follow.

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