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Seed Sourcing for Restoration in an Era of Climate Change

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ABSTRACT: Proper sourcing of seed for ecological restoration has never been straightforward, and it is becoming even more challenging and complex as the climate changes. For decades, restoration practitioners have subscribed to the “local is best” tenet, even if the definition of “local” was often widely divergent between projects. However, given our increasing ability to characterize habitats, and rapid climate change, we can no longer assume that locally sourced seeds are always the best or even an appropriate option. We discuss how plants are responding to changing climates through plasticity, adaptation, and migration, and how this may influence seed sourcing decisions. We recommend focusing on developing adequate supplies of “workhorse” species, undertaking more focused collections in both “bad” years and “bad” sites to maximize the potential to be able to adapt to extreme conditions as well as overall genetic diversity, and increasing seed storage capacity to ensure we have seed available as we continue to conduct research to determine how best to deploy it in a changing climate.

Index terms: assisted migration, climate change, provenance, restoration, seed sourcing

BACKGROUND

As anthropogenic disturbance and destruction of natural areas increase, so does the need for native plant seed for restoration and revegetation projects. From the pioneering work of Turesson (1922) and Clausen et al. (1940) on plant adaptation to the present, hundreds of studies have shown that plant populations are often adapted to their local environment, eventually leading to ecotypic variation or even speciation (reviewed in Linhart and Grant 1996; Huford and Mazer 2003). For example, plants have been demonstrated to adapt to winter temperature and length (Balduman et al. 1999), water availability (Dudley 1996a, 1996b; Fenster 1997), soil type (Sambatti and Rice 2006), herbivory (Crémieux et al. 2008), competitive regime (Leger 2008), pests and pathogens (Thrall et al. 2002), and many other biotic and abiotic factors. This leads to the assumption that locally sourced seed should perform better in restorations than nonlocal seed.

The assumption that “local is best” is incorporated into seed sourcing decisions in a variety of ways. When working in regions or with species where local adaptation has not been studied, the most basic approach is to put limits on geographic distances from which seed can be sourced for restoration projects. A recent survey of several restoration practitioners in the greater Chicago area found seed sourcing guidelines ranging from within 40 to 320 kilometers of the site to be restored or within the county where the restoration is occurring (Saari and Glisson 2012). However, geographic distance is not necessarily, nor even generally, the best descriptor of where to obtain

the best adapted or most appropriate plant material (Leimu and Fischer 2008). Local adaptation is a function of the rate of change in environmental gradients for abiotic and biotic factors (temperature, precipitation, soil chemistry, pests and pathogens, pollinators, etc.) and the ability of populations to adapt to these changes, rather than simply distance (Hereford 2009; Johnson et al. 2010). Instead of putting strict geographic limits on sourcing, a more complex approach is to source seed from environmentally or ecologically similar habitat, as long as the restoration site has not been profoundly altered (Knapp and Rice 1994; Lesica and Allendorf 1999; Montalvo and Ellstrand 2000; McKay et al. 2005; Kramer and Havens 2009).

Information on patterns of local adaptation, garnered largely from time and resource-intensive common garden and reciprocal transplant studies, has been used to delineate seed transfer zones for a growing number of species with high economic or restoration value (Johnson et al. 2004). Seed transfer zones are geographic areas within which seeds can be moved around with minimal risk of maladaptation (Kramer and Havens 2009). Unfortunately, for those who seek an easy answer to sourcing decisions, there is tremendous spatial and temporal variation in patterns of local adaptation among species (Leimu and Fischer 2008; Johnson et al. 2010). This means seed transfer zones will be species-specific and are influenced by many factors, including mating system and patterns of gene flow, geographic distribution of the species, the heterogeneity of the landscape and climate where the species occurs, and other biotic and

abiotic factors (Johnson et al. 2004). For example, annuals that are highly selfing, with gravity-dispersed seed and historically occurring in discrete, isolated populations are predicted to be more locally adapted than long-lived, wind-dispersed species, especially those that have experienced recent range expansion (Ennos et al. 1998; Hufford and Mazer 2003; Broadhurst et al. 2008). Seed transfer zones have been empirically derived for several timber species (Johnson et al. 2004), as well as some grasses and forbs commonly used in restoration, but are still lacking for the vast majority of native plant species.

In an effort to provide some general guidelines on seed sourcing for species lacking experimentally determined seed transfer zones, some authors have suggested using ecoregions as a proxy for seed transfer zones. For example, Johnson

et al. (2010) suggested using Omernik Level IV ecoregions (Omernik 1987) as a conservative definition of a local seed source for unstudied species. Recent research has found that Level IV ecoregions are generally effective in capturing local adaptation measured in a grass (Erickson et al. 2004) and even Level III ecoregions were effective for five forb species (Miller et al. 2011) in the western United States. Scientists with the US Forest Service recently developed provisional seed zones based on a combination of minimum winter temperature zones, aridity, and Omernik's Level III ecoregions (Figure 1; Bower et al. 2014). Both of these approaches offer useful starting points for thinking about seed sourcing issues, but as Kramer et al. (this issue) show, each species is different and it is challenging to predict which proxy seed zones may work best for a particular

species.

EFFECTS OF CLIMATE CHANGE ON PLANTS AND SEED SOURCING DECISIONS

Until fairly recently, most seed transfer zone delineation and management prescriptions involving seed sourcing have assumed at least implicitly that the environment, including the climate, is relatively stable (Millar et al. 2007). We now know that the climate is changing at a greatly accelerated rate and will continue to do so for the foreseeable future (IPCC 2007). Plant species can respond to a rapidly changing climate in several ways. They can cope with the changes through plasticity (Sultan 2000), which may include phenological changes such as leafing out earlier in warmer years, senescing earlier or flowering later in

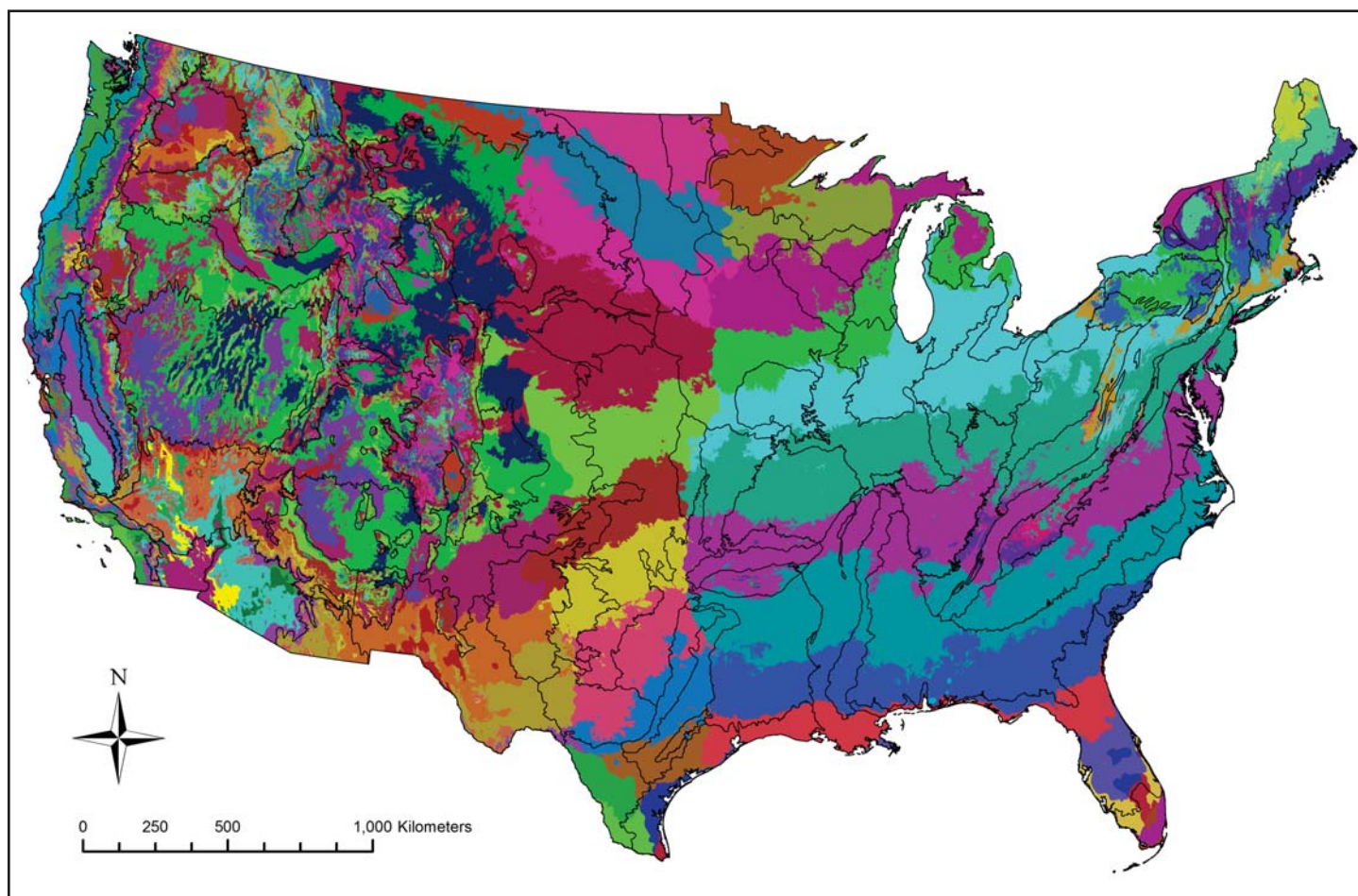


Figure 1. Provisional seed transfer zones developed by the USDA Forest Service for the continental United States. (Bower et al. 2014; available at <www.fs.fed.us/wwetac/threat_map/SeedZones_Intro.html>). Geographical areas that share a color should be able to exchange seed with minimal risk of maladaptation.

drought years (Sherry et al. 2007). Species can also adapt through natural selection to environmental changes (Hoffmann and Sgro 2011), for example, becoming more heat or drought tolerant over several generations. Additionally, species can migrate to regions with more suitable climates. Lacking one or more of these responses, plant species (or populations in some portion of their current range) will likely go extinct as the climate changes (Williams et al. 2008).

Species Distribution Modeling (SDM) has been used to predict where species may need to migrate given various climate change scenarios. SDM uses bioclimatic variables, such as those available from WorldClim (Hijmans et al. 2005; <www.worldclim.com>), and current (and “recent” historical) locality data to begin to understand the relationship between species ranges and climate. Some modeling approaches may incorporate additional variables such as soil and other habitat requirements, while mechanistic approaches include physiological restrictions to understand the limits of species distributions, but these are less common because such characteristics remain unknown for the vast majority of species. Many authors model the current distribution of species, and then project those models into the future under one or more time steps to determine potential range shifts under climate change. As modeled, the responses appear to be relatively species-specific, with each species responding to different suites of climate or other variables.

We provide two examples of such projected species responses from our own work (see Appendix for methods). Figure 2 depicts the response of Siler’s pincushion cactus (*Pediocactus sileri* (Engelm. ex J.M. Coul.) L.D. Benson) under the CCCMA CGCM2 A2a climate change scenario. The center of the suitable climatic envelope for this species is predicted to shift 75 km. to the northwest by the 2080s. In Figure 3, we summarize the results of these models for rare species in the intermountain western United States (91 taxa) and in the northeastern United States (17 taxa). The direction of range shift is more consistent in the Northeast, with most species mov-

ing north and east, whereas in the western United States, climate envelope shifts happen in all directions. The distance of range shift is also quite different, with species needing to move much longer distances in the Northeast to remain in their optimal climate. This is due in part to the rare species in the Northeast having larger ranges currently, but also due to the relative homogeneity in elevation and habitats in that part of the country.

Seed sourcing for both short-term restoration efforts and long-term resiliency in the face of climate change can benefit from the use of the many predictive tools available. In Australia, for example, the National Climate Change Adaptation Research Facility at the University of Queensland has used SDMs to predict the impact of climate change, with and without restoration activities, on 355 species of threatened plants. They concluded that 59 of those considered could completely lose their climatically suitable range (i.e., their suitable climate will no longer exist in Australia) by 2085 under the “business as usual” climate change scenario, while four plant species face almost certain extinction due to complete loss of suitable range even under the most optimistic mitigation scenario tested (Maggini et al. 2013). However, using such model results to determine seed sourcing strategies can be complicated by the indirect climatic responses of interacting species, which have been shown to influence and even reverse the direct effects of climate change (Angert et al. 2013). For example, Suttle et al. (2007) found that experimentally extending the rainy season in a California grassland community initially caused increases in plant production. However, after the second year, the accumulation of grass litter suppressed forb species and caused steep declines in plant species richness.

Some recent studies have pointed out that in an era of rapid climate change, local seed sources may not outperform other sources, and in some cases may underperform (Wilkinson 2001; Maschinski et al. 2013; Wilczek et al. 2014) as populations find themselves marooned at sites to which they are no longer adapted. This has led to the concepts of dynamic seed transfer

zones and assisted migration (also called managed relocation and assisted colonization), which take into account the effects of climate change on plant distributions (Ying and Yanchuk 2006; Kramer and Havens 2009; Vitt et al. 2010). Dynamic seed transfer zones incorporate the idea that zones are not static through time; their boundaries will shift as the climate changes. SDMs are being used by our research group and others to attempt to forecast how far seed zones will shift, in what direction, and over what time frame. The forestry community has been working on this issue for economically important tree species over two decades (Billington and Pelham 1991; Rehfeldt et al. 1999; Rehfeldt 2004; Ying and Yanchuk 2006; O’Brien et al. 2007; Potter and Hargrove 2012).

In the past, our research group has defined assisted migration as “the purposeful movement of species to facilitate or mimic natural range expansion, as a direct management response to climate change” (Vitt et al. 2010). Here we extend that definition to, “the purposeful movement of individuals or propagules of a species to facilitate or mimic natural range expansion or long distance gene flow within the current range, as a direct management response to climate change.” This change acknowledges that propagule movement within a species range beyond typical gene flow distances or between disjunct populations is a type of assisted migration (Figure 4), sometimes referred to as facilitated adaptation (Aitken and Whitlock 2013). Excluding extreme definitions (e.g., Thomas et al. 2013), facilitated adaptation attempts to incorporate both local genetic diversity and genes from populations adapted to projected climate changes, allowing natural selection to then operate on this expanded pool of genetic diversity.

The concept of assisted migration has been met with much skepticism by the conservation community. Some fear that moving genotypes long distances within current range limits will lead to maladaptation and/or outbreeding depression (a decrease in fitness of offspring when parents are genetically dissimilar) (Weeks et al. 2011). Others point out that moving plants outside their

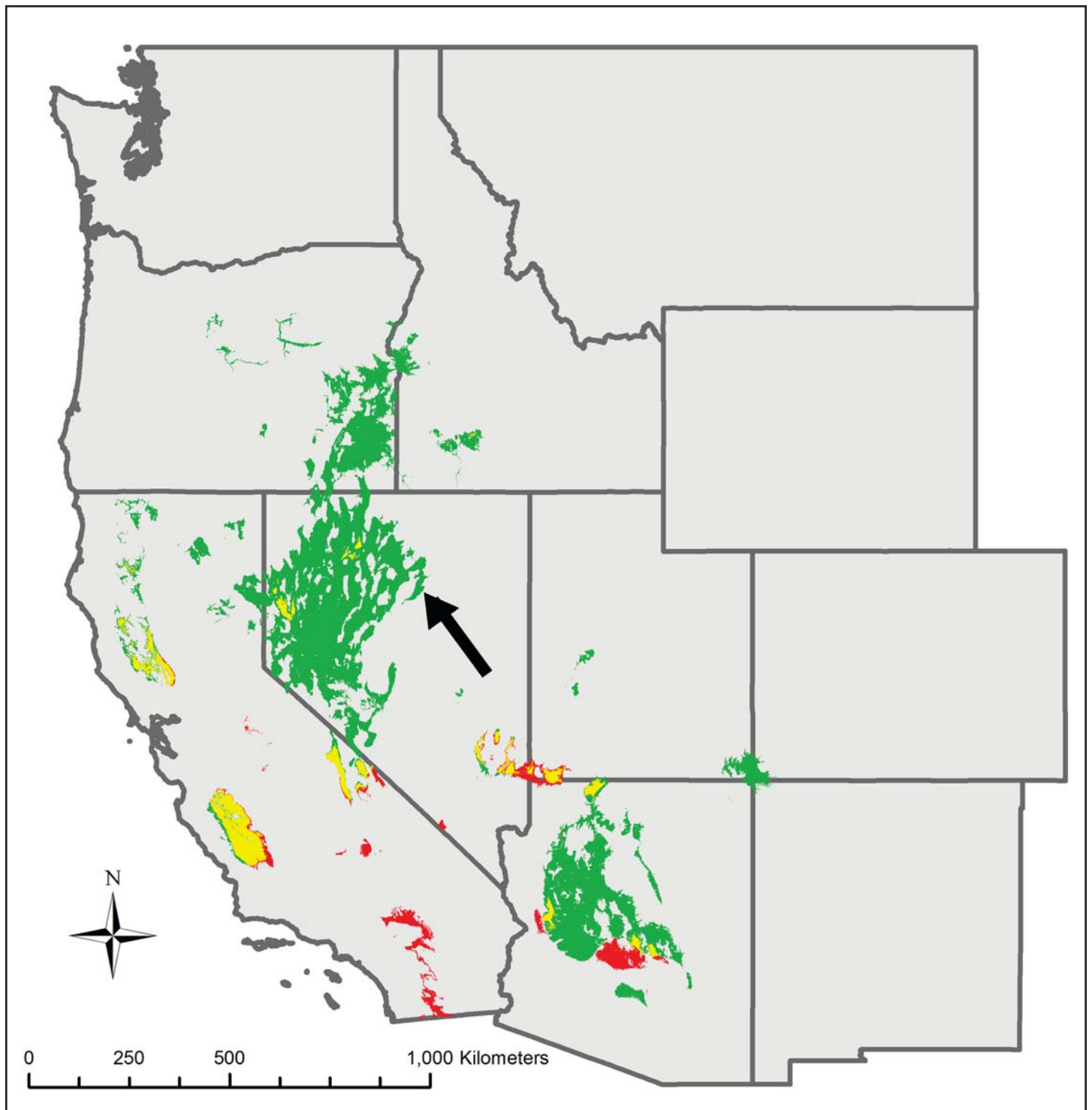


Figure 2. A species distribution model for Siler's pincushion cactus (*Pediocactus sileri*), showing the predicted change in climatic niche by the 2080s under the CCCMA CGCM2 A2a climate change scenario. Green represents areas of predicted expansion of climatic niche; yellow represents areas of no change of climatic niche; red represent areas of predicted contraction of climatic niche. The arrow indicates the direction and distance of the change at the centroid of the predicted climatic niche between now and the 2080s.

historic range may lead to problems with invasive behavior (Mueller and Hellmann 2008; Riccardi and Simberloff 2009). Still others have cited the huge costs associated

with large scale implementation of assisted migration (Hunter 2007) or lack of confidence in climate models (McLachlan et al. 2007). While these risks and costs

merit consideration, so too do the risks and costs of choosing to do nothing. Some recent studies have examined the risk of invasiveness with relatively short-distance

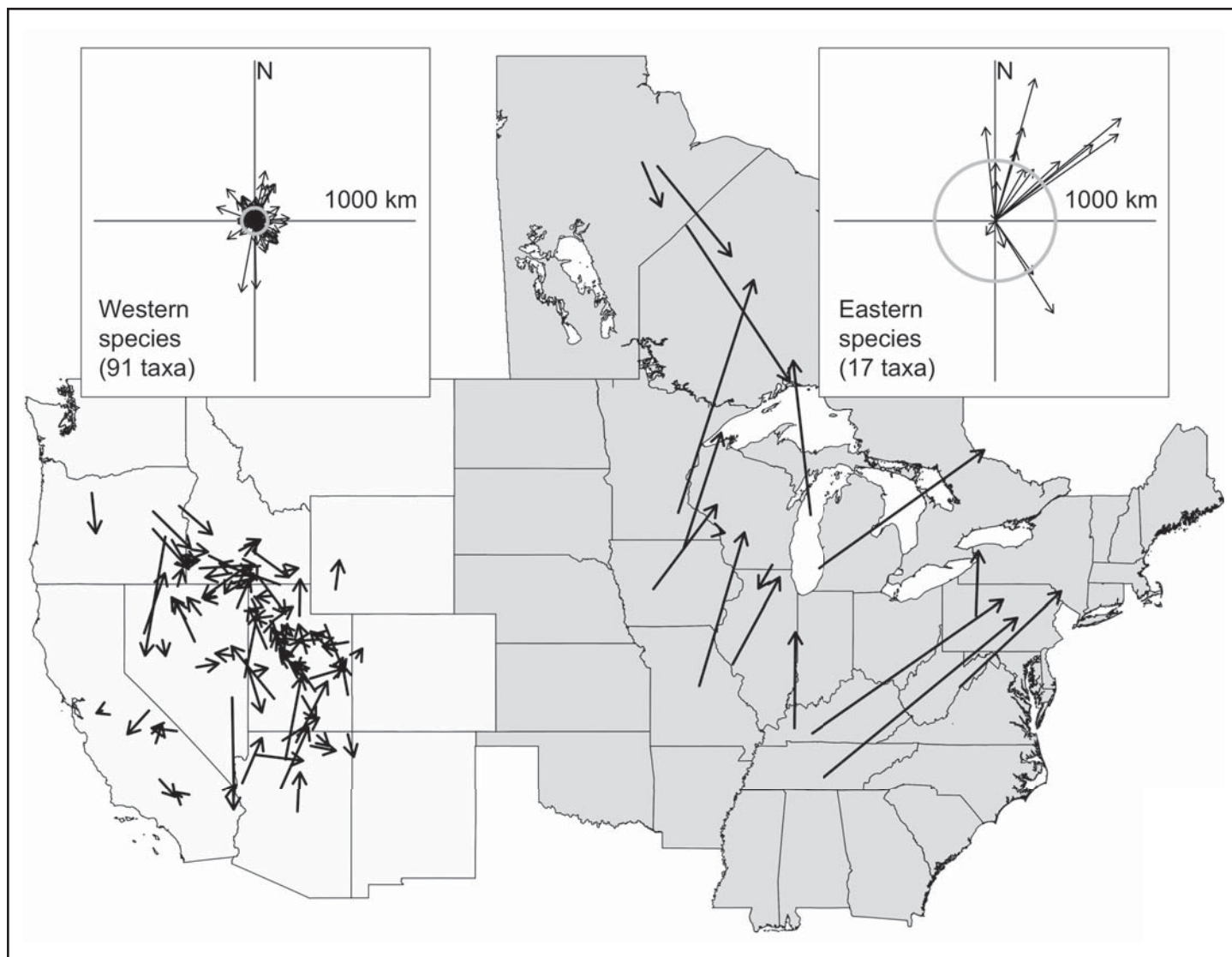


Figure 3. Map showing the change in the distribution of the climatic niche for rare (threatened, endangered, or candidate) species in the western United States and northeastern United States by the 2080s under the CCCMA CGCM2 A2a climate change scenario. The arrows indicate the direction and distance of the change at the centroid of the predicted climatic niche between now and the 2080s. The windroses summarize the direction and distance for each region. The ring plotted on each windrose represents the geometric mean (solid grey) for the change in distribution of climatic niche in each region. The axis bars for each windrose are scaled to 1,000 km (from 0,0 to tip).

intracontinental movement of plants and found them to be relatively small (Mueller and Hellman 2008; Reichard et al. 2012). In addition, the cost of assisted migration is lowered when its implementation is planned within a restoration context. In other words, assisted migration could be accomplished by changing one's seed sourcing guidelines with little incremental cost increase for restoration projects.

The lines between restoration seed sourcing and assisted migration have already begun to blur. Many restoration practitioners are sourcing seed less conservatively (from

more distant provenances, often with climate change in mind) either deliberately or out of necessity when local sources are not available in the preferred quantity or price (BLM 2000). A recent paper by Breed et al. (2013) outlines four seed sourcing strategies: local provenancing, composite provenancing (first proposed by Broadhurst et al. 2008), admixture provenancing, and predictive provenancing (summarized in Table 1). They provide a decision tree to help practitioners choose an appropriate seed sourcing method based on the use of climate change distribution modeling and known differences (genetic and/or

environmental) between populations. Their recommendations assume seeds can be collected from multiple, diverse populations, including capturing samples from various soil and climatic conditions. Others have distinguished between a strict local provenancing approach (originating from the site itself or an extremely close site within typical gene flow distance) and a relaxed local provenancing approach that focuses on matching ecological conditions between source and recipient sites and collecting from large populations, and often multiple populations, even if they are further away. This relaxed approach accomplishes both

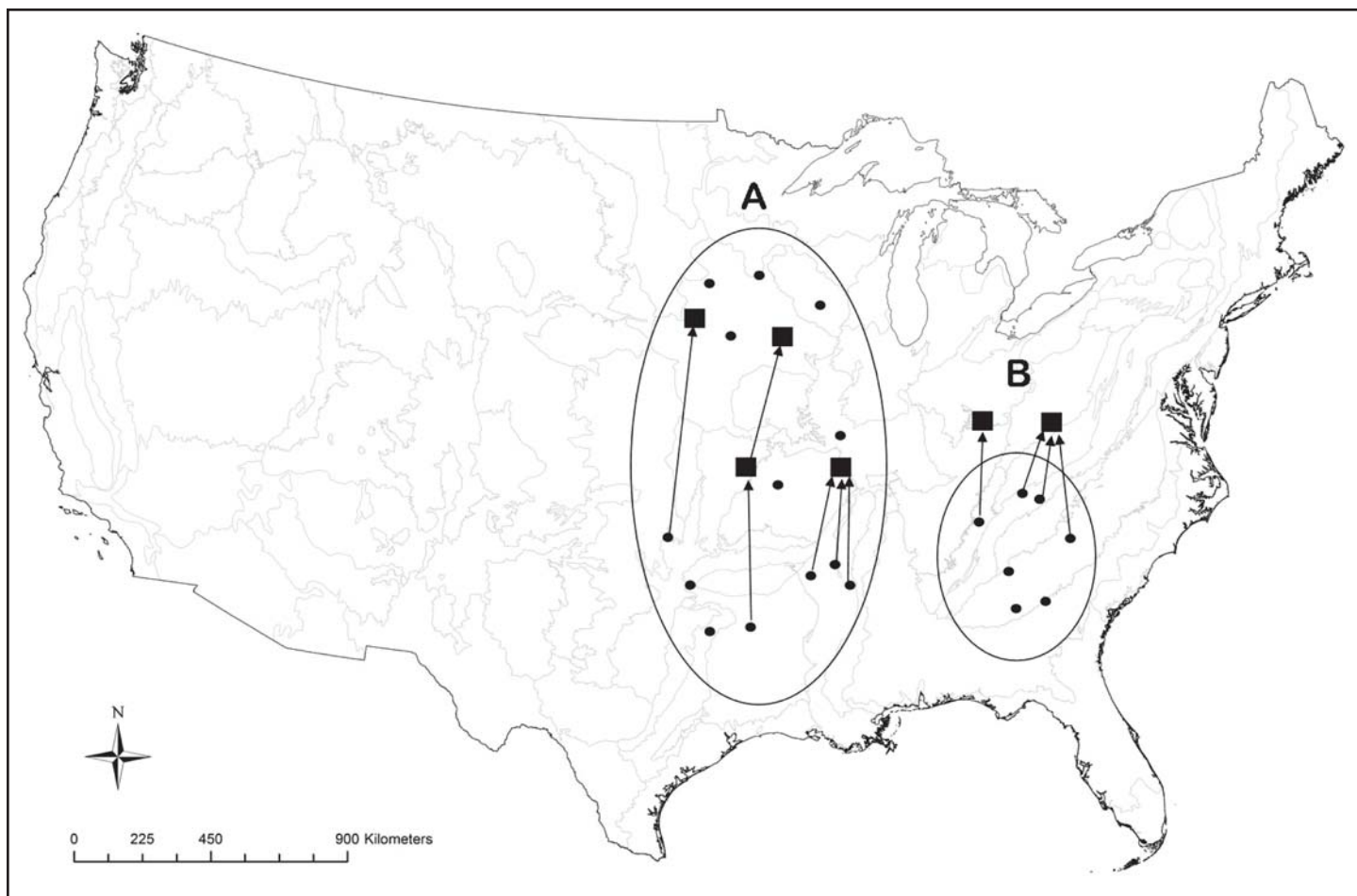


Figure 4. Various scenarios for assisted migration. Restorations (indicated by filled squares) can source propagules from single or multiple populations (indicated by filled circles). Assisted migration within a species' range (A) can include movement of propagules connecting disjunct portions of a range (shown at left) or can take place over time in a stepping stone fashion (shown in center). Example B shows assisted migration beyond a species' historical range.

local provenancing and increased genetic diversity if multiple sources are used (Kaye 2001; Broadhurst et al. 2008; Ward et al. 2008). The predictive provenancing approach has been applied to some commercially important conifers (Rehfeldt and Jaquish 2010; Thomson et al. 2010) but the research required to do so, including common garden experiments, is prohibitively costly and time-consuming for most species. Potter and Hargrove (2012) took an approach that avoids common garden experiments, describing 30,000 "seed transfer ecoregions" globally, then projected the locations of those ecoregions in 2050 and 2100 using different emission scenarios and global circulation models. Their results can be used to answer two important questions: (1) "Where should I source seed now so that my restoration (in a given location) will be well-adapted in the future?" and (2) "Where should my

seeds (from a given location) be planted to ensure they will be well-adapted in the future?" (Potter and Hargrove 2012). However, planting a "pre-adapted" restoration runs the risk of failure in early years if seeds do not establish well under current conditions, so facilitating adaptation must be balanced with avoiding maladaptation to current climates (Bower and Aitken 2008). It may be best to think about assisted migration as moving germplasm in a stepwise manner and in an experimental context to test these ideas about predictive provenancing. However, all of this research highlights a recent trend in restoration ecology. It is no longer sufficient to have the goal of a restoration project be the return to pre-disturbance (or even pre-settlement) conditions. Our restoration targets must be more responsive and proactive to changing conditions as we move into the future

(Harris et al. 2006).

OTHER FACTORS AFFECTING SEED SOURCING DECISIONS

There are numerous other factors that may affect how one sources seed for a restoration project, some biological (Table 2), some practical. For instance, the condition of the site to be restored should be considered. If it is highly degraded or altered from the original condition, local provenance may not be as important. Previously adapted populations may no longer be appropriate when soil chemistry or structure, fire regime, or other properties have been drastically changed (Leger 2008). Introduced pests and pathogens, such as *Phytophthora cinnamomi* (Rands) in Australia, can similarly change environments enough that local seed sources, or

Table 1. Types of seed sourcing, modified from Breed et al. (2013), with their description, benefits, risks and most appropriate uses.

Seed sourcing type	Definition	Benefits	Risks	Best Used When
Strict local provenancing	Using seed only from the site where restoration is occurring or populations within normal gene flow distance	<ul style="list-style-type: none"> • little risk of maladaptation (at least short term) 	<ul style="list-style-type: none"> • narrow genetic base • possible inbreeding • genetic drift • lack of adaptive potential 	<ul style="list-style-type: none"> • disturbance is minimal • large local population present at or adjacent to restoration • predicted distribution change is low
Relaxed local provenancing	Mixing seed from geographically close populations with a focus on matching environment of source and recipient sites	<ul style="list-style-type: none"> • little risk of maladaptation (at least short term) • avoids inbreeding • increases adaptive potential 	<ul style="list-style-type: none"> • can have narrow genetic base • lack of adaptive potential for the longer term 	<ul style="list-style-type: none"> • disturbance is minimal • predicted distribution change is low
Composite provenancing	Mixing seed from populations of close and intermediate distance (or environmental match) to mimic long distance gene flow	<ul style="list-style-type: none"> • avoids inbreeding • increases adaptive potential 	<ul style="list-style-type: none"> • maladaptation • outbreeding depression 	<ul style="list-style-type: none"> • disturbance is minimal • fragmentation is high • predicted distribution change is moderate
Admixture provenancing	Mixing seed from many populations of varying distances throughout the range of the species	<ul style="list-style-type: none"> • highest adaptive potential 	<ul style="list-style-type: none"> • largest risk of maladaptation • outbreeding depression • possibly invasive genotypes 	<ul style="list-style-type: none"> • disturbance is high • predicted distribution change is high
Predictive provenancing	Using genotypes adapted to predicted conditions (e.g. 2050 climate projections) based on models and transplant experiments	<ul style="list-style-type: none"> • deals best with changing conditions, if predictions are correct 	<ul style="list-style-type: none"> • projections may be wrong • requires much research (high initial cost) 	<ul style="list-style-type: none"> • disturbance is low to moderate • predicted distribution change is high and well understood

even species, cannot succeed (Lesica and Allendorf 1999; Broadhurst et al. 2008; Johnson et al. 2010). Another factor to consider is landscape history. Patterns of genetic diversity and their applications for seed zone delineation may be quite different in relatively young, postglacial landscapes like the US tallgrass prairie compared to more ancient, stable landscapes like the southwest Australia floristic region (Hopper 2009; Kramer and Havens 2009). One might expect a greater degree of

local adaptation and consequently smaller seed zones in ancient landscapes, but this remains to be tested on a broad scale.

For individual species, local seed sourcing may be more important for geographically narrow endemics and edaphic endemics than for more widespread species. The same may be true for species that have a long history of existing in relatively isolated sites with little gene flow between them, compared to those from recently

fragmented sites that were historically connected by long distance gene flow (Fenster and Galloway 2000; Frankham et al. 2011). For example, in populations that have had minimal gene flow for over 500 years or 20 generations, outbreeding depression leading to maladaptation becomes increasingly likely, and it may be more important to match environmental conditions (between source and restoration sites) in order to limit potential negative

Table 2. Species and habitat characteristics that may influence seed sourcing decisions.

More conservative/local seed sourcing		More relaxed/longer distance seed sourcing
Species characteristics		
Narrow and/or edaphic endemic	↔	Widely distributed
Taxonomic uncertainty (potential for cryptic species)	↔	Taxonomic stability (well-studied)
Little long-distance gene flow	↔	Extensive long-distance gene flow
Habitat characteristics		
Historically fragmented	↔	Recently fragmented
High quality	↔	Highly disturbed/degraded
Ancient/stable landscape	↔	Younger/dynamic landscape

effects (Frankham et al. 2011).

On the more practical side, the scale and urgency of restoration will factor into seed sourcing decisions. Some projects are able to wait until appropriate seed sources are collected and bulked. For instance, the planned restoration of a few hundred acres of grazed pastureland to native tallgrass prairie may be able to wait a few years in order for suppliers to produce the materials specified for the project by the land manager. At the other extreme, restoration (or at least rehabilitation/revegetation) may need to happen almost immediately after severe wildfires, especially in mountainous regions because of erosion risks. These fire events are unplanned, unpredictable, and large-scale; millions of hectares burn every year in the United States. It is impossible to have enough local, source-identified seed of all the species needed to address every postwildfire restoration need immediately. These projects may need to be approached in a stepwise manner. For instance, an annual or short-lived cover crop could stabilize the site, followed by planting of a few appropriately sourced early seral species, followed by the addition of materials specified and grown for the project in later years. This approach would require the development and storage of source-identified “work horse” species representing numerous seed zones for several early seral species. Increased seed storage capacity, such as the recently built Bureau of Land Management Seed

Warehouse in Nevada, will be critical to the success of these projects.

RECOMMENDATIONS

At this point in time, scientists working in restoration ecology can offer best management practices based on research to date, but much remains to be tested. Land managers are left balancing those scientific recommendations with consideration of availability of plant materials and costs. We offer the following recommendations to the restoration community, which we hope will improve restoration outcomes:

1. Develop regional lists of essential or “workhorse” species for plant communities most in need of restoration and rehabilitation. Seed collection and nursery production efforts should focus on developing large quantities of source-identified seed of these relatively few species for long-term storage. These are the plant materials that can be deployed immediately after disturbances to begin the restoration/rehabilitation process. The Native Seed Network website (nativeseednetwork.org) provides an excellent starting point for ecoregional species lists, and they encourage the restoration community to help refine those lists.
2. Collect and bank genetically diverse seed samples of as many species as possible, especially those species important for restoration. Current collection strategies often capitalize on “good” years and sites, only collecting species when and

where seed production is high. This strategy should be reconsidered, as the seed produced in “bad” years, such as drought years, may harbor important genetic variation needed as the climate changes. In addition, collections from “bad” sites (heavily invaded or environmentally harsh) may provide species or ecotypes that are more competitive with invasive species (Mealor and Hild 2007; Leger 2008), and may be considered “native winners.” Focusing collection efforts on range edges and ecologically dissimilar sites may capture additional important variation (Rice and Emery 2003; Darling et al. 2008). The desire for large seed collections should not trump the importance of capturing this diversity.

3. Increase short-term (cool) and long-term (frozen) seed storage capacity to be able to store the seeds from the efforts described above. Having stored seed will also allow sourcing strategies to be diversified by sourcing temporally as well as spatially. Having a greater selection of species from multiple sources will allow for faster responses to the immediate and diverse demands associated with many short-term rehabilitation projects, including postwildfire restoration and erosion control. Similarly, the efforts of the Native Seed Network to improve the availability of native seeds and support the native seed market place will also increase options for restoration.

4. Expand experimental tests of different provenancing practices and types of

assisted migration. Empirical results are needed from a wide variety of species and locations before best practices can be recommended.

5. Maintain good records and monitor restoration outcomes. In a sense, every restoration project is an experiment. Future meta-analyses of successes and failures will allow us to improve restoration practices. A national clearinghouse or database of restoration project outcomes, perhaps modeled on or using the platform of the Conservation Registry (<<http://www.conservationregistry.org/>>), would enhance this capacity enormously.

CONCLUSIONS

Making appropriate seed sourcing decisions will depend on many factors, including the suite of species one is attempting to restore, the landscape context, and the size and urgency of the restoration project. In the eastern and midwestern United States, obtaining appropriate materials may be easier because the scale of restoration projects is relatively small, provisional seed zones are relatively large, and the effects of climate change on plant distributions appear to be more predictable. Restoration in the western United States will undoubtedly prove more challenging, where many restoration projects are immense, the scale of local adaptation tends to be finer grained and consequently seed zones are smaller, and species distribution models find less predictable responses to climate change. Nevertheless, we are encouraged by the large-scale Native Plants Development Program led by the Bureau of Land Management to collect, grow, and store large quantities of source-identified native seed materials (NPM DP 2009). This is an essential step in improving restoration outcomes, especially in western states where the program is focused. Having a seed bank of ecologically and genetically diverse, source-identified native seed keeps our options open for future projects as restoration science catches up with restoration needs.

As we change from looking to the past to preparing for the future in restoration ecology, one wonders if creating future-proof

plant communities is more “prestation” than restoration. Regardless of what we call our activities, the challenge of developing and maintaining resilient and adaptable communities is becoming ever more challenging and ever more important in our rapidly changing world.

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Appendix. Species distribution modeling methods used in Figures 3 and 4.

We modeled 91 rare species that occur in the western United States and 17 species that occur in the northeastern United States. For all taxa, we used the current climatic data set and one future climate model acquired from WorldClim (Hijmans et al. 2005; www.worldclim.org). The species distribution modeling methods for the taxa from the western United States were completed following the protocol by Still et al. (this issue) with two differences to the models. The projected model extent for all taxa presented here is the entire western United States (AZ, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY) and only one future global circulation and emission scenario model was run. The five bioclimatic variables used in the models were annual mean temperature, mean temperature of wettest quarter, mean temperature driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter.

The 17 species found in the northeastern United States were modeled using MaxEnt and the projected model extent included 33 U.S. states (ME, NH, VT, CT, RI, MA, NY, PA, DE, VA, MD, WV, SC, NC, GA, MS, LA, AK, TN, KY, OH, IN, IL, WI, MN, MI, MO, IA, OK, NE, KS, SD and ND) and two Canadian provinces (Ontario and Manitoba) for which we had locality data. ENMTools was used to determine the correlation values between each of 19 bioclimatic variables, and a subset of six uncorrelated variables (mean diurnal, mean temperature of wettest quarter, mean temperature of coldest quarter, precipitation seasonality, precipitation of warmest quarter, and precipitation of coldest quarter) were used to create individual models for each species.

Following the methods of VanDerWal, Murphy et al. (2012), the change in distance and bearing for climatic niches for all taxa were calculated by first calculating the center of gravity on continuous surface models for the current and future ranges using the SDMTools package (VanDerWal, Falconi et al. 2012) in R 3.0.1 (R Core Team 2013). The SDMTools package was then used to calculate the speed and direction of climatic niche change.
