

UN DECADE ON ECOSYSTEM RESTORATION

STRATEGIC ISSUES ARTICLE

Community-level assisted migration for climate-appropriate prairie restoration

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Climate change threatens the long-term survival of highly fragmented habitats such as North American tallgrass prairie. De novo plantings into former agricultural sites can contribute to efforts to conserve prairie biodiversity, but past planting practice (including our own) has focused on the use of local species and genotypes. Climate change makes this “local-only” practice obsolete because of rapidly shifting species’ ranges. We propose that new prairie plantings incorporate assisted migration at the community level; all species and genotypes that are viable in the changed climate and potentially could reach the site in an unfragmented landscape should be considered for inclusion. Selecting and sourcing species for climate-appropriate restorations is possible with minimal additional cost or expertise. Based on best-available estimates of current and future climate, species richness of future prairie plantings at our Minnesota study site could be increased by over one-third (26 new species). Potential risks to such extensive use of assisted migration are offset by the drastic conservation challenge of highly fragmented communities under climate change.

Key words: assisted colonization, climate change, habitat fragmentation, prairie reconstruction, range shift, seed source

Implications for Practice

- Restoration plantings traditionally have used local species and seed sources, because these are presumably adapted to local conditions.
- However, rapid anthropogenic climate change may mean that multiple nonlocal species could thrive in restorations. Even for species with local populations, local genotypes may be poorly adapted to future climate conditions.
- Unassisted migration to introduce climate-appropriate species and genotypes is nearly impossible currently, especially for highly fragmented habitats such as tallgrass prairie.
- We propose that future prairie plantings include all suitable species that could reach the planting site in an unfragmented landscape.
- For species that already occur locally, local seeds should be mixed with seed from climate-appropriate locations to allow in situ adaptation to changing climates.

...management and conservation of the biological world, and our place in it, requires a transition from trying to minimize biological change to one in which we facilitate dynamism that accelerates the rates at which species and ecosystems adjust to human-associated drivers of change. (Thomas 2020)

The Challenge of Tallgrass Prairie Conservation and Restoration

North American temperate grasslands rank as Critically Endangered (Hoekstra et al. 2005), among the most threatened

ecoregions globally. From 80 to 99.9% of original tallgrass prairie has been lost, mainly due to conversion to agriculture (Gibson 2009). The remaining fragments of tallgrass prairie are mostly small and isolated in the landscape, and suffer from high rates of local extinction (Alstad et al. 2016). To maintain prairie biodiversity in these circumstances, a favored approach of conservationists has been to establish prairie communities in places where none currently exist (i.e. reconstruction; Gann et al. 2019). In many locations, including the area in which we work, reconstructed prairie is more common on the landscape than native prairie remnants. Thus, planted prairies may be the only hope for long-term maintenance of some functioning version of this community. Establishing best practices for de novo prairie plantings is essential to achieve conservation goals, yet current approaches often fail to consider how climate change will affect success.

The primary goal of restorations typically has been to maximize species richness and other measures of biodiversity of prairie plants (Ruiz-Jaen & Aide 2005; Wortley et al. 2013). The

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benchmark for success of establishing a prairie community has been comparison with local prairie remnants (e.g. Barak et al. 2017; Newbold et al. 2020). Geographic location of seed source (“provenance”) for prairie plantings has received considerable attention (McKay et al. 2005; Dupré la Tour et al. 2020). Reconstructions typically have used seed only from nearby remnants, because local genotypes are presumed to be best adapted to site-specific conditions.

Our own practices in the Cowling Arboretum at Carleton College (Northfield, MN, U.S.A.) serve as an example of traditional restoration practices. Areas of prairies have been established in the Arboretum since the late 1970s, and there are currently approximately 64 ha of planted prairie. M.J.M. has been involved in planning and assessing these plantings since 1987, serving as Arboretum Director from 1991 to 2007 and as Research Supervisor from 2007 to present. The site had essentially no prairie species present when our work began, and most of what is now prairie was in row-crop agriculture for many decades previously. Our goal for these reconstructions was to recreate the local prairie plant community as completely as possible, similar to most other prairie planting efforts at this time. We viewed our relatively large plantings as a potential means to rescue species that could be lost elsewhere on the local landscape, which contains only a tiny proportion of the originally extensive prairies. Our planting was restricted to species that occurred locally, based on either current occurrence or records from the time of European settlement to present. Whenever possible, we chose seed from local remnants, preferably within approximately 30 km.

In many ways these prairie plantings have been successful. A diverse community of prairie species has developed (McKone & Hernández unpublished data; Camill et al. 2004), with relatively few problems with invasive species. Soil carbon and nitrogen have begun to recover since planting (Hernández et al. 2013). The prairie has also attracted a number of animals of conservation concern, such as grassland birds (Beck et al. 2016). However, the reality of climate change forces us to reconsider the goals and practices that have guided us for decades.

Assisted Migration in Response to Climate Change

Anthropogenic climate change already has had an impact on many natural communities (reviewed in Scheffers et al. 2016), and this can only increase as the rate of change accelerates. Local extinctions due to climate change are occurring in plants and animals (Wiens 2016), and projections suggest that species-wide extinctions are likely to accelerate greatly in future climates (Urban 2015; Román-Palacios & Wiens 2020). Under these circumstances, current areas set aside for conservation may lose their ability to maintain native species diversity (Hannah et al. 2007; Batllori et al. 2017). Current practices for habitat restoration that emphasize planting native species from local sources fail to account for the impacts of a changing climate and threaten the resilience of these systems into the future (Prober et al. 2019). New best practices must be based on the realities of climate change while still being practical for land managers (Heller & Zavaleta 2009).

Assisted migration, “the intentional translocation of individuals within or outside the natural range of a species” (Aitken & Whitlock 2013), is one of the most commonly proposed active responses to climate change (Frankham et al. 2017; Hällfors et al. 2017; Prober et al. 2019). The projected rate of climate change is significantly faster than the most rapid rates at the end of the last glaciation, and perhaps for the last 65 million years (Diffenbaugh & Field 2013). Recent range shifts already have been observed in some species (Chen et al. 2011), and transplant experiments have demonstrated that some species can now grow well outside their previous range (e.g. Wang et al. 2019). However, many species will not be able to track the rapidly changing climate (Corlett & Westcott 2013; Svenning & Sandel 2013). The problem is exacerbated by extensive fragmentation of native habitats in human-dominated landscapes, making migration across the landscape much more difficult for many species (Frankham et al. 2017).

Human intervention is the only realistic means for the ranges of many species to keep up with rapidly moving climate envelopes in fragmented habitats (Vitt et al. 2010; Butterfield et al. 2017). Given the rate of movements of climate envelopes, the principle of use of only locally occurring species and genotypes in habitat restoration is questionable at best. Some local species may be lost entirely if their climate envelopes move outside the local area. Multiple species that grow elsewhere would thrive in restorations if they were able to migrate to new locations, but this is prevented by the speed of climate change and the difficulty of dispersal across fragmented landscapes. To restore the natural process of migration, restorations should include species from locations that are likely to match current and future climates (Havens et al. 2015; Vitt et al. 2016; Butterfield et al. 2017).

Use of nonlocal seed sources also should be reconsidered for species that already occur locally. There is ample evidence from reciprocal transplant experiments that plant populations are often adapted to local conditions (Leimu & Fischer 2008) including climate variables such as temperature, day length, and precipitation. The rapidly changing climate will render populations increasingly maladapted to local conditions. Any resulting reduction in reproductive potential could lead to extinction unless populations are able to evolve rapidly to track climate change (Davis & Shaw 2001; Jump & Peñuelas 2005; Sgrò et al. 2011). The genotypes adapted to changed climates are most likely to occur in nonlocal populations (e.g. Etterson et al. 2020), but gene flow from climate-appropriate source populations is severely limited by habitat fragmentation (Davis & Shaw 2001; Jump & Peñuelas 2005). Thus, it may be necessary to introduce genotypes from parts of the current range of a species that match current or future climate conditions (Hoffmann & Sgrò 2011; Frankham et al. 2017).

Community-Level Assisted Migration in Prairie Restoration

We here examine the role of assisted migration to plant prairies that will be successful in a changing climate. To frame our discussion, it is essential to recognize that *all prairie reconstructions are by definition examples of assisted migrations*. Prairie

species that are planted into former agricultural land require intentional human dispersal from elsewhere. The question therefore is not *whether* to use assisted migration in prairie plantings, but how to *optimize* the practice of assisted migration to accommodate climate change. We propose that future prairie restorations include any species that could exist under climate change if there were a landscape of continuous prairie habitat. For both local and nonlocal species, introductions should include sufficient genetic variation to allow species to adapt to changing climate.

The argument for assisted range expansion is particularly strong for tallgrass prairie. The range of many prairie species is expected to shift significantly with climate change (Lyon et al. 2019). Most prairie plants are herbaceous and not animal dispersed, generally the class of plant that was most likely to lag Holocene climate change (Butterfield et al. 2019). There is limited colonization from remnant prairies into reconstructed prairies even when they are adjacent, and mostly on a scale of 10s of meters (Sperry et al. 2019). The extreme habitat loss and fragmentation of prairies in the current landscape makes it highly unlikely that unassisted migration will occur over long distances (Galatowitsch et al. 2009).

Given the dire long-term conservation prospects for maintenance of prairie biodiversity, the best option for prairie plantings is to introduce any species with a climate-based range envelope that has expanded into the focal area. This is a radical departure from the “local is best” approach to seed provenance that we have utilized for decades in our own plantings. We build on other generally similar proposals (e.g. Havens et al. 2015; Ramalho et al. 2017; Lyon et al. 2019) by explicitly expanding to include consideration of an *entire plant community* within the framework of assisted migration, both for range expansion and climate-adjusted provenancing. That is, there should be *community-level assisted migration*.

Once it is acknowledged that climate change requires use of nonlocal seed in restorations, a new basis for seed provenance is necessary. A variety of proposals have been made for the optimal strategy for use of nonlocal seed sources (Breed et al. 2013; Prober et al. 2015). For example, “predictive provenancing” would be use of seed from a location that closely matches the predicted climate in the planting area. However, this strategy requires both an accurate climate prediction and a seed source in the targeted source area. A more flexible approach is “climate-adjusted provenancing” (Prober et al. 2015; Ramalho et al. 2017), the use of seed both from local and from multiple nonlocal populations, biased in the direction of expected climate change (Fig. 1). Such a strategy ensures that local genotypes are maintained, but the addition of nonlocal genotypes will maximize heritable variation for climate-related traits. Given uncertainty about the exact rate of climate change and about the distribution of climate-appropriate genotypes, such a mixed strategy is a powerful means to maximize the probability that planted populations will be able to adapt to current and future conditions. Use of seed samples from multiple source populations, both distant and local, could help ameliorate the effects of genetic drift in prairie populations (Frankham et al. 2017; Ralls et al. 2018; Bell et al. 2019).

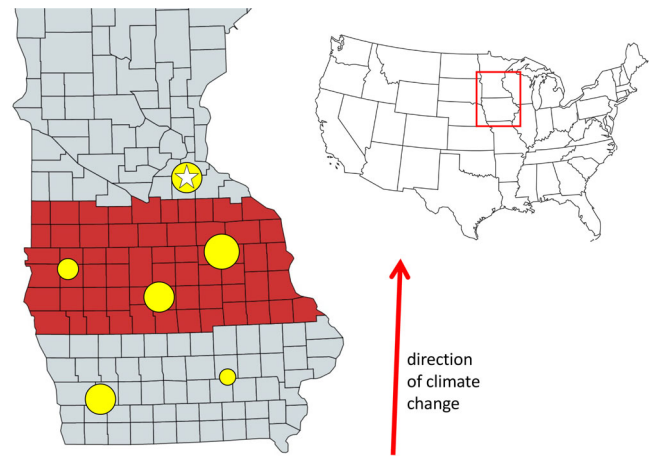


Figure 1. Source area identified for potential assisted migration to match 2020 conditions (counties in red). Star marks the planting site, and yellow circles show conceptually where seed sources could be used for climate-adjusted provenancing. Seeds would include local sources, sources that match the 2020 climate (red counties), and some sources that match future climate. County map created by MapChart (<https://mapchart.net>).

Feasibility

Achieving the goal of community-level assisted migration might appear to be a daunting prospect for land managers, because there are inevitably limited resources available to evaluate new planting methods. To demonstrate feasibility, we show here that these goals can be achieved with relatively low investments of time, money, and expertise. We followed our revised goals to design a future planting at our field site in the Cowling Arboretum.

Climate-based species distribution models can be used to predict climate-shifted ranges (Butterfield et al. 2017; Lyon et al. 2019). However, such modeling would not be feasible on the community level because sufficiently detailed range and climate measurements are only available for a limited number of species; Lyon et al. (2019) found sufficient occurrence information to build models for only 14 out of the 26 prairie species they considered.

To make a selection of seed provenance locations, it is necessary to know how the local climate has shifted since the onset of climate change. Sufficiently precise data can be derived from Multivariate Adaptive Constructed Analogs (MACA) that downscale global climate models to predict local climates. These models are available cost-free online (<http://www.climatologylab.org/mac.html>) and do not require modeling expertise to use. We used MACA models to determine the areas where plants existed in past climates that match our study site in 2020. The target area identified (Fig. 1) generally included southern Minnesota (southern two tiers of counties) and northern Iowa (northern four tiers of counties). Though there is a strong east–west gradient in precipitation across central North America (Galliat et al. 2020), the predicted location of future climates for our specific target area is predominantly to the south (Galatowitsch et al. 2009).

To choose appropriate species for our planned reconstruction, we determined the source area to the south where plants could

grow at our study site in the 2020 climate. We then used the county-level distribution maps from the Biota of North America Program (Kartesz 2015) to determine the range of each of the approximately 1,958 species in 774 genera found in Iowa (Eilers & Roosa 1994). There were 216 plant species that occurred in this target source area but not currently at our study site.

From these, we wanted to select candidate species that are prairie specialists, rather than generalist species that are common in other habitats as well. One way to find such species is use of the widely available conservatism index (C-value). The index is based on two factors: tolerance to disturbance and occurrence in specific habitat types (Freyman et al. 2016). The index has a range of values from 0 (disturbance-tolerant, found in multiple community types) to 10 (disturbance-intolerant,

Table 1. Plant species that could be introduced into prairie plantings at the study site from climate-appropriate areas further south. Species are generally ranked jointly by distribution in target area (number of counties) and average value of the conservatism index (C-value). See text for details. Nomenclature follows Kartesz (2015).

| Candidate Species | Family | No. of Counties in Target Area | Mean C-Value |
|---------------------------------|---------------|--------------------------------|--------------|
| <i>Arnoglossum plantagineum</i> | Asteraceae | 46 | 8.8 |
| <i>Polytaenia nuttallii</i> | Apiaceae | 11 | 8.3 |
| <i>Parthenium integrifolium</i> | Asteraceae | 18 | 7.7 |
| <i>Dodecatheon meadia</i> | Primulaceae | 15 | 7.3 |
| <i>Asclepias amplexicaulis</i> | Apocynaceae | 12 | 7.3 |
| <i>Echinacea pallida</i> | Asteraceae | 22 | 7.0 |
| <i>Asclepias longifolia</i> | Apocynaceae | 18 | 7.0 |
| <i>Aristida purpurea</i> | Poaceae | 12 | 6.7 |
| <i>Liatris squarrosa</i> | Asteraceae | 7 | 7.0 |
| <i>Erythronium mesochoreum</i> | Liliaceae | 9 | 6.0 |
| <i>Rudbeckia subtomentosa</i> | Asteraceae | 13 | 5.3 |
| <i>Hypericum sphaerocarpum</i> | Hypericaceae | 8 | 6.3 |
| <i>Pediomelum tenuiflorum</i> | Fabaceae | 5 | 7.7 |
| <i>Melica nitens</i> | Poaceae | 6 | 6.8 |
| <i>Senna marilandica</i> | Fabaceae | 4 | 7.5 |
| <i>Silphium integrifolium</i> | Asteraceae | 13 | 4.5 |
| <i>Asclepias stenophylla</i> | Apocynaceae | 4 | 7.3 |
| <i>Liatris hirsuta</i> | Asteraceae | 4 | 7.0 |
| <i>Astragalus missouriensis</i> | Fabaceae | 3 | 7.0 |
| <i>Asclepias purpurascens</i> | Apocynaceae | 3 | 7.0 |
| <i>Lomatium foeniculaceum</i> | Apiaceae | 3 | 7.0 |
| <i>Phlox bifida</i> | Polemoniaceae | 4 | 6.0 |
| <i>Desmodium paniculatum</i> | Fabaceae | 3 | 6.0 |
| <i>Mentzelia decapetala</i> | Loasaceae | 4 | 5.0 |
| <i>Pycnanthemum tenuifolium</i> | Lamiaceae | 4 | 4.3 |
| <i>Ruellia humilis</i> | Acanthaceae | 4 | 4.0 |

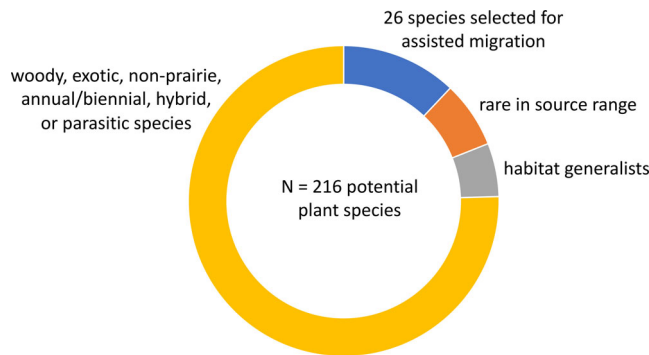


Figure 2. Selection of candidate species for community-level assisted migration. Of 216 potential species identified by range in the target area (Kartesz 2015), 163 were eliminated because of inappropriate habitat preference or life history, 12 were eliminated because they were not prairie specialists, and 15 were eliminated because they were not widespread in the target area. This left 26 candidate species for assisted migration (Table 1).

found in narrow range of community types). Since we have already chosen plants that are identified as present in prairie, high C-values would indicate prairie specialists. Though the management of the conservatism index remain controversial (as reviewed by Matthews et al. 2015), they are widely used by land managers. For our potential species, we used the compiled C-values available online (<https://universityofiowa.org>) from nearby states: Minnesota, Iowa, North and South Dakota (aggregated), Nebraska, Missouri, and Wisconsin. We averaged the assigned C-values across these six databases. Species with C-values below 4 are generally considered widespread and disturbance tolerant (Freyman et al. 2016). Thus, we eliminated the 12 species on our list with average C-values < 4. This left 26 species (Table 1) that would be appropriate for our planned prairie (Fig. 2).

We propose the assisted migration of these 26 new species into our planting by range expansion, as well as assisted gene flow from southern populations of up to 60 local species. This constitutes assisted migration at the community level, and we are not aware of other such ambitious proposals.

If successful, the addition of 26 new species would increase species richness of our reconstructed prairies by more than a third compared to previous plantings. Increased diversity of that magnitude could have multiple benefits (Fig. 3), such as greater resistance of productivity to climate extremes (Isbell et al. 2015) and increased energy use efficiency across trophic levels (Buzhdygan et al. 2020). Each additional species would interact with a variety of other species, including competitors, mutualists, and consumers. Additional species might help to replace the functional role of local species that are predicted to be lost due to climate change. The addition of southern genotypes of already-present local species can be expected to increase the likelihood of evolutionary adaptation to climate change, as well as to help alleviate inbreeding depression in local fragmented populations.

The economic cost of community-level assisted migration could be surprisingly modest. Many prairie plantings already depend on purchasing seed from commercial sources. A primary

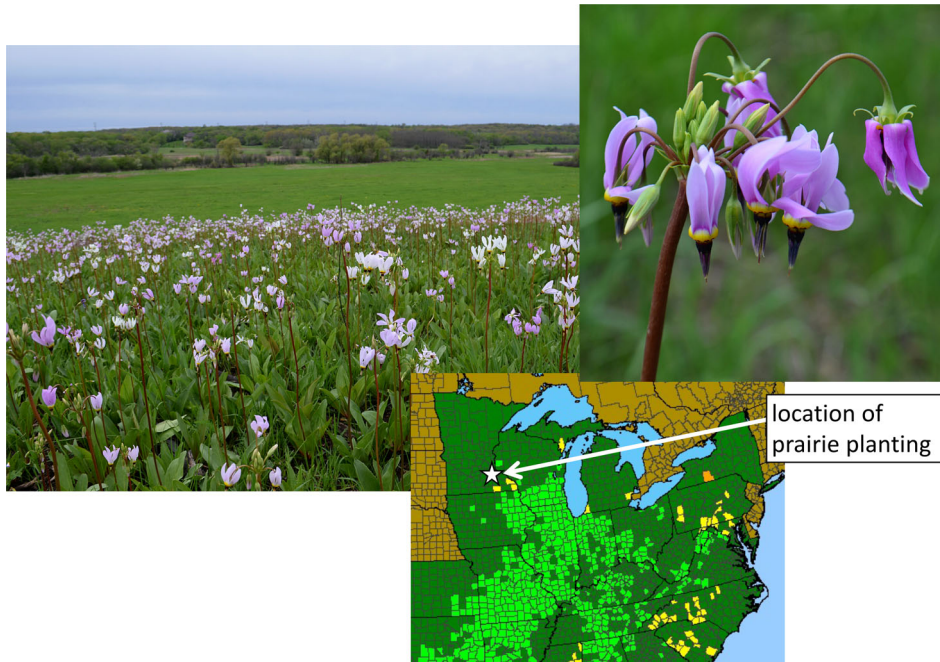


Figure 3. *Dodecatheon meadia* is a high-priority candidate species for range expansion into prairie plantings in the Cowling Arboretum, Northfield, MN, U.S.A. The current range map from BONAP (Kartesz 2015, used by permission) and site of our reconstruction are shown. Counties are colored light green when the species is present and not rare, yellow when present and rare, and orange when extirpated; states where species is present are dark green. Addition of this species would significantly increase phylogenetic diversity, as it would be the first member of the Family Primulaceae. *D. meadia* is among the earliest flowering species in prairies (Anderson & Schelfhout 1980), and its buzz-pollinated flowers are utilized by a variety of bees, especially in the genus *Bombus* (Macior 1964). Addition of an early-flowering resource such as *D. meadia* could significantly improve habitat quality of our reconstructions for *Bombus* spp. such as the federally endangered *Bombus affinis*, queens of which are known to visit *D. meadia* (Macior 1964). Plant images copyright Christopher David Benda.

driver of cost of restoration is the diversity of the seed mix (Kimball et al. 2015) rather than the geographical source of the seed. Assisted migration simply requires changing the provenance of purchased seed. For our example, approximately 80% (21 of 26) of nonlocal species were available from suppliers that collect in or near our target source area. There could be extra time and cost required to get seed from multiple sources, as required for climate-adjusted provenancing. In cases where resources for planning restorations are severely limited, we would advocate simply acquiring seed from a supplier within the climate-appropriate range.

Potential Risks

There has been a long and lively debate about whether to use assisted migration to help ameliorate the impact of climate change (reviewed in Hewitt et al. 2011; Schwartz et al. 2012; Prober et al. 2019). Potential risks to assisted migration would be magnified if the process occurs on the scale of entire communities.

The most commonly stated argument against assisted migration is that the resulting range expansions could create novel invasive species (Hewitt et al. 2011). However, assisted migration across relatively small distances on the same continent is fundamentally different from the intercontinental introductions that are the source of most harmful invasive species. Intracontinental invasive species are much

less common than intercontinental invasives (Mueller & Hellmann 2008; Simberloff et al. 2012; Bellemare et al. 2017). The rare examples of intracontinental invasives are typically tied to anthropogenic disturbance (Simberloff et al. 2012). For our proposed prairie restoration, most of the plant species we would introduce currently coexist in prairies in the source area. Thus, few novel combinations of species will be created by planting them together in a new location.

Outbreeding depression is another potential problem when plantings include a mix of genotypes from multiple source locations. However, outbreeding depression is uncommon compared to inbreeding depression and is often short-lived (Frankham et al. 2017). Even when present initially, successful genetic combinations of parental ecotypes will survive and reproduce. Thus natural selection would be predicted to allow populations of mixed ecotypes to survive (Frankham et al. 2017), and therefore adapt to local conditions.

More broadly, there is a high probability that some of the species or genotypes we introduce will not survive in our reconstructions given the uncertainties inherent in predicting climate change and resulting range shifts. There would seem to be few negative consequences of such a “failure.” Propagules surely are dispersed repeatedly outside the viable range of all species, and simply do not survive there. There is likely to be little biological consequence of failed dispersal.

Ethical Considerations

Assisted migration is an active intervention that departs from the conservation ideal of setting reserves aside to allow them to function naturally, apart from the influence of humans (Schwartz et al. 2012). But to preserve biodiversity in the face of climate change, management decisions must adapt to the pervasive global pressures of human activity (Heller & Zavaleta 2009; Camacho 2010; Vitt et al. 2010; Ralls et al. 2018; Prober et al. 2019).

Two over-riding human impacts have already taken place: habitat destruction and global climate change. Rather than restoring a previous *condition*, community-level assisted migration restores the natural *process* that occurred in response to past episodes of more gradual climate change in a continuous landscape (Rohwer & Marris 2016; Siipi & Ahteensuu 2016). Given the severe conservation challenges for the tallgrass prairie community, the cost of inaction is greater than the comparatively minor risks associated with assisted migration.

Conclusions

We here propose the most extensive assisted migration project of which we are aware. Though we acknowledge uncertainty of success and potential risks of such an enterprise, we believe it is justified by the confluence of extreme threats to tallgrass prairie biodiversity posed by extensive habitat loss and rapid climate change.

If community-level assisted migration is used as the basis for future prairie restorations, restoration practitioners would need to reverse the widely held “local is best” precept for prairie plantings. A combination of both local and strategically defined “non-local” would be the criterion for optimal seed provenance. Such a change in approach would require a different message in public education efforts about the role of prairie plantings in the long-term conservation of this highly endangered community.

The tallgrass prairie community is a special case in some ways. Prairie conservation has depended heavily on *de novo* plantings, which already require assisted migration regardless of guidelines for seed provenance. A different set of trade-offs could apply in areas with existing native populations. However, we urge managers of remnant native communities to evaluate options in light of climate change. For example, our simple methods would allow managers to predict broadly how many species could be lost from a reserve. Would local extinctions cause the loss of important ecological functions? If so, assisted migration for range expansion could be essential. Similarly, introduction of nonlocal genotypes from locations that match current and future climates might give local species a greater chance for evolutionary rescue.

There is universal agreement on the urgent need for more experimental work to evaluate the potential effectiveness of assisted migration (Prober et al. 2019). Carefully monitored community-level assisted migration could offer critical data to help evaluate the broader application of such an approach, and could foster societal discourse on how best to conserve nature under climate change.

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Our study site is located on the homelands of the Wahpekute and Mdewakanton bands of the Dakota Nation. We honor with gratitude the people who have stewarded the land through the generations and their ongoing contributions to this region. We acknowledge the ongoing injustices that we have committed to the Dakota Nation, and we wish to interrupt this legacy, beginning with acts of healing and honest story telling about this place.

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