

Meetings

Evolutionary approaches to seed sourcing for grassland restorations

An organized workshop in Minneapolis, MN, USA, 21 March 2019

Large-scale conversion and fragmentation of biologically diverse, productive, temperate grasslands has impaired key ecosystem services, including carbon storage (Ahlering *et al.*, 2016), pollination (Hendrickson *et al.*, 2019), and maintenance of soil structure, and hydrological services (Power, 2010; Lark *et al.*, 2015; Comer *et al.*, 2018). With increased anthropogenic stresses, including climate disruption, the need for grassland restoration has increased. Applying restoration strategies that establish and maintain long-term resiliency will be critical to regaining some of the lost ecosystem services. One of the major challenges to establishing restorations is an apparent tension that exists between evolutionary theory and restoration practice. Maintenance of evolutionary potential may require introduction of genetic variation following decades of reduced gene flow due to anthropogenic fragmentation or inbreeding (Ralls *et al.*, 2018). However, evolutionary studies have yielded abundant evidence of local adaptation, which implies that local selective pressures have contributed to differentiation in traits important to contemporary adaptation across environmentally heterogeneous landscapes (Hufford & Mazer, 2003; McKay *et al.*, 2005). Balancing the prevalence of local adaptation while maintaining evolutionary potential is necessary to sustain long-term adaptability in restored grassland communities (Aitken & Bemmels, 2016; Bucharova *et al.*, 2018). Moreover, to meet the demands of restoration, the collection, propagation and production of seed for restoration poses its own evolutionary challenges (Espeland *et al.*, 2017; Breed *et al.*, 2018). The goal of this workshop was to ask how key evolutionary processes contribute to individual-, population-, and community-level variation across the landscape and to ask how restoration practice may affect these processes and ultimately restoration success.

This workshop focused on the role of evolution in restoration, including understanding the scale and extent of adaptation to current, local conditions, estimating the impact of gene flow across scales, and quantifying the capacity for adaptation to novel selective environments. A large body of work has demonstrated that plant populations tend to be adapted to local conditions (Leimu & Fischer, 2008; Hereford, 2009); however, the eco-geographic scale of adaptation is virtually unknown for most species (McKay *et al.*, 2005). In addition, as restoration site conditions

commonly diverge from pre-disturbance environments, locally sourced populations could be maladapted following restoration (Lesica & Allendorf, 1999). Whether conditions change for these or other reasons, genetic variation is a prerequisite for adaptive evolution (Lewontin, 1974). While gene flow may hamper adaptive divergence or cause outbreeding depression due to the breakup of co-adapted gene complexes (Aitken & Whitlock, 2013; Janes & Hamilton, 2017), it can also mitigate the deleterious effects of inbreeding and genetic drift to which small, fragmented populations are especially susceptible (Falk *et al.*, 2006; Hamilton & Miller, 2016). Thus, a core challenge remaining, for both restored and natural populations, especially in fragmented landscapes, is to minimize maladaptation to current conditions while maintaining adaptive potential in uncertain environments.

Oral presentations focused on the intersections of adaptation, gene flow, and the maintenance of adaptive capacity at varied levels of biological organization. A number of research programs are currently addressing the question 'How local is local?'. Marissa Ahlering (The Nature Conservancy, Minneapolis, MN, USA) noted that there is a substantial range in how we define local, and this has bearing on local, regional, and national seed management efforts. Shelby Flint (University of Minnesota, Saint Paul, MN, USA) summarized ongoing evaluation of the geographic scale of local adaptation in common grassland perennials. Flint noted that the signature of local adaptation is not consistent across species in an ongoing study. Jill Hamilton (North Dakota State University, Fargo, ND, USA) presented assessments of the eco-geographic scale of differentiation for a range of quantitative traits. Hamilton identified differences in the scale of trait differentiation across landscapes for different quantitative trait classes, including morphological, resource allocation, and stomatal traits. Hamilton suggested that different functional trait classes may be suitable for establishing seed transfer guidelines and that suitability may depend on climate–trait associations (Yoko *et al.*, In press). Lars Brudvig (Michigan State University, East Lansing, MI, USA) discussed a recently established experiment examining the consequences of intra- and inter-specific diversity on restored populations, communities, and ecosystem functions. Establishing this experiment as a large-scale restoration, Brudvig will be evaluating the impact population genetic diversity and species diversity may have on community diversity across restored ecosystems over time. Similarly, Ahlering described a new project comparing short-term success and longer-term persistence of single- and multi-source seed mixtures in large-scale restorations. These studies address fundamental questions regarding the scale of adaptation across levels of biodiversity while applying large-scale tests of composite provenancing approaches in restorations (Bucharova *et al.*, 2018).

Understanding the balance between adaptation, gene flow and demographic variation can require long-term empirical studies, particularly when considering the maintenance of connectivity

across dynamic landscapes. Stuart Wagenius (Chicago Botanic Garden, Glencoe, IL, USA) discussed feedbacks between evolution and demography. Wagenius's long-term studies combining natural population observations with common garden experiments indicated substantial consequences of inbreeding depression and considerable variability in fitness across different life history stages in the long-lived perennial, *Echinacea angustifolia* (Wagenius *et al.*, 2010). Lauren Sullivan (University of Missouri, Columbia, MO, USA) presented ongoing research into the consequences of pollen and seed dispersal using a range of grassland species. Sullivan's fine-scale assessment of the impact of dispersal mode and distance on connectivity within and among populations of prairie forbs has implications for landscape-level site acquisition and management. While gene flow is important to the maintenance of diversity and connectivity across grassland ecosystems, it can be associated with risk, particularly if seed transfer increases the likelihood of introducing nonnative species into areas they have not reached. Holly Bernardo (US Geological Survey, Reston, VA, USA) discussed existing seed availability and the use of spatially explicit models to evaluate the risk of introducing nonnatives and its dependence on seed transfer distances. Bernardo's research identifies an optimized geographic distance for seed transfer that balances the trade-offs between distance, seed availability, and the risk of nonnative introductions. Additionally, range shifts can establish gene flow between previously allopatric taxa, leading to inter-specific hybridization (Hamilton & Miller, 2016). For rare species, hybridization with more widespread congeners may be undesirable (Zlonis & Gross, 2018). Briana Gross (University of Minnesota Duluth, MN, USA) summarized the population genetic consequences of gene flow between rare, isolated disjunct populations with their more common relatives asking whether hybridization is a threat to native population genetic structure. Understanding when hybridization may be viewed as a conservation threat or a conservation tool will be important to species conservation (Chan *et al.*, 2019).

Considering the maintenance of adaptive capacity, Charles Fenster and Michele Dudash (South Dakota State University, Brookings, SD, USA) advocated the use of genetic rescue, the introduction of genetic variation to counter the genetic and demographic consequences of small, fragmented populations, as a management tool for native plant populations (Carlson *et al.*, 2014; Ralls *et al.*, 2018). They offered a decision tree considering environmental conditions, breeding system, and risk of outbreeding depression as a basis for decisions on the use of genetic rescue within a restoration context (Frankham *et al.*, 2017). Taking a direct approach to estimating evolutionary potential, Ruth Shaw (University of Minnesota, St Paul, MN, USA) discussed predicted and experimentally estimated values of additive genetic variance for fitness (Fisher, 1930; Lewontin, 1974) using *Chamaecrista fasciculata* and *E. angustifolia*. Shaw suggested targets for evolutionary rescue, which differs from genetic rescue in its reliance on evolutionary change from standing genetic variation, would be populations where observed fitness is lower than predicted. Interestingly, Shaw noted that estimates of additive genetic variance for fitness based on a number of life history traits suggest a substantial capacity for adaptation. Together, this research points

to the importance of maintaining genetic variance in native populations not only for current conditions, but also considering the maintenance of adaptive potential across generations.

Several participants addressed the interface between applied and theoretical considerations in the context of seed sourcing for restoration. One of the current challenges facing restoration is seed availability as demand consistently surpasses supply (Broadhurst *et al.*, 2008, 2016). Nicholas Goldsmith (University of Minnesota, St Paul, MN, USA) characterized obstacles faced by users and producers of locally sourced seed, which included uncertainty and risks associated with funding and production of seed, limited lead time on project-specific needs, and variable growing conditions that can dramatically affect seed supply and demand. Julie Etterson (University of Minnesota Duluth, MN, USA) discussed the extent and consequences of genetic bottlenecks and unconscious selection during accession, propagation, and production of farmed seed for restoration. In an experiment, Etterson noted farmed seed exhibited reduced fecundity and stress tolerance relative to wild collected seed. Etterson identified approaches to minimize selection during propagation; including increasing the number of maternal families sampled per population, harvesting at multiple times across a season, and mixing hand collections with mechanical harvesting for large-scale restorations (Espeland *et al.*, 2017). Despite growers' efforts to maintain genetic diversity, Jill Hamilton presented evidence of genomic differences between native and commercial seed sources. Although the consequences of these differences to quantitative trait variation remain to be tested, the effective population size of commercial seed sources was reduced relative to native populations. Finally, although accessibility of native seed was identified as a major limitation to implementation, new regional initiatives have the potential to improve seed availability. The newly established Native Plant Initiatives at South Dakota State University addresses some of the concerns associated with farmed sources of native seed pairing research with production (Lora Perkins, South Dakota State University, Brookings, SD, USA). Efforts that integrate research and application with education of local communities and stakeholders will be key to establishing, implementing, and maintaining these new initiatives.

Among workshop participants, there was consensus that, especially now as environmental conditions change rapidly, it is crucial to maintain and in some cases supplement existing genetic variation to enable adaptive evolutionary change. Genetic and evolutionary rescue may combat the combined impact of drift, inbreeding, and reduced gene flow due to fragmentation, ameliorating the risk of local extinctions and promoting resilience (Whitely *et al.*, 2015; Hamilton *et al.*, 2017). In addition, considering the spatial and temporal scale over which responses to changing conditions are evaluated will be important (Baythavong, 2011). Many existing experimental studies reflect seasonal weather responses, rather than long-term responses to climatic variation. Considering short- and long-term responses to selection, as well as plasticity, will be needed, both for assessing adaptive potential, designing seed mixes, and establishing seed transfer guidelines. There are clear benefits to establishing seed selection, production and transfer guidance for native grassland species, and there is much to be learned from the existing expertise implemented across

different systems (Breed *et al.*, 2018; Bucharova *et al.*, 2018). With increasing need for native seed, the impact of unconscious selection on seed production will require evaluation. Finally, focusing restoration on capacity for continuing adaptation, rather than on 'local' sourcing alone, appears key to maintaining evolutionary potential. While there is debate over the definition or scale of 'local', there is consensus that maintaining and enhancing the adaptive capacity of our native grasslands is necessary. As evidence accumulates that species are maladapted to contemporary environments, identifying and implementing restoration strategies that consider the capacity for ongoing adaptation will be necessary to preserving grassland ecosystems and their evolutionary potential.

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References

- Ahlering M, Fargione J, Parton W. 2016. Potential carbon dioxide emission reductions from avoided grassland conversion in the northern Great Plains. *Ecosphere* 7: e01625.
- Aitken S, Bemmels JB. 2016. Time to get moving: assisted gene flow in forest trees. *Evolutionary Applications* 9: 271–290.
- Aitken SN, Whitlock MC. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution and Systematics* 44: 367–388.
- Baythavong BS. 2011. Linking the spatial scale of environmental variation and the evolution of phenotypic plasticity: selection favors adaptive plasticity in fine-grained environments. *The American Naturalist* 178: 75–87.
- Breed M, Harrison PA, Bischoff A, Durruty P, Gellie N, Conzales EM, Haven K, Karmann M, Kilkenny F, Krauss SI *et al.* 2018. Priority actions to improve provenance decision-making. *BioScience* 68: 510–516.
- Broadhurst LM, Jones TA, Smith FS, North T, Guja L. 2016. Maximizing seed resources for restoration in an uncertain future. *BioScience* 66: 73–79.
- Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesik PA, Yates C. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 587–597.
- Bucharova A, Bossdorf O, Holzel N, Kollmann J, Prasse R, Durka W. 2018. Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. *Conservation Genetics* 20: 7–17.
- Carlson SM, Cunningham CJ, Westley P. 2014. Evolutionary rescue in a changing world. *Trends in Ecology & Evolution* 29: 521–530.
- Chan WY, Hoffmann AA, van Oppen MJH. 2019. Hybridization as a conservation management tool. *Conservation Letters* 12: e12652.
- Comer PJ, Hak JC, Kindscher K, Muldavin E, Singhurst J. 2018. Continent-scale landscape conservation design for temperate grasslands of the Great Plains and Chihuahuan Desert. *Natural Areas Journal* 38: 196–211.
- Espeland EK, Emery NC, Mercer KL, Wooldbright S, Mettenring KM, Gepts P, Etterson JR. 2017. Evolution of plant materials for ecological restoration: insights from the applied and basic literature. *Journal of Applied Ecology* 54: 102–115.
- Falk DA, Richards CM, Montalvo AM, Knapp EE. 2006. *Population and ecological genetics in restoration ecology*. Washington, DC, USA: Island Press.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford, UK: Clarendon Press.
- Frankham R, Ballou JD, Ralls K, Eldridge M, Dudash MR, Fenster CB, Lacy RC, Sunnucks P. 2017. *Genetic management of fragmented animal and plant populations*. Oxford, UK: Oxford University Press.
- Hamilton JA, Miller JM. 2016. Adaptive introgression as a resource for management and genetic conservation under climate change. *Conservation Biology* 30: 33–41.
- Hamilton JA, Royauté R, Wright JW, Hodgskiss PD, Ledig FT. 2017. Genetic conservation and management of the California endemic, Torrey pine (*Pinus torreyana* Parry): implications of genetic rescue in a genetically depauperate species. *Ecology and Evolution* 7: 7370–7381.
- Hendrickson JR, Sedivec KK, Toledo D, Printz J. 2019. Challenges facing grasslands in the Northern Great Plains and North Central Region. *Rangelands* 41: 23–29.
- Hereford J. 2009. A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist* 173: 579–588.
- Hufford KM, Mazer SJ. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology & Evolution* 18: 147–155.
- Janes JK, Hamilton JA. 2017. Mixing it up: the role of hybridization in forest management and conservation under climate change. *Forests* 8: 237.
- Lark TJ, Salmon JM, Gibbs HK. 2015. Cropland expansion outpaces agricultural and biofuel policies in the United States. *Environmental Research Letters* 10: 044003.
- Leimu R, Fischer M. 2008. A meta-analysis of local adaptation in plants. *PLoS ONE* 3: e4010.
- Lesica P, Allendorf FW. 1999. Ecological genetics and the restoration of plant communities: mix or match? *Restoration Ecology* 7: 42–50.
- Lewontin RC. 1974. *The genetic basis of evolutionary change*. New York, NY, USA: Columbia University Press.
- McKay JK, Christian CE, Harrison S, Rice KJ. 2005. "How local is local?" – a review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13: 432–440.
- Power A. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Proceedings of the Royal Society B: Biological Sciences* 365: 2959–2971.
- Ralls K, Ballou JD, Dudash MR, Eldridge MDB, Fenster CB, Lacy RC, Sunnucks P, Frankham R. 2018. Call for a paradigm shift in the genetic management of fragmented populations. *Conservation Letters* 11: e12412.
- Wagenius S, Hangelbroek HH, Ridley CE, Shaw RG. 2010. Biparental inbreeding and interremnant mating in a perennial prairie plant: fitness consequences for progeny in their first eight years. *Evolution* 64: 761–771.
- Whitely AR, Fitzpatrick SW, Funk WC, Tallmon DA. 2015. Genetic rescue to the rescue. *Trends in Ecology & Evolution* 30: 42–49.
- Yoko ZG, Volk K, Dochtermann NA, Hamilton JA. In press. The importance of quantitative trait differentiation in restoration: landscape heterogeneity and functional traits inform seed transfer guidelines. *AOB Plants*. In press.
- Zlonis KJ, Gross BL. 2018. Genetic structure, diversity, and hybridization in populations of the rare arctic relict *Euphrasia hudsoniana* (Orobanchaceae) and its invasive congener *Euphrasia stricta*. *Conservation Genetics* 19: 43–55.

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