ON THE NATURE OF THINGS: ESSAYS
New Ideas and Directions in Botany

Adapting to a warming world: Ecological restoration, climate change, and genomics[1]

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Global climate change and other anthropogenic influences are rapidly transforming the habitats of many species. A species' ability to cope will depend on its capacity to tolerate these changes in situ or migrate to more suitable conditions. In this essay, we will briefly discuss how adaptive variation within managed species can be assessed and how this information might be used to maximize the possibility of in situ adaptation to climate change. We also make recommendations to improve ecological restoration outcomes and discuss how restoration projects could provide invaluable insight into general ecological and evolutionary processes.

Local adaptation is a process by which divergent natural selection in response to local environmental conditions causes resident populations to outperform foreign populations in their home environment (Kawecki and Ebert, 2004; Savolainen et al., 2013). Meta-analyses reveal that local adaptation is relatively common, occurring in about 71% of studies (Leimu and Fischer, 2008; Hereford, 2009). While by no means ubiquitous, the home-site advantage associated with adaptive differentiation has long been recognized in agriculture, forestry, and conservation. Many management strategies source nearby individuals when restoring or supplementing natural populations to maintain local adaptation or in some cases to conserve local lineages (Vander Mijnsbrugge et al., 2010). However, as climates are shifting, the "local is best" paradigm may not apply if these changing environmental factors are a major driver of local adaptation.

Can we make use of adaptive differences among populations to deal with changing climates? Assisted gene flow, where individuals or their gametes are moved within a species range, has been touted as an option to facilitate in situ adaptation to climate change (Broadhurst et al., 2008; Weeks et al., 2011; Aitken and Whitlock, 2013; Aitken and Bemmels, 2016). Because existing adaptive differences among populations have already been vetted by selection, these differences have the potential to be an important source of genetic variation to enable populations to respond to future

challenges. For restoration and conservation efforts, assisted gene flow can be implemented via approaches like composite provenancing, whereby a combination of source populations is used to re-establish populations (Broadhurst et al., 2008). However, the challenge is to determine the best composition of source populations, especially given uncertainty regarding the importance of adaptive differentiation among specific populations and future climate conditions.

Assisted gene flow has a number of benefits for managed populations. Regardless of population size, assisted gene flow can introduce or increase the frequency of preadapted alleles that may allow populations to more rapidly evolve to track changing climates. For small populations suffering from inbreeding and loss of genetic variation, assisted gene flow can also alleviate inbreeding depression, increase adaptive potential and provide a demographic safeguard from extinction by boosting population size. However, not all species/populations will be amenable to assisted gene flow. Outbreeding depression, or the reduced fitness of crosses between individuals from different populations, is a particular concern for populations with ploidy or other large-scale chromosomal differences. Other intrinsic incompatibilities and local adaptation to nonclimate-related factors also could reduce the fitness of introduced migrants or their descendants, but simulations have shown that if incompatibilities are not complete, population fitness can quickly rebound when beneficial alleles are also introduced (Aitken and Whitlock, 2013).

How can we identify which species might benefit from assisted gene flow because they exhibit substantial local adaptation to climate? Identifying local adaptation generally requires significant experimental effort to demonstrate a home-site advantage, such as reciprocal transplant experiments, where fitness of local and foreign genotypes is compared at each site, or common gardens, where individuals from different populations are grown in controlled environmental conditions. Provenance trials, where seeds are sourced from many populations and performance is assessed in multiple field sites, have been instrumental in guiding reforestation policies for many economically important tree species and are impacting planting decisions with respect to climate change (Wang et al., 2006; O'Neill et al., 2008). Provenance trials are not readily employed for

other plant species involved in ecological restoration (Bower et al., 2013; but see St. Clair et al., 2013) and could be developed as a standard experimental tool for illuminating patterns of local adaptation to climate or other environmental factors. These experimental approaches can be challenging to implement in some species, such as those that are long-lived, and the cost and effort involved may be beyond the capacity of many scientists. However, automated, high-throughput phenotyping systems for the field and greenhouse are becoming suitable for a wide range of organisms and will likely transform the scale and repeatability of these standard phenotypic studies in the coming decades as they have for crops and model species (Fiorani and Schurr, 2013; Fahlgren et al., 2015).

Could genomic studies provide a useful avenue to identify local adaptation to climate? Studies of genomic variation are providing insight into the genetic basis of local adaptation across an ever-growing number of organisms (Savolainen et al., 2013). Sequencing technologies are improving and providing higher quality data at ever decreasing cost. Sophisticated experimental and statistical frameworks are being developed to differentiate candidate loci governing local adaptation from genomic variation primarily driven by neutral processes (e.g., Günther and Coop, 2013; Whitlock and Lotterhos, 2015). Theoretical work has clarified our understanding of how genomic architecture will evolve under various evolutionary scenarios (e.g., Yeaman, 2015). As our understanding of the genomic architecture of adaptation expands, so too will our capacity to make prior assessments regarding the benefits of assisted gene flow for particular populations using genomic data. Yet, many obstacles remain to be overcome before fitness outcomes across environmental gradients can be predicted from genomic data. For example, local adaptation governed by many loci of small effects is particularly difficult to detect (Le Corre and Kremer, 2012; Yeaman, 2015). Despite such difficulties, correlations between climatic factors and genomic variation, once demographic history is accounted for statistically, can be a signal of local adaptation to climate. However, whether such population genomic "short-cuts" will work in place of long-term provenance trials or whether they will frequently be stymied by population history or complex genetic architecture remains to be empirically tested.

Can ecological restoration act as "real-world" experiments? Even if provenance trials or genomic investigations are beyond the capacity of current managers, restoration activities represent important opportunities for investigation into fundamental ecological and evolutionary processes and evaluation of assisted gene flow approaches. Over the short term, the ecological consequences of using different source populations could be examined by monitoring population demography, species interactions and population responses to stress. Structured decision-making and adaptive management (frameworks for making management decisions under uncertainty) are increasingly used in conservation (Runge, 2011). These methods could be used to formalize the design, monitoring and comparison of multiple provenancing strategies in management situations, enabling management approaches to change as we learn more about the system and the success of different restoration strategies. Over the longer term, rapid evolutionary response to environmental change could be captured through ancestor–descendant comparisons (Franks et al., 2008). Preserving tissue samples from the stocks used for restoration will allow the tracking of genomic changes over time, while seed preservation will also enable direct comparisons of phenotypic changes of ancestral and descendant populations in the same common gardens. Restoration

programs are good candidates for ancestor preservation, especially those implemented in protected areas with a lower risk of future transformation, because they allow for larger-scale implementation of "experimental" populations beyond what can be managed by a single laboratory or within a single funding cycle.

Climate change is not the only stress experienced by plant populations, which are also subject to habitat loss, fragmentation, eutrophication, changed disturbance regimes, and biological invasions. Because stressors, both ecological and genetic, often interact, it is important to manage these other threats to maximize adaptive potential to climate change. Such management will boost the effective population size and potentially minimize the demographic costs of selection to multiple stressors.

Future prospects and recommendations: It is currently challenging to identify when local adaptation is important and how climatic factors will impact restoration. However, guidelines for managers pertaining to assisted gene flow and other types of translocations have been developed (Broadhurst et al., 2008; Weeks et al., 2011; Aitken and Whitlock, 2013; Ottewell et al., 2015; Bower et al., 2013). We encourage further efforts to provide practical recommendations and baseline information relating to climatic variability, the scale and degree of local adaptation, genetic diversity and differentiation, and the adaptive genetic landscape for species involved in ecological restoration to enhance the implementation of these guidelines. Classic experimental approaches and rapidly advancing genomic and phenotyping technologies will aid in the selection of seed sources for key species. We can also assist adaptation to climate change by reducing stress from other threatening processes. However, there are limited resources for assessment and monitoring of restoration sites as well as important practical constraints for target species, such as seed limitations (Broadhurst et al., 2008). We stress that an information limitation should not hamper current restoration efforts and that structured decision-making and adaptive management can be used to focus our monitoring and resolve uncertainties while implementing the best management given the information that is currently available. Finally, saving genetic material or seed stocks used in restoration to track adaptation over time is an easy, cheap, and useful thing to do.

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