

REVIEW

Evolution of plant materials for ecological restoration: insights from the applied and basic literature

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Summary

1. Restoration is normally conducted with the goal of creating plant populations that establish, survive, successfully reproduce, contribute to ecosystem function and persist in the long term. Restoration often relies on revegetation that, on large scales, requires agronomic increase of native plant materials. During this propagation process, restoration populations are subject to genetic sampling as well as natural and artificial selection that could result in adaptation contrasting sharply with that of native populations.

2. Here we draw on insights from the evolutionary and agricultural literature to illustrate how changes in the amount and type of genetic variation in *ex situ* repositories (source collections and production farms) could affect plant performance in restoration. The consequences of intentional and/or inadvertent evolutionary modification of restoration materials are discussed with respect to population viability and ecosystem function.

3. *Synthesis and applications.* We conclude that sampling effects and intentional and unintentional selection during collection, propagation and restoration planting have the potential to diminish restored populations. We describe testing for evolutionary change in plant materials using neutral molecular markers and/or field observations. Six practices, multiple collections through time, multiple collections through space, large effective population size, provenance tracking, promoting gene flow and reducing selection comprise 'evolutionarily enlightened management' that decreases the potential for unintentional evolution and maladaptation.

Key-words: ecological restoration, ecosystem function, ecosystem services, genetic drift, local adaptation, plant materials, plant propagation, revegetation, seed provenance, selection

Introduction

In an age of surging human population growth and unprecedented anthropogenic global change, conservation practice is shifting to restoration of degraded habitats from preservation of increasingly rare intact populations, communities and ecosystems (Caro *et al.* 2012; Corlett 2015). Restoration typically includes revegetation that requires substantial propagule input. Successful restoration depends upon these propagules establishing,

surviving, successfully reproducing, contributing to ecosystem function and persisting in the long term. Regulations or local mores may require restored plant populations with a genetic composition that closely resembles nearby, natural populations, and as we show in this paper, this resemblance may determine the contribution of restoration populations to ecosystem function. Restoration efforts can be hindered by the lack of availability and high cost of appropriate native material (Peres *et al.* 2003; Menges, Guerrant & Hamzé 2004; Merritt & Dixon 2013), and restoration material (seeds or other propagules) will be increasingly subject to agronomic increase

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(or, propagation) to meet future demands (Rehfeldt *et al.* 1999; Merritt & Dixon 2013).

It is inevitable, based on lessons of the agricultural and evolutionary literature, that industrial-scale propagation and harvesting will alter the genetic constitution of restoration material (Roundy, Shaw & Booth 1997; Dyer, Knapp & Rice 2016). Given that these evolutionary changes have the potential to undermine the most fundamental goals of restoration (i.e. functional, sustainable, and resilient populations), we must understand how these influences are manifested during the process of propagation and how their effects can be minimized. This claxon call for understanding has been made by others (Broadhurst *et al.* 2008; Byrne, Stone & Millar 2011; Breed *et al.* 2013; Carroll *et al.* 2014), with only a few existing studies supplying data (Table S1, Supporting Information). Nevertheless, there is a considerable literature that can be applied to understand the expected evolutionary impacts of propagation, including sampling of wild populations, increase of propagules in an agronomic setting, and

planting and establishment in the restoration setting on the genetic composition of restoration materials (Fig. 1). We draw on lessons from the basic and applied literature to highlight key processes that impose evolution on the restoration gene pool in three ways: (i) by changing the amount of genetic variation during propagule collection and production; (ii) by changing the type of genetic variation during propagule collection and production; and (iii) by responding to selection at the restoration site. Next, we explain tests that can be readily accomplished to determine whether evolution has occurred. We conclude with set of six general guidelines that inform evolutionarily enlightened management of restoration material.

PROCESS 1: CHANGES IN THE AMOUNT OF GENETIC VARIATION DURING PROPAGULE COLLECTION AND PRODUCTION

Seed collection from wild populations is a first step in propagation of restoration materials (Basey, Fant &

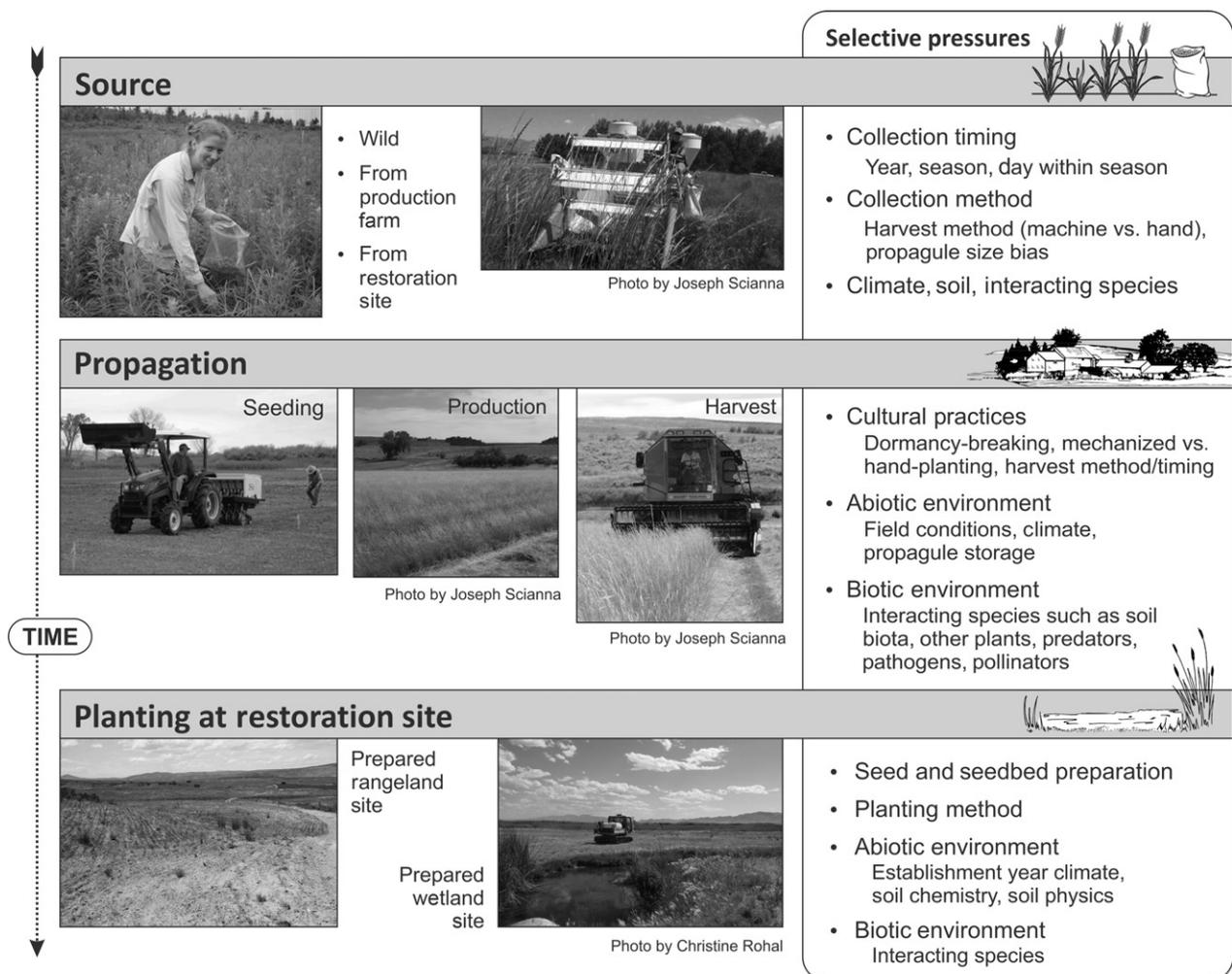


Fig. 1. Increase of restoration materials occurs in three phases: (i) collection; (ii) production/propagation; and (iii) planting at the restoration site. Sources may be wild-collected and directly installed into restoration sites, or selected from wild collections or cultivars and then cycled through an increase step in a production farm prior to being introduced to the restoration site. Cultural practices at each phase and environmental factors in each growing environment can influence the genetic composition of restoration material.

Kramer 2015). By taking a relatively small sample from a relatively large population, seed collection can cause genetic drift, that is, a change in the frequency of gene variants due to sampling, affecting population genetic and phenotypic variation and sometimes means. Genetic drift can lead to an overall reduction in genetic variation and a greater risk of future inbreeding through mating between genetically similar individuals (Fig. 2, Scenario 1a and 2a, reviewed in Angeloni, Ouborg & Leimu 2011). Genetic drift reduces the capacity of a population to respond to selection and is captured in a parameter called effective population size, N_e , which accounts for not only the census number of individuals in a population but also their genetic variability (Wright 1938). In other words, N_e is

not just the number of plants that successfully establish on the production farm from wild collections, but also reflects their genetic diversity. For example, if growers repeatedly propagate annual species or increase population size by dividing plants (i.e. cloning), the decision of which plants and how many of their propagules to include in the next generation will strongly influence how much genetic variation is retained over time (Fant *et al.* 2008). There is a substantial literature regarding the maintenance of N_e in *ex situ* collections (e.g. Hamilton 1994) and how N_e affects fitness (reviewed in Ellstrand & Elam 1993). Each stage leading up to the restoration planting could be considered short-term *ex situ* repositories (e.g. Johnson, Bradley & Evans 2005) and N_e must be considered

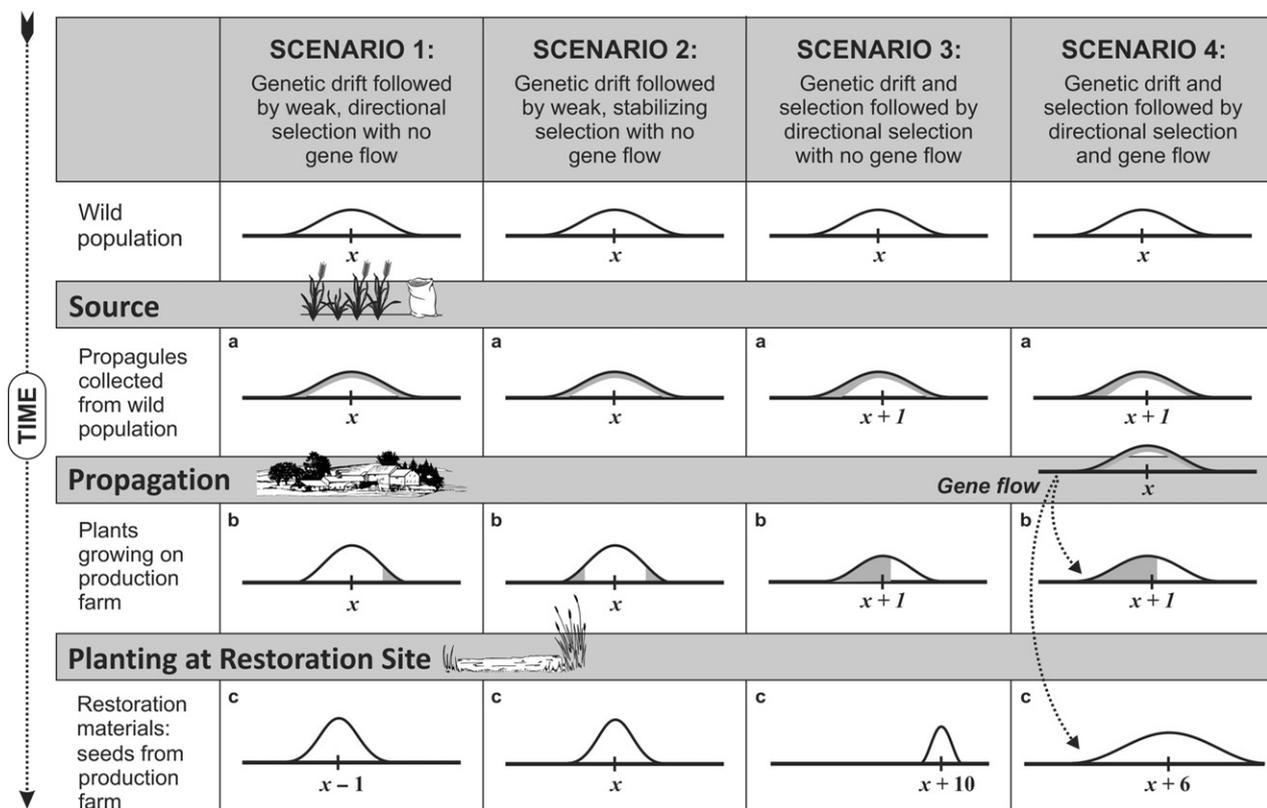


Fig. 2. Four hypothetical scenarios that illustrate how the genetic base of restoration populations can be altered over time through the three phases of increase: source collection, plant propagation on production farms and planting at the restoration site. For each scenario, a single original source population that has a specific mean phenotype (x) and range of variation (curve). We use flowering time as an arbitrary genetically based trait to describe the process of evolution during increase. Scenario 1: (1a) Random sampling results in general reduction in genetic variation among the propagules collected from the wild population (shaded area under the curve) but no change in their average flowering time, x . (1b) During seed production, plants that flower later are systematically excluded because of, for example, the timing of harvest (shaded area under the curve). (1c) This results in the production of restoration material with that flowers earlier, on average ($x-1$) and has reduced genetic variation for flowering time (narrower curve). Scenario 2: (2a) As in Scenario 1, random sampling results in a reduction in genetic variation. (2b) Harvesting seeds at the peak of production exclude plants that have already shed their seed as well as plants that have not yet matured their seed. (2c) This ‘stabilizing selection’ (i.e. loss of the extremes) further reduces genetic variation. Scenario 3: (3a) In addition to sampling effects, in this scenario seed collection is conducted at a time that excludes plants that flowered early and have already shed their seeds. (3b) As a consequence, the mean flowering time of plants growing on the production farm is later ($x+1$). This change is exacerbated by late seed harvesting that selects against plants with early and intermediate flowering time. (3c) Consequently, the restoration material is characterized by severely reduced genetic variance and later flowering. Scenario 4: (4a) As in Scenario 3, both drift and inadvertent selection influence the mean and variance of flowering time. (4b) However, in this scenario, gene flow from adjacent natural populations that arrives either naturally or intentionally by farm managers restores variation to some extent. (4c) Ongoing gene flow at the restoration site augments genetic diversity and reduces the strong effect of later flowering induced by late harvesting.

because the sequence of sampling seeds from the wild to establish a production farm and sampling seeds from farm-raised plants for restoration planting will together reduce genetic diversity (Hamilton 1994).

Reduction in N_e at the time of seed collection from source populations can increase the risk of producing inbred seed on the propagation farm. The negative effects of inbreeding in plants are extremely well documented, starting with foundational work of Darwin (Darwin 1876). The genetic underpinnings of inbreeding depression have been thoroughly explored in theoretical models (Lande & Schemske 1985; Husband & Schemske 1996), and its negative impact has repeatedly been demonstrated in both experimental studies (Galloway, Etterson & Hamrick 2003; Angeloni, Ouborg & Leimu 2011) and in natural conditions (reviewed in Keller & Waller 2002; Angeloni, Ouborg & Leimu 2011). Inbreeding depression is widespread in natural populations, and its consequences vary depending on factors such as the plant trait being measured, the breeding system, the life span of individuals within the species and environmental factors (Angeloni, Ouborg & Leimu 2011). Affected traits vary among species, but can include lower germination rates (e.g. Buza, Young & Thrall 2000), increased prevalence of chlorophyll deficiencies that can be lethal (Willis 1992), slower growth and smaller size (Sorensen & Miles 1982), altered flowering time (Galloway, Etterson & Hamrick 2003) and reduced fecundity (Nason & Ellstrand 1995). Considered jointly, this suite of traits can destabilize population demography (O'Grady *et al.* 2006). Although intensive experimental inbreeding suggests that it is possible to purge the genetic load of deleterious alleles that causes inbreeding depression (Barrett & Charlesworth 1991), evidence that this actually occurs in natural conditions is equivocal (Byers & Waller 1999). Consequently, measures to avoid reductions in N_e , and consequent risks of inbreeding, are warranted during the collection and production of restoration materials.

Genetic diversity (N_e) and phenotypic diversity have also been shown to confer stability at the ecosystem level (reviewed in Hughes *et al.* 2008; Hautier *et al.* 2015). Key biotic and abiotic interactions that drive community structure and ecosystem patterns and processes are deeply affected by intraspecific genetic variation in foundation plant species. For example, the amount of genetic diversity within populations can influence competitive interactions between species and ultimately alter plant community composition (Michalet *et al.* 2011). Genetic diversity can also drive community structure that extends across multiple trophic levels (Whitham *et al.* 2012) and can sometimes be more important than interspecific diversity within the plant community (Crawford & Rudgers 2013). The phenotypically driven contribution of genetic diversity to ecosystem function is covered in process 2 below.

Reductions in genetic variation during the course of production may limit a population's response to selection.

Capacity for evolutionary change is proportional to genetic variance for fitness and traits (Fisher 1930; for a meta-analysis of empirical studies, see Leimu *et al.* 2006), so the amount of variation in traits that influence performance will determine the potential for a population to evolve within a restoration (e.g. Harris *et al.* 2006; Broadhurst *et al.* 2008; Jump, Marchant & Penuelas 2008; Weeks *et al.* 2011; Kettenring *et al.* 2014). Evolutionary capacity is linked to the ability of a population to persist through typical environmental variation, climate change, other alterations in anthropogenic impacts and introductions of new invasive species. In the shorter-term, genetic diversity also aids a population in overcoming suboptimal adaptation to a site (Matyas 1996).

PROCESS 2: CHANGES IN THE TYPE OF GENETIC VARIATION DURING PROPAGULE COLLECTION AND PRODUCTION

While the index N_e reflects genetic diversity and can be maximized by proper management, it is not just the *amount* of genetic variation that influences restoration success, but also the *type* of genetic variation that will ultimately determine evolutionary sustainability (e.g. Koester *et al.* 2014). Typically, natural plant populations are genetically diverged to some degree and differences in the phenotypes that they express contribute to local adaptation (reviewed in Latta 2004). Thus, the type of genetic variation in restoration populations is influenced by sourcing decisions as well as intentional and unintentional selection throughout the propagation process.

There are multiple ways to determine optimal areas from which to source wild population propagules for restoration. One involves using seed transfer zones. Seed transfer zones delineate areas within which plant materials can be relocated with reduced risk of being poorly adapted to their new location and have been heavily researched for forestry species in North America and Europe (e.g. Ying & Yanchuk 2006). Seed zones for forestry species focus on maximizing above-ground growth in addition to assessing translocation risk (Hamann, Gylander & Chen 2011). The establishment of seed zones relies on the correlation of phenotypes and collection environments (determined in common garden studies). In general, common garden studies can provide basic information on genetic differentiation between populations across the species range (reviewed in Kawecki & Ebert 2004). When common gardens are established at multiple test sites, an understanding of local adaptation and the fitness consequences of translocation can also be assessed (e.g. Rehfeldt *et al.* 1999). In reality, most native species have not received such detailed study and, in these cases, provisional seed transfer zones have been suggested that are based on key environmental attributes such as winter minimum temperature and aridity (Bower, St. Clair & Erickson 2014). These analyses give basic information on intraspecific phenotypic variation and on phenotypes that

may be particularly important for species persistence in different climates. These studies also provide information on the range of phenotypes that occur at the species level on the landscape.

Another, contentious, sourcing strategy is to use strictly geographically local genotypes because those genotypes are most likely to be adapted to the conditions of the restoration site and therefore most likely to establish successfully. The preference for local genotypes is predicated on the idea that the restoration site is ecologically similar to nearby, natural populations. This ecological similarity may not be the case (e.g. Lesica & Allendorf 1999; Jones 2013). Populations that are closest to the restoration site may be small and genetically depauperate with limited potential for adapting to future environmental change (Harris *et al.* 2006), particularly if they are small and relatively isolated from other populations (e.g. Broadhurst *et al.* 2008; Weeks *et al.* 2011). In addition, nearby populations, although local, may have been evolved under a different ecological context and lack relevant adaptive variation for the restoration site (Montalvo & Ellstrand 2000; Bischoff *et al.* 2006). Nevertheless, small populations that grow in environments similar to those in restoration may house genotypes particularly important to success (Rowe & Leger 2011; Basey, Fant & Kramer 2015). The focus on local genotypes for restoration is shorthand for increasing the likelihood that adaptive genetic diversity is included in the restoration gene pool. The adaptationist strategy (as in Gould & Lewontin 1979) of this approach is also reflected in the sourcing method that matches genotypes to the planting environment using climate change models (e.g. Vitt *et al.* 2010). Given how little we know about the genotypes that do well in restoration and multiple findings that other populations often do better at a site compared to the local collection (e.g. Rehfeldt *et al.* 1999; Bischoff, Steinger & Müller-Schärer 2010; Grady *et al.* 2011; but see Bucharova *et al.* 2016), adaptationist shorthand for determining the optimal type of genetic diversity has significant shortcomings. In order to choose appropriate sources, we need to understand the traits that are important for successful restoration. Tests such as those performed by Kulpa & Leger (2013) that compare the traits of plants that establish in restoration to those of the propagule source population (Test 2 below) will help us identify phenotypes that are adapted to restoration.

Collecting practices in the wild and on-farm selection may alter plant traits with unintended consequences in the restoration setting. Domestication traits in crops resulting from intentional and unintentional selection (Table S1) have been shown to negatively impact plant fitness in nature [see reviews on the fitness effects of timing of flowering (Elzinga *et al.* 2007), seed size (Leishman *et al.* 2000), dispersal ability (Nathan & Muller-Landau 2000) and dormancy (Honnay *et al.* 2008)]. For example, seed retention (or, dispersal ability) is likely to have opposite selection pressures on-farm and in a restoration setting.

Shattering (the converse of retention) is advantageous in the wild because it leads to the dispersal of seeds across the landscape and into hospitable microsites for germination. In contrast, seed retention is advantageous in production systems because seeds remain attached to the plant until harvested. In agronomic settings, non-shattering seed heads are intentionally selected to increase yields. Seed shatter has been shown to be controlled by few genes (Raman *et al.* 2014), and non-shattering phenotypes can evolve quickly under strong directional selection (Gepts 2004). Perennial grasses used for restoration in the United States vary in their degree of seed retention, both within and among populations (e.g. Jones 1998) and thus could evolve greater seed retention through differential collection in the wild and during propagule production.

Seed dormancy is another example of a trait that is important for fitness in nature that can be lost during propagation in agronomic conditions (Basey, Fant & Kramer 2015). Rapid germination may be valuable at restoration sites and production farms that are characterized by homogeneous conditions, low levels of competition and high resource availability because seed that germinates abundantly and rapidly may be more likely to occupy niches prior to weed encroachment (e.g. Rowe & Leger 2011). In contrast, seed dormancy is essential for wild population maintenance when year-to-year climate variation results in non-optimal germination conditions in some years (Pywell *et al.* 2003; Schroeder & Prasse 2013). Perennial grasses used for restoration in the United States vary in germination rates, both within and among populations (e.g. Schantz & Espeland 2016), indicating that they may be likely to evolve in response to propagation. When source populations vary in traits known to evolve quickly under agricultural practices (Table S1), evolution in response to propagation is likely. A handful of studies show that intentional selection of wild species to produce more vigorous, uniform or reliably establishing cultivars results in an overall reduction in genetic variability (Larson *et al.* 2000; Fant *et al.* 2008).

A meta-analysis of restoration experiments confirms that high germination (ruderality) is important for establishment, but also asserts that competitive dominance is important for persistence (Pywell *et al.* 2003). However, complete competitive dominance may not be ultimately desirable in restoration since genotypes that support species coexistence (e.g. Michalet *et al.* 2011) may promote colonization by native species from remnant populations surrounding the restoration area (e.g. Prach, Jongepierova & Rehounkova 2013), conferring sustainability. The traits that confer invasion resistance by weedy species while simultaneously promoting colonization by native species should be further explored within the restoration and invasion literature.

A final example of a trait likely to respond to on-farm selection is rapid growth. Increased growth rate can result in a genetically correlated reduction of defensive compounds (Herms & Mattson 1992; Massey & Hartley 2000).

In addition, vigorous growth of *Pinus edulis* at the seedling stage is a strong predictor of susceptibility to the stem-boring moth *Dioryctria albobittella* (Ruel & Whitham 2002). Damage by moths results in extreme changes in tree architecture that virtually eliminate seed production, reducing reproductive ability and negatively impacting avian and mammalian seed dispersers (Christensen & Whitham 1991). Thus, restored populations selected for increased growth could be at risk for causing problems for entire food webs. Moth and needle-scale herbivory in *Pinus edulis* has been shown to alter ecosystem-level traits such as decomposition rate (Classen *et al.* 2007) and nutrient flow (Chapman *et al.* 2003; Classen *et al.* 2013). However, selection for moth-resistant genotypes as part of restoration practice may *also* result in undesirable outcomes because moth-resistant trees can be less drought-tolerant than moth-susceptible trees (Sthultz, Gehring & Whitham 2009).

PROCESS 3: RESPONSE TO SELECTION AT THE RESTORATION SITE

Just as the traits that influence plant fitness differ between agricultural and natural contexts (as in Weiner *et al.* 2010), genotypes adapted to the restoration environment may differ from those adapted to the farm and from those adapted to natural habitats. Restoration sites and production farms that propagate herbaceous plant species are similar: typically large, open sites with a negligible existing plant community, high light availability and unbuffered fluctuations in soil surface temperature and moisture availability (e.g. Kettenring & Galatowitsch 2011). However, farms are typically located in areas where plants grow easily while restoration sites are typically marginal. The environment of the restoration site may be stressful, and this can increase the expression of deleterious effects of inbreeding that may have accrued during the process of propagation (Armbruster & Reed 2005).

The selective landscape of restoration sites will change over time: cover increases as plants establish and grow. Therefore, the degree of similarity between restoration sites and production farms will be reduced as the restored plant community at the restoration site matures. As noted above, traits that confer short-term restoration success may be very different than those determining long-term persistence (e.g. Pywell *et al.* 2003). In addition to overcoming demographic and immediate ecological constraints to establishment, populations must persist under changing conditions and, as described previously, this capacity hinges upon the amount and nature of genetic variation that persisted through the process of producing restoration materials.

Two tests for evolutionary change in restoration materials

Here we present two specific tests for evolutionary change in restoration materials that focus on different

fundamental types of genetic variation: neutral and adaptive (McKay & Latta 2002). Genetic variation that is 'neutral' does not directly affect fitness (i.e. survival and fecundity). Neutral genetic variation is typically assayed at the molecular sequence level as short repeated DNA sequences (i.e. microsatellites), or the size and/or DNA sequence of random fragments of the genome (i.e. RFLPs). With time, more methods for measuring molecular genetic variation have surfaced that can allow us to explore the genome more completely, including the use of abundant single nucleotide polymorphisms (SNPs) and genotyping by sequencing (GBS). Both of these methods pick up variation at neutral loci, but also at loci underlying phenotypic traits (for more information on the application and history of the full suite of available molecular markers see Doveri *et al.* 2008). Neutral molecular variation is especially valuable for providing information about the evolutionary history of populations, as well as the genetic structure, gene flow and dispersal among contemporary populations (Falk *et al.* 2006; Holderegger, Kamm & Gugerli 2006). Molecular techniques have been extensively used in the practice of conservation (e.g. Allendorf, Hohenlohe & Luikart 2010), but these techniques have been less broadly applied in restoration to date (Kettenring *et al.* 2014; Mijangos *et al.* 2015).

Neutral molecular variation is not directly correlated with variation in traits that undergo selection (for meta-analyses see Pfrender *et al.* 2000; Reed & Frankham 2001). Variation in traits that have direct links to fitness (e.g. seed dormancy, germination, growth, flowering, and seed production and seed dispersal) typically have a complex genetic basis that is best understood using quantitative genetics, the approach used most widely in agriculture, where genetic variation is assessed based on pedigree structure (i.e. the extent of resemblance among relatives and unrelated groups of individuals; for a review of the application of quantitative genetics to native species see Lynch 1996; Storfer 1996; Frankham 1999). In recent decades, molecular and quantitative genetic techniques have been merged to answer basic evolutionary questions in native species (reviewed in Wu *et al.* 2008) and assist with the goals of applied sciences, such as crop improvement (reviewed in Collard *et al.* 2005). Both molecular and quantitative genetics can provide important tools for monitoring changes in genetic variation over the course of collection, propagation and restoration. For a thorough review of current technologies, including promises and pitfalls, see Williams, Nevill & Krauss (2014).

TEST 1: INFORMING RESTORATION PRACTICES WITH NEUTRAL MOLECULAR INFORMATION

Numerous practical guides describe how to conduct an assessment of neutral genetic variation in wild and restoration populations of interest (Henry 2006; Selkoe & Toonen 2006; Newton 2007); DNA extracted from plant tissue is then sent to a genomics facility for processing at

a nominal cost. These comparisons of neutral genetic variation can be conducted in collaboration with a practitioner at a federal laboratory or academic facility that has access to the facilities for DNA extraction and data analysis.

When these collaborations can be established, valuable information regarding genetic change in propagation and restoration can be obtained from this approach. For example, the extent to which N_e has been reduced during the process of propagation can be quantified by comparing molecular variation in natural source populations, propagation populations, material deployed at the restoration site and established restorations. If substantial reductions in the effective population size are observed, methods of augmenting genetic diversity are warranted (see specific suggestions in the 'guidelines' section below). Gene flow at the production or restoration sites can also be measured; it may be prudent to facilitate gene flow (see Guideline 5 below) to maintain genetic variation over time. Finally, this approach could be used to decide whether source populations should be genetically mixed. Neutral genetic information has been used extensively for restoration of rare plant populations to understand genetic distances among populations in order to prioritize their inclusion in new populations and determine if admixture is likely to affect fitness (Falk & Holsinger 1991). If some populations are genetically unique, then admixture between populations may not be advisable until the importance of underlying trait differentiation is assessed.

TEST 2: DETECTING CHANGES IN TRAITS

The first step to ascertain any genetic changes that may have accrued during the process of propagation for restoration is to compare the traits of plants in source populations to those at production farms and in restored populations (Fig. 3a). Traits that indicate genetic problems such as inbreeding or maladaptation might include flowering time, reproductive output, seed dormancy and viability, or frequency of chlorophyll deformities (e.g. leaf-bleaching or yellowing is a sign of inbreeding in predominantly outcrossing species, Ohnishi 1982; Willis 1992). If differences between populations are observed, there is cause for concern but not necessarily alarm because these differences could simply be a function of plant growth responses to contrasting growth environments (i.e. phenotypic plasticity).

A test to determine whether trait differences are a function of a genetically based evolutionary shift or are plastic responses is to grow a subset of plants from the wild, propagation and restoration populations in a common garden. If phenotypic differences among populations disappear in a common garden, then it is likely that the changes that were originally observed in field conditions were simply a function of the environmental response (Fig. 3b) and this result indicates that action does not

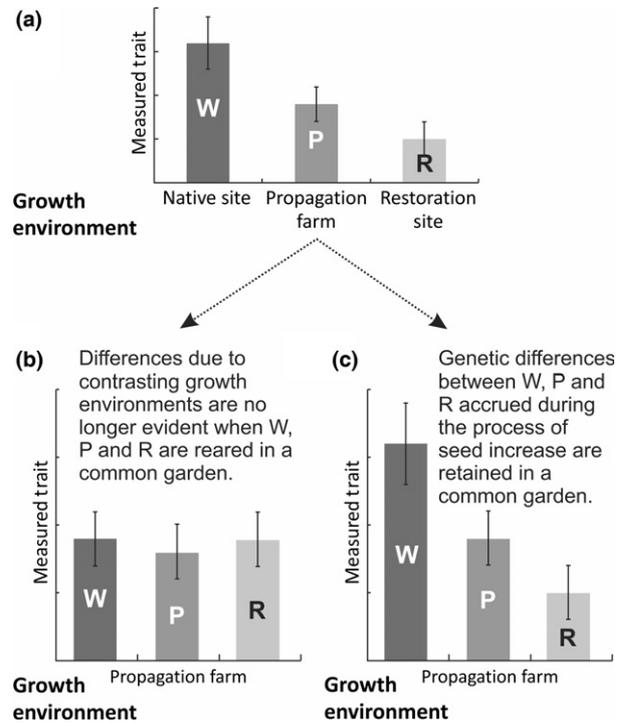


Fig. 3. (a) Based on measurements of plants growing in wild source population (W), on a production farms (P), and in a restoration site (R), it appears that a phenotype (measured trait) has shifted during through the three phases of increase. However, this is not necessarily the case. The observed phenotypic differences could simply reflect plant growth responses to contrasting environments (i.e. may not influence evolutionary potential) rather than genetic modification of the restoration material (i.e. influences evolutionary potential). To disentangle these effects with contrasting importance to population sustainability, it is necessary to grow representatives of W, P and R in a common garden where environmental influences on the plant trait are the same for each population. For example, representatives of W, P and R could be reared together at the production farm. (b) If population differences disappear when they are grown together at a site, then the original observed differences (panel a) must have been due to environment effects at the growth sites and, therefore, are not a cause for concern to growers. (c) However, if the differences are retained in the common garden, then evolution has modified the gene pool through the process of increase. These genetic differences could be due to a loss of genetic diversity, inadvertent selection, or both which may have detrimental effects on short- and long-term performance of materials at restoration sites.

need to be taken. However, if population differences are retained (Fig. 3c), then evolutionary change has occurred and appropriate remedial actions should be considered (see 'guidelines' section below for specific suggestions).

Flowering time may be a good choice of an index trait of evolutionary change because it is easy to measure and has broad ecological relevance. Timing of flowering is a heritable trait (Etterson 2004) that has been shown repeatedly to evolve rapidly (Franks, Sim & Weis 2007). Flowering phenology is also an important ecological trait because flowers that bloom at different times draw in pollen from donors at different spatial scales, thereby affecting genetic diversity in the population (Ison *et al.* 2014).

Selection on flowering time may also alter traits that negatively impact fitness in natural conditions (Burgess, Etterson & Galloway 2007). Variation in flowering time may be a good proxy for genetic variation in the offspring population because this trait is generally controlled by multiple loci distributed over entire genomes (Buckler *et al.* 2009; Salomé *et al.* 2011; Huang *et al.* 2012; Charmantier, Garant & Kruuk 2014). Therefore, a test that may provide important information about the genetic divergence and health of propagation and restoration populations is to measure differences in flowering time when source populations are reared in a common garden (for more details about experimental design and associated inferences see Etterson 2008). Other candidate traits are seed dormancy and seed shatter, or any array of traits commonly used in genecology studies (e.g. Bower, St. Clair & Erickson 2014). Measuring more than one trait is preferable due to the fact that evolution of traits depends on their genetic architecture as well as reproduction: selection on flowering time and dormancy are likely to be reinforced via assortative mating whereas traits like shattering may be less strongly reinforced.

Recommendations to manage evolution during the restoration process

Currently, our inability to track materials across the stages of collection, propagation and ultimate performance in restoration obstructs our determination of how selection in materials management impacts plant performance in restorations. Strong geographic ties between collectors, producers and restoration practitioners are necessary to track source performance in restoration and understand factors that lead to resilient planted populations. Research in traditional agriculture shows that *in situ* preservation of the evolutionary processes shaping crop genetic resources must necessarily occur at the local level (Bellon 1996; Brush 2004). While there is virtually no scientific information regarding how success of restoration populations can be altered by modifying collection and production practices, we can implement practices that will help us understand and mitigate negative effects of intentional and unintentional selection.

Ongoing management of restored sites using evolutionarily informed practices can facilitate the maintenance of genetic variation over time and increase the likelihood for population persistence. Best practices should focus on preserving patterns of genetic variation observed in 'healthy' natural populations, particularly for dominant or foundation plant species (the ones most frequently planted in restoration). This would mean having as much adaptive or quantitative genetic trait variation within the restored population as is typically found in natural populations, including similar trait values. An index of 'minimum viable interacting population' (MVIP, Wymore *et al.* 2014), defined as the minimum size of a population needed to preserve the level of genetic diversity required

by dependent and interacting species, is a potential benchmark for genetic diversity of restoration populations. MVIP differs from N_e by accounting for interspecific interactions, while N_e protects only the ability of a population to maintain its own genetic variation. While the ecosystem-level effects of genetic variation are quite well studied (e.g. Michalet *et al.* 2011; Hautier *et al.* 2015), this research has not yet been applied to designing foundation restoration materials that support ecosystem function (but see Kettenring *et al.* 2014). Without specific knowledge of how genetic variation within keystone restoration species affects dependent ecosystem dynamics, variation within restored populations that mirrors the scope of variation in natural populations may be an adequate proxy for MVIP.

When we choose source populations, propagation protocols and restoration management techniques, we do so with the ultimate aim of a particular phenotypic and genotypic composition of restoration populations. Management tools and restoration genetic targets will differ depending on the mating systems, modes of reproduction and dispersal strategies of the taxa involved (reviewed in Loveless & Hamrick 1984; Hamrick & Godt 1990). For instance, obligate outcrossing species may have substantial genetic diversity within populations, whereas highly selfing or predominantly clonal species may harbour their diversity among populations. For species where diversity is maintained at the landscape level (selfing and predominantly clonal species), high levels of genetic diversity within restoration populations may not be desirable or ultimately sustainable. Seed zones for these species may be smaller in scope than seed zones for outcrossing species (Hufford & Mazer 2003). For species where diversity is housed among (not within) populations, a coordinated approach to maintaining genetic diversity among populations requires consistent effort across years and across agencies.

Guidelines for managing evolution in propagation and restoration

In absence of specific knowledge regarding traits needed for long-term persistence of restoration populations, best practice should be evolutionarily enlightened management of the propagation and restoration process. Below we provide six specific guidelines to achieve the goal of restoration populations that house appropriate levels of genetic variation.

GUIDELINE 1: CONDUCT MULTIPLE COLLECTIONS FROM SOURCE AND PRODUCTION POPULATIONS OVER TIME

Genetic samples that are obtained from a population may differ over time (within a growing season and between years); therefore, propagule collection and harvest should be conducted periodically throughout the period of seed

maturation and, if practical, in multiple years. The genetic constitution of seeds produced by a single plant can differ both between years (Nakanishi *et al.* 2005) and within a single year (Ison *et al.* 2014). Biotic and abiotic conditions such as drought and herbivory can affect the amount of seed production. Thus, the timing and frequency of seed collection from the same population, even the very same plants, can influence the genetic composition of restoration materials. Multiple harvests increase the likelihood of sampling the full suite of genetic variation that is harboured in a population. This practice includes genotypes with diverse phenologies as well as those that reproduced at different times because of biotic and abiotic influences in the field. Intentionally selecting for a range of phenologies by using multiple collections ensures that seeds from earlier- and later-maturing individuals are maintained within restoration populations (Dyer, Knapp & Rice 2016).

GUIDELINE 2. USE SOURCES FROM SEVERAL NATIVE POPULATIONS THAT ARE IN CLOSE PROXIMITY

When local seed is required by regulatory or other standards, a strategy for maximizing the adaptive potential of a restored population is to use an initial seed mix containing local genotypes (Grady *et al.* 2011; Dyer, Knapp & Rice 2016), and genotypes from ecologically similar, but geographically more distant populations (Montalvo & Ellstrand 2000; Bischoff *et al.* 2006; Broadhurst *et al.* 2008; Woolbright *et al.* 2014). Pooling propagules from several source populations will prevent inadvertently sampling from a single population with low diversity (Kettenring *et al.* 2014). Although admixture between genetically diverged populations could lead to outbreeding depression (or, the loss of local adaptation, Ellstrand & Elam 1993; Hufford & Mazer 2003; Verhoeven *et al.* 2011) and low fitness because of intrinsic genetic incompatibility (Galloway & Etterson 2005), the duration of these negative effects is not well known and could persist for only a few generations (Erickson & Fenster 2006; Pickup & Field 2013). Increasing multiple source locations within a single production farm or restoration site may mimic the frequent trading of seeds and active maintenance of genetic diversity in landrace production (e.g. Abbo, Lev-Yadun & Gopher 2010; Bellon, Hodson & Hellin 2011; Soleri *et al.* 2013), which augments genetic diversity in traditional farming systems. Therefore, agricultural research shows that, under conditions where genetics and phenotypes are known, this approach can increase performance reliability while evolutionary research highlights the risks of this approach.

GUIDELINE 3: MAINTAIN LARGE N_E ON THE PRODUCTION FARM

Collection of propagules from the wild is the most important step for maximizing effective population size.

Maximizing genetic variation from the seed source and maintaining that variation at harvest will increase sampling benefits (i.e. increasing the probability that important genotypes are included, e.g. Bischoff, Steinger & Müller-Schärer 2010) and portfolio effects (i.e. increasing the probability that important intergenotypic emergent properties occur, e.g. Crowe & Parker 2008). Support for maximizing genetic variation in restoration populations comes from other work including basic demography, local adaptation and adaptive capacity (Matyas 1996; Lesica & Allendorf 1999; Broadhurst *et al.* 2008; Bischoff, Steinger & Müller-Schärer 2010; Weeks *et al.* 2011). While some authors (Bischoff, Steinger & Müller-Schärer 2010) recommend tracking the number of maternal plants in each *ex situ* repository (source collection and production farm), we expect that industrial-scale collection and propagation and subsequent management of gene flow (see Guideline 5 below) will lead to large maternal numbers that adhere to or exceed the general guidelines of the 50/500 rule for N_e (Jamieson & Allendorf 2012).

GUIDELINE 4. TRACK SOURCE THROUGH PROPAGATION AND RESTORATION PLANTINGS

A critical step in understanding how the amount and type of genetic diversity influences restoration success is tracking the source (or provenance) of restoration material. Data gained from the very first provenance trials with forestry species in the late 1800s were the first to show that source can determine successful establishment (Matyas 1996). This type of study is best conducted on foundation species that are produced and planted at extremely large scales. Adequate documentation includes source location and date(s) of collection and location and dates of harvest from the production farm. This documentation will improve our knowledge regarding the contribution of source (compared to seeding practices, environmental variation and site characteristics) to restoration success and lead to better information regarding how propagation and source choice affect ultimate plant performance (Merritt & Dixon 2013).

GUIDELINE 5: INTENTIONALLY PROMOTE GENE FLOW

When local provenancing is not required, practitioners can make provenancing decisions that intentionally mix source populations. These strategies have been reviewed in Breed *et al.* (2013). In addition to promoting gene flow by mixing source populations, production and restoration practices can also be modified to augment or introduce adaptive genetic variation into populations (Hufford & Mazer 2003; Vitt *et al.* 2010; Aitken & Whitlock 2013). Gene flow between propagation and natural populations can counter the loss of genetic diversity (Fig. 2. Compare Scenarios 3 and 4, panels b and c). Higher rates of gene flow bring greater degrees of genetic similarity among populations, except in the case of extremely strong

selection against immigrant alleles (Gonzalo-Turpin & Hazard 2009). Also, higher rates of gene flow between populations will produce a greater potential for populations to harbour genetic diversity (Tero *et al.* 2003). In the context of propagation for restoration, gene flow from natural populations into adjacent production farms could serve to maintain and perhaps enhance genetic diversity over time. In the case where a production farm propagates genotypes that drastically differ from local populations, gene flow may not be appropriate. Swamping and/or outbreeding depression can occur when populations are not mixed appropriately (Hufford & Mazer 2003; Aitken & Whitlock 2013).

Intentional gene flow can be especially valuable for genetic rescue from inbreeding (Richards 2000) or maladaptation (Heschel & Paige 1995), and this tool can be useful in response to a finding of inbreeding or maladaptation in the tests we describe above. Because genetic diversity at restoration sites may be reduced due to strong selection from interannual climatic variation or other factors that vary among years, assisted gene flow into restoration sites may be necessary. Overseeding (i.e. seeding additional genotypes into an already established restoration) is an excellent approach. The source of these genotypes should be well considered and may match the source of the original restoration planting.

Depending on the plant taxon, management and restoration of pollinator populations may be required to manage appropriate gene flow. Large-scale restoration in the United States has mostly focused on wind-pollinated trees and grasses as foundation species (e.g. Bower, St. Clair & Erickson 2014) and therefore does not depend on pollinator services for population maintenance. More complex systems with dependent species will require multitrophic management for persistence and perhaps even restoration of faunal taxa (e.g. Mijangos *et al.* 2015). Pollinator species diversity and the stability of pollination services can be enhanced by interplanting diverse species mixes in large-scale field conditions (Ebeling *et al.* 2008). The presence of a robust pollinator community facilitates genetic exchange within the restoration populations and across the broader landscape (Westphal, Steffan-Dewenter & Tscharntke 2003).

GUIDELINE 6: REDUCE SELECTION

Reducing selection within production farms will maintain genetic diversity (Dyer, Knapp and Rice 2016). For example, restoration practitioners and production farmers may pre-treat seeds to break dormancy (e.g. Kettenring & Galatowitsch 2007), thereby reducing selection on dormancy by removing the expression of that variation in on-farm or restoration populations. Managing the origin of populations and choosing appropriate production environments minimizes the effects of selection. Production farms that mimic moisture, light, nutrient or disturbance levels and their variation found in the wild should

minimize unintentional abiotic selection. This approach may contradict typical practice and reduce on-farm propagule yields, but will help ensure long-term fitness in the restoration environment (Kettenring *et al.* 2014). The approach of mirroring the restoration environment at the production farm may also confer adaptive maternal effects upon propagules, although available research shows that maternal effects on restoration taxa are minimal in restoration environments (Espeland & Richardson 2015; Espeland *et al.* 2016). When different genotypes are favoured in different microhabitats (Harris *et al.* 2006), genetic variation may be best preserved at the vendor scale by pooling propagules across production farms. Production fields that are differentiated in biotic, edaphic, hydrologic or microclimatic factors and subsequent pooling of propagules from those different habitats would then sample the available diversity. This practice is mirrored by farmers in traditional agriculture who often cultivate multiple fields to maintain broad tolerance (i.e. canalized phenotypes) and yield stability (as in Steinberg 1999). Heterogeneity at the restoration site itself may also increase the maintenance of diversity and decrease unintentional selection. Thus, rather than attempting a strict match of production farms to restoration conditions, managing for microsite heterogeneity across farms and within restorations could significantly improve genetic diversity and decrease the potential for narrowed genetics in each population.

Typical propagation practice of monoculturing creates strong unintentional biotic selection for high intraspecific competitive ability and low tolerance of biotic heterogeneity (Weiner *et al.* 2010). Producers can mimic the wild by growing multiple species in polyculture (e.g. Piper 1999; Malézieux *et al.* 2009), thereby maintaining traits that promote interspecific coexistence. In addition, polycultures can provide ecosystem services to producers, such as pest and disease control, improved carbon and nutrient cycling, enhancement of beneficial organisms and increased production per area of each species compared to monocultures (reviewed in Oestergaard *et al.* 2009). In a larger scale polyculture or interspecific planting, harvesting multiple species that have different seed production morphologies, phenologies and plant statures requires special equipment, such as vacuum harvesters and stripper headers (e.g. Burton & Burton 2002; USDA NRCS 2004).

CONCLUSIONS

It is important to consider the potential for inadvertent evolution of restoration materials as global demand for restoration propagules quickly outpaces the availability of propagules from wild populations (Merritt & Dixon 2013). We have highlighted important ways that both the amount and type of genetic variation could be altered throughout the multistage process of producing large quantities of restoration material. Successful restoration outcomes depend on genetically informed practices that

minimize the negative effects of reduced variation and inadvertent selection at the harvesting and seed production stages and facilitate the maintenance of diversity in restored populations after planting. Others have concluded that genetically diverse restoration materials are the most appropriate for managing risk in the restoration environment. We support that conclusion with the caveat that higher diversity in restoration populations than what we find in naturally occurring populations may indicate the presence of some maladapted genotypes. We have applied existing literature to show that research is needed to determine the genotypic and phenotypic traits that confer restoration success and that these traits may be undermined by evolutionary processes in propagation. In the face of these unknowns, we have provided practical considerations for plant materials management. These guidelines represent approaches that may be used to improve the adaptive capacity and the potential to positively contribute to ecosystem function and services in restoration populations.

Acknowledgements

Thanks to Beth Redlin for expert graphics assistance. Thanks to the Etterson laboratory, Nicole Soper Gordon, Lora Perkins, RC Johnson and John Gaskin for helpful comments on the manuscript.

Data accessibility

Data used in this paper have been taken from the references and additional citations listed in Data sources. For more information see Table S1.

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Received 9 January 2016; accepted 29 June 2016

Handling Editor: Joslin Moore

Data Sources

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Examples from the evolutionary (e), agricultural (a), and restoration (r) literatures that demonstrate response to selection at the three process stages of restoration materials management (seed collection, propagation, installation of restoration).