

REVIEW

Application of genetic diversity–ecosystem function research to ecological restoration

Karin M. Kettenring^{1,2*}, Kristin L. Mercer³, Carrie Reinhardt Adams⁴ and Jes Hines^{2,5}

¹Ecology Center and Department of Watershed Sciences, Utah State University, Logan, UT, USA; ²Smithsonian Environmental Research Center, Edgewater, MD, USA; ³Department of Horticulture and Crop Science, The Ohio State University, Columbus, OH, USA; ⁴Department of Environmental Horticulture, University of Florida, Gainesville, FL, USA; and ⁵Department of Experimental Limnology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Neuglobsow, Germany

Summary

1. Three common goals for restoration are (i) rapid plant establishment, (ii) long-term plant persistence and (iii) restoration of functioning ecosystems. Restoration practitioners often use cultivars optimized for rapid plant establishment under highly disturbed conditions to achieve the first goal; locally adapted genotypes are championed for the second because they can be well suited for local environmental conditions. Restoring functioning ecosystems is considered a loftier goal that practitioners struggle to achieve because we lack proven techniques.

2. Similar to the demonstrated benefits of species, functional and phylogenetic diversity for ecosystem functions (EFs), recent genetic diversity (GD)–ecosystem function (EF) experiments have shown that increases in plant GD can positively influence many different EFs. Would the introduction of diverse plant genotypes of a given species into a restoration enhance ecosystem functioning and the evolutionary potential of restored populations?

3. In this review, we first examine three propagule-sourcing approaches: cultivar, local adaptation and GD. Next, we raise questions that if addressed, could help practitioners implement a GD approach in restoration: (i) How might the selection, relatedness and arrangement of genotypes be optimized to restore functioning ecosystems, (ii) How do traits that affect an EF relate to neutral or adaptive diversity, more common measures of GD and (iii) at which spatial and temporal scales does GD influence EFs in restorations?

4. *Synthesis and applications.* Although each propagule-sourcing approach may be best suited for a particular restoration goal, each approach may simultaneously benefit other goals. Yet cultivars and locally adapted populations that have experienced artificial and/or natural selection may not possess the levels of diversity that will confer expected benefits to different ecosystem functions. Future research should determine the relative value of each approach (or a combination of approaches) for simultaneously achieving multiple restoration goals. Restoration experiments, where plant genetic diversity (GD) is manipulated and monitored over scales relevant to restoration, could reveal the true promise of a GD approach to restoration.

Key-words: community genetics, ecological restoration, ecosystem functions, ecosystem multifunctionality, ecosystem services, genetic diversity, genotype richness, genotypic diversity, plant materials, restoration genetics

Introduction

The ultimate test of our understanding of ecological systems depends on whether we can actively reverse

ecosystem degradation to regain biodiversity and fully functioning ecosystems through ecological restoration (Benayas *et al.* 2009). Research has revealed that plant diversity can influence many ecosystem processes (hereafter referred to as ‘EFs’ when describing multiple ecosystem functions, or ‘EF’ when referring to an individual

*Correspondence author. E-mail: karin.kettenring@usu.edu

ecosystem function; Cardinale *et al.* 2012). Many levels of plant diversity including species, functional and phylogenetic diversity affect particular EFs (Cardinale *et al.* 2009; Cadotte, Carscadden & Mirotchnick 2011; Srivastava *et al.* 2012). Therefore, biodiversity ecosystem function (BEF) research suggests tangible means to achieve the lofty and often elusive goal of restoring fully functioning ecosystems (i.e. to restore a broad suite of EFs including the services they provide to humans; Costanza *et al.* 1997; Ehrenfeld 2000; Benayas *et al.* 2009; Montoya, Rogers & Memmott 2012). Restoration experiments have shown that introducing more plant species (e.g. Doherty, Callaway & Zedler 2011) or greater plant functional diversity (e.g. Montoya, Rogers & Memmott 2012) can increase particular EFs (Benayas *et al.* 2009). However, the importance of genetic diversity (GD) within plant species for EFs has received less attention in the context of restoration.

Recent genetic diversity–ecosystem function (GD-EF) research has demonstrated that genetic variation within plant species (such as genotypic or allelic richness as reviewed in Hughes *et al.* 2008) has consequences for plant communities (Booth & Grime 2003; Fridley & Grime 2009). These GD effects can also extend to affect diversity of higher trophic levels (Wimp *et al.* 2005; Johnson, Lajeunesse & Agrawal 2006), primary productivity (Crutsinger *et al.* 2006; Kotowska, Cahill Jr & Keddie 2010), decomposition (Schweitzer *et al.* 2004; Madritch, Donaldson & Lindroth 2006), invasion resistance (Crutsinger, Souza & Sanders 2008; Vellend, Drummond & Tomimatsu 2010) and the ability of ecosystems to recover from a disturbance such as episodic herbivory or extreme weather events (Hughes & Stachowicz 2004; Reusch *et al.* 2005). These results suggest that increasing plant GD may enhance restoration of functioning ecosystems. For instance, a recent study in the Chesapeake Bay found that increased allelic diversity of seagrass *Zostera marina* plantings positively affected invertebrate habitat, primary productivity and nutrient retention (Reynolds, McGlathery & Waycott 2012).

Despite major advances provided by the GD-EF literature, questions remain that limit the application of this research to restoration. Without experimental results that soundly demonstrate anticipated benefits of increased GD to restoring functioning ecosystems while achieving other goals essential to restoration, some may question the added challenges posed by sourcing genetically diverse plant materials. For example, we would expect high GD plantings to foster the evolutionary potential of restored populations (Rice & Emery 2003; Falk *et al.* 2006; Broadhurst *et al.* 2008) and hence a common restoration goal of long-term population persistence, but this diversity benefit has not been explicitly evaluated in GD-EF studies. Simultaneously, GD-EF research has paid limited attention to the source of the genotypes used in experiments, including common restoration sources of locally adapted genotypes or cultivars (but see Bischoff, Steinger & Müller-Schärer 2010), which may affect experimental outcomes.

In this review, we highlight the compelling promise GD-EF research offers for restoring functioning ecosystems, while acknowledging the gap between that potential and the application of GD-EF research to restoration. First, we review three propagule-sourcing approaches for restoration – cultivar, local adaptation and GD. We discuss how each sourcing approach relates to three main restoration goals: plant establishment, long-term persistence and restoring fully functioning ecosystems. Next, we explain what we see as the main research avenues that could facilitate the application of GD-EF research to restoration. Finally, given that restoration projects often have diverse goals, we explore how to combine propagule-sourcing approaches for greatest benefit.

Key restoration goals

Restoration practitioners often try to achieve multiple goals while balancing complicated biological and social constraints. We focus here on three main goals of restoration (Fig. 1), of which the first two are most common. The first – to maximize plant establishment – is an especially important goal under degraded soil conditions, in highly altered environments, or with large-scale restorations at risk of invasion by undesirable species (Lesica & Allendorf 1999; Broadhurst *et al.* 2008). The second goal is long-term persistence (on the order of decades or more) of restored plant communities (Lesica & Allendorf 1999; McKay *et al.* 2005), which necessitates restoring populations with the potential to evolve in response to environmental change (Rice & Emery 2003; Broadhurst *et al.* 2008). The third goal is to restore fully functioning ecosystems (Ruiz-Jaen & Mitchell 2005; Choi *et al.* 2008; Suding 2011). For example, a restored ecosystem should fully support local food webs, maintain nutrient and

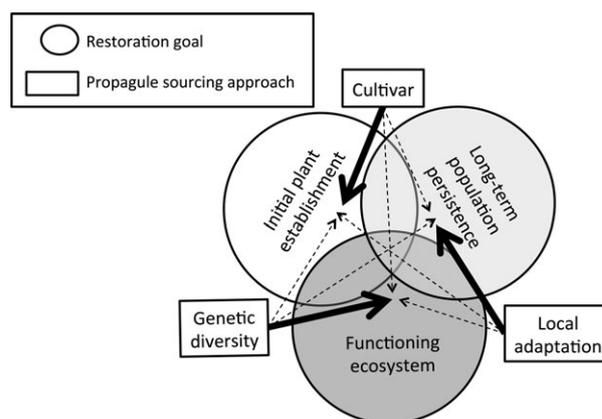


Fig. 1. Three common goals for restoration include initial establishment of plants, long-term population persistence and restoration of a functioning ecosystem. Three propagule-sourcing approaches (cultivar, local adaptation and genetic diversity) can target a specific primary restoration goal (solid arrows) while also benefitting a secondary goal (dashed arrows). When restoration scenarios require a focus on multiple goals (overlapping circle spaces), an integrated approach may be required (see Fig. 2).

hydrologic cycling and recover from disturbances. While there are abundant examples of how to successfully restore particular EFs in restorations (e.g. Klopff & Baer 2011), restoration of fully functioning ecosystems is difficult because we lack proven strategies (Moreno-Mateos *et al.* 2012). In practice, introducing high species and/or functional diversity has proved to be an extremely challenging (e.g. Kindscher & Tieszen 1998; Martin, Moloney & Wilsey 2005) but nonetheless worthwhile approach given the inherent societal value of biodiversity and its role in restoration of multiple ecosystem functions (see Introduction). Here, we propose that emphasizing the use of high GD in sourcing propagules could increase the likelihood of restoring functioning ecosystems.

Approaches to sourcing propagules for restoration

Traditionally, ecological restoration has applied both horticultural and ecological approaches, and a good dose of pragmatism, to plant propagule sourcing. Practitioners may be working with especially large or disturbed sites (Lesica & Allendorf 1999), have low availability of

propagules, be constrained by time and cost, and have issues with funding and legal compliance. Therefore, their primary concern may simply be to find sufficient propagules that will establish on a site, which unfortunately does not ensure long-term persistence or restoration of a functioning ecosystem. Sourcing propagules using cultivar, local adaptation or GD approaches can support goals of rapid establishment, long-term persistence and restoration of functioning ecosystems, respectively. Of course, to some degree these goals overlap (Fig. 1). For instance, long-term persistence requires good plant establishment, and the GD introduced for restoring a functioning ecosystem likely enhances a population's evolutionary potential and long-term persistence (Falk *et al.* 2006). Nevertheless, we address each approach individually because any specific restoration may require emphasis on one goal and approach over another.

CULTIVAR APPROACH

Planting cultivars with desirable traits can achieve rapid plant establishment (Seliskar 1998; Lesica & Allendorf 1999; Lambert, Baer & Gibson 2011). Cultivars are

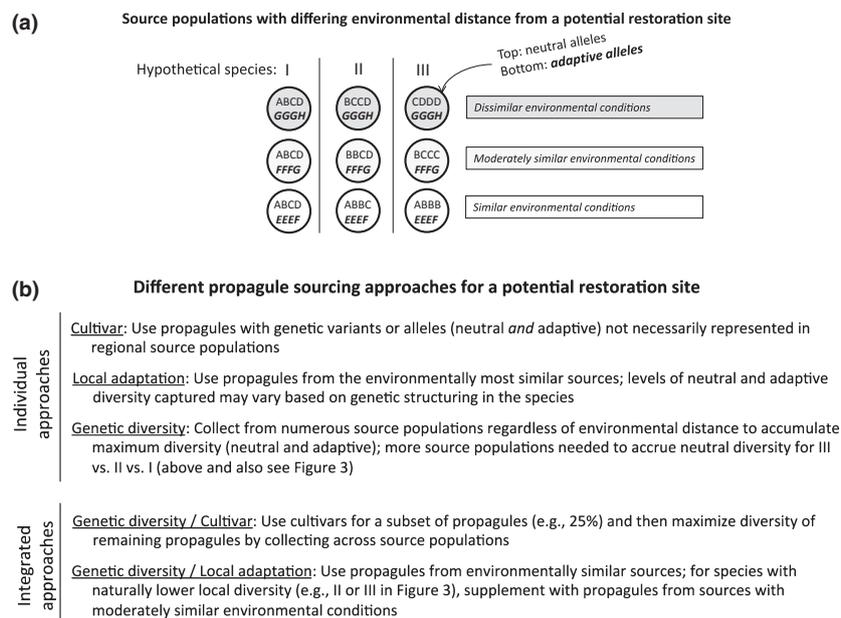


Fig. 2. (a) Source populations with differing environmental distance from a potential restoration site for species with different natural genetic structuring (e.g. species I–III in Fig. 3). Circles in ‘similar’, ‘moderately similar’ and ‘dissimilar’ rows represent example source populations of each hypothetical species found at increasing environmental distances from a restoration. Letters in each circle represent the frequency of genetic variants (i.e. alleles) found in a population; repeated letters indicate that the allele has a greater frequency. These variants are alleles at one neutral locus (alleles A–D in top line of circles) and at one locus with a strong effect on the response of fitness to the environment (i.e. adaptive locus; alleles E–H shown in lower line in bold and italics). For species I, which has low differentiation among populations for neutral alleles (see Fig. 3), all source populations have identical neutral alleles. Species III has higher differentiation among populations for neutral alleles, and few shared neutral alleles among populations. Species II is intermediate in this regard. In this example, species I–III possess equal levels of diversity at the adaptive locus within source populations because, for all species, strong selection from local environmental conditions dominates over gene flow. Alleles for traits associated with an ecosystem function (EF; not shown) could follow the structuring patterns for adaptive loci if those EF traits also had a strong effect on fitness, while EF traits with a negligible impact on fitness would be structured more similarly to the neutral loci (See Fig. 3). (b) Different propagule-sourcing approaches discussed in the text. Some approaches take into account a species' natural genetic structuring when collecting propagules or considering the environmental distance between propagule source populations and the restoration site.

collected from natural populations, selected or bred for superior performance, and propagated for wide-scale use in restorations, often in regions where they may not naturally occur (e.g. Casler *et al.* 2007). Cultivars have characteristics optimal for establishment – such as high germination rates, productivity and stress tolerance – even when sites are highly degraded or situated within degraded landscapes (Lesica & Allendorf 1999; Jones 2003; McKay *et al.* 2005; Johnson *et al.* 2010). Cultivars may contain a single genotype (e.g. *Spartina alterniflora* clones for marsh reclamation in northern Gulf of Mexico (Harrison *et al.* 2001)) or multiple genotypes (e.g. ‘seed orchards’ of *Panicum virgatum* for prairie restoration (Casler *et al.* 2007)).

Yet, there are a number of concerns with a cultivar approach (Fig. 2). First, while a cultivar approach may help restore some EFs (e.g. enhanced performance of cultivars may lead to increased productivity; Lambert, Baer & Gibson 2011), the development of cultivars can lead to a reduction in GD and therefore may diminish positive effects of GD on ecosystems. Secondly, cultivars may hybridize with surrounding, locally adapted genotypes leading to ‘genetic pollution’ (Lesica & Allendorf 1999; Rowe & Leger 2011; but see Casler *et al.* 2007). Thirdly, cultivars with enhanced competitive ability under disturbed conditions may exclude establishment of other native species. For instance, cultivars with enhanced physiological performance and biomass production may out-compete and replace locally adapted plants, even if an important EF was restored (e.g. primary productivity; Lambert, Baer & Gibson 2011). Despite these concerns, relatively few experiments have tested impacts of cultivars on other establishing genotypes, and large projects planted with cultivars are rarely monitored long term. A recent experimental grassland restoration showed that even with demonstrated superior cultivar performance (Gustafson, Gibson & Nickrent 2004), seed source (cultivar vs. non-cultivar) did not affect community assembly after four years (Gibson *et al.* 2013). In support of these findings, Wilsey (2010) suggests that cultivars may not competitively reduce other species’ recruitment because what cultivars gain in increased vigour they lack in fitness due to reduced local adaptation. Restoration guidance recommends the cultivar approach only for severely disturbed lands (Johnson *et al.* 2010), but more research is needed.

LOCAL ADAPTION APPROACH

Use of locally adapted propagules presumably increases the long-term persistence of restored populations since they can tolerate biotic and abiotic site conditions (McKay *et al.* 2005). This local adaptation approach (Fig. 2) can be especially relevant in restoration sites with minimal disturbance, since locally adapted propagules should maintain high fitness and will not pollute local populations with poorly adapted genotypes (Ellstrand 1992; Lesica & Allendorf 1999). Although local adapta-

tion is ubiquitous (Clausen, Keck & Hiesey 1948; McKay *et al.* 2001; Angert & Schemske 2005), the scale and relative strength of local adaptation vary across species (Schmitt & Gamble 1990; Galloway & Fenster 2000; Garrido *et al.* 2012). Additionally, due to patchy habitat distribution, populations from environmentally similar, but distant, habitats may have more similar adaptations than geographically close populations from distinct habitats (e.g. Bischoff *et al.* 2006). Thus, practitioners seeking locally adapted propagules should collect propagules from sites that are environmentally similar to the proposed restoration rather than relying on those that are simply close geographically.

Conversely, strict adherence to the local adaptation approach may not facilitate long-term persistence for five reasons. First, local adaptation may be less common than is presumed (Leimu & Fischer 2008; Hereford 2009). Secondly, solely introducing propagules adapted to current conditions could limit persistence if environmental conditions change dramatically (Rice & Emery 2003; Sgrò, Lowe & Hoffmann 2011; Breed *et al.* 2013). Thirdly, the highly altered restoration environment may radically differ from surrounding ecosystems (i.e. so altered they are considered novel ecosystems (Hobbs, Higgs & Harris 2009)), making local adaptations irrelevant. Fourthly, locally adapted source populations may be genetically depauperate due to strong directional selection (Rice & Emery 2003; Broadhurst *et al.* 2008), reducing potential benefits to restoring functioning ecosystems, evolutionary potential and the ability to recover from disturbances while increasing the likelihood of inbreeding depression and genetic drift (Rice & Emery 2003; Broadhurst *et al.* 2008; Sgrò, Lowe & Hoffmann 2011; Breed *et al.* 2013). Finally, locally adapted propagules may be costly or unavailable in large quantities for restorations (Burton & Burton 2002).

GENETIC DIVERSITY APPROACH

Introducing diverse genotypes could facilitate restoration success by influencing numerous EFs, although this GD approach remains experimental (See Table S1, Supporting information; Fig. 2). In most GD-EF studies, genotypic richness is manipulated, and the resulting effects on an EF or suite of EFs are evaluated (Table S1, Supporting information). The observed benefits of genotypic richness on an EF could result from three non-mutually exclusive mechanisms: (i) the sampling effect, due to the higher probability that more diverse populations contain one or more highly functioning genotypes, (ii) the selection effect, whereby a highly functioning genotype comes to dominate a population over time and (iii) complementarity, due to increasing resource capture efficiency due to variation among genotypes (i.e. niche partitioning) and/or facilitation among genotypes, which enhances an EF or suite of EFs (Loreau & Hector 2001). All three mechanisms occur in experimental plots, singly or in combination (Table S1,

Supporting information). We suggest that in a restoration context, the relative importance of each mechanism may change over time, as has been shown in species diversity research where complementarity effects on primary production increased over time (Cardinale *et al.* 2007). If the restoration site is highly heterogeneous or degraded, planting diverse genotypes may be a good bet-hedging strategy whereby the sampling effect will ensure at least some successful establishment. The selection, and particularly complementarity, effects may become more important over the long term for various EFs (Table S1, Supporting information). Here, we briefly discuss two EFs – invasion resistance and the ability to recover from disturbance – to illustrate how a GD approach could improve an EF in the context of restoration. For a review of the effects of GD on several other EFs, see Hughes *et al.* (2008).

Restored ecosystems must be invasion resistant since disturbance from the restoration process itself often makes restorations inherently invasion prone (D'Antonio & Meyerson 2002; DeMeester & Richter 2010). A diverse assemblage of genotypes may improve invasion resistance by filling all available niches better than a relatively uniform group of genotypes, such as in some cultivars. For example, increasing genotypic richness of tall goldenrod *Solidago altissima* led to higher stem densities and greater niche complementarity, thereby reducing the biomass of old field invaders (Crutsinger, Souza & Sanders 2008). This suggests that planting a diversity of genotypes could limit invasions in restorations.

Another important goal for restored ecosystems is that they will be able to recover from myriad other disturbances, such as episodic herbivory (e.g. Hughes & Stachowicz 2011; Parker, Salminen & Agrawal 2010), or extreme weather events, such as those predicted with climate change. Reusch *et al.* (2005) demonstrated that genotypically rich seagrass *Zostera marina* plantings had higher density and biomass production than low-diversity plots under near-lethal water temperatures. Given the unpredictability of future climate conditions, the benefits of GD in response to disturbance in restorations are considerable.

Using a GD approach, however, introduces the potential for outbreeding depression if non-local genotypes are used (GD-EF research to date has not fully addressed the importance of local vs. non-local genotypes to effects on EF). The use of non-local genotypes could result in 'genetic dilution' and/or the disruption of co-adapted gene complexes during intraspecific hybridization (Hufford & Mazer 2003; McKay *et al.* 2005; but see Frankham *et al.* 2011). In addition, introducing non-local genotypes that could potentially become invasive is extremely problematic (e.g. *Phragmites australis*; Saltonstall 2002), in part because such cryptic invaders would be nearly impossible to distinguish from local genotypes for future control. Given the uncertainty involved with a GD approach, a risk assessment that considers aspects of the species' biol-

ogy (particularly mating systems; Fig. 3), including 'natural' degree of inbreeding/outbreeding and restoration conditions (e.g. size of the restoration in relation to surrounding natural populations), could help guide decision-making regarding propagule diversity targets.

Key research avenues for ensuring successful application of a genetic diversity approach to restoration

To use the GD approach with confidence in restoration, we must advance three key avenues of research: (i) optimal selection, relatedness and arrangement of genotypes, (ii) relating traits that affect an EF to neutral and adaptive diversity and (iii) evaluation of GD-EF effects using temporal and spatial scales appropriate for restoration.

SELECTION, RELATEDNESS AND ARRANGEMENT OF GENOTYPES

It remains unclear whether the magnitude of effects on an EF or suite of EFs found in GD-EF experiments reflects the GD-EF relationships at work in natural populations. In particular, an over- or under-representation of GD in experiments, compared to diversity in natural populations (Fig. 3), could skew the importance of diversity for an EF relative to other factors for restoration (Hersch-Green, Turley & Johnson 2011; Tack, Johnson & Roslin 2012). A meta-analysis found that the influence of plant GD on the structure of insect communities had been overstated because researchers often collected plant genotypes across broad areas, but conducted experiments in relatively small, environmentally homogenous plots (Tack, Johnson & Roslin 2012), which may or may not be relevant to restoration. When we examined how and where propagules were acquired across GD-EF experiments, we found that researchers used disparate approaches of extremely varied distances to the experimental site with a broad range of collection area sizes (Table S1, Supporting information). Also, some researchers intentionally maximized phenotypic differences in genotypes used for experiments (e.g. Kotowska, Cahill Jr & Keddie 2010) or, by contrast, excluded phenotypic extremes (e.g. Weltzin *et al.* 2003). These practices can over- (by maximizing phenotypic differences) or under-estimate (by excluding phenotypic extremes) the GD effect compared to natural populations. Therefore, it is important to consider the spatial scales of both genotype collection and experimentation to clarify the relative effects of GD vs. other ecological factors on communities and different EFs (Hersch-Green, Turley & Johnson 2011; Tack, Johnson & Roslin 2012). Because restorations are not natural (though many attempt to imitate natural populations; Fig. 3), restoration practitioners may consider genotype acquisition and selection choices as a method to preferentially enhance the influence of GD on an EF or suite of EFs.

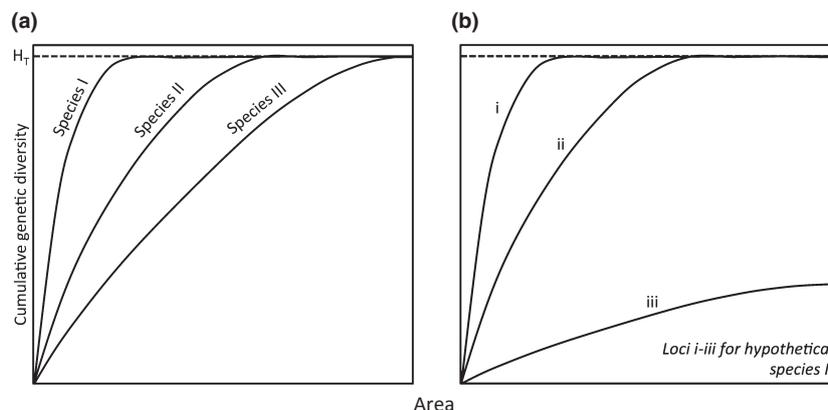


Fig. 3. Genetic diversity within hypothetical species I–III increases with area and, thus, the number of populations sampled; modified from Neel and Cummings (2003) for (a) neutral loci and (b) those that control phenotypic traits. The rate diversity accumulates depends on the partitioning of genetic variation within and among populations; total diversity (H_T) is the sum of variation within and among populations (see graph asymptote above). (a) Considering neutral diversity, species I has higher variation within populations and lower differentiation among populations (see Falk *et al.* 2006 for a review of related genetic concepts). Species III has lower variation within populations and higher differentiation among populations. A sexually reproducing, outcrossing species with long-distance seed dispersal might resemble species I; an asexually reproducing species with local propagule dispersal would be most like species III; and a species with intermediate life-history traits would resemble species II (reviewed in Loveless & Hamrick 1984; Hamrick & Godt 1990). (b) For a hypothetical species (e.g. II here), the structuring of genetic diversity at loci encoding phenotypic differences will differ for loci that have strong effects on fitness responses to environments (i.e. that are adaptive; curve i; also see Fig. 2); have ecological relevance (e.g. drive an ecosystem function or phenotypic differentiation) without affecting fitness (effectively neutral; curve ii); or are adaptive at very large spatial scales (e.g. alleles that are fixed within a region; curve iii).

Importantly, genetic effects on EFs may depend not only on genotypic richness, but also on the degree of genetic relatedness among individuals (Stachowicz *et al.* 2013). More distantly related genotypes may better support particular EFs through trait differentiation and niche complementarity (Stachowicz *et al.* 2013), analogous to the importance of phylogenetic or functional diversity over species richness to different EFs (Cadotte, Carscadden & Mirotchnick 2011; Srivastava *et al.* 2012). A second (not mutually exclusive) hypothesis suggests that more closely related genotypes may enhance particular EFs due to kin recognition and cooperation (Stachowicz *et al.* 2013). Given that these mechanisms may result in contrasting impacts on various EFs, future GD-EF research should consider genetic relatedness to better guide restoration propagule choice. Although this may seem to be merely a finer degree of resolution of diversity effects among hierarchical classifications, these effects become more important at the subspecies level due to the effects of hybridization and inbreeding/outbreeding depression on restoration success.

Finally, regardless of the genotypes chosen for use in restoration, the spatial arrangement of the genotypes in plantings may have important implications for different EFs, as has been demonstrated with interspecific diversity (e.g. Yurkonis, Wilsey & Moloney 2012). The common practice of using randomized and gridded plantings of genotypes in GD-EF experiments (Table S1, Supporting information) may reduce competition among closely related genotypes (assuming niche complementarity and not kin cooperation is driving a positive effect on EF) relative to what is seen in natural populations with more

natural clustering of propagules following dispersal. Similar gridded arrangements are used in restoration plantings, and their effects on different EFs remain unknown. Thus, the benefits of manipulating genotype planting arrangements for restoring functioning ecosystems are important areas for future research.

RELATING TRAITS THAT AFFECT AN ECOSYSTEM FUNCTION TO NEUTRAL AND ADAPTIVE DIVERSITY

Advances in inexpensive molecular techniques have made it feasible to examine patterns of genetic structuring for more species (Fig. 3) (e.g. Fant *et al.* 2008; Ritchie & Krauss 2012; Sweetman, Kettenring & Mock 2013). However, this neutral diversity is poorly correlated with quantitative trait variation, which suggests that neutral diversity may not represent adaptive traits of interest for restoration (Reed & Frankham 2001; McKay & Latta 2002). These non-neutral sources of variation are likely essential for bolstering lifetime fitness, evolutionary potential, long-term persistence and restoration of functioning ecosystems.

Although GD-EF research has suggested mechanisms by which GD can enhance different EFs (e.g. complementarity), we lack a comprehensive understanding of how traits affecting individual performance relate to traits affecting EFs. This conceptual disconnect is caused because studies focusing on selection on adaptive traits consider effects on individual performance, whereas studies on plant traits that affect EFs often do not. The evolutionary forces governing either neutral or adaptive diversity could dominate patterns of diversity in traits

affecting EFs (Fig. 3). For instance, evening primrose *Oenothera biennis* genotypes vary in their bolting timing, an adaptive trait that affects fitness (Parker, Salminen & Agrawal 2010). In diverse assemblages, this ‘phenological complementarity’ led to increased resistance to herbivores, an important EF. In contrast, some traits that drive an EF may have less of an impact on fitness (e.g. traits driving decomposition of plant litter may not influence plant fitness, at least not at the same time-scale). In such species where adaptive and EF traits are not correlated, genetic structuring of traits affecting EFs would likely be more similar to patterns of neutral diversity. When sampling plants to accrue diversity for a GD approach in restoration, there is therefore no singular rule about how diversity related to traits affecting EFs would relate to patterns of neutral or adaptive diversity. To improve propagule-sourcing recommendations, we need to discern the spatial distribution of traits driving different EFs so practitioners can collect the diversity required to facilitate restoration goals.

MISMATCHED SPATIAL AND TEMPORAL SCALES

The spatial and temporal scales at which GD-EF research is performed may limit direct application to restoration (Reynolds, McGlathery & Waycott 2012). We found that most studies used plots $\leq 1 \text{ m}^2$ that were monitored for < 2 years (Fig. 4). These findings are not surprising since the rigorous experimental designs of GD-EF studies call for replication of each level of diversity, which makes them logistically challenging, and because this is a relatively recent field of inquiry, so long-term data sets are not yet available. Nonetheless, these spatial and temporal

scales are mismatched with common restoration projects, which can be hundreds if not thousands of square metres in area (a similar scale mismatch exists between BEF research and conservation; Srivastava & Vellend 2005) and should be monitored for multiple years to assess responses over a range of environmental conditions (Blossey 1999; Petrov & Marrs 2000; Palmer 2009). The utility of GD for restoring functioning ecosystems should be empirically tested by manipulating GD in restorations. Synthesis of decades of research on BEF relationships suggests that diversity benefits remain even at large spatial scales and may increase with time (Cardinale *et al.* 2012); similar relationships may occur with GD and a suite of EFs in restorations.

Selecting propagules in realistic restoration scenarios with multiple goals

Unique challenges presented by individual restoration projects require that different combinations of approaches for sourcing propagules be used to achieve diverse, inter-related goals (Ehrenfeld 2000). Yet exactly how to do this remains elusive. There may be redundancy or contradictions among the three propagule-sourcing approaches, which raises some interesting questions.

COMBINING CULTIVAR AND GENETIC DIVERSITY APPROACHES

Combining the cultivar and GD approaches for sourcing propagules (Fig. 2) could be most appropriate where rapid establishment of native vegetation is critical, but the long-term goal remains restoring functioning ecosystems.

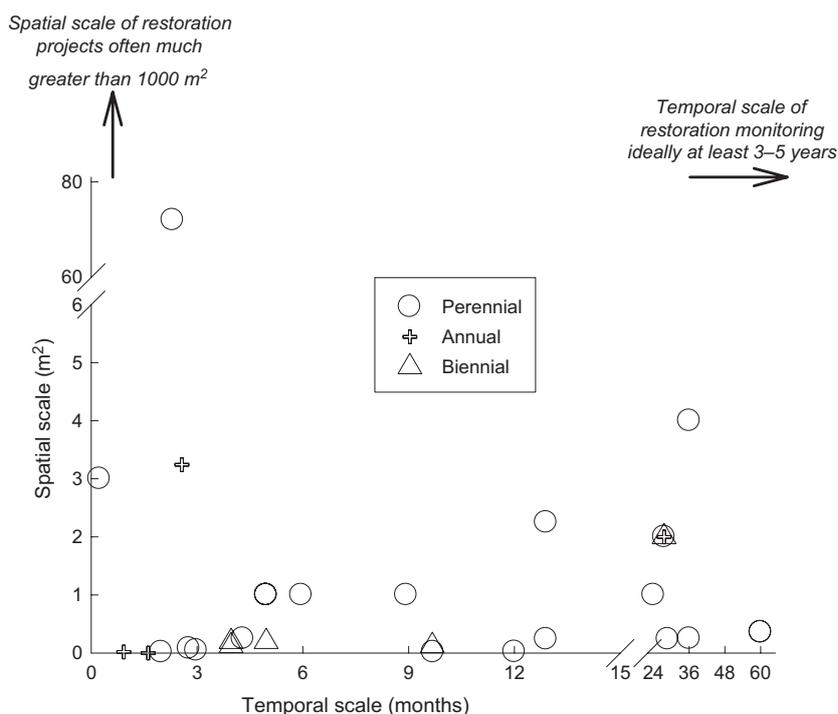


Fig. 4. The scale of genetic diversity–ecosystem function studies (see Table S1, Supporting information) in relation to the temporal and spatial scale at which restorations typically occur. Symbols show life cycles of focal plant species.

This may be the case in highly altered sites in high conservation value ecosystems. Yet, the cultivar approach, which focuses on one or very few genotypes for rapid vegetation establishment, runs contrary to the premise of restoring high GD in a GD approach; there may be long-term consequences of selecting cultivars while neglecting genetic diversity.

Perhaps diversity among cultivars could be used to enhance restoration of functioning ecosystems? Amassing a range of cultivars with particular traits (e.g. early flowering, limited seed dormancy) may increase the functioning of ecosystems unless they still lack key adaptive diversity. The use of less genetically uniform cultivars could be beneficial here. Alternatively, cultivars could be added to a genetically diverse propagule mix, ensuring rapid establishment, while also positively influencing the restoration of a functioning ecosystem (Fig. 2). For instance, cultivars of native grasses quickly revegetate degraded areas around decommissioned oil wells in tundra wetlands, but these cultivars are intensely competitive and inhibit colonization of other plants even after a decade (McKendrick 1997; Streever *et al.* 2003); supplementing the cultivar planting with diverse populations has not been pursued, but could add needed diversity, and thereby assist with restoration of a functioning ecosystem. Either of these combined approaches would be more costly than a pure cultivar approach, and therefore, experimental evidence is required before widespread implementation.

COMBINING THE LOCAL ADAPTATION AND GENETIC DIVERSITY APPROACHES

Combining the local adaptation and GD approaches (Fig. 2) would be most appropriate for goals of long-term persistence of native plants and restoring functioning ecosystems. To combine these two approaches, a practitioner could amass a diverse array of genotypes by sourcing propagules from several areas environmentally similar to the restoration site. Yet, it may be more complicated based on the following three questions.

First, how much diversity exists within and among locally adapted populations? The level of diversity naturally present varies by species (Figs 2 & 3), and amounts of variation can differ across the genome (Slatkin 1987; Storz 2005). A species may have, for instance, high variation within populations at many neutral loci, while having low diversity at the specific loci conferring local adaptation or an EF. Thus, practitioners might obtain genotypes from numerous populations expecting to artificially inflate GD levels and capturing all relevant alleles, but their efforts will be greatly affected by the distribution of diversity across the genome *and* the landscape (Figs 2 & 3).

Secondly, to what degree does local adaptation enhance different EFs? For instance, if a population is locally adapted to saturated soils, it may retain traits that increase relevant EFs, such as capacity for water filtra-

tion, than would a population from dry areas. Some of these traits could be important for their local adaptation – if that EF had an important effect on the plant's fitness – but others may not be. Thus, questions remain about synergistic effects on related EFs of locally adapted propagules.

Thirdly, what is the relative value of locally adapted genotypes vs. genetically diverse genotypes for achieving long-term persistence and restoration of functioning ecosystems? Unfortunately, there is little research to guide this assessment. However, Bischoff, Steinger and Müller-Schärer (2010) found that, for one wildflower species, higher GD and the use of non-local seeds resulted in both increased seed production and height, which could be correlated with primary productivity. Similar studies looking at both persistence traits and EFs in tandem would help illuminate the effects of diversity and locally adapted propagules on such factors.

SUMMARY AND CONCLUSIONS

Here, we have emphasized ecological restoration as a potential application of GD-EF research and have identified novel avenues for future GD-EF studies. In particular, future work should explore: (i) the effect of genotype selection, relatedness and physical arrangement on the restoration of functioning ecosystems, (ii) the relationship of traits that affect an EF to neutral and adaptive diversity, (iii) the extent to which GD-EF relationships remain at larger and longer scales and (iv) whether the integration of approaches for sourcing propagules can help achieve multiple restoration goals. Research to address these questions will simultaneously advance GD-EF theory, while allowing for appropriate application of the GD approach to restoration.

Advancing GD-EF theory is particularly useful to restoration scientists who must justify their recommendations to practitioners with sound science due to the costs of implementing new propagule-sourcing approaches. For example, the identification and propagation of locally adapted propagules from the wild are costly and logistically difficult. The integrated approaches that we highlighted will present further challenges to practitioners, which may be warranted if they lead to successful plant establishment, long-term persistence and restoration of functioning ecosystems.

Acknowledgements

We thank Jared Baker and Rebekah Downard for data collection assistance and Marc Cadotte, Erin Espeland, Michael Kane, Brian Wilsey and Scott McArt for manuscript feedback.

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Received 20 September 2013; accepted 25 November 2013

Handling Editor: Brian Wilsey

Supporting Information

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

Table S1. Methodological details of representative GD-EF studies.