# Ecosystem restoration: Recent advances in theory and practice

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**Review**

# Ecosystem restoration: recent advances in theory and practice

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**Abstract.** Restoration of damaged ecosystems is receiving increasing attention worldwide as awareness increases that humanity must sustain ecosystem structure, functioning, and diversity for its own wellbeing. Restoration will become increasingly important because our planet will sustain an increasingly heavy human footprint as human populations continue to increase. Restoration efforts can improve desirable ecological functioning, even when restoration to a historic standard is not feasible with current practice. Debate as to whether restoration is feasible is coupled to long-standing disputes regarding the definition of restoration, whether more-damaged lands are worthy of restoration efforts given limited financial resources, and ongoing conflicts as to whether the novel ecosystem concept is a help or a hindrance to restoration efforts. A willingness to consider restoration options that have promise, yet would have previously been regarded as 'taboo' based on the precautionary principle, is increasing. Functional restoration is becoming more prominent in the scientific literature, as evidenced by an increased emphasis on functional traits, as opposed to a simple inventory of vascular plant species. Biodiversity continues to be important, but an increasingly expansive array of provenance options that are less stringent than the traditional 'local is best' is now being considered. Increased appreciation for soil health, plant–soil feedbacks, biological crusts, and water quality is evident. In the United States, restoration projects are becoming increasingly motivated by or tied to remediation of major environmental problems or recovery of fauna that are either charismatic, for example, the monarch butterfly, or deliver key ecosystem services, for example, hymenopteran pollinators.

**Additional keywords:** ecosystem functions, natural selection, plant adaptation, plant restoration, seed dispersal, soil ecology.

Received 1 April 2017, accepted 20 July 2017, published online 30 August 2017

## Introduction

Rising human populations are largely responsible for the environmental degradation that ecological restoration seeks to repair (Dietz *et al*. 2003). Although world populations will continue to rise in the near future, birthrates are in decline throughout the world and 70 countries now fall below the replacement fertility rate (Stout 2008). Remarkably, the absolute number of children on Earth is already in decline (Stout 2008). The outcome of this trend is not only that the world's population will age, but also that it will eventually begin to decrease in size (Stout 2008). Thus, a period of increasing human footprint and collateral environmental damage will likely be followed by a quickly deescalating population (Stout 2008). Historically, declining populations are associated with economic decline (Stout 2008). Thus, the discipline of ecological restoration is likely to face its greatest challenges at a time when human capital and economic resources will be inadequate for the scale of the problem. This is a sobering assessment that emphasises the necessity that society must become considerably more effective with limited restoration resources than has been possible in the past.

## Rationales for restoration are varied

Clewell and Aronson (2006) have described five rationales for ecological restoration. These include the idealistic, heuristic, technocratic, biotic, and pragmatic rationales. Jax (2010; ch. 7) discussed three of the above and offered a sixth, the physiognomic rationale. Each rationale offers opportunities, and each may suffer pitfalls.

The *idealistic rationale* values the convergence of nature and human culture. It is motivated by an obligation to atone for society's damage to the environment, a desire to commune with nature on the part of many urbanites, the wish of indigenous peoples to reconnect their culture to nature, and a need for spiritual renewal. A pitfall is that it is difficult to sustain a geographically large effort with a volunteer work force that wishes to pursue restoration at a leisurely pace. The *physiognomic rationale* (Jax 2010) is based on the desire to maintain physical features and dominant life forms, with minimal attention paid to specific species and ecosystem processes. This rationale follows from the tradition of Alexander von Humboldt (1769–1857), the father of plant geography. Its primary drawback is that the approach may be regarded as lacking in detail or dated, particularly as it lacks a

modern scientific foundation. The *heuristic rationale* proposes to deduce ecological principles from experiments embedded in restoration projects. Its pitfalls are that heterogeneous restoration sites do not easily lend themselves to designed experiments and independent variables are often confounded. The *technocratic rationale* is typically directed by a government entity or some other large institution, entails management of public lands, and is administered through a top-down authoritative bureaucracy. One pitfall is that accomplishment is typically measured by orders, contracts, and permits issued rather than actual restoration accomplishments (Clewell and Aronson 2006; Svejcar *et al.* 2017). In addition, the work of large bureaucracies tends to be mediocre and the public is generally less supportive if it is not directly engaged in the restoration effort (Clewell and Aronson 2006). The *biotic rationale* involves the conservation of biodiversity. This is an appealing goal in general, but in practice it presents a steep challenge, as biodiversity conservation crosses several scales, ranging from the genetic diversity coded by DNA sequences to species diversity to biodiversity across landscapes. In contrast, the *pragmatic rationale* is motivated by the restoration of natural capital, i.e. products and services that contribute to human economic wellbeing, and amelioration of climate change. This rationale has the scientific advantage of offering concrete variables and quantifiable responses to treatments. However, its greatest pitfall may be its scientific orientation, which may make it difficult to engage large segments of the general public. Despite the considerable recent attention being given to ecosystem services and climate change, the pragmatic rationale is probably the least well developed of the six rationales in the literature.

All six restoration rationales will continue to contribute to the practice of ecological restoration. However, the scientific community has most heavily invested in the biotic and pragmatic rationales. The commitment of the conservation biology discipline to the biotic rationale has been high, but whether the results justify the large expenditures of effort and finances is increasingly being called into question (Kareiva and Marvier 2012). Nevertheless, changes in orientation away from the biotic rationale in the direction of the pragmatic rationale can be expected to be met with fierce resistance (Caro *et al.* 2012; Miller *et al.* 2014; Murcia *et al.* 2014). However, given current societal emphases on ecosystem goods and services and amelioration of climate change, it is likely that the pragmatic rationale will stimulate the greatest amount of theory development in the near future. Thus, it is likely that the pragmatic rationale will increase in significance over the next 10–20 years. Over the last couple of decades, scientific underpinnings for the restoration of biological entities, on the one hand, and the restoration of ecological functioning and ecosystem services, on the other, have become well developed. Future advances can be expected with the synthesis of new approaches that are able to combine favourable outcomes of the biotic and pragmatic rationales.

## Is restoration feasible?

An ongoing struggle in defining ecological restoration between those who wish to root it to a specific historical mooring and those who seek to apply a broader and perhaps more realistic approach has marked the history of the restoration discipline nearly since its

inception. But over its short history, the definition of ecological restoration has expanded rather than contracted, most notably in 2004 when SERI changed its definition from 'the process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems' (Jackson *et al.* 1995) to 'the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed' (SERI 2004). It should be noted that the 1995 definition, with its emphasis on indigenous ecosystems, corresponds more closely with the biotic rationale, whereas the 2004 definition corresponds more closely with the pragmatic rationale. At the moment, the back-and-forth debate over novel ecosystems (from Hobbs *et al.* 2014*a*; to Murcia *et al.* 2014; to Hobbs *et al.* 2014*b*; and then to Aronson *et al.* 2014) characterises this divergence of opinion over which definition of restoration is most appropriate.

In short, there are many approaches to restoration, and the choice of approach should arguably be based on (1) which is most appropriate given the objectives and (2) which provides the greatest likelihood of success. As is nearly always the case for disciplines of a practical nature, one size does not fit all. Although descriptors such as rehabilitation, recreation, reclamation, and revegetation have value, such projects should not be regarded as subordinate in quality to true restoration projects. After all, among these are the most difficult and messy jobs with some of the greatest potential for net improvement of the environment. Hobbs *et al.* (2011) proposed the term 'intervention ecology' to encompass a multiplicity of approaches, for example, those that are both legitimate and relevant (Miller and Bestelmeyer 2016). Likewise, 'altered' ecosystems should not be automatically equated with degraded land (Hobbs 2016; Miller and Bestelmeyer 2016), though many are.

The novel ecosystem concept has stimulated discussion among scientists, managers, and policymakers, with some feeling that the idea has not been sufficiently scrutinised scientifically (Murcia *et al.* 2014). Specifically, some regard the legitimacy of novel ecosystems as a violation of the precautionary principle and as a policy threat, equating their recognition to a 'get out of jail free' card (Murcia *et al.* 2014; Simberloff and Heins 2014). Simberloff and Heins (2014) argue that restoration is not restricted by the presence of intransigent ecological thresholds that circumscribe novel ecosystems, but rather merely by fiscal resources and political will. In retort, Miller and Bestelmeyer (2016) concluded that 'burying the novel ecosystem concept is no longer an option'.

There is little question that the novel ecosystem issue has led to a certain degree of acrimony, but this is hardly surprising given its context in a discipline that many have considered to be rooted to a historic benchmark. It is interesting that many of the arguments regarding novel ecosystems parallel the earlier debate about local provenance between Wilkinson (2001, 2004*a*) and Sackville Hamilton (2001). Such a paradigm shift as novel ecosystems will likely take time to become generally accepted. However, given the general acceptance of climate change and its undesirable impacts, the general taboo against climate-change denial, plus the expanding presence of invasive species worldwide, it will be increasingly difficult to reject the validity of novel ecosystems as a concept. This is particularly true as novel ecosystems have become commonplace and familiar to many (Perring and Ellis 2013). Due to the increasingly heavy

human footprint, novel ecosystems will certainly not disappear but will rather inevitably increase in extent and degree of novelty over time. Thus, the next generation of restoration scientists and practitioners, having 'grown up' with novel ecosystems, will likely find them not only to be minimally controversial but also to be useful as a construct for understanding how ecosystems function, assemble, and may be restored. For example, nearly 70% of restoration professionals queried already question the relevance of historical baselines given global change (Hagerman and Satterfield 2014). A public sold on the idea of global change is likely to entertain new ideas concerning ecological and evolutionary change. At the same time, the idea of functional analogues has become more prominent in the literature (Jones 2003; Parker *et al*. 2010; Ostertag *et al*. 2015). In a changing world, processes are likely to assume precedence over the more-ephemeral entities, leading us directly back to Wilkinson (2004*a*).

## The use of 'taboo' options in restoration practice is increasing

Currently underway, though incomplete, is a paradigm shift in restoration practice towards greater support for approaches that have been widely considered to be 'taboo' in the past (Hagerman and Satterfield 2014). Driving this paradigm shift are the increasingly important factors of climate change (Minteer and Collins 2010; Sgrò *et al*. 2011; Aitken and Whitlock 2013; Hagerman and Satterfield 2014; Havens *et al*. 2015) and novel ecosystems (Harris *et al*. 2006). In Hagerman and Satterfield's (2014) survey, conservation experts were in near-unanimous agreement with a set of unconventional policy recommendations previously considered taboo, whereas half still responded negatively towards specific interventions that logically corresponded to these policy recommendations. Taboo topics in the survey included assisted migration and triage-based decision-making, i.e. abandoning elements considered to be lost causes. Another example is intentionally establishing novel ecological assemblages that may be better adapted to the changed conditions (Hagerman and Satterfield 2014; Jones *et al*. 2015). Researchers were more likely to respond negatively than practitioners to such interventions in conservation areas, as were women relative to men, but no differences in response were found related to employment group, political perspective, age, or feelings towards intervention in general (Hagerman and Satterfield 2014).

As previously stated, the short history of ecological restoration has been punctuated by a debate between those emphasising preservation and biodiversity apart from human influence and others emphasising ecosystem processes inclusive of human impacts. This debate is as vocal now as it has ever been, particularly as there is growing acceptance that we have moved into a new epoch known as the Anthropocene. This debate is subtly and not-so-subtly shaping current restoration efforts, but these efforts are being directed not just by the debate itself but also by the reality of the world in which we live. As the most vocalised environmental issue of our time is global climate change, this will have the largest impact on how ecological restoration is to be done in the near future.

An approach towards restoration rooted in the economically based concept of ecosystem services has become increasingly prominent in recent decades. Palmer *et al*. (2004) called for the design of 'well-functioning' ecosystems that optimise ecosystem services as part of a future sustainable world. Such purposeful intervention will require management and may admittedly shift attention and funding away from the preservation of historical undisturbed ecosystems (Palmer *et al*. 2004; Wilkinson 2004*b*). This school of thought contends that there are few truly wild places left on the planet, but the net impact of 'domesticated nature' is positive (Kareiva *et al*. 2007). This model acknowledges the importance of the preservation of biodiversity (Kareiva and Marvier 2012), but it encompasses the belief that the separation of humanity from Nature on a planet dominated by humans is an unsustainable course (Kareiva *et al*. 2007). Nonetheless, the argument is made that humans can manage Nature more thoughtfully and wisely than has been done in the past (Kareiva *et al*. 2007). Such an approach embraces the social sciences and humanities and prioritises human welfare, as evidenced by the emphasis on provisioning ecosystem services (Kareiva and Marvier 2012). Conservation is envisioned as being 'for people' instead of 'from people' and views Nature as resilient rather than fragile (Kareiva and Marvier 2012). This model embraces the Anthropocene, promising no return to Eden and anticipating triage (Voosen 2012). It may be regarded as the most viable option, given that the scale of change sustained by the planet may preclude the attainment of goals associated with preservation (Wilkinson 2004*a*). Apparently this view is gaining credence, as the slogan of The Nature Conservancy has been changed from 'saving the last great places on Earth' to 'protecting nature, preserving life' (Voosen 2012). Other non-governmental organisations have followed The Nature Conservancy lead, de-emphasising the preservation argument in favour of a renewed emphasis on ecosystem services (Voosen 2012).

## Functional restoration is emerging as a useful restoration approach

As increasing attention is being paid to ecological functioning and ecosystem services, functional restoration is beginning to assume a more prominent position. Functional restoration may be a viable approach when the restoration objective entails an improved environmental state, for example, improved water quality, reduced weed populations, or increased plant cover. Soil and vegetation data have been used to develop criteria to ascertain whether restoration practice is necessary to restore ecological functioning (Pyke *et al*. 2002), to qualitatively assess ecosystem health at a single point in time (Pyke *et al*. 2002), and to identify which ecological processes have been compromised and should be targeted for renewal (Tongway and Hindley 2004). Identification of species and genotypes that contribute to the restoration of ecological functioning implies quantitative measurement of plant functional traits and environmental variables to address objectives and measure success, respectively. Functional traits are those that impact ecological fitness, i.e. the ability of an organism to survive, reproduce, and persist across generations. Because traits are universal, functional trait analysis has the intuitive appeal of elucidating correlative relationships among traits and suggesting mechanistic explanations for fitness that can be generalised to other species or sites (Clark *et al*. 2012). Plant materials may be selected for use or developed on the basis of trait expression (Jones *et al*. 2010). Traits may be mapped

genetically (Larson *et al.* 2006; Larson and Kellogg 2009) and used to generate seed transfer zones (Johnson *et al.* 2004).

Pywell *et al.* (2003) used a meta-analysis of 25 experiments on species traits to predict restoration performance of 13 grasses and 45 forbs on arable sites in lowland Britain. The relationship between traits and performance was weak for grasses, but for forbs, establishment was linked to colonisation ability, while traits related to competitive ability, vegetative growth, and seed bank persistence became more important over time. To build models to predict restoration species performance and diversity in the Willamette Valley of Oregon, Roberts *et al.* (2010) seeded various mixtures of 28 native species representing three functional groups and measured 11 functional traits in monoculture field plots and a growth chamber. Species establishment in monoculture was the trait most closely related to establishment and cover in mixture. Clark *et al.* (2012) found that a 27-trait model explained nearly as much variation in cover as a species model despite the former's lower complexity. Mitchell *et al.* (2015) evaluated functional traits of Australian grasses, legumes, and shrubs to assess their amenability for pasture production. Larson *et al.* (2015) used path analysis models of traits and key life transitions (germination, emergence, establishment, seedling survival) to identify traits that confer success at these transitions in eastern Oregon. Across 47 grass varieties, they found that germination and emergence were the most critical factors for successful restoration, whereas seed mass and coleoptile tissue density were associated with successful germination and emergence, respectively. Using six seed traits and eight seedling traits, Larson *et al.* (2015) clustered these 47 varieties into six 'functional types' corresponding to general recruitment strategies. Using multivariate-analysis techniques, Ostertag *et al.* (2015) drew functional profiles of species in order to create a hybrid ecosystem in Hawai'i that would meet management goals, as restoration of the native ecosystem was not economically feasible. Laughlin (2014) used trait-based models to choose restoration species to counter Dalmatian toadflax (*Linaria dalmatica* [L.] Mill.), an invasive species in forest understories in the south-western United States. Laughlin *et al.* (2017) developed a model to choose species to meet trait-based restoration objectives based on predicted changes in the climate of mixed conifer forests in the south-western United States. These forests would be no-analogue assemblages of native species that do not currently exist in contemporary landscapes.

Many of the arguments against the functional approach emphasise non-scientific issues of perception or strategy. Caro *et al.* (2012) worried that the idea of the Anthropocene would undermine the legitimacy of conservation and restoration goals. For example, a belief that pervasive human influence is inevitable might generate feelings of hopelessness on the part of practitioners or trigger advantage taking by capitalists. Concomitant with this is the fear that alteration of land use may become normalised, as degradation has already occurred. Finally, if conservation is regarded as futile, funding may be diverted.

## The measurement of adaptation is becoming better grounded statistically

Local adaptation (LA), generally presumed to be frequent and sizable, has been a topic of great interest in the field of restoration. In the first meta-analysis (36 studies with 1032 estimates of LA)

reported on this topic, Leimu and Fischer (2008) opined that LA appears to be less common in plants than generally assumed. In a second meta-analysis (74 studies with 892 estimates of LA), Hereford (2009) reported an average 43% relative fitness advantage for local. Both studies found that 71% of the time, the local population was better than a randomly selected non-local population in one-on-one comparisons. However, the frequency of local superiority, i.e. local is best, would be expected to decline when multiple non-local populations are compared with the local population, as opposed to one-on-one comparisons. Hereford (2009) found that trade-offs among environments were likely too weak to preclude simultaneous adaptation to multiple environments, a necessary condition for the evolution of specialist genotypes. Kawecki and Ebert (2004) explained why LA is not an automatic consequence of evolution. Countering or limiting forces include gene flow, genetic drift, natural selection due to temporal (as opposed to spatial) variation, insufficient genetic variation, and genetic architecture of plant traits. Temporal variation limits natural selection, favouring generalist phenotypes, whereas spatial variation favours natural selection for specialist phenotypes.

Blanquart *et al.* (2013) clarified how LA may be detected and quantified statistically using the sympatric versus allopatric contrast. This contrast compares performance of a pair of genotypes at each of their local sites (sympatric) to performance at the two non-local sites (allopatric). Its calculation requires the inclusion of multiple demes for each population in the experiment to provide replication and an error term to assess the significance of the sympatric versus allopatric contrast effect. Blanquart *et al.* (2013) showed statistically how sympatric versus allopatric contrast is a more powerful and accurate test than other statistical techniques.

Although LA has received considerable attention, general adaptation (GA) has been mostly ignored (Jones 2013*a*). Experimentally, GA corresponds to a main effect for genotype, whereas specific adaptation (SA) is the deviation of a specific genotype in a specific environment after genotype and environment main effects have been fitted. Then LA may be thought of as the special case of SA for a local population. Assessment of GA effects for plant populations may be very useful in selecting populations for widespread restoration applications. Next-generation DNA sequencing technology may potentially lead to a more advanced understanding of adaptation due to the volumes of data it can generate at low cost (Williams *et al.* 2014). It may prove useful for elucidating how GA and SA are genetically controlled.

In theory, cross-pollinating species may respond most rapidly to natural selection for LA due to their high degree of genetic recombination. However, unlike in the temperate northern hemisphere, most Australian grasses lack self-incompatibility mechanisms that enforce outcrossing, suggesting that they are less likely to display LA (Whalley *et al.* 2013). Whalley *et al.* (2013) proposed that native grass taxa that can both cross- and self-pollinate may possess an evolutionary advantage. In such taxa, cross-pollination allows production of a diversity of genotypes upon which natural selection may operate, and self-pollination allows rapid replication of selected (locally adapted) genotypes. Cross-pollination also promotes evolutionary resilience to changing environmental conditions.

## A new emphasis on evolutionary processes has broadened choices for plant provenance

Although ecological processes have been central to restoration practice since its beginning, evolutionary processes are just beginning to have a significant impact on thinking concerning how restoration efforts may be most effective (Sgrò *et al*. 2011). The 'local is best' paradigm of plant provenance is now frequently questioned (e.g. Broadhurst *et al*. 2008; Sgrò *et al*. 2011; Weeks *et al*. 2011; Havens *et al*. 2015), and it is better regarded as a testable hypothesis than as unquestioned dogma (Jones 2013*b*). Numerous studies of Australian native grasses have found that local superiority is equivocal, and performance is better predicted by the similarity of the provenance and test sites for environmental variables and historical selection pressures than by geographical proximity (Whalley *et al*. 2013).

Many evolutionary biologists recommend genetically diverse sources of seed that provide raw material upon which natural selection can act (Broadhurst *et al*. 2008; Weeks *et al*. 2011). Such seed sources may provide ecological and genetic novelty (Weeks *et al*. 2011) through hybridisation (Hoffmann and Sgrò 2011), and they may enhance evolutionary resilience (Sgrò *et al*. 2011) when ecological and environmental change are the norm (Sgrò *et al*. 2011). Plant materials of diverse geographic origin developed specifically for greater genetic diversity have promise (Larson *et al*. 2000; Jones 2003), but they may be slow to gain acceptance, as they are 'not local anywhere'.

'Assisted evolution' may be applied by implementing plant materials that (1) reflect general historical evolutionary patterns, (2) display adaptation to the modified environment, (3) adapt to contemporary selection pressures, and (4) contribute to the recovery of ecosystem structure and function (Jones and Monaco 2009). Such an approach may combine alleles that are desirable locally with alleles that are favourable in a more general set of environments, including those that have been modified. By enhancing stress tolerance through the acceleration of natural processes, van Oppen *et al*. (2015) proposed assisted evolution as an approach to facilitate coral reef recovery. van Oppen *et al*. (2015) have proposed a biological tool box that would include the induction of acclimatisation, genetic modification of microbial symbionts for stress tolerance, selective breeding, and experimental evolution of algal symbionts.

Evolution has often been thought of as a slow process, but it may be rapid and ongoing (Sgrò *et al*. 2011). Contemporary evolution, that which occurs over short time frames and often as a consequence of anthropogenic change (Stockwell *et al*. 2003), can lead to the construction of novel ecologically adapted genotypes (Kinnison *et al*. 2007). This may be the best way to preserve a genetic future for threatened species, but it necessarily entails high mortality due to natural selection (Hoffmann and Sgrò 2011).

We note 26 species/provenance selection approaches that are either currently practiced or have at least been proposed in the literature, ranging from geographically local populations to synthetic biology (Table 1). As suggested by this large number, viewpoints on these issues encompass a broad spectrum of thought. The 26 approaches encompass four levels of intrusion that correspond to the four restoration gene pools described by Jones (2003) and Jones and Monaco (2007). Of the 26 approaches, eight involve no selection, seven involve selection

among species, six involve selection among populations, and five involve selection within populations. The assisted evolution paradigm (Jones and Monaco 2009; van Oppen *et al*. 2015) encompasses 13 of the 26 approaches.

In criticising the long-term introduction of plants to Ascension Island in the South Atlantic, Gray (2004) asserted that genotypes must not only be adapted but also possess evolutionary potential. In this vein, he asserted that local genotypes are preferable due to their purported fitness resulting from local selection pressures. Yet, at the same time exotics are suspect because they may be too fit, becoming invasive and either displacing or hybridising with local genotypes, which may lead to outbreeding depression (Gray 2004). Thus, the argument for local may vacillate between 'local is strong' and 'local is weak.' Does preference for local really depend on adaptation or evolutionary potential? Or is the choice of 'local' affirmed simply because it is local, i.e. the genetic identity argument? Hagerman and Satterfield (2014) discussed how ancillary arguments are commonly used to justify a predetermined and preferred choice. Although the genetic identity argument is perfectly legitimate, it should be acknowledged that preservation of genetic identity is preferred, at least in part, because it fulfills a predetermined restoration objective.

The move away from strictly local plant materials is gaining traction because (1) plant material collected from fragmented populations may be depauperate in genetic diversity (Broadhurst *et al*. 2008), (2) concerns surrounding the issue of outbreeding depression (Hufford and Mazer 2003) have been largely allayed (Frankham *et al*. 2011), (3) a consensus has been reached that climate change is occurring, (4) novel ecosystems are becoming widely recognised, and (5) data do not support the assumption of a fitness trade-off among local and non-local sites (Hereford 2009; Sgrò *et al*. 2011). Thus, many scientists have come to believe that there may be justifiable reasons for the relaxation of the precautionary principle for plant provenance (Broadhurst *et al*. 2008; Havens *et al*. 2015). Taking a preservationist approach to genotypes under changing conditions can be self-defeating (Lankau *et al*. 2011; Havens *et al*. 2015) by working against natural selection instead of working with it. Strategic mixing of populations has been recognised as both practical and cost-effective (Jones 2003; Weeks *et al*. 2011; Whalley *et al*. 2013), and the development and use of 'pre-adapted' seeds for novel future environments has been suggested (Lankau *et al*. 2011; Sgrò *et al*. 2011; Jones 2013*a*; Jones *et al*. 2015). When local is not best (Jones 2013*b*; Whalley *et al*. 2013), justification of local genotypes based on the precautionary principle of restoration may be seen as a misapplication of that principle (Whalley *et al*. 2013).

Despite the genetic disadvantages of local plant materials, they will continue to have an intangible appeal to segments of society, even when they are not 'best,' simply because they are local (Rossi 2013; ch. 1) and hence curtail ecologic homogenisation (Wood *et al*. 2015). Although research may deliver more-effective plant materials for use by restoration practitioners, any ecological, genetic, and economic advantages they may provide will need to be weighed against the appeal of 'local' on a case-by-case basis. Despite local's intrinsic appeal, the array of approaches to selection of species, provenance, or selection within provenance has greatly expanded in recent years

**Table 1.    Twenty-six strategies to population or species selection for ecological restoration listed from non-intrusive to most-intrusive**

| | Strategies | Selection[A] | RGP[B] | AE[C] | References |
|---|---|---|---|---|---|
| | *Non-intrusive strategies* | | | | |
| 1. | Selection of 'native winner' species | AS | n/a | – | Barak *et al.* (2015) |
| 2. | Species selection based on functional traits | AS | n/a | – | Pywell *et al.* (2003), Funk *et al.* (2008), Laughlin (2014), Mitchell *et al.* (2015), Ostertag *et al.* (2015) |
| 3. | Geographically local population | NS | 1°A | – | Namkoong (1969), Joshi *et al.* (2001), Sackville Hamilton (2001), Hancock *et al.* (2013) |
| 4. | Seed transfer zones | NS | 1°B | – | Rehfeldt (1989, 1994), Westfall (1992), Johnson *et al.* (2004), St. Clair *et al.* (2013) |
| 5. | Focal point seed zones | NS | 1°B | – | Parker (1992), Ukrainetz *et al.* (2011) |
| 6. | Plant adaptation regions/provisional seed zones | NS | 1°B | – | Vogel *et al.* (2005), Bower *et al.* (2014) |
| 7. | Climate similarity analysis | NS | 1°B | – | Doherty *et al.* (2017) |
| 8. | Composite provenancing | NS | 1°B | x | Broadhurst *et al.* (2008) |
| 9. | Ecologically similar provenance | NS | 1°B | x | Raabová *et al.* (2007), Vander Mijnsbrugge *et al.* (2010) |
| 10. | prescriptive gene flow | NS | 1°B | x | Sexton *et al.* (2011) |
| 11. | Trait selection within a local or similar population (either #3, 4, 5, 6, 8, or 9) | WP | 1°C | x | Atwater *et al.* (2015), Ferguson *et al.* (2015) |
| | *Less-intrusive strategies* | | | | |
| 12. | Trait selection among populations | AP | 2°A | x | Kitchen and Monsen (1994); Asay *et al.* (2003) |
| 13. | Predictive provenancing | AP | 2°A | x | Crowe and Parker (2008), Wang *et al.* (2010), Sgrò *et al.* (2011) [cited by Prober *et al.* (2015)] |
| 14. | Climate-adjusted provenancing | AP | 2°B | x | Prober *et al.* (2015) |
| 15. | Admixture provenancing/assisted gene flow | AP | 2°B | x | Breed *et al.* (2013), Aitken and Whitlock (2013), Zavodna *et al.* (2015) |
| 16. | Assisted migration | AP | 2°B | x | Minteer and Collins (2010), Vitt *et al.* (2010) |
| 17. | Selection of remnant plants post-disturbance | WP | 2°C | x | Leger (2008), Ferrero-Serrano *et al.* (2011), Goergen *et al.* (2011), Rowe and Leger (2011), Bergum *et al.* (2012) |
| 18. | Trait selection within a non-local population | WP | 2°C | x | Jones (2009), Jones *et al.* (2010), Chivers *et al.* (2016) |
| 19. | Genomic selection | WP | 2°C | x | Heffner *et al.* (2009) |
| 20. | Genetic rescue | AP | 2°C | x | Frankham (2015), Waller (2015) |
| 21. | Genome editing | WP | 2°C | – | Jones (2015), Ledford (2015) |
| | *More-intrusive strategies* | | | | |
| 22. | Interspecific hybridisation among native species | AS | 3° | x | Larson *et al.* (2006), Frascaria-Lacoste *et al.* (2011) |
| 23. | Genetically modified (transgenic) organisms | AS | 3° | – | Wolfenbarger and Phifer (2000) |
| | *Most-intrusive strategies* | | | | |
| 24. | Restoration with allopatric native species | AS | 4°A | – | Butterfield *et al.* (2016), Laughlin *et al.* (2017) |
| 25. | Introduced species | AS | 4°B | – | Robertson *et al.* (1966), Hull (1974), Goodenough (2010), Davis *et al.* (2011), Blank *et al.* (2015), Davies *et al.* (2015), Friday *et al.* (2015) |
| 26. | Synthetic biology (creation or resurrection of species) | AS | 4°B | – | Tucker and Zilinskas (2006), Stanturf *et al.* (2014) |

[A]Selection among species (AS), no selection (NS), selection among populations (AP), selection within populations (WP).
[B]Restoration gene pool as defined by Jones and Monaco (2007).
[C]Assisted evolution (Jones and Monaco 2009; van Oppen *et al.* 2015) strategies indicated by 'x'.

(Table 1). This suggests that the potential for future progress in developing more-effective plant materials is bright. Consequently, the number, diversity, and quality of native plant materials that may be available to restoration practitioners are likely to continue an upward trajectory.

## The use of 'islands' has become a viable approach when resources for restoration are scarce

When the availability of restoration seeds is limited by either supply or price, such that it is infeasible to seed large areas, implementation of restoration 'islands' may be an attractive option for the practitioner. Islands may also be useful for ecological reasons, for example, to provide a patchy (heterogeneous) distribution that confers desired ecosystem functioning or to stimulate the nucleation process of succession by facilitating colonisation by later-successional species (Holl *et al.* 2011). Native grass islands in Australia boosted native seed banks outside the perimeter of the islands (Bean *et al.* 2016). Planting tree islands in old pasture in Costa Rica was more attractive from cost and labour standpoints than traditional plantation-style plantings (Cole *et al.* 2010). Cole *et al.* (2010) measured seed rain on trees from ~2–3.5 years of age. Islands received fewer zoochorous seeds than plantation plantings, but the difference was not significant. However, islands received about three times the number of tree seeds as control (natural recovery) plots where no trees had been planted. However, no evidence was found for dispersal of tree or shrub seed beyond

the islands' edges. Zoochorous tree and shrub seeds were dispersed preferentially to large ($144\,m^2$) or medium-sized ($64\,m^2$) islands, as opposed to small ($16\,m^2$) islands or areas distant from island edges, suggesting that island size may be important.

Islands may be generated inadvertently by wildfire skips of vegetation (Longland and Bateman 2002). These authors suggest that big sagebrush (*Artemisia tridentata*) islands in the semiarid western United States may possess ecological benefits by serving as refugia for shrub-associated plant and animal species. This would be particularly important for sagebrush-obligate species, such as greater sage-grouse (*Centrocercus urophasianus*) and pygmy rabbit (*Brachylagus idahoensis*). Islands may provide habitat or serve as sources for seed dispersal, thus accelerating post-fire recovery. By providing refugia for rodents, sagebrush islands may benefit prey species. Islands might be intentionally generated at low cost using prescribed fire methodology or via fire-fighting efforts.

### Soil-mediated legacy effects will be useful for delineating realistic restoration goals

Soils and the organisms that occupy them will receive greater attention in restoration than in the past because they have often been compromised by degradation, yet they are emerging as keys to understanding and furthering the advance of secondary succession and resultant ecosystem recovery. Soil legacies, the result of ongoing effects that emanate from historical events or management practices that have disrupted soils, may persist indefinitely and impact nutrient cycling, plant growth, and ecosystem recovery (Foster *et al*. 2003). Activities that induce legacies may include forestry, agriculture, modification of natural disturbance regimes, for example, fire, and manipulation of animal populations (Foster *et al*. 2003). For example, tillage homogenises topsoil up to a 30-cm depth, leaving a uniform $A_p$ horizon that may persist for hundreds of years (Foster *et al*. 2003). Across the southern United States, abandoned cotton fields were replaced with secondary pine forests where old-growth hardwoods had originally dominated. The soils of the pine replacement forests have only 64% of the nitrogen and 59% of the carbon as remaining old-growth hardwood forest (Foster *et al*. 2003).

In the semiarid western United States, passage of the Enlarged Homestead Act of 1909 encouraged dry farming, the practice of cropping of land without irrigation water (Morris and Rowe 2014). Dry farming was successful at first during a sequence of wet years accompanied by government-subsidised wheat prices during World War I, but homesteads began to be abandoned within a decade following the war due to lower wheat prices, drought, and general unsuitability of the land for cultivation (Morris 2011). Nevertheless, due to legacy effects, the impact of dry farming on current vegetation can still be seen in aerial photos (Morris *et al*. 2011). Even after 90 years, native vegetation has not recovered from cultivation, as compared with adjacent never-cultivated lands. Additional major impacts were conferred by fencing and building of homesteads, logging, cultivation, mining, forage seedings, water diversions, altered fire regimes, introduction of invasive species, unregulated livestock grazing, and animal trapping, hunting, and control (Morris and Rowe 2014). The effects of unregulated livestock grazing before passage of the Taylor Grazing Act of 1934 have been described as 'unprecedented, swift, and devastating' (Morris and Rowe 2014). The cumulative effects of all these impacts have had a dramatic impact on the land's response to restoration treatments, including native-plant and invasive-species growth (Morris *et al*. 2013).

In Australia, Gibson-Roy *et al*. (2010) used a 'scalping' treatment to treat former agricultural sites in order to facilitate seedings of herbaceous native species. Removal of 100 mm of surface soil by scalping reduced exotic weed seed banks and lowered excessively high phosphorus levels induced by historical applications of superphosphate. Scalped areas showed dramatically greater densities of desirable sown native species and dramatically lower densities of undesirable non-sown exotic species. These areas were able to be used as seed-production areas to provide seeds for additional restoration projects.

### Plant–soil feedbacks are now being recognised for their critical role in directing secondary succession

Plant–soil feedbacks (PSF) are plant-induced changes in their soils that impact subsequent plant growth. The primary action of PSF is now believed to be via soil organisms, such as pathogens, nematodes, and mycorrhizae, rather than by soil nutrient levels (Kardol *et al*. 2006, 2007). These feedbacks are believed to provide a mechanistic explanation for ecological processes such as secondary succession and plant invasion (Kardol *et al*. 2007; Kulmatiski *et al*. 2008). Negative PSF inhibit growth of the test species, whereas positive PSF stimulate its growth, possibly leading to a monoculture (Kardol *et al*. 2007). Plant–soil feedbacks can be measured experimentally in a two-stage experiment, where soil exposed to the test species in the first stage is used to assay its growth in the second stage (Kardol *et al*. 2007). Research has shown that PSF are commonly but not exclusively negative (Kardol *et al*. 2007), but their magnitude may vary widely. For example, PSF of grasses and forbs are more negative than those of woody plants, annuals are more negative than perennials, early-seral species are more negative than late-seral species, and monocultures are more negative than species mixtures (Kulmatiski *et al*. 2008). A negative PSF of an early-successional species may contribute to its replacement by a later-successional species that displays a less-negative PSF (Middleton and Bever 2012). Furthermore, PSF become less negative as succession proceeds (Kardol *et al*. 2006), and their effect may be long lasting, thereby maintaining late-successional status (Kardol *et al*. 2007). Thus, PSF may be considered soil-legacy effects.

Armed with the theoretical knowledge that PSF may direct succession, scientists have conducted experiments to determine if and how the process of secondary succession may be manipulated to help achieve restoration goals. This is of particular interest because response to restoration treatments may hinge on the ability of a degraded soil to recover (Middleton and Bever 2012). Creating 'islands' using soil inoculant may be an effective restoration technique, as the restoration of a plant community may hinge on a restored soil-microbial community. Early-successional species were inhibited on former agricultural land in Indiana, USA inoculated with soil taken from a remnant grassland (9% by volume), whereas mid- and late-successional tallgrass prairie species were stimulated (Middleton and Bever 2012).

The inoculant's effect was found to extend from a distance of 0.25–2.0 m over the course of this 4-year study in support of the 'nucleation model' of succession. This suggests that soil microbes can disperse via small quantities of inoculant, making soil inoculation a potentially feasible restoration practice. The effectiveness of inoculum may be greater when applied at an early successional stage (Middleton and Bever 2012).

In a 6-year experiment, Dutch researchers successfully steered plant communities on previously cultivated soil towards contrasting targets, i.e. grasslands or heathlands, by using soils obtained from grassland and heathland communities, respectively (Wubs *et al.* 2016). Soils were planted with a mixture of 10 early-, 10 mid-, and 10 late-successional species, and their response over time was evaluated. Inoculants did not impact early- or mid-successional species, but late-successional species were favoured. Compared with inoculation, greater effectiveness was achieved by complete removal of topsoil and replacement with the target soil, thereby avoiding legacies from the cultivated soil. In the United States, efforts are underway to characterise the soil biota of never-tilled tallgrass prairie-remnant soils. These soils have been found to be dominated by Verrucomicrobia, a phylum of bacteria that is associated with carbon rather than nitrogen metabolism and that declines in the presence of nitrogen fertiliser (Fierer *et al.* 2013). A better understanding of the biota of late-seral soils may lead to practices that enhance restoration success.

## Biological soil crusts are extending the pallet of plants for restoration beyond vascular species

Biological soil crusts (also known as microphytic or cryptogamic crusts) may serve as ecosystem engineers in ecosystems subject to high abiotic stress (Young *et al.* 2016). These crusts are non-vascular communities of cyanobacteria, lichens, algae, mosses, and heterotrophs (Young *et al.* 2016) that are critical structural and functional ecosystem components (Bowker 2007). They require high light at the soil surface, thus they are particularly important on aridlands, though they may exist ephemerally in wetter climates. Biological soil crusts enhance soil quality by aggregating soil particles, reducing runoff, and fixing nitrogen and carbon, and they are useful as an indicator of soil health. Biological soil crusts are subject to damage by hoofed animals. Field-scale restoration of these crusts is now an active research area (Bowker *et al.* 2016). Biological soil crust organisms are being greenhouse-reared for transplantation to field sites where they have been lost due to past disturbance (Bowker *et al.* 2016).

## Two examples from North America

Major restoration efforts continue to be connected to dramatic environmental-damage events, disruptions of important ecosystem services, and declines in charismatic animal species. I offer examples from North America for the latter two categories that have parallels throughout the world.

### (i) The annual North American migration of monarch butterflies is an iconic behaviour worthy of preservation

The monarch butterfly (*Danaus plexippus*) is a charismatic species that has been listed as a species of special concern in Canada since 2003, but it has no special status at the federal level in the United States. The eastern migratory population of the monarch butterfly is the largest in the world (Vidal and Rendón-Salinas 2014). This population enters reproductive diapause in the fall and overwinters in Mexico at a cluster of locations discovered in 1975 and declared a reserve in 2000. In the spring, monarch adults begin to migrate northward towards the mid-western and eastern United States, reproducing through the remainder of the breeding season before returning to Mexico. Monarch numbers in Mexico peaked in 1996 and then posted a steady decline totalling 90% from 2006 to 2013. Adult monarchs are floral nectar generalists, but their larvae are obligate feeders on milkweed (*Asclepias* spp.) (Dumroese *et al.* 2016). Common milkweed (*A. syriaca* L.) is the most important of 75 native milkweed species. Three hypotheses have been advanced to explain monarch decline – loss of overwintering habitat in Mexico due to illegal logging, loss of breeding habitat in the United States and Canada, and occasional extreme weather events (Brower *et al.* 2012; Flockhart *et al.* 2015).

Pleasants and Oberhauser (2013) estimated annual monarch egg production in the mid-western United States from 1999 to 2010 and correlated it with population estimates for the previous and subsequent overwintering population in Mexico. Annual egg production in the United States Midwest was uncorrelated with the previous winter's population size in Mexico, indicating that breeding season weather conditions in the Midwest are more important than initial population size in Mexico for determining the size of the year's breeding population. However, annual egg production in the Midwest was positively correlated with the following winter's population size in Mexico. Unfortunately, egg production in the Midwest dramatically declined from 1999 to 2010 because milkweed declined by 31% for non-agricultural land and 81% for agricultural land. Because agricultural milkweed produces 3.89 times the number of eggs as non-agricultural milkweed, the overall estimated decline in egg production in the Midwest between 1999 and 2010 was 72%.

This decline in egg production, particularly that on agricultural land, is a consequence of the rapid adoption of glyphosate-resistant maize and soybean varieties in the United States Corn Belt starting in the late 1990s (Pleasants and Oberhauser 2013; Flockhart *et al.* 2015). Herbicides used previously in these agricultural fields were not particularly effective on milkweed, whereas glyphosate is quite effective, thus the dramatic decline of milkweed and monarch egg production in agricultural fields in the Midwest (Pleasants and Oberhauser 2013). Prior to 1999, maize and soybean fields produced monarchs at a rate similar to other habitats (Oberhauser *et al.* 2001). Consequently, monarch decline in the Midwest has been blamed on industrial agriculture (Flockhart *et al.* 2015), with the virtual disappearance of milkweeds in agricultural fields being termed 'inevitable' (Pleasants and Oberhauser 2013). In the eastern United States, where maize and soybeans are less prominent crops, the monarch decline has been less conspicuous.

An earlier debate surrounding genetically engineered crops involved *Bt* maize hybrids resistant to European corn borer (*Ostrinia nubilalis*) (Losey *et al.* 1999; Gatehouse *et al.* 2002). The initial report (Losey *et al.* 1999) claimed that survival of monarch larvae is compromised by the consumption of *Bt* maize pollen present on milkweed leaves. However, monarch populations were found not to decline in response to high rates of adoption of

insect-resistant *Bt* maize hybrids (Gatehouse *et al*. 2002). These researchers questioned the validity of the experimental procedure of Losey *et al*. (1999).

Recommendations for restoration of the monarch butterfly are to protect and restore habitat for foraging, breeding, and migration; to utilise integrated pest management to reduce insecticide use; to provide tools and guidelines to inform conservation efforts; and to propagate seed stocks of milkweed species for restoration use (Vidal and Rendón-Salinas 2014). Because the monarch flyways extend from Mexico to Canada through the United States, all three countries need to be involved in protection of monarch habitat (Vidal and Rendón-Salinas 2014). In the United States, monarch habitat continues to be lost due to increased demand for biofuels, which leads to conversion of Conservation Reserve Program land to glyphosate-resistant maize production (Brower *et al*. 2012). In 2010 mid-western roadsides accounted for 20% of all milkweeds in the region, and they may become increasingly important as monarch habitat if managed for that purpose (Pleasants and Oberhauser 2013). Monarch conservation may be furthered by providing a broad phenological array of *Asclepias* species in restoration efforts (Dumroese *et al*. 2016). The Xerces Society for Invertebrate Conservation (2017) has compiled a series of 15 regional nectar plant lists from a database of nearly 24 000 monarch nectaring observations.

### (ii) Maintaining healthy populations of native pollinators is necessary to maintain pollination of native plant species as an ecosystem service

Abundant evidence now points to a decline in native and domesticated pollinators and the native plants they pollinate (Potts *et al*. 2010). In a central Illinois, USA forest understory community, forb and pollinator populations and their interactions have changed dramatically over a 120-year period (Burkle *et al*. 2013). Though no forbs were lost, 50% of bee species have been extirpated, all since 1971. Only 24% of the original forb-pollinator interactions remained intact, with a net interaction loss of 46%. Of 4067 lost interactions, 45% were due to bee extirpations. Specialist bees were lost to a greater extent than generalists, thus the quantity and quality of pollination services declined more than actual species loss. Phenological and spatial shifts of forbs and bees negatively impacted several interactions. Degradation of network structure and function likely equates to reduced resilience to future environmental change.

Rather than due to a single cause (Naug 2009; Potts *et al*. 2010), pollinators' decline is due to multiple anthropogenic stresses, such as diseases, parasites, insecticides, intensive land use, habitat loss, climate change, and spread of invasive plants (Vanbergen *et al*. 2013). Multiple drivers may interact synergistically, as the sublethal effects of one driver may increase the lethality of others, for example, overwinter mortality (Potts *et al*. 2010). Climate change can cause differential migration and phenological mismatches between bee and plant species (Vanbergen *et al*. 2013). Non-native plants may compete with native plants for native pollinators. Managed pollinators can compete with native pollinators or compromise them by spreading pests and disease. Species richness and abundance of native bees declines with distance from wild habitat (Potts *et al*.

2010), and honeybee colony loss and low honey production are associated with low prevalence of wildlands across the United States (Naug 2009). It is believed that energetically stressed honeybees may require more foraging, yet lack the ability to find or return to the hive. This hypothesis would explain the lack of dead bees in the vicinity of abandoned hives that is a characteristic of colony collapse disorder (Naug 2009).

Over 400 species of bees are estimated to occur in the United States (Konkel 2016), most of which are solitary and ground-nesting (Ogle *et al*. 2011). Better habitat with greater plant diversity attracts pollinators, and an array of species that collectively flower sequentially from spring to fall provides nutrition that sustains and increases bee populations throughout the year (Konkel 2016). For example, seeding islands of diverse species including green rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G. L. Nesom & Baird), which blooms in the fall when few other plant species are blooming, can support restoration goals for native pollinators and native plants (Dumroese *et al*. 2016). Pollinator decline led United States President Obama (2014) to charge a newly organised Pollinator Health Task Force with development of a strategy for increasing native vegetation through affordable 'pollinator-friendly' seed mixes. Native plant species that attract a greater number and diversity of bees may be considered pollinator-friendly, and restoration seed mixes should contain one or more of such species (Cane and Love 2016).

Kleijn *et al*. (2015) cautioned that the ecosystem services argument is inadequate for conservation of native pollinators. This is because most of the economic impact of pollinators is generated by a few common species that can be otherwise enhanced through simple management techniques. Therefore, a clear moral argument based on biodiversity is needed to justify the preservation of threatened pollinator populations.

### Conclusion

As human populations have increased, environmental degradation has become both more extensive and intensive. Reversion to 'pristine' conditions is often not feasible. A dramatic increase in the diversity of restoration challenges is increasing the scope of what is considered to be restoration, thereby expanding its definition. Restoration projects increasingly address connections among floral, edaphic, and faunal communities, as well as among biotic and abiotic components of the ecosystem. The ecological orientation of restoration, with its emphasis on secondary succession, is increasingly being interfaced with the disciplines of physiology, genetics, and evolution. Thus, restoration is poised to become a truly integrated and collaborative field.

### Conflicts of Interest

The author declares no conflicts of interest.

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