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Restoration demography and genetics of plants: when is a translocation successful?

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Abstract. Restorations are complex, often involving restoring ecological processes, vegetation structure, and species' populations. One component of restorations is translocation of key species. Translocations (introductions, reintroductions, augmentations) are often necessary to recover species diversity and install key species. In this review, I consider the ways translocations have been evaluated at various stages during the process of restoration. Vital rates (survival, growth, fecundity) of propagules (seeds, transplants) are commonly used to evaluate initial success. Transplants usually provide greater initial success than do sown seeds. Beyond initial rates, completion of the life cycle through flowering, fruiting, dispersal and subsequent seedling recruitment is a key benchmark. Modelling population viability of translocated populations is a logical next step and can bring in many powerful inferential tools. Of factors affecting the success of translocations, genetic issues are paramount, as restorationists need to consider inbreeding depression, reproductive viability, local adaptation, and evolutionary potential of translocated populations. The success of translocations is also clearly context-dependent, with herbivory, disturbance, competition and other ecological factors important. Future translocations need to make better use of comparisons with reference populations, a long-term perspective on success and an experimental framework that can provide both practical and basic knowledge. Demographic data collection and analysis in restorations has great potential to elucidate causes of translocation failure and improve the prognosis of future restorations.

Introduction

In the sentimental baseball movie 'Field of Dreams', the character played by Kevin Costner is encouraged by God (voice-typecast by James Earl Jones) to 'Build It and He Will Come'. So, Costner 'Builds It', it being a baseball stadium in the middle of a cornfield, hoping 'He' (deceased baseball legend Shoeless Joe Jackson) will appear for a game. In a Hollywood miracle, Jackson and his teammates materialise from the surrounding cornfields. Jackson later asks Costner if he is in heaven; Costner replies, no, it's Iowa.

Restoration is a broad process that may include re-establishing natural disturbance regimes, ecological gradients and vegetation structure. Restorationists often wish that by restoring ecosystem structure and function (Building It) most species will return. In Iowa, creating a heavenly restoration could be done by providing periodic summer fire and grazing to a prairie that was over-dominated by C4 grasses (Howe 1994). Or, prairie restorations might require more intensive measures such as restoring hydrology (Galatowitsch and van der Valk 1996), herbiciding exotic species (Masters *et al*. 1996), adding dominant species (Martin *et al*. 2005) or adding seeds and plants of nitrogen-fixing species (Kindscher and Tieszen 1998).

Sometimes, if you build it, they will come. For sites that are only moderately degraded, on-site species populations may expand with ecosystem restoration. Passive revegetation approaches to restoration rely on recruitment from seed banks and seed dispersal to allow ecosystems to self-design in response to the restoration of a suitable disturbance regime (e.g. hydrologic restoration; DeSteven *et al*. 2006). For example, experimentally manipulated fire, irrigation and soil disturbance interacted differentially to release the seed bank in the groundcover of longleaf pine sandhills (Cox *et al*. 2004). Recovery from seed banks will vary among ecosystems and be affected by conditions during restoration. For instance, hydrologic restoration and overstorey cutting led to substantial recruitment of herbaceous wetland species from a seed bank. However, the extent of undesirable woody plant competition varied over time, being negatively affected by periodic drought (DeSteven *et al*. 2006). The ability of certain species to form long-term persistent seed banks can provide dramatic population recovery (e.g. after fires) if seed banks have not been depleted (Menges and Quintana-Ascencio 2004). Restoration efforts that depend on seed dispersal are more successful when there is good connectivity between restoration sites and sites serving as seed sources (Muller *et al*. 1998).

However, direct addition of propagules often needs to be one component of a restoration. The success of the population spawned or encouraged by these additions is a component of the success of the restoration as a whole. Translocation is the deliberate release of organisms into the wild for the purpose of establishing a new population (introduction), re-establishing an extirpated population (reintroduction), or augmenting a critically small population (modified from Wolf *et al*. 1996; this definition of translocation is similar to the general definition of reintroduction used by some authors, e.g. Guerrant and Kaye

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2007). The primary goal of augmentations is to increase local population size, whereas introductions and reintroductions serve to increase the number of populations and perhaps enhance favourable metapopulation dynamics. The ultimate goal of these activities is establishing viable, self-sustaining populations (Griffith *et al*. 1989; Maunder 1992; Gordon 1996). Although there are many ways to evaluate demographic success (Pavlik 1996), a focus on whether populations are viable will require many years of data and/or projections based on data-hungry demographic models (Menges 2000). Nonetheless, initial stages of success such as seedling recruitment, plant growth and plant reproduction are reasonable milestones (Guerrant and Pavlik 2007).

In the present review, I consider the ways in which ecologists and restoration biologists have evaluated translocations, ranging from simple and short-term to more complex and long-term. I also consider factors that contribute to translocation success, including the type of propagules, translocation strategy, breeding systems, local adaptation, genetic variation, and interactions of translocated plants with herbivores, disturbances, and other ecological factors. Finally, I outline potential new approaches to evaluating translocations and learning from them. I draw most of my examples from the recent literature on restorations.

Defining translocation success

Vital rates of propagules: assessing the initial fate of translocations

Perhaps the most intuitive approach to assessing translocation success is to ask what happened to the seeds or plants that were brought to the site. Did they survive? Did they grow? How many seeds did they produce? These are essentially questions about the vital rates of the translocated population. A successful new population should be able to carry on basic life-cycle processes such as establishment, reproduction and dispersal (Pavlik 1996). The tools to analyse individual success are the tools of descriptive demography.

What happens to seeds?

Seeds are the propagules of choice for many translocations. They have the advantages of being relatively easy to collect and transport. Use of seeds avoids the additional costs and risks of propagating plants, as well as the potential for artificial selection in greenhouse and garden locales (Lesica and Allendorf 1999). The trade-off, of course, is that a far lower percentage of seeds survive, germinate and establish relative to transplants (Bell *et al*. 2003; Jusaitis *et al*. 2004).

Seed germination and seedling emergence are the first steps in the process of seed-based translocations. Monitoring of both individual seeds and groups of sown seeds is possible, although with different implications for analyses of results. Certainly, frequent monitoring will be required to ‘catch’ most cases of successful emergence. This may be important because different management treatments may be successful in encouraging either seedling emergence or subsequent seedling survival. For example, in an introduction of an annual grassland forb in California, clipping treatments increased recruitment, although eventually the introduction was unsuccessful no matter which treatment was applied (Holl and Hayes 2006). Clipping and fire treatments influenced successful seedling establishment of a rare mint in Florida (Gordon 1996).

What happens to plants?

Plants produced by propagating seedlings, cuttings or from tissue culture (e.g. Wang *et al*. 2006) often have better success than seeds directly sown onto the restoration site (Maschinski and Wright 2006; Guerrant and Kaye 2007). If monitoring is conducted following translocation, vital rates of translocated individuals are commonly followed through time. Transplant survival (establishment) is, by far, the most common vital rate monitored, at intervals ranging from frequent (e.g. biweekly; Gennet *et al*. 2004) to annual (Monks and Coates 2002) to infrequent (e.g. after 7 years for 24 species; Mottl *et al*. 2006).

Survival is not the only measure of transplant success. Measures of individual plant growth provide evidence that the site chosen is suitable for an introduction. In the case of Florida Ziziphus (*Ziziphus celata*; Fig. 1), transplants at one site had high survival but little growth, whereas transplants at a second site had slightly lower survival but faster growth (Weekley *et al*. 2007). Strong positive growth of *Jacquemontia reclinata* transplants in southern Florida restorations was considered a sign of early translocation success (Maschinski and Wright 2006). In a longer-term (10-year) study, lack of consistent plant growth in wetland restorations was one of the pieces of evidence used to suggest that mitigation sites were not following desired trajectories towards reference conditions (Zedler and Callaway 1999). Fire was seen as a positive management treatment in experimental restorations of *Asclepias meadii*, promoting higher growth and survivorship (Bowles *et al*. 1998).

Life-cycle completion: a critical benchmark

A key qualitative measure of the ultimate fate of translocations is the ability of transplants to flower and set fruit, often considered a

Fig. 1. Narrow central Florida scrub endemic *Ziziphus celata*, protected from herbivory by cages at an introduction site, being monitored for growth and survival. Introduced populations are being designed with propagules from multiple wild populations in order to overcome breeding-system limitations imposed by cross-incompatibility and limited genetic variation (Weekley *et al*. 2002). Photograph by Carl Weekley.

critical achievement in transplantations (e.g. Tyndall and Groller 2006). Beyond merely producing some fruit, quantitative reproductive success (e.g. seed output per plant) is an assessment of the initial success of a restoration. For example, Morgan (2000) found that plants in introduced populations of the threatened grassland daisy *Rutidosis leptorrhynchoides* had seed production and germination similar to those of plants in natural populations, suggesting that small population size in the introduced population was not causing reductions in reproductive success.

Many plants reproduce clonally, so the success of transplanted clonal offshoots and, ultimately, their ability to spread clonally, can be important. An increase in the shoot number of an endangered clonal shrub was evidence for initial success in one transplant study (Braham *et al*. 2006).

Ultimately, dispersal is a key to a successful translocation (Pavlik 1996). Translocations themselves are one way to overcome dispersal limitations for sites and species where passive restoration has not been successful. However, most species' distributions, even within restorations, are likely to be dispersal-limited (Tobias *et al*. 2003). Monitoring reintroduction success needs to include looking up from the site of transplantation itself and assessing successful dispersal within and among sites.

Population-level assessments of translocation success

Population states

For a snapshot of translocation success, many authors consider static (state) objectives (Pavlik 1996) such as population size, area covered by plants and percentage of suitable habitats occupied. Number of plants is a common measure used to evaluate reintroductions and other translocations (Howald 1996; Lindborg and Eriksson 2004). Tracking plant numbers (Level 2 monitoring of Menges and Gordon 1996) is far less labour-intensive than the individual tracking necessary to measure vital rates. Changes in population size over time are also measures of initial translocation success. This calculation can be done within newly introduced populations, or by evaluating the contribution of translocations to metapopulation size (Maschinski and Wright 2006). Of course, short-term increases in population size do not provide much assurance of future trends. For example, an introduced population of *Cordylanthus maritimus* var. *maritimus* started by seed-sowing increased almost 3-fold in 3 years. Still, because opportunities for subsequent seed germination and establishment were considered to be limiting to population growth, researchers did not consider the success of the introduction guaranteed (Parsons and Zedler 1997).

Modelling population viability in introduced populations

Long-term persistence is a key measure of the success of translocations (Pavlik 1996; Maschinski and Wright 2006). However, restorationists would like to project persistence as soon as possible, and figure out ways to increase the chances of population persistence. Population viability analyses can give useful information on the projected future success of introductions and translocations. Such analyses input demographic data (e.g. survival, growth, fecundity, recruitment, dispersal) and project future population sizes, stage structures, population growth rates (deterministic or stochastic), time-to-extinction and extinction probabilities (Menges 2000). Further analyses can evaluate the sensitivity of population growth rates to individual vital rates (Mills *et al*. 1999) and partition past variation in population growth rates to ecological factors or treatments (Life Table Response Experiments; Caswell 2001). These analyses have been used to analyse potential and past management effects on demography and persistence of populations (Morris and Doak 2002).

In some senses, introduced populations offer great opportunities for these analyses, as more may be known about starting conditions (e.g. number of transplants, dates of introduction) than is known for wild populations. Despite this, few population viability analyses have been attempted on introduced populations.

The first population viability analysis on an introduced population was accomplished by Bell *et al*. (2003) on Pitcher's thistle (*Cirsium pitcheri*; Fig. 2), an endemic monocarpic perennial herb that grows on sand dunes of the western Great Lakes in North America. Repeated introductions into protected land near Chicago were closely followed to obtain demographic data for transplants and naturally recruited individuals. Data on these two groups showed different

Fig. 2. *Cirsium pitcheri* flowering plant translocated into a restoration site in Wisconsin, USA. Introduced populations of Pitcher's thistle show a similar range of vital rates, but greater variation in these rates, than wild populations (Bell *et al*. 2003). Photograph by Tim Bell.

demographic outcomes. The translocated population had a similar range of finite rates of increase (lambda ranging from 0.66 to 1.21) as did nearby natural populations (lambda ranged from 0.87 to 1.21), although variation in vital rates for the translocated population was relatively high (Bell *et al*. 2003). Although this translocation has been successful (T. Bell, pers. comm.), greater variance suggests a higher extinction risk than for similar-sized natural populations.

A sophisticated population viability analysis melding demography and genetics was published by Kirchner *et al*. (2006) on the narrow endemic *Centaurea corymbosa* (Fig. 3). Data were extracted from studies of six wild populations to inform planned introductions. The authors' goals were to compare population growth and extinction risk for different seed-introduction strategies. Population persistence was highest when many seeds were introduced into multiple sites (Kirchner *et al*. 2006). Introductions into multiple sites also minimised the loss of self-incompatibility alleles.

Close tracking of plants inherent in collecting data for a population viability analysis allows comparisons of potential population growth with and without translocations. The analysis of the endangered palm *Pseudophoenix sargentii* in the Florida Keys showed that reintroduced plants had faster maturation and higher population growth rates than did wild plants and that reintroductions have expanded the species range (Maschinski and Duquesnel 2007).

Fig. 3. Flowering individual of the narrow endemic *Centaurea corymbosa* growing in limestone outcrops in southern France. Multiple introductions from many source populations were most successful in creating new populations (Kirchner *et al*. 2006). Photograph by Bruno Colas.

Factors that contribute to success of translocations

Seeds or plants and how?

The type of propagules (seeds, transplants, plantlets) used in translocations affects success. Demographic monitoring of different propagule treatments is common in the restoration literature. As expected, seedlings and other transplants have greater success than sown seeds (Guerrant 1996; Bowles *et al*. 1998; Bell *et al*. 2003; Jusaitis *et al*. 2004; Maschinski and Wright 2006; Guerrant and Kaye 2007) and larger plants have greater success (survival, growth) than smaller plants (Guerrant 1996). However, the propagation of seedlings is expensive and time-consuming relative to sowing seeds. For example, Kaye and Cramer (2003) found that, although seeding and transplanting were both successful approaches to restoring populations of Kincaid's lupine in Oregon, direct seeding was far less expensive. However, if seeds are in short supply, direct seeding may be wasteful of seeds relative to greenhouse propagation programs (Guerrant and Kaye 2007). In addition to comparisons of seeds *v*. transplants, other studies have compared different seed-sowing techniques (Cox *et al*. 2004; Wilson *et al*. 2004), different types of transplants (e.g. bare root plants, potted plants, plants of different sizes; e.g. Alley and Affolter 2004) and combinations of transplant age with different site environments (Kindell *et al*. 1996).

Translocation strategies

Rout *et al*. (2007) considered how the number of individuals translocated should be parsed among two populations. If long-term persistence is the goal, then creating conditions for expanding populations is more important than translocation decisions. If creating a large overall population is the overall goal, contributing mainly to populations that are already increasing is favoured. However, this analysis does not consider the advantages of spreading propagules among various sites to avoid catastrophic events that could eliminate introduced populations. Potentially, catastrophic events, such as fire, disease and overgrazing, are aggregated in space. Dispersion of populations across wide spatial extents, especially if there are intervening barriers to the spread of catastrophes (e.g. firebreaks, barriers to disease dispersal, barriers to grazers) will provide buffering of the metapopulation. Thus, the extent of metapopulation, along with abundance, should be a key goal of translocation. Potential parameters to consider include the number and distribution of populations (Pavlik 1996). Even small numbers of translocations can be effective at increasing metapopulation viability (Lubow 1996).

Genetics of translocated propagules

A newly introduced population that cannot reproduce cannot be considered a success. Genetic issues that limit or prevent reproduction are a key issue in translocations (Gordon 1994; Vergeer *et al*. 2004). Limitations owing to breeding systems and inbreeding depression are important, but additional considerations may be outbreeding depression and genetic mixing, genetic representativeness, founder effects and retaining the potential for further evolution. Because most translocations are necessarily limited in the number of plants introduced, issues of small population size will always be important.

Breeding systems, inbreeding depression and reproductive viability

For species that cannot reproduce except by crosses among different mating types, small populations may be at risk from extinction because of the loss of key mating types. For example, Lakeside daisy (*Hymenoxys acaulis* var. *glabra*) populations in Illinois were all of a single mating type, so no recruitment occurred within the state (DeMauro 1993). In contrast, interplant matings among Ohio Lakeside daisy plants were largely successful in producing viable seeds (Moran-Palma and Snow 1997). Subsequent restoration efforts in Illinois required moving genotypes from another state (Ohio) to produce progeny.

Florida ziziphus (*Ziziphus celata*) reproduction also appears limited by the availability of mating types. Most natural populations are uniclonal and produce no fruits (Weekley *et al*. 2002). Recruited seedlings been observed only in an *ex situ* collection with multiple mating types. Restorations are currently underway (Fig. 1), using propagated material representing cross-compatible mating types from multiple populations, as determined by experimental crosses (Weekley and Menges 2005). The hope is that crosses between plants (once they mature to flowering size) will provide recruitment into the introduced populations.

In some cases, poor reproduction in natural populations may be caused by ecological factors. Mowing and lack of fire have created populations of Mead's milkweed with few genotypes (Hayworth *et al*. 2001), so that introductions from multiple populations may be necessary for translocation success.

Small populations, especially those of obligate outcrossers, are at risk from inbreeding depression. Inbreeding depression can reduce the survival of introduced populations, as was the case for various-sized populations of *Silene* spp. introduced in Oregon (Kephart 2004). Introductions made from small, selfed populations (in predominately outcrossing species) may be particularly disadvantaged in experimental introductions (Vergeer *et al*. 2004).

Finally, reproductive viability may be a function of seedling recruitment. For example, natural populations of blue oak (*Quercus douglasii*) in California have exceedingly rare seedling recruitment despite abundant production of viable acorns (Rice and Emery 2003). Restoration of woodlands dominated by these oaks will require identification and correction of factors that limit seedling survival.

Local adaptation and outbreeding depression

In many species, individuals from the local site have higher fitness than individuals from other sites. This local adaptation (home-site advantage; Montalvo and Ellstrand 2000) appears to be quite common. Even in the absence of demonstrated local adaptation, high levels of population differentiation argue for caution in translocations (Gravuer *et al*. 2005).

Locally adaptive genetic variation is a key to restoration success. Although molecular genetic variation has been used as a proxy for adaptive genetic variation, molecular and adaptive variation may not be strongly correlated (McKay and Latta 2002). Quantitative genetic variation is useful in ascertaining what sources to use in translocations, but relevant data are not likely to be available. In a sense, translocations for conservation purposes are also common garden or (partial) reciprocal transplant experiments, and reciprocal transplant experiments have been used to assess local adaptation and translocation strategies; (Kindell *et al*. 1996; Hufford and Mazer 2003; Sanders and McGraw 2005).

A balance needs to be struck between providing genetic variation (which may need to be garnered from many sites) and avoiding outbreeding depression (Vergeer *et al*. 2004). Outbreeding depression, the dilution of local adaptation or genomic co-adaptation, is a potential negative consequence of augmentation (Hufford and Mazer 2003; Gravuer *et al*. 2005; McKay *et al*. 2005). One guideline is to use local sources, but draw from as much genetic variation as possible (Lesica and Allendorf 1999). However, it may be necessary to use mixtures of non-local sources when restoring severely disturbed areas (Lesica and Allendorf 1999) or when dealing with breeding-system problems (Moran-Palma and Snow 1997). Where propagules from several local or non-local sources are combined, local ecotypic variation may be lost. Evidence that genetic variation from one source population would be insufficient for successful restoration may, therefore, be desirable.

If it is necessary to mix genetic sources, the use of material from populations in similar environments may be an approach that balances the need for genetic variation with the avoidance of introducing individuals of different ecotypes (McKay *et al*. 2005). Sanders and McGraw (2005), drawing on the results of reciprocal transplant studies, suggested that multiple sources and multiple sites be used, but that introduced populations be spatially segregated by source population. Similarly, Gordon (1994) recommended that new populations composed of propagules from multiple sources be located where crosses with natural populations are unlikely.

This leads to a practical question; namely, from what distances can propagules be drawn for successful translocations? Geographic-distance effects can interact with restoration treatments in affecting transplant performance (Smith *et al*. 2005). Inbreeding species and those with poor dispersal will have stronger local adaptation. Translocations with these species will be more successful in restorations that draw from relatively small geographic areas. Variation in the spatial scale of local adaptations makes the creation of distance rules counterproductive (McKay *et al*. 2005). Instead, translocations should try to minimise movement across climatic, edaphic or biotic regimes (Gordon and Rice 1998; Hufford and Mazer 2003). Close demographic scrutiny of introduced material can help determine which maternal lines are adapted to the site and therefore enhance the chances of future translocation success.

Genetic variation

Introductions may serve as inadvertent founder events that may result in severe genetic bottlenecks (Hufford and Mazer 2003). This is particularly relevant if the donor population was already under bottleneck conditions, if only portions of populations were sampled for propagules, if a few plants contributed most of the propagules (Robichaux *et al*. 1997; Krauss *et al*. 2002) or if introduced population sizes were small. Among four introduced populations of pink sand verbena (*Ambronia umbellata* subsp. *breviflora*) in Oregon, populations smaller than 1000 individuals had lower genetic variation than did larger populations (McGlaughlin *et al*. 2002).

The ideal situation may be when a new introduction contains (and retains) levels of genetic variation similar to wild populations. This was the case with introductions of the vernal pool endemic composite, *Lasthenia conjugens* (Ramp *et al*. 2006), which had patterns of genetic diversity similar to that of natural populations (Fig. 4). Such a series of introductions can be considered an initial restoration success from a genetic point of view. Far more common, unfortunately, is the situation where genetic variation, particularly the distribution of rare alleles, is lower in introduced than in source populations (Helenurm and Parsons 1997; Robichaux *et al*. 1997).

Even when populations are founded with substantial genetic variation, genetic erosion is an insidious problem. In translocations of the endangered *Grevillea scapigera*, which was unusually well monitored genetically, genetic losses occurred resulting from errors in transplanting, inbreeding and unequal contributions to the F1 generation (Krauss *et al*. 2002). Although this is a serious issue in restorations, these patterns suggest that experimental restorations can be used to explore the degree to which stochastic events and selection alter the genetic signature of translocations. They also point out that a metapopulation approach to translocations may be critical to maintaining genetic diversity and species viability (Krauss *et al*. 2002).

Interactions of translocations with herbivory, disturbances, competition and other factors

The success of translocations is, of course, dependent on context and on events that occur during the translocation. In many translocations, these factors vary stochastically among sites and microsites, whereas in others, researchers attempt to control these factors. Such experiments have a long history in ecology, although the synergy of restoration and experimental ecology has not been fully realised. Certainly, many researchers could utilise (or design) translocations that would both benefit biodiversity and answer basic research questions. By varying introduction conditions, one can discover optimal conditions as well as allowing various ecotypes to express their fitness in a range of conditions.

Fig. 4. Vernal pool endemic composite *Lasthenia conjugens*. Introductions of this species have levels of genetic variation similar to those of wild populations (Ramp *et al*. 2006). Photograph by Sharon Collinge.

Herbivores may exert a toll on introduced seeds, seedlings and plants. Exclosures to limit these effects are often a given, but sometimes an experimental treatment as well. In many cases, herbivores suppress seedling recruitment (Sweeney *et al*. 2002; Maschinski *et al*. 2004); however, effects on transplants have also been found (Jusaitis 2005). Besides direct negative effects, indirect positive effects are possible. In tallgrass prairie restoration in the USA, ungulates increased light availability and, if seed limitation was eliminated, increased seedling emergence (Martin and Wilsey 2006).

Disturbance regimes are often manipulated in restorations. In natural systems, fire is often manipulated and responses of individual species studied (e.g. Menges and Quintana-Ascencio 2004). However, fewer studies use fire as an experimental treatment for translocations. Fire increased survival and growth of translocated populations of *Asclepias meadii* in prairie restorations in mid-western USA (Bowles *et al*. 1998). Fire has been used as a site treatment before translocations of Florida ziziphus, although intense fires created aggressive oak resprouting that reduced transplant survival (C. Weekley and E. Menges, unpubl. data). Smaller-scale disturbance experiments in restorations have involved varying gap size (Westbury *et al*. 2006) and clipping frequency (Holl and Hayes 2006).

Competition from surrounding vegetation can affect the success of transplants. Aggressive weeds, a common problem in restorations, can have an impact the success of transplants (e.g. Scade *et al*. 2006). High-productivity sites hampered survival of introduced plants of *Nassella pulchra*, suggesting that its original habitat may have been more marginal sites (Lombardo *et al*. 2007). Similarly, competition among transplants reduced survival in multispecies clumps in South African deserts (Blignaut and Milton 2005). Clipping may reduce aboveground competition, but may also interact with other factors to influence translocation success. Survival of transplanted *Conradina glabra* individuals and subsequent seedling establishment was higher where a clipping treatment also reduced fire intensity adjacent to translocated plants (Gordon 1996). Manipulation of the light regime is also a common treatment in experimental restorations. Survival of several species was highest with shaded conditions in restoration of coastal sandscapes in Lake Superior (van Stappen 2004).

Secondary effects of translocations

The success of translocations can go beyond the establishment of populations of individual species. For species that have important roles to play in the ecosystem (keystone species), their introduction may trigger changes that are seen as beneficial.

Translocated species can facilitate the establishment of other species. Restoring cover of native plants suppressed exotic weeds in tallgrass prairie restorations in the USA (Blumenthal *et al.* 2003). Transplants can be used to increase cover in invasion-prone communities and block the influx of exotic species into restorations (Wang *et al.* 2006).

In the case of *Rhinanthus minor*, its introduction into species-poor British grasslands served to increase diversity (Westbury *et al.* 2006). The use of an early successional shrub species as a nurse plant increased oak survival in a restoration in Spain (Castro *et al.* 2006) and increased survival of *Olea europaea* ssp. *cuspidata* in grazed Ethiopian restorations (Aerts *et al.* 2007). Woody plants serve as perches for avian dispersers, thereby increasing the speed of pasture restoration into tropical forests (Holl *et al.* 2000). However, translocations sometimes fail to create a restoration trajectory towards reference sites (Wilkins *et al.* 2003).

New directions

Restoration ecology, and the imbedded subject of translocation, are changing rapidly as experimental approaches are expanded, more projects are better-documented and new techniques (e.g. population viability analyses) are brought to bear in evaluation. There are several emerging directions that will undoubtedly receive more emphasis in the near future. These include the use of reference populations, longer monitoring windows and better integration of the practice and science of restoration.

Comparison of translocations to reference populations

Many reports of introductions consider vital rates such as survival, growth and fecundity in a vacuum. While higher vital rates may be preferable to lower vital rates, placing results into the context of wild populations may provide some solace. In the long run, an introduced population should be as demographically capable as its wild counterparts (Pavlik 1996). In wild populations of most plants, seedling emergence and survival can be very low. These variables were compared in natural *v.* experimental introduction habitats with the endangered limestone endemic shrub *Purshia subintegra.* Seedling vital rates during 5 years at the restoration site, although not high, were higher than for seedlings recruited in natural populations (Maschinski *et al.* 2004). The use of reference populations, akin to reference sites (White and Walker 1997), for comparisons of translocation success, should become a routine part of restoration ecology (e.g. used by Bell *et al.* 2003).

A long-term view

Long-term monitoring of introductions is essential. Short-term results can be misleading, especially in variable environments. For example, the interpretation of the effects of cages to exclude herbivores, and the assessment of success of the translocation, varied depending on the length of data collection (Maschinski *et al.* 2004). For some species, little will be learned from any short-term study. Slow-maturing plants clearly require a long-term perspective on their success. For long-lived plants, it may take decades for translocated plants to become reproductive (Maschinski and Duquesnel 2007). The long-term viability of most reintroduction projects has not been assessed (Maunder 1992). Similarly, long-term data will be needed to assess the success of most restorations (Zedler and Callaway 1999).

Experimental restoration and demography

Restoration activities, including translocations, provide feedback that can be useful in subsequent restorations. However, without appropriate experimental design, the scope of these inferences is limited (Fig. 5). More rigorous experiments are likely to provide information that can be useful beyond the species and sites of the experiment. In addition, ecological restoration has been seen as providing ideal experimental settings for tests of ecological theory (Bradshaw 1987; Sarrazin and Barbault 1996; Young *et al.* 2005); however, this potential has not been fully realised by plant population biologists. Reintroduction projects are best designed as scientific experiments that test explicit hypotheses (Guerrant and Kaye 2007); by trying different approaches within an experiment, the restorationist is bet-hedging while gaining knowledge even if the reintroduction fails. For example, introducing seeds at various densities can provide practical guidance on how to best balance logistical and seed-number limitations (Kirchner *et al.* 2006), while providing data on whether density-dependent germination or seedling survival is important.

Finally, theoretical predictions can be used to design restorations (Fig. 5). For example, Maschinski and Wright (2006) listed a series of generalisations from ecological theory (e.g. migration between spatially linked patches can provide a rescue effect) that imply particular restoration approaches (e.g. introducing populations that are clumped together in the landscape).

Experiments, failure and learning

Scientific studies of experimental restorations need to be as objective as possible. Unfortunately, published restoration

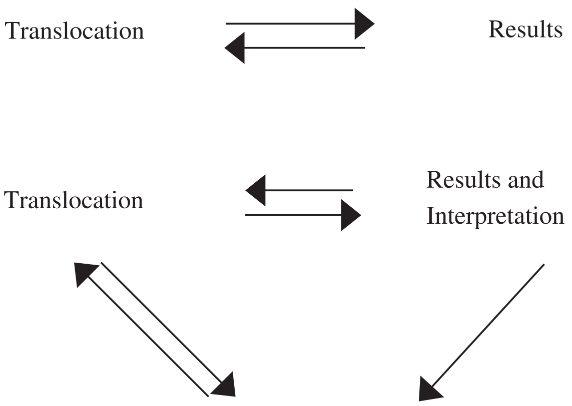

Fig. 5. Conceptual flow chart contrasting basic translocations (top) with experimental translocations informed by ecological theory (bottom). Results from basic translocations can help inform the next translocation, although the scale of inference is local. Experimental translocations informed by ecological theory can provide the same local inference. However, appropriate experiments can test ecological theory, which can be used to draw broader inferences. In addition, ecological theory can inform translocation experiments.

results are probably biased towards successes because of the natural human motivation (in practitioners and in editors) to accentuate successes and minimise failures. However, failures, if well documented, can be instructive. Nothing defines success better than a good, solid failure (Pavlik 1996). Documenting what went wrong helps define the set of what could be right, and helps the next restoration ecologist define an efficient, relevant experiment.

Beyond 'building it', restorationists are 'bringing them (translocated plants)' to their 'fields of dreams'. Whether 'they' stay or perish is not only an outcome but an opportunity to learn. Lessons learned will inform future restorations.

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