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PERSPECTIVE

Assessing the benefits and risks of translocations in changing environments: a genetic perspective

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Introduction

Increasingly, consideration is being given to the movement of individuals, populations and species across landscapes to enhance or maintain biodiversity, either as part of ecological restoration programmes or to increase the number or size of populations of threatened species. These intentional movements, termed translocations, are among the most powerful tools for biodiversity conservation, as habitat loss, introduced species, disease epidemics and climate change threaten species worldwide. Translocation programmes for ecological restoration and

Abstract

Translocations are being increasingly proposed as a way of conserving biodiversity, particularly in the management of threatened and keystone species, with the aims of maintaining biodiversity and ecosystem function under the combined pressures of habitat fragmentation and climate change. Evolutionary genetic considerations should be an important part of translocation strategies, but there is often confusion about concepts and goals. Here, we provide a classification of translocations based on specific genetic goals for both threatened species and ecological restoration, separating targets based on 'genetic rescue' of current population fitness from those focused on maintaining adaptive potential. We then provide a framework for assessing the genetic benefits and risks associated with translocations and provide guidelines for managers focused on conserving biodiversity and evolutionary processes. Case studies are developed to illustrate the framework.

species conservation share the ultimate goals of population persistence and resilience, but rates of success have been low for both restoration (Wuethrich 2007; Palmer and Filoso 2009; Godefroid et al. 2011) and conservation translocations (Griffith et al. 1989; Dodd and Seigel 1991; Germano and Bishop 2009). It is unusual for conservation relocations to have follow-up monitoring; so outcomes are often unknown and causes of failures are rarely understood (Fischer and Lindenmayer 2000). Because of rapid recent and predicted rates of environmental change, the role of translocations is being re-evaluated in the context of maximizing persistence

and resilience for both rare and restricted species, and common species.

Although conservation scientists and managers consider translocation a primary tool for management, controversy remains over how the goals for translocations should be prioritized and measured, and how success can best be achieved. For example, the often stated aims of ecological restoration (including biodiversity corridors or 'biolinks') are as follows: (i) increased species diversity and structure, (ii) presence of indigenous species, (iii) functionality both within the community and the broader ecological landscape, (iv) an appropriate physical environment, (v) reduction or elimination of threats and (vi) persistence and resilience to environment stresses (SER 2004; Ruiz-Jaén and Aide 2005; Damschen et al. 2006). In contrast, the aims of conservation translocations are usually to create or maintain viable populations of a single, focal species, with measures of success based on abundance (establishment, fecundity and population size), extent (dispersal, number of populations), resilience (genetic variation, resistance to perturbation) and persistence (Pavlik 1996; Vallee et al. 2004). Achieving the common goals of resilience and persistence of translocated populations will depend upon a suite of factors including species' physiology, ecology, genetic diversity, plasticity, local adaptation and population and community dynamics (Dodd and Seigel 1991; Armstrong and Seddon 2008).

Here, we discuss translocations in the light of their genetic implications and outline the evolutionary benefits and risks for these different types of translocations. We suggest that perceived, but generally unsubstantiated, risks place too much constraint on current management options, commonly leading to inaction. Instead, we advocate that more attention should be given to the strategic mixing of populations as a practical and cost-effective method of establishing viable populations that are capable of persisting in the face of environmental change. We provide a simple risk-assessment framework for managers that can be used to determine courses of action in restoration and conservation to maximize genetic potential, even in the face of limited information. We then apply this risk-assessment framework to several case studies, highlighting the approach for managers.

A genetic view of translocations

Translocation is defined by the International Union for Conservation of Nature (IUCN) as 'the movement of living organisms from one area with free release in another' (IUCN 1987). The IUCN recognizes three different types of translocations; *augmentation* (movement of individuals into a population of conspecifics), *introduction* (movement of an organism outside its historical range) and *re-introduction* (movement of an organism into a part of its

native/historical range from which it has disappeared) (IUCN 1987). From a genetic perspective, however, translocations are defined by the underlying goal of the translocation. For instance, augmentation can be used in threatened species programmes to increase population size to avoid the stochastic loss of a small population, but from a genetic viewpoint, it can alleviate detrimental genetic effects that arise in small fragmented populations such as genetic load, inbreeding depression and reduced genetic variation (Hedrick 1995; Westemeier et al. 1998; Vila et al. 2003; Pickup and Young 2008; Hedrick and Fredrickson 2010). The target of the genetic translocation in this case is to improve reproductive fitness (which includes both survival and fertility components) leading to genetic rescue, and/or increase genetic variation leading to genetic restoration (see Table 1). Genetic rescue occurs when the introduction of new genes into a small population counters the expression of deleterious genes (genetic load), while genetic restoration is essentially focussed on increasing levels of genetic variation and adaptive potential.

While translocations are well defined by the IUCN, the genetic implications are less clear. In Table 1, we outline five different types of genetic translocations based on the intended outcome. Most of these have been described in some form elsewhere (Hedrick 1995; Broadhurst et al. 2008; Hedrick and Fredrickson 2010), although we introduce some new concepts (e.g. genetic capture). Importantly, we also define secondary actions that are often implied, but not specifically mentioned when these genetic translocations have been discussed previously. These different types of genetic translocations all share the goal of increasing/maintaining genetic variation and reducing genetic load and differ only in whether they specifically target adaptive potential and/or environmental change (e.g. *introduction* translocation). *Genetic capture*, *genetic rescue* and *genetic restoration* are generally applicable to threatened species and aimed at the short/medium term. *Genetic adaptation* is aimed at species used in restoration, which often includes a range of keystone and common species, or species likely to be impacted by environmental change, with long-term persistence the ultimate goal.

We introduce *genetic capture*, because it is applicable to endangered and critically endangered species where source individuals or seed are scarce or where captive breeding programmes are initiated or a seed orchard is established. Often, genetic factors are ignored in these situations, but we argue that they are critical for success. By translocating 20–50 individuals or seed (either to captivity/seed orchard or the wild), the aim is to capture >95% of the standing genetic variation within the source population (or populations of a species, particularly if there is a high level of clonality or inbreeding), if we assume an equal contribution to the next generation by each of these

Table 1. Types of genetic translocation for conservation and restoration.

Translocation Type	Primary action: Introduction/Augmentation	Outcome	Secondary action: Population size/ gene flow	Outcome	When applicable	Increase evolutionary potential	IUCN categories applicable
Genetic capture	20–50 breeding individuals	Capture >95% genetic variation from source population	Increase N_e to >1000 within a few generations	Retain >90% genetic variation from source population	Captive breeding colony; translocation to new environment	Short term	Critically endangered; Endangered
Genetic rescue	20% source into recipient population	Reduce genetic load, genetic isolation Reduce inbreeding depression Keep locally adapted alleles	–	–	Population suffering inbreeding depression/genetic load; drastic loss of genetic variation	Short term	Endangered; Vulnerable
Genetic restoration	20% source into recipient population	Increase genetic variation Reduce genetic load, genetic isolation Reduce inbreeding depression Keep locally adapted alleles	Continued gene flow at approximately OMPG into recipient population	Increase genetic variation	Population suffering inbreeding depression/genetic load; drastic loss of genetic variation	Short to medium term	Endangered; Vulnerable; Near threatened
Genetic adaptation (recipient population)*	One or more source populations into recipient population, 20% overall	Increase genetic variation and adaptive potential Introduce new alleles for traits important for environmental change	Continued gene flow at approximately OMPG into recipient population; $N_e > 1000$	N_e is maximized for long-term evolution	Reconnection of fragmented populations; translocations to new environments	Long term	Vulnerable; Near threatened; Least concern but likely to experience environmental changes in near future
Genetic adaptation (new environment)*	Introduction into new environment	Generate genetic variability that increases adaptation to new and future environment	–	Genetic variation is maximized (e.g. composite provenancing) for adaptation	Establishing populations outside historical range	Long term	Least concern but likely to experience environmental change, keystone species for restoration

*There are no signs of inbreeding depression in recipient population. N_e , effective population size; OMPG, one migrant per generation; IUCN, International Union for Conservation of Nature.

individuals or seeds. Ideally, this new population should reach an effective population size of approximately 1000 individuals within several generations of the translocation by rapid expansion or continued introductions, as genetic variation is lost at the rate of $1/2N_e$ per generation (N_e being the effective population size; allelic neutrality is assumed). In some situations (e.g. endangered mammals), continued introductions are likely to be the only way to negate or limit the effects of small population size.

Generally, with any genetic translocation, longer-term success will depend on how quickly the effective population size can be increased to >1000 individuals, which is considered an approximate threshold minimum for maintaining adequate adaptive potential and evolvability in the face of environmental change (Willi et al. 2006). While some species can persist with small effective population sizes, their long-term success is likely to be compromised. If the effective population size cannot be increased beyond 1000 within several generations after the translocation event, then gene flow from the source to the recipient population is recommended with a minimum of one migrant per generation (OMPG; Franklin 1980; Frankel and Soule 1981; Allendorf 1983; Mills and Allendorf 1996). The source population in this case should have an effective population that exceeds 1000 individuals (or connected by gene flow to other subpopulations that exceed a total effective population size of 1000). The OMPG concept has been modelled and shown to obviate the effects of small population size (build up of deleterious alleles/genetic load and inbreeding depression, but see Mills and Allendorf 1996; Vucetich and Waite 2000), without swamping any adaptive alleles that are unique to the recipient population (Hedrick 1995). As long as one migrant is interpreted as one genetically effective migrant, OMPG is apparently quite robust to violations of its many simplifying assumptions (Wang 2004).

Hedrick (1995) has shown that augmentation translocations into recipient populations should not exceed a level of 20% gene flow from the source population(s) to reduce the detrimental genetic load (and inbreeding depression if present) of the recipient population without losing uniquely adapted alleles in the recipient population. Similarly, when planning for future environmental change (see below), *genetic adaptation* translocations should also not exceed 20% gene flow from the source population(s) to avoid the loss of locally adapted alleles from the recipient population(s).

Augmentation for genetic rescue and genetic restoration

Rescuing threatened populations

A 20% level of gene flow is recommended for the genetic rescue of populations (Hedrick 1995). For restoration,

ongoing gene flow is recommended at the rate of at least OMPG (Hedrick 1995; Mills and Allendorf 1996), although this may be considerably higher with fluctuating population size (Mills and Allendorf 1996; Vucetich and Waite 2000). The translocation of several individuals per generation (rather than an initial 20% level of gene flow) is likely to be enough to reduce the detrimental consequences of inbreeding, while minimizing the risks of outbreeding depression (Box 1) (Hedrick 1995; Lopez et al. 2009; Hedrick and Fredrickson 2010). This may be the only available option for some endangered species where populations are small and cannot be increased above 1000 individuals. The risk of outbreeding depression, however, should be carefully weighed against the substantial risk that ongoing loss of genetic diversity and inbreeding poses to the long-term persistence of populations (Edmands 2007; Lopez et al. 2009; Frankham et al. 2011), a point we discuss further below.

Although there is clear empirical evidence that mixed populations can have high vigour (e.g. Binks 2007), the predominant view among conservation managers is that locally adapted populations are the most appropriate sources for translocations. Unfortunately, this pervasive position has discouraged attempts to mix source populations and as a consequence limited the use of translocations. Their rationale is that locally adapted populations are most likely to establish and persist under similar environmental conditions (although this may not be the case for small threatened populations that are prone to genetic drift and therefore maladaptation; Lopez et al. 2009) that 'genetic pollution' by alien genotypes with a strong competitive ability (Saltonstall 2002) is limited (*sensu* Potts et al. 2003) and that outbreeding depression is avoided (see Box 1; Hufford and Mazer 2003). This is a conservative view when translocating for genetic rescue and restoration, but nearby (presumably locally adapted) populations do not exist in many cases for threatened species. Similarly, in highly fragmented and degraded landscapes where there are local source populations, they are often small and isolated, with low levels of genetic variation and likely to have increased levels of inbreeding and possibly hybridization (Field et al. 2008).

Genetic risks: outbreeding depression versus heterosis and avoiding inbreeding depression

Perhaps the greatest perceived risk to performing translocations concerns outbreeding depression (Box 1). However, this risk has most likely been greatly overstated, and there are some clear, predictive risk-factors for strong outbreeding depression (Frankham et al. 2011). The risk of outbreeding depression depends on population size

and structure, gene flow, breeding system (Box 2), the environments of the source/recipient populations, the degree of adaptive differentiation among source and

Box 1: Definitions relating to genetic translocations

Adaptive evolution: Genetic change because of natural selection that improves the reproductive fitness of a population in its environment.

Effective population size (N_e): The number of individuals that would result in the same loss of genetic diversity, inbreeding or genetic drift among replicate populations if they behaved in the manner of an idealized population.

F1: the offspring produced in the first generation of a cross/mating.

Gene flow: Movement of alleles between populations via migrants or gametes that contribute to the next generation.

Genetic erosion: Loss of genetic diversity in small populations.

Genetic rescue: Improvement in reproductive fitness and increase in genetic diversity because of outcrossing of a population previously suffering low genetic diversity and inbreeding.

Genetic restoration: Restoration of genetic diversity towards former levels in a population.

Genotype \times environment interaction (GE): Differential performance of the same genotype in different environments.

Heterosis: Hybrid vigour. Superior performance of hybrid genotypes, normally indicating fitness superior to both parental genotypes.

Inbreeding: The production of offspring from mating of individuals related by descent, e.g. self-fertilization, brother \times sister or cousin matings.

Inbreeding depression: Deleterious change in the mean for a quantitative trait because of inbreeding, especially for reproduction or survival.

Local adaptation: Situations where local population has higher fitness when tested in its own environment than any introduced population.

Outbreeding depression: Reduction in any pre- or postmating aspect of reproductive fitness because of attempted crossing of distinct lines/populations, subspecies or even species).

Reproductive fitness: The number of fertile offspring surviving to reproductive age contributed by an individual in their lifetime. Encompasses mating ability, fertilization capacity, fecundity and survival. Often referred to as fitness.

recipient populations and rates of environmental change that populations are likely to experience. These factors will determine whether populations are likely to suffer substantial outbreeding depression after translocation, and whether population fitness and adaptability will be affected by a loss of genetic diversity, and whether genetic rescue will improve fitness [heterosis; (Box 1)].

The prevailing assumption is that outbreeding depression will always occur when individuals from differently adapted populations are crossed, and that translocations among distinct lineages will therefore be universally deleterious; consequently, genetic translocations are yet to be routinely considered a viable conservation management tool. However, the risk of outbreeding depression has until recently been poorly predicted (see Edmands 2007; McClelland and Naish 2007) and therefore overemphasized in the literature (Frankham et al. 2011) and also by managers. For many species, common-garden or field-based experiments involving crosses among populations will assist in assessing the risk of genetic translocations, subsequent outbreeding depression and any fitness recovery (which can be substantial and rapid; Edmands et al. 2005; Erickson and Fenster 2006). Combined with estimates of genetic divergence using neutral genetic markers, this type of information can help decision-making by conservation managers about the feasibility of genetic translocations (Holmes et al. 2008). However, common garden or transplant experiments are not possible for many species of immediate conservation concern, given need for rapid action, and low availability of individuals for experimentation. For these cases, Frankham et al. (2011) have proposed a framework for evaluating the risk of outbreeding depression, based upon questions about taxonomic status, fixed chromosomal differences, historical gene flow, evolutionary relationships, environmental differences between populations and the number of generations in different environments. In many conservation efforts, options for increasing genetic diversity and adaptive potential are often limited (see *Burramys parvus* example below); these must be judged differently as the loss of genetic diversity and increased genetic load could lead to the rapid extinction of unique populations or species. The risk of outbreeding depression therefore must be weighed against the immediate risk of population decline/extinction in the absence of translocation.

Weighing the risks

Translocations can either have beneficial (heterosis) or deleterious effects on reproductive fitness (outbreeding depression), that can change over time, and both effects can occur simultaneously (Marshall and Spalton 2000).

Box 2. Impacts of different breeding systems and their implications for translocations

Asexual Species: Asexual eukaryotic species and populations without genetic diversity have limited potential to show adaptive evolution, as they rely on recent mutations for genetic change. In the absence of sexual reproduction, neither inbreeding nor outbreeding depression can occur, unless there is some sexual reproduction. When considering translocations for asexual species, it is crucial to identify and characterize different clones. For a purely asexual species, the best clones in terms of adaptation to the translocation site would usually be recommended for use.

Selfing Species: Strictly selfing species do not outcross, and so outbreeding depression will not occur. However, most selfing species have at least occasional outcrossing. They typically exhibit less inbreeding depression than outbreeding species (Byers and Waller 1999). When considering translocations, the one or two populations best genetically adapted to the translocation site would generally be recommended for use. A single translocated selfing population would typically have very limited ability to adapt to the translocation site, particularly as selfing species can lack genetic variation, and translocations might benefit from using multiple source populations for maximizing future evolutionary potential.

Self-incompatible species: Self-incompatible species have a higher requirement for gene flow among populations than for other diploids. High levels of gene flow maintain adequate levels of self-incompatibility alleles (see (Young et al. 2000a) and require that multiple populations are used as sources for translocations, or that recipient populations are augmented frequently.

Haplodiploid Species: Haplodiploid species are less sensitive to inbreeding depression than equivalent diploid species, because of purging of deleterious alleles in haploid males (see Peer and Taborsky 2005; Frankham 2010). Haplodiploid species have a higher requirement for gene flow among populations than for diploids. This is required to maintain adequate numbers of alleles at sex-determining loci (see Zayed and Packer 2005). Inbreeding depression and heterosis are less important concerns for translocations of haplodiploids than diploids, while the risk of outbreeding depression is greater. Further, the need for genetic restoration in haplodiploids is greater than for diploids, to maintain sex allele genetic diversity.

Polyploid Species: We do not expect the recommendations for translocations to differ materially for polyploid versus diploid species. In general, polyploids will be less susceptible to small population size, self incompatibility and limited gene flow than diploids.

For example, crosses between three subspecies of deer mice (*Peromyscus* spp.) were overwhelmingly beneficial (see Frankham et al. 2011). However, F2 and backcross generations also showed deleterious effects of outcrossing, but these effects were small and restricted to subspecies adapted to different environments. The benefits of crossing populations (F1 and/or F2 compared to parental means) typically increase as the parental populations are more inbred (Fenster and Galloway 2000). Conversely, the risks of outbreeding depression increase when the populations are adapted to different environments (but see Hereford 2009), or when they are characterized by fixed chromosomal differences (Frankham et al. 2011). Neutral locus divergence is a poor predictor of outbreeding depression (McClelland and Naish 2007), but rather shows a positive relationship with F1 mean for quantitative characters (McClelland and Naish 2007), predicting heterosis rather than outbreeding depression.

Even when mixing populations results in outbreeding depression, natural selection acting on enhanced genetic diversity can remove the deleterious fitness effects over time and in some cases yield fused populations with higher fitness than either parent (Carney et al. 2000; Erickson and Fenster 2006). Deleterious effects of outbreeding depression may also be mitigated via a range of management strategies. In cases of revegetation, planting excess seeds/seedlings should allow poorly adapted genotypes to be removed via natural selection (Broadhurst et al. 2008). Backcrossing to parental stocks may also obviate the immediate effects of outbreeding depression.

Introductions to maintain evolutionary potential under environmental change

Translocations and environmental change

As well as translocating threatened species for augmentation or re-introduction, there is also interest in using translocations to alleviate threats of detrimental environmental change including climate change (Hunter 2007; McLachlan et al. 2007; Grueber and Jamieson 2008; Hoegh-Guldberg et al. 2008; Menges 2008; Ricciardi and Simberloff 2009; Richardson et al. 2009). This may involve moving species beyond their current range (Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009; Richardson et al. 2009) to future suitable climates (Mueller and Hellmann 2008) or as an option for species at immediate risk of extinction (Hoegh-Guldberg et al. 2008). For these introductions (also termed 'assisted colonization', 'managed relocation' and 'assisted migration') (Seddon 2010), a different set of genetic issues becomes important. Source populations must be 'genetically matched' to recipient sites to ensure that genotypes adapted to local conditions at the recipient site

Table 2. Outcomes, risks and consequences associated with different types of translocations.

Outcome	Risk	Consequence	Likelihood	Mitigation/Research
Augmentation				
Translocation occurs	Outbreeding depression	Decreased fitness of offspring from crosses	Variable, depends on past isolation, chromosome incompatibility	Evaluate in preliminary crosses, compensate through higher numbers; Obtain genetic data (nuclear and mtDNA) and evaluate according to Frankham et al. (2011)
	Loss of local adaptation	Decreased population fitness	Variable, depends on genotype–environment interactions	Use mix of source populations, compensate through higher numbers to allow natural selection Allow/enable backcrossing to recipient population
	Replacement of recipient genetic background	Loss of uniqueness, local adaptability	Low to medium: depends on donor numbers/fitness	Restrict donor numbers to minimize impact if considered a threat
	Disease transmission	Spread of disease could have disastrous consequences	Low: depends on species	Ensure only healthy material is translocated; If appropriate, quarantine prior to release
Translocation abandoned	Inbreeding and genetic load	Loss of genetic diversity, decreased fitness, increased extinction risk	Medium to high, depends on population size and gene flow	Increase potential for gene flow; controlled crossing strategy to minimize inbreeding
	Environmental change in remnant population	Loss of evolvability, increased extinction risk	Medium to high, particularly given climate change, fragmentation etc	Consider other translocation sites; Consider captive breeding as insurance
	Demographic stochasticity	Loss of evolvability, possibility of extinction	Low to high, depending on population size	Consider other translocation sites; Consider captive breeding as insurance
Introduction/reintroduction				
Translocation occurs	Displacement of species following hybridization, although hybridization can also be beneficial	Loss of local biodiversity, although genetic variance can also be increased	Low, depends on presence of closely related species	Assess presence of species from same genus, evaluate past hybridization in target group with molecular markers
Translocation abandoned	Ecological catastrophe	Sharp decrease in population size or extinction	Medium to high, unless species is widely distributed	Consider other translocation sites; Consider captive breeding as insurance

are translocated. Further, evolutionary genetic potential (or *genetic adaptation*, see Table 1) must be a primary consideration to ensure that threatened populations can adapt to future environmental changes.

These issues are relevant to more common species as well as threatened species that have been the focus of discussion around augmentation, introduction and re-introductions. Increased rates of species invasions (Walther et al. 2009), rapid rates of environmental change driven by global warming (Croxford et al. 2002) and human-mediated habitat fragmentation and modification have enormous impacts on ecological and evolutionary processes (Parmesan 2006). Therefore, species likely to be threatened in the future include many that are currently common (Gaston 2010). Even when species are not threatened, their role as keystone species in ecological commu-

nities may be at risk (Gaston 2010), such as coniferous forests under the threat of bark beetles triggered by warming conditions (Cudmore et al. 2010). In these cases, augmentation and genetic matching may be pivotal to enhancing adaptation to current and future conditions and restoring gene flow across fragmented landscapes (Rice and Emery 2003). Increasing genetic diversity by using a mixture of individuals from several source populations will promote adaptive potential for evolutionary change and enhance the establishment and persistence of the translocated populations (Broadhurst et al. 2008; Sgrò et al. 2011). This approach would also address other critical issues associated with the use of genetically limited stock as sources for translocations, including avoiding the deleterious effects of inbreeding and the possibility of creating ‘genetic ghettos’ (Frankel 1974; Moritz 1999).

When translocations are focussed on increasing the adaptability of populations under environmental change rather than just increasing genetic variation, they depend on generating variation at adaptive genetic loci. These are being rapidly isolated by a variety of techniques (Hoffmann and Willi 2008; Nadeau and Jiggins 2010) including the extent to which putative adaptive markers are differentiated from neutral variation when populations adapted to different conditions are compared (e.g. Hohenlohe et al. 2010; Narum et al. 2010). Genetic differentiation at neutral markers then reflects population processes unrelated to adaptation including patterns of recent gene flow and changes in population size as well as historical connectivity, and a combination of mitochondrial markers as well as microsatellites or other nuclear markers is often used to separate these processes (e.g. Mitrovski et al. 2007; Boissin et al. 2010).

Importance of evolutionary potential

Recent studies of contemporary evolution have demonstrated rapid evolution of traits in a number of taxa (Hendry et al. 2008; Gingerich 2009). Thus, evolutionary adaptation is an important way for natural populations to counter stressful conditions arising from recent climate change, rather than relying solely on plasticity or evading these conditions through dispersal. The evidence for rapid evolution in response to climate change in several short-lived species is clear (Umina et al. 2005; Reusch and Wood 2007), suggesting that many organisms have the capacity to respond to climate change within a timeframe of tens of years (Bradshaw and Holzapfel 2008). These responses depend on the presence of genetic variation in populations; in the absence of genetic variation, there is now strong evidence for an increased risk of extinction in wild populations (Spielman et al. 2004).

Population genetic and evolutionary models suggest that effective population sizes need to be in the thousands to obviate the effects of random genetic drift on genetic variation and thereby maintain adequate adaptive potential and evolvability under different types of selection (Lande 1995; Willi et al. 2006). Yet, many species now exist in fragmented landscapes, with restricted gene flow amongst populations. This has resulted in isolated populations that are often well below adequate effective population sizes for maintaining their adaptive potential. The imperative for conservation managers should now be conservation and restoration practises that maintain and increase genetic diversity within species, thereby promoting *in situ* adaptive processes. Translocations must be targeted at increasing gene flow between isolated populations of a species or populations that are likely to be challenged by future environmental change (see Table 1). The long-term

implications of ignoring adaptability when planning translocations will extend well beyond the persistence of species, with potential impacts on biodiversity and ecosystem function (Bailey et al. 2009) and resilience in response to climate extremes (Reusch et al. 2005).

Genetic risk: losing local adaptation

The potential for translocations to maximize population adaptability under climate change is increasingly being considered in the context of landscape restoration (Menges 2008; Jones and Monaco 2009); however, the perceived risk of losing local adaptation is a serious impediment to this approach being put into practice. Loss of local adaptation (Box 1) has long been considered a risk to the success of translocations, and the focus has been on using local source populations (or provenances) when making decisions about which germplasm to source for restoration and reintroduction programmes (Callahan 1964; Keller et al. 2000; McKay et al. 2005; O'Brien et al. 2007). Although it is widely assumed that local adaptation will always result in a fitness trade-off between local and nonlocal environments, fitness trade-offs are not ubiquitous and are often weak with no long-term consequences (Hereford 2009). For instance, local adaptation in the pancontinental common reed, *Phragmites australis*, has not been sufficient to prevent the invasion of local North American populations by a haplotype introduced from Europe (Howard et al. 2008).

Despite this evidence, an emphasis on local provenance prevails. A '*local is best*' sourcing practise misses two important points that may impact restoration or reintroduction success in the face of future climatic changes (Sgrò et al. 2011). The first is that there is a risk of encouraging the establishment of populations that do not harbour sufficient genetic variation and evolutionary potential resulting in the selection of inbred or genetically depauperate seed sources (Broadhurst et al. 2008). The second issue is that environmental conditions driving local adaptation can change very rapidly such that the conditions, for example, under which a 100-year-old tree established are likely to be quite different to those existing today. Source material from more distant (geographically and ecologically) populations may often harbour adaptations that more closely match the environment of the focal restoration site today and into the future.

Weighing the risks: genotype–environment interaction and gene flow

In moving beyond local provenance, the prevalence and strength of genotype–environment (GE) interactions (Box 1) must be considered both in the context of

current and predicted future climates. Sgrò et al. (2011) suggest natural gene flow dynamics that facilitate the redistribution of genetic variation within a species also need to be considered. Where GE interactions appear weak or have not been tested, it may be sensible to simulate leptokurtic gene flow dynamics, where most propagules disperse proximally, but with a significant proportion moving over longer distances (Byrne et al. 2007, 2008; Sgrò et al. 2011). Such a restoration practise would mix locally sourced material, taken from genetically healthy stock, with proximate and ecogeographically matched sources. In addition, a smaller proportion of material, depending on the natural gene flow dynamics of the focal species, should be sourced from much further afield to increase genetic variation and promote adaptation. This practise, defined as using a combination of source populations or ‘composite provenancing’ by Broadhurst et al. (2008), represents a cautionary strategy that might also be appropriate for species where GE interactions are strong but the predicted changes in climate are small or unknown.

Circumstances under which translocations might also be considered in the context of evolutionary resilience and climate change can involve situations where there is strong local adaptation (Sgrò et al. 2011). Moving individuals from warm-adapted populations to currently colder locations that are experiencing climatic warming may increase the probability of adaptation, and thus persistence and resilience of cold-adapted populations under a warming

climate. Such translocations could be considered in recently fragmented landscapes where a species displays a wide altitudinal or latitudinal range and ecological risks are likely to be minimal (Hoegh-Guldberg et al. 2008; Lopez et al. 2009). The long-term aim of such translocations is to create populations that harbour the adaptive genetic diversity to enable ongoing adaptation to climate change and other environmental threats. This may be considered a management tool for species that are not currently threatened, but are likely to be so under a climate warming scenario (e.g. the platypus, *Ornithorhynchus anatinus*). Such intervention, while potentially controversial, may remove the need for ongoing intervention and management, though it can only reasonably be considered when predictions of environmental trajectories are clear.

Source provenances for new environments

Introductions of species into areas where they currently or historically have not existed are being considered a way of tackling climate change in restoration and revegetation programmes (Hoegh-Guldberg et al. 2008). A number of issues need to be considered to increase the likelihood of successful establishment; this depends on levels of genetic variability in source populations and the nature of environmental gradients along which populations are being introduced (Fig. 1). Where levels of genetic variation are high in source populations, and there is a clear environmental gradient such as associated

	Genetic diversity of source population	Distribution of source population	Solution	Schematic
1	High	Continuous	Take from entire distribution, or tip if this matches target area ecologically	
2	High	Fragmented along cline	Take from fragment(s) that matches target area ecologically. This might be closest population (particularly in altitudinal series)	
3	High or low	2+ populations – large disjunction – no population adapted to site	Cross and pool (especially if low)	
4	Low	Fragmented along cline	Take from multiple populations to augment diversity and adaptation, match ecologically if possible, if altitudinal pool populations at similar altitude	

Figure 1 Genetic considerations in establishing populations outside the current or historical distribution of a species. Relevant scenarios depend particularly on whether levels of genetic variability in the populations are high or low, but also on the distribution of populations along the gradient.

with elevation or aridity, material could mostly be sourced from adjacent populations (Fig. 1, scenarios 1–4). The likelihood of suitable genetic source material could also be enhanced by composite provenancing (Broadhurst et al. 2008), sourcing some individuals from multiple populations to increase adaptive potential, as insurance for uncertainty in climate predictions. While invasive species are generally successful for a number of biological/ecological reasons, they highlight the importance of climate- and habitat-matching for successful *introductions* (Lopez et al. 2010). By moving species into habitats that are likely in the future to match current climatic conditions, genotypes can potentially be matched to future climate and habitat predictions. Maximizing genetic diversity, mixing genotypes by composite provenancing and matching genotypes to future habitat/climate predictions (predictive provenancing; Atkins and Travis 2010) are all options that need to be considered in future introductions for restoration and revegetation.

The movement of species beyond their current range has also been suggested as an option for species at immediate risk of extinction (Hoegh-Guldberg et al. 2008) and has been undertaken as a last resort in some instances (Jamieson et al. 2006; Grueber and Jamieson 2008; Miskelly et al. 2009). Unfortunately, species at immediate risk of extinction are often already suffering from a genetic viewpoint (inbreeding depression, losses of genetic diversity, maladaptation etc), and these translocations are used to free them from immediate threats such as predation, disease and habitat loss. In these instances, *genetic capture* (Table 1) is the only available genetic translocation option, but unless effective population size can be increased dramatically, then genetic diversity will continue to decline. Consideration should be given to using *introduction* translocations and future climate/habitat matching for threatened species that are predicted to continue to decline under climate change scenarios. In these instances, genetic variation, genetic mixing and genotype-matching may all be considered in introductions (Fig. 1). To increase genetic variation and take advantage of heterosis, it may be sensible to source material from multiple populations even when these are located along a gradient (Fig. 1, scenarios 5–9).

Genetic risks: hybridization

Introductions into new environments carry the risk of increasing the chance of hybridization events between closely related species, particularly in plants. Interspecific hybridization is often thought of as being an evolutionary dead end with hybrids typically less fit than either parent (Mayr 1963). Similarly, intraspecific hybridization between two distantly related populations is also thought

to be maladaptive [see ‘outbreeding depression’ above and in (Box 1)]. Furthermore, some have suggested that the effects of hybridization can be particularly deleterious when dealing with rare species with narrow distribution (Levin et al. 1996) and that in situations where there is weak pre-mating isolation hybridization can cause extinction in just a few generations (Rieseberg 2006). Although interspecific hybridization between abundant alien and rare native species can threaten populations of the native species, such situations should be infrequent where proposed translocations or restoration is adequately planned and assessed and take into account common close relatives to any locally rare species where hybridization may occur and lead to species or genomic extinction.

Alternatively, there is much evidence that suggests adaptive radiations can be linked to hybridization events (Dowling and Secor 1997; Seehausen 2004; Stelkens et al. 2009; Arnold and Martin 2010) because they introduce novel genotypes upon which natural selection can act. For example, in the annual sunflower *Heliathus*, interspecific hybridization has led to the generation of new species that occupy new environments showing that hybridization has facilitated ecological novelty (Rieseberg et al. 2003). Although the risks of outbreeding depression are greater for interspecific hybrids (see above), it is worth noting that hybridization can increase the rate of adaptive evolution, particularly for making major ecological shifts (Rieseberg et al. 2003; Arnold and Martin 2010; Grant and Grant 2010), and could be considered in conservation and restoration efforts as a possible mitigation strategy against a changing environment where other options for maintaining adaptive potential are not available.

One obvious situation however in which intraspecific hybridization is to be avoided is when the species under consideration is made up of several chromosome races. In this case, mating between individuals sourced from populations with different ploidy levels will generally result in the production of progeny that are infertile because of meiotic irregularities resulting in the production of unbalanced gametes. Such an extreme case of hybrid dysgenesis is more likely in plants, where interfertile chromosome races are not uncommon. A good example of such a situation is in the Australian grassland herb *Rutidosia leptorrhynchoides* which exists as both diploid and tetraploid populations, the triploid progeny of which occur at low frequencies and have significantly reduced pollen fertility (Young and Murray 2000).

A simple risk-assessment framework for translocations

Based on the different risks associated with translocations, we have developed a simple decision tree (Fig. 2) and

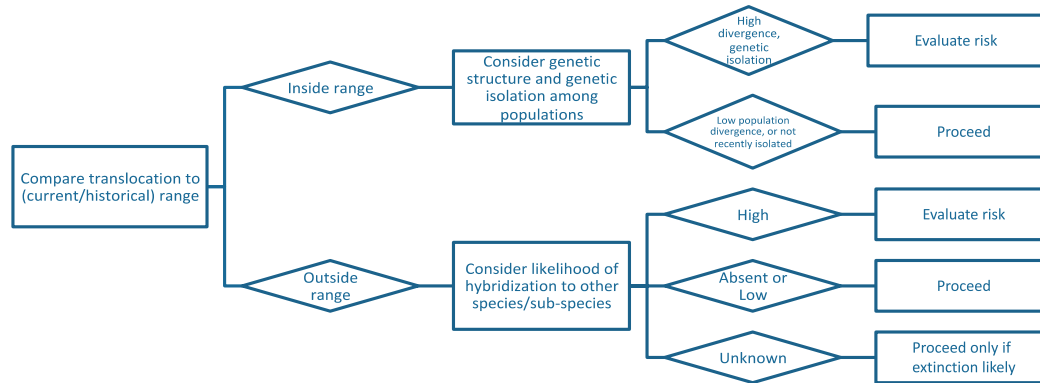


Figure 2 Simplified decision tree for determining whether to proceed or assess risk in translocation.

risk-assessment framework (Table 2) that provides a guide for managers considering translocations. That is, implementation of translocations within a risk management framework will enable the benefits of translocation to be realized while minimizing potential negative impacts. It also identifies those risks that can be mitigated via additional management decisions. Importantly, this risk management framework will guide decisions about translocations even in the absence of detailed information on the reproductive biology and genetics of the species concerned, a situation often faced by managers.

The first consideration in the decision tree (Fig. 2) is whether the translocation will occur inside (reintroduction or augmentation) or outside (introduction) the recent historical range of the species. Note that genetic data can contribute information about the history of genetic isolation among populations (e.g. indicate whether target and source populations for translocations have been connected recently in evolutionary time) as well as patterns of genetic divergence. Small populations in a fragmented landscape might show a high level of divergence even though they have not been isolated for a long time. In cases where divergence is low or isolation relatively recent, a translocation might then proceed without the need to consider the risk-assessment table (Table 2). However, a manager will often need to evaluate the risk of a conservation or restoration translocation (for instance, if there is genetic structure within a species or the possibility of interspecific hybridization). If so, the risks associated with either proceeding with a translocation or abandoning it must be weighed alongside any mitigation steps that can be undertaken to minimize risks (Table 2). Below we apply this risk-assessment framework to case studies from the literature. The case studies generally are in favour of translocations; however, there are examples in the literature where proceeding with a translocation would not be recommended (e.g. the infamous *Capra ibex ibex* where two closely

related species from different regions that were adapted to breed in different seasons were introduced into the former Czechoslovakia and subsequent hybrids failed because of timing of breeding; Hunter and Gibbs 2007; Frankham et al. 2011).

Note that understanding genetic structure and evolutionary relationships within a species is an important evaluation step for a translocation in a risk-assessment framework, especially for assessing gene flow and predicting outbreeding depression (Frankham et al. 2011). While Table 2 can be used to evaluate the risk of a translocation in its absence, it is highly recommended that genetic data be generated to help with the risk-assessment process. Genetic structure can be evaluated relatively easily, with either maternally inherited (mitochondrial or chloroplast DNA) or nuclear sequence/marker data in a relatively short timeframe (approximately 1–6 months, depending on method). If a translocation is undertaken, it is strongly advised that genetic data are also obtained to monitor the effectiveness of the translocation in achieving the goals. Effective monitoring is often lacking in translocations, yet is critical for understanding success and failure (Armstrong and Seddon 2008; Seddon 2010).

Applying the risk-assessment framework to case studies

Burrhamys parvus and the restoration of genetic diversity in the Mt Buller population

Burrhamys parvus, the mountain pygmy possum, is endemic to the alpine areas of Australia and restricted to three mountain ranges (the Mt Higginbotham-Loch/Bogong High Plains, Mt Kosciuszko and Mt Buller) and is considered critically endangered by the IUCN. The Mt Buller population has gone through a dramatic population crash in the last 15–20 years, and Mitrovski et al. (2008) subsequently documented one of the most rapid declines in genetic diversity for mammalian species ever recorded.

Genetic diversity (as measured by heterozygosity and allelic diversity at microsatellite loci) on the Mt Buller population was reduced by over 65% between 1996 and 2006, and inbreeding was a significant issue (Mitrovski et al. 2008). The populations in the central (Mt Higginbotham-Loch/Bogong High Plains) and northern (Mt Kosciuszko) regions are genetically distinct from the southern (Mt Buller) population based on microsatellite and mtDNA (Mitrovski et al. 2007), but have maintained a significantly higher genetic diversity in the same period. It has been suggested that individuals from the central region should be translocated to the Mt Buller population to alleviate the effects of inbreeding and genetic load, restore genetic diversity and increase the adaptive potential and long-term persistence of this population (Mitrovski et al. 2008). Under the scheme proposed in Table 2, this would be an *augmentation* translocation with the aim of *genetic rescue* and *genetic restoration*.

Applying this situation to the decision tree (Fig. 2), the proposed translocation is inside the species current range, genetic structure is high between mountain ranges and populations (Mitrovski et al. 2007) and therefore the outcome is to 'evaluate risk' through Table 2. If we consider the outcome *Translocation occurs* first, there are four areas of risk to evaluate. (i) For risk of outbreeding depression, the consequence is reduced fitness and likelihood is moderate given that these populations have been evolving independently for approximately 20 000 years (Mitrovski et al. 2007). A mitigation strategy would be to evaluate preliminary crosses, either in the field or in captivity (see below). (ii) For risk of loss of local adaptation, the consequence is decreased fitness, likelihood is moderate (in the absence of direct knowledge) and a mitigation strategy would be to allow backcrossing to recipient population. (iii) For risk of replacement of recipient genetic background, the consequence is replacement of Mt Buller genome with Central genome, likelihood is low and mitigation would be to translocate only males and monitor the frequency of gene flow into the population via neutral markers (applying the *genetic rescue* translocation approach in Table 1). (iv) For risk of disease transmission, the consequence could be introduction of a disease that could cause extinction of the Mt Buller population, likelihood is minimal given that there are no known diseases present in populations of *B. parvus*, and a mitigation would be to vet check the animals (and quarantine if appropriate).

If the outcome of the decision tree is *translocation abandoned*, then the risks will all have similar consequences, with a continued loss of genetic variation, an increase in genetic load and relatedness amongst Mt Buller individuals, and a high extinction threat. Demographic stochasticity and an ecological catastrophe, given the

current population size of approximately 30 individuals, are highly likely to cause extinction. The only mitigation strategy would be to undertake a captive breeding colony for short-term viability.

If we compare *translocation occurs* with *translocation abandoned*, then the recommendation under this risk-assessment would be to proceed with repeated translocations with a number of mitigation steps added (above) and the improvement of habitat to sustain a larger population. The major mitigation strategy would be to evaluate any large negative effects of outbreeding depression either by limiting the introduction in the field to a defined area on Mt Buller and assessing the viability of hybrids or assessing this and sterility in captivity. It would be recommended that the guidelines for *genetic rescue* and *genetic restoration* are followed (Table 1).

A population translocation of the vulnerable *Acacia attenuata*

Acacia attenuata is an endemic shrub species confined to south-eastern Queensland, Australia (Brownlie 2007). This species is listed as Vulnerable under the Environment Protection and Biodiversity Conservation Act Australia (Brownlie 2007) and is found in a highly fragmented distribution, particularly in the southern and central regions across its range of approximately 400 km between north Bundaberg and the Gold Coast in Queensland. Seedling recruitment in *A. attenuata* is disturbance dependent, with fire strongly associated with mass seedling recruitment. Inappropriate fire regimes can greatly affect the recruitment of seedlings, with some species of *Acacia* suffering population declines and even localized extinction due either to an increase in frequency of fire (high seedling mortality) or a decrease in fire frequency (resulting in very low recruitment levels). Combined with urbanization, fire regimes have likely led to the rapid decline and fragmentation of *A. attenuata* throughout its range. An urban development was planned within an area that contained one of the largest and most genetically diverse populations of *A. attenuata*, at the southern end of its distribution at Bundilla (Brownlie et al. 2009). A Compensatory Habitat Project was initiated that considered the genetic and ecological implications of the development and then proposed a translocation of mature plants to a nearby site that would capture the genetic diversity found within the Bundilla population. This would be defined as a *reintroduction* translocation with the aims of *genetic capture* of the existing source population.

Applying this situation to the decision tree (Fig. 2), the translocation is inside the species current/historical range, and therefore, we need to consider the genetic structure

of the species before deciding whether to undertake the translocation. Brownlie et al. (2009) have recently performed a population genetic study using allozymes of 14 populations throughout the distributional range of *A. attenuata* in Queensland. The data indicate deviations from Hardy–Weinberg equilibrium and high levels of inbreeding within populations, with some structuring amongst populations. However, this did not follow an isolation-by-distance pattern, and several subpopulations sampled around the Bundilla development site that border the proposed translocation site were not significantly different (suggesting that these may be remnants of a recently continuous population). Given that genetic structure is low in populations, and that there is no evidence of structure between the populations immediately around Bundilla and the proposed translocation site, then we would recommend proceeding with the translocation based on the decision tree (without a need to proceed to Table 2). It is recommended that the guidelines for *genetic capture* (Table 1) are followed for this translocation.

Population augmentation of the grassland herb *Rutidosia leptorrhynchoides*

Rutidosia leptorrhynchoides (the Button Wrinklewort) is a self-incompatible grassland herb endemic to the temperate grasslands of southeastern Australia. The species is listed as Endangered under the Environmental Protection and Biodiversity Conservation Act Australia (Morgan 1995) and is now only found in 23 fragmented populations in two geographical groups one in eastern New South Wales and the Australian Capital Territory and the second in western Victoria (Young et al. 1999). Demographic analysis of populations has shown strong relationships between population size and seed set with small populations of <200 individuals (which make up approximately half of current populations) setting less than a third of the seed of those bigger than 1000 flowering plants (Morgan 1995; Young et al. 2000c). Analysis of pollinator limitation, inbreeding levels and genetic diversity at the self-incompatibility locus show this reduction in seed set to be directly because of loss of S alleles in these small populations leading to genetic mate limitation which reduces fertilization success (Young et al. 2000c; Young and Pickup 2010). Simulation modelling shows these small populations to exhibit significantly reduced population viability as measured by both population size and extinction probability (Young et al. 2000b). Interpopulation crossing studies have demonstrated that mate limitation can be eliminated and seed set restored in small populations by introducing new S alleles from other populations (Pickup and Young 2008). Based on this, augmentation of small populations with germplasm from

larger populations has been listed as a management action in the *R. leptorrhynchoides* species Recovery Plan (NSW DEC 2010). This would require moving germplasm (plants, seed or pollen) between the disjunct northern and southern parts of the range as populations in the south are generally small.

Looking at this situation, it represents an example of genetic rescue (Table 1). Applying the decision tree (Fig. 2), the action would be moving plants within the current range and the issue then becomes is there ecologically important genetic structure among populations and across the range? Young et al. (1999) undertook an allozyme-based study of genetic structure in this species and demonstrated only modest genetic differentiation among populations in terms of neutral markers, even between the north and south of the range. However, these data did reveal evidence of polyploidy in some southern populations. The presence of autotetraploid populations was confirmed by Murray and Young (2001) using cytogenetic analysis of chromosome number and karyotype. These data showed that while northern populations are exclusively diploid ($2n = 2x = 22$), southern populations were a mixture of both diploid and autotetraploid ($2n = 4x = 44$) populations, and that the two chromosome races are interfertile (Young et al. 2000c). Given such very strong genetic differentiation, that would have severe consequences for fitness if diploid and tetraploid populations were mixed, we would recommend that augmentation of small populations can only proceed once the cytogenetic make up of both target and source populations has been established. Once this is carried out, guidelines for genetic rescue (Table 1) should be followed.

Translocations outside historical range: introduction of the eastern barred bandicoot

There are few examples where translocations have been undertaken to move individuals outside their historical range for a genetic reason. One such introduction being considered is the translocation of Victorian eastern barred bandicoot, *Perameles gunnii*, to French Island (17 000 ha) in Victoria, Australia (Richard Hill, personal communication). This species, once widespread across western Victoria (Australia), is now extinct in the wild on mainland Australia and only persists as part of a captive breeding programme at Zoos Victoria (Winnard and Coulson 2008). However, 20 years of captive breeding has seen a continual decline in genetic diversity, with a loss of approximately 30–40% over this period (Weeks 2010). A subspecies is widespread in Tasmania (Australia), but also thought to be in decline. The Victorian and Tasmanian *P. gunnii* have likely been isolated for approximately

10 000 years (Weeks 2010). Consideration is being given to crossing Victorian and Tasmanian *P. gunnii* to increase genetic diversity and introducing these hybrids to French Island, which sits outside its historical range, but importantly does not contain a key introduced predator, the red fox, *Vulpes vulpes*.

In this situation, the translocation is outside the current/historical range, there are no related species on the island, although the individuals translocated to the island are likely to be F1 hybrids between Victorian and Tasmanian *P. gunnii*. Weeks (2010) showed that there is quite high divergence at the nuclear level between these populations, and therefore, the outcome of the decision tree is to evaluate risk. In Table 2, if the translocation occurs, the greatest risk will be outbreeding depression between Tasmanian and Victorian *P. gunnii*. To mitigate this risk, careful evaluation of hybrid offspring and outbreeding depression is recommended in captivity. If the translocation is abandoned, continued loss of genetic diversity would occur in captivity, with extinction the likely long-term scenario. Therefore, we would recommend the translocation proceed, but only after outbreeding depression has been evaluated in captivity.

Conclusions

Threats to species or population persistence from changing environments are increasing the need for translocations as conservation management actions to increase resilience and persistence in climate change adaptation programmes. Genetic issues are likely to be critical to the aims and success of many translocation programmes, and their importance is likely greater in the face of environmental change. To ensure long-term persistence of populations and species, programmes should focus more on increasing genetic adaptive potential as well as restoring genetic variability. Genetic targets must be established for all programmes, and the best ways of achieving these targets should be an integral part of any management plan. Translocations provide an insurance mechanism for populations to adapt to future conditions, but there are risks that need to be weighed carefully on a case-by-case basis. Evolutionary issues must be considered in translocation programmes even when data on genetic variation and adaptation are unavailable, but these data should be collected routinely in management programmes.

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