

REVIEW ARTICLE

# Restoring species through reintroductions: strategies for source population selection

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Only a quarter of reintroduction programs succeed in restoring a self-sustaining population of an extirpated species. Optimal source population selection for restoration efforts can increase the fitness of translocated individuals and improve reintroduction success. Here, we describe the support for two strategies for selecting source populations: pre-existing adaptation and adaptive potential. The pre-existing adaptation strategy focuses on source populations with a high frequency of genotypes that confer adaptations, and within this strategy we detail the ancestry matching approach and environment matching approach. The adaptive potential strategy focuses on source populations with high heritable genetic variation that confer the potential to adapt, and within this strategy we detail the single source population approach and multiple source population approach. We review empirical tests of the different approaches, and find stronger support for the pre-existing adaptation strategy than the adaptive potential strategy. We provide a framework for source population selection based on the two strategies, highlighting the importance of gathering information on key environment features in the source and restoration locations, as well as detail the knowledge gaps. Filling these knowledge gaps is important for validating and potentially revising our proposed framework, and ultimately improving the success rate of restoring extirpated populations.

**Key words:** adaptability, environment features, extirpated species, genetic similarity, geographic distance, population size

## Implications for Practice

- Explicitly incorporating evolutionary and ecological considerations into source population selection for reintroduction programs could greatly improve their success at restoring self-sustaining populations.
- Both shared ancestry and environmental similarity are useful for improving restoration program success, although the benefits of adaptive potential remain unconfirmed.
- Measuring the population growth rate (intrinsic  $r$ ) of multiple source populations across gradients of genetic similarity, environment similarity, and heritable genetic variation will help clarify the effectiveness of the source population selection approaches.

## Introduction

Restoration ecology has a focus on improving degraded ecosystems by restoring fundamental processes and habitat features (Seddon et al. 2007). This restoration often emphasizes the physical habitat and assumes that extirpated species will recolonize by natural dispersal (Lipsey & Child 2007). However, in the event of a barrier to natural dispersal, the ecosystem functions provided by native species may be unfulfilled, resulting in incomplete restoration of ecosystem services and integrity (Worm et al. 2006; Lipsey & Child 2007).

Reintroduction programs, in which conspecific individuals are translocated into formerly occupied locations, have emerged

as an important tool for reversing extirpations and restoring ecosystem function (Lipsey & Child 2007; Seddon et al. 2007; Armstrong & Seddon 2008; Seddon 2010; IUCN 2013). These programs are intuitively appealing as a means of restoring populations and communities toward an historical baseline, and have been practiced for over a century (Kleiman 1989). In particular, there has been a pronounced increase in the number of reintroduction programs, rising from 124 species in the early 1990s to 424 species in 2005 (Seddon et al. 2014). However, even in the absence of obvious barriers to population restoration, only 25–30% of reintroduction programs are successful at restoration (Fischer & Lindenmayer 2000; Godefroid et al. 2011). To increase success, a better understanding of the factors contributing to the outcome of reintroduction programs is needed.

A number of guidelines and best practices for reintroduction programs have emerged, which largely focus on habitat restoration and the demographics and logistics of translocation (Montalvo et al. 1997; Armstrong & Seddon 2008). For example, these guidelines indicate that population restoration

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should be considered only if the original causes of the extirpation have been addressed and the habitat has been restored to a state that should again be capable of supporting the species (Dobson et al. 1997; Palmer et al. 1997; Cochran-Biederman et al. 2015). Other guidelines suggest avoiding source populations that could suffer from deleterious genetic effects such as low heritable genetic variation, inbreeding depression, or domestication (Montalvo et al. 1997; Weeks et al. 2011). Adequate heritable genetic variation might be important for adaptation to environment changes, such as those associated with global climate change and anthropogenic disturbance (Jones 2003, 2013; Broadhurst et al. 2008; Sgrò et al. 2011; Weeks et al. 2011; Breed et al. 2013; Kettenring et al. 2014; Jahnke et al. 2015). Inbreeding depression may occur in source populations when fitness-related traits (e.g. survival and reproductive traits) are reduced by inbreeding, and typically results from either the expression of deleterious recessive alleles or the loss of diversity at loci where heterozygosity is advantageous (Allendorf et al. 2013). Small, declining, or fragmented populations should thus be avoided as source populations because they may have low adaptability due to low heritable genetic variation and may also suffer from inbreeding depression (Breed et al. 2013). Source populations may also be impaired by domestication selection that can result in the accumulation of alleles that are deleterious to individuals released into the wild (Allendorf et al. 2013). Domestication selection may be especially problematic when a population has had multiple generations of captive breeding (Lynch & O'Hely 2001; Araki et al. 2007). These recommendations on the genetics of source populations have largely been incorporated into reintroduction programs (Armstrong & Seddon 2008; Vander Mijnsbrugge et al. 2010; Weeks et al. 2011; IUCN 2013; Mijangos et al. 2015).

Despite potentially major effects on the outcome of population restoration efforts, few clear guidelines exist on how to optimally select source populations for translocation (Cochran-Biederman et al. 2015). Based on case studies reviewed by the World Conservation Union (Soorae 2008, 2011), reintroduction programs typically select one source population for restoration based on: (1) the only remaining source population; (2) a source population of sufficient size that it should not have a reduction in viability if individuals are removed for translocation; or (3) the closest geographic source population to the restoration location. However, we propose that source population selection based on an evolutionary and ecological perspective could greatly improve the success of reintroduction programs, and the strategies for identifying these source populations are the focus of this review. Previous work on source population selection can be broadly categorized into the *pre-existing adaptation strategy*, which focuses on populations with a high frequency of genotypes that confer adaptations (i.e. high fitness) in the restoration location, or the *adaptive potential strategy*, which focuses on populations with high heritable genetic variation that confer the potential to adapt (i.e. respond to selection pressures) in the restoration location. Here, we review the theoretical and empirical support for these two strategies and develop needed recommendations for selecting source populations.

### Pre-Existing Adaptation Strategy

Source populations may differ in their viability in the restoration location because of genetically based differences in individual fitness resulting from local adaptation. Local adaptation is a genotype by environment pattern in which the genotypes of local individuals have higher fitness in their local environment than they do in a foreign environment (Kawecki & Ebert 2004). Local adaptation is both taxonomically and geographically widespread, with fitness advantages of local populations observed in 71% of reciprocally translocated plants and animals (Hereford 2009). Knowledge of local adaptation could therefore serve as a basis for identifying source populations with adaptations to the key environment features of the restoration location. The fitness advantage of local adaptation tends to be positively correlated with the genetic similarity and environment similarity between the source and foreign locations (Raabová et al. 2007; Hereford 2009; Fraser et al. 2011). Identifying source populations with adaptations to the key environment features of the restoration location can therefore be accomplished using genetic or environment similarity. We term these two approaches (1) ancestry matching and (2) environment matching, which are not mutually exclusive.

**Ancestry Matching Approach.** Using an ancestry matching approach, a source population is selected for translocation based on genetic similarity to the extirpated population. This approach is based on the premise that close genetic relatives could share genes that confer adaptations to the key environment features of the restoration location. The same genes may occur in both the source and extirpated populations because they were present in a recent common ancestor or were transferred between populations through gene flow (Moritz 1999). Reintroduction programs could use historical samples of the extirpated population, if available, and collect samples from source populations to directly measure genetic similarity. Similarity is typically estimated from phylogenetic relationships or historical gene flow calculated using genetic markers (for methods see Holder & Lewis 2003; San Mauro & Agorreta 2010; Marko & Hart 2011). Typically, several unlinked genetic markers, such as microsatellite loci or single nucleotide polymorphisms (SNPs), need to be used to provide sufficient resolution for estimating the genetic similarity between populations (Beaumont & Nichols 1996; Parker et al. 1998; Williams et al. 2014). Genetic similarity at neutral markers can also be examined in concert with similarity at functional markers to confirm that close genetic relatives share genes underlying adaptations (for methods see Krauss et al. 2013; Stingemore & Krauss 2013). Alternatively, geographic distance between the source and foreign locations can be used as a proxy for genetic similarity as there is often a correlation between the two variables (e.g.  $r = 0.22-0.52$  for two studies on plants, Montalvo & Ellstrand 2000; Raabová et al. 2007); albeit, direct estimates of genetic similarity had a stronger relationship with the fitness-related traits of translocated populations than geographic distance in these two studies.

**Environment Matching Approach.** Using an environment matching approach, a source population is selected for translocation based on environment similarity between the source and restoration locations. Locations containing similar key environment features tend to produce individuals with similar phenotypes, either through selection on the same genes (e.g. Campbell & Bernatchez 2004; Turner et al. 2010; Schumer et al. 2011) or on different genes that produce similar phenotypes (e.g. Nachman et al. 2003; Campbell & Bernatchez 2004; Hoekstra et al. 2006). Regardless of the underlying mechanism, reintroduction programs could measure the similarity of key environment features between source and restoration locations. Analysis of similarity is typically accomplished using distance matrices constructed of measurements of the key environment features (for methods see Montalvo & Ellstrand 2000; Raabová et al. 2007; Lawrence & Kaye 2011). Environment similarity can also be examined in concert with similarity at functional markers or quantitative traits to confirm that candidate environment matches possess adaptations for the restoration location (for methods see Garnier-Géré & Ades 2001; Krauss et al. 2013; Stingemore & Krauss 2013). Alternatively, geographic distance between the source and foreign locations can be used as a proxy for environment similarity as there is often a correlation between the two variables (e.g.  $r = 0.22$ – $0.75$  in Montalvo & Ellstrand 2000; Raabová et al. 2007); albeit, direct estimates of environment similarity had a stronger relationship with the fitness-related traits of translocated populations than geographic distance in these two studies (also see Lawrence & Kaye 2011).

#### Adaptive Potential Strategy

The second strategy for selecting source populations is to emphasize the potential to adapt to the key environment features of the restoration location. This strategy favors the translocation of source populations with high heritable genetic variation. Fisher's fundamental theorem of natural selection predicts that the rate of change in mean individual fitness should be equal to the heritable genetic variation in individual fitness of a population (Fisher 1930). Similarly, using the breeder's equation, the evolutionary response ( $R$ ) to selection is based on the selection pressure ( $S$ ) and the amount of heritable genetic variation ( $h^2$ ) underlying the phenotype ( $R = Sh^2$ ; Falconer & Mackay 1996). That is, for a given selection pressure, such as that exerted by a key environment feature, there is a stronger evolutionary response (genetically induced change in phenotype) when there is a greater amount of heritable genetic variation underlying phenotypes. An association between the amount of heritable genetic variation and the potential to adapt is supported by laboratory populations of *Drosophila melanogaster* (Reed et al. 2003). The amount of heritable genetic variation is also associated with local persistence in metapopulations of butterflies (*Melitaea cinxia*) (Saccheri et al. 1998). Two approaches that provide high heritable genetic variation are translocations of individuals from (1) a single source population that has high heritable genetic variation and (2) multiple source populations that are genetically or environmentally dissimilar from each other.

**Single Source Population Approach.** Using a single source population approach, a source population is selected for translocation because it possesses a high amount of heritable genetic variation. The amount of within-population genetic variation is typically estimated using neutral markers and indices such as heterozygosity, allelic richness, or the proportion of polymorphic loci (for methods see Excoffier & Heckel 2006; Williams et al. 2014). This approach assumes that heritable genetic variation scales with neutral genetic variation, which is supported in laboratory populations of *Drosophila* (Briscoe et al. 1992). Alternatively, population size can be used as a proxy for the amount of neutral genetic variation because of a correlation between the two variables ( $r = 0.7$  for animal populations, reviewed by Frankham 1996). However, a concern with these methods is that neutral genetic markers do not always correctly predict the amount of heritable genetic variation (Reed & Frankham 2001; McKay & Latta 2002). Quantitative genetic methods can instead be used to directly estimate the amount of heritable genetic variation for survival and fitness-related traits through parent–offspring correlation or breeding designs that examine variance among sibling groups (for methods see Falconer & Mackay 1996; Lynch & Walsh 1998). Although such analyses are often costly and infrastructure intensive, they have an advantage of being able to target specific traits that are thought to be important for fitness (e.g. Puurtinen et al. 2009).

**Multiple Source Population Approach.** Using a multiple source population approach, two or more source populations with distinctive genetic or environmental backgrounds are selected for translocation, which combined as a mixed-source group should produce a high amount of heritable genetic variation (Breed et al. 2013). Distinctive source populations can be identified based on genetic and environment dissimilarity, using methods similar to those described for identifying ancestry and environment matches. However, some caution is warranted when using the multiple source population approach because of two major concerns.

First, translocations from multiple source populations may result in interpopulation breeding, which can lead to outbreeding depression or hybrid breakdown (Lesica & Allendorf 1999; Weeks et al. 2011; IUCN 2013; Cochran-Biederman et al. 2015), especially with increasing genetic or environmental distance between the source populations (Montalvo & Ellstrand 2001; Frankham et al. 2011; Hufford et al. 2012). Outbreeding depression may arise in hybrids because of genetic incompatibilities between populations (Lynch 1991; Neff et al. 2011) and may not be detected until the second generation of interpopulation breeding (Edmands 2007). For example, outbreeding depression led to reduced growth of second-generation interpopulation hybrids when multiple source populations of Slimy sculpin (*Cottus cognatus*) were translocated into Minnesota as part of a reintroduction program (Huff et al. 2011). In general, outbreeding depression is predicted for hybrids produced from populations that have fixed chromosomal differences, exchanged no genes in the last 500 years, or inhabit different environments (Frankham et al. 2011).

Second, the multiple source population approach is essentially a bet-hedging strategy (Kettenring et al. 2014), and may delay the identification of a best source population. For example, a mixed-source group might by chance contain an ancestry or environment match, which has high fitness because of pre-existing adaptation and not because of adaptive potential. Post-translocation monitoring could identify the source population with highest fitness and direct subsequent translocations. However, if the best population was selected using a priori criteria, then the initial fitness of translocated individuals would be higher than for the multiple source population approach.

### Empirical Evaluation of the Approaches

Using the Web of Science, we conducted a literature search for studies that examined the fitness of different source groups translocated into foreign locations previously occupied by the target species or into locations containing small numbers of conspecifics. We included studies if they provided a coefficient of determination ( $r^2$  or a Pearson correlation,  $r$ ) between fitness-related traits from different source groups and the genetic similarity to the group at the foreign location, the environment similarity between the source and foreign locations, or the amount of heritable genetic variation within the translocated groups. We also included studies that compared fitness-related traits among different source groups. For the multiple populations approach, we included studies that examined the contributions of each source population to the restored population. Correlations between fitness-related traits and the genetic similarity and environment similarity are tests of the usefulness of the two approaches within the pre-existing adaptation strategy. Similarly, correlations between fitness-related traits and the amount of heritable genetic variation of the translocated groups are tests of the usefulness of the two approaches within the adaptive potential strategy. We identified 26 studies that met these criteria, including 18 studies that provided coefficients of determination (Table S1 in Appendix S1, Supporting Information) and eight studies that compared the relative fitness-related traits among different source groups. A detailed summary of the empirical support of the strategies is provided in Table S2 in Appendix S1.

### Empirical Tests of the Pre-Existing Adaptation Strategy

There was no significant difference between the effect sizes for the ancestry matching approach and the environment matching approach (Wilcoxon rank sum,  $W = 128$ ,  $p = 0.58$ ), albeit there was a large range of effect sizes (mean = 24%, range 0–87%, Table S1 in Appendix S1). Ancestry matching by genetic similarity was supported by nine studies that detected positive correlations with fitness-related traits (mean = 21%, range = 0–56%, Table S1 in Appendix S1). Similarly, environment matching was supported by 12 studies that detected positive correlations with fitness-related traits (mean = 26%, range = 0.4–87%, Table S1 in Appendix S1). Three additional studies found support for environment matching but did not

provide a coefficient of determination between fitness-related traits and environment similarity (Appendix S1).

Only five studies directly compared the effects of ancestry matching and environment matching on fitness-related traits (Appendix S1). The degree of environment alteration relative to historical conditions was not reported. In all five studies, environment matching was a better predictor of fitness than ancestry matching; albeit, the single best population was sometimes an ancestry match and sometimes an environment match.

### Empirical Tests of the Adaptive Potential Strategy

Seven studies examined fitness-related traits as a function of the number of alleles, heterozygosity, or the percentage of polymorphic loci using neutral genetic markers. There were generally, but not always, positive correlations between these markers and fitness-related traits (Appendix S1). Three studies examined fitness-related traits as a function of source population size—a proxy of within-population genetic variation—and found that larger populations had greater fitness than smaller populations following translocation (Appendix S1). One potential caveat with the interpretation of these studies is that none directly estimated the amount of within-population heritable genetic variation for fitness-related traits or the response to selection, so fitness differences could not be directly linked to adaptation following translocation.

Three studies examined translocations using multiple source populations (Appendix S1). None of the studies provided a coefficient of determination between fitness-related traits and a measure of the amount of heritable genetic variation within the translocated mixed-source group, although high heritable genetic variation was inferred because of the distinctive genetic and environmental backgrounds of each source. For all three studies, selection in the restoration location removed certain source groups, resulting in a single source group that disproportionately contributed to the restored population. However, it is not clear if this result was due to adaptation following translocation because there was no fitness comparison between the restored population and its translocated group.

### Source Population Selection Framework

Building upon previous recommendations (Seddon & Soorae 1999; McKay et al. 2005; Weeks et al. 2011; IUCN 2013; Kettenring et al. 2014; Cochran-Biederman et al. 2015), we constructed a novel source population selection framework (Fig. 1). Our framework has an a priori expectation that the habitat can support the target species; otherwise habitat restoration is recommended before considering a reintroduction (Dobson et al. 1997; Palmer et al. 1997; Cochran-Biederman et al. 2015). The assessment of local and regional genetic structure is also recommended to identify and characterize candidate source populations (i.e. for ancestry matching and adaptive potential) and to define relevant management units (Olsen et al. 2014). The framework is presented as a guide to selecting source populations with the highest probability of possessing adaptations to



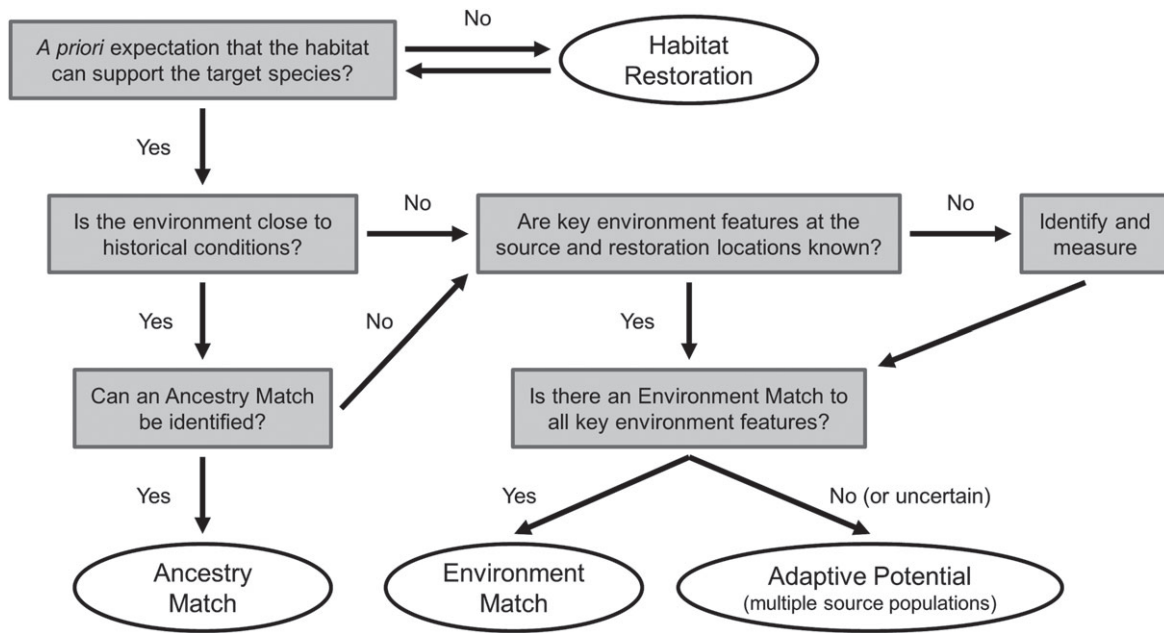


Figure 1. A framework for selecting source populations for reintroduction. Steps may be skipped due to cost, difficulty, or time constraints; however, skipping steps is likely to reduce the probability of a successful reintroduction.

the key environment features of the restoration location. Cost, difficulty, and time constraints may be issues for certain steps and such steps can be skipped; however, skipping steps may lower the probability that the source populations possess adaptations needed for successful restoration. Our framework offers three key advantages and clarifications to previous recommendations: (1) it offers guidelines for choosing between ancestry and environment matching; (2) it highlights the importance of identifying and measuring key environment features between the source and restoration locations; and (3) it prioritizes the pre-existing adaptation strategy above the adaptive potential strategy.

The placement of ancestry matching and environment matching is dependent on the state of the habitat relative to historical conditions (e.g. no major change in soil conditions and no abundant exotic species). If the habitat is largely unchanged and an ancestry match is available, then the ancestry match should be translocated into the restoration location (Lesica & Allendorf 1999; O'Brien & Krauss 2008). The ancestry match may possess adaptations to unidentified (cryptic) environment features that may be absent in a source population chosen using environment matching (Garcia de Leaniz et al. 2007; Fraser 2008). In addition, ancestry matching has the greatest potential to restore an extirpated population to its near-original state, which may be particularly valuable when restoring populations of cultural or evolutionary significance (Moritz 1999). If there is no ancestry match or the habitat differs from historic conditions, then key environment features including temperature, competitors, predators, prey type, parasites, and pathogens should be used to identify an environment match. If an environment match to all key environment features at the restoration location can be identified, then the environment match should be translocated

(Lesica & Allendorf 1999; Jones 2003, 2013; Weeks et al. 2011; Kettenring et al. 2014).

If there is no environment match to current conditions, or high uncertainty in the key environment features, then multiple source populations should be translocated as a bet-hedging strategy, preferably source populations with high heritable genetic variation or source populations from diverse genetic and environmental backgrounds. The fitness of the translocated individuals should then be monitored to determine whether a single source population (or group of individuals) has higher fitness. That source population (or group of individuals) should then be the focus of future restoration efforts if further translocations are necessary.

Across all approaches, post-translocation monitoring (e.g. survival, body size, and population size) for at least 10 years is recommended for measuring restoration success (Fischer & Lindenmayer 2000; Menges 2008; Godefroid et al. 2011). In addition, models suggest that an effective size of at least 1,000 can improve the capacity of a population to respond to additional selection pressures, such as global climate change (Willi & Hoffmann 2009; Sgrò et al. 2011). To achieve this effective population size in a few generations, sustained translocations may be required at the restoration location (Weeks et al. 2011).

If translocations do not re-establish a self-sustaining population, additional effort may be needed to determine if unidentified features of the environment are preventing a successful reintroduction and if additional habitat restoration is required. Trying another source population is cautioned unless a cause of the initial reintroduction failure is identified because there is a high likelihood that a new source population will also fail to re-establish a self-sustaining population (e.g. Cochran-Biederman et al. 2015).

**Table 1.** Summary of knowledge gaps and the benefit of the knowledge for selecting source populations.

<i>Knowledge Gap</i>	<i>Details</i>	<i>Benefit of the Knowledge</i>
(1) Can fitness-related traits predict reintroduction outcome?	Measure per capita growth rate instead of fitness-related traits	Per capita growth rate is a better predictor of population growth in the restoration location
(2) What are the key environment features for environment matching?	Determine the features that have major influences on fitness, which should be used for the environment matching criteria	A better understanding of key features may enhance the implementation of the environment matching approach
(3) Does the adaptive potential strategy affect the outcome of translocations?	Compare the fitness of the reintroduced population and its translocated group in the new location to identify adaptation following translocation	Will determine if high heritable genetic variation is beneficial because of adaptive potential

### Knowledge Gaps and Research Needs

By examining the empirical literature on translocations, we have identified three major knowledge gaps (Table 1). Filling these gaps is critical to validate, and potentially revise, our source population selection framework. First, most studies have not measured fitness as per capita growth rate or intrinsic  $r$  but have measured fitness-related traits that do not necessarily capture population growth rate (Hendry & Gonzalez 2008). For reintroduction programs, there is a large interest in re-establishing a self-sustaining population with a growing ( $r > 0$ ) or stable ( $r = 0$ ) population size in the restoration location (Menges 2008). Thus, per capita growth rate is a more useful measure than fitness-related traits and should be estimated in translocation studies. In addition, there may be benefits to comparing different candidate source populations in experimental settings prior to large-scale restoration efforts. For example, experiments could measure the relative fitness of different candidate source populations exposed to key environmental features in laboratory settings (e.g. van Katwijk et al. 1998, 2009) or small-scale natural settings of the restoration location (e.g. Houde et al. 2015).

Second, environment matching is a challenging source population selection approach to implement because identifying key environment features can be difficult, time consuming, and costly. Most of the studies that examined environment matching in our analysis were on plants, possibly because of the better understanding of the key environment features for these taxa (e.g. competitors and temperature), as well as a general emphasis on plants over animals in restoration ecology (Mijangos et al. 2015). A better understanding of the key environment features for other taxa, such as animals, would increase the usefulness of environment matching. Overall, an improved understanding of key environment features would also allow the fitness effects of environmental changes from historical conditions to be better predicted, which would help inform the choice between ancestry and environment matching. Identifying key environment features can be accomplished using local adaptation methods, e.g. common garden and reciprocal translocation experiments (Kawecki & Ebert 2004), or assessing the influence of select features on the fitness of individuals in natural populations.

Third, it is not yet clear if the adaptive potential strategy is of practical benefit in reintroduction programs. This strategy aims to translocate a group with high heritable genetic variation, with the goal of facilitating adaptation from this variation through

evolutionary processes. However, even when this strategy works as intended, many individuals from the translocated group will likely have low fitness in the restoration location (Lande & Shannon 1996; Newman & Pilon 1997; Rice & Emery 2003; Breed et al. 2013). Consequently, the benefits of the adaptive potential strategy will be fully realized only after multiple generations, once selection has acted on the translocated group to remove individuals with genotypes that confer low fitness in the restoration location. No studies have directly compared the fitness of a restored population and its translocated group, so it is difficult to estimate the magnitude of the fitness benefits resulting from the adaptive capacity strategy (i.e. adaptation following translocation). Further research is needed to determine the role of adaptive capacity in translocation outcome and whether populations with high heritable genetic variation are more likely to re-establish a population in the restoration location than populations with low heritable genetic variation. At this time, there is limited evidence that the adaptive potential strategy affects translocation outcome.

### Summary and Conclusion

We have discussed the theoretical and empirical underpinnings for source population selection and used this research to produce a framework based on the pre-existing adaptation and adaptive potential strategies. We have argued that the pre-existing adaptation strategy should be considered prior to the adaptive potential strategy. Our source population selection framework is based largely on evolutionary and ecological theory, as our search of the primary literature revealed few empirical studies that spoke to the effectiveness of these strategies. This paucity of data highlights the need for further research assessing the relationships between reintroduction outcomes and gradients of genetic similarity, environment similarity, and heritable genetic variation. Filling three critical knowledge gaps will increase our understanding of how best to select source populations for reintroduction programs and ultimately help improve the success rate of restoring self-sustaining populations.

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## LITERATURE CITED

- Allendorf FW, Luikart G, Aitken SN (2013) Conservation and the genetics of populations. Blackwell Publishing, Oxford, United Kingdom
- Araki H, Cooper B, Blouin MS (2007) Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318:100–103
- Armstrong DP, Seddon PJ (2008) Directions in reintroduction biology. *Trends in Ecology and Evolution* 23:20–25
- Beaumont MA, Nichols RA (1996) Evaluating loci for use in the genetic analysis of population structure. *Proceedings of the Royal Society of London B* 263:1619–1626
- Breed MF, Stead MG, Ottewell KM, Gardner MG, Lowe AJ (2013) Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics* 14:1–10
- Briscoe DA, Malpica JM, Robertson A, Smith GJ, Frankham R, Banks RG, Barker JSF (1992) Rapid loss of genetic variation in large captive populations of *Drosophila* flies: implications for the genetic management of captive populations. *Conservation Biology* 6:416–425
- Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesk PA, Yates C (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 1:587–597
- Campbell D, Bernatchez L (2004) Generic scan using AFLP markers as a means to assess the role of directional selection in the divergence of sympatric whitefish ecotypes. *Molecular Biology and Evolution* 21:945–956
- Cochran-Biederman JL, Wyman KE, French WE, Loppnow GL (2015) Identifying correlates of success and failure of native freshwater fish reintroductions. *Conservation Biology* 29:175–186
- Dobson AP, Bradshaw AD, Baker AJM (1997) Hopes for the future: restoration ecology and conservation biology. *Science* 277:515–522
- Edmunds S (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Molecular Ecology* 16:463–475
- Excoffier L, Heckel G (2006) Computer programs for population genetics data analysis: a survival guide. *Nature Reviews Genetics* 7:745–758
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Longman, Harlow, United Kingdom
- Fischer J, Lindenmayer DB (2000) An assessment of the published results of animal relocations. *Biological Conservation* 96:1–11
- Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford, United Kingdom
- Frankham R (1996) Relationship of genetic variation to population size in wildlife. *Conservation Biology* 10:1500–1508
- Frankham R, Ballou JD, Eldridge MDB, Lacy RC, Ralls K, Dudash MR, Fenster CB (2011) Predicting the probability of outbreeding depression: predicting outbreeding depression. *Conservation Biology* 25:465–475
- Fraser DJ (2008) How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications* 1:535–586
- Fraser DJ, Weir LK, Bernatchez L, Hansen MM, Taylor EB (2011) Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity* 106:404–420
- García de Leaniz C, Fleming IA, Einum S, Verspoor E, Jordan WC, Consuegra S, et al. (2007) A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. *Biological Reviews* 82:173–211
- Garnier-Géré PH, Ades PK (2001) Environmental surrogates for predicting and conserving adaptive genetic variability in tree species. *Conservation Biology* 15:1632–1644
- Godefroid S, Piazza C, Rossi G, Buord S, Stevens A-D, Aguruiaru J, et al. (2011) How successful are plant species reintroductions? *Biological Conservation* 144:672–682
- Hendry AP, Gonzalez A (2008) Whither adaptation? *Biology & Philosophy* 23:673–699
- Hereford J (2009) A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist* 173:579–588
- Hoekstra HE, Hirschmann RJ, Bunday RA, Insel PA, Crossland JP (2006) A single amino acid mutation contributes to adaptive beach mouse color pattern. *Science* 313:101–104
- Holder M, Lewis PP (2003) Phylogeny estimation: traditional and Bayesian approaches. *Nature Reviews Genetics* 4:275–284
- Houde ALS, Smith AD, Wilson CC, Peres-Neto PR, Neff BD (2015) Competitive effects between rainbow trout and Atlantic salmon in natural and artificial streams. *Ecology of Freshwater Fish*, DOI: 10.1111/eff.12206
- Huff DD, Miller LM, Chizinski CJ, Vondracek B (2011) Mixed-source reintroductions lead to outbreeding depression in second-generation descendants of a native North American fish. *Molecular Ecology* 20:4246–4258
- Hufford KM, Krauss SL, Veneklaas EJ (2012) Inbreeding and outbreeding depression in *Stygidium hispidum*: implications for mixing seed sources for ecological restoration. *Ecology and Evolution* 2:2262–2273
- IUCN (International Union for Conservation of Nature) (2013) Guidelines for reintroductions and other conservation translocations. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, United Kingdom
- Jahnke M, Olsen JL, Procaccini G (2015) A meta-analysis reveals a positive correlation between genetic diversity metrics and environmental status in the long-lived seagrass *Posidonia oceanica*. *Molecular Ecology* 24:2336–2348
- Jones TA (2003) The restoration gene pool concept: beyond the native versus non-native debate. *Restoration Ecology* 11:281–290
- Jones TA (2013) When local isn't best. *Evolutionary Applications* 6:1109–1118
- Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecology Letters* 7:1225–1241
- Kettenring KM, Mercer KL, Reinhardt Adams C, Hines J (2014) Application of genetic diversity-ecosystem function research to ecological restoration. *Journal of Applied Ecology* 51:339–348
- Kleiman DG (1989) Reintroduction of captive mammals for conservation. *BioScience* 39:152–161
- Krauss SL, Sinclair EA, Bussell JD, Hobbs RJ (2013) An ecological genetic delineation of local seed-source provenance for ecological restoration. *Ecology and Evolution* 3:2138–2149
- Lande R, Shannon S (1996) The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50:434–437
- Lawrence BA, Kaye TN (2011) Reintroduction of *Castilleja levisecta*: effects of ecological similarity, source population genetics, and habitat quality. *Restoration Ecology* 19:166–176
- Lesica P, Allendorf FW (1999) Ecological genetics and the restoration of plant communities: mix or match? *Restoration Ecology* 7:42–50
- Lipsey MK, Child MF (2007) Combining the fields of reintroduction biology and restoration ecology. *Conservation Biology* 21:1387–1388
- Lynch M (1991) The genetic interpretation of inbreeding depression and outbreeding depression. *Evolution* 45:622–629
- Lynch M, O'Hely M (2001) Captive breeding and the genetic fitness of natural populations. *Conservation Genetics* 2:363–378
- Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland, Massachusetts
- Marko PB, Hart MW (2011) The complex analytical landscape of gene flow inference. *Trends in Ecology and Evolution* 26:448–456
- McKay JK, Christian CE, Harrison S, Rice KJ (2005) "How local is local?" A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13:432–440
- McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTL and traits. *Trends in Ecology and Evolution* 17:285–291
- Menges ES (2008) Restoration demography and genetics of plants: when is a translocation successful? *Australian Journal of Botany* 56:187–196
- Mijangos JL, Pacioni C, Spencer PBS, Craig MD (2015) Contribution of genetics to ecological restoration. *Molecular Ecology* 24:22–37

- Montalvo AM, Ellstrand NC (2000) Transplantation of the subshrub *Lotus scoparius*: testing the home-site advantage hypothesis. *Conservation Biology* 14:1034–1045
- Montalvo AM, Ellstrand NC (2001) Nonlocal transplantation and outbreeding depression in the subshrub *Lotus scoparius* (Fabaceae). *Australian Journal of Botany* 88:258–269
- Montalvo AM, Williams SL, Rice KJ, Buchmann SL, Cory C, Handel SN, Nabhan GP, Primack R, Robichaux RH (1997) Restoration biology: a population biology perspective. *Restoration Ecology* 5:277–290
- Moritz C (1999) Conservation units and translocations: strategies for conserving evolutionary processes. *Hereditas* 130:217–228
- Nachman MW, Hoekstra HE, D'Agostino SL (2003) The genetic basis of adaptive melanism in pocket mice. *Proceedings of the National Academy of Sciences of the United States of America* 100:5268–5273
- Neff BD, Garner SR, Pitcher TE (2011) Conservation and enhancement of wild fish populations: preserving genetic fitness versus genetic diversity. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1149–1154
- Newman D, Pilson D (1997) Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution* 51:354–362
- O'Brien EK, Krauss SL (2008) Testing the home-site advantage in forest trees on disturbed and undisturbed sites. *Restoration Ecology* 18:359–372
- Olsen JL, Coyer JA, Chesney B (2014) Numerous mitigation transplants of the eelgrass *Zostera marina* in southern California shuffle genetic diversity and may promote hybridization with *Zostera pacifica*. *Biological Conservation* 176:133–143
- Palmer MA, Ambrose RF, Poff NL (1997) Ecological theory and community restoration ecology. *Restoration Ecology* 5:291–300
- Parker PG, Snow AA, Schug MD, Booton GC, Fuerst PA (1998) What molecules can tell us about populations: choosing and using a molecular marker. *Ecology* 79:361–382
- Puurtinen M, Ketola T, Kotiaho JS (2009) The good-genes and compatible-genes benefits of mate choice. *The American Naturalist* 174:741–752
- Raabová J, Münzbergová Z, Fischer M (2007) Ecological rather than geographic or genetic distance affects local adaptation of the rare perennial herb, *Aster amellus*. *Biological Conservation* 139:348–357
- Reed DH, Frankham R (2001) How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55:1095–1103
- Reed DH, Lowe EH, Briscoe DA, Frankham R (2003) Fitness and adaptation in a novel environment: effect of inbreeding, prior environment, and lineage. *Evolution* 57:1822–1828
- Rice KJ, Emery NC (2003) Managing microevolution: restoration in the face of global change. *Frontiers in Ecology and the Environment* 1:469–478
- Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. *Nature* 392:491–494
- San Mauro D, Agorreta A (2010) Molecular systematics: a synthesis of the common methods and the state of knowledge. *Cellular and Molecular Biology Letters* 15:311–341
- Schumer M, Krishnakant K, Renn SCP (2011) Comparative gene expression profiles for highly similar aggressive phenotypes in male and female cichlid fishes (*Julidochromis*). *Journal of Experimental Biology* 214:3269–3278
- Seddon PJ (2010) From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restoration Ecology* 18:796–802
- Seddon PJ, Armstrong DP, Maloney RF (2007) Combining the fields of reintroduction biology and restoration ecology. *Conservation Biology* 21:1388–1390
- Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP (2014) Reversing defaunation: restoring species in a changing world. *Science* 345:406–412
- Seddon PJ, Soorae PS (1999) Guidelines for subspecific substitutions in wildlife restoration projects. *Conservation Biology* 13:177–184
- Sgrò CM, Lowe AJ, Hoffmann AA (2011) Building evolutionary resilience for conserving biodiversity under climate change: conserving biodiversity under climate change. *Evolutionary Applications* 4:326–337
- Soorae PS (ed) (2008) Global re-introduction perspectives: re-introduction case-studies from around the globe. IUCN/SSC Re-introduction Specialist Group, Abu Dhabi, U.A.E.
- Soorae PS (ed) (2011) Global re-introduction perspectives: 2011. More case studies from around the globe. IUCN/SSC Re-introduction Specialist Group and Abu Dhabi Environment Agency, Gland, Switzerland and Abu Dhabi, United Arab Emirates
- Stingemore JA, Krauss SL (2013) Genetic delineation of local provenance in *Persoonia longifolia*: implications for seed sourcing for ecological restoration. *Restoration Ecology* 21:49–57
- Turner TL, Bourne EC, Von Wettberg EJ, Hu TT, Nuzhdin SV (2010) Population resequencing reveals local adaptation of *Arabidopsis lyrata* to serpentine soils. *Nature Genetics* 42:260–263
- Vander Mijnsbrugge K, Bischoff A, Smith B (2010) A question of origin: where and how to collect seed for ecological restoration. *Basic and Applied Ecology* 11:300–311
- van Katwijk MM, Bos AR, de Jonge VN, Hanssen LSAM, Hermus DCR, de Jong DJ (2009) Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. *Marine Pollution Bulletin* 58:179–188
- van Katwijk MM, Schmitz GHW, Hanssen LSAM, den Hartog C (1998) Suitability of *Zostera marina* populations for transplantation to the Wadden Sea as determined by a mesocosm shading experiment. *Aquatic Botany* 60:283–305
- Weeks AR, Sgrò CM, Young AG, Frankham R, Mitchell NJ, Miller KA, et al. (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications* 4:709–725
- Willi Y, Hoffmann AA (2009) Demographic factors and genetic variation influence population persistence under environmental change. *Journal of Evolutionary Biology* 22:124–133
- Williams AV, Nevill PG, Krauss SL (2014) Next generation restoration genetics: applications and opportunities. *Trends in Plant Science* 19:529–537
- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790

## Supporting Information

The following information may be found in the online version of this article:

**Appendix S1.** Empirical evaluation of the approaches.

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