

Evolutionary Restoration Ecology

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Restoration Ecology and Evolutionary Process

Restoration activities have increased dramatically in recent years, creating evolutionary challenges and opportunities. Though restoration has favored a strong focus on the role of habitat, concerns surrounding the evolutionary ecology of populations are increasing. In this context, previous researchers have considered the importance of preserving extant diversity and maintaining future evolutionary potential (Montalvo et al. 1997; Lesica and Allendorf 1999), but they have usually ignored the prospect of ongoing evolution in real time. However, such *contemporary evolution* (changes occurring over one to a few hundred generations) appears to be relatively common in nature (Stockwell and Weeks 1999; Bone and Farres 2001; Kinnison and Hendry 2001; Reznick and Ghalambor 2001; Ashley et al. 2003; Stockwell et al. 2003). Moreover, it is often associated with situations that may prevail in restoration projects, namely the presence of introduced populations and other anthropogenic disturbances (Stockwell and Weeks 1999; Bone and Farres 2001; Reznick and Ghalambor 2001) (Table 6.1). Any restoration program may thus entail consideration of evolution in the *past*, *present*, and *future*.

Restoration efforts often involve dramatic and rapid shifts in habitat that may even lead to different ecological states (such as altered fire regimes) (Suding et al. 2003). Genetic variants that evolved within historically different evolutionary contexts (the past) may thus be pitted against novel and mismatched current conditions (the present). The degree of this mismatch should then determine the pattern and strength of selection acting on trait variation in such populations (Box 6.1; Figure 6.1). If trait variation is heritable and selection is sufficiently strong, contemporary evolution is likely to occur and may have dramatic impacts on the adaptive dynamics of restoration scenarios. Adaptation to current conditions (the present) may in turn influence the ability of such populations to subsequently persist and evolve over short or long periods (the future). Thus, the success (or failure) of a restoration effort may often be as much an evolutionary issue as an ecological one.

It is also useful to recognize that contemporary evolution may alter the interactions of species with their environments and each other. Restoration ecologists may thus be faced with a changed cast of players, even if many of the same nominal species are restored. Efforts that assume species and populations are evolutionarily stagnant may face frustrating and

TABLE 6.1

Examples of contemporary evolution in plants and animals in nature.

Context/Example	Traits	Evolutionary agent	References
Colonization			
Threespine stickleback (<i>Gasterosteus aculeatus</i>)	Lateral plate armor	Freshwater habitat	Bell et al. 2004
Pacific salmon (<i>Oncorhynchus</i> spp.)	Development and growth, morphology, reproductive timing, ovarian investment	Breeding environment (temperature, flow, migratory rigor)	Hendry et al. 2000; Hendry et al. 2001; Kinnison et al. 2001; Quinn et al. 2001; Koskinen et al. 2002
European Grayling (<i>Thymallus thymallus</i>)	Length at termination, yolk-sac volume, growth rate, survival	Water temperature	
Guppies (<i>Poecilia reticulata</i>)	Age and size at maturity, offspring size, antipredator behavior	Predator regimes	Endler 1980; Reznick et al. 1997; O'Steen et al. 2002
Mosquitofish (<i>Gambusia affinis</i>)	Size at maturity, fat storage	Environmental constancy, thermal environment	Stearns 1983; Stockwell and Weeks 1999
White Sands pupfish (<i>Cyprinodon tularosa</i>)	Pgdh (Phosphogluconate dehydrogenase); body shape	Salinity/flow	Stockwell and Mulvey 1998; Collyer et al., 2005
Dark-eyed juncos (<i>Junco hyemalis</i>)	Morphology (amount of white in tail)	Sexual selection	Rasner et al. 2004; Yeh 2004
Rabbits (<i>Oryctolagus cuniculus</i>)	Morphology	Ecoregional variation (temperature and aridity)	Williams and Moore 1989
Isopod (<i>Asellus aquaticus</i>)	Pigmentation	Predation	Hargeby et al. 2004
<i>In situ</i> disturbance	Tolerance to metals (e.g., copper)	Metal contaminated soils (e.g., mine waste piles)	Jain and Bradshaw 1966; Antonovics and Bradshaw 1970; Wu and Kruckeberg 1985; Macnair 1987; Bone and Farres 2001
Numerous plant species, including <i>Mimulus guttatus</i> , <i>Anthoxanthum odoratum</i> , <i>Agrostis tenuis</i> , <i>Lupinus bicolor</i> , <i>Lotus persianus</i> , <i>Anthoxanthum odoratum</i>	pH tolerance	Fertilizer, altered soil pH	Snaydon and Davies 1972; Davies and Snaydon 1976; Bone and Farres 2001
<i>Plantago major</i>	Growth rate	High ozone concentration	Davison and Reiling 1995
<i>Arabidopsis thaliana</i>	Seed production	CO ₂ concentration	Ward et al. 2000
Oligochaete (<i>Limnodrilus hoffmeisteri</i>)	Loss of cadmium resistance	Removal of cadmium	Levinton et al. 2003

Numerous insect species back moths (<i>Plutella xylostella</i>) Soapberry bugs (<i>Jadera haematoloma</i>) Pitcher plant mosquitoes (<i>Wyeomyia smithii</i>) Water flea (<i>Daphnia galeata mendotae</i>)	Pesticide resistance (e.g., resistance to <i>Bt</i>) Beak length Photoperiodic diapause response Resistance to poor/toxic diet	Selective mortality or sterility, <i>Bt</i> -related mortality Introduced host fruit size	Mallet 1989; Tabashnik 1994 Carroll et al. 2001
Galapagos finches (<i>Geospiza fortis</i>) Red squirrels (<i>Tamiasciurus hudsonicus</i>) Selective harvest European Grayling (<i>Thymallus thymallus</i>) Northern cod (<i>Gadus morhua</i>) Bighorn sheep (<i>Ovis canadensis</i>) Introgession Ducks, canids, salmonids, sunflower, etc.	Body size, beak shape Breeding season Age and size at maturity Size, age at maturity Male body and horn size Morphology (other aspects likely)	Global warming Cyanobacteria increase following eutrophication Drought effects on food resources Global change (increased temperatures) Selectivity of harvest methods and gear (e.g., mesh size of nets) Harvest of large cod Selective harvest of large males Hybridization among wild species and between wild and domestic (sub)species	Bradshaw and Holzapfel 2001 Hairston et al. 1999 Grant and Grant 2002 Réale et al. 2003 Haugen and Vøllestad 2001 Olsen et al. 2004 Coltman et al. 2003 Rhymer and Simberloff 1996; Al-lendorf et al. 2001; Grant and Grant 2002

Box 6.1

Evolutionary Change in Quantitative Traits

For a quantitative trait (influenced by multiple genes, often of small effect), a simple equation can be used to predict how adaptation should proceed, at least under a number of simplifying assumptions (Lande and Arnold 1983). Specifically, $\Delta z = G\beta$, where Δz is the change in mean trait value from one generation to the next, G is the additive genetic variance for the trait and β is the selection gradient acting on the trait (slope of the relationship between the trait and fitness). When considering a single trait, this equation is analogous to the traditional “breeder’s equation” (evolutionary response = heritability * selection; $R = h^2S$) because $G/P = h^2$ and $S/P = \beta$, where P is the phenotypic variance and S is the selection differential (difference between the mean trait value before and after selection). When considering multiple traits, Δz becomes a vector of changes in mean trait values, G becomes a matrix of additive genetic variances/covariances, and β becomes a vector of selection gradients. That is, $\Delta z = G\beta$ (Lande and Arnold 1983; Schluter 2000; Arnold et al. 2001). In the case of two traits, the multivariate equation expands to

$$\begin{bmatrix} \Delta z_1 \\ \Delta z_2 \end{bmatrix} = \begin{bmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix},$$

where Δz_i is the evolutionary response for trait i , G_{11} and G_{22} are the additive genetic variances for the two traits, G_{12} and G_{21} are identical and are the additive genetic covariance between the two traits, and β_i is the selection gradient acting on the trait. Selection gradients are commonly estimated as partial regression coefficients from a multiple regression of both traits on fitness. In this case, selection gradients represent the effect of each trait on fitness after controlling for the effect of the other trait (i.e., “direct” selection). This equation shows how the evolutionary response for each trait will be a function of selection acting directly on that trait, the additive genetic variance for that trait, selection acting on the other trait, and the additive genetic covariance between the traits. That is, $\Delta z_1 = G_{11}\beta_1 + G_{12}\beta_2$ and $\Delta z_2 = G_{22}\beta_2 + G_{21}\beta_1$. This formulation illustrates how apparently paradoxical evolutionary changes can be observed in some situations. For example, the first trait can evolve to be smaller even if it is under selection to be larger (e.g., Grant and Grant 1995). This can occur when $G_{12}\beta_2 < 0$ and $|G_{12}\beta_2| > G_{11}\beta_1$; that is, when the negative indirect effect of selection on the first trait is stronger than the positive direct effect of selection. These negative indirect effects should increase as selection on the second trait becomes stronger and as the genetic covariance becomes stronger, with one of these quantities necessarily being negative.

Phenotypes in an undisturbed population should be centered around an optimal value (i.e., the population is well adapted). In a restoration context, however, a disturbance to the environment may shift the phenotypic optimum away from the current phenotypes (Figure 6.1). This shift leads to a mismatch between current phenotypes and optimal phenotypes, leaving the population maladapted and subject to directional selection. Under a number of assumptions, the strength of this selection can be represented as:

$$\beta = \frac{-(z - \theta)}{\omega^2 + P}$$

where z is the mean trait value, θ is the optimal trait value, P is the phenotypic variance, and ω^2 is the strength of stabilizing selection around the optimum (for simplicity, we assume ω^2 is

the same around the optimum before and after the disturbance). Smaller values of ω^2 correspond to steeper fitness functions and therefore stronger stabilizing selection around the optimum. When a disturbance shifts the optimum away from the current phenotypes, directional selection on the population increases (larger $|\beta|$), causing evolution toward the new optimum.

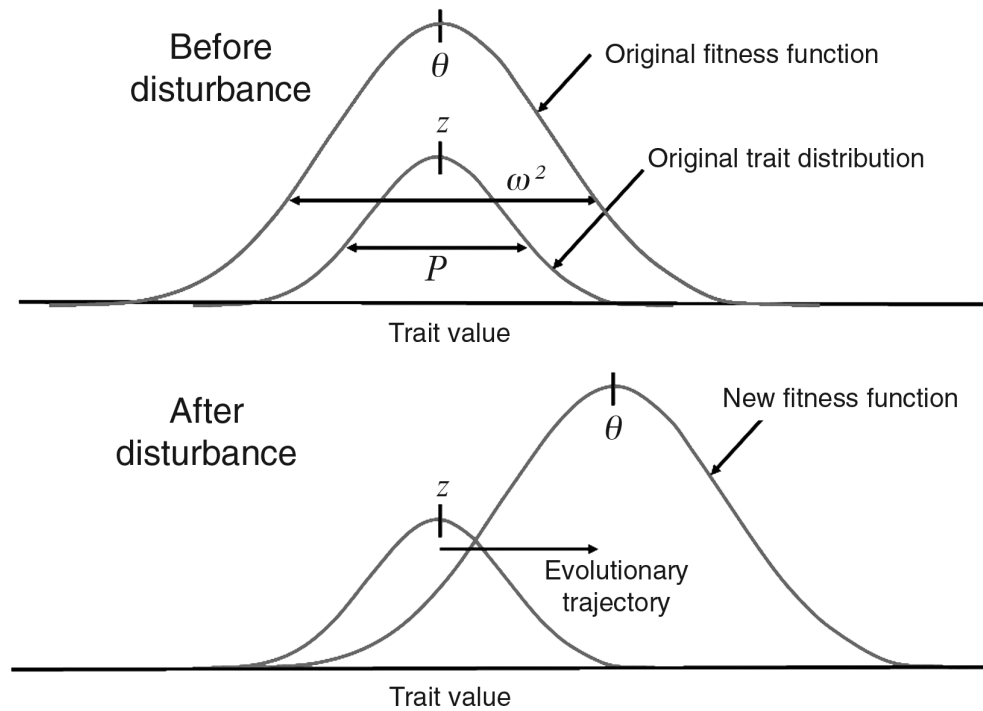


FIGURE 6.1 The distribution of trait values is shown in relation to the fitness function before and after a disturbance (native habitat versus restoration habitat), where z is the mean trait value, θ is the optimal trait value, P is the phenotypic variance, and ω^2 is the strength of stabilizing selection around the optimum. The width of the fitness function reflects the strength of stabilizing selection, which is denoted by ω^2 .

These equations can be used to predict the evolutionary responses of traits following a disturbance and have proven effective in predicting evolutionary responses in natural populations (Grant and Grant 1995, 2002). Figure 6.2 shows evolutionary responses for a population in relation to different additive genetic variances ($G = 0.1-0.5$) and strengths of stabilizing selection ($\omega = 2-5$; i.e., $\omega^2 = 4-25$). In each case, we assume the mean trait value is larger than the optimum ($z - \theta = 1$) and the phenotypic variance is $P = 1$. In general, evolutionary responses will increase as genetic variance increases (G increases) and the strength of stabilizing selection increase (ω decreases). Evolutionary responses will also increase with increasing differences between the mean trait value and the new optimal trait

value. However, it is important to recognize that several factors can lead to discrepancies between predicted and observed evolutionary responses (Merilä et al. 2001b; see Box 6.2).

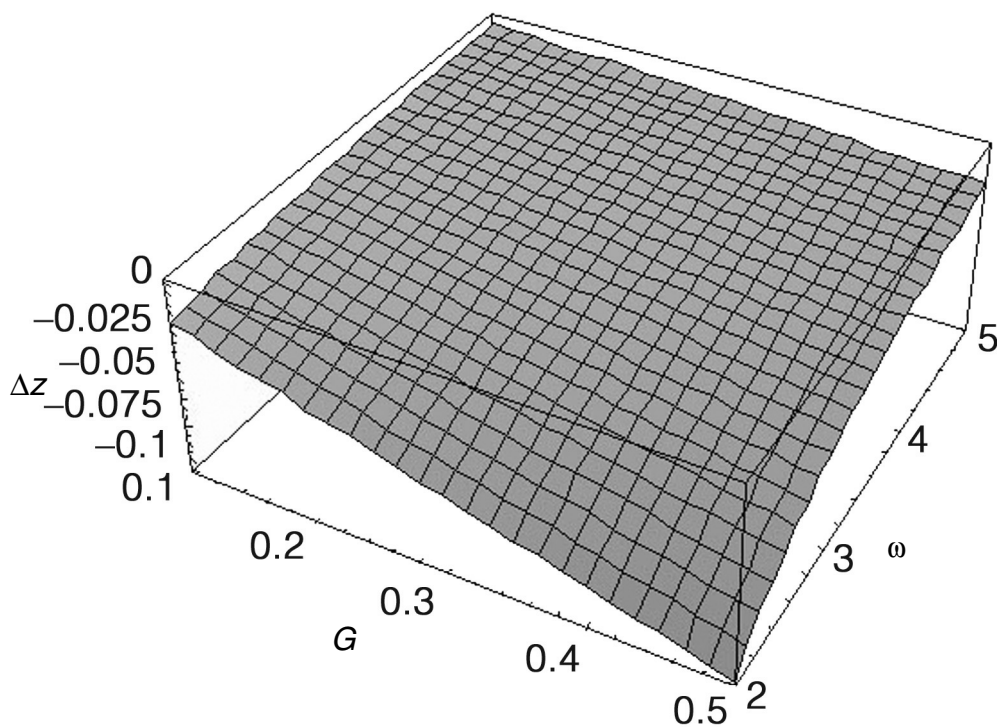


FIGURE 6.2 The evolutionary response (Δz) of a population is shown for different additive genetic variance ($G = 0.1$ – 0.5) and strengths of stabilizing selection ($\omega = 2$ – 5).

unanticipated outcomes. For instance, mounting evidence suggests that sustained harvest results in rapid life-history evolution toward less preferred phenotypes (e.g., smaller body size) (Haugen and Vøllestad 2001; Coltman et al. 2003; Olsen et al. 2004), potentially influencing both the ecological roles of these species in their communities and our own ecological interactions with them (e.g., rates of harvest).

Simply acknowledging, or even anticipating, that evolution will occur in restoration contexts is, however, probably not an entirely satisfying message for many readers of this book. We wish to go further and suggest that restoration ecology may include evolutionarily enlightened approaches or even constructive management of evolutionary processes. Regardless, it is our hope that the study of evolution may not only inform restoration, but that restoration may also inform the study of evolution. Indeed, the tempo and mode of contemporary evolution is still not well understood (Kinnison and Hendry 2001), and restoration ecology offers an opportunity to study the mechanics of evolution for diverse taxa under a variety of circumstances.

In this chapter, we consider the roles of evolutionary processes in both ecological endangerment and restoration. Because our actions as practitioners of restoration are largely lim-

ited to the present, much of our discussion will surround interactions with contemporary evolution. First, we describe the conditions under which contemporary evolution occurs and the factors by which it may be facilitated or constrained. Second, we discuss approaches and tools available for assessing evolutionary mechanics acting in populations of restoration concern. We consider evolutionary dynamics in a landscape context because restoration schemes will generally involve contributions from, and interactions with, the larger metapopulation and metacommunity (Maschinski, this volume; Menninger and Palmer, this volume). Our approach links historically established genetic diversity (the past) with contemporary evolution (the present) and long-term evolutionary potential (the future). Third, we provide an evolutionary perspective on traditional topics within the field of restoration ecology, such as the identification of suitable seed sources. We conclude by discussing research areas ripe for evaluation in the context of evolutionary restoration ecology.

Evolutionary Ecology and Contemporary Evolution

Evolutionary ecology, by analogy to other areas of ecology, is the study of processes that influence the *distribution* and *abundance* of individuals with different genotypes (genetic forms within a species or population). These processes often involve interactions of organisms with their abiotic and biotic environments. The term *evolution* is reserved for *heritable* changes in the relative abundance of trait values among generations. Often, adaptive evolution results from natural selection driven by correlations between heritable trait variation and *fitness* (the likelihood that an individual will contribute to future generations). However, a suite of additional factors, including anthropogenic effects, influence the likelihood and outcome of adaptive evolution and, by association, the performance and sustainability of populations.

In fact, anthropogenic activities are often associated with cases of evolution on contemporary time scales. We use the general term, *contemporary evolution*, in lieu of the other commonly used term, *rapid evolution*, which carries a historic perspective that such evolution is exceptional. In reality, contemporary evolution is now widely documented, and there is no evidence to suspect that it is either uncommon or exceptionally fast, given time-scaling effects (Kinnison and Hendry 2001; Stockwell et al. 2003). In general, contemporary evolution should occur whenever there is sufficient heritable variation for a trait under directional selection (Box 6.1; Figure 6.1). In a restoration program, we might expect a mismatch between the optimal trait value and the actual mean trait value for the given population. This mismatch causes directional selection to act on the trait: that is, selection favoring a shift in the mean trait value toward the optimum (highest net fitness value) (Figure 6.1). If the phenotypic variation has some genetic basis, the population mean should shift toward the optimum in the next generation (i.e., adaptation to the restoration environment). Of course, the population may go extinct, even while it is adapting, if the population is too small or if selection is too strong (Figure 6.3; also see Lynch 1996).

Contemporary evolution should occur in the above situation in general, but efficient adaptation can be opposed by many factors, including population size, gene flow, antagonistic pleiotropy, and life-history constraints (Table 6.2; see also Box 6.2). Small populations are less likely to evolve for two reasons. First, low population size may not provide sufficient phenotypic variation for selection to act (Lande 1995; Lynch 1996). Second, small populations are less likely to persist through the initial reduction in population size during the early stages

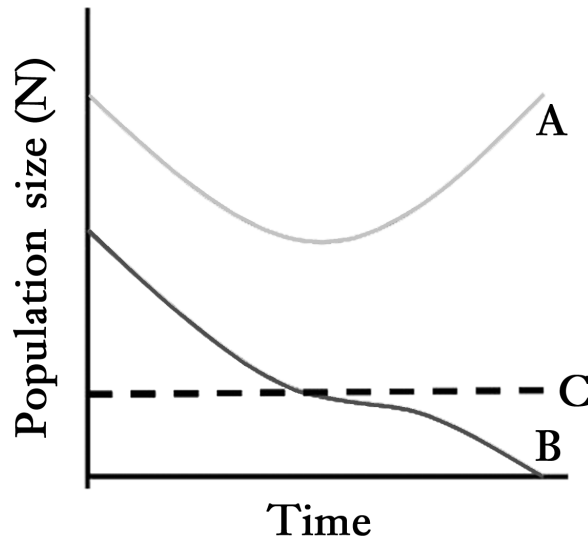


FIGURE 6.3 For large populations (A), novel selection is expected to cause an initial decline in population size (N) until the population adapts and population size increases (A). However, small populations (B) are more vulnerable to extinction because they are more likely to reach sizes where demographic stochasticity becomes overwhelming (C).

TABLE 6.2

Factors constraining and facilitating contemporary evolution.

Factors facilitating contemporary evolution	Reference
High genetic variation	Boulding and Hay 2001
Strong selection (directional, stabilizing)	Hendry, 2004
Absence of gene flow	Boulding and Hay 2001
Large populations	Gomulkiewicz and Holt 1995; Lande 1995; Lynch 1996; Lynch and Lande 1998; Franklin and Frankham 1998
Factors constraining contemporary evolution (in addition to the converse of those listed above)	
Antagonistic pleiotropy	Etterson and Shaw 2001
Life history constraints	Reznick et al. 2004
Environmental deterioration (evolution masked)	Merilä et al. 2001b

of adaptive evolution (Figure 6.3). Gene flow has the potential to slow adaptation by introducing maladapted genes from adjacent populations, an effect we discuss at length below. Antagonistic pleiotropy may impede adaptation when two genetically correlated traits (e.g., both partly influenced by same underlying genes) are under different patterns of selection. Life-history constraints can hinder adaptation by limiting a population's growth rate under selection (Reznick et al. 2004). For instance, populations with delayed maturity were at high extinction risk when introduced to sites with greater predation risk (Reznick et al. 2004).

Box 6.2

The Effects Of Gene Flow and Stabilizing Selection on Evolutionary Divergence

One such complication relevant to restoration is gene flow, where populations may be held from separate optima by genetic exchange among populations. The equations from Box 6.1 can be modified quite simply to include the effects of gene flow (Hendry et al. 2001). For example, when selection acts on each population and then some individuals move between populations (e.g., adults but not juveniles move), the difference in mean phenotype between the two populations for a single trait (ΔD) will change according to:

$$\Delta D = -\hat{m}D + [1 - \hat{m}][G_j\beta_j - G_i\beta_i],$$

where \hat{m} is the proportion of individuals exchanged between populations, D is the current difference between the populations, and G and β are the additive genetic variance and selection gradient for the trait in population i and population j . As above, a multivariate version of the equation would replace ΔD , D , G and β with their matrix or vector equivalents. One can then predict the equilibrium difference in trait value between the two populations (D^*), by setting $\Delta D = 0$ and solving for D :

$$D^* = \frac{[1 - \hat{m}]}{\hat{m}} [G_j\beta_j - G_i\beta_i].$$

As noted in Box 6.1, it is often useful to express β as a function of the deviation of the mean trait value from the optimum for that population, the strength of stabilizing selection around the optimum, and the phenotypic variance for the trait. Assuming ω^2 , P , and G are the same in both populations, the equilibrium difference when selection takes place before movement is:

$$D^* = D_0 \left[\frac{G[1 - \hat{m}]}{G[1 - \hat{m}] + [\omega^2 + P]\hat{m}} \right],$$

where D_0 is the difference in the optimum trait value between the two populations. Figure 6.4 uses this last equation to explore how the equilibrium difference between two populations will be a function of varying gene flow ($\hat{m} = 0 - 0.05$) and stabilizing selection ($\omega = 2 - 10$; i.e., $\omega^2 = 4 - 100$). The analysis assumes a typical heritability ($G = 0.3$, $P = 1$, therefore $h^2 = 0.3$) and an optimal difference in mean trait value of $D_0 = 1$. Figure 6.4 shows that relative adaptation (deviation from the optimum) decreases with increasing gene flow even when gene flow is quite low and with weaker stabilizing selection around the optimum. The negative effect of gene flow on adaptation is strongest when stabilizing selection is quite weak, as is thought to be the case in nature (Kingsolver et al. 2001).

In the context of restoration, these relationships have implications for how the restored site(s) interacts with surrounding sites. In general, we would expect that increases in gene flow between populations in different environments will reduce their adaptive divergence and therefore fitness (see also Boulding and Hay 2001). This potential negative effect of gene flow should therefore be considered when contemplating artificial manipulations of population density or movements of individuals between environments. These negative effects of gene flow, however, will need to be balanced with the consideration of positive effects that

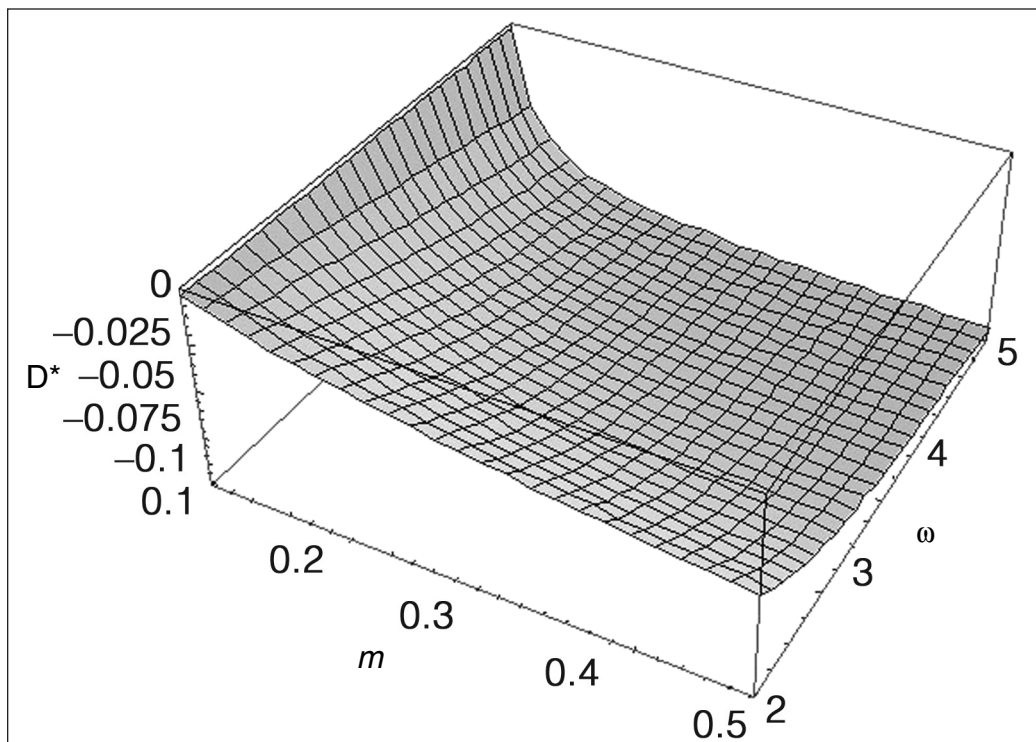


FIGURE 6.4 The effects of gene flow ($m = 0 - 0.05$) and stabilizing selection ($\omega = 2 - 10$) on relative adaptation (D^* , divergence from the optimum) are shown. Adaptation decreases with even modest increases in gene flow as long as stabilizing selection is weak, as is thought to be the case in nature.

might arise when populations are inbred (Hedrick 1995), or when gene flow allows a new or marginal population to persist long enough to then adapt to their environment (Holt and Gomulkiewicz 1997; Kawecki and Holt 2002).

Landscape Genetics and Restoration

A profitable way to evaluate current evolutionary processes and future evolutionary potential is through *landscape genetics* (*sensu* Manel et al. 2003; Guillot et al. 2005), which, at its simplest, is the quantification of genetic variation within and among populations (i.e., population genetics) in the context of a spatially and temporally complex landscape. Genetic variation within populations is important because it mediates adaptive evolution in response to changing conditions (Houle 1992; Bürger and Lynch 1995; García-Ramos and Rodríguez 2002; Reed et al. 2003). Genetic variation among populations is important as a reflection of local adaptation and the potential role of gene flow. In some situations such gene flow may be an important source of variation, whereas in others it may prove an impediment to local adaptation (Box 6.2).

Strong adaptation to different ecological environments implies that restoration efforts might benefit from choosing source populations that have phenotypes similar to those at the restoration site or, equivalently, source populations that occupy similar environments. If the restoration site is a novel environment and local adaptation is strong, it may be better to generate a genetically diverse group by mixing source populations. Selection at the restoration site can then weed through the various combinations based on their relative fitness (Lesica and Allendorf 1999; Falk et al., this volume; Maschinski, this volume). Restoration thus has two possible relationships to contemporary evolution. On one hand, the practitioner or researcher should be aware that contemporary evolution is likely in a restoration context. On the other hand, some researchers may choose to modify the conditions of restoration in such a way as to intentionally influence evolutionary change.

One way in which evolution may be managed is by managing gene flow to and from the restoration site. Gene flow is most commonly viewed as a constraining force in adaptive divergence (e.g., Storfer et al. 1999; Riechert et al. 2001; Hendry et al. 2002; Calsbeek and Smith 2003; see also Box 6.2) that contributes to a “migrational load” (Lenormand 2002) limiting the fitness of local populations (Boulding and Hay 2001). Restoration practitioners may consider restricting the rate or pattern of gene flow in cases where migrational load is expected and mediated by anthropogenic influences. For example, translocation rates might be reduced after initial establishment of restoration populations to allow them to adaptively diverge from their sources. However, negative effects of gene flow need to be weighed against potential positive effects, such as reduced inbreeding depression, increased genetic variation, and increased potential for future adaptation (e.g., Hedrick 1995; Newman and Tallmon 2001). Precedent already exists for providing artificial gene flow for the purpose of genetically “rescuing” inbred populations (Hedrick 1995). In either case, information about genetic variation within and among populations, habitat heterogeneity, and dispersal over landscapes would be essential to any attempted management of gene flow.

Landscape genetics, including the assessment of local adaptation, gene flow, and genetic variation, is commonly based on surveying molecular markers (neutral or selected) and quantitative traits (phenotypic traits coded for by multiple loci) (Falk et al., this volume). Variation in neutral markers generally reflects the combined effects of mutation, gene flow, and genetic drift. Variation in markers under selection or in quantitative traits is influenced by these same factors, but also by the strength and direction of selection. In the following section, we consider methods and inferences based on (1) neutral markers, (2) selected markers, and (3) quantitative traits.

Neutral Markers

Much of landscape genetics focuses on variation at presumed neutral loci, including some allozymes, microsatellites, mitochondrial DNA, AFLPs (amplified fragment length polymorphisms), RAPDs (random amplified polymorphic DNA), and SNPs (single nucleotide polymorphisms). Genetic variation at such markers can be summarized with a variety of metrics, the most common being various versions of F_{ST} , the amount of genetic variation among populations (v_a) for a given locus relative to the total variation among (v_a) and within (v_w) populations:

$$F_{ST} = \frac{v_a}{v_a + v_w}.$$

For a single locus with two alleles, F_{ST} will equal zero when none of the genetic variation is found among populations (i.e., they have the same allele frequencies), but will equal unity when all of the genetic variation is found among populations (i.e., they are fixed for alternative alleles) (Wright 1969). The situation is more complicated for highly polymorphic markers (Hedrick 1999).

The magnitude of F_{ST} at equilibrium will theoretically reflect three factors: the effective population size (N_e), the rate of mutation (μ), and the rate of gene flow (m , proportion of populations that are immigrants). When mutation is low relative to gene flow (and a number of other assumptions are adopted; Whitlock and McCauley 1999), mutation can be ignored, leaving a simple relation between genetic divergence and gene flow: $F_{ST} = 1/(1+4N_e m)$. This simplicity has led to the frequent use of F_{ST} to infer the amount of historical (i.e., long-term) gene flow, a quantity typically indexed as the effective number of migrants ($N_e m$). However, it is also useful to estimate the *rate* of gene flow (m), because it is this latter quantity that has a direct effect on divergence in selected traits (Hendry et al. 2001). Estimation of m from $N_e m$ therefore requires the estimation of N_e .

The above estimation procedure has been criticized heavily (Whitlock and McCauley 1999), largely because it rests on a number of dubious assumptions, particularly an “island” model of population structure. Alternatively, gene flow can be estimated using methods such as the rare alleles method or coalescent approaches that are a bit less restrictive to some assumptions (e.g., Slatkin 1985; Beerli and Felsenstein 1999; Pearse and Crandall 2004). Ultimately, however, all of these methods require relatively low rates of gene flow and equilibrium between gene flow and genetic drift, which may take thousands of generations to achieve (Waples 1998). Restoration sites, and the landscapes around them, are often far from equilibrium, and so estimates of historical gene flow must be interpreted with caution. Specifically, gene flow will be overestimated when populations are still diverging from a common ancestor under drift (Kinnison et al. 2001) but underestimated during periods of increased gene flow among previously divergent populations (Whitlock 1992). Fortunately, the problem of non-equilibrium conditions can sometimes (but not always) be circumvented by estimating “current” immigration with genetic assignment methods (Berry et al. 2004; Paetkau et al. 2004). However, practitioners should note that these methods detect immigrants that might not actually contribute to genetic introgression. Further, assignment power should be taken into account before attributing mis-assigned individuals as immigrants.

Gene flow estimates in restoration scenarios can be used to infer evolutionary potential: low gene flow facilitates the independent evolution of different populations, whereas high gene flow constrains it (Hendry et al. 2001; Lenormand 2002). This generalization is largely true for divergence in neutral markers but is heavily nuanced for divergence in selected markers or traits. Large numbers of effective migrants may belie strong selection that weeds out an even larger number of unsuitable immigrants, or their offspring, while favoring more suitable individuals. Selected markers or traits can thus undergo adaptive divergence even in the face of apparently moderate gene flow (Hendry et al. 2001). In short, gene flow estimates can be useful tools in restoration contexts, but are best interpreted along with an understanding of selection acting on traits in the populations of concern.

Selected Markers

Some molecular markers reflect traits that are under direct selection or are physically linked to loci under selection (Mitton 1997). If these markers can be identified, surveying them within and among populations can reveal the amount and structure of adaptive genetic variation. For example, allozyme loci are sometimes under selection (Mitton 1997) and can be easily and quickly assayed for large numbers of individuals. Indeed, variation in allozyme markers has already been considered in a restoration context (Stockwell et al. 1996; Stockwell and Mulvey 1998). For instance, approximately 75% of recently established populations have low allelic diversity relative to their ancestral source (Stockwell et al. 1996). Further, contemporary evolution has been reported for several allozymes (Mitton and Koehn 1975; Smith et al. 1983; Stockwell and Mulvey 1998). For example, allele frequencies at the phosphoglucate dehydrogenase (*Pgdh*) locus are correlated with salinity in native and recently introduced populations of the White Sands pupfish (*Cyprinodon tularosa*). This variation likely reflects adaptive variation across space and time (Stockwell and Mulvey 1998).

Another approach to quantifying divergence for selected markers is to infer quantitative trait loci (QTL) based on associations between phenotypic differences and particular alleles at marker loci (e.g., Hawthorne and Via 2001; Peichel et al. 2001). Unfortunately, QTL analyses have a number of limitations. From a practical perspective, they are time consuming and expensive, often requiring a breeding program coupled with extensive controlled rearing. Even if these practical problems can be overcome, however, a serious theoretical limitation is that divergence at QTLs is unlikely to reflect the divergence in the traits influenced by those QTLs (Latta 1998; Pfrender et al. 2000; Le Corre and Kremer 2003). QTL surveys may therefore provide little information about the genetic basis and adaptive significance of phenotypic variation. And so, QTLs may be of limited use in most conservation and recovery programs, which are more concerned with heritable adaptive differences than in the number, nature, and genomic locations of loci influencing those differences.

An emerging approach to the study of adaptation at the molecular level is the use of cDNA (complimentary DNA) microarrays for examining differences in gene expression between populations in different environments (reviews: Gibson 2002; Jackson et al. 2002). At present, microarrays have been developed for only a handful of model species (e.g., *Arabidopsis*) and are very costly and time consuming. For most conservation concerns, microarrays will therefore be prohibitive for the foreseeable future. Ultimately, however, this approach might provide a powerful tool for selecting populations for recovery efforts that best match the gene expression patterns appropriate for a particular restoration environment.

Quantitative Traits

Heritable variation in quantitative traits arguably provides the most direct link to evolutionarily important phenotypic patterns. By far the easiest and most widespread method for estimating such variation is to measure phenotypic traits on wild individuals. The resulting patterns will reflect a combination of genetic and environmental influences, which may interact in complicated ways. For example, phenotypic differences among individuals or populations may not have a genetic basis (e.g., James 1983) if trait expression is directly influenced by environmental factors (i.e., phenotypic plasticity). In this case, the offspring of individuals transplanted between environments may express traits that are expected to suit individuals in

those environments. Alternatively, phenotypic similarity among individuals or populations may be maintained by substantial genetic differences that override environmental heterogeneity (e.g., countergradient variation: Conover and Schlutz 1995). In this case, individuals subjected to identical environments may subsequently differ dramatically in trait expression. These two examples illustrate how inferences about heritable variation are tenuous when based on phenotypic variation in the wild alone.

Genetic variation *within* populations is important because it influences the ability of a population to adapt to changing environments (Houle 1992; Bürger and Lynch 1995; García-Ramos and Rodríguez 2002; Reed et al. 2003). The influence of genetic variation on short-term evolutionary potential can be assessed by measuring the narrow-sense heritability (i.e., additive genetic variance divided by total phenotypic variance) of fitness-related traits (Roff 1997), or of fitness itself. With this information, one can predict the evolutionary response of a trait to a given intensity of selection (Box 6.1). The influence of genetic variation on long-term evolutionary potential can be considered by assessing the “evolvability” of the trait (i.e., coefficient of variation of additive genetic variance) (Houle 1992). In some cases features that are strongly correlated with fitness (i.e., under strong selection) may retain less variation for future evolutionary challenges. Hence, current adaptation and future adaptive potential can be at odds with each other.

The most direct, robust, and informative way to infer heritable adaptive differences is through the use of reciprocal transplants (O’Hara Hines et al. 2004). Differences in trait expression and overall performance (e.g., survival, growth, reproductive success) between individuals in “home” versus “foreign” environments can then be used to infer adaptive genetic differences. The optimal design of reciprocal transplant experiments has many important nuances (O’Hara Hines et al. 2004), which we do not discuss further because such experiments are often prohibitively difficult in a restoration context. A more common and tractable approach is to rear/grow individuals from different populations in controlled environments, such as a greenhouse, where conditions can sometimes be set to mimic environmental features at natural sites. Such “common-garden” experiments can reveal whether phenotypic variation within or among populations is heritable, and can incorporate breeding designs that reveal the quantitative genetic architecture (e.g., additive, dominance, epistasis) of that variation.

Although such rearing experiments are useful and prevalent, they have important limitations. A seemingly obvious point, often forgotten or ignored, is that genetic variation *within* populations (e.g., significant heritability) does not mean that phenotypic differences *among* populations necessarily have a genetic basis, only that genetic variation exists for evolution of a given population. Common-garden experiments should include all populations about which inferences are to be made. Even when this can be achieved, the phenotypic expression of genetic variation will depend on the specific rearing/growing conditions (Roff 1997; Hoffmann and Merilä 1999). Accordingly, differences observed in a specific common environment may not reflect differences that would be observed under other rearing environments, or in nature. Moreover, common-garden experiments do not directly demonstrate the adaptive significance of phenotypic variation, because they do not expose organisms to the full suite of challenges they would encounter in nature.

Instead, the adaptive significance of heritable phenotypic variation among populations might be inferred by comparing *genetic* divergence in phenotypic traits (i.e., estimated in a

common garden) to divergence expected under the absence of natural selection (i.e., based on mutation and genetic drift alone). When additive genetic differences *exceed* these “neutral” expectations, selection is inferred as the basis of phenotypic divergence (review: Turelli et al. 1988). At present, neutral models of trait evolution are limited in that they rarely consider gene flow, variable demographics, or founder effects. Moreover, although the rejection of a neutral model provides evidence that phenotypic patterns are the product of selection, *failure* to reject a neutral model does not provide evidence for or against anything; there is no reason selection cannot produce values consistent with neutral expectations.

A recent extension of such approaches is to estimate the neutral expectation directly from the genomes of the populations under consideration. For example, an analog of F_{ST} has been developed for quantitative traits (termed Q_{ST} by Spitze 1993):

$$Q_{ST} = \frac{\sigma_a^2}{\sigma_a^2 + 2\sigma_w^2},$$

where σ_a^2 is the additive genetic variance among populations and σ_w^2 is the additive genetic variance within populations. Neutral and selected variation within and among population are both subject to the same patterns of demography and immigration. When phenotypic traits are not under selection, Q_{ST} should approximately equal F_{ST} as estimated from neutral markers (Lande 1992; Spitze 1993; Whitlock 1999; but see Hendry 2002). Q_{ST} values greater than F_{ST} thus imply that phenotypic differences are driven by selection and are therefore adaptive.

Q_{ST}/F_{ST} comparisons have attracted considerable recent interest. A point of general agreement is that Q_{ST} often exceeds F_{ST} , suggesting that divergence in quantitative traits is the result of selection (Merilä and Crnokrak 2001; McKay and Latta 2002). Nonetheless, Q_{ST} is sometimes appreciably less than F_{ST} , implying parallel or convergent patterns of selection on some traits in some systems (e.g., Lee and Frost 2002). A point of general disagreement is whether or not F_{ST} and Q_{ST} are correlated. If they are, the easy-to-measure F_{ST} might be used to infer the difficult-to-measure Q_{ST} , which generally requires rearing experiments to estimate genetic variances. Some authors argue that these measures are correlated (Merilä and Crnokrak 2001; Crnokrak and Merilä 2002) and others, that they are not (Pfrender et al. 2000; McKay and Latta 2002; Latta and McKay 2002). Regardless, the correlation is clearly not very strong (see also Reed and Frankham 2001). F_{ST} is therefore unlikely to provide a reliable estimate of relative heritable trait divergence. Despite this limitation, Q_{ST}/F_{ST} comparisons are useful for revealing phenotypic traits that are under strong divergent selection even in the face of some gene flow.

Owing to the difficulty of formally estimating Q_{ST} , several short-cuts have been proposed. The simplest, and hence most appealing, is to assume that phenotypic variation reflects additive genetic variation. If so, Q_{ST} might be estimated simply by measuring the phenotypes of individuals captured from the wild (perhaps with some correction using known heritabilities). Although quantitative trait divergence estimated using additive genetic variation (Q_{ST}) and phenotypic variation (perhaps we can call this P_{ST} by analogy) may sometimes be equivalent, there is no fundamental expectation (see arguments above) or empirical data to support this. Additive genetic variation within populations might be estimated in the wild using phenotypic similarity and genetic relatedness or pedigree (Ritland 2000), but such ap-

proaches would not address the problem of estimating heritable variation among populations. Despite all these concerns, evidence that Q_{ST} or P_{ST} exceed F_{ST} would support the importance of environmental heterogeneity in determining trait variation over the landscape.

Application of Contemporary Evolution to Restoration Ecology

Restoration ecology includes a number of strategies that can be considered in the context of contemporary evolution. First, the temporal and spatial context of the restoration site is important. The need for restoration suggests that the site has undergone dramatic transformations. The legacy of previous land uses such as pesticide residue may continue to generate important selective pressure during and after restoration. Alternatively, organisms that persist during a cleanup may actually evolve to post-cleanup conditions (Levinton et al. 2003). As already discussed, the spatial context is also important because the site will interact spatially within its local region in terms of gene flow (or absence thereof). Here, we consider various restoration strategies in an evolutionary context.

Selection of Seed Sources

The restoration of populations to environments from which they have been extirpated requires the selection of suitable source populations (i.e., seed sources). The first order question faced in such cases may be whether to use a captive lineage derived from that site prior to extirpation or to use an exogenous source. If an exogenous source is selected, geographically proximate sources are often chosen under the assumption that these are more likely to have structure and function similar to that required at the restoration site (Jones 2003). However, adaptive divergence and geographic distance are not always well correlated. As a result, more optimal seed sources may be quite distant from the target site. It is also important to remember that populations undergoing restoration may affect surrounding populations through dispersal and gene flow, and this impact will again depend on spatial variation in selection and adaptation (Falk et al., this volume).

Rice and Emery (2003) recommend an approach in which source populations are matched to the general ecological conditions at the restoration site, but the source mixture includes populations from representative microclimates. The idea here is that the general population is sufficiently matched to manage genetic load, but that the mixture from various microclimates maximizes evolutionary potential. We feel that general rules such as these are likely to engender a false sense of security. It is quite possible that increasing the number of sources without respect to understanding their actual performance in the new habitat may simply increase the proportion of individuals that are maladapted and hence the genetic load. Selection of seed sources based on insights into patterns of selection, genetic variation, and local adaptation for the landscape under consideration may have higher odds of success. However, such information is often not readily available. We suggest that the most pragmatic alternative is to start with releases (even small scale) of a suite of likely candidate sources, and then recompose further (and perhaps larger) releases based on *empirical* insights into the best performing sources (e.g., tagging or genetic studies). If a local population takes hold, further empirical evaluations can be made to determine if continued supplementation from outside sources is likely to be beneficial or detrimental.

An additional complication is that preferred donor sites may have limited seed surplus, making it necessary to consider less preferred alternatives. Other options that have been pursued include multiple origin polycrosses, the use of related taxa or interspecific hybrids, or unrelated species that serve a similar function (Jones 2003). Each of these approaches can have important implications in the context of contemporary evolution, and each should again be evaluated *empirically* on a limited scale before risking continued long-term supplementation with the same sources. Literature on exotic and invasive species suggests that some of these options, such as releases of related taxa, carry risks of creating pestiferous invasions. Hence, issues of containment or eradication should be carefully ensured before even performing test releases.

Although captive populations are commonly used in restoration efforts and may retain the traits best suited to a restoration site, they could pose some severe drawbacks. In particular, captive populations may have limited genetic variation, suffer from inbreeding or introgression, and may be adapted to captive conditions ("domestication," see Frankham et al. 2000; Woodworth et al. 2002; Gilligan and Frankham 2003). Such adaptation need not involve intentional selection, or even obvious differences between captive and wild environments. Instead, captive populations can evolve simply due to relaxed selection pressures (Heath et al. 2003). These changes may have negative impacts on the evolution of native populations when captive lines are used for supplementation (Heath et al. 2003). For instance, relaxed selection pressure presumably selected for smaller egg size in a hatchery population of chinook salmon (*Oncorhynchus tshawytscha*) (Heath et al. 2003). Populations supplemented with large numbers of fish from this hatchery showed a reduction in egg size that theoretically could be detrimental to fitness (Heath et al. 2003).

How then might captive populations be managed to prevent unwanted evolutionary changes? Common prescriptions include (1) maintaining limited inputs from any remaining wild source, (2) continual release of captive offspring into the wild to ensure their exposure to natural selection, and (3) manipulations of the captive environment to better match the wild environment. The issue for many captive populations may thus come down to approaches for preventing their domestication and adaptation to captive conditions. Preventing evolution or adaptation is a difficult proposition for the reasons described above. Unfortunately, the evidence that these approaches are effective is limited and considerable debate exists on the role that captive populations should play in conservation and restoration. Captive propagation has been credited with the persistence and reintroduction of some populations and species (e.g., California condor, red wolf). However, supportive releases from captive lineages or even artificial propagation of otherwise wild populations have also been implicated as ineffective or damaging for recovery of remaining wild populations (e.g., salmon) (Myers et al. 2004). Ultimately, fully controlled comparisons simply do not exist to indicate whether already declining wild populations would have fared better or worse in the absence of such measures.

An interesting, but as yet untested, approach may be to mimic natural selection when implementing captive breeding programs. However, accurately determining natural selection is extremely difficult (Hersch and Phillips 2004), and mimicking this selection in captivity is likely to be equally difficult. At present, captive breeding programs usually focus on retaining or increasing genetic variation, reducing inbreeding, and removing individuals with obvious deleterious traits (color variants, deformities, etc.). As noted above, however,

supplementation with exogenous sources may actually reduce population fitness if the population is already partly adapted. We suggest that practitioners consider the value of a hybrid approach that favors propagation of individuals having phenotypes/genotypes well suited for the restoration site, while specifically avoiding inbreeding (i.e., not mating with close relatives).

Inoculation, Stocking and Natural Colonization

One philosophy of restoration is “if you build it, they will come.” That is, restoration sites with suitable environmental characteristics will be naturally recolonized by appropriate species. However, the rate of natural colonization can be slow and may vary as a function of species vagility and habitat fragmentation (Maschinski, this volume). Brady et al. (2002) used mesocosms to compare the merits of inoculation versus natural colonization of experimental wetlands. They found that natural colonization resulted in higher species richness but lower species diversity (as measured by richness and evenness) and generally mimicked a natural wetland. Snails dominated inoculated mesocosms, whereas naturally colonized mesocosms were dominated by chironomids. This difference in community structure is likely to influence local selective pressures for a variety of species. For instance, snails act as intermediate hosts for a suite of parasites that also infect fish (Hoffman 1999) and so these different approaches may produce habitats that vary considerably in parasitism risk for various fish species.

The alternative strategies of introduction or colonization may also have important implications for genetic variation. Restoration efforts that proceed by introduction often result in reduced genetic variation at presumably neutral markers (Stockwell et al. 1996; Helgen and Parsons 1997), which can compromise evolutionary potential. In contrast, Travis et al. (2002) found that naturally colonized sites had high genetic variation. These results suggest that natural colonization is preferable, when possible, but more research should be conducted to confirm these conclusions and to evaluate alternative introduction approaches.

Managing “Refuge” Populations in the Context of Contemporary Evolution

For many actively managed species, refuge populations are sometimes established as a hedge against extinction (Stockwell et al. 1996; Stockwell and Weeks 1999). This approach is especially common for desert fishes, due to the precarious nature of their habitats in the face of anthropogenic disturbance. In most cases, refuge populations are intended as “genetic replicates” of native populations, but this goal can be undermined when refuge populations face different selection pressures to which they adapt. This adaptation may increase the long-term viability of refuge populations, but also decrease their value as genetic replicates of the source population. If adaptive divergence is substantial, refuge populations may no longer possess adaptive variation suited to the original site, although they nonetheless preserve the evolutionary legacy of the lineage. Management actions designed to limit the local adaptation of refuge populations would slow the decay of genetic equivalence but might reduce sustainability of the refuge population.

An example of evolution in refuge populations is provided by White Sands pupfish (*Cyprinodon tularosa*) in New Mexico. Native populations of this species occur at Malpais Spring (brackish spring) and Salt Creek (saline river). These two populations are genetically

distinct at microsatellite markers and have nearly fixed differences at an allozyme marker (Stockwell et al. 1998). Circa 1970, two populations of *C. tularosa* were established at Mound Spring (brackish spring) and Lost River (saline river) (Stockwell et al. 1998; Pittenger and Springer 1999). These refuge populations underwent subsequent changes in allele frequencies at an allozyme locus (Stockwell and Mulvey 1998) and in various aspects of body shape (Collyer et al., 2005). Thus, the Mound Spring population has lost some of its value as a genetic replicate of the Salt Creek population. We contend that refuge populations should not necessarily be managed to maintain evolutionary stasis but should instead be managed as reserves of the evolutionary legacy of species (Stockwell et al. 1998, 2003).

Summary and Research Opportunities

Recent work has suggested that contemporary evolution is common, and decades of research support the significance of natural selection, gene flow, and other evolutionary mechanisms in determining the fate of populations. Evolutionary ecology should thus be considered a central element of a more comprehensive restoration science. Indeed, the non-equilibrium conditions associated with restoration efforts are likely to promote evolutionary changes and the success or failure of such efforts is as much an evolutionary problem as an ecological one. Further, *evolutionary restoration ecology* should be considered from the genotype to the landscape scales. After all, it is the heterogeneity of the landscape that determines patterns of selection and gene flow and thus the potential distribution of individuals and their traits.

We have spent the bulk of this chapter describing potential contributions of evolutionary ecology to restoration. However, restoration activities also provide excellent opportunities for evolutionary biologists to study population genetics, natural selection, and contemporary evolution. From an evolutionary biology perspective, exciting opportunities may be afforded by the manipulative experiments in evolution posed by restoration activities. Here we identify a few topics that we think are ripe for collaborative attention.

- *The relationship between contemporary evolution and ecological function:* Seliskar (1995) reported that the genetic background of the founding stock may have profound influence on the ecological function of an introduced population (cord grass, *Spartina alterniflora*). It is also possible that subsequent contemporary evolution may alter the functional role of a species. Collaborations between functional ecologists, evolutionary biologists and restoration practitioners may provide exciting opportunities to explore the cause and effect relationships of contemporary evolution and ecosystem function.
- *Contemporary coevolution:* Species interactions, such as predation and herbivory, are important selective factors associated with contemporary evolution. This creates the potential for contemporary coevolution (e.g., herbivory/defense) or trophic evolutionary cascades (Thompson 1998). For example, selection for smaller size at maturity may lead to a reduction in gap size and a shift in diet, thus releasing (or changing) predation pressure on prey species. This change might lead to evolution in the prey species, which could have cascading effects on additional species.
- *Managed releases:* The traditional approach for reintroduction efforts is to use large numbers of individuals to maintain genetic variation. An alternative is to not only in-

produce suitable sources, but to select phenotypes within those sources that are best matched to the new environment (Stockwell et al. 2003). This alternative may result in lower initial genetic variation but may facilitate contemporary adaptation. After all, adaptation and population productivity are the product of natural selection associated with reduction of maladaptive variation from the population. Again, the best phenotypes may be gleaned empirically by monitoring preliminary releases. These and other approaches for source selection could be compared in experiments in which multiple sites are targeted for restoration with comparable species and sources.

- *The evolutionary control of exotics:* Some investigators have advocated an evolutionary approach to the control of exotic and weedy species (Palumbi 2001; Stockwell et al. 2003). For instance, simulations by Boulding and Hay (2001) showed that high gene flow among locally adapted populations may cause population extirpation. Perhaps gene flow can be increased in situations where extinction would be desirable (e.g., of an exotic), though the risk of genetically enhancing such populations also exists. Another evolutionary control method may be the simultaneous use of multiple control agents to slow the evolutionary compensation of disease/pest organisms (Palumbi 2001). We agree that evolutionary approaches may be useful for control efforts but caution that the various options must first be evaluated in replicated experiments.
- *Reversing the evolutionary trajectory for managed species:* As indicated above, most populations are likely to evolve when faced with new patterns of selection and such selection is expected to result in some loss of genetic variation. This raises the possibility that they are no longer adapted to their native habitats. A question of critical importance for some actively managed populations may be whether and how rapidly they might evolve back toward their original condition if needed. Restoration ecologists may have unique opportunities to evaluate the reversibility of contemporary evolution by studying cases where exploitation is ceased, for example, when captive lineages are reintroduced to the wild, or where refuge populations are reintroduced to native habitats.
- *The evolution of fitness:* Most studies of contemporary evolution examine changes in just one or a few traits. This atomization of an organism's phenotype will not capture the full implications of contemporary evolution on population productivity and persistence. Much greater insights would be provided by measuring the evolution of fitness itself (Kinnison et al., forthcoming). For example, one might introduce a population to a restoration site, allow that population to adapt for several generations, and then compare its performance (survival and reproductive success) in the introduction site against more individuals from the source population. This sort of comparison would reveal the rate at which fitness evolves in restoration contexts. Such studies would provide a more comprehensive understanding of the implications of contemporary evolution for restoration ecology.

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