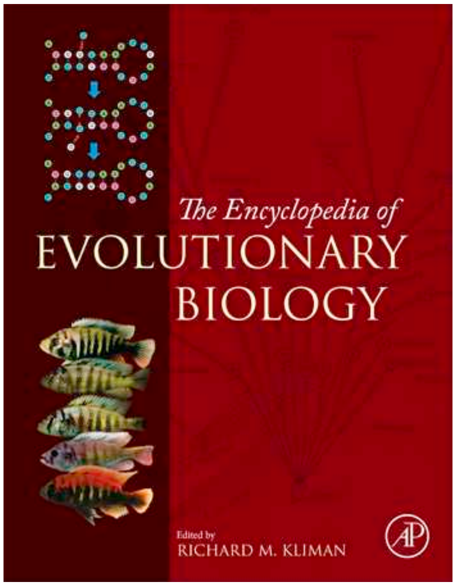

Hays, C.G., and Fagan, C.M. (2016) Conservation Biology, Evolution and. In: Kliman, R.M. (ed.), Encyclopedia of Evolutionary Biology. vol. 1, pp. 347–353. Oxford: Academic Press.

Conservation Biology, Evolution and

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Glossary

Heterozygosity A measure of the genetic variation within individuals in a population; mean observed heterozygosity refers to the proportion of individuals sampled carrying two different alleles at a given loci.

Demographic rates Per capita (per individual) birth and death rates, these determine the rate at which a population grows or declines over time.

Density-dependent population growth When the rate of increase of a population is not a constant, but varies as a function of population size.

Overdominance Also referred to as 'heterozygote advantage'; individuals with two different alleles at a loci have the highest fitness.

Quantitative trait A trait that is the result of the cumulative effects of many genes and the environment; quantitative traits (such as body size, and limb length) vary among individuals such that the range of phenotypes is continuous, rather than falling into discrete categories.

Stochastic Describes a process for which the outcome is determined at least by one random factor.

Introduction

Conservation biology as a discipline is deeply rooted in evolutionary biology. The overarching goal of conservation biology is to protect and maintain biodiversity, and biodiversity spans multiple levels of biological organization, including the diversity of genes, species, communities, and ecosystems. Evolutionary processes determine or influence diversity at all levels in this hierarchy. For example, loss of genetic diversity within a population can decrease population growth rate and persistence (Frankham *et al.*, 2002); genetic diversity within a population can also have important ramifications for community and ecosystem-level processes, such as the strength and stability of species interactions, community structure, primary productivity, and nutrient cycling (e.g., Lankau and Strauss, 2007; see review by Hughes *et al.*, 2008).

Within conservation biology, the subdiscipline of conservation genetics focuses on the application of genetic tools and methods pulled from a range of evolutionary fields (including systematics, phylogeography, population genetics, and increasingly genomics) to conservation problems. Conservation genetics is an active and growing field of study: a peer-reviewed journal of that name has been in print since 2000, in addition to the many papers exploring genetic topics in conservation published in journals with broader conservation or ecological themes. Conservation genetics has also received thoughtful attention in several textbooks (e.g., Groom *et al.*, 2005; Carroll and Fox, 2008); we recommend these sources and others listed at the end of this article for further reading.

Here we briefly discuss some of the areas where evolutionary biology and molecular genetics intersect with conservation biology. We divide our review into two broad topics: first, we consider some of the many ways in which molecular genetic patterns have been used to inform current conservation practice. Then we review the evolutionary processes most important for the persistence of small, demographically threatened populations, and how evolutionary principles might be incorporated into active management plans.

Pattern: What Can Genetic Patterns Tell Us about Biodiversity and Taxa of Conservation Concern?

The use of genetic techniques to answer ecological questions has exploded in frequency over the last decade as molecular techniques have become increasingly powerful, efficient, and inexpensive. Molecular markers such as microsatellites and DNA sequences have provided conservation biologists valuable insight into the basic biology (e.g., mating system, dispersal) and demographic history of species of concern. For example, molecular analyses have been used to illuminate the effect of kinship on social behavior of African elephants (Archie and Chiyo, 2012), and estimate the pre-whaling abundance of gray whales (Alter *et al.*, 2008). Molecular markers have also been utilized for forensic applications, such as identifying the geographic origins of captive chimpanzees (Goldberg, 1997), and determining what species of whale meat is being sold in Japanese markets (Baker and Palumbi, 1996).

Identification of Units of Biodiversity

'DNA barcoding,' the standardized use of short (~600 bp), highly conserved regions of the genome to distinguish species-level taxonomy (see review by Kress *et al.*, 2015), can be used to identify cryptic species and resolve taxonomic disputes. For example, analysis of the mitochondrial gene encoding cytochrome *c* oxidase subunit 1 (CO1; the most common 'barcode' marker used for animal taxa) revealed that the neotropical skipper butterfly *Astraptes fulgerator* represents a complex of at least 10 well-resolved species (Hebert *et al.*, 2004). Molecular genetic analysis has also been applied extensively to document variation within species, and to identify populations that are sufficiently differentiated that they require separate management. This is the idea behind evolutionarily significant units, or ESUs (Ryder, 1986). ESUs are recognized by the Endangered Species Act and have been broadly embraced by management agencies since first proposed in the mid-1980s, in spite of the fact that there is ongoing debate about the practical

doi:10.1016/B978-0-12-800049-6.00301-2

application of the label, and what, exactly, counts as evolutionary significance (see review by Crandall *et al.*, 2000). Of key concern is the relative importance of adaptive divergence versus longstanding reproductive isolation. Neutral or nearly neutral molecular markers (i.e., noncoding DNA) are most often used to evaluate population divergence, and these may not reflect the same patterns as quantitative traits or adaptive differences among populations (McKay and Latta, 2002).

Conservation Planning

Most terrestrial conservation efforts are based upon a framework of protecting habitat; thus an active field of conservation biology (systematic conservation planning) involves developing methods for prioritizing different areas for conservation. These assessments typically use information on species distributions or their proxies (e.g., vegetation type, environmental parameters) and maximize representation of diversity based on different criteria, such as within-site species richness and complementarity of species assemblages, patterns of endemism or restricted-range species, and representation of threatened species. An ongoing challenge is to better incorporate genetic and trait diversity below the species level into conservation assessment. There are theoretical reasons why genetic diversity and species diversity might be broadly correlated across space, since they are influenced by processes that act in parallel at both scales (e.g., connectivity, habitat heterogeneity; see review by Vellend and Geber, 2005). However, empirical evidence thus far is mixed; thus conservation planning based on species-level patterns may not adequately protect within-species patterns of divergence (e.g., Thomassen *et al.*, 2011; Rissler *et al.*, 2006; Moritz, 2002).

Another way that evolutionary biology has been used to inform spatial conservation planning is by incorporating species' evolutionary history into the 'ranking' process. Some species are more important than others for maintenance of diversity from an ecological perspective (e.g., keystone species, ecosystem engineers); other species are more important from an evolutionary perspective, arguably because they represent greater evolutionary depth (e.g., basal taxa), or because they are more evolutionarily labile and thus (may) have higher potential for future diversification (e.g., species-rich clades). A variety of metrics have been proposed to integrate taxonomic diversity into conservation planning (e.g., Steel *et al.*, 2007; Graham and Fine, 2008; Rosauer *et al.*, 2009). The most commonly used metric currently is phylogenetic diversity, or PD (Faith, 1992), which incorporates both the topology of the phylogenetic tree as well as branch lengths for the species in question. A recent example of this approach is the Zoological Society of London's Evolutionarily Distinct and Globally Endangered (EDGE) program, which pairs PD with information on extinction risk, as assessed by the International Union for Conservation of Nature (IUCN) Red List criteria (Isaac *et al.*, 2007).

The primary challenge facing conservation planning is to preserve not just the existing patterns of genetic and species diversity, but also the evolutionary processes that create and maintain these patterns (Moritz, 2002; Hendry *et al.*, 2011; Brooks *et al.*, 2015). Cowling and Pressey (2001) tackle this problem for a major biodiversity hotspot, the Cape Floristic Region in southwestern Africa. They identified key landscape components thought to contribute to the evolutionary process, especially gradients (fine scale, edaphic gradients as well as macrogeographic climatic gradients), and corridors of movement allowing exchange between inland and coastal areas. This example is exceptional in that the Cape Floristic Region is better studied than many other regions of conservation concern; however, the basic message – preserve gradients, species interactions, and dispersal – is broadly applicable.

Process: The Problem of Small Populations

Much of conservation genetics has focused on the challenges facing small, fragmented populations, for obvious reasons. Of central concern is the loss of genetic diversity as populations decline in size, and the resulting interplay between genetic diversity and population demography. Preservation of genetic diversity is considered critical for two reasons. First, genetic diversity within individuals (e.g., heterozygosity) can directly influence individual fitness, and thus have immediate impacts on demographic rates in small, inbred populations. Second, loss of genetic diversity at the scale of the population broadly equates to a loss of evolutionary potential. This idea can be traced back to Fisher's Fundamental Theorem: under selection, the rate of change of mean fitness is equal to the additive genetic variance in fitness (Fisher, 1958). As the environment shifts, small populations may lack the heritable variation in functional traits necessary to respond adaptively.

Adaptive genetic change that allows a declining population to avoid extinction is called 'evolutionary rescue' (reviewed by Gonzalez *et al.*, 2013; Carlson *et al.*, 2014). Both theory (e.g., Holt and Gomulkiewicz, 1997) and increasing experimental evidence (Bell and Gonzalez, 2009) show that the likelihood of evolutionary rescue depends on the direct and interactive effects of three factors: the degree of mismatch between mean phenotype and environment, the supply of genetic variation, and population size. In general, population size is positively correlated with genetic diversity, at least as measured by neutral or nearly neutral molecular markers (Frankham, 1996). Spielman *et al.* (2004) conducted a meta-analysis of 170 taxonomically paired comparisons of threatened and nonthreatened species; they found that in 77% of cases, heterozygosity (measured at microsatellite or allozyme loci) was lower in the threatened species (**Figure 1**). However, Mendelian molecular markers are often a poor predictor of quantitative diversity (Reed and Frankham, 2001), and adaptive variation may be maintained by selection while neutral variation is lost (McKay and Latta, 2002). Empirical data collected thus far suggest that only the smallest populations show reduced evolutionary potential (see review by Willi *et al.*, 2006). Nevertheless, the trajectory of evolutionary rescue is a race with extinction – even if small populations do contain individuals with appropriate traits (or if these appear by mutation or gene flow), small populations will have a more difficult time achieving rescue than larger ones, both because the rate at which adaptation must occur is faster and because stochastic processes (like genetic drift, discussed below) dominate in small populations.

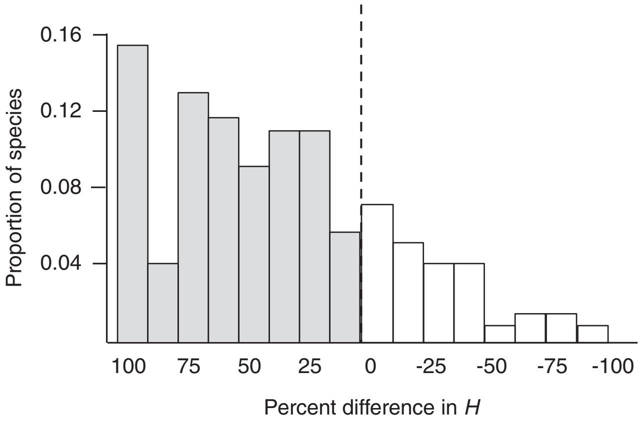

Figure 1 Distribution of percent differences in heterozygosity (*H*) between threatened and taxonomically related non-threatened taxa. Shaded bars (77% of all comparisons) show cases where *H* is lower in the threatened taxa. Data from Spielman, D., Brook, B.W., Frankham, R., 2004. Most species are not driven to extinction before genetic factors impact them. Proceedings of the National Academy of Sciences of the United States of America 101, 15261–15264.

Genetic Drift

Genetic drift is the change in allele frequencies in a population over time due to random sampling events (e.g., differences among individuals in survival or fecundity that are unrelated to their phenotype/genotype). Although the specific genetic consequences of genetic drift during a given demographic bottleneck are unpredictable, the overall effect of drift is to erode genetic diversity.

Effective population size, or N_e, is a measure of how sensitive a population is to genetic drift. N_e is defined as the size of a hypothetical, theoretically ideal population that would experience the same level of inbreeding, loss of heterozygosity, and genetic drift per generation as the real population in question (Kimura and Crow, 1963). Other factors besides the census size of a population will influence the change in allele frequencies over time (e.g., an uneven sex ratio, past fluctuations in population size, nonrandom variation in family size); by excluding these factors, N_e makes it possible to evaluate and compare measurements of drift across species with very different life histories. There are different ways to empirically estimate N_e over both short- and long-term time scales (see review by Hare *et al.*, 2011), but N_e is virtually always smaller, and often much smaller, than the census size of a population. Frankham (1995) reviewed published estimates of N_e/N for wildlife species, and found that N_e averaged only 10–11% of total census size.

In large (unthreatened) populations, it takes a long time to see a major effect of genetic drift on allele frequencies; genetic diversity represents a balance between mutation and natural selection. However, when $N_e s \ll 1$, where s is the selection coefficient describing the difference in fitness between two alleles, drift can counter selection, and the alleles will behave as if they are neutral (Wright, 1931). Thus through this mechanism, small populations may show greater maladaptation (i.e., mismatch between environment and mean phenotype) than larger ones. By similar logic, mildly deleterious mutations will tend to accumulate in small populations, because selection is ineffective at removing them. This can lead to 'mutational meltdown': as deleterious mutations become fixed, they drive down population growth rate (and size), making the population progressively more susceptible to fixation of future mutations (Lynch *et al.*, 1995).

Inbreeding and Inbreeding Depression

Small populations are often subject to inbreeding, or the mating of closely related individuals. Inbreeding per se does not affect allele frequencies; however, because closely related individuals are likely to share alleles that are identical by descent, this increases the likelihood that progeny will inherit the same allele from both parents. Thus inbreeding causes a decline in mean heterozygosity. This in turn can lead to inbreeding depression, typically defined as the relative reduction in fitness of inbred progeny compared to outbred progeny. This fitness differential varies with environment: the expression of inbreeding depression is often greatest in physiologically stressful environments (reviewed by Reed *et al.*, 2012). For example, inbreed white-footed mice (*Peromyscus leucopus*) displayed equivalent survival to outbreed mice in the lab but significantly reduced survival when released into the wild (Jimenez *et al.*, 1994). Similarly, Keller *et al.* (1994) showed that a severe winter selected against relatively inbred individuals in a wild population of song sparrows (*Melospiza melodia*).

Inbreeding depression can be caused by several different genetic mechanisms: the expression of deleterious recessive alleles (i.e., alleles that were 'masked' in the heterozygous state, but expressed in homozygotes), or the loss of overdominance at loci where heterozygotes have the highest fitness. Reduction in fitness caused by the first mechanism can be alleviated over time by selection, assuming that inbreeding occurs gradually and selection against homozygous recessive individuals is not overwhelmed by genetic drift. This process is referred to as purging the genetic load. Support for the role of purging in declining populations is mixed; some reviews suggest that purging only occurs in some cases and does not completely remove fitness costs associated with inbreeding (Ballou, 1997; Byers and Waller, 1999), which underscores the need to better understand the genetic mechanism of inbreeding depression across taxa (Crnokrak and Barrett, 2002).

Interplay between Genetic versus Nongenetic Processes Affecting Demography

In addition to genetic drift and inbreeding, there are also critical nongenetic processes that influence the viability and persistence of small populations. For example, small populations may be subject to positive density-dependent population growth (called an Allee effect, or depensation in fisheries science). Any mechanism that causes a particular component of individual fitness (e.g., individual survival, growth rate or fecundity) to increase with increasing population size or density is considered a 'component Allee effect'; if the net result of all component Allee effect (plus possible compensatory changes in other components of fitness) is an increase in population growth rate, this is a 'demographic Allee effect' (Stephens *et al.*, 1999). The three most commonly reported mechanisms leading to an Allee effect are mate limitation, cooperative defense behavior, and predator satiation (see review by Kramer *et al.*, 2009). For example, groups of bighorn sheep (*Ovis canadensis*) smaller than five individuals show reduced group vigilance in spite of the fact that individuals in these small groups increase their vigilance behavior; further, the per capita risk of predation is greater in small groups if a predator attack does occur (Mooring *et al.*, 2004).

Small populations are also vulnerable to environmental and demographic stochasticity. Year-to-year variation in population growth rate, as well as larger environmental perturbations ('catastrophes'; e.g., storms, fires, etc.), will have a greater impact on small populations than larger ones, simply because larger populations have a greater numerical buffer between the number of individuals at any given time and extinction. Demographic stochasticity is the variation in realized population growth rate that occurs even when the underlying vital rates (e.g., birth and death rates) that determine population growth are constant – the result of applying a rate to real (whole) numbers. Like genetic drift, the relative magnitude of this effect increases as population size declines.

The relative importance of genetic versus nongenetic factors for population persistence has been debated since the inception of conservation genetics (see review by Brook, 2008). Demographic processes are often thought to impact small populations before genetic effects become important; this idea dates back to an influential paper by Lande (1988). However, there is no doubt that inbreeding depression can be an important cause of decline for wild populations (Keller and Waller, 2002). A direct link between inbreeding and extinction risk has been shown in experimental populations of *Drosophila* (Wright *et al.*, 2008), the whitefly *Bemisia tabaci* (Hufbauer *et al.*, 2013), the plant *Clarkia pulchella* (Newman and Pilson, 1997), and in both experimental and wild populations of the Glanville fritillary butterfly *Melitaea cinixi* (Saccheri *et al.*, 1998; Nieminen *et al.*, 2001). Further, the processes described above do not act in isolation: any negative consequences of inbreeding for population growth rate will have implications for all other processes mediated by population size. Gilpin and Soule (1986) first coined the term 'extinction vortex' to describe the sequence of events and synergy between direct and indirect (genetic) demographic consequences of small population size (**Figure 2**). If an ecological impact (e.g., harvest, pollution, or an invasive species) reduces population size, this exposes the population to demographic stochasticity and possible Allee effects; these in turn reduce population growth rate and size, increasing the likelihood of inbreeding and the magnitude of genetic drift, further reducing population growth rate and size.

Dispersal and Gene Flow

One of the fundamental processes that affects population dynamics and persistence is the movement of individuals (dispersal) and their genes (gene flow) from one population to another. This movement may either help or hinder the recovery of threatened populations, depending on the particular circumstances. First consider dispersal alone: on the

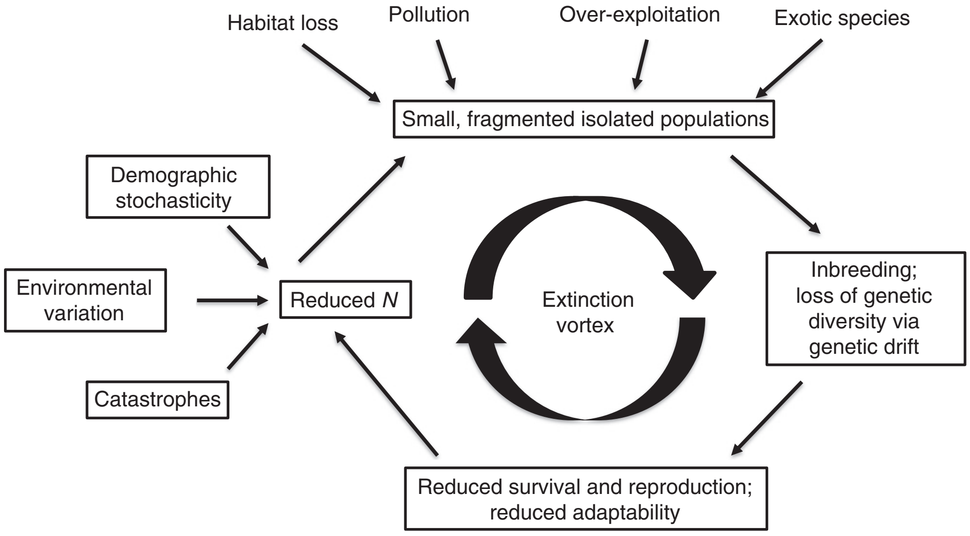

Figure 2 The interplay between genetic and demographic consequences of small population size can lead to an 'extinction vortex.' Reproduced from Frankham, R., Ballou, J.D., Briscoe, D.A., 2002. Introduction to Conservation Genetics. Cambridge: Cambrige University Press.

one hand, the movement of individuals into a declining population serves to pump up population size, and thus can reduce the impact of Allee affects, demographic stochasticity, and genetic drift. Thus, dispersal can have a positive impact on adaptive evolution and population persistence, even in the absence of corresponding gene flow, by potentially maintaining a population in decline (i.e., a demographic sink) long enough for adaptation to occur (Holt *et al.*, 2003). However, in theory, dispersal could also increase population size past its local carrying capacity, thus reducing the fitness of all genotypes; this would make it harder for a new beneficial allele to increase in frequency (Gomulkiewicz *et al.*, 1999).

The effect of gene flow on population dynamics and adaptation is equally complicated (see review by Garant *et al.*, 2007). Gene flow typically acts to increase the genetic diversity within populations; if gene flow increases additive genetic variation for ecologically relevant traits, this can increase the adaptive potential of small populations. New alleles brought in via gene flow can alleviate inbreeding depression and cause population growth rate to rebound – this phenomenon is called genetic rescue (reviews by Tallmon *et al.*, 2004; Whiteley *et al.*, 2015). However, gene flow is not a panacea: gene flow can increase within-population diversity, but it homogenizes genetic differences among populations – if these differences are adaptive, then gene flow will have a negative effect on mean fitness. This is called outbreeding depression, defined as a reduction in fitness of progeny produced by the matings of genetically divergent individuals. When gene flow links populations or groups of individuals experiencing different selection pressures, gene flow can counter the effect of natural selection on allele frequencies, and 'swamp' local adaptation. Outbreeding depression may also occur even if populations have experienced similar selective environments, if the populations have evolved different genetic 'solutions' involving multiple interacting loci (i.e., epistasis). Gene flow between populations can break up these coadapted gene complexes, leading to low fitness in the progeny.

There have been several high profile examples of successful genetic rescue in the last decade, perhaps the most famous of which is the Florida panther (*Puma concolor coryi*). The Florida panther is the last surviving subspecies of the puma in eastern North America. By the early 1990s, Florida panthers were reduced to a single population of ~25 individuals suffering from physical complications linked to inbreeding, including heart defects, high loads of infectious diseases, kinked tails, and adult males with low sperm quality and undescended testes (Johnson *et al.*, 2010). After eight female panthers were translocated from Texas into Southern Florida, the frequency of these traits declined, the population tripled in size, and population growth rate went from 5% annual decline to 4% growth (Benson *et al.*, 2011).

There are far fewer empirical examples of outbreeding depression than of inbreeding depression, but the fitness consequences for declining populations can be equally damaging (review by Edmands, 2007); thus active translocation of individuals by humans, or 'assisted gene flow' (Aitken and Whitlock, 2013), must be approached with some caution. This is one of several areas in which genomic methods (i.e., high-throughput, massively parallel sequencing) offer tremendous promise for conservation. Genomics allows the screening of thousands of markers across the entire genome, providing a powerful tool for exploring the genetics of adaptation (Ouborg *et al.*, 2010; Harrisson *et al.*, 2014). Genomic methods can be used to select appropriate source populations for assisted gene flow, and even to identify individuals within those populations that are likely to have the greatest 'rescuing' effect, either because they have highest genome-wide genetic diversity, or because they possess particular alleles associated with fitness (Whiteley *et al.*, 2015).

Concluding Thoughts

There is now broad recognition that the distinction between so-called ecological time scales (i.e., days to years) and evolutionary time scales (i.e., thousands of years) is a false one – microevolutionary changes can occur rapidly, within human lifespans. Thus, effective conservation must consider both the evolutionary and ecological consequences of any management action or inaction (Ashley *et al.*, 2003; Stockwell *et al.*, 2003). Latta (2008) points out two ironies that challenge our ability to control our evolutionary impact on nature: first, humans select against the very traits that we most value in the wild species that we harvest. For example, fisheries typically select against the largest and fastest-growing individuals, removing those genotypes from the gene pool (Biro and Post, 2008), just as trophy hunting selects against the traits that hunters most prize (Coltman *et al.*, 2003). The second irony is that the species and populations we often wish would remain static (such as insect pests, weedy plants, and pathogens) usually have the greatest potential to evolve resistance to our actions, while the species we hope would adapt to environmental change (i.e., rare, endangered taxa) are least likely to be able to do so. Thus the challenge facing conservation biology is to find ways to proactively manipulate evolutionary processes to achieve conservation goals. To thwart unintended anthropogenic selection, this might mean establishing reserves to act as reservoirs of particular genotypes (e.g., Baskett *et al.*, 2005); to promote adaptation to climate change, this could mean translocating more drought- or heat-tolerant genotypes from a lower latitude to a higher one (Aitken and Whitlock, 2013). Applied evolution has been successfully used in agriculture and medicine; although there are inherent risks associated with attempting to harness and shape evolutionary processes, the need for applied or prescriptive evolution in conservation and resource management has never been greater (see reviews by Hendry *et al.*, 2011; Lankau *et al.*, 2011; Smith *et al.*, 2014).

See also: Biogeography, Conservation. Conservation Biology, Quantitative Genetics in. Invasive Species, Evolution and. Responses to Climate Change, Evolution and

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