Prescriptive Evolution to Conserve and Manage Biodiversity

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Abstract

We are witnessing a global, but unplanned, evolutionary experiment with the biodiversity of the planet. Anthropogenic disturbances such as habitat degradation and climate change result in evolutionary mismatch between the environments to which species are adapted and those in which they now exist. The impacts of unmanaged evolution are pervasive, but approaches to address them have received little attention. We review the evolutionary challenges of managing populations in the Anthropocene and introduce the concept of prescriptive evolution, which considers how evolutionary processes may be leveraged to proactively promote wise management. We advocate the planned management of evolutionary processes and explore the advantages of evolutionary interventions to preserve and sustain biodiversity. We show how an evolutionary perspective to conserving biodiversity is fundamental to effective management. Finally, we advocate building frameworks for decision-making, monitoring, and implementation at the boundary between management and evolutionary science to enhance conservation outcomes.

1. INTRODUCTION

Evolutionary mismatch: a measure of maladaptation that describes the deviation between a population's phenotypic distribution and the optimum for its environment

Applied evolution: the use of evolutionary biology to manage, analyze, and problem solve

The planet recently marked two troubling milestones that anticipate the tremendous challenges ahead for the future of biodiversity: The world's human population surpassed 7 billion, and the concentration of carbon dioxide in the atmosphere rose above 400 ppm. The growth of the middle class, estimated to approach 5 billion over the next 17 years (Homi 2010), will require huge resources, further taxing a planet where two-thirds of the world's land area is already devoted to supporting human activities (Millenn. Ecosyst. Assess. 2005). Although land use change is currently the main driver of species' declines and extinctions (Hoffmann et al. 2010), the impacts of climate change may well rival this in the near future (Natl. Res. Counc. 2013). As a consequence, we are witnessing a global, but unplanned, evolutionary experiment with the biodiversity of the planet. Evolutionary mismatch between the environments to which species are well adapted and those in which they now exist is becoming commonplace and is having negative impacts on species viability (Hendry et al. 2011, Smith & Bernatchez 2008, Stockwell et al. 2003). More effective approaches are needed to mitigate these threats and preserve biodiversity (Dawson et al. 2011, Moritz & Agudo 2013).

A central motivation for why these issues need greater attention is that unmanaged and unwanted evolution has, in fact, become pervasive (Smith & Bernatchez 2008). For example, overharvested organisms have evolved to mature at smaller sizes (Darimont et al. 2009), exotic species introduce novel genes into native populations (Rhymer 2008), and habitat loss and fragmentation increase inbreeding depression in vulnerable species (Smith & Bernatchez 2008). Unmanaged evolution owing to human activities alters the traits and resilience of existing species, but is rarely tracked or examined for its impacts. These go unnoticed while populations and ecosystems continue to be managed using traditional approaches. We can either choose to manage evolutionary processes or not, but evolutionary change will proceed regardless. Given the immediacy and magnitude of the threats, we believe that meeting these challenges will require new and audacious approaches. The goal of this review is to examine past efforts, stimulate discussion, and suggest ways of building new applied evolutionary approaches that can be employed to better conserve and manage biodiversity. We hope that by using an applied evolutionary approach to management, we can shape the outcomes in more beneficial ways.

Managing evolution of natural populations is not a new concept but actually has its roots in game management of the early nineteenth century. Aldo Leopold recognized the potential deleterious effects of hybridization on non-native trout populations, but also the opportunity of releasing fish that might be well adapted into "empty" waters (Leopold 1918). Leopold's land ethic emphasized the interconnections between humans and the land and the complex evolutionary history on which it is grounded (Leopold 1970), but today we recognize the value in conserving such empty waters. The utility of evolutionary principles in species management was appreciated later (Soule & Orians 2001) with the focus on threats to small populations, particularly the effects of genetic drift and inbreeding depression (Frankham 2002). These and subsequent applications eventually led to the explosion of evolutionary conservation, especially the widespread use of molecular genetic approaches (Avise 2008, Ouborg et al. 2010, Smith & Wayne 1996), and to today's emerging field of conservation genomics (Ouborg et al. 2010).

Managed evolution in its current formulation places more emphasis than traditional conservation genetics on phenotypes, ongoing selection, contemporary trait change, and the adaptive capacity of wild and human-supported populations (Carroll & Fox 2008, Smith et al. 1993, Stockwell et al. 2003). It considers not just genotypic diversity but genotype-environment interactions, including phenotypic plasticity and epigenetics, which determine trait expression and its consequences for individual and population performance. In particular, applied evolution seeks to not just predict but also to manage adaptation and plasticity to influence population persistence or even community and ecosystem conditions. Applied evolution also considers macroevolutionary processes and the unique ecological functions and values of a diversity of evolutionary lineages (Devictor et al. 2010, Faith et al. 2004).

We recognize that there are a number of excellent reviews on applied evolution (Bull & Wichman 2001, Carroll et al. under review, Hendry et al. 2011, Losos et al. 2013). However, ours is distinct in its focus on the contributions and opportunities of applied evolution to preserving biodiversity and the risk-taking we believe will be necessary. Specifically, we introduce the concept of prescriptive evolution, to describe how one can proactively leverage evolutionary principles, especially those important to adaptation, and apply them to conservation challenges. The next five sections are organized as follows: In Section 2, we explore the utility of evolutionary approaches for biodiversity conservation and why it matters. Section 3 examines important concepts, challenges, and salient examples of evolution in the Anthropocene. Section 4 summarizes previous efforts to incorporate evolutionary approaches into biodiversity management. Section 5 discusses the translational challenges between evolutionary biology and management, and how prescriptive evolutionary approaches can promote biodiversity conservation. Finally, Section 6 emphasizes the importance of evolutionary stewardship.

Prescriptive evolution: the use of planned manipulations of evolutionary processes to achieve conservation outcomes while assessing, balancing, and mitigating potential evolutionary and ecological risks

Anthropocene: the current geological age, in which human activity has been the dominant influence on climate and the environment

2. WHY AN EVOLUTIONARY APPROACH TO CONSERVATION MATTERS

In principle, three fundamental determinants shape the fate of individuals and populations—genotypes, environment, and chance processes. These three elements interact to shape phenotypes, selection, and trait change through time. Conservation biology has typically focused on managing environmental conditions, such as habitat quality and quantity, and on buffering populations from chance processes, such as demographic stochasticity. But the management of adaptive genetic variation and phenotypes has lagged. Although some conservation approaches do target phenotypes, such as vaccinations to improve survival in the wild or choosing appropriate regions for restoration, these phenotypic interventions are rarely performed with a prescriptive evolutionary goal in mind (but see Hedrick 1995 and below). Likewise, the most commonly stated genotypic goals of larger conservation initiatives (e.g., the Convention on Biological Diversity) are limited to preserving genetic diversity (e.g., avoiding genetic drift) and the avoidance of inbreeding. Few programs identify interventions that involve prescriptive phenotypic evolution as a pathway to recovery. Common rationales for not including evolutionary approaches in management are that (*a*) evolution acts too slowly relative to ecological threats, (*b*) evolution is beyond our ability to manage, and (*c*) manipulating evolution runs counter to the integrity of natural processes (Smith & Bernatchez 2008). The latter two concerns, that prescriptive evolution is more than we can or ethically should aspire to, are considered in a later section. In the remainder of this section we focus on the first.

The concern that evolution acts too slowly to matter can be considered from two perspectives: (*a*) Are evolutionary threats of a similar magnitude to ecological ones, and (*b*) can evolution work rapidly enough to aid population recovery? The influential paper by Lande (1988) stating that inbreeding depression and loss of genetic variation are secondary concerns to saving threatened species compared with stochastic demographic or environmental threats may have hindered evolutionary conservation approaches. Recent work parses the relative contributions to population growth of genetic diversity versus initial population size in models and field experiments and suggests genetic variation can, in fact, be quite important. In an experiment evaluating the effect of different source populations on population growth of Allegheny woodrats (*Neotoma magister*),

Contemporary evolution: current evolution, particularly that occurring at rates relevant to ecological dynamics (observable over less than a few hundred years)

Evolutionary constraints: limitations to adaptation imposed by genetic makeup, functional trade-offs, and the pace of environmental change relative to the organism's demography

Evolutionarily informed management (evolutionarily enlightened management, evolutionary management): management that integrates consideration of past or current evolution such as evolutionary constraints, gene flow, or selection response

translocations were made from either more or less genetically diverse populations. More diverse translocations increased population allelic richness and heterozygosity, and these populations also increased in abundance relative to populations receiving lower diversity translocations (Smyser et al. 2013). In a similar study involving *Bemisia* whiteflies, populations were founded by factorially manipulating the number of individuals and their genetic background (inbred or outcrossed). Genetic diversity, but not numbers of individuals, affected the net reproductive rate of populations, with a greater effect in harsh environments (Hufbauer et al. 2013). Other experimental studies also show the importance that the source of gene flow can have on fitness and population increases (Bell & Gonzalez 2009, Sexton et al. 2011). Thus, although there is no doubt about the importance of demographic and environmental stochasticity on population declines or extinctions, the role of evolutionary processes should not be underestimated.

Does evolution work rapidly enough to be meaningful for conservation? Results indicate that contemporary evolution frequently operates at rates consistent with management concerns (months to a few hundred years) and in ways that can influence management outcomes (Stockwell et al. 2003). Evolutionary rates tend to scale negatively with time, such that, on average, total trait change expected over a generation is not much less than that expected over a decade or century (0.53 versus 0.58 versus 0.63 standard deviations) (Hendry et al. 2008, Kinnison & Hendry 2001). The similarity of these rates of trait change over short and long periods is thought to reflect the combined effects of phenotypic plasticity and temporal averaging of opposing patterns of evolution in response to naturally fluctuating selection in the wild (Hendry et al. 2008, Siepielski et al. 2013). In contrast, management actions, such as havesting practices, often result in consistent directional selection. Accompanying this directional selection are associated directional trait changes in species: Average rates of human-driven trait change are closer to 1.0 standard deviation per generation (Hendry et al. 2008). These metrics suggest that considerable trait change can happen rapidly, particularly when both selection and phenotypic plasticity favor it (Ghalambor et al. 2007).

Evidence for faster evolutionary rates associated with anthropogenic disturbance may involve more than just the capacity for humans to accelerate and sustain trait change. Slower-evolving populations may go extinct without ever being measured, due to their inability to keep pace with human disturbances (Hendry et al. 2008). This is a reminder that although evolutionary rescue may be the hope (Bell & Gonzalez 2009), the demographic costs imposed by strong selection can contribute to extinction (Holt et al. 2005). This, however, is not a reason to dismiss evolutionary considerations in management. Clearly, few conservation practitioners would dismiss habitat restoration as a conservation tool merely because it sometimes doesn't work to recover a species. A holistic conservation framework that considers both the evolutionary potential and evolutionary constraints of populations is essential. The concept of "evolutionary mismatch" in populations constrained to evolve slowly, discussed below, is part of such a framework (e.g., Hendry et al. 2011).

Evolutionary mismatch is a measure of maladaptation that describes the deviation between a population's phenotypic distribution and the optimum for its current environment. Fundamentally, mismatch may best be understood through an examination of preanthropogenic conditions or rapid environmental change, such as might be inferred from reconstructions of climate and habitat in the recent or distant past. The degree of mismatch can be considered an indicator of the intensity of selection acting on a population, as well as the potential demographic cost (i.e., loss of individuals from the population) and loss of genetic variation that contributes to extinction risk. Populations limited in evolvability, such as those with low genetic variation, long generation times, or gene flow from maladapted sources, will generally be more likely to become mismatched, especially in rapidly changing environments.

The framework of evolutionarily informed management is useful in highlighting complementary approaches to reduce mismatch, including managing for environmental suitability or promoting adaptive genetic change (evolution) and changes in the phenotypes expressed by populations (phenotypic plasticity). The low evolutionary potentials of many mismatched taxa often first require environmental rather than genetic interventions, such as providing refuge environments to which organisms are adapted and translocating maladapted populations to more favorable regions. It is worth noting that even long-lived organisms, such as trees, can adapt in contemporary time when selection is sustained (Kinnison & Hairston 2007), as might occur when mature adults are hardy and long-lived, and when selection acts most strongly on juveniles (Vourc'h et al. 2001).

Challenged by climate mismatches predicted in the future, conservation approaches could include moving threatened species proactively ahead of environmental change to conserve them (McLachlan et al. 2007, Wang 2010). Ideally, environmental manipulations might solve many issues posed by mismatch, but that is probably not realistic. Hence, most environmental manipulations could be augmented with evolutionary interventions to reduce mismatch and the intensity of selection and its demographic costs.

Manipulation of phenotypes offers another means to buffer the costs of mismatch (Hendry et al. 2011). Trait expression reflects not just genetic changes across generations but also interactions of genes and environment through adaptive phenotypic plasticity, maternal effects, and epigenetic imprinting (Ghalambor et al. 2007). All of these processes involve adaptive induction of "evolutionary algorithms" (Schlaepfer et al. 2005, Schlichting & Pigliucci 1998) that can improve performance of individuals in response to an environmental cue experienced by that individual, its parents, or more distant ancestors. These inducible algorithms were themselves shaped by historic selection favoring the ability to produce different phenotypes in variable environments. They may serve as bridges across adaptive valleys (Ghalambor et al. 2007), facilitating evolutionary rescue (Chevin et al. 2010) of threatened taxa by reducing phenotypic mismatch enough that populations can sustain the costs of selection. However, as with environmental manipulations, these inducible mechanisms are unlikely to be a panacea. Because mismatches arise from evolved adaptations to past environments they may be insufficient or even antagonistic when environments exceed historic conditions, the reliability of existing cues degrades (Reed et al. 2010), or new false cues trap individuals into lower fitness outcomes (Ghalambor et al. 2007, Schlaepfer et al. 2005, Schlaepfer et al. 2010). Plasticity may thus be maladaptive when the relationships between cues, phenotypes, and fitness are lost in new environments (Chevin et al. 2013).

We define prescriptive evolution as a set of management actions that result in a better match between the phenotypes of threatened taxa and their environment. These encompass both genetic and plastic responses of taxa. We can point to a clear record of prescriptive evolution in fields outside of classical natural resource management and conservation, such as medicine and agriculture (Carroll et al. under review). Below we provide examples of how prescriptive evolution can be employed or is already employed in management. Human actions, whether management related or otherwise, have already inadvertently caused evolutionary change (Smith & Bernatchez 2008, Stockwell et al. 2003). We must now decide whether these will occur in a planned or unplanned fashion.

3. EVOLUTIONARY CHALLENGES IN THE ANTHROPOCENE AND THEIR IMPLICATIONS FOR THE CONSERVATION OF BIODIVERSITY

> *"The history of climate on the planet—as read in archives such as tree rings, ocean sediments, and ice cores—is punctuated with large changes that occurred rapidly, over the course of decades to as little as a few years."* (Natl. Res. Counc. 2013)

Classical examples of rapid evolution driven by humans such as industrial melanism (Kettlewell 1956)—once considered unusual—are becoming commonplace. Indeed there are now thousands of known cases of human-mediated contemporary evolution (Hendry et al. 2008, Smith & Bernatchez 2008). Human-caused evolution in native species can result from direct selection on traits or from selection arising from more indirect effects. Examples such as overharvesting of large fish and the application of pesticides impose strong selection directly on the traits of the targeted organisms. Such selection is often strongly directional. Populations facing persistent directional selection face the problem that genetic variation for favored traits may become rapidly depleted, or, even if variation is maintained, populations may face a persistent mismatch (lag load). Other selective effects of humans can exert more complex and often multivariate selection. For example, when humans dump toxins into the environment, "stacked" pollutant stressors that depend on different detoxification pathways may be much more difficult to adapt to for native species than pollutants that are metabolized through shared pathways (e.g., Cyp1A; see Monosson 2013 for examples).

Applied evolution strategies: management based upon evolutionary principles

In contrast to these direct effects of selection, human-caused selection may also be indirect, diffuse, or variable over time. Diffuse selection may result from non-natives or extinction of key species that drive evolution in other community members (Palkovacs et al. 2011). Variable selection resulting from extreme environmental fluctuations, such as predicted under future climate models (Natl. Res. Counc. 2013), may also be a factor. Complex and diffuse indirect effects of human-imposed selection are predicted to be more difficult to predict and reverse than many direct effects.

To this set of challenges, we can add another complication for evolutionary recovery efforts. Without considerable historical data on past genetic diversity or trait variation, it is difficult to know the complex ways in which human-modified landscapes have already altered genetic structure and evolution—in other words the natural "baseline" is unknowable (Holderegger & Di Giulio 2010, Warmuth et al. 2013). For example, the Silk Road facilitated gene flow among horse populations (Warmuth et al. 2013), but other roads have reduced gene flow (Garcia-Gonzalez et al. 2012, Holderegger & Di Giulio 2010, Riley et al. 2006). Without insights into the past, conventional approaches risk conserving genetic structure that arose because of human disturbance. This and related shifting-baselines issues in conservation biology (Pauly 1995) underline the importance of museum collections and archiving genetic samples discussed below. In the following sections, we describe how evolution is integral to conservation challenges and how management of selection and adaptation are emerging as new paradigms.

3.1. Climate Change

The need to incorporate applied evolution strategies is well illustrated by current efforts to mitigate the impacts of climate change (McMahon et al. 2011, Natl. Res. Counc. 2013). Faced with an environmental shift away from favorable conditions, species have three options for avoiding extinction: (*a*) respond plastically, (*b*) evolve adaptively in place (Gienapp et al. 2007, Williams et al. 2008), and (*c*) move to more favorable habitats. With increasing habitat fragmentation and urbanization, opportunities for dispersal to suitable new habitats will be limited. Many assessments of the effects of climate change on biodiversity involve species distribution models that predict range contractions and widespread extinctions due to climate change (Dawson et al. 2011). Thus, for many species, responding to climate change via plastic responses or adaptive evolution will likely be crucial for avoiding extinction.

To manage natural populations, several groups have proposed the movement of targeted phenotypes, genes, or genotypes to genetically depauperate populations, to populations poorly suited to current conditions, and/or to populations inhabiting extreme environments. These approaches are referred to as genetic restoration (Hedrick 1995), assisted migration (Vitt et al. 2010), assisted translocation (Coles & Riegl 2013), assisted colonization, managed gene flow, assisted gene flow (Aitken & Whitlock 2013), prescriptive gene flow (Sexton et al. 2011), facilitated gene flow

(Thomas & Bell 2013), genetic rescue, and evolutionary rescue (Chevin et al. 2013, Kinnison & Hairston 2007, Pelletier et al. 2009). Forestry has made some of the most extensive forays into these approaches (Aitken & Whitlock 2013). Evolutionary management includes planting more heat- or drought-tolerant genotypes from lower elevation or latitude populations to higher elevations or latitudes (Aitken & Whitlock 2013, O'Neill et al. 2008) or planting stocks genetically modified to better withstand climate (O'Neill et al. 2008). In a 10-year experiment with quaking aspen in North America, seeds moved 800 or 1,600 km northward produced almost twice the biomass of local aspen seeds, suggesting local phenotypic mismatch (Schreiber et al. 2013). If biotic interactions with antagonists and mutualists are also important determinants of range (e.g., Ettinger & HilleRisLambers 2013, Kaarlejarvi et al. 2013), traits other than climate tolerance will also need to be considered.

Increased frequency of extreme weather events will require different management approaches from those managing for shifts in mean change (Natl. Res. Counc. 2013). The selective load associated with more variable environments can cause bottlenecks that leave a genetic imprint different from the response to trends in climate means. Demographic and selective costs of fluctuating environments may deplete genetic variation and hasten extinction. Few studies have documented environment-induced reduction in genetic variation in natural populations, subsequent impacts on demography, and the resilience of such populations to future stressors. After flooding due to extreme rainfall events, marble trout populations exhibited reduced genetic variation within populations (Pujolar et al. 2013) and much greater among-population differentiation. Reduced genetic variation is also associated with range edge populations, which are expected to experience climatic extremes. At the xeric range edge of sessile oaks (*Quercus petraea*), genetic variation is reduced in several loci, and these loci exhibit a cline in variation associated with seasonality and/or precipitation across the range, suggesting divergence due to selection rather than founder effects or drift (Borovics & Matyas 2013). The developmental effects of severe genetic bottlenecks have been most extensively studied in humans, where it leads to a higher incidence of genetic disorders (Guha et al. 2012). The Florida Panther is a famous case in natural populations, in which long-term inbreeding reduced population viability and panthers were "rescued" with genetic variation introduced by individuals imported from Texas (Hedrick 1995).

3.2. Unforeseen Hybridization

Adaptive diversification results from natural selection acting differently among populations in heterogeneous environments. Anthropogenic loss of environmental heterogeneity can result in increased contact and hybridization of recently diverged taxa, leading to a loss of differentiation that reverses the speciation process (Seehausen et al. 2008). For example, the feeding of seeds by humans to the Galapagos ground finch (*Geospiza fortis*) is hypothesized to have eliminated bimodality in the beak size in semiurban areas (Hendry et al. 2006). Introduced species may have similar effects, as in the case of introgression between recently differentiated Enos Lake benthic and limnetic stickleback (*Gasterosteus aculeatus*) populations due to the biophysical influences of nonnative crayfish (Behm et al. 2010). Crayfish activities led to lake conditions intermediate between previous environments and preferred by the intermediate phenotypes of hybrid sticklebacks, causing coalescence of the differentiated forms (Seehausen 2007). Another analogous process with potentially different consequences is the masking or degradation of signals of differentiation when in fact the important aspects of the environment remain distinct. Eutrophication in African Rift Valley Lakes threatens to reverse cichlid fish adaptive radiations by reducing the visibility of otherwise species-specific gender and courtship coloration (Seehausen et al. 1997). Finally, chemical pollution can alter mate choice and break down sexual isolation between species as feared for endocrine disrupting chemicals that are persistent in the environment, bioaccumulate, and have effects at low doses (Shenoy & Crowley 2011). Evolutionary management of unwanted hybridization can entail manipulating aspects of environments that disfavor hybrids. For example, in the California tiger salamander hybrid zone with nonnative barred salamanders, more rapid drying of ponds favored primarily native genotypes relative to more introgressed ones (Johnson et al. 2013).

3.3. Pesticide Resistance Evolution

Lessons from the evolution of pesticide resistance may be important for conservation management in agricultural regions. Agricultural lands harbor a large proportion of biodiversity, and the billions of pounds of pesticides applied annually (Grube et al. 2011) place these habitats under special threat (Geiger et al. 2010). Despite the numerous potential impacts on biodiversity, the evolutionary effects of toxic chemicals are understudied (Lawler et al. 2006). As noted above, evolution might be expected from either direct effects of poisoning or indirect effects from changes in community interactions. For example, avian diversity in agroecosystems declines with pesticide use, with agrarian-specialist birds being most affected due to herbicides altering native plant communities (Chiron et al. 2014). Similarly, plummeting monarch butterfly (*Danaus plexippus*) populations appear to reflect declines in their milkweed host plants (*Asclepias* spp.) with glyphosate-based weed control (Pleasants & Oberhauser 2013). Pesticide runoff from farms is a particularly serious contaminant of aquatic systems. Although the evolution of resistance to environmental toxins is rarely studied in nontarget species (Jansen et al. 2011), physiological tolerance to the common organophosphate insecticide chlorpyrifos was recently discovered in wild frog populations breeding close to agricultural lands in the northeastern United States, suggesting adaptation to an otherwise toxic pesticide (Cothran et al. 2013). De Laender et al. (2014) modeled the influence of toxin gradients on species diversity and found that such within-species variability in tolerance contributes strongly to biodiversity maintenance under environmental pollution. Resistant populations might serve as translocation sources for other populations threatened by pesticide use, but in which resistance has not (yet) evolved.

In addition, prescriptive actions aimed specifically at preventing pest evolution have the potential to reduce pesticide applications (Wilson et al. 2013). More than 11,000 cases of pesticide resistance have been documented in nearly 1,000 species of insects and plants (Tabashnik et al. 2014). Prescriptive controls increasingly used to slow pest adaptation include cycling different chemicals in sequence (Lagator et al. 2013), stacking multiple controls simultaneously (Roush 1998), and setting aside nontreated "refuge" areas from which nonresistant genotypes can later spread to disrupt adaptation in treated areas (Tabashnik et al. 2013). When combined with such prescriptive resistance management, less broadly harmful pesticides may allow more sustainable control practices with reduced nontarget impacts on wild species (Brookes & Barfoot 2013).

3.4. Invasive Species

A growing number of studies point to the importance of evolutionary processes in facilitating invasions (reviewed by Dlugosch & Parker 2008). The best predictor of invasion success appears to be propagule pressure, the number and size of introductions into a new environment (Simberloff 2009). Introductions from many source populations may enhance genetic diversity and facilitate adaptation to new habitats (Dormontt et al. 2011, Prentis et al. 2008), though there is also evidence that even bottlenecked populations sometimes respond successfully to selection based on new expressions of standing genetic variation in novel environments (reviewed by Carroll 2011). Although comparatively little is known about the genetic basis of evolution in invading populations, adaptive evolution appears to have contributed to invasion success in a number of cases (Keller et al. 2009, Xu et al. 2010). Within invading species, some adaptation may occur due to a combination of phenotypic plasticity in some traits and evolution in others (Lucek et al. 2014). Because postarrival evolution can be an important component of success in invaders arriving with small population sizes and with low genetic diversity, it may also prove important in the recovery of native species reduced to small population sizes with low genetic diversity.

Evolutionary impact statements: required before major construction and development projects are undertaken; entail collecting baseline genetic data and considering habitat changes in light of patterns of gene flow, dispersal, and levels of adaptive variation

Extinction of natives is one (macroevolutionary) consequence of species invasions (Zamora et al. 2005), and hybrid introgression with non-native relatives may also lead to the loss of distinct native taxa (reviewed by Rhymer 2008). Increasingly, studies document rapid microevolutionary change in native populations in response to invaders. Examples include the effects of invasive predators (Kiesecker & Blaustein 1997), food sources (Carroll et al. 2005), and competitors (Lankau 2012, Lau et al. 2008). Short-term snapshots of biotic resistance shortly after invasion may underestimate the long-term regulatory potential of natives (Carlsson et al. 2009). The practical upshots may include rapid evolution of capacities for tolerance or biological control of invaders by native species (Carroll 2011) and using invader-experienced phenotypes and genotypes for restoration (Deck et al. 2013, Felker-Quinn et al. 2013, Leger & Espeland 2010).

4. LEVERAGING EVOLUTIONARY BIOLOGY PRINCIPLES TO CONSERVE BIODIVERSITY

4.1. The Potential of Applied Evolution and the Importance of Risk-Taking

The potential benefits of integrating evolutionary approaches into conservation management are enormous. For example, new technologies, such as next generation sequencing, provide more accurate assessments of genetic diversity and might eventually be used to optimize the evolutionary rescue of declining populations (**Table 1**). However, time is of the essence as many species are declining precipitously and will almost surely become extinct without dramatic or even radical intervention—employing evolutionary thinking may offer solutions. Many of the most aggressive interventions to save threatened species, such as captive breeding programs, though a means to buy time, are not sustainable solutions on their own. These programs risk inadvertent adaptation to captivity, genetic drift, inbreeding, and exposure to novel diseases that may prevent return to the wild (Snyder et al. 1997). It is important to overcome the fear of experimentation, such as the prohibition on experiments in National Parks and protected areas or with listed species that face apparent adaptive limitations. At the very least, recovery programs should consider identifying threshold conditions beyond which imminent extinction is apparent and experimentation presents little added threat (Possingham & Kinnison 2010).

Evolutionary experiments are not the only way that evolutionary approaches might improve conservation. Like environmental impact statements, there is also a need for evolutionary impact statements before major construction/development projects are undertaken. Such assessments might collect baseline genetic data, and consider habitat changes in light of patterns of gene flow and dispersal, as part of efforts to create marine protected areas or the formation of other core reserve areas for slowing the loss of genetic diversity.

Along with evolutionary assessments, such as impact statements, the development of a framework for evolutionary early warning signs and the establishment of a monitoring network is needed. With most species of conservation concern, we typically focus on saving populations that are already undergoing severe population declines, when in fact evolutionary interventions are more likely to succeed the earlier problems are detected. One early warning sign, in which the trait in question is known, might be when the strength of selection or rate of contemporary trait change

Table 1 Management actions that affect the evolution of organisms

Management action	Outcome without an evolutionary approach	Outcome using an evolutionary approach
Pathogen control	Administration of vaccines to endangered vertebrates in order to control viruses that spillover from domestic animals.	Because indiscriminate vaccination leads to the evolution of resistance, managers could use an evolutionary vaccination strategy that allows some resistant mutants to grow without imposing strong selective pressure for the evolution of resistance.
	Example: Vaccination of the endangered African wild dog (*Lycaon pictus*) against distemper and rabies [S1][a].	Example: Wild dogs could be vaccinated with several different vaccines that interact epistastically (hypothetical). The use of multiple drugs would create a moving target for the virus, making it harder for highly resistant strains to evolve.
	Application of antimicrobials (herbicides and fungicides) to wild plant populations.	Managers screen the host species to identify resistant populations, which are bred to replace susceptible populations.
	Example: Use of fungicides to control fungus (*Hymenoscyphus pseudoalbidus*) that is causing high mortality of common ash trees (*Fraxinus excelsior*) in Europe [S2].	Example: Managers could test ash populations for fungal sensitivity and breed populations that exhibit high resistance (hypothetical).
Translocation (individuals from a different population are introduced to breed with a declining population)	Unless managers select populations that are genetically compatible, offspring may have reduced fitness (outbreeding depression).	The donor population is selected for genetic compatibility with the recipient population through at least F2 generation with backcrossing.
	Example: Reduced F1 fitness following translocation of black rhinoceros (*Diceros bicornis* minor) from Kenya to breed with South African populations [S3].	Example: With careful population management, black rhinos translocated to Zimbabwe have high heterozygosity and do not suffer from outbreeding depression [S4].
Habitat restoration	Decision-makers should select founder populations with high genetic diversity. Otherwise, when the population expands in the restored habitat, overall genetic diversity may be low due to founder effects.	Managers select individuals from several different source populations to colonize the restored habitat, which reduces founder effects as the population expands.
	Example: The terrestrial orchid (*Dactylorhiza incarnate*) inhabits coastal dune habitats in Belgium [S5]. The orchid experienced a population bottleneck due to dune loss in the 1970s. After recent dune restoration, population size is expanding but genetic diversity remains low.	Example: Managers could seed the restored dunes with individuals from several different orchid populations to combat the loss of genetic diversity resulting from the 1970s bottleneck.

[a]See **Supplemental Literature Cited** for references. (Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**.)

Supplemental Material

is potentially unsustainable (Olsen et al. 2012). Still other signs of trouble might be inferred from unsustainably strong selection in response to growing mismatch or rates of contemporary trait change that exceed theoretical or empirical expectations for long-term persistence (Chevin et al. 2013). Many of these signs would require regular monitoring of populations for phenotypes or genotypes but this is becoming feasible (Bailey et al. 2010). Moreover, given the substantial decrease in the cost of genome sequencing, cheap, accurate genomic assays can readily be integrated into population management.

One important way that conservation strategies can incorporate evolutionary processes is to protect as much intraspecific phenotypic and genetic variation as possible (Sgro et al. 2011, Smith & Grether 2008, Thomassen et al. 2011, Tymchuk et al. 2010, Vandergast et al. 2008). Such variation could either directly form the basis of an evolutionary response to future environmental change or be a proxy for the loci involved in adaptation. In other words, in addition to preserving hotspots identified on the basis of species richness and levels of threat, a focus could be on identifying and preserving regions of high adaptive genetic turnover (Smith & Grether 2008, Thomassen et al. 2011). Although policy makers have acknowledged the importance of conserving genetic and phenotypic variation (Millenn. Ecosyst. Assess. 2005), efforts to incorporate these measures into protected area design and climate change mitigation have lagged.

Evosystem services: environmental services that are provided by the product of past or ongoing evolution, such as when native species evolve to control introduced species

Selection on standing genetic variation is not the only factor determining the capacity for adaptive trait change. Gene flow will often provide a more ready source of genetic variation than mutation (Hendry et al. 2011, Kinnison & Hairston 2007). Using wildlife tunnels or bridges to connect habitats' increasing meta-community connectivity can foster long-term persistence, thus reducing the risk of extinction due to demographic stochasticity and the chance of inbreeding depression (Dornier & Cheptou 2012, Staddon et al. 2010). However, though tunnels and bridges can sometimes effect such exchange, they do not always work (Beebee 2013), and facilitated or prescriptive gene flow should then be considered as a management tool.

Work is needed to develop guidelines on levels and sources of gene flow suitable for sustaining adaptive genetic diversity for evolution while limiting migration load and outbreeding depression (Bailey et al. 2010, Sexton et al. 2011). However, such developments will require important distinctions with respect to the objectives of the manipulation and characteristics of the migrant pool. In some cases, gene flow may draw at random from a source population or mixture of populations to establish entirely new refuge populations or to bolster genetic variation and facilitate evolutionary rescue (Bell & Gonzalez 2009). In others, there may be more interest in targeting specific populations or phenotypes/genotypes to more directly accelerate adaptation in a recipient population, as might occur when sourcing individuals from warm-adapted populations and moving them to the warmer edges of the range.

One hazard of managing gene flow is the possibility of maladaptation as a result of outbreeding depression. This can occur when novel genes are introduced to a population that are poorly suited locally or disrupt locally adapted gene complexes, reducing the fitness of individuals in the population. In theory, natural selection is expected to cull poor combinations over time, but if the "load" of outbreeding depression is too high it could result in rapid population declines and extinction.

Models of evolutionary recovery in small populations may also assist in the development of risk assessment models for managed gene flow. For example, the dynamics of evolutionary recovery in many evolutionary rescue models (Chevin et al. 2013, Pelletier et al. 2009) are characterized by a first stage in which population size decreases to a minimum owing to maladaptation, after which the population starts growing again because of adaptive evolution. A condition for persistence is that populations do not dip below the critical size when Allee effects and/or demographic stochasticity govern population dynamics.

Finally, there is often an overemphasis of ecological factors, such as ecosystem services when making conservation decisions without considering evolutionary processes or evosystem services that might also be at work (Carroll et al. 2014, Faith et al. 2010). A hypothetical example might involve a group of related but allopatric vertebrate frugivores that provide ecosystem services by dispersing tree seeds. Managers wishing to enhance seed rain might connect forest fragments to facilitate movement of dispersers. However, the use of such a strategy without considering how closely related the disperser species are, or if they hybridize (or if they are native species), might backfire. Over the long term, hybridization of dispersers might lead to less efficient seed dispersal and ultimately a decline in ecosystem services. From a policy standpoint, advocating general evolutionary principles may be one approach, such as maintaining genetic variability with the broader goal of preserving adaptive diversity—a useful bet-hedging strategy in the face of rapid environmental change.

4.2. Prescriptive Evolution

Three major concerns for implementing prescriptive evolution include: (*a*) When should evolutionary concerns be integrated alongside recognized ecological ones, (*b*) how can we best implement prescriptive evolution in real world situations, and (*c*) what risks do we assume in managing evolution? We believe that managers can begin by asking how evolutionary processes are influenced by current practices and proceed from there to consider evolutionary manipulations less tied to current practices, ranking evolutionary manipulations among other management strategies, and monitoring the effectiveness of the strategies once implemented (**Figure 1**). As to risk, unplanned evolution often presents greater risk than planned. The inadvertant evolutionary responses in natural populations are inherently unmanaged, sometimes inefficient, and not necessarily to the benefit of the organisms in question or human interests. In contrast, proactively managing evolutionary processes opens the door to more positive outcomes. Although some unintended consequences are inevitable, active engagement permits managing risk in a less haphazard fashion. Indeed, a fundamental component of what we consider truly prescriptive evolution is the weighing and management of risk through the development of evolutionary early warning indicators, the assessment and ranking of risk tied to alternate management scenarios, implementation of controlled experiments, and monitoring to ensure that evolutionary actions have the desired consequences or at least inform future use of such manipulations. We concede that many evolutionary management schemes may be irrevocable, but emphasize that irrevocable unwanted evolution is ongoing in many regions in the absence of action.

To illustrate the utility of evolutionary risk management approaches, consider the need to identify areas for conserving rare and threatened species (**Table 2**). Conservation organizations currently spend enormous resources conducting surveys to identify populations at risk. Rare populations present a challenge in that their scarcity makes it difficult to collect such data. A recent method that uses evolutionary principles has shown that identifying intraspecific genetic and morphological variation in common species is an effective predictor for mapping distributions of rare species (Fuller et al. 2013). The advantage of this approach is that the data can be collected and analyzed economically. For example, Fuller et al. show that, compared with a less evolutionarily informed approach, the use of intraspecific genetic and morphological traits protects twice as many threatened species in a 64,000-km^2 area of dry forest in western Ecuador (Fuller et al. 2013). Furthermore, by identifying critical conservation areas more quickly and cost-effectively, the evolutionary approach reduces the risk of loss of important species from delays required by reliance on traditional surveys. A risk in this approach is that the use of common species as surrogates has not yet been widely tested across ecosystems (**Table 2**; Gregory et al. 2012, Guisan et al. 2013, and see **Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). However, this risk can be mitigated by limiting implementation to areas in which the modeled relationships are supported and by recognition that long-term monitoring may suggest further modifications.

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A second example involves assisted migration (McLachlan et al. 2007), and the establishment of new extralimital populations, to reduce the phenotype-environment mismatch and conserve lineages that might otherwise be lost to impending envionmental change (**Table 2**). A major

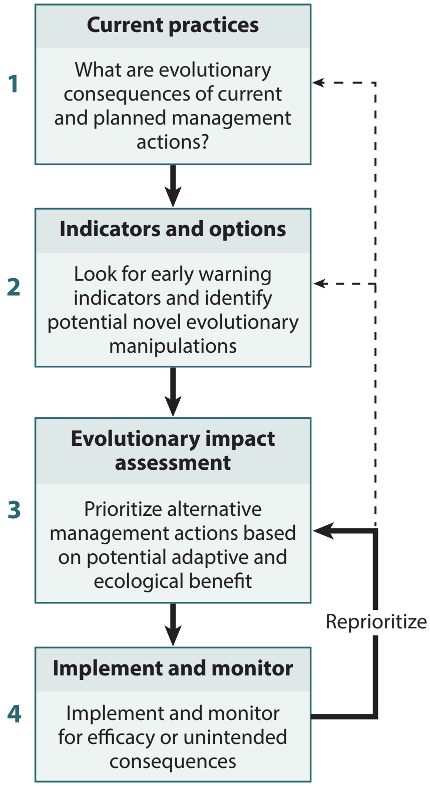

Figure 1

Steps to implementing prescriptive evolution. (*Step 1*) Given that many systems already have active management in place, the first step is often to determine whether and how current practices might influence evolution. (*Step 2*) Where evolutionary problems may be suspected from current practices, early warning indicators might be developed to trigger further action and other evolutionary mechanisms identified that could be beneficial outside current management practices. (*Step 3*) Recognizing that there are often many evolutionary dimensions to a management problem, a next step may be to prioritize these with respect to relative risk or benefit. (*Step 4*) Once implemented, high-priority actions should be assessed for efficacy or unintended outcomes. In some cases, there may be a need to reprioritize to make future progress (*Step 3*) or new information may come to light requiring consideration of new evolutionary challenges (*dashed lines*).

challenge is determining when to implement this measure in place of, or in addition to, continued in situ conservation. An indicator for using this prescriptive approach is cases in which current or impending enviromental changes are too extreme for the species to adapt and population declines are obvious or imminent. By moving to a better matched environment, demographic costs of selection may be reduced. Risk concerns for these approaches include the ecological release of a potential invasive species, introgression with related species, or other negative ecological interactions with the recipient community (e.g., disease transmission). Initial risk mitigation consists of controlled release and experimentation before full implementation, followed by continued monitoring to ensure that the long-term adaptational and demographic goals are achieved. The risk management requirements of this evolutionary approach can be integrated into ecological risk management.

Additional highly controversial evolutionary management approaches entail genetic engineering of organisms with genes from other species. Whole amphibian faunae are threatened by chytrid fungus (Wake & Vredenburg 2008), to which there appears to be limited standing genetic

Table 2 Examples of prescriptive evolutionary solutions to conservation challenges

Challenge	Approach	Advantages	Risks	Risk mitigation	References[a]
Need to identify areas for conservation of rare and threatened species	Use intraspecific genetic and morphological variation in common species to predict distribution of threatened species	Data from common species are easily collected and economically analyzed	Generality of these relationships are unknown	Further studies to confirm relationship between common and threatened species	[S7]
Low genetic diversity/ inbreeding depression	Introduction of genes from suitable sources; genetic monitoring	Increased adaptive potential and augmented population size	Loss of distinctiveness and disruption of coadapted gene complexes; threat of novel diseases	Controlled experimental breeding studies; disease screening	[S8]
Genetically constrained mismatch (low evolutionary potential in mismatched rare taxa)	Evolutionary rescue—add genetic variation in general, versus targeted/ customized/directed types of genetic additions	Increased fitness of population	Nature of the mismatch may be difficult to understand; maladaptive gene flow lowers population density to critical levels	Studies to understand the characteristics of the mismatch; supplement populations with additional individuals to buy time for evolutionary rescue	[S9]
Environmental changes too extreme for species to adapt	Assisted migration and translocations of individuals likely to be better adapted to new areas; translocation of additional sources of genetic variation from similar harsh regimes	Allows populations in affected areas to persist or provides new populations where extirpated	Unanticipated ecological effects, e.g., invasion, introgression, loss of coadapted gene complexes	Small-scale experimental translocations and intensive monitoring	[S10, 11]
Promoting persistence of species and populations threatened by pests	Source, training, early exposure, “seed” with populations adapted or experienced to threat; inoculate disease-threatened taxa with attenuated strains	Reduce or eliminate deleterious effects of pests or invaders	Unintended release and exposure of pathogen to nontarget taxa	Controlled laboratory experimental trials	[S12]
Prioritizing protected areas under climate change	Identify regions of high adaptive variation particularly ecological gradients across which selection and migration can interact to maintain population viability and adaptive genetic diversity	Maximize adaptive variation preserved; bet-hedging approach; genomic tools allow adaptive genetic variation to be more easily assessed	Regions of adaptive variation across taxa do not overlap; regions identified unsuitable for conservation efforts	Pilot studies	[S13, S14]

(*Continued*)

Table 2 ***(Continued)***

Challenge	Approach	Advantages	Risks	Risk mitigation	References[a]
No genetic variation for specific threat	Introduce genes from other species to promote adaptation (GMOs)	Extinction prevention	Exposure of nontarget taxa to novel genetic material; expensive and may not be possible	Genetic engineering to deter accidental release	[S15]
Promote persistence of regional or meta populations threatened by habitat loss, degradation, and fragmentation	Maintain or enhance genetic variation with respect to fitness and historic gene flow; assist migration and translocation of individuals likely to be more adapted to new areas	Maintain adaptive potential	Gene flow may reduce local adaptation and disrupt social structure	Monitoring population growth	[S16]
Maintaining or promoting evo- and ecosystems services	Manage to maximize phylogenetic diversity protected	Aid in protecting ecosystem function	Inattention to diversity within clades, depauperate clade may be insufficient to sustain function	Maximize sampling to ensure important functions are retained; improve understanding of inter- and intraclade diversity	[S17]

[a]See the **Supplemental Literature Cited** for references. (Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**.)

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variation for resistance in many populations. In this case, it is possible that the same resistance gene(s), if found, could provide resistance to many species. Such engineering approaches, though extreme, are not without precedent. Researchers have already genetically modified American chestnut trees with wheat oxalate oxidase resistance genes to potentially allow the recovery of this grand species, brought to its knees by exotic pathogens to which it was evolutionarily naive (Newhouse et al. 2014). Another prescriptive evolution approach harnesses plasticity, epigenetics, and genes by considering the evolutionary history of individuals used for restoration or translocation with respect to a particular threat. For example, experience with an invader has been shown to reduce impact of that invader on offspring of native species. Seedlings of tree species exposed to invasive garlic mustard become less dependent on mycorrhizal mutualists that are killed by garlic mustard (Lankau 2012). Plants grown from seeds of individuals experienced or naive to invasion by the exotic grass *Holcus lanatus* show different responses to soil biota, germinate earlier, and reach canopy height sooner when invader-experienced (Deck et al. 2013). In animals, prey species have been trained to avoid foxes to which they were naive; such cultural evolution may speed adaptation (Griffin et al. 2001).

In sum, we believe prescriptive evolutionary approaches, in addressing and facilitating the speed of adaptation, could offer means of attaining not only short-term but long-term conservation goals while balancing and mitigating forms of risk that are present, but rarely identified, under current approaches. Some of the manipulations available to prescriptive evolution push the bounds of not just technology but of what some might even consider conservation (e.g., genetic engineering). Scientific and societal debate over where to draw the prescriptive line will be ongoing as technology and needs emerge, but in the near term we face an even more pragmatic concern—how best to translate even modest evolutionary prescriptions into management policy.

Boundary science: in conservation refers to research that both advances scientific understanding and contributes to decision-making

5. LOST IN TRANSLATION: THE CHALLENGE OF TRANSLATING EVOLUTIONARY PRINCIPLES INTO POLICY

Prescriptive evolutionary approaches can be tested as tools for intervention and mitigation to improve outcomes and their utility for managers. Although management is nuanced, a set of general principles is likely to emerge and allow more proactive and pre-emptive interventions. We also expect over time that prescriptive approaches will become more easily translated among conservation disciplines and management contexts, paralleling developments in evolutionary agriculture and medicine. Indeed, there is already evidence of this occurring on broad scales (Carroll et al. under review, Hendry et al. 2011, Losos et al. 2013), but the most important translational goal is the most basic, to bridge the knowledge-action boundary so that science-based initiatives can be implemented. The gulf between conservation science and the implementation of its recommendations is less a scientific challenge than a social one. This may be remedied when managers and decision makers work together to define problems, understand the constraints, and then do the science, together, leading to better management decisions (Mace & Purvis 2008). Providing training in prescriptive evolutionary approaches to early career managers is one constructive avenue (Cook et al. 2013). Institutional frameworks that provide mechanisms for decision-making at shared boundaries, referred to as "boundary science," can likewise smooth implementation, improving scientific knowledge and conservation outcomes [(Cook et al. 2013, Guisan et al. 2013); for an example of how the content of **Table 2** can be placed in such a structured decision-making process (Gregory et al. 2012), see **Supplemental Table 1**]. Finally, museums and genomic archives need to be expanded to provide better temporal records. Collecting and archiving genetic samples gives a longitudinal perspective on evolutionary processes through time (Losos et al. 2013). Encouraging agencies to invest in genomic techniques would also help make evolutionary approaches standard tools for managers. What are the best practices for evolutionary monitoring? How do we decide what is enough gene flow? An IPCC-like intergovernmental science-policy platform for biodiversity, currently being debated by policy makers, could be a first step (Larigauderie & Mooney 2010).

Supplemental Material

6. EVOLUTIONARY STEWARDSHIP

"To keep every cog and wheel is the first precaution of intelligent tinkering."—Aldo Leopold

Inherent in taking a prescriptive evolutionary approach is the recognition that we are forever putting our signature on the diversity of life. We recognize that some readers may see our recommendation to intercede in the evolution of other species as crossing an ethical line between our desires to preserve nature and the freedom of natural systems to run their own course. But there are no firewalls between humanity and nature—our everyday actions and inactions shape evolution across the globe. The choice of prescriptive evolution is one of deliberate or haphazard actions. A guiding principle for thoughtful stewardship is Aldo Leopold's "intelligent tinkering" (Leopold 1970), but in an evolutionary context it is important to recognize that the loss, addition, and change in the function of parts is likely. The use of an evolutionary framework to conserve biodiversity is a collective responsibility that we believe is fundamental to wise management.

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