Conservation Biology

Special Section Essay

Future Human Intervention in Ecosystems and the Critical Role for Evolutionary Biology

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In 1978, at the first conference to discuss the emerging field of conservation biology, there were 4 billion people on Earth. Now there are more than 7 billion, with 10.1 billion projected by 2100. Sustainably meeting the needs of 10 billion people and conserving natural resources at the same time will require profound creativity and innovation. Scholars who study human-caused climate change have a word for this creativity, adaptation. Adaptation involves some acceptance that change is occurring and will continue to occur and an acknowledgment that new forms and combinations of nature are being created. Adaptation also requires humans to design new tools, draw upon new theories and resources, and manage natural and social systems to a greater degree than we have before.

To allow successful adaptation of ecosystems to global change, conservation biology will have to shift its perspective from backward to forward looking. Restoring and maintaining ecosystems to a historic baseline has been a common goal of conservation, but alterations in land cover, climate change, and environmental contaminants are making it impossible to recreate the past. Instead, society has to ask what kind of nature it would like to create and what ecosystem functions it would like to maintain.

We think conservation biology should strive to preserve economic, cultural, aesthetic, and option value with little or no reduction in the biological diversity that underlies that value. To achieve this, however, society will need to maintain genetic diversity and functioning ecosystems alongside humans. And it will be necessary to foster biotic changes that are achievable given the realities of global change.

We argue that adaptation of nature by humans to global changes such as climate change, habitat loss and fragmentation, and nutrient deposition will require a sophisticated understanding of evolutionary theory and genome biology because evolution is a key, and inevitable, response of organisms to changes in their environment. Furthermore, evolutionary factors can be manipulated to foster particular conservation outcomes. In other words, acknowledging and harnessing evolutionary adaptation will be critical to enabling humans to facilitate adaptation of ecosystems to global change. Fortunately, evolutionary biology already has a rich history in conservation biology, and we believe that its role will expand over the next 25 years.

History of Evolutionary Biology in Conservation

The initial focus within conservation biology on evolution and genetics was small populations. The realization that many small populations were threatened by a lack of genetic variation, for example, led to recommendations for minimum viable population sizes that mitigate inbreeding (Hedrick & Kalinowski 2000) and random genetic drift (Lande & Barrowclough 1987). Associated management strategies included tracking of pedigrees and equalization of family size. Fragmentation of a species' habitat and loss of connectivity among populations can exacerbate genetic drift; thus, the role of migration and connectivity as a source of genetic variation was also emphasized by early conservation geneticists.

Technological advances in the 1980s and 1990s (e.g., capillary sequencing machines, microsatellite loci) stimulated research on patterns of genetic diversity and the degree of subdivision in natural populations. These studies often used DNA sequences that do not code for proteins, and are not exposed to natural selection, to indirectly estimate effective population size and connectivity. The importance of DNA that codes for adaptive genetic variation was also recognized. For example, studies showing a lack of variation in genes involved in immune

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responses of felids suggested that extensive inbreeding was occurring in many species of large cat (O'Brien et al. 1985). In the case of the Florida panther (*Felis concolor coryi*), managers increased adaptive genetic variation by introducing unrelated individuals. An additional link to population genetics was forged by a growing awareness that lineages have unique evolutionary histories and independent evolutionary trajectories (Moritz 1994), allowing management priorities to be informed by phylogenetic distinctiveness (Avise 2000).

Over the last 25 years, quantitative genetic theory has focused on mutations that replenish genetic variation lost through drift, rates of and limitations to adaptation, and the connection among environmental change, adaptation, and population persistence. Scientists have asked, for example, what is the maximum rate of environmental change a population can track via adaptation? For instance, Gomulkiewicz and Holt (1995) combined demographic and genetic models to quantify when and how adaptation can prevent populations from becoming extinct. In these models, adaptive genetic variation enables evolution.

Beginning in the 1990s, studies demonstrating evolution over decades placed ecology and evolution on a comparable temporal scale and reinforced the relevance of evolutionary theory to conservation biology. This relevance was further emphasized by the emergence of the new field of community genetics, which emphasizes the relation between genetic variation in one species and traits in other species (Whitham et al. 2006). For example, genetic variation in secondary compounds among hybrid *Populus* trees affects species diversity of herbivores and rates of nutrient cycling (Bailey et al. 2009). Study of the causal relation between evolution and ecosystem dynamics (eco-evo dynamics [Post & Palkovacs 2009]) incorporates time into community genetics. These advances led to recognition that selection occurs at multiple biological levels.

Growing Role for Evolutionary Biology

Building on this history, we think the role of evolutionary principles in conservation biology will expand in the future so that the following objectives of ecosystem adaptation can be achieved.

1. Reveal the effects of global change on biological diversity.

The first of four roles that we see for evolutionary biology (evolutionary adaptation) in dynamic conservation management (adaptation to global change) is identifying when and how environmental change stresses populations and species. Specifically, the relation between population mean fitness and environmental change must be determined and the level of natural selection acting on populations must be revealed. Environmental change can increase the level of selection and decrease population mean fitness by moving the optimal phenotype away from the current mean phenotype (Fig. 1). This shift, and concomitant decrease in fitness, is a selective load that can contribute to demographic declines and a decrease in the probability of population persistence.

Gauging the ability of populations to evolve and track a moving optimum in changing environments, when the relation between phenotype and fitness varies through time, requires an understanding of the genetic basis of evolutionary adaptation. What genes are responsible for adaptation in a particular environmental context? How many are responsible genes and to what effect? Are the routes to adaptation through regulatory changes in gene

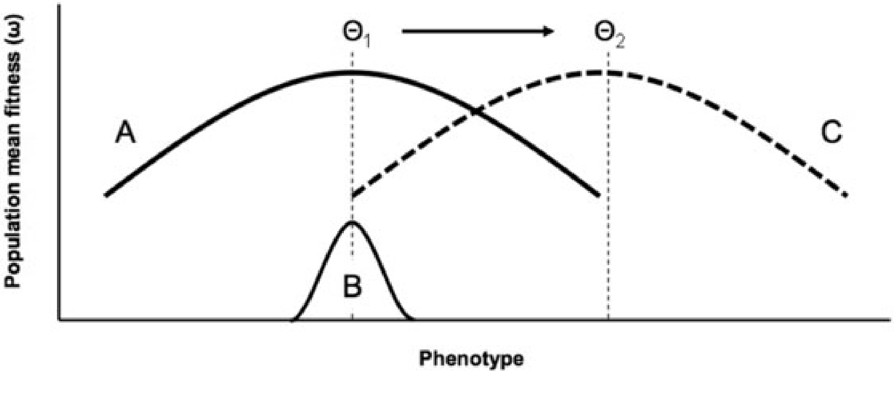

Figure 1. A simplified fitness landscape (A) and the distribution of phenotypes (B) for a population with mean phenotype at the optimum for this landscape (Θ_1). A change in the environment shifts the landscape (C), and the mean phenotype of the population is now some distance from the new optimum (Θ_2). This shift imposes a selective cost proportional to the distance to the new fitness optimum. If this cost is great, the population size may decrease and the likelihood of extinction through stochastic demographic events may increase. Whether populations can avoid this cost, and the associated reduction in size, is a function of the distance of the optimum shift, the amount of available adaptive genetic variation, and the rate of change in the landscape. See also Reed et al. 2011.

expression patterns or via functional changes in protein-coding sequences?

Quantitative genetic experiments are often relied on to estimate genetic variation (e.g., h^2) or candidate genes, such as those involved in thermal adaptation in model systems such as *Drosophila* (Hoffmann et al. 2003). However, quantitative genetic approaches do not identify the genes underlying the phenotype, and candidate-gene approaches often infer gene function on the basis of similar sequences in unrelated taxa. Consequently, these approaches are limited in their ability to identify the genetic material involved in evolutionary responses.

Recent advances in genomics may facilitate access to the genes directly involved in evolutionary adaptation. The increasing number of whole genome sequences available, and the relative ease of sequencing transcriptomes, allows the construction of functional genomic tools such as gene-expression microarrays. Expression arrays applied to organisms adapted to varied environmental conditions can quickly identify the genes that underlie adaptive differences across the entire genome (Whitehead & Crawford 2006). Additionally, strategies for surveying genetic diversity across the genome (e.g., RAD-tags [Hohenlohe et al. 2010]) and for conducting population genomics (Futschik & Schlotterer 2010) are beginning to be adopted widely. These innovations allow the techniques of genomic biology to be applied even to the most endangered of organisms so that the mechanisms that cause decreases in biological diversity are revealed.

2. Understand natural resilience to global change.

Describing the abundance and distribution of adaptive genetic variation is necessary to increase understanding of natural resilience to environmental change (Fig. 2). Enhancing natural resistance will be a key strategy in increased ecosystem management for global change. A convenient measure of resilience is the ability of a population to maintain high population mean fitness in a changing environment. Populations can increase mean fitness and persist if they disperse and track abiotic and biotic resources, respond directly to the environment via phenotypic plasticity, or move closer to the local fitness peak via adaptive evolution (Fig. 1). In the models of Bürger and Lynch (1995) and Gomulkiewicz and Holt (1995), evolutionary adaptation increases persistence time by reducing the selective cost imposed by a moving optimum in the fitness landscape and increasing fitness to the extent that populations can maintain a sufficiently large size and thereby reduce the chance of local extinction due to stochastic demographic events. Populations lacking sufficient variation to track a moving optimum experience an increasing lag load (Bürger & Lynch 1995; Hellmann & Pineda-Krch 2007). The rate of input of mutational variation and the effective population size determine the amount of available genetic variation and the maximum rate of change a population is able to withstand.

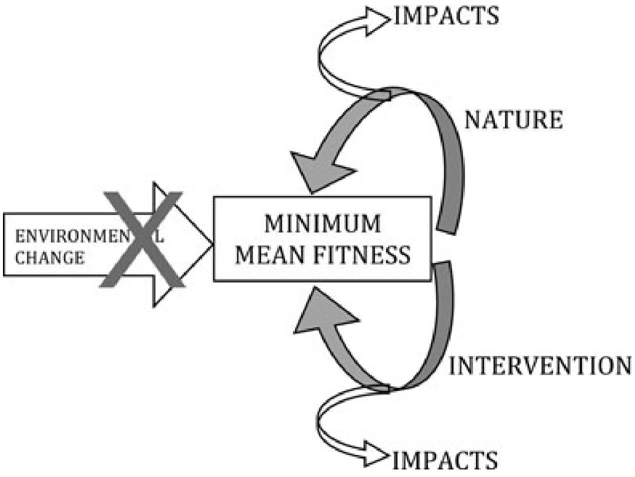

Figure 2. As the environment changes (large arrow), fitness of populations currently at their fitness optimum declines (Fig. 1). For a population to persist, minimum mean fitness must be maintained so that per capita rate of increase is greater than zero. The direct method to achieve this is to prevent environmental change that is unfavorable for the population (gray X). Alternatively, selective pressures in nature will drive evolution (upper gray arrow), and humans can facilitate this process through intervention (lower gray arrow). Both natural evolution and evolution facilitated by humans have ecological effects (open arrows).

However, these theoretical treatments lack realism. For example, evolutionary trajectories in natural populations do not always follow a simple uphill path (Fig. 1). Real adaptive landscapes are complex and adaptive trajectories are likely constrained by genetic correlations among traits. Evolutionary adaptation may be further limited by functional constraints at the genetic, protein, or phenotypic level. In addition, adaptive evolution in response to environmental change can alter interactions in communities. Incorporating this complexity into current theory is needed to understand the extent of natural resilience to environmental change.

3. Craft interventions to minimize effects of global change.

Where natural resilience is inadequate to preserve biological diversity in the face of global change, managers will turn to direct intervention. The goal of intervention at the species level is long-term population persistence, and we emphasize here interventions that enable populations to track changing environments through evolution (Fig. 1). Conservation biology has traditionally relied on interventions that preserve habitats to maintain large populations and genetic diversity. The genetic and evolutionary effects of these efforts are often not quantified, however, and additional interventions are possible.

More direct and aggressive intervention will require extensive information about functional genetic variation and the direction and intensity of selection. For example, to combat mortality from heat stress caused by increases in summer temperatures, one might augment poleward movement of populations of a species with warm-adapted alleles. One could do this by introducing individuals from warmer locations into the target populations, but it may be more effective to identify specific genes that confer a fitness advantage given a particular stressor and then to introduce those genes directly through controlled crosses, artificial hybridization, or even genetic engineering. Different species will require different techniques for this kind of manipulation, techniques that are based on the biology of the organism and its environmental context.

One also could intervene to geographically match genotype and environment as the environment changes. This concept is called managed relocation and involves translocating individuals (and their genes) from areas of historic occupancy to new regions where they are likely to persist in the future (Richardson et al. 2009). Managed relocation can be motivated by several objectives, from simple genetic preservation to production of an ecosystem good or service. Managed relocation must consider the genetic composition of introduced populations and account for their future evolutionary trajectory, including projections of mean population fitness, to ensure that the introduction is viable over the long term. Managed relocation can also include management after introduction, including genetic augmentation or even the removal or control of introduced individuals or particular genotypes.

4. Predict responses to intervention.

Evolutionary biology is critical to the understanding of the effects of management interventions. Many historic interventions have had undesired effects (e.g., the introduction of kudzu [Alderman 2004]), but there also is a long history in natural resource management of successful, often aggressive, intervention (e.g., Messing & Wright 2006). Because future intervention may be more directed and possibly larger in scope than has been typical in the past (Fig. 2), anticipating and monitoring its effects and understanding the underlying drivers of these effects will be critical.

Any intervention will trigger evolution across entire communities, whether the intervention mimics a natural process or is highly artificial. The effects of natural phenomena and human interventions could be similar or different, but neither is neutral in effect (Fig. 2). From an ethical and legal perspective, the effects of natural phenomena may be perceived differently than the effects of large human interventions (Moore 1996), and these differences need to be discussed and debated.

A Vision for the Future

We expect that considerable philosophical and conceptual change will occur within conservation biology over the next 25 years. If we acknowledge that the human population is growing and that the rapid pace of global change, including climate change, will continue, then we need to begin managing systems that are constantly changing—we can no longer look to the past for guidance on how an ecosystem is supposed to be. We argue that more intensive management, with an emphasis on helping biological diversity persist through global change, will rely on evolutionary biology, its theories, and its genomic tools and techniques. For example, any intervention that enables populations, and thereby species, communities, and ecosystems, to maintain the highest possible mean fitness will require extensive information about the factors driving evolution.

Conservation professionals and the public need to define the key objectives of conservation and find ways to achieve those objectives. Toward the former, we suggest a goal of maximizing genetic diversity to encourage adaptive evolution and increased recognition that populations and communities are likely to change in profound ways. To the latter, we argue that evolutionary principles offer the greatest potential to understand the future trajectory of biological diversity and enhance the likelihood of desirable conservation outcomes.

The conservation biology we are describing—one that helps ecosystems tolerate increasing global change—has an increasing array of sophisticated tools at its disposal with which to investigate the distribution of functional diversity and intervene to maximize diversity and its function. For new technology to exist (e.g., to sequence an entire genome) but remain untapped would be unfortunate. There must be a community of trained professionals to interpret the biological significance of these data and act on this information to develop management strategies. This vision requires a major investment in natural resource management and training, investment that is higher than current natural resource budgets.

We also recognize that increased intervention or management comes with considerable risks. In many cases, these risks may be counterbalanced by the risks of inaction (Schwartz et al. 2009). Many interventions may fail to meet their objectives, but we expect these interventions will be pursued with good intentions, with open acknowledgement of the potential risks and benefits, and with rigorous risk assessment and experimentation.

Supporting Information

A list of additional references (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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