



Contemporary evolution meets conservation biology

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Recent research has revealed that evolution often occurs on contemporary timescales, often within decades. Contemporary evolution is associated with the same factors that are driving the current extinction crisis: habitat loss and degradation, overharvesting and exotic species. Thus, it is relevant to many conservation situations. First, habitat fragmentation might influence the potential of a population to adapt in response environmental degradation. Second, certain harvesting strategies can result in the evolution of life-history traits, ultimately resulting in negative impacts on harvestable yield. Third, the establishment of exotic species can be influenced by their adaptive potential and our ability to limit that potential. Furthermore, contemporary evolution is of concern for intensively managed species, because it might reduce their fitness in native habitats. Ultimately, contemporary evolution is influenced by complex interactions among population size, genetic variation, the strength of selection, and gene flow, making most management scenarios unique. In a world filled with contemporary evolution, conservation efforts that ignore its implications will be less efficient and perhaps even risk prone.

Humans have become an evolutionary force of extraordinary influence [1], evidenced most obviously by an unprecedented extinction rate that is attributable to their activities [2]. Human activities are also associated with evolutionary changes that can occur within a few hundred years, otherwise known as CONTEMPORARY EVOLUTION (see Glossary) [3–5].

The discipline of conservation biology is underpinned by evolutionary theory [2]. For instance, conservation biologists acknowledge the importance of population size and genetic variation for future evolutionary potential [6,7]. Evolutionary concerns are also reflected in the designation of conservation units [8,9] and management plans that seek to conserve both process and pattern [10,11]. However, most research considers evolution to be a long-term concern, whereas the evidence for contemporary evolution suggests that it should also be a short-term concern. Here, we argue that contemporary evolution is relevant to conservation biology in many contexts, including the establishment of exotic species, the response of species to environmental change, and the management of endangered populations.

What is contemporary evolution?

Many recent studies have reported ‘rapid evolution’ in contemporary populations facing environmental change. However, evolutionary rates that have been called ‘rapid’ in such studies vary by orders of magnitude [3,4], leaving the phrase with little meaning. We prefer the term ‘contemporary evolution’ in reference to evolutionary changes observable over less than a few hundred years [3,4]. Such rates can indeed be ‘rapid’ but this assertion is empty without actually quantifying and comparing evolutionary rates. One evolutionary rate measure is the haldane, which quantifies phenotypic change in standard deviations per generation [3]. In general, evolutionary rates tend to scale negatively with time interval (measured as the number of generations), owing, in part, to a negative self-correlation caused by plotting rates, which have time in the denominator, versus time itself [12,13] (Fig. 1). For this reason, fast or slow rates need to be interpreted relative to the time interval over which they were measured, or as positive or negative deviations from the overall time-scaling trend [4]. From this, it is evident that the range of evolutionary rates for different taxa over the same number of generations can be quite large.

A common historical perception was that contemporary evolution was relatively rare and examples, such as industrial melanism in the peppered moth *Biston betularia*, were atypical. However, once biologists started measuring the strength of natural selection in the wild, they found that it was often stronger than expected [14], suggesting that contemporary evolution could also be quite

Glossary

Contemporary evolution: heritable trait evolution observed in contemporary time (i.e. less than a few hundred generations).

Directional selection: individuals with trait values at one extreme have higher fitness, resulting in a directional shift in the population mean value for that trait.

Gene flow: exchange of genes among populations because of successful reproduction by migrants.

Genetic drift: random changes in gene frequencies because of sampling error, often observed in small populations.

Heritability (h^2): proportion of the phenotypic variation for a trait that has an additive genetic basis.

Metapopulation: spatial collection of partially isolated populations that have some level of gene flow among them. Local populations can go extinct, but these patches can subsequently be re-colonized.

Selection gradient: correlation between fitness and a particular trait, holding effects of other traits constant.

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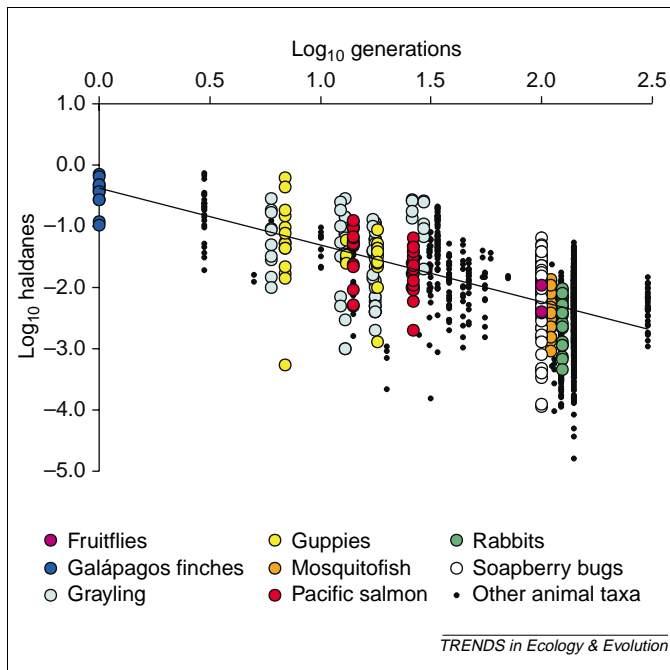


Fig. 1. Evolutionary rates in haldanes (standard deviations of change per generation), relative to time interval, for a survey of 2104 rates. Colored circles represent estimated rates for taxa represented in Table 1. Because evolutionary rates tend to scale negatively with time, a trend line is provided as means of judging rates faster or slower than the mean predicted value over a given time interval (slope = -0.962 ; intercept = -0.274). Most studies estimating multiple rates tend to find a mixture of faster and slower than average values. Figure adapted, with permission, from [4].

common. Moreover, unprecedented rates of anthropogenic perturbations are expected to cause particularly strong selection, further increasing the potential for contemporary evolution [5,14].

Numerous examples of contemporary evolution have now been reported in the literature [3,5,15,16]. For example, Reznick and co-workers documented the contemporary evolution of wild guppy *Poecilia reticulata* populations in response to a change in predation pressure [17]. In several replicate cases, dramatic and parallel life-history evolution was observed within 4–11 years [17]. Introductions of Pacific salmon *Oncorhynchus* spp. have also resulted in different populations adapting to different breeding environments within 13–26 generations. Furthermore, some of these populations also show evidence of partial reproductive isolation from each other over this same timescale [18–20].

Similar cases of contemporary evolution have been reported for a variety of taxa and situations. Table 1 presents selected examples for plants and animals (including some highlighted in Fig. 1), most of which include the demonstration of a heritable basis for the observed evolution. Many of the examples result from the establishment of new populations (colonization) or the alteration of environments experienced by extant populations (*in situ* disturbance). Contemporary evolution can also result from artificial propagation, introgression among populations or species, and selective exploitation.

Table 1. Examples of contemporary evolution in plants and animals

Example	Traits	Evolutionary agent	Refs
Colonization			
Goldenrods <i>Solidago</i> spp.	Phenology and growth	Latitudinal effects	[64]
Copepods <i>Eurytemora affinis</i>	Low salinity tolerance	Freshwater colonization	[65]
Fruit flies (wild) <i>Drosophila subobscura</i>	Wing dimensions	Latitudinal effects	[41]
Mosquitofish <i>Gambusia affinis</i>	Size at maturity and fat storage	Thermal environment	[15]
Guppies <i>Poecilia reticulata</i>	Age and size at maturity, offspring size and antipredator behavior	Predator regimes	[17,66]
Pacific salmon <i>Oncorhynchus</i> spp.	Development and growth, morphology, reproductive timing and ovarian investment	Features of breeding environment (temperature, flow and migratory rigor)	[18–20]
Rabbits <i>Oryctolagus cuniculus</i>	Morphology	Ecoregional variation (temperature and aridity)	[42]
In situ disturbance			
Numerous plant species (e.g. <i>Mimulus guttatus</i>)	Tolerance to metals (e.g. copper)	Metal contaminated soils (e.g. mine waste piles)	[16,31]
Numerous insect species (e.g. diamondback moths <i>Plutella xylostella</i>)	Pesticide resistance (e.g. resistance to <i>Bacillus thuringiensis</i>)	Selective mortality or sterility (e.g. <i>Bacillus thuringiensis</i> -related mortality)	[46,67]
Soapberry bugs <i>Jadera haematoloma</i>	Beak length	Fruit size of introduced host species	[40]
Pitcher plant mosquitoes <i>Wyeomyia smithii</i>	Photoperiodic diapause response	Global warming	[35]
Water flea <i>Daphnia galeata</i>	Resistance to poor/toxic diet	Increase in cyanobacteria following eutrophication	[68]
Galápagos finches <i>Geospiza fortis</i>	Body size and beak shape	Climatic effects on food resources	[23]
Other			
Artificial propagation (e.g. salmon in hatcheries <i>Oncorhynchus/Salmosp.</i>)	Life history, morphology and behavior	Inadvertent selection, genetic drift and inbreeding	[54]
Selective harvest (e.g. European grayling <i>Thymallus thymallus</i>)	Age and size at maturity	Selectivity of harvest methods and gear (e.g. mesh size of nets)	[30]
Introgression (e.g. ducks, canids, salmonids and sunflowers)	Morphology (other aspects likely)	Hybridization among wild species, and between wild and domestic (sub)species	[69,70]

Box 1. Evolutionary change in quantitative traits

For a quantitative trait (influenced by multiple genes, often of small effect), adaptation should proceed according to $\Delta z = G\beta$ where Δz is the change in mean trait value from one generation to the next, G is the additive genetic variance for the trait and β is the selection gradient acting on the trait (slope of the relationship between the trait and fitness). When considering a single trait, this equation is analogous to the traditional 'breeder's equation' (evolutionary response = heritability \times selection; $R = h^2 S$) because $G/P = h^2$ and $S/P = \beta$, where P is the phenotypic variance and S is the selection differential (difference between the mean trait value before and after selection). When considering multiple traits, Δz becomes a vector of changes in mean trait values, G becomes a matrix of additive genetic variances/covariances, and β becomes a vector of selection gradients [a–c].

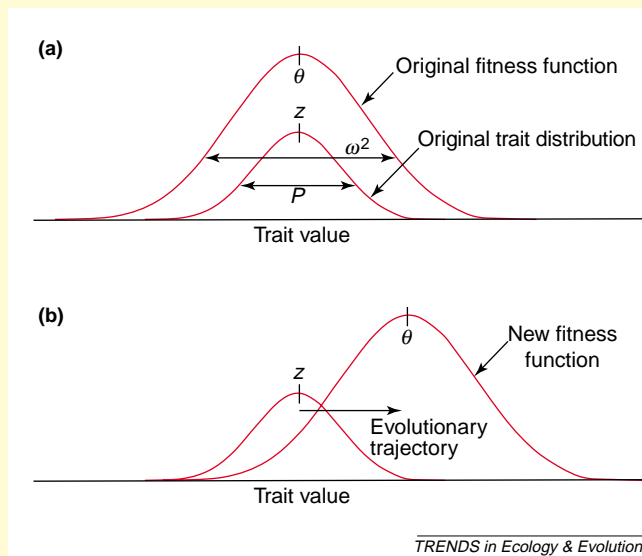


Fig. 1. A representation of trait variation and selection before (a) and after (b) a disturbance. The upper curve in each panel represents the fitness function acting on a trait (the higher the curve the higher the fitness of a given trait value). The lower curve represents the frequency distribution of trait values in the population. P is the phenotypic variance, θ is the optimal trait value, ω^2 is the strength of stabilizing selection around the optimum, and z is the mean trait value.

In a conservation context, we might imagine that phenotypes in an undisturbed population are centered around an optimal value (i.e. the population is well adapted) but that a disturbance shifts the phenotypic optimum to a new location (Fig. 1). This shift leads to a mismatch between current phenotypes and optimal phenotypes, leaving the population maladapted and subject to directional selection. The strength of this selection can be represented as Eqn 1:

$$\beta = \frac{-(z - \theta)}{\omega^2 + P} \quad \text{[Eqn 1]}$$

where z is the mean trait value, θ is the optimal trait value, P is the

These empirical results, as well as theoretical predictions, have generated a reasonable set of expectations for conditions under which contemporary evolution should occur. In general, evolutionary responses should be relatively high in cases of high trait HERITABILITY and following an increase in the intensity of DIRECTIONAL SELECTION. In natural populations, directional SELECTION GRADIENTS follow a negative exponential distribution with many small values, a few large values, and a median of 0.16 [21]. Given this 'typical' strength of selection and a moderate heritability ($h^2 = 0.25$), evolutionary changes of one standard deviation could take place in as few as 25 generations [22] (Box 1).

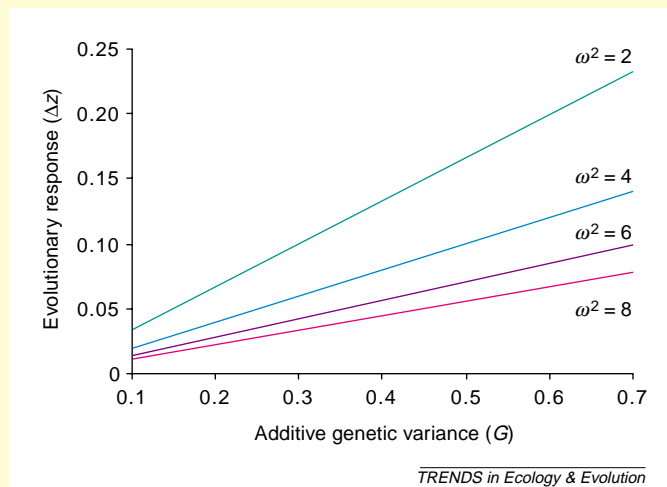


Fig. 2. The relationship between evolutionary response (Δz) and additive genetic variance (G), as a function of the strength of stabilizing selection (ω^2). The curves are calculated using $z = 10$, $\theta = 11$, and $P = 1$, where z is the main trait value before the disturbance, θ is the optimal trait value, and P is the phenotypic variance.

phenotypic variance, and ω^2 is the strength of stabilizing selection around the optimum (for simplicity, we assume ω^2 is the same around the optimum before and after the disturbance) [b]. Smaller values of ω^2 correspond to steeper fitness functions and therefore stronger stabilizing selection around the optimum. When the optimum shifts, a steeper fitness function to either side leads to stronger directional selection on the population (larger β) and faster evolution toward the new optimum.

These equations predict the evolutionary responses of traits following a shift in optimal trait values, and have proven useful in predicting evolutionary responses in natural populations. However, it is important to recognize that several factors can lead to discrepancies between predicted and observed evolutionary responses [d]. In general, however, evolutionary responses will increase as genetic variation or the strength of selection increase (Fig. 2). Evolutionary responses will also increase with increasing differences between the mean trait value and the new optimal trait value.

References

- a Lande, R. and Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution* 37, 1210–1226
- b Arnold, S.J. *et al.* (2001) The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* 112–113, 9–32
- c Schluter, D. (2000) *The Ecology of Adaptive Radiation*, Oxford University Press
- d Merilä, J. *et al.* (2001) Explaining stasis: microevolutionary studies in natural populations. *Genetica* 112–113, 199–222

The above scenario is simplistic because it assumes a constant strength of selection through time, which is unlikely in nature [23]. Instead, an introduction or rapid environmental change is akin to shifting the location of a fitness peak on an adaptive landscape (Box 1). Selection should often be strongest and adaptation most rapid soon after a disturbance, followed by a gradual leveling off as the new adaptive peak is approached [3,4,16] (Box 1). It is also unlikely that evolution will follow the smooth trajectories of deterministic equations. Instead, it should follow a jagged path driven by spatial and temporal variation in the conditions that influence the new optimum [23]. When the

Box 2. Interactions between selection and demography

A complex set of factors can facilitate or constrain contemporary evolution, and hence impact the outcome of conservation efforts. Thus, a major challenge when incorporating evolutionary theory into recovery programs is the accurate assessment of interactions among selection, gene flow and demography. The relative roles of these factors are context specific.

Small populations are often considered to have limited potential for adaptive evolution. Estimates of the EFFECTIVE POPULATION SIZE (see Box Glossary) necessary for long-term adaptive evolution vary from 500 to 5000 [a,b]. These guidelines are obviously rough and ignore the fact that increasing population sizes do not ensure adaptation over contemporary time, as the following scenarios illustrate. First, artificially enhancing population sizes to unnaturally high levels, particularly when associated with habitat loss, could introduce density-dependent risks to even the fittest genotypes. Second, increasing the size of a population could reduce demographic risk and genetic drift, but, by itself, might not increase the genetic variation required for adaptation. Third, artificial propagation and enhancement designed to increase population sizes can disrupt natural mating and patterns of selection, potentially slowing adaptation or even causing evolution that makes the population maladapted for its natural environment.

The effects of selection are also difficult to generalize. Following an environmental disturbance, an increase in selection causes an initial decline in population size ('N' in Fig. 1), a decline that will continue until adaptation or the relaxation of density dependence increase mean fitness past the replacement level (Fig. 1, line A) [c,d]. If selection is strong, a population could decline to extinction or to a size where the demographic risk of extinction is high (below 'C' in Fig. 1), even if it is evolving in an adaptive direction (Fig. 1, line B) [c,d].

Genetic constraints can also influence the ability of populations to respond to natural selection. For example, if selection favors an increase in two traits that are negatively genetically correlated with each other (antagonistic pleiotropy), the rate of adaptive evolution will slow [e,f]. Such constraints could increase the chances that selective mortality will out-strip fitness gains. The potential influences of gene flow are considered in Box 3.

Box Glossary

Effective population size (N_e): the size of an idealized population that would lose genetic variation at the same rate as the actual population.

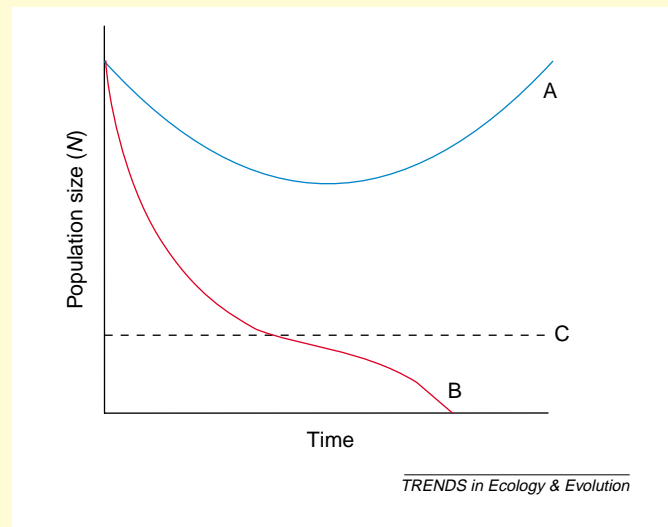


Fig. 1. Population trajectories for two scenarios of contemporary evolution. Under both scenarios, population size declines in response to selection. Under scenario A, adaptation increases mean fitness and enables population recovery. However, if selection is very strong (B), then the population could decline to extinction or to a size where the risk of demographic extinction (C) is high. Figure modified, with permission, from [c].

References

- a Franklin, I.R. and Frankham, R. (1998) How large must populations be to retain evolutionary potential. *Anim. Conserv.* 1, 69–73
- b Lynch, M. and Lande, R. (1998) The critical effective size or a genetically secure population. *Anim. Conserv.* 1, 70–72
- c Gomulkiewicz, R. and Holt, R.D. (1995) When does evolution by natural selection prevent extinction? *Evolution* 29, 201–207
- d Lynch, M. (1996) A quantitative-genetic perspective on conservation issues. In *Conservation Genetics: Case Studies from Nature* (Awise, J.C. and Hamrick, J.L. eds), pp. 471–501, Chapman and Hall
- e Barton, N. and Partridge, L. (2000) Limits to natural selection. *Bioessays* 22, 1075–1084
- f Etterson, J.R. and Shaw, R.G. (2001) Constraint to adaptive evolution in response to global warming. *Science* 294, 151–154

strength of selection is excessive, a population might go extinct even if it is undergoing adaptive evolution [24].

Many other factors influence the rate, trajectory and consistency of evolution. In particular, interactions among population size, GENE FLOW, genetic variances and covariances, and complex patterns of selection can lead to a variety of outcomes (Boxes 2,3). Given this complexity, 'rules of thumb' will be of limited use. Instead, conservation biologists will need to become increasingly fluent in the mechanics of evolutionary theory if they are to deal effectively with the evolutionary challenges that face managed species [25].

Contemporary evolution and the 'Evil Quartet'

Diamond [26] coined the term 'evil quartet' to refer to the most important anthropogenic factors that cause contemporary extinction: overharvesting, habitat fragmentation and degradation, exotic species and chains of extinction. The first three factors currently seem most important in their association with extinction risk [27] and are also likely to be potent agents of selection.

Overharvesting

Harvesting is often selective with respect to phenotypic traits (e.g. harvesting the largest individuals) and can therefore exert strong directional selection. This selection is likely to cause contemporary evolution in harvested populations, particularly when harvest rates exceed natural mortality rates [28]. Recent experimental work, mimicking various harvest patterns on captive populations of Atlantic silversides *Menidia menidia*, provided strong evidence that selection can cause substantial life-history evolution within a few generations [29]. Furthermore, harvesting the largest individuals resulted in a significant decline in biomass yield [29]. This was attributed to evolutionary changes in traits that influence population growth and productivity, including juvenile growth, egg size and larval growth [29].

Another example comes from a natural fishery. European grayling *Thymallus thymallus* populations around Norway evolved earlier age and smaller size at maturity after exposure to a gill-net fishery [30]. Relaxation of fishing pressure then led to an increase in age and size at

Box 3. Gene flow and contemporary evolution

Gene flow is the Jekyll and Hyde of conservation, where every benefit can be spun into a corresponding cost. Jekyll: gene flow increases genetic variation within populations, limiting inbreeding depression and increasing evolutionary potential [a,b]. Hyde: but gene flow could limit local adaptation [c] and the introgression of foreign genes into a locally adapted population can lead to population declines or even extinction [d,e]. These effects will be strongest when immigrants are abundant, are maladapted to local conditions, and are able to mate freely with residents [c,f]. Jekyll: indeed, but this cost could be used as a tool in efforts to eradicate, or at least control, unwanted exotics: maladapted individuals could be introduced into unwanted populations to depress their fitness [e]. Hyde: but if an invasive population is limited primarily by genetic variation, continued gene flow could potentially instigate further adaptation and population growth, thus contributing to the emergence of invasive species after multiple introductions. Jekyll: true, but this could have a positive use in promoting adaptation in depleted indigenous populations (i.e. rescue-effect gene flow).

The effect of the same proportion of immigrants in contributing to gene flow can also change over time. For example, as populations become more divergent, gene flow between them might decline if the relative fitness of immigrants and hybrids declines. Additionally, hybrid matings that result in offspring with lower fitness might select for prezygotic isolation (i.e. reinforcement). As gene flow declines, the selection-gene flow equilibria might shift, enabling further adaptation in a self-reinforcing feedback loop. More effective conservation might thus vary patterns of selection, gene flow, or artificial enhancement over the course of a recovery programme. For example, rescue effect gene

flow or captive propagation could be used to raise a population above a demographically critical size [b], but subsequent reduction or cessation of these factors might be required to enable further adaptation and greater population productivity. In one case study, Hedrick considered the costs of gene flow owing to loss of local adaptation against the benefits of genetic restoration [b]. His modeling showed that substantial initial gene flow, followed by reduced levels of gene flow might allow for the genetic restoration of the Florida panther *Felis concolor coryi*, whilst minimizing loss of locally adapted alleles [b]. These results were based on a single locus model, but illustrate how the relative costs and benefits of gene flow can be evaluated on a case-by-case basis.

References

- a Frankham, R. (1995) Conservation genetics. *Annu. Rev. Genet.* 29, 305–327
- b Hedrick, P.W. (1995) Gene flow and genetic restoration: the Florida panther as a case study. *Conserv. Biol.* 9, 996–1007
- c Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends Ecol. Evol.* 17, 183–189
- d Boulding, E.G. and Hay, T. (2001) Genetic and demographic parameters determining population persistence. *Heredity* 86, 313–324
- e Tufto, J. (2001) Effects of releasing maladapted individuals: a demographic-evolutionary model. *Am. Nat.* 158, 331–340
- f Rhymer, J.M. and Simberloff, D. (1996) Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27, 83–109

maturity [30], changes that could play a role in population recovery. However, cessation of fishing might not always lead to rapid recovery [28]. A more probable scenario is that directional selection continues over protracted periods as fisheries continue to harvest the largest available individuals.

Habitat degradation and fragmentation

Habitat degradation can lead to novel selection pressures and the potential for contemporary evolution. In fact, many cases of contemporary evolution are associated with localized cases of habitat degradation [5,16,31]. This suggests that certain species might be able to cope adaptively with habitat degradation but, unfortunately, habitat degradation is also often associated with an increased risk of extinction [27,32]. Associated declines in population size, unless reflective of adaptation, are likely to limit the adaptive responses of such populations.

Habitat fragmentation is often associated with reductions in population size, as well as increased isolation. These conditions can impede adaptive responses to selection. For example, global warming will force organisms to move or adapt [33]. A fragmented landscape is generally expected to limit movement (but see [34]) and slow the spread of adaptive genes across the landscape, whilst small population sizes might simultaneously compromise their ability to respond adaptively to environmental change (Box 2). Recent studies have reported contemporary evolution in response to photoperiod shifts and altered carbon dioxide regimes [35,36], but it remains uncertain whether these rates of change are sustainable [37], particularly in smaller populations.

Under habitat degradation and fragmentation, the restoration of population connectivity and gene flow

might be a management option. However, uncritical application of artificial gene flow can have negative consequences [38]. If recently fragmented populations have diverged appreciably, efforts to initiate or restore gene flow could result in diminished adaptation and increased risk of extinction [39] (Box 3). The optimal amount of gene flow in a METAPOPOPULATION will depend on a variety of factors, including the degree to which subpopulations are adapted to local conditions [38].

Exotic species

Exotic species are reputedly one of the greatest threats to biodiversity [2,26,27], a threat that could become increasingly difficult to counter as exotics adapt to their new environments. Many empirical examples of contemporary evolution involve exotic species [15,19,20,40–42], perhaps because they experience high levels of selection, or simply because they have been the focus of more research. Regardless, contemporary evolution probably plays an important role in the establishment and success of certain exotics. Furthermore, contemporary evolution might influence how rapidly exotics spread from their point of origin [43].

Typically, exotic species persist at low (often undetectable) numbers when they first colonize an area, and then ‘explode’ to become invasive at some future time [44]. This pattern might reflect populations that: (1) need to spend an initial period of time adapting to local conditions before they can enter a period of rapid expansion; or (2) are held in demographic check until suitable environmental conditions arise. In the former case, small population sizes could initially limit the potential for evolution. In either case, new populations should be most vulnerable immediately after colonization, and managers should focus control efforts on these stages.

Contemporary evolution might also play an important role in the invasion dynamics of exotic species. For instance, García-Ramos and Rodríguez [43] examined how the invasion of species into new habitats is influenced by their adaptation across spatially heterogeneous environments. They found that evolutionary responses and the speed of invasion increased with high heritability and low spatial heterogeneity [43]. Interestingly, reduced spatial heterogeneity can result from successful invasion by exotics [45]. Thus, the establishment of one exotic species could provide the conditions (reduced spatial heterogeneity) that further promotes the invasion of additional exotic species.

How might evolution play a role in the control of invasive species? In some ways, contemporary evolution works against attempted control measures. For example, traditional approaches to the control of weedy species have involved mass application of herbicides and pesticides, which exert strong selection on the target species and, not surprisingly, result in the evolution of resistance [46–48]. Acknowledging the costs of evolved resistance, some control programs are beginning to include treatments that reduce evolutionary potential in the target species. Examples of such programs include the temporal rotation of different classes of chemicals (fluctuating selection), and the setting aside of nontreated areas from which non-resistant genotypes can later spread to compromise adaptation in treated areas [1,46]. The second of these approaches relies on expectations that increased gene flow will decrease the rate of contemporary adaptation [39,49], reduce mean population fitness [50], and perhaps even lead to population extinction [39]. This second approach will be limited to situations in which exotic species have discontinuous distributions, as is the case with exotic species of fish that have undergone contemporary evolution in response to local environments [15,19,20].

Conserving endangered species

Contemporary evolution is also relevant to the conservation of intensively managed species. Captive and wild ‘refuge’ populations are often established as a hedge against the extinction of endemic populations. Such refuge populations often show reduced genetic diversity [51] and might undergo evolutionary divergence from their ancestral populations [15]. For instance, contemporary evolution has been observed in captive populations that ‘become domesticated’ [52–54]. This causes concern when these populations are established as ‘genetic replicates’ of targeted taxa. If the refuge population diverges from the native population, it might become maladapted to its ancestral habitat [5,15,40] and therefore more difficult to reintroduce [55]. In these cases, maintaining some gene flow from wild populations into captive populations could prevent captive populations from diverging too far from their wild form [49].

Other management approaches could also reduce the likelihood of evolutionary divergence of refuge populations. For instance, captive environments can be modified to mimic natural conditions more closely [53]. The response to selection might also be reduced by maintaining smaller populations [56], although this can simultaneously increase

risks of inbreeding and GENETIC DRIFT. Alternatively, the ubiquity of contemporary evolution suggests that we should shift our view of captive populations from static reserves of particular trait values to dynamic reserves of evolutionary potential. Indeed, attempts to impede adaptation of refuge populations can compromise their ability to grow and persist, and hence diminish their value for preserving species in a changing world.

Future directions

We challenge conservation biologists to consider evolution in the short term rather than just the long term. This is especially important given that evolution can occur within timeframes that are relevant to most conservation plans (decades). The prospect that adaptive evolution occurs on short timescales calls for conservation planners to reconsider traditional approaches to the genetic management of populations. Here, we provide suggestions for future conservation strategies that increasingly consider evolutionary principles.

Adaptation: now or later?

Much current conservation emphasis is on the characterization of genetic variation within and among populations, methods of preserving that variation, and ways to minimize the impacts of lost variation (e.g. inbreeding and genetic drift) [57]. With the exception of concerns about adaptation to captivity [57] and the rapid loss of genetic variation [51], little applied research has considered contemporary evolution as a conservation risk or tool.

Conservation goals of maintaining population abundance, promoting population persistence, conserving genetic variation and maintaining adaptation might not be fully compatible. Most forms of adaptation entail a selective loss of genetic variation through an increase in the frequency of genotypes that improve fitness. Management strategies that emphasize the retention of genetic diversity within populations could thus decrease mean population fitness and impede adaptation in the present, even if they increase the potential for future evolutionary change. Likewise, the value of increasing genetic variation within populations through gene flow must also be balanced against its current and future impacts on adaptation. Optimal strategies will therefore depend on a host of factors, including the degree of location adaptation, the amount of gene flow and history of inbreeding.

Conservation programs thus need to prioritize clearly their goals of current adaptation versus preservation of genetic diversity (perhaps for future adaptation). Determining when and how managers should favor current adaptation relative to the preservation or enhancement of genetic variation should be one of the emerging goals of conservation genetics.

Quantitative traits and conservation

The field of conservation genetics has struggled for years to infer adaptive significance from patterns of neutral genetic variation [38,57,58]. Although quantitative variation and molecular variation are at times correlated, adaptive population structuring often far exceeds neutral population structuring [38,58,59], even for populations diverging over

contemporary time [60]. Nonequilibrium conditions (drift versus gene flow versus selection), which might characterize many populations of conservation concern, could make the connection between neutral and adaptive variation even more tenuous.

Management based on the absence of strong population structuring at neutral markers is particularly problematic. For example, translocations to establish gene flow among populations, based on evidence of minimal neutral marker structuring, could lead to outbreeding depression [61] if the populations are locally adapted. Such a scenario can occur when patterns of adaptation or gene flow have changed over contemporary time. However, no simple standards exist for delineating the levels of neutral divergence that indicate insignificant adaptive divergence. Thus, surveys of neutral genetic variation should be increasingly complemented by genetic analyses of quantitative traits [38].

Managing selection (pilot releases)

Another central question for conservation biologists is to what degree, and in what manner, should we attempt to manipulate evolution to attain conservation goals? For instance, adaptive evolution in response to captivity might be considered an undesirable outcome that should be avoided; whereas adaptive evolution in response to a changing environment in the wild might be desirable and should be promoted.

Selection in the wild might sometimes be too strong for populations to adapt before they go extinct [24] (Box 2). Enabling generations of selection in intermediate environments could help buffer such effects. Another possibility might be to screen family groups before release to 'select' those that are most likely to respond favorably to the novel environment. This could be done for certain species by monitoring patterns of selection on pilot groups released into the wild [62]. Future large-scale releases could then be tailored toward genotypes that showed maximum fitness in the natural environment, such as close relatives of the individuals that survived well in pilot releases.

Research within restoration efforts

Although much has been learned from the introduction of populations to novel environments, current concerns regarding exotics make experimental transplants less feasible and, in many cases, unethical. However, the field of restoration ecology offers tremendous opportunity to conduct replicated field experiments that examine evolutionary processes in newly altered or restored habitats. Furthermore, many recovery plans for protected species call for the use of translocations, providing opportunities to study evolution in recently established populations [63]. Even the US Endangered Species Act (section 10j) allows for the creation of experimental populations of endangered and threatened species, and these might be used to study and evaluate evolutionary management [63].

Concluding comments

We have provided an overview of how contemporary evolution is relevant to conservation biology, a discipline that, although ostensibly based on evolutionary principles,

does not typically consider contemporary evolution [25]. This is probably because evolution has traditionally seemed far removed from the immediate crisis of retaining existing biodiversity. We have discussed a few examples of conservation concerns related to contemporary evolution. Given that most endangered species are influenced by a combination of anthropogenic factors [27], including over-harvesting, habitat degradation and exotics, the contemporary evolution facing many populations could be significantly more complex than we have portrayed. Nonetheless, the apparent prevalence of contemporary evolution argues that conservation practitioners must now consider evolution over contemporary timescales. Some readers might be dismayed that the effects we discuss often seem contradictory and that we have not drawn hard and fast rules. However, this is currently inappropriate because the application of contemporary evolution to conservation biology is still very much in its infancy. We therefore hope that our discussion inspires research that can help disentangle the importance of diverse evolutionary forces to a variety of conservation scenarios.

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References

- 1 Palumbi, S.R. (2001) *The Evolution Explosion: How Humans Cause Rapid Evolutionary Change*, Norton
- 2 Meffe, G.K. and Carroll, C.R. (1997) *Principles of Conservation Biology*, Sinauer Associates
- 3 Hendry, A.P. and Kinnison, M.T. (1999) The pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53, 1637–1653
- 4 Kinnison, M.T. and Hendry, A.P. (2001) The pace of modern life II. From rates of contemporary microevolution to pattern and process. *Genetica* 112–113, 145–164
- 5 Reznick, D.N. and Ghalambor, C.K. (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112–113, 183–198
- 6 Franklin, I.R. and Frankham, R. (1998) How large must populations be to retain evolutionary potential. *Anim. Conserv.* 1, 69–73
- 7 Lynch, M. and Lande, R. (1998) The critical effective size for a genetically secure population. *Anim. Conserv.* 1, 70–72
- 8 Moritz, C. (1994) Defining 'Evolutionarily Significant Units' for conservation. *Trends Ecol. Evol.* 9, 373–375
- 9 Fraser, D.J. and Bernatchez, L. (2001) Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol. Ecol.* 10, 2741–2752
- 10 Crowling, R.M. and Pressey, R.L. (2001) Rapid plant diversification: planning for an evolutionary future. *Proc. Natl. Acad. Sci. U.S.A.* 98, 5452–5457
- 11 Moritz, C. (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. *System. Biol.* 51, 238–254
- 12 Gingerich, P.D. (2001) Rates of evolution on the time scale of the evolutionary process. *Genetica* 112–113, 127–144

- 13 Sheets, H.D. and Mitchell, C.E. (2001) Why the null matters: statistical tests, random walks and evolution. *Genetica* 112–113, 105–125
- 14 Endler, J.A. (1986) *Natural Selection in the Wild*, Princeton University Press
- 15 Stockwell, C.A. and Weeks, S.C. (1999) Translocations and rapid evolutionary responses in recently established populations of western mosquitofish (*Gambusia affinis*). *Anim. Conserv.* 2, 103–110
- 16 Bone, E. and Farres, A. (2001) Trends and rates of microevolution in plants. *Genetica* 112–113, 165–182
- 17 Reznick, D.N. *et al.* (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275, 1934–1937
- 18 Hendry, A.P. *et al.* (2000) Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290, 516–518
- 19 Kinnison, M. *et al.* (2001) Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* 55, 1656–1667
- 20 Quinn, T. *et al.* (2001) Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern rate, and process. *Genetica* 112–113, 493–513
- 21 Kingsolver, J.G. *et al.* (2001) The strength of phenotypic selection in natural populations. *Am. Nat.* 157, 245–261
- 22 Conner, J.K. (2001) How strong is natural selection? *Trends Ecol. Evol.* 16, 215–217
- 23 Grant, P.R. and Grant, B.R. (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296, 707–711
- 24 Lynch, M. (1996) A quantitative-genetic perspective on conservation issues. In *Conservation Genetics: Case Studies from Nature* (Avise, J.C. and Hamrick, J.L. eds), pp. 471–501, Chapman and Hall
- 25 Ashley, M.V. *et al.* (2003) Evolutionary enlightened management. *Biol. Conserv.* in press
- 26 Diamond, J.M. (1989) Overview of recent extinctions. In *Conservation for the Twenty-first Century* (Western, D. and Pearl, M.C. eds), pp. 37–41, Oxford University Press
- 27 Wilcove, D.A. *et al.* (1998) Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615
- 28 Conover, D. (2000) Darwinian fishery science. *Mar. Ecol. Prog. Ser.* 208, 299–313
- 29 Conover, D.O. and Munch, S.B. (2002) Sustaining fisheries yields over evolutionary time scales. *Science* 297, 94–96
- 30 Haugen, T. and Vøllestad, A. (2001) A century of life-history evolution in grayling. *Genetica* 112–113, 475–491
- 31 Macnair, M. (1987) Heavy metal tolerance in plants: a model evolutionary system. *Trends Ecol. Evol.* 2, 354–359
- 32 Richter, B.D. *et al.* (1997) Threats to imperiled freshwater fauna. *Conserv. Biol.* 11, 1081–1093
- 33 Noss, R.F. (2001) Beyond Kyoto: forest management in a time of rapid climate change. *Conserv. Biol.* 15, 578–590
- 34 Young, A. *et al.* (2002) The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.* 17, 413–418
- 35 Bradshaw, W. and Holzapfel, C. (2001) Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci. U.S.A.* 98, 14509–14511
- 36 Ward, J.K. *et al.* (2000) Is atmospheric CO₂ a selective agent on model C₃ annuals? *Oecologia* 123, 330–341
- 37 Bürger, R. and Lynch, M. (1995) Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution* 49, 151–163
- 38 McKay, J.K. and Latta, R.G. (2002) Adaptive population divergence: markers, QTL and traits. *Trends Ecol. Evol.* 17, 285–291
- 39 Boulding, E.G. and Hay, T. (2001) Genetic and demographic parameters determining population persistence. *Heredity* 86, 313–324
- 40 Carroll, S.P. *et al.* (2001) Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. *Genetica* 112–113, 257–272
- 41 Huey, R.B. *et al.* (2000) Rapid evolution of a geographic cline in size of an introduced fly. *Science* 287, 308–309
- 42 Williams, C. and Moore, R. (1989) Phenotypic adaptation and natural selection in the wild rabbit, *Oryctolagus cuniculus*, in Australia. *J. Anim. Ecol.* 58, 495–507
- 43 García-Ramos, G. and Rodríguez, D. (2002) Evolutionary speed of invasions. *Evolution* 56, 661–668
- 44 Schmitz, D.C. *et al.* (1997) The ecological impact of nonindigenous plants. In *Strangers in Paradise* (Simberloff, D. *et al.*, eds), pp. 39–61, Island Press
- 45 McKinney, M.L. and Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453
- 46 Tabashnik, B. (1994) Evolution of resistance to *Bacillus thuringiensis*. *Annu. Rev. Entomol.* 39, 47–79
- 47 Barrett, S.C.H. (2000) Microevolutionary influences of global changes on plant invasions. In *Invasive Species in a Changing World* (Mooney, H.A. and Hobbs, R.J. eds), pp. 115–139, Island Press
- 48 Goerghiou, G.P. and Lagunes-Tejeda, A. (1991) *The Occurrence of Resistance to Pesticides in Arthropods*, Food and Agriculture Organization of the United Nations
- 49 Ford, M.J. (2002) Selection in captivity during supportive breeding may reduce fitness in the wild. *Conserv. Biol.* 16, 815–825
- 50 Riechert, S.E. *et al.* (2001) High gene flow levels lead to gamete wastage in a desert spider system. *Genetica* 112–113, 297–319
- 51 Stockwell, C.A. *et al.* (1996) Translocations and the preservation of allelic diversity. *Conserv. Biol.* 10, 1133–1141
- 52 Fleming, I.R. and Gross, M.R. (1993) Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecol. App.* 3, 230–245
- 53 Campton, D.E. (1995) Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: what do we really know? In *Uses and Effects of Cultured Fishes in Aquatic Ecosystems* (Schramm, H.L.J. and Piper, R.G. eds), pp. 335–337, American Fisheries Society
- 54 Reisenbichler, R. and Rubin, S. (1999) Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *ICES J. Mar. Sci.* 56, 459–466
- 55 Lynch, M. and O'Hely, M. (2001) Captive breeding and the genetic fitness of natural populations. *Conserv. Genet.* 2, 363–378
- 56 Margan, S.H. *et al.* (1998) Single large or several small? Population fragmentation in the captive management of endangered species. *Zoo. Biol.* 17, 467–480
- 57 Frankham, R. (1995) Conservation genetics. *Annu. Rev. Genet.* 29, 305–327
- 58 Merilä, J. and Cronkrak, P. (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *J. Evol. Biol.* 14, 892–903
- 59 Reed, D.H. and Frankham, R. (2001) How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55, 1095–1103
- 60 Koskinen, M.T. *et al.* (2002) Contemporary fisherian life-history evolution in small salmonid populations. *Nature* 419, 826–830
- 61 Leberg, P.L. (1993) Strategies for population reintroduction: effects of genetic variability on population growth and size. *Conserv. Biol.* 7, 194–199
- 62 Hendry, A.P. *et al.* (2003) Estimating natural selection acting on stream-dwelling Atlantic salmon: implications for the restoration of extirpated populations. *Conserv. Biol.* in press
- 63 Stockwell, C.A. and Leberg, P.L. (2002) Ecological genetics and the translocation of native fishes: merging experimental approaches. *West. N. A. Nat.* 62, 32–38
- 64 Weber, E. and Schmid, B. (1998) Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. *Am. J. Bot.* 85, 1110–1121
- 65 Lee, C. (1999) Rapid and repeated invasions of freshwater by the copepod *Eurytemora affinis*. *Evolution* 53, 1423–1434
- 66 O'Steen, S. *et al.* (2002) Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 56, 776–784
- 67 Mallet, J. (1989) The evolution of insecticide resistance: have the insects won? *Trends Ecol. Evol.* 4, 336–340
- 68 Hairston, N. *et al.* (1999) Rapid evolution revealed by dormant eggs. *Nature* 401, 446
- 69 Rhymer, J. and Simberloff, D. (1996) Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27, 83–109
- 70 Allendorf, F. *et al.* (2001) The problems with hybrids: setting conservation guidelines. *Trends Ecol. Evol.* 16, 613–622