An evolutionary conservation biology

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DOI:10.1093/acprof:oso/9780199214211.003.0008

Abstract and Keywords

This chapter begins with a discussion of human impact on biodiversity. It then discusses human impact on evolutionary processes, evolutionary responses of harvesting, conservation of evolutionary potential, and establishment of the concepts of evolutionarily significant units (ESUs) and management units.

Keywords: evolution, biodiversity, evolutionary significant units, conservation units
Humans have had and continue to have devastating effects on global biodiversity. It has been estimated that in just the last 400 years 127 named bird species have died out, all of them most probably due to human action (Newton 2003). These extinctions are not only actions of the modern industrialized culture, because as many as a thousand endemic island bird species may have disappeared following early human colonization in the pre-historic period (Milberg and Tyrberg 1993). Many extant bird species are at present critically endangered by human action. It is predicted that deforestation will cause just under 100 endemic bird species to become extinct on the islands of the Philippines and Indonesia alone in the near future (Brooks et al. 1996). Of existing tropical forests, 16 million ha are lost annually (Achard et al. 2002). It is forecasted that one in eight bird species may become extinct over the next 100 years worldwide (Sodhi et al. 2004). Nearly all (99%) of the threats are due to human activities such as deforestation and hunting (Butchart et al. 2004).

These numbers and bleak predictions are not just confined to birds but apply to all organisms. The rate of loss of populations and habitat for animal and plants is estimated to be about 1% per year (Balmford et al. 2003). On a regional scale in Britain, extinctions of butterflies, birds, and vascular plants were found to be correlated (Thomas et al. 2004). Thus the losses of birds mentioned in the previous paragraph are without doubt accompanied by losses in other taxa. There is also direct evidence that humans are impacting plants, too, as in Britain there is a relationship between the loss of scarce plants and human population density (Thompson and Jones 1999).

A recent summit on ‘Evolutionary Change in Human-altered Environments’ was hosted by the Institute of the Environment at the University of California in February 2007. In the report it is stated: ‘As a consequence of [human-induced] impacts, we are witnessing a global, but unplanned, evolutionary experiment with the biotic diversity of the planet. Growing empirical evidence indicates that human-induced evolutionary changes impact every corner of the globe. Such changes are occurring rapidly, even at the level of a human lifespan, bear huge (p.140) economical costs and pose serious threats to both humans and the biodiversity of the planet’ (Smith and Bernatchez 2008). Humans have not only destroyed habitats and extinguished species, they have also changed species by domestication, moved them around the world, and released
alien species into the wild. All these statements could also have been written in the present tense with an additional note to say that species are now not only transformed by traditional breeding but also by transgenic techniques. One of the major threats to human welfare is the spreading of resistance to antibiotics and pesticides among pests and disease organisms, a clear example of contemporary Darwinian evolution (Palumbi 2001). It is clear that humans have affected and are affecting the evolutionary process.

8.1 Human impact on evolutionary processes
As mentioned in Chapter 6, evolution was previously regarded as a slow process. However, evolutionary changes can occur within short periods of time (e.g. Reznick 1997, Hendry 2000, 2006, Bradshaw and Holzapfel 2001, Quinn 2001). Moreover, it has been recognized that what is primarily driving contemporary evolution are the same factors that are behind the present biodiversity crisis and the on-going extinction. The factors that have been identified as drivers of contemporary evolution are: habitat loss and fragmentation, overharvesting, and introduction of alien and invasive species (Stockwell et al. 2003). Rates of evolutionary change are measured in haldanes (in honour of one of the founders of modern evolutionary biology, J.B.S. Haldane), which is defined as standard deviations of phenotypic change per generation. Obviously the scale of change alters with time: the more generations that pass, the greater the change. Therefore, to judge whether a change has been faster or slower than expected, the residuals from this relationship need to be calculated (Fig. 8.1). It is obvious that evolutionary rates occur on timescales that can be observed and quantified but also that the range of evolutionary rates for different taxa over the same number of generations varies considerably.

Not all changes in morphology, behaviour, and life history observed in response to environmental perturbation (human-induced or not) are due to genetic microevolutionary change. For example, many saltwater species also occur in the brackish waters of the Baltic Sea and are thus able to reproduce and live at considerably lower salinities compared to that in which they are usually found (Johannesson and André 2006). Whether local Baltic populations have truly
adapted to the lower salinity in the Baltic or if they represent species that are phenotypically plastic remains unclear.

Both microevolutionary change and phenotypic plasticity seem to matter for explaining occurrences of saltwater species in the Baltic. In flounder *Platichthys* (<p.141>)

... there are two forms that differ in egg characteristics (Florin and Höglund 2008). One is a pelagic spawning form that lays small and buoyant eggs and the other shows demersal spawning with larger, more robust eggs that sink to the bottom. In the Baltic, salinities fall from the Sound to the east and northwards. The demersal spawning form is more common in the more brackish waters of the northern Baltic. The buoyant eggs of pelagic spawners cannot float in the lower salinities in the north Baltic and suffer great mortality. On the other hand, the sinking eggs of demersal spawners are more robust and can survive the mechanic forces on the bottom of the spawning banks. It is likely that this difference in spawning behaviour and egg characteristics represents a microevolutionary response to salinity.

The turbot, *Psetta maxima*, is another flatfish that occurs in marine waters and in the Baltic. Their ability to survive and reproduce at low salinity is more likely to be explained by phenotypic plasticity as we could find no population structure among fish caught on the saline west coast of Sweden and fish caught in the Baltic (Florin and Höglund 2007).

In a review of existing studies it was found that observed phenotypic changes were greater when the environmental change was anthropogenic than natural (Hendry *et al.* 2008).
This difference may be explained by phenotypic plasticity rather than genetic change. In quantitative genetic studies that were designed to minimize the effects of phenotypic plasticity there was no difference among studies in which the change was anthropogenic or natural. However, the effect was evident for studies of wild-caught individuals in which both genetic and plastic responses may be present.

Due to the erection of hydroelectric power dams, the spawning waters of salmonid fishes have been affected. Several measures have been implemented to counteract the damage to fish stocks induced by these changes. They include the introduction of fish ladders so that migrating fish can pass the dams and several variants of supportive breeding using hatchery-reared fish. A growing body of evidence has shown that these altered selection regimes can result in genetic changes (Fleming et al. 2000, Hutchings and Fraser 2008, Waples et al. 2008).

In the River Dalälven in Sweden, large numbers of hatchery-produced trout have been raised and released for decades to compensate for the loss of natural reproduction caused by several hydroelectric power plants. This captive stock was founded using wild fish caught in the river. When comparing wild and hatchery-produced fish, phenotypic differences with a presumed genetic basis were observed (Petersson and Järvi 1993, 1995, Petersson et al. 1996). However, careful genetic studies using microsatellites and allozymes have shown that there was no genetic differentiation among the stocks (Palm et al. 2003a). Unfortunately, the experiments testing for phenotypic differences were not designed in a way that allowed for discrimination between phenotypic plasticity and genetic effects. However, an explanation for the differences among the stocks in morphology and behaviour may be that the observed phenotypic differences represent the actions of non-genetic maternal effects. Such may be mediated, for example, by egg-size differences among wild and hatchery-reared females (Jonsson et al. 1996).

Thus not all phenotypic changes observed in relation to human-induced changes are of genetic origin and instead represent plastic phenotypic responses. However, phenotypic plasticity also has a genetic component and may thus respond to selection (Via and Lande 1985, Stearns and Koella 1986, Scheiner 1993). It may be that human-induced changes select
for species that have evolved the ability of phenotypic plasticity: species that are pre-adapted to live in stressed and unstable environments. On the other hand, it has been suggested that phenotypic plasticity is one of the traits that may be lost when fish become domesticated in hatcheries (Hutchings and Fraser 2008).

8.2 Evolutionary responses of harvesting
In harvested or managed populations evolutionary change induced by selective harvesting can be rapid and has been documented in a number of cases. It is predicted from life-history theory that increased mortality favours evolution towards earlier sexual maturation at smaller size. Commercial fishing that is selective with respect to size, maturity status, behaviour, or morphology has been shown to cause such shifts (Jørgensen et al. 2007; Table 8.1). Moreover, from the point of view of the harvester these changes cause undesired changes: easily caught (p.143)

Table 8.1 Harvest-induced evolutionary changes in fish. For some stocks (n) the magnitude of change was quantified (from Jørgensen et al. 2007).

<table>
<thead>
<tr>
<th>Change, % (n)</th>
<th>No. of studies</th>
<th>No. of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maturation at lower age</td>
<td>10 23–24 (1)</td>
<td>6</td>
</tr>
<tr>
<td>Maturation at smaller size</td>
<td>13 20–33 (3)</td>
<td>7</td>
</tr>
<tr>
<td>Lower PMRN midpoint</td>
<td>10 3–49 (13)</td>
<td>5</td>
</tr>
<tr>
<td>Reduced annual growth</td>
<td>6 15–33 (3)</td>
<td>6</td>
</tr>
<tr>
<td>Increased fecundity</td>
<td>4 5–100 (3)</td>
<td>3</td>
</tr>
<tr>
<td>Loss of genetic diversity</td>
<td>3 21–22 (2)</td>
<td>3</td>
</tr>
</tbody>
</table>

large fish will be removed from the population while smaller and more difficult-to-catch fish are left behind (Lande et al. 1997).
A similar effect has been noted in hunted game populations. Trophy hunting selects against spectacular traits like large horns and antlers meaning that the hunted populations consist of fewer and fewer trophy animals (Coltman et al. 2003).

These evolutionary effects should come as no surprise. Ever since the dawn of evolutionary biology, predators have been believed to be important for shaping adaptations in prey (Reznick and Travis 1996, Swaddle and Lockwood 1998, Reznick et al. 2001). Humans, just like any top predator, impose selective pressures that have changed and will continue to change the properties of their prey populations.

Latta (2008) pointed out a corollary with human-imposed selective pressures. On the one hand humans select for undesirable features in some organisms, for example by inducing smaller and more uncatchable fish and game, resistant pests and disease organisms, and resilient weeds. On the other hand, human action has made it hard for us to change populations that we do want to alter. As discussed in Chapter 1, selection is a less potent evolutionary force in small and endangered populations and thus there are limits to the adaptive potential in such small populations, which cannot evolve despite our conservation efforts (Willi et al. 2006). It has therefore been proposed that a major focus of conservation biology should be to preserve the evolutionary potential of natural populations.
8.3 Conserving evolutionary potential

Conservation and evolution are to some extent a contradiction in terms. Evolution implies change and conservation implies no change. However, in this context conservation should be understood in terms of providing conditions making it possible for future change. It has long been recognized that practical conservation decisions should be based on evolutionary considerations. Erwin (1991) argued that, in a phylogeny of evolutionary lineages, the part in which species radiated the most should be given priority in protection. The part of the phylogeny in which rare endemics are found would be doomed to extinction in any case as such life forms obviously are not evolving. The radiating part of the phylogeny, on the other hand, represents evolutionary potential. If followed, this strategy would be different from many practical policies in which rare endemic species are considered conservation priorities. Arguments to preserve processes rather than patterns have also been made by several others (e.g. Smith et al. 1993, Thompson 1996, Stockwell et al. 2003).

A similar debate about conservation priorities prevails when it comes to prioritising among populations within species. Should conservation efforts and resources be put into large and thriving populations that have good future prospects or should they be put into small and peripheral populations? Lesica and Allendorf (1995) argued that the conservation value of peripheral populations depends upon their genetic divergence from other conspecific populations (Fig. 8.2). If peripheral populations are genetically and morphologically divergent from central populations such populations contribute to the overall genetic
diversity within a species and would add to their long-term conservation. They argued further that peripheral populations are potentially important sites of future speciation events. In California valley oak, *Quercus lobata*, some populations were more threatened than others. When such populations consisted of individuals with distinctive histories and genetic composition, they should be given priority in reserve network design or else valuable evolutionary information would be lost for this species (Grivet et al. 2008).

In Eurasian populations of the nominate subspecies of the black-tailed godwit *Limosa limosa limosa*, unique and rare mitochondrial haplotypes were found in peripheral populations on the Baltic islands Öland and Gotland (Högland et al. 2008). These islands harbour small fringe populations and yet mitochondrial diversity was much higher in these populations than in the much larger population breeding in the Netherlands. Clearly unique mitochondrial haplotypes would be lost if the Baltic populations should perish. Unfortunately, population-size trajectories have been negative in the past years and at the time of writing the Baltic populations are on the very brink of extinction.

What would be the optimal way to incorporate knowledge of evolutionary processes and the distribution of genetic diversity into conservation planning? Moritz (2002) argued for separation of genetic diversity into two dimensions, one concerned with adaptive variation and the other with neutral
divergence caused by isolation. Conservation of species and specific areas should emphasize protection of historically isolated lineages or so-called evolutionarily significant units (ESUs) because these cannot be recovered. By contrast, adaptive features may best be protected by maintaining the context for selection, heterogeneous landscapes, and viable populations, rather than protecting specific phenotypes.

Moritz proposed to (1) identify areas that are important for representing species and vicariant genetic diversity (by vicariant he meant genetic diversity specific to a particular area) and (2) within these areas maximize the protection of contiguous environmental gradients across which selection and migration can interact to maintain population viability and (adaptive) genetic diversity.

8.4 Conservation units
The need to identify conservation priorities has lead to the establishment of the concepts of ESUs (Ryder 1986) and management units (MUs; Moritz 1994), topics that have been touched upon previously in this book. How to best define such units is unclear (Crandall et al. 2000) and a heated debate on this topic used to prevail in the literature (see Fraser and Bernatchez 2001 for a review).

Many definitions of an ESU have been provided, each stressing different factors as important (Table 8.2). The ESU concept was first proposed to deal with the problems and vagueness of using subspecies definitions as a guide in conservation work. The original definition stressed that an ESU should be defined as a group of organisms that has been isolated from other conspecific groups for a sufficient period of time to have undergone meaningful genetic divergence from those other groups (Ryder 1986). In reality ESUs have been delimited by identifying groups of reciprocally monophyletic mitochondrial DNA lineages. Thus to qualify as an ESU, all lineages within a group must share a more recent common ancestor than any other lineage from another group (Moritz 1994).

Many conservation projects have also collected allele frequency data from allozymes and microsatellites. Such data were not easily applicable to the ESU concept and it was suggested that MUs could be used as a subcategory to ESUs.
To qualify as MUs, populations should show significant differences in allele

**Table 8.2 Evolutionarily significant unit (ESU) criteria (after Dyland and Bernatchez 2001).**

<table>
<thead>
<tr>
<th>Study</th>
<th>Criteria</th>
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<tbody>
<tr>
<td>Ryder 1986</td>
<td>Subsets of the more inclusive entity species, which possess genetic attributes significant for the present and future generations of the species in question</td>
</tr>
<tr>
<td>Waples 1991</td>
<td>A population or group of populations that:</td>
</tr>
<tr>
<td></td>
<td>(i) is substantially reproductively isolated from other conspecific population units; and</td>
</tr>
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<td></td>
<td>(ii) represents an important component of the evolutionary legacy of the species</td>
</tr>
<tr>
<td>Dizon et al. 1992</td>
<td>Populations or groups of populations demonstrating significant divergence in allele frequencies</td>
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<tr>
<td>Avise 1994</td>
<td>Sets of populations derived from consistently congruent gene phylogenies</td>
</tr>
<tr>
<td>Moritz 1994</td>
<td>Populations that:</td>
</tr>
<tr>
<td></td>
<td>(i) are reciprocal monophyletic for mtDNA alleles; and</td>
</tr>
<tr>
<td></td>
<td>(ii) demonstrate significant divergence of allele frequencies at nuclear loci</td>
</tr>
<tr>
<td>Vogler and DeSalle 1994</td>
<td>Groups that are diagnosed by characters which cluster individuals or populations to the exclusion of other such clusters</td>
</tr>
<tr>
<td>Crandall et al. 2000</td>
<td>Abandon the term ESU for a more holistic concept of species, consisting of populations with varying levels of gene flow evolving through drift and selection</td>
</tr>
</tbody>
</table>
Study | Criteria
--- | ---
Fraser and Bernatchez 2001 | A lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level (lineage) of the species

(p.147) distributions (Moritz 1994). In an ecological context an MU was defined as a group in which local population dynamics are determined primarily by birth and death rather than immigration and emigration (Moritz 1995).

The applicability of ESUs in situations where populations are continuously distributed has been questioned (Paetkau 1999). However, the main critique of the use of ESU is that when applied, the decision to call a species or population an ESU has most often been based on neutral characters. More genetic markers and the inclusion of non-neutral markers have been called for (Pertoldi et al. 2007).

This argument may be illustrated by a study of populations of the endangered North American Karner blue butterfly, *Lycaeides melissa samuelis* (Gompert et al. 2006). This subspecies is morphologically distinct from the nominate subspecies the Melissa blue butterfly, *Lycaeides melissa melissa*. It was shown that the presence of Melissa blue mitochondrial haplotypes in western Karner blue populations were the result of mitochondrial introgression. Thus western Karner blues were indistinct from Melissa blue butterflies on the basis of mtDNA whereas eastern populations were distinct. The subspecies were clearly separated in nuclear DNA which illustrates the risks of using data from a single locus for diagnosing ESUs.

The concept ESU has been important in practical management and legislation. In a review Fallon (2007) found that a taxonomic unit was much more likely to be included under the US Endangered Species Act if it had been assigned ESU status based on genetic data. Moreover, the type and amount of genetic data used was correlated with whether or not genetic distinction was discovered (the more and the better the data the more distinctions). The author called for guidelines for the evaluation of genetic information to list or delist organisms under the Endangered Species Act and advocated the use of multiple genetic markers.
In an attempt to reconcile the many views on ESU, Fraser and Bernatchez (2001) advocated what they called ‘adaptive evolutionary conservation’. In this approach many differing criteria could be used alone or in combination depending on the situation to determine the conservation status of species and other taxonomic units. They argued that a rigid, universal definition of an ESU across all species may not be possible. Instead they concluded that the main conservation goal should be to preserve both evolutionary processes and the ecological viability of populations. This would be accomplished by maintaining as many populations within the species as possible so that the process of evolution will not be constrained. To my knowledge this approach has not been applied and ESUs are still in use although more markers, and also non-neutral ones, are used.

The debate over ESU may partly reflect which markers have been in fashion. In the early 1990s mtDNA and phylogenetic reconstructions dominated the scene. With the advent of microsatellites in the mid-1990s there was a call for using allele frequency differences and hence the MU was introduced. Now when selected markers have become more common there is a call to also include (p.148) non-neutral information. Ironically, the debate over non-neutral versus neutral variation was a major impetus for the initiation of the current debate. The debate over ESUs also parallels the endless discussion of species concepts (Fraser and Bernatchez 2001). Advocates of the phylogenetic and related species concepts tend to favour ESU criteria based on historical and phylogenetic foundations while advocates of biological and similar species concepts have advocated the use of frequency differences and adaptive markers.

Now, with the advent of comparative data on whole genomes it has become clear that genomic variation is quite complex. Parts of the genome may be extremely conserved (e.g. coding genes) whereas other regions are more liable to change. Phylogenetic reconstruction of the evolutionary relationships between species works because lineage sorting by genetic drift makes species monophyletic over time. However, as has become evident in the debate over ESUs, incomplete lineage sorting has the consequence that closely related species may share gene sequences. As an example, in North American prairie grouse, the three species of the genus Tympanuchus all share mitochondrial haplotypes (Lucchini et al. 2001). Also,
even in cases when conservationists are dealing with good
taxonomic species, gene pools are not closed. Horizontal gene
transfer occurs via viruses and other vectors. Gene trees are
not the same as species trees (Pamilo and Nei 1988, Nichols
2001). To reconstruct the phylogeny and hence guide
conservation decisions the information from many genes need
to be considered.

8.5 Concluding remarks
How should a science of evolutionary conservation biology be
framed? Pertoldi, Biljsma, and Loeschcke (2007) listed five
problems affecting conservation genetics that should be
addressed by future studies. I agree on four of these, which
are listed here.

1 The lack of sufficient integration of the sub-disciplines
of conservation genetics. Being a multidisciplinary and
applied subject, conservation genetics is borrowing
theory, techniques, and analytical tools from related
subjects. Although much progress has been made with
publication of books and journals devoted to the field,
researchers may still have their background and some
of their other research in nearby fields. Evolution is a
unifying theory of biology and it should be apparent
that evolutionary studies and evolutionary thinking has
much to offer in conservation research and practice. To
resolve this worry, there should be less focus on new
techniques and markers and more focus on asking and
resolving relevant questions.

(p.149)

2 Inferring selection by means of neutral markers. As
has been argued in this book and elsewhere (Hedrick
2001, Gilligan et al. 2005), the correlation between
molecular diversity (e.g. heterozygosity) and
quantitative genetic variation (e.g. heritability) is weak
and becomes even weaker in expanding or declining
populations. Much current research is focused on
finding the molecular basis for quantitative variation
and while there is much optimism that these issues may
be resolved with new genomic techniques there are
theoretical limits to what can be gained. Fisher's
fundamental theorem of natural selection (see Chapter
2) tells us that the heritability of fitness-related traits is
transitory and generally low. One needs to be very
lucky to detect quantitative trait nucleotides for fitness-related traits in natural populations.

3 Inferring population dynamics by means of neutral markers. As was reviewed in Chapter 4, there is quest for inferring population processes from genetic data. However, many different demographic scenarios may produce similar genetic footprints. There is clearly a need for more integration among metapopulation ecological theory and population genetics. It is also the case that geneticists, systematists, and ecologists have slightly different views on what they mean by a population (Waples and Gaggiotti 2006). Geneticists tend to stress units that are in Hardy–Weinberg and linkage equilibrium whereas ecologists may define populations as entities in which there is density-dependent mortality and reproduction.

4 Genetic consequences of increased environmental variability (the answer to which is actually integrated with the fifth problem listed by Pertoldi et al. (2007); that is, lack of ecological relevance). As has been discussed in Chapter 4, climate change is one of the major challenges of today. Climates in the future are not only going to be warmer but more fluctuations are also predicted. We do not yet have good knowledge of these effects on genetic variability and how populations are going to respond evolutionarily to more stochastic environments. The conservation genetic paradigm is that the more variation there is, the better. This can be illustrated using a metaphor: the more tools in the tool box, the more problems can be solved. However, is there an upper limit to how large the tool box should be? In other words, should conservation genetic projects ultimately always be aimed at preserving and restoring as much variation as possible? Theoretical considerations suggest that genetic variation actually lowers fitness under selection (Lande and Shannon 1996).
Ecology and genetics, good old-fashioned ecological genetics, will continue to cross foster each other's disciplines and both subjects are integral parts of the study of evolution. One area where ecology, genetics, and evolution come together is in understanding disease dynamics. A more complex understanding of immunogenetics—linking studies of disease, genetic variation, and demographic—declines is high on the list of future research priorities. It has become clear that pathogens are emerging and re-emerging as significant threats to wildlife and human health at an increasing rate (Acevedo-Whitehouse and Cunningham 2006). Infectious disease may well be the final causative agent which makes small and endangered populations go extinct. Infectious disease has had large effects on feral populations when a disease to which there is no resistance has been introduced, not least in our own species. Thus a fuller and deeper understanding of the ecology and evolution of disease and disease resistance is not only of academic interest but also of importance in practical conservation. Conservation genetics can be seen as the effort to influence the evolutionary process in ways that enhance the persistence of population (Latta 2008). To do so we obviously first need to know about genetic variation in threatened species and much of the research throughout the history of the discipline has been aimed at studying and describing this variation. In Sweden, the Natural Environmental Protection Agency recently financed and published a survey of all genetic studies on wild plants and animals in the country (Andersson et al. 2007). Accompanying the report was an explicit proposal to the government on how to collect, store, and use such data in practical conservation in the future. International guidelines on how to set up and run such services have also been proposed (Schwartz et al. 2006). The time has come to implement these suggestions and to ask relevant questions about the evolutionary fate of endangered populations around the globe.