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Introduction

Régis Ferrière, Ulf Dieckmann, and Denis Couvet

Evolution has molded the past and paves the future of biodiversity. As anthropogenic damage to the Earth's biota spans unprecedented temporal and spatial scales, it has become urgent to tear down the traditional scientific barriers between conservation studies of populations, communities, and ecosystems from an evolutionary perspective. Acknowledgment that ecological and evolutionary processes closely interact is now mandatory for the development of management strategies aimed at the long-term conservation of biodiversity. The purpose of this book is to set the stage for an integrative approach to conservation biology that aims to manage *species* as well as ecological and evolutionary *processes*.

Human activities have brought the Earth to the brink of biotic crisis. Over the past decades, habitat destruction and fragmentation has been a major cause of population declines and extinctions. Famous examples include the destruction and serious degradation that have swept away over 75% of primary forests worldwide, about the same proportion of the mangrove forests of southern Asia, 98% or more of the dry forests of western Central America, and native grasslands and savannas across the USA. As human impact spreads and intensifies over the whole planet, conservation concerns evolve. Large-scale climatic changes have begun to endanger entire animal communities (Box 1.1). Amphibian populations, for example, have suffered widespread declines and extinctions in many parts of the world as a result of atmospheric change mediated through complex local ecological interactions. The time scale over which such biological consequences of global change unfolds is measured in decades to centuries. The resultant challenge to conservation biologists is to investigate large spatial and temporal scales over which ecological and evolutionary processes become closely intertwined. To tackle this challenge, it has become urgent to integrate currently disparate areas of conservation biology into a unified framework.

1.1 Demography, Genetics, and Ecology in Conservation Biology

For more than 20 years, conservation biology has developed along three rather disconnected lines of fundamental research and practical applications: conservation demography, conservation genetics, and conservation ecology. *Conservation demography* focuses on the likely fate of threatened populations and on identifying the factors that determine or alter that fate, with the aim of maintaining endangered species in the short term. To this end, stochastic models of population dynamics are combined with field data to predict how long a given population of an endangered

Box 1.1 Global warming and biological responses

Increasing greenhouse gas concentrations are expected to have significant impacts on the world's climate on a time scale of decades to centuries. Evidence from long-term monitoring suggests that climatic conditions over the past few decades have been anomalous compared with past climate variations. Recent climatic and atmospheric trends are already affecting the physiologies, life histories, and abundances of many species and have impacted entire communities (Hughes 2000).

Rapid and sometimes dramatic changes in the composition of communities of marine organisms provide evidence of recent climate-induced transformations. A 20-year (1974 to 1993) survey of a Californian reef fish assemblage shows that the proportion of northern, cold-affinity species declined from approximately 50% to about 33%, and the proportion of warm-affinity southern species increased from about 25% to 35%. These changes in species composition were accompanied by substantial (up to 92%) declines in the abundance of most species (Holbrook *et al.* 1997).

Ocean warming, especially in the tropics, may also affect terrestrial species. Increased evaporation levels generate large amounts of water vapor, which accelerates atmospheric warming through the release of latent heat as the moisture condenses. In tropical regions, such as the cloud forests of Monteverde, Costa Rica, this process results in an elevated cloud base and a decline in the frequency of mist days, a trend that has been associated strongly with synchronous declines in the populations of birds, reptiles, and amphibians (Pounds *et al.* 1999).

Since the mid-1980s, dramatic declines in amphibian populations have occurred in many parts of the world, including a number of apparent extinctions. Kiesecker *et al.* (2001) presented evidence that climate change may be the underlying cause of this global deterioration. In extremely dry years, reductions in the water depth of sites used by amphibians for egg laying increase the exposure of their embryos to damaging ultraviolet B radiation, which allows lethal skin infection by pathogens. Kiesecker *et al.* (2001) link the dry conditions in their study sites in western North America to sea-surface warming in the Pacific, and so identify a chain of events through which large-scale climate change causes wholesale mortality in an amphibian population.

species is likely to persist *under given circumstances*. Conservation demography can advertise some notable achievements, such as devising measures to boost emblematic species like the grizzly bear in Yellowstone National Park, planning the rescue of Californian condors, or recommending legal action to protect tigers in India and China.

A different stance is taken by *conservation genetics*, which focuses on the issue of preserving genetic diversity. Although the practical relevance of population genetics in conservation planning has been heatedly disputed over the past 15 years, empirical studies have lent much weight to the view that the loss of genetic diversity can have short-term effects, like inbreeding depression, that account for a significant fraction of a population's risk of extinction (Saccheri *et al.* 1998). There

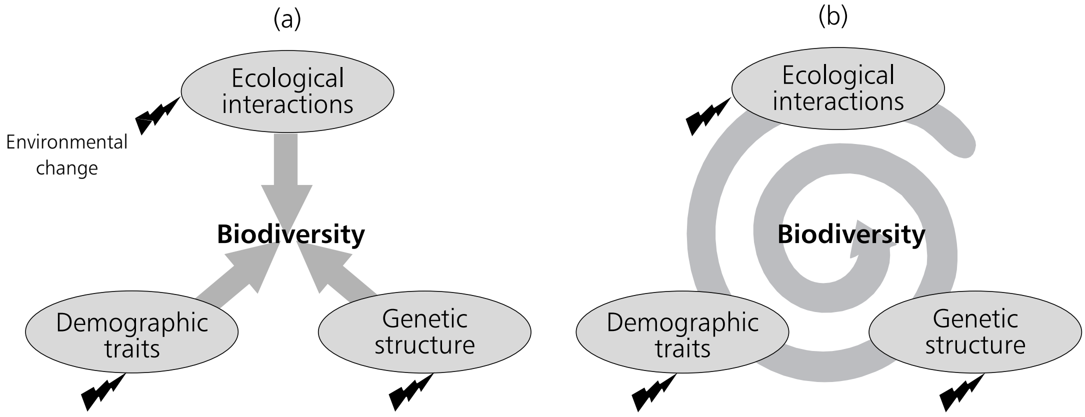


Figure 1.1 The integrative scope of evolutionary conservation biology (b) reconciles the three traditional approaches to the management of biodiversity (a).

is even experimental support for the contention that restoring genetic variation (to reduce inbreeding depression) can reverse population trajectories that would otherwise have headed toward extinction (Madsen *et al.* 1999).

The third branch of conservation biology, *conservation ecology*, relies on utilizing, for ecosystem management, the extensive knowledge developed by community ecologists and ecosystem theorists, in particular of the complicated webs of biotic and abiotic interactions that shape patterns of biodiversity and productivity. All the species in a given ecosystem are linked together, and when disturbances – such as biological invasions, disease outbreaks, or human overexploitation – cause one species to rise or fall in numbers, the effects may cascade throughout these webs. From a conservation perspective, one of the central questions for community and ecosystem ecologists is how the diversity and complexity of ecological interactions influence the resilience of ecosystems to disturbances.

All ecologists and population geneticists agree that evolutionary processes are of paramount importance to understand the genetic composition, community structure, and ecological functioning of natural ecosystems. However, relatively little integration of demographic, genetic, and ecological processes into a unified approach has actually been achieved to enable a better understanding of patterns of biodiversity and their response to environmental change (Figure 1.1). This book demonstrates why such an integrative stance is increasingly necessary, and offers theoretical and empirical avenues for progress in this direction.

1.2 Toward an Evolutionary Conservation Biology

All patterns of biodiversity that we observe in nature reflect a long evolutionary history, molded by a variety of evolutionary processes that have unfolded since life appeared on our planet. In this context, should we be content with safeguarding as much as we can of the current planetary stock of species? Or should we pay equal, if not greater, attention to fostering ecological and evolutionary processes that are responsible for the generation and maintenance of biodiversity?

Evolutionary responses to environmental changes can, indeed, be so fast and so strong that researchers are able to witness them, both in the laboratory and in the wild. Some striking instances (Box 1.2) include:

- Laboratory experiments on fruit flies that illuminate the role of intraspecific competition in driving fast, adaptive responses to pollution;
- Experiments on Caribbean lizards under natural conditions that demonstrate rapid morphological differentiation in response to their introduction into a new habitat; and
- Statistical analysis of extensive data on harvested fish stocks, from which we learn that the overexploitation of these natural resources can induce a rapid life-history evolution that must not be ignored when the status of harvested populations is assessed.

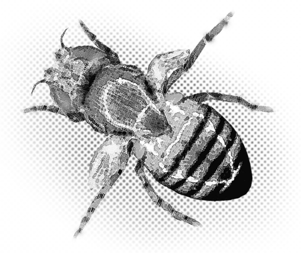
From their review of the studies of microevolutionary rates, Hendry and Kinnison (1999) concluded that rapid microevolution perhaps represents the norm in contemporary populations confronted with environmental change.

Looking much further back, analysis of macroevolutionary patterns suggests further evidence that the interplay of ecological and evolutionary processes is essential in securing the diversity and stability of entire communities challenged by environmental disturbances. Striking patterns of ecological and morphological stability observed in some paleontological records (e.g., from the Paleozoic Appalachian basin) are now explained in terms of "ecological locking": in this view, selection enables populations to respond swiftly to high-frequency disturbances, but is constrained by ecological conditions that change on an altogether slower time scale (Morris *et al.* 1995). Rapid microevolutionary processes driven and constrained by ecological interactions are therefore believed to be critical for the resilience of ecosystems challenged by environmental disturbances on a wide range of temporal and spatial scales.

Such empirical evidence for a close interaction of ecological and evolutionary processes in shaping patterns of biodiversity prompts a series of important questions that should feature prominently on the research agenda of evolutionary conservation biologists:

- How do adaptive responses to environmental threats affect population persistence?
- What are the key demographic, genetic, and ecological determinants of a species' evolutionary potential for adaptation to environmental challenges?
- Which characteristics of environmental change foster or hinder the adaptation of populations?
- How should the evolutionary past of ecological communities influence contemporary decisions about their management?
- How should we prioritize conservation measures to account for the immediate, local effects of anthropogenic threats and for the long-term, large-scale responses of ecosystems?

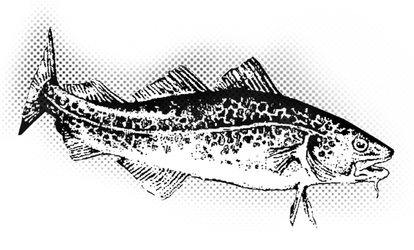
Box 1.2 Fast evolutionary responses to environmental change



Pollution raises threats that permeate entire food webs. Ecological and evolutionary mechanisms can interact to determine the response of a particular population to the pollution of its environment. This has been shown by Bolnick (2001), who conducted a series of experiments on fruit flies (*Drosophila melanogaster*). By introducing cadmium-intolerant populations to environments that contained both cadmium-free and cadmium-laced resources, he showed that populations experiencing high competition adapted to cadmium more rapidly, in no more than four generations, than low-competition populations. The ecological process of intraspecific competitive interaction can therefore act as a potent evolutionary force to drive rapid niche expansion.

Reintroduction of locally extinct species and reinforcement of threatened populations are important tools for conservation managers. A study by Losos *et al.* (1997) investigated, through a replicated experiment, how the characteristics of isolated habitats and the sizes of founder populations affected the ecological success and evolutionary differentiation of morphological characters. To this end, founder populations of 5–10 lizards (*Anolis sagrei*) from a large island were introduced into 14 much smaller islands that did not contain lizards naturally, probably because of periodic hurricanes. The study indicates that founding populations of lizards, despite their small initial size, can survive and rapidly adapt over a 10–14 year period (about 15 generations) to the new environmental conditions they encounter.

Overexploitation of natural ecosystems is a major concern to conservation biologists. Heavy exploitation can exert strong selective pressures on harvested populations, as in the case of the Northeast Arctic cod (*Gadus morhua*). The exploitation pattern of this stock was changed drastically in the early 20th century with the widespread introduction of motor trawling in the Barents Sea. Over the past 50 years, a period that corresponds to 5–7 generations, the life history of Northeast Arctic cod has exhibited a dramatic evolutionary shift toward earlier maturation (Jørgensen 1990; Godø 2000; Heino *et al.* 2000, 2002). The viability of a fish stock is therefore not just a matter of how many fish are removed each year; to predict the stock's fate, the concomitant evolutionary changes in the fish life-history induced by exploitation must also be accounted for. These adaptive responses are even likely to cascade, both ecologically and evolutionarily, to other species in the food chain and have the potential to impact the whole marine Arctic ecosystem.



Tackling these questions will require a variety of complementary approaches that are based on a solid theoretical framework. In Box 1.3, we outline the concept of the "environment feedback loop" that has been proposed as a suitable tool to link the joint operation of ecological and evolutionary processes to the dynamics of populations.

1.3 Environmental Challenges and Evolutionary Responses

Complex selective pressures on phenotypic traits arise from the interaction of individuals with their local environment, which consists of abiotic factors as well as conspecifics, preys and predators, mutualists, and parasites. Phenotypic traits respond to these pressures under the constraints imposed by the organism's genetic architecture, and this response in turn affects how individuals shape their environment. This two-way causal relationship – from the environment to the individuals, and back – defines the environment feedback loop that intimately links ecological and evolutionary processes.

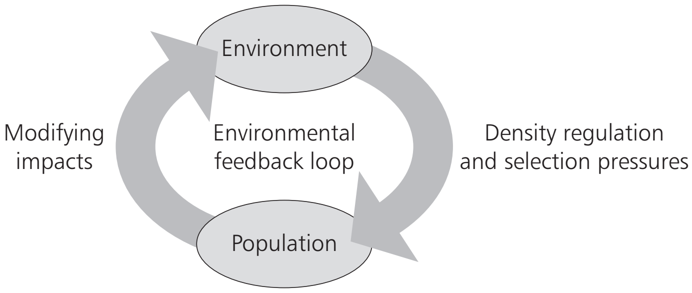
The structure of this feedback loop is decisive in determining how ecological and evolutionary processes jointly mediate the effects of biotic and abiotic environmental changes on species' persistence and community structure (Box 1.4). Three kinds of phenomena may ensue:

- Genetic constraints and environmental feedback can result in "evolutionary trapping", a situation in which a population is incapable of escaping to an alternative fitness peak that would ensure its persistence in the face of mounting environmental stress.
- Frequency-dependent selection may sometimes hasten extinction by promoting adaptations that are beneficial from the perspective of individuals and yet detrimental to the population as a whole, leading to processes of "evolutionary suicide".
- By contrast, "evolutionary rescue" may occur when a population's persistence is critically improved by adaptive changes in response to environmental degradation.

The relevance of evolutionary trapping, suicide, and rescue was first pointed out in the realm of verbal or mathematically simplified models (Wright 1931, Haldane 1932, Simpson 1944). Now, however, these concepts help to explain a wide range of evolutionary patterns in realistic models and, even more importantly, have also been documented in natural systems (Box 1.5). Among the most remarkable examples, the study of a narrow endemic plant species, *Centaurea corymbosa*, provides a clear-cut illustration of evolutionary trapping. The collection and analysis of rich demographic and genetic data sets led to the conclusion that *C. corymbosa* is stuck by its limited dispersal strategy in an evolutionary dead-end toward extinction: while variant dispersal strategies could promote persistence of the plant, they turn out to be adaptively unreachable from the population's current phenotypic state. In general, the possibility of evolutionary suicide should not come as a surprise in species that evolve lower basal metabolic rates to cope with the stress imposed

Box 1.3 The environmental feedback loop

Populations alter the environments they inhabit. The environmental feedback loop characterizes these interactions of populations with their environments and thus plays a key role in describing their demographic, ecological, and adaptive dynamics.



The environmental feedback loop goes beyond the self-evident interaction between a population and its environment. In fact, the concept aims to capture the pathways along which the characteristics of a resident population affect the variables that describe the state of its environment and how these, in turn, influence the demographic properties of resident or variant phenotypes in the population (Metz *et al.* 1996a; Heino *et al.* 1998). Some illustrative examples of variables that belong to these three fundamental sets are given below.

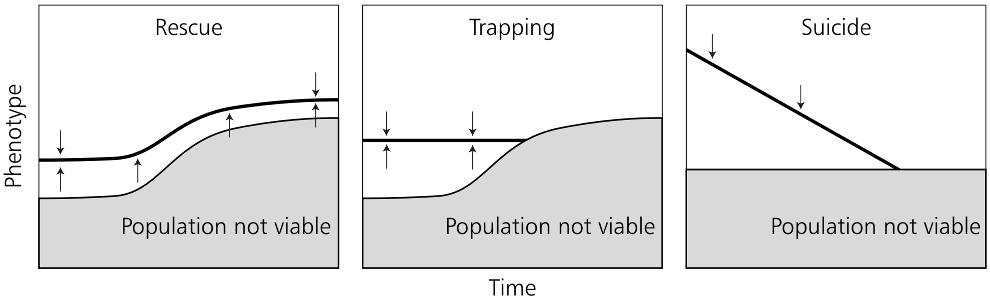
- Population characteristics: mean phenotype, abundance, or biomass, number of newborns, spatial clumping index, sex ratio, temporal variance in population size, etc. All these variables may be measured, either for the population as a whole or for stage- or age-specific subpopulations.
- Environmental variables: resource density, frequency of intraspecific fights, density of predators, helpers, or heterospecific competitors, etc.
- Demographic properties: rate of growth, fecundity, mortality, probability of maturation, dispersal propensity, etc.

The resultant loop structure involves precisely those environmental variables that are both affected by population characteristics and also impact relevant demographic properties. Specifying the environmental feedback loop therefore enables a description of all density- and/or frequency-dependent demographic mechanisms and selection pressures that operate in a considered population.

The minimal number of environmental variables or population characteristics that are sufficient to determine the demographic properties of resident and variant phenotypes is known as the dimension of the environmental feedback loop (Metz *et al.* 1996a; Heino *et al.* 1998; see also Chapter 11). This dimension has two important implications. First, it acts as an upper bound for the number of phenotypes that can stably coexist in the population (Meszéna and Metz 1999). Second, adaptive evolution can operate as an optimizing process and maximize population viability, under the constraints imposed by the underlying genetic system, only if the environmental feedback loop is one-dimensional (Metz *et al.* 1996a).

Box 1.4 Evolutionary rescue, trapping, and suicide

Populations that evolve under frequency-dependent selection have a rich repertoire of responses to environmental change. In general, such change affects, on the one hand, the range of phenotypes for which a population is not viable (gray regions in the panels below) and, on the other hand, the selection pressures (arrows) that, in turn, influence the actual phenotypic state of the population (thick curves).



Three prototypical response patterns can be distinguished:

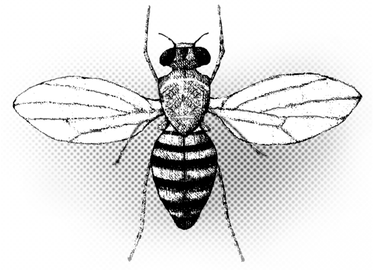
- Evolutionary rescue (left panel) occurs when environmental deterioration reduces the viability range of a population to such an extent that, in the absence of evolution, the population would go extinct, but simultaneously induces directional selection pressures that allow the population to escape extinction through evolutionary adaptation.
- Evolutionary trapping (middle panel) happens when stabilizing selection pressures prevent a population from responding evolutionarily to environmental deterioration. A particularly intriguing case of evolutionary trapping results from the existence of a second evolutionary attractor on which the population could persist: unable to attain this safe haven through gradual evolutionary change, the population maintains its phenotypic state until it ceases to be viable.
- Evolutionary suicide (right panel) amounts to a gradual decline, driven by directional selection, of a population's phenotypic state toward extinction. Such a tendency can be triggered and/or exacerbated by environmental change and is the clearest illustration that evolution cannot always be expected to act in the "interest" of threatened populations.

by an extreme environment, as exemplified by many animals living in deserts. A species that undergoes a reduction in metabolic rates must often divert resources away from growth and reproduction to invest in maintenance and survival. In consequence, reproductive rates fall and population densities decline, while the species' range may shrink. These adaptations confer a selective advantage to particular individuals, but run against the best interest of the species as a whole (Dobson 1996). Evolutionary rescue, on the other hand, is thought to be ubiquitous to maintain the diversity of communities. One example has recently been worked out in detail: the persistence of metapopulations of checkerspot butterflies (*Melitaea cinxia*) in degrading landscapes has been shown to depend critically on the potential for dispersal strategies to respond adaptively to environmental change.

Box 1.5 Evolutionary trapping, suicide, and rescue in the wild

Centaurea corymbosa (Asteraceae) is endemic to a small geographic area (less than 3 km^2) in southeastern France. Combining demographic and genetic analysis, Colas *et al.* (1997) concluded that the scarcity of long-range dispersal events associated with the particular life-history of this species precludes establishment of new populations and thus evolution toward colonization ability, even though nearby unoccupied sites would offer suitable habitats for the species. Thus, *C. corymbosa* seems to be trapped in a life-history pattern that will lead to its ultimate extinction.

Evolution of lower basal metabolic rates in response to environmental stress seems to pave the way for evolutionary suicide. Exposing *Drosophila* to dry conditions in the laboratory for several generations leads to the evolution of a strain of fruit fly with lowered metabolic rates and an increased resistance to dessication; incidentally, this also leads to a greater tolerance to a range of other stresses (starvation, heat shock, organic pollutants). These individuals, however, exhibit a reduction in their average birth rate, and thereby place their whole population at a high risk of extinction.



Evolutionary rescue can occur in a realistic metapopulation model of checkerspot butterflies (*Melitaea cinxia*) subject to habitat deterioration (Heino and Hanski 2001). In these simulations, which have been calibrated to an outstanding wealth of field data, habitat quality deteriorates gradually. In the absence of metapopulation evolution, habitat change leads to extinction as habitat occupation falls to zero. By contrast, the adaptive response of migration propensity results in evolutionary rescue.

Evidently, current communities must have gone through a series of environmental challenges throughout their history. Evolutionary trapping and suicide must thus have eliminated many species that lacked the ecological and genetic abilities to adapt successfully, and current species assemblages are expected to comprise those species that are endowed with a relatively high potential for evolutionary rescue (Balmford 1996). This cannot but strengthen the view that to maintain the ecological and genetic conditions required for the operation of evolutionary processes should rank among the top priorities of conservation programs.

1.4 Evolutionary Conservation Biology in Practice

In a few remarkable instances, management actions have already been undertaken with the primary aim of maintaining the potential for evolutionary responses to environmental change.

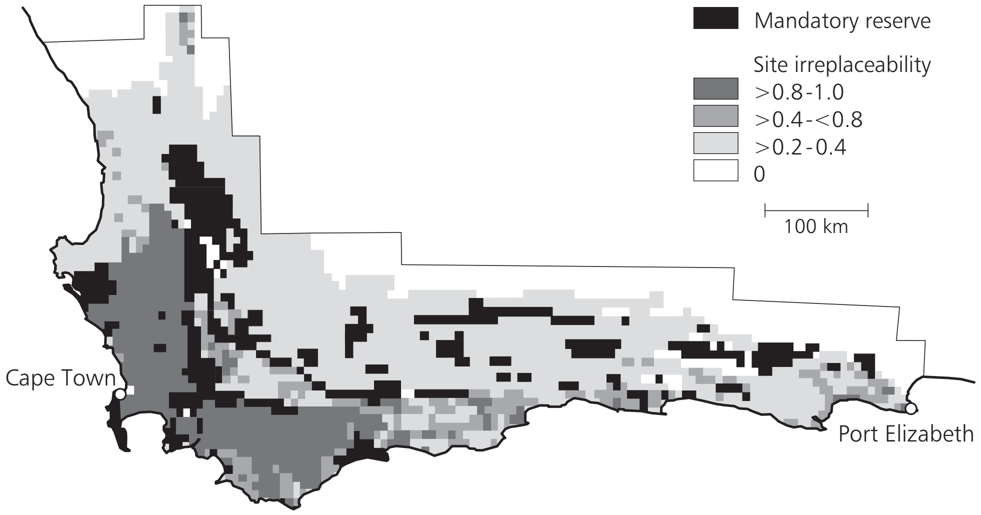
One such example is provided by the conservation plan devised for the Florida panther (*Felis concolor coryi*). Management of such an apex predator could be critical for the ecological and evolutionary functions of the whole web of interactions to which it is connected. After inbreeding depression was identified as a major threat to the panther population, a conservation scheme was implemented to manage genetic diversity. The aim was to reduce the short-term effects of inbreeding depression, but at the same time preserve those genetic combinations that render the Florida panther adapted to its local environment. Reinforcement with individuals that originated from a different subspecies, the Texas panther *F. concolor stanleyana*, was recognized as the only way to alleviate the deleterious effects of inbreeding in the remnant population of Florida panthers. The two taxa, however, are neither genetically nor ecologically “exchangeable”, in the sense of Crandall *et al.* (2000), which implies that they are genetically isolated and adapted to different ecological conditions. A particular challenge for this evolutionary conservation plan was, therefore, to avoid loss of the genetic identity and local adaptation attained by the Florida panther. To address this problem, a mathematical model was constructed to evaluate the proportion of introduced individuals that would eliminate the genes responsible for inbreeding depression and maintain both the genes responsible for local adaptations and the neutral genes expressed by typical characters that distinguish the two subspecies morphologically (Hedrick 1995). Action was then undertaken according to these predictions.

Another characteristic example of a conservation program devised from an evolutionary perspective targets the Cape Floristic Region (CFR), a biodiversity hotspot of global significance located in southwestern Africa. To conserve ecological processes that maintain evolutionary potential, and thus may generate biological diversity, is of central concern to managers of the CFR. Over the past few decades, considerable insights have been gained regarding evolutionary processes in the CFR, especially for those that involve plants. Now the goal has been set to design a conservation system for the CFR that will preserve large numbers of species and their ecological interactions, as well as their evolutionary potential for fast adaptation and lineage turnover (Box 1.6). The currently proposed plan recognizes that extant CFR nature reserves are not located in a manner that will sustain eco-evolutionary processes. The plan also highlights difficult trade-offs between the conservation of either pattern or process, as well as between the requirements for biodiversity conservation and other socioeconomic factors.

The ultimate goal of conservation planning should be to foster systems that enable biodiversity to persist in the face of anthropogenic changes. The two examples mentioned above illustrate the grand challenges that evolutionary conservation biology ought to tackle by identifying ways to preserve or restore genetic and ecological conditions that will ensure the continued operation of favorable

Box 1.6 Evolutionary conservation biology in practice: the Cape Floristic Region

There are very few ecosystems in the world for which an attempt has been made to develop conservation schemes aimed to preserve biodiversity patterns and eco-evolutionary processes in the context of a rapidly changing environment. One such is a conservation scheme suggested for the Cape Floristic Region (CFR) of South Africa, a species-rich region that is recognized as a global priority target for conservation action (Cowling and Pressey 2001). A distinctive evolutionary feature of the CFR is the recent (post-Pliocene) and massive diversification of many plant lineages. Over an area of 90 000 km^2, the CFR includes some 9000 plant species, 69% of which are endemic – one of the highest concentrations of endemic plant species in the world. This diversity is concentrated in relatively few lineages that have radiated spectacularly. There is evidence for a strong ecological component of the diversification processes, which involves meso- and macroscale environmental gradients and coevolutionary dynamics in plant–pollinator systems.



Conservation planning for the CFR aims to identify and conserve key evolutionary processes. For example, gradients from uplands to coastal lowlands and interior basins are assumed to form the ecological substrate for the radiation of plant and animal lineages. Suggested conservation targets amount to preserving at least one instance of a gradient within each of the major climate zones that are represented in the region. In addition, recognized predator–prey coevolutionary processes are motivating recommendations for the strict protection of three “mega wilderness areas”. Altogether, seven types of evolutionary processes have been listed for conservation management, and by selecting from areas in which one or more of these seven processes are operating, a system of conservation areas has been designed, based on a map of “irreplaceability” (shown above). Units at the highest irreplaceability level (dark gray) include areas of habitat that are all essential to meet conservation goals, whereas units with lowest irreplaceability (white) comprise patches of habitat in a largely pristine state for which conservation goals can be achieved through the implementation of alternative measures. Black indicates units in which existing reserves cover more than 50% of the area. Each planning unit is sufficiently large to ensure the continual operation of critical ecological and environmental processes (in particular through plant–insect pollinator interactions) and a regular regime of natural fire disturbances.

eco-evolutionary processes in a rapidly changing world. In fact, while protecting species may be hard, there is widespread agreement that the conservation of ecological interactions and evolutionary processes will be more efficient and cost-effective than a species-by-species approach (Noss 1996; Thompson 1998, 1999b; Myers and Knoll 2001). This does not rule out management measures directed at particular species (based on traditional tools such as population viability analysis), but suggests that we reconsider the motivation for doing so. Species-oriented conservation efforts are expected to be more rewarding when they target endangered species that have passed through the extinction sieve of a long history of natural and anthropogenic disturbances, and therefore should possess a higher potential for evolutionary rescue. Management must also prioritize species that are likely to play a crucial role in mediating the effect of global change on the integrity of entire networks of ecological interactions.

1.5 Structure of this Book

This volume is divided into five parts. In Part A, the basic determinants of population extinction risks are reviewed, after which Part B surveys the empirical evidence for rapid adaptive responses to environmental change. Unfolding the research program of evolutionary conservation biology, Part C shows how to integrate demographic, genetic, and ecological factors in models of population viability. Part D explains how these treatments can be extended to describe spatially heterogeneous populations, and Part E discusses embedment into the overarching context of community dynamics.

This structure leads to a development of ideas as follows:

- Part A explains how to devise population models that integrate interactions between individuals (sharing resources, finding mates) with sources of random fluctuations (demographic and environmental stochasticity). Such models are the basis for extinction-risk assessment. Different forms of dependence – which lie at the heart of population regulation and the environmental feedback loop – are shown to differ dramatically in their impact on population viability. In particular, the life cycles and spatial structure of populations must be considered if extinction risks are to be evaluated accurately.
- One motivation behind denial of a role for adaptive evolution in the dynamics of threatened populations might come from a belief that evolutionary change always occurs so slowly (e.g., at the geological time scale of paleontology) that it does not interact significantly with ecological processes and rapid environmental changes. To help overcome this widespread conception, Part B reviews recent observational and experimental studies that provide striking demonstrations of fast adaptive responses of morphological and life-history traits to environmental change. Convincing evidence is available for the existence of substantial genetic variation in life-history traits, and a current exciting line of research investigates whether genetic variability can sometimes even be enhanced by stressful environmental conditions.

- The challenge to assess the quantitative impact of life-history adaptation on extinction risk has nourished new developments in evolutionary theory. Three different stances are presented in Part C. A first option is to capitalize on a well-established modeling tradition in population genetics to investigate how mutations affect the extinction risks of small or declining populations in constant environments. Quantitative genetics offers an elegant alternative approach and allows the study of the conditions under which selection enables a population to track a changing environmental optimum. Integration of all the components of the environmental feedback loop requires the effects of density- and frequency-dependent ecological interactions to be respected, and the framework of adaptive dynamics has been devised to enable this.
- Issues that arise from the spatial dimensions of population dynamics and environmental change are tackled in Part D. Spatial heterogeneity – be it intrinsic to a habitat's structure (given, for instance, by an uneven distribution of resources) or resulting from a population's dynamics (leading to self-organized patterns of abundance) – modifies existing selection pressures and creates new ones. In particular, the option of individual dispersal as an evolutionary alternative to local adaptation exists only in spatially structured settings. In this context, the ecological and evolutionary role of peripheral populations must be analyzed carefully. Empirical studies suggest that processes of evolutionary rescue and evolutionary suicide may have occurred through adaptive responses of dispersal strategies to environmental degradation.
- Today, a scarcity of biological information still tends to confine the scope of viability analyses to single populations. Nevertheless, it is clear that the network of biotic interactions in which endangered species are embedded can strongly affect their viability. Environmental change may impact the focal species directly, or indirectly through its effects on other interacting species. Specific environmental changes that directly act on a single population only may be echoed by feedback responses from interacting species. To elevate our exploration of the adaptive responses to environmental change to the community level provides the motivation for the final Part E.

In addition to pursuing the main agenda of ideas outlined above, this volume also offers coverage of a broad scope of transversal themes. Chapters written in the style of an advanced textbook can be used to access up-to-date and self-contained reviews of key topics in population and conservation biology and evolutionary ecology. Crosscutting topics include:

- Extinction dynamics of unstructured and physiologically structured populations (Chapters 2 and 3);
- Dynamics of metapopulations and evolution of dispersal (Chapters 4, 14, and 15);
- Adaptive responses of natural systems to climate change, pollution, and habitat fragmentation (Chapters 5, 12, and 15);

- Empirical studies of life-history evolution in response to environmental threats (Chapters 6, 7, and 8);
- Population genetics and quantitative genetics of small or declining populations and of metapopulations (Chapters 9, 10, 12, 13, and 15);
- Adaptive dynamics theory and its applications (Chapters 11, 14, 16, and 17);
- Explorations of the demographic and genetic causes and consequences of rarity (Chapters 5, 9, 14, 15, and 18); and
- Community dynamics through evolutionary change in interspecific relations (Chapters 16, 17, and 18).

Merging these approaches will make it possible to acquire new insights into the responses of ecological and evolutionary processes to environmental change, as well as into the implications of these responses for population persistence and ecosystem diversity. The chapters herein are intended to pave the way for such integration.

The aim of this volume is to convince readers of the urgent need for systematic research into eco-evolutionary responses to anthropogenic threats. This research needs to account for, as accurately as is practically feasible, the type of environmental change, the species' life cycle, its habitat structure, and the network of ecological interactions in which it is embedded. This is a call for innovative experimental work on laboratory organisms, for a more integrative assessment of the living conditions of threatened populations in the wild, and for an extension of our theoretical grasp of processes involved in extinction and rescue. We hope that the book will entice students and researchers in ecology, genetics, and evolutionary theory to step into this open arena.

References

References in the book in which this chapter is published are integrated in a single list, which appears on pp. 365–410. For the purpose of this reprint, references cited in the chapter have been assembled below.

Balmford A (1996). Extinction filters and current resilience: The significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution* **11**:193–196

Bolnick DI (2001). Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* **410**:463–466

Colas B, Olivieri I & Riba M (1997). *Centaurea corymbosa*, a cliff-dwelling species tottering on the brink of extinction: A demographic and genetic study. *Proceedings of the National Academy of Sciences of the USA* **94**:3471–3476

Cowling RM & Pressey RL (2001). Rapid plant diversification: Planning for an evolutionary future. *Proceedings of the National Academy of Sciences of the USA* **98**:5452–5457

Crandall KA, Bininda-Emonds ORP, Mace GM & Wayne RK (2000). Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution* **15**:290–295

Dobson AP (1996). *Conservation and Biodiversity*. Scientific American Libraries. New York, NY, USA: Freeman

Godø OR (2000). *Maturation Dynamics of Arcto-Norwegian Cod.* IIASA Interim Report IR-00-024. Laxenburg, Austria: International Institute for Applied Systems Analysis

Haldane JBS (1932). *The Causes of Evolution*. Ithaca, NY, USA: Cornell University Press

Hedrick P (1995). Gene flow and genetic restoration: The Florida Panther as a case study. *Conservation Biology* **9**:996–1007

Heino M & Hanski I (2001). Evolution of migration rate in a spatially realistic metapopulation model. *The American Naturalist* **157**:495–511

Heino M, Metz JAJ & Kaitala V (1998). The enigma of frequency-dependence. *Trends in Ecology and Evolution* **13**:367–370

Heino M, Dieckmann U & Godø OR (2000). Shrinking cod: Fishery-induced change in an oceanic stock. *Options*, Spring, pp. 6–8. Laxenburg, Austria: International Institute for Applied Systems Analysis

Hendry AP & Kinnison MT (1999). The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* **53**:1637–1653

Holbrook S, Schmitt RJ & Stephens JS (1997). Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications* **7**:1299–1310

Hughes L (2000). Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution* **15**:56–61

Jørgensen T (1990). Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil International pour l'Exploration de la Mer* **46**:235–248

Kiesecker JM, Blaustein AR & Belden LK (2001). Complex causes of amphibian population declines. *Nature* **410**:681–684

Losos JB, Warhelt KI & Schoener TW (1997). Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* **387**:70–73

Madsen T, Shine R, Olsson M & Wittzell H (1999). Restoration of an inbred adder population. *Nature* **402**:34–35

Meszéna G & Metz JAJ (1999). *Species Diversity and Population Regulation: The Importance of Environmental Feedback Dimensionality*. IIASA Interim Report IR-99-045. Laxenburg, Austria: International Institute for Applied Systems Analysis

Metz JAJ, Geritz SAH, Meszéna G, Jacobs FAJ & van Heerwaarden JS (1996). Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems*, eds. SJ van Strien & SM Verduyn Lunel, pp. 183–231. Amsterdam, Netherlands: North Holland

Morris PJ, Ivany LC, Schopf KM & Brett CE (1995). The challenge of paleontological stasis: Reassessing sources of evolutionary stability. *Proceedings of the National Academy of Sciences of the USA* **92**:11269–11273

Myers N & Knoll AH (2001). The biotic crisis and the future of evolution. *Proceedings of the National Academy of Sciences of the USA* **98**:5389–5392

Noss RF (1996). Ecosystem as conservation targets. *Trends in Ecology and Evolution* **11**:351

Pounds JA, Fogden MPL, Campbell JH & Savage JM (1999). Biological responses to climate change on a tropical mountain. *Nature* **398**:611–615

Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W & Hanski I (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**:491–494

Simpson GG (1944). *Tempo and Mode in Evolution*. New York, NY, USA: Columbia University Press

Thompson JN (1998). Rapid evolution as an ecological process. *Trends in Ecology and Evolution* **13**:329–332

Thompson JN (1999). The evolution of species interactions. *Science* **284**:2116–2118

Wright S (1931). Evolution in Mendelian populations. *Genetics* **16**:97–159