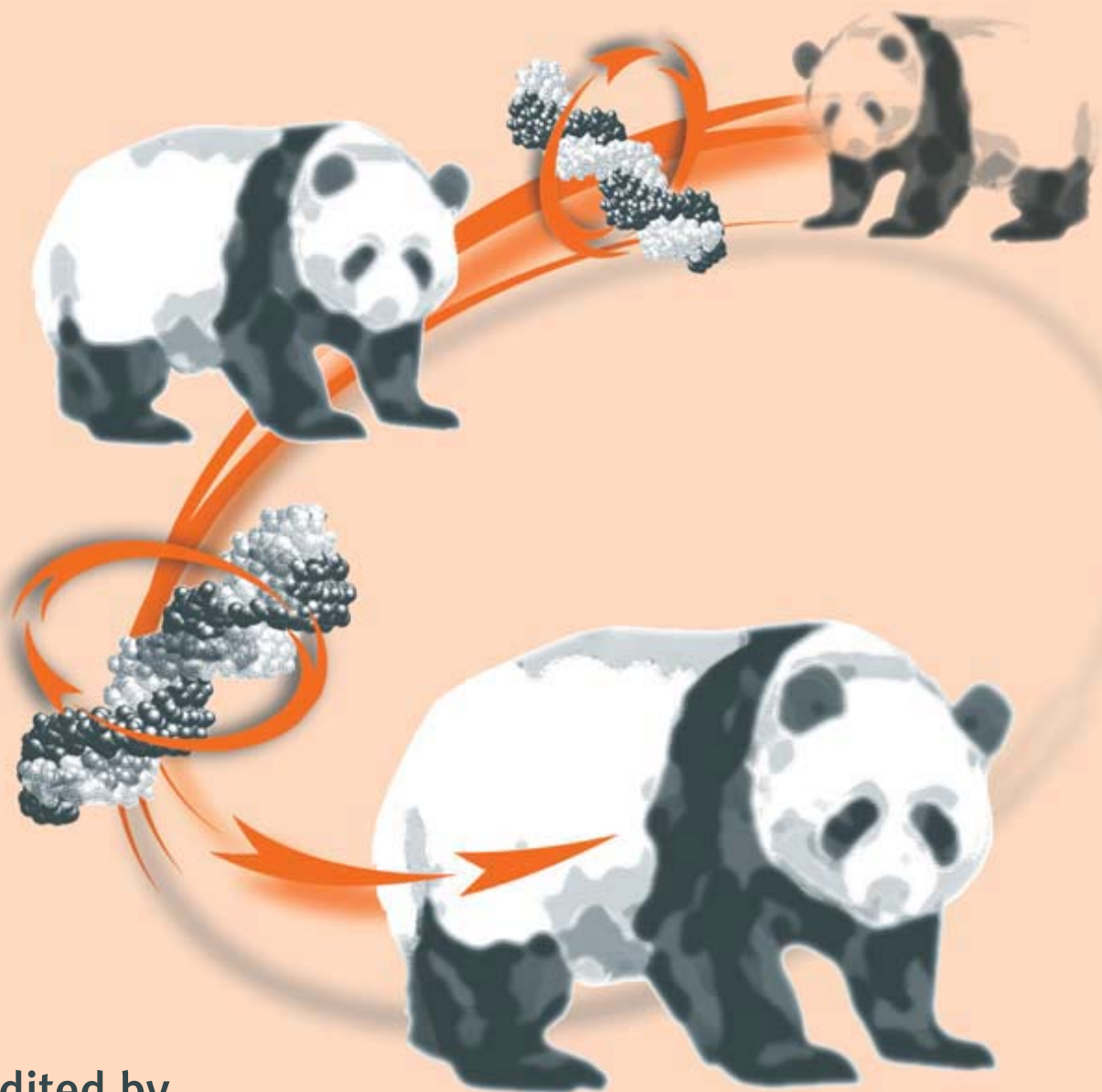


Cambridge Studies in Adaptive Dynamics

Evolutionary Conservation Biology



Edited by
R. Ferrière, U. Dieckmann, and D. Couvet

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PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom
CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK <http://www.cup.cam.ac.uk>
40 West 20th Street, New York, NY 10011-4211, USA <http://www.cup.org>
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain

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First published 2004

Printed in the United Kingdom at the University Press, Cambridge

Typefaces Times; Zapf Humanist 601 (Bitstream Inc.) System \LaTeX

A catalogue record for this book is available from the British Library

ISBN 0 521 82700 0 hardback

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Acknowledgments

Development of this book took place at the International Institute of Applied Systems Analysis (IIASA), Laxenburg, Austria, at which IIASA's former directors Gordon J. MacDonald and Arne B. Jernelöv, and current director Leen Hordijk, have provided critical support. Two workshops at IIASA brought together all the authors to discuss their contributions and thus served as an important element in the strategy to achieve as much continuity across the subject areas as possible.

Financial support toward these workshops given by the European Science Foundation's Theoretical Biology of Adaptation Programme is gratefully acknowledged. Régis Ferrière and Ulf Dieckmann received support from the European Research Training Network *ModLife* (Modern Life-History Theory and its Application to the Management of Natural Resources), funded through the Human Potential Programme of the European Commission.

The success of any edited volume aspiring to textbook standards very much depends on the cooperation of the contributors in dealing with the many points the editors are bound to raise. We are indebted to all our authors for their cooperativeness and patience throughout the resultant rounds of revision. The book has benefited greatly from the support of the Publications Department at IIASA; we are especially grateful to Ewa Delpos, Anka James, Martina Jöstl, Eryl Maedel, John Ormiston, and Lieselotte Roggenland for the excellent work they have put into preparing the camera-ready copy of this volume. Any mistakes that remain are, however, our responsibility.

Régis Ferrière
Ulf Dieckmann
Denis Couvet

Notational Standards

To allow for a better focus on the content of chapters and to highlight their interconnections, we have encouraged all the authors of this volume to adhere to the following notational standards:

α	Ecological interaction coefficient
b	Per capita birth rate
d	Per capita death rate
r	Per capita growth rate
R_0	Per capita growth ratio per generation
K	Carrying capacity
N	Population size
N_e	Effective population size
x, y, z	Phenotypic or allelic trait values
G	Genetic contribution to phenotype
E	Environmental contribution to phenotype
P	Phenotype
V_G	Genetic variance(–covariance)
V_E	Environmental variance(–covariance)
V_P	Phenotypic variance(–covariance)
V_A	Additive genetic variance(–covariance)
V_D	Dominance genetic variance(–covariance)
V_I	Epistatic genetic variance(–covariance)
$V_{G \times E}$	Genotype–environment variance(–covariance)
h^2	Heritability
S	Selection coefficient/differential
R	Response to selection
u	Per locus mutation rate
U	Genomic mutation rate
L	Mutation load
F	Inbreeding coefficient
H	Level of heterozygosity
f	Fitness in continuous time ($f = 0$ is neutral)
W	Fitness in discrete time ($W = 1$ is neutral)
t	Time
T	Duration
τ	Delay time

n	Number of entities other than individuals
p, q	Probability or (dimensionless) frequency
i, j, k	Indices
$\mathbb{E}(\dots)$	Mathematical expectation
$\Delta \dots$	Difference
$\bar{\dots}$	Average
$\hat{\dots}$	Equilibrium value

1

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

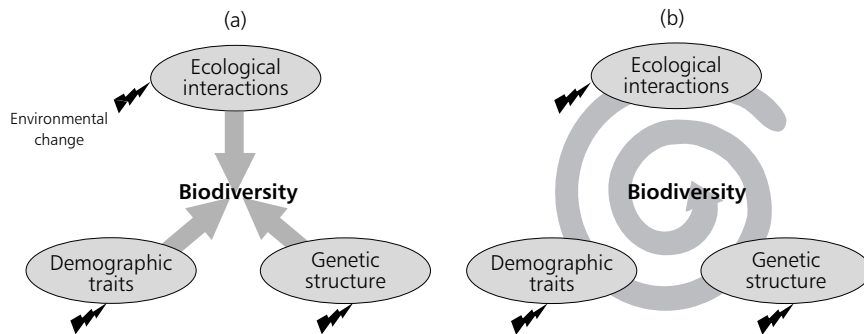


Figure 1.1 The integrative scope of evolutionary conservation biology (b) reconciles the three traditional approaches to the management of biodiversity (a).

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

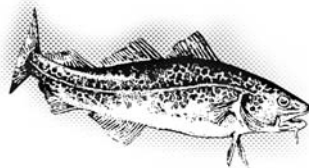
Pollution raises threats that permeate entire food webs. Ecological and evolutionary mechanisms can interact to determine the response of a particular population to the pollution of its environment. This has been shown by Bolnick (2001), who conducted a series of experiments on fruit flies (*Drosophila 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.

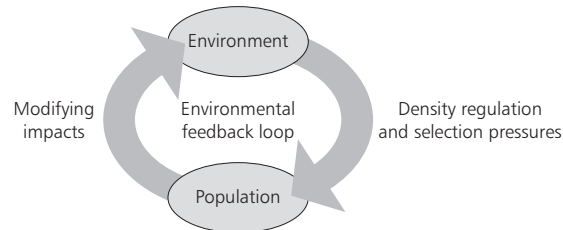
The structure of this feedback loop is decisive in determining how ecological and evolutionary processes jointly mediate the effects of biotic and abiotic environmental changes on species’ persistence and community structure (Box 1.4). Three kinds of phenomena may ensue:

- 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.

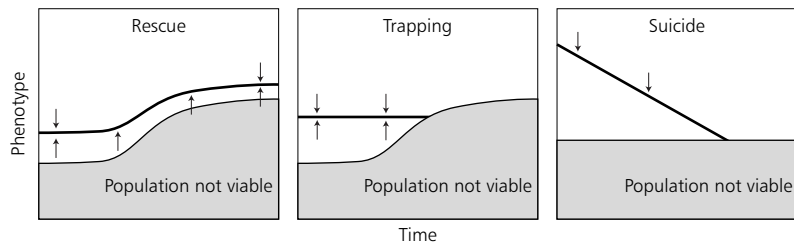
- Population characteristics: mean phenotype, abundance, or biomass, number of newborns, spatial clumping index, sex ratio, temporal variance in population size, etc. All these variables may be measured, either for the population as a whole or for stage- or age-specific subpopulations.
- Environmental 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 km²) 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 desiccation; 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.

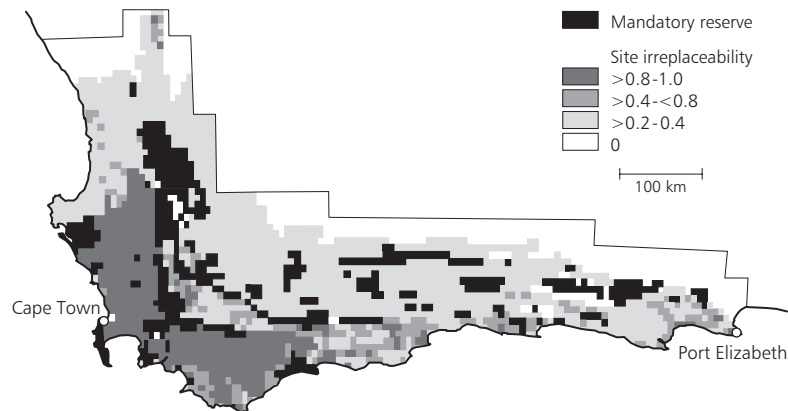
One such example is provided by the conservation plan devised for the Florida panther (*Felis concolor coryi*). Management of such an apex predator could be critical for the ecological and evolutionary functions of the whole web of interactions to which it is connected. After inbreeding depression was 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 km², 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.

Part A
Theory of Extinction



Introduction to Part A

Local changes in biodiversity happen through migration or speciation and through extinctions. The latter have been at the focus of conservation biology since the field's inception, and the purpose of this opening part is to review the rich theoretical foundations for our understanding of population extinction.

Specifically, we aim to understand how mechanisms that operate at the level of individuals scale up to the dynamics of populations and thus determine extinction risks. In the context of evolutionary conservation biology, this step is necessary to identify potential targets that impact on population viability. Such targets include classic life-history traits (e.g., demographic parameters such as survival probabilities, fecundity, or age at maturity) and behavioral traits that determine the effective interactions between individuals (e.g., propensities to move or migrate, competitive ability, or mate choice).

Connecting individual characteristics to population properties is also necessary to understand the origin of the selective pressures by which populations exert a feedback to individuals. Adaptive evolution usually proceeds by small steps: new phenotypes arise from mutation or recombination, and the individuals thus affected must compete with their conspecifics. Questions of viability and extinction are therefore important to address in assessing whether evolutionary innovations are retained through the persistence of their carriers or, instead, are eliminated through their extinction.

The theoretical material in this part should also be relevant to investigators with a primary interest in population viability analysis (PVA). For more than two decades, PVA has provided a fruitful approach to the quantitative assessment of endangered species; it is used to facilitate the design of management programs and to compare the relative merits of alternative conservation measures prior to their implementation. The species-oriented and short-term perspective of PVAs is not necessarily at odds with the ecosystem-oriented and long-term perspective suggested in this book: there are at least two important reasons for emphasizing the role of PVAs in the context of evolutionary conservation biology.

First, PVAs often target large vertebrates that are the ecological and evolutionary cornerstones of their ecosystems. Major ecological and evolutionary knock-on and ripple effects are expected for smaller species (and, indeed, for biotas as a whole) from the decline or extinction of such keystone species. An example is the current decline of elephants in African savannas. This species and many other large mammals have little hope of innovation in their evolutionary future, but their role in the ecosystem is so central that their extinction could alter the ecological interactions and evolutionary paths of many other species in a disastrous manner. Thus, PVAs are very useful to help maintain keystone species, especially if these are perched on the brink of extinction. This may sometimes win sufficient time

to design and implement management measures at the broader level of communities and ecosystems. In a similar vein, the implementation of reserve systems to conserve ecological and evolutionary processes, like the ambitious conservation plan for the Cape Floristic Region, can only be gradual. It is therefore critical that actions be undertaken to minimize the extent to which conservation targets are compromised before measures of evolutionary conservation can take effect.

Second, the endangerment of species targeted by PVAs may often have an evolutionary basis. We now understand that small population size and a resultant high vulnerability to environmental stress can arise as a by-product of behavioral and life-history evolution toward large body size and competitive superiority, both of which have to be traded against low reproductive output. Species that have evolved such attributes are likely to have low abundance; such species must have passed through highly selective extinction sieves during their evolutionary history, and only those endowed with particular demographic and genetic features that enabled them to buffer environmental disturbances have been retained. Thus, rare species still extant today presumably are properly “equipped” by the evolutionary and co-evolutionary processes to cope with perturbations. Conservation managers should therefore be aware of how and to what extent current and forthcoming challenges posed by human activities (often unprecedented in their scope and interaction) differ from the evolutionary history and context of a threatened species.

The three chapters in this part introduce the theoretical tools needed to evaluate the risk of extinction for a given population. This issue is addressed, in turn, for unstructured populations (Chapter 2), populations with structured life cycles (Chapter 3), and spatially structured populations (Chapter 4).

How do interactions between individuals influence a population’s risk of extinction? In Chapter 2, Gabriel and Ferrière address this question by investigating the properties of unstructured population models in which populations are regulated through density dependence. These models are appropriate for organisms with simple life cycles. Extinction risks, which are inversely proportional to average times to extinction, respond differently to changes in different demographic parameters. Important scaling relationships depend upon the types of stochastic fluctuations to which populations are exposed. Demographic stochasticity originates from the random timing of birth and death events, from individual variation in birth and death rates, and from random fluctuations in the sex ratio. By contrast, external stochastic influences on population dynamics include environmental noise and rare catastrophes. Chapter 2 shows how the type and “color” of stochastic fluctuations interfere with the nonlinear mechanisms of population regulation to shape patterns of population viability and extinction.

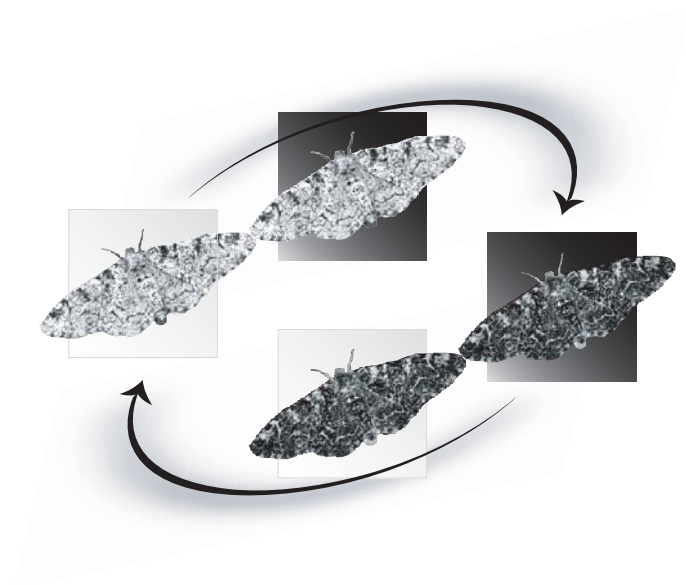
As few life-history traits are required to parametrize unstructured population models, these models are particularly amenable to mathematical analysis. Such simplification, however, carries the cost of ignoring those life-history traits that govern transitions in a species’ life cycle. This is problematic since developmental transitions, as well as intraspecific interactions that occur in different ways between particular developmental stages, often critically affect population dynamics.

Chapter 3 by Legendre introduces, in a didactical manner, the concepts and tools needed to relate population dynamics to the structure and parameters of life cycles that involve discrete stages. The chapter first focuses on age-dependent stages and transitions. After a review of the basic theory, it is explained how to extend classic models to account for the influence of sexual reproduction on population viability. Traits and interactions involved in mating processes can have a dramatic impact on the extinction risks of populations. As a genetic factor of demographic change induced by sexual reproduction, the consequences of inbreeding depression are discussed.

Space introduces an extra dimension of population structure and presents new challenges for the modeling of extinction dynamics. In Chapter 4, Gyllenberg, Hanski, and Metz describe a general framework for modeling spatially fragmented populations. This enables evaluation of the effects on population viability and persistence of traits that determine spatial population structure (such as offspring dispersal). Although the general treatment is mathematically rather sophisticated, the authors demonstrate the utility of their approach for particular examples, which allows the essentials to be grasped easily. The question of metapopulation growth or decline is addressed by deriving the metapopulation's basic reproduction ratio from life-history traits and environmental characteristics. Relating these parameters to metapopulation viability requires the effects of finite population size to be taken into account, which naturally leads to a discussion of stochastic metapopulation models. The resultant analysis disentangles the relative importance of local resource dynamics, regional habitat structure, and life-history traits on the extinction risk of metapopulations.

Part B

The Pace of Adaptive Responses to Environmental Change



Introduction to Part B

“How fast, as a matter of fact, do animals evolve in nature?” was asked by George Gaylord Simpson (1944) in his renowned book *Tempo and Mode in Evolution*. Ecological and evolutionary processes are often thought to occur on different time scales, so much so that it is common to hear biologists talk about ecological time in contrast to evolutionary time. However, several decades of study in evolutionary ecology and evolutionary genetics have revealed that the time scales of ecological and evolutionary processes can overlap for many crucial questions posed by ecologists. A number of recent studies have reported on the rapid evolution of morphological, physiological, behavioral, and demographic traits over time scales of a few decades, or tens of generations, which coincides with the time horizon of many conservation schemes. How robust is the evidence that leads to the conclusion of commensurate time scales? What do we know about the ecological and genetic conditions under which fast evolutionary change is likely to occur? How relevant are these conditions from the vantage point of conservation biology? The purpose of Part B is to address these important questions.

One of the classic examples of rapid adaptation in response to environmental change is the celebrated case of the peppered moth (*Biston betularia*). At the end of the 19th century, air pollution caused by a thriving industry in the UK and other parts of Europe killed the gray lichen that covered tree trunks on which the moth, with its lichen-mimetic wings, could rest almost invisibly to its predators. As a consequence, this light-colored phenotype was exposed to heavy predation, which promoted the rapid spread of a dark (melanic) mutant, an adaptation that may have rescued the peppered moth from likely extinction. Decreasing air pollution in the 1970s has triggered a similarly rapid evolutionary resurrection of the light-colored phenotype. Whereas the detailed evolutionary mechanisms that underlie this phenomenon are still vigorously debated (Majerus 1998), the case clearly demonstrates how quickly organisms can respond to environmental changes and how ecological predictions that do not account for such adaptations can be in error qualitatively. Not only can adaptations to new environmental conditions occur rapidly, but also they may be amazingly broad in their geographic scope. The rapid evolutionary establishment of a geographic cline in the body size of a fruit fly species (*Drosophila subobscura*), introduced to the New World at the end of the 1970s, shows rates of evolutionary change on a continental scale that exceed almost all previously measured natural rates. Other famous examples of rapid adaptations over large geographic scales are known to involve coevolution of interacting species: rapid and concomitant changes in the virulence of the myxoma virus and the resistance of its host, the European rabbit (*Oryctolagus cuniculus*), were recorded over as few as five years after the disease had spread through Australia in the 1950s.

Evidence for rapid adaptations has been obtained experimentally, too. These experiments fall into four major groups, depending upon whether environmental changes qualify as primarily abiotic (like habitat pollution or climatic change) or biotic (involving, for example, the introduction or removal of predators); and whether these changes correspond to environmental degradation or amelioration. The relevance of such experiments in the context of evolutionary conservation biology can hardly be overestimated: they highlight the important role that common organisms, widely bred in the laboratory, can play in developing an experimental approach to address questions in this emerging field.

Basic empirical evidence for rapid evolutionary responses to environmental threats is reviewed in Chapter 5. After examining the major types of environmental change and their different temporal and spatial scales, Frankham and Kingsolver present a variety of examples for swift responses:

- Recently established latitudinal gradients in fruit flies and codling moths;
- Rapid local adaptation in sockeye salmon;
- Range expansion in admiral butterflies;
- Industrial melanism in peppered moths;
- Acquisition of metal resistance in maple trees; and
- Evolution of heat tolerance in fruit flies and in the bacterium *Escherichia coli*.

The chapter also explains how to assess the evolutionary potential of a threatened population and discusses the special challenges experienced by small populations.

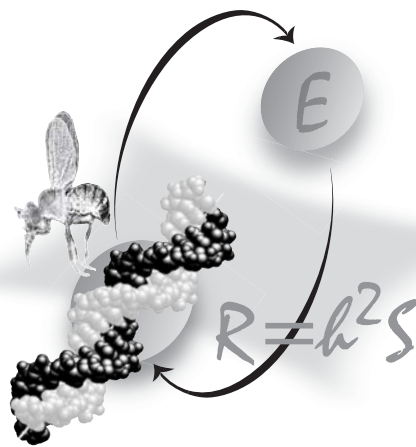
In Chapter 6, Reznick, Rodd, and Nunney present a fascinating review of empirical examples of rapid evolution in natural populations and conclude that fast adaptive changes are not limited to artificially selected organisms. The chapter also examines the sort of ecological and genetic mechanisms that might hamper fast evolution. One important message is that conservation actions that involve environment restoration offer great potential for species recovery to be accelerated by concomitant adaptation.

Genetic variability in life-history traits is necessary for selection to proceed, but selection is also expected to deplete such variability. In Chapter 7, Hughes and Sawby describe the mechanisms that can maintain variability for life-history traits in natural populations. The authors review the empirical evidence, mainly from *Drosophila*, for variability in these traits, and discuss the kinds of mechanisms that could be responsible for the maintenance of variation. Finally, they examine the extent to which these traits are affected by inbreeding depression, and conclude with a review of the evidence for purging inbreeding depression in small populations – a highly controversial topic in conservation biology.

Genetic variation may be depleted or enhanced in the course of adaptations. In Chapter 8, Imasheva and Loeschcke examine the fascinating possibility that external stresses that trigger adaptive responses may also accelerate the production of genetic variation. The chapter offers a review of empirical evidence for such enrichment, and examines the consequences such processes have on the pace and scope of phenotypic evolution.

A review of contemporary rates of evolution (Hendry and Kinnison 1999) concluded that “Claims of rapid microevolution should not necessarily be considered exceptional, and perhaps represent typical rates of microevolution in contemporary populations facing environmental change. [...] Perhaps the greatest contribution that [the study of] evolutionary rates will ultimately make is an awareness of our own role in the present microevolution of life and a cautious consideration of whether populations and species can adapt rapidly enough to forestall the macroevolutionary endpoint of extinction.” What is still required, though, is a quantitative assessment of the consequences of rapid evolutionary change on extinction dynamics and population viability. Part C makes theoretical steps forward in this direction, paving the way for the most warranted experimental insights.

Part C
Genetic and Ecological Bases
of Adaptive Responses



Introduction to Part C

As Part B shows, there is now strong empirical evidence that a rapid adaptive evolution of life-history traits may occur in response to environmental change in the wild. However, very few empirical studies document the consequences such adaptations have for population dynamics and viability.

Continuing the establishment of a theoretical platform for evolutionary conservation biology, begun in Part A for populations with a static genetic composition, Part C introduces models to assess the extent to which contemporary evolutionary change can contribute to, or hamper, population persistence in the face of environmental threats. For this purpose we need to understand how the different components of the evolutionary process affect population viability under different types of environmental change. This agenda involves a series of more specific questions:

- *How does genetic variation influence population viability?* In populations unaffected by immigration, mutation is the ultimate long-term source of all the genetic variation upon which selection may act. The effect of mutation on population viability is complex. While a large mutation rate implies that new favorable mutations become available relatively quickly, most mutations have primarily deleterious effects. In large populations, selection is expected to remove such deleterious mutations efficiently. In small populations, however, random genetic drift is likely to result in the fixation of deleterious mutations. At the same time, the rates at which beneficial mutations are incorporated decrease with population size. The interplay between these effects suggests the existence of a threshold population size below which the net effect of mutation on population viability is negative. Estimation of this threshold and understanding how it depends on the genetic system under consideration is important in conservation.
- *When is adaptive change expected to be fast enough to promote evolutionary rescue from a degrading environment?* In simple models of phenotypic evolution, a population possesses an optimal phenotype that depends on the given environment. As environmental conditions vary, a crucial question is whether the population has any opportunity to track the optimal phenotype. The risk of extinction increases and adaptation may fail to rescue the population if the lag between its phenotypic composition and the optimal phenotype becomes too large. How closely a population can track its evolutionary optimum depends on the available genetic variability, on the strength of selection, and on the type and pace of environmental change that causes the evolutionary optimum to vary.
- *Under which conditions does the selective process promote phenotypes that enhance population viability?* The metaphor of evolutionary optimization is suitable only if the fitness (i.e., the rate of increase from low density) of phenotypes is independent of the population's frequency distribution and the total

density of individuals that express different phenotypes. Only under these conditions does the phenotype that maximizes fitness, given the genetic constraints (e.g., linkage disequilibria), also minimize a population's risk of extinction. In contrast, as has already been pointed out by Haldane (1932), a phenotypic adaptation that confers an advantage to an individual may be detrimental to the population as a whole. Under frequency- and/or density-dependent selection, conditions for population viability are not related to conditions for evolutionary stability, and the actual direction of selection may therefore not always coincide with the one that leads to the most efficient reduction in extinction risk. To understand the interplay between population viability and evolutionary dynamics requires complete knowledge of the environment feedback loop that describes the dependence of selection pressures on the adaptive status of populations.

The following chapters address these three important questions for closed single-species populations. The challenges of how to extend these approaches to spatially structured habitats and to multispecific interactions are tackled in Parts D and E, respectively.

In Chapter 9, Whitlock and Bürger investigate, within the framework of population genetics models, the effects of reduced or declining population sizes on population viability. The authors review the current understanding of a process known as "mutational meltdown" and discuss several of the genetic and demographic features of species that can substantially affect this process. Elaborating on the classic results of Malécot and Kimura concerning the rate of fixation of alleles, the process of fixation of beneficial and deleterious mutations in small or declining populations is explored. The review concludes with several strong qualitative statements on how genetic components of evolutionary processes are likely to influence the extinction risks of populations that experience reductions in their population sizes.

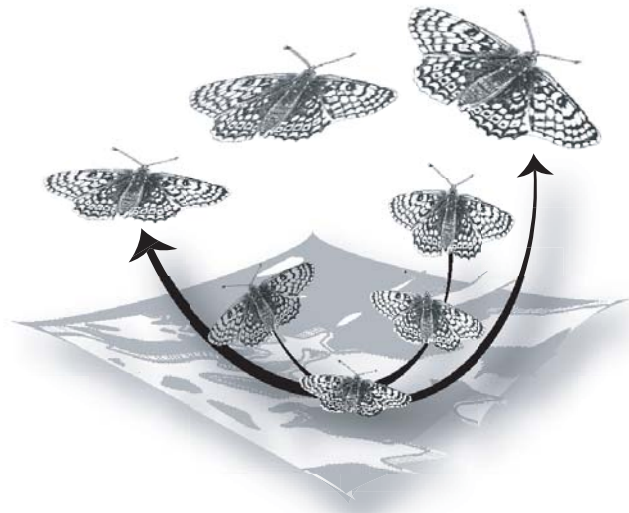
The dynamics of environmental change are considered explicitly in the quantitative genetics models that Bürger and Krall present in Chapter 10. The authors investigate how effective the adaptive response to environmental degradation can be given the amount of genetic variation, the strength of selection, and the pace of environmental change. Three types of environmental variation are envisioned: stationary environmental stochasticity (temporally correlated or not), directional change (like gradual habitat loss or increased pollution), and a single catastrophic change. The outcome is that the speed and predictability of environmental deterioration are critical in determining the effect of adaptation on population viability. The authors discuss the conditions under which evolutionary rescue is expected to occur and the conservation measures that back up such natural processes. The chapter also draws attention to situations in which genetic variability detrimentally affects population persistence.

The dichotomy between rescuing and suicidal adaptive responses to environmental change is probed further in Dieckmann and Ferrière's Chapter 11. In contrast with quantitative genetics models (in which ecological interactions are usually subsumed in a few compound parameters that describe environmental change and

selection), this chapter focuses on the ecological factors that determine the evolutionary responses of threatened populations. After highlighting the importance of eco-evolutionary feedback between populations and their environment, the authors review the theory of adaptive dynamics as a versatile tool for examining the evolutionary consequences of environmental change. The chapter then describes how evolutionary processes directly influence biodiversity. First, the diversity of communities is enhanced through speciation, which is recognized increasingly as being driven by frequency-dependent selection that results from ecological interactions. Second, diversity is reduced evolutionarily through selection-induced extinction, a process during which a species' adaptive dynamics jeopardize its viability. Based on various examples, the chapter delineates the ecological conditions that favor the evolutionary enhancement or reduction of biodiversity.

The material presented in this part has two basic implications for the improvement of conservation strategies. First, conservation planning is most efficient when it is proactive, such as by implementing measures that prevent the decline of populations and thus prevent the harmful genetic effects associated with small population size. Yet, it must be kept in mind that the restoration of abundances or habitat may result in conflicting selection pressures, either by introducing new phenotypes that have undergone different selection histories, or by opening up new habitats that induce different selection pressures. Second, understanding interactions between individuals turns out to be essential for the long-term success of conservation efforts. This applies not only to predicting the short-term fate of populations in a static world (see Chapter 2), but also to assessing the direction and relative strength of selection pressures that act on life-history traits in response to environmental change, and to the eventual impact of such adaptive responses on population viability.

Part D
Spatial Structure



Introduction to Part D

Human population growth and economic activity convert vast natural areas to serve for settlement, agriculture, and forestry, which leads to habitat destruction, habitat degradation, and habitat fragmentation. These forces are among the most potent causes of species decline and biodiversity loss. Habitat destruction contributes to the extinction risk of three-quarters of the threatened mammals of Australasia and the Americas, and of more than half of the world's endangered birds. Populations confronted with the degradation of their local environment (in excess of the tolerance conferred by phenotypic plasticity) can exhibit two basic types of evolutionary response: either they stay put and adapt to the new local environmental conditions, or they adapt in ways that allow individuals to shift their spatial range efficiently in search of better habitats. In Parts B and C, attention is focused on the former type of adaptation. It is evident that to account for spatial heterogeneity in populations and habitats raises formidable empirical and theoretical challenges. Part D reviews the current achievements and challenges in understanding the role of spatial processes in the persistence of natural populations.

Increased fragmentation typically reduces the size of local populations and/or the flow of migrants between them. This enhances extinction risks, because of either a higher sensitivity of the isolated local populations to demographic stochasticity, or a diminished probability of rescue through immigration. Also, increased fragmentation may affect evolutionary processes in many ways, through a variety of conflicting genetic and demographic effects. First, isolation of population fragments increases the rate of inbreeding on the regional scale, which may in turn exacerbate inbreeding depression, while simultaneously relaxing any existing outbreeding depression. Second, recurrent migration into an open population can either foster or hamper evolutionary rescue: incoming dispersers provide an infusion of genetic variation upon which local selection can act, while, at the same time, potentially swamping existing local adaptation. To predict the overall direction and speed of evolutionary change in spatially structured populations thus requires the selection pressures that operate at all the relevant spatial scales to be accounted for. Chapters in this part follow a path toward increasing levels of complexity in the description of spatially structured populations and culminate in a review of empirical studies on the effects of spatial heterogeneity on population viability.

In Chapter 12, Gaggiotti and Couvet examine how the genetic structure of spatially extended populations is shaped by so-called isolation by distance. The chapter describes the effects of several factors that alter spatial differentiation, including the overall rate of local extinction, the intensity of selection (when traits for which differentiation is measured are not selectively neutral), and the local demographic

balance. The authors also discuss the extent to which sink populations can participate in maintaining genetic variation.

The role of sink habitats for evolutionary rescue is probed further in Chapter 13 by Holt and Gomulkiewicz. The authors provide a review of the effect of local adaptation on population persistence in ecological settings for which processes of immigration cannot be neglected. The chapter presents two different modeling frameworks with which to address this issue. Source–sink models are particularly suited to fragmented populations, in which individual patches depend on immigration for persistence. By contrast, focus–periphery models assume continuously distributed populations, in which low-density fringes surround high-density strongholds. It is shown that a fundamental conflict between the supply of variant genetic material and a danger of swamping local adaptation in marginal habitats is central to understanding evolutionary change in both of these frameworks.

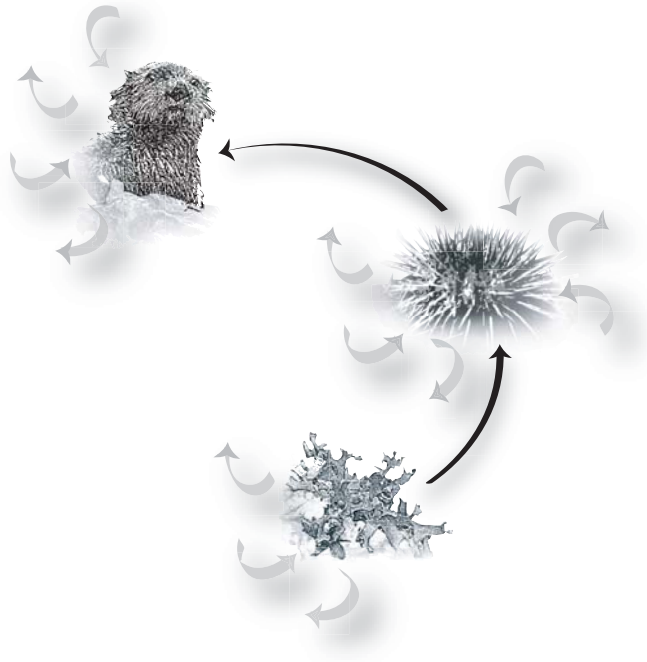
In Chapter 14, Parvinen presents metapopulation models that incorporate both individual parameters and environmental characteristics. These models are applied to predict evolutionary change in metapopulations, with a particular focus on the evolution of dispersal traits. A classification of evolutionary outcomes for different environmental conditions advances our understanding of how adaptive processes that operate on dispersal traits are affected by different types of environmental change, and thus influence metapopulation dynamics and viability. This helps to identify combinations of demographic profiles and types of environmental changes that are more likely to result in evolutionary rescue, evolutionary trapping, or evolutionary suicide.

Chapter 15 reviews empirical evidence for fast evolutionary change in response to landscape fragmentation. Colas, Thomas, and Hanski examine examples of metapopulation adaptation – involving local adaptations, adaptation of migration rates, or interactions of such effects – and assess the consequences of such adaptations for metapopulation viability. Examples involve studies of butterfly and plant populations, for which it is shown that the adaptive response of migration rates depends on the fine details of how the metapopulation fragmentation processes unfolds. Such processes may generate different patterns of correlation between patch size, local demographic dynamics, and rates of local extinction. The authors show that local adaptations can occur quite rapidly in response to habitat change. Empirical material presented in this chapter underlines that the evolution of dispersal traits can result in evolutionary rescue as well as evolutionary trapping or suicide.

The study of spatial effects in the context of evolutionary conservation biology is still in its infancy. Nevertheless, several implications for conservation practitioners have already emerged. First, the theory suggests that the absence of changes in the geographic range of a species must not be misconstrued as evidence for resilience to large-scale environmental deterioration. Second, to prioritize protection actions on the basis of local demographic wealth can easily go awry – “sink” habitats characterized by reproductive deficits may prove critical to maintain genetic

variability on a regional scale. Third, when planning population reinforcement, the addition of individuals with new dispersal phenotypes (resulting, for instance, from artificial selection under conditions of captive breeding, or from importation from other populations evolved under different selection pressures) may have undesired effects on population viability.

Part E
Community Structure



Introduction to Part E

“No man is an island”, and no species of conservation interest exists in isolation from others. Ecosystems define the ecological theater, not only for any evolutionary play, but also for unfolding tales of population decline or rescue. This book therefore ends with a part on the community-level aspects of evolutionary conservation biology. In this way, we establish several additional perspectives to our general question on the ecological, demographic, and genetic conditions that enable or hinder populations to overcome extinction threats through adaptation.

On the ecological side, many density-dependent and frequency-dependent selection pressures emerge from interspecific interactions. It is the dependence of focal populations on the abundance of their resources, preys, predators, mutualistic partners, and competitors that creates complex webs of fitness effects and thus determines the strength and direction of natural selection. An interesting level on which to express such dependences is the flow of nutrients through ecological systems. Measures of nutrient cycling not only serve as indicators of ecosystem functioning, but also provide a convenient platform for resolving the interaction between organisms and their environment and for characterizing the implications of anthropogenic change.

On the demographic side, density regulation in communities is often nonlinear and can result in the coexistence of multiple demographic attractors. Anthropogenic change can, temporarily or permanently, tilt the established balance between regulating forces, and so lead to shifts of or even switches between demographic equilibria. Attractor switches are bound to bring about qualitatively new selection pressures and will often prove to be particularly resilient to conservation efforts directed at their reversal. Such complex dependences explain why ecosystems can react to altered conditions by displaying intricate cascades of ecological and evolutionary responses. Since such responses tend to act on different time scales, their study is critical to understand the expected ultimate impact of detrimental perturbations as well as conservation interventions.

By definition, genetic factors almost always act within species, not within communities. Exceptions can occur through interspecific gene flow. Hybridization is a prime example of such a process and can either exacerbate or ameliorate the perils of extinction experienced by small populations. However, because of the introgression of variant genetic material, hybridization may sometimes rescue only the demographic and ecological, but not the genetic, identity of challenged populations.

To consider issues of conservation and adaptation at the community level necessitates that the primary target of conservation efforts be clarified. Are we most interested in the conservation of life-history patterns, evolutionary lineages, networks of ecological interactions, current equilibrium states of ecosystems, their

diversity, or their ecological function? Different targets mandate different types of interventions.

It is clear that conservation biology, and especially evolutionary conservation biology at the community level, is stretching current empirical and theoretical knowledge beyond its limits. The contributions to this part must therefore be appreciated as attempts to push these limits forward. The analyses presented are, of necessity, more tentative and hypothetical than those offered in the earlier parts of this volume.

In Chapter 16, Bronstein, Dieckmann, and Ferrière point out why a single-species focus may often be too narrow when investigating ecological and evolutionary responses to extinction threats. This is especially obvious for tightly coupled ecological associations, such as those involving mutualists. After a review of the range of anthropogenic threats to which mutualists are exposed today, the authors show how the reduction of an established species or the invasion of a non-native species can have dramatic repercussions for mutualistic partners. Expected responses range from benign resilience through the addition or replacement of mutualistic partners to the linked extinction of populations. The potential for such complex reaction patterns underlines that environmental threats can induce ecological and evolutionary effects that cascade through entire ecological communities.

Chapter 17 describes a framework for conducting analyses of adaptive responses from a whole-ecosystem perspective. Loreau, de Mazancourt, and Holt explain how to extend the “classic” view of environments being external to evolving populations and constant during their adaptation, by incorporating, first, organism–environment feedbacks for the operation of natural selection and, second, sufficient ecological resolution to describe such environments. One level on which to resolve evolutionarily relevant feedbacks is that of nutrient transport: the indirect ecological and evolutionary effects of nutrient cycling are sometimes so strong as to modify or even prevail over the selective pressures that arise from direct ecological interactions. Based on examples from plant–herbivore evolution and extending their findings to coevolution in other exploiter–victim systems, the authors argue that a comprehensive approach to evolutionary conservation biology will have to merge population-level and ecosystem-level perspectives to predict the responses of ecological systems to environmental degradation.

Turning from the ecological to the genetic implications of community-level interactions, Chapter 18 shows how the fate of endangered species can depend on hybridization with sexually compatible individuals of another species. Illustrated by a variety of empirical examples, Levin points out that the contact between an endangered species and its congener can lead to the rapid disappearance of the former. Hybrids may happen to be sterile or the congener itself may possess a higher fitness than the endangered species. From a conservation point of view, intermediate situations, in which hybrid derivatives are stabilized, have to be regarded as mixed successes, because the original genetic identity of the endangered species is sacrificed, an outcome that is most likely for insular species. At the opposite end

of the spectrum, hybridization may also rescue an endangered species, by conferring the required local adaptations or by alleviating the deleterious effects of inbreeding.

Integration of insight at the community level will eventually enable conservation managers to interact, reliably and effectively, with our ecological environment. Years of inventive empirical and theoretical research still separate us from this ultimate goal.

19

Epilogue

Régis Ferrière, Ulf Dieckmann, and Denis Couvet

“Ecologists traditionally have sought to study pristine ecosystems to try to get at the workings of nature without the confounding influences of human activity. But that approach is collapsing in the wake of scientist’s realization that there are no places left on Earth that don’t fall under humanity’s shadow” (Gallagher and Carpenter 1997).

19.1 Introduction

Indeed, the preoccupation of evolutionary ecologists with the pristine reflects a long tradition in western culture and a philosophy that separated humanity and nature (Latour 1999; Gould 2000; Western 2001).

As highlighted by the quote above, currently a large fraction of the world’s ecosystem structure and dynamics is dominated by human effects (Vitousek *et al.* 1997; Palumbi 2001). By the 20th century, domestic production and settlement had visibly transformed nearly half of the world’s land surface, and as we enter the 21st century, human activity is altering biogeochemical cycles and climate on a global scale (Hammond 1998; Western 2001). As a consequence, we must face the prospect of large-scale extinctions in the near future. While this could become comparable in magnitude to some of the catastrophic mass-extinction events of the past, the current biodiversity crisis has a unique feature: humankind as the primary cause. The threat is intrinsic, and because the originator of the trauma has a presumed capacity to mitigate its own deleterious impact, conservation action may be warranted (Novacek and Cleland 2001).

In this closing chapter we argue that evolution in the wake of human-induced environmental change should be the default prediction and should therefore be part of every thorough conservation analysis. By appreciating the potential speed and pervasiveness of anthropogenic evolutionary change, by predicting evolutionary trajectories where possible, and by managing evolutionary threats and responses with foresight, evolutionary conservation biologists can help to reduce or steer our evolutionary impact on the biosphere and thus ameliorate the economic and social costs of altered eco-evolutionary processes.

19.2 Humans as the World’s Greatest Evolutionary Force

The ecological role humans now play in the world and the industrialization of our agriculture, medicine, and landscape mean that humankind has an overwhelming impact on the evolutionary processes that produce, maintain, and sometimes

doom biodiversity (Palumbi 2001). One striking feature of contemporary human activities is that they raise highly diverse combinations of threats to ecosystems, at a probably unprecedented pace. The evolutionary history of life is marked with environmental challenges, in response to which local adaptations, dispersal, and phenotypic plasticity have evolved.

Do historical adaptations to previous environmental challenges help or hinder populations to respond adequately to current, multifaceted environmental changes? An answer to this question is far from obvious. For example, the alternation of glaciation and deglaciation episodes during the past million years caused repeated drastic changes in the distributions of most temperate-zone species (Dynesius and Jansson 2000). While today's loss and deterioration of habitats, which result from urban and agricultural development, might be envisaged as imposing similar challenges for the adaptation of species, the accompanying habitat fragmentation represents a novel impediment to range shifts and gene flow (see Chapters 11 to 14 for theoretical accounts of this issue, and Chapters 12 and 15 for an empirical perspective; see also Davis and Shaw 2001). A wealth of evidence from controlled experiments, artificial selection in plant and animal breeding and analyses of paleontological records underscores that adaptive evolution can proceed on short time scales (Chapters 5 and 6). On the other hand, however, it has also been demonstrated that, sometimes, genetic interdependence among traits (Chapter 7) can retard evolutionary responses to a point at which evolutionary rescue becomes unlikely (Davis and Shaw 2001; Etersson and Shaw 2001).

Human activities also impact greatly on the genetic and specific variation of communities upon which selective forces operate, often with deleterious consequences. The loss of genetic diversity is expected to hamper adaptation and trap populations in evolutionary dead ends (Chapters 1 and 5). By contrast, biotic exchanges, for which humans are effective agents in all regions of the globe, result in injuriously accelerated evolution (Vitousek *et al.* 1996; Mooney and Cleland 2001; Novacek and Cleland 2001; Chapters 17 and 18). Some of the more dramatic examples, such as the introduction of Nile perch into Lake Victoria and the resultant loss of at least 200 endemic cichlid species (Witte *et al.* 1992), offer sobering experimental evidence for the potentially catastrophic effects of invasive species – aggravated in this case by the further alteration of the food web that resulted from the lake's eutrophication in the 1980s (Verschuren *et al.* 2002). Invaders in general can be expected to affect community adaptation in a rapid manner, by matching local selection pressures and by inducing evolutionary responses in native species (Thompson 1998; Huey *et al.* 2000).

Biotechnology introduces more human-mediated mechanisms that generate evolutionary novelty. Some genetically modified organisms result from the insertion of exogenous genes into domestic plants and animals – effectively increasing the rate at which new traits and trait combinations become available, and thus acting akin to macromutations (Chapter 8). When modified traits cross from domestic

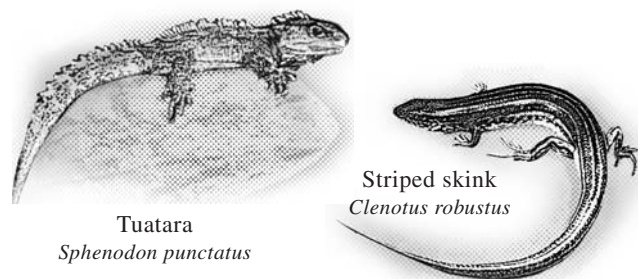
into wild species, they can undergo rapid spread and thus add to the fuel of evolution in natural populations (Abbo and Rubbin 2000; Palumbi 2001). The introgressive hybridization of cultivars and their “wild” ancestors can eventually lead to the evolution of aggressive weeds, the disruption of ecological processes, and the loss of native species (Chapter 18). Macromutations with unknown genetic effects may also arise as a result of increases in background mutagen concentrations, from increases in the ultraviolet B (UVB) mediation of ozone depletion by nitrous oxide and chlorofluorocarbons, and from nuclear waste storage. Such potentially serious threats will require vigilance and careful assessment by evolutionary conservation biologists.

19.3 Evolutionary Conservation in Anthropogenic Landscapes

Evolutionary conservation biology must aim at practical and effective conservation strategies in a world in which human populations and wildlife communities are highly integrated. One of the most acute challenges is raised by changes in land use, ranked as the most intensive driver of terrestrial environmental change in the 21st century (Sala *et al.* 2000; Novacek and Cleland 2001). Projections for the expected impact of land-use change on the planet’s biota are so stark that any conservation efforts must be geared realistically against a continual tide of human activities. There already are two major directions in the effort to constrain the rampant destruction of natural habitats, to which evolutionary conservation biology should contribute:

- To identify “biodiversity hotspots” at the local scale of preserved areas, and to establish management priorities accordingly (Myers *et al.* 2000);
- To define and implement sustainable practices and management programs at the larger scale of highly populated areas.

On which basis should biodiversity hotspots be identified and ranked for intensive study and conservation efforts? Realizing that the current composition and structure of ecosystems represent the “canopy” of a forest of evolutionary trees, evolutionary conservation biology raises the issue of whether and how we should account for evolutionary history in defining such conservation targets. It has been argued that even if we lose 90% of the species on the planet, we may lose only 20% of the phylogenetic diversity (because most genera have several species, and the survival of one might capture most of the genetic variability that exists within the whole clade; Nee and May 1997). So is one tuatara worth 200 species of skinks? The tuatara has been dubbed “the world’s most unique reptile” for being the last surviving species in an order that stretches right back to the Mesozoic (other such “living fossils” include the coelacanth fish, the horseshoe crab, and the native frogs of New Zealand). As emphasized by Loreau *et al.* (Chapter 17), evolutionary conservation biology in natural sanctuaries does value the phylogenetic uniqueness of the tuatara, but perhaps most importantly stresses the value for long-term and global conservation of a web of ecological interactions, such as those in which highly diverse communities of skinks are embedded (Woodruff 2001). As



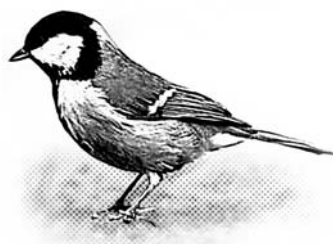
far as priorities are concerned, two lines of action should therefore be pursued and balanced under the constraints of limited financial and technical resources:

- Species-specific conservation effort, advocated not only as a matter of esthetics or biophilia, but most importantly whenever such species are critical to maintaining the basic ecological relationships and evolutionary processes within a community (Chapters 1–4 and 16–18);
- Conservation of groups of less charismatic and often poorly known organisms that may perform apparently redundant roles in an ecosystem, so-called “functional groups”, to preserve the way that nature evolved to hedge its bets in the face of an uncertain future (Western 2001; Chapter 17).

Species-specific management in biodiversity hotspots raises several important issues for the genetic arm of evolutionary conservation biology (Hedrick 2001):

- *Detecting genetic erosion.* Genetic erosion, which is both a symptom and a cause of endangerment of small populations, can become a dominant concern in isolated wildlife reserves. The very detection of genetic erosion in small populations is problematic and requires integrated surveys of demography and genetics, and their interaction.
- *Linking inbreeding and adaptations.* As a consequence of genetic erosion, inbreeding is expected to impair adaptation primarily (Chapter 5); but, although the deleterious impact of inbreeding on population demography has been demonstrated clearly (Nieminen *et al.* 2001), the long-term consequences on and through the eco-evolutionary feedback loop remain poorly understood (Chapters 3 and 5). For example, habitat fragmentation has a direct effect on local levels of inbreeding, which may in turn alter selective pressures that act on dispersal, and thereby further modify rates of inbreeding (Chapter 12; Perrin and Mazalov 2000; Ebert *et al.* 2002).
- *Managing gene flow in the face of local maladaptation.* A fragmented habitat is also the substrate of local maladaptation (Chapters 13 and 15), which can be amplified by regional environmental change (as demonstrated in a demographic and physiological study of great tits, *Parus major*, by Thomas *et al.* 2001b). Thus, gene flow in fragmented landscapes subject to global change is not necessarily beneficial to population persistence and adaptability, and could be an important target of active management (Templeton *et al.* 2001).

Even when the priorities listed above are adequately fulfilled, the global network of biodiversity hotspots and other protected areas is likely to remain too small to avert a rash of extinctions. Overharvesting, resource depletion, and the growing ripples of by-products of human activities result in ecological homogenization, simplification, and dysfunction in human-dominated landscapes (Western 2001). The 1992 Rio Convention on Biological Diversity and a plethora of national



Great tit
Parus major

biodiversity strategies testify to the consensus about the environmental threats of overconsumption and the need for sustainable practices at a global scale (Hempel 1996). Even those biodiversity hotspots that do or should receive the highest degree of official protection are highly vulnerable to threats from outside the system, including climate change, pollution, nitrogen deposition, and biological invasions (Dobson 1996). On the other hand, even in human-dominated landscapes not all species are losing ground to us. Some live with us and

prosper – in German, these are known as *Kulturfolger*, culture followers. It is part of the research agenda of evolutionary conservation biologists to help discover how to share anthropogenic habitats with wild species to maintain and promote their diversity (Rosenzweig 2001, 2003). A growing number of studies pave the way in this respect. For example, “countryside biogeography” shows that some styles of land use are already compatible with the ecological and evolutionary needs of many species (Greenberg *et al.* 1997; Daily *et al.* 2001). “Reconciliation ecology” aims to combine controlled experiments and the analyses of large-scale ecological patterns to find how to preserve biodiversity in habitats that host high levels of human activity (Rosenzweig 2003).

To maintain and restore the evolutionary potential of ecosystems that persist in areas heavily impacted by human activities, evolutionary conservation biologists should seek ways to harness the forces of evolution to their advantage. Rarely has this been attempted so far (Ewald 1994, p. 215; Palumbi 2000), although encouraging examples come from virulence and pest management, on the basis of a fruitful dialogue between theory and practice (Dieckmann *et al.* 2002). A striking example is provided by the use of chemical control in which resistance includes a severe metabolic cost, and so makes resistant organisms less fit when the chemicals are removed (McKenzie 1996; Palumbi 2001). Methods currently used to achieve successful virulence management impact all three factors that drive evolutionary change: variation in fitness-related traits (e.g., in human immunodeficiency virus 1 by limiting the appearance of resistance mutations; Wainberg *et al.* 1996), directional selection (e.g., by varying the choice of antibiotics over time, Lipsitch *et al.* 2000), and heritability of fitness-related traits (e.g., by artificially increasing the proportion of individuals without resistance alleles; Mallet and Porter 1992). However, seldom have all three evolutionary factors been manipulated in the same

system, and seldom has the engineering of the evolutionary process been attempted in a systematic fashion. In this vein, recent experimental work on selection at the level of the ecosystem (Swenson *et al.* 2000) opens interesting new directions of research, which may eventually lead to innovative practices in restoration ecology.

19.4 Culture's Role in the Eco-evolutionary Feedback Loop

The future of biodiversity will be shaped by our awareness of the global threats and our willingness to take suitable action. Our ability to do so is currently hampered by several factors, including the poor state of our biospheric and geospheric knowledge, the ignorance of human impact, and the lack of guidelines for sustainability. The paucity of good policies and the lack of incentives to adopt practices in daily life that would be compatible with sustainability are related to the presently still weak connection between biodiversity and human welfare (Western 2001). Put in a pointed manner, our systematic alteration of eco-evolutionary processes is indeed hard to fault based on our own evolutionary success to date.

Anthropogenic challenges to biodiversity take on a different complexion, however, when the growing problems of overconsumption, ecological and evolutionary side effects, and rising costs are considered (Western 2001). The cost of growing human consumption can be measured in falling yields, mounting pollution, and rising production costs (Botsford *et al.* 1997; Daily 1997; Myers and Kent 1998). Nearly half of the world's marine fish stocks are fully exploited and another quarter are overexploited (Botsford *et al.* 1997; FAO 1999), and a three-fold increase in the amount of pesticides used in agriculture is expected by 2050 (Tilman and Lehman 2001). Overall, the real costs of food, resource, energy, and materials production are disguised by subsidies and an oversight of negative externalities (Myers and Kent 1998).

The costs of the side effects of anthropogenic environmental change are more immediately visible, as they often have a direct bearing on human health. Ozone thinning and increased UV levels, toxic pollutants, endocrine-mimicking substances, immune suppression (Chivian 1997), and the emergence and spread of resistant diseases, including HIV, Ebola, and Marburg (Daszak *et al.* 2000), all cause grave concerns and mandate increasing health expenditures. Not even a money scale is required to assess the magnitude of the tragedy of "environmental refugees" – millions of people who can no longer gain a secure livelihood in their homelands because of drought, soil erosion, desertification, deforestation, and other human-induced environmental problems (Myers 2002). Thus, eco-evolutionary responses of ecosystems to human activities result in a global reduction of ecosystem services to humanity (Daily 1997; Ehrlich 2001). This occurs through the loss of species, genetic diversity, and ecological interactions (as with pollination; Chapter 16; Pimentel *et al.* 1997), through rising costs, and even through our sheer inability to access the remaining ecosystem services and avoid the side effects of our impact. This adds to Odum's (1971), McDonnell and Pickett's (1993), and O'Neill and Kahn's (2000) views that both ecology

and socioeconomics, because of their limited paradigms, have artificially isolated *homo oeconomicus* from the ecosystems in which it functions.

That large-scale changes in ecosystem function can lead to dramatic societal changes – including population dislocations, urban abandonment, and state collapse (a process that, at a conceptual level, is perhaps akin to evolutionary suicide) – has been documented in several outstanding case studies drawn from New



Maya site of Tikal
(ca. 800 AD)

and Old World civilizations, including the classic Maya empire of Mesoamerica and the Akkadian empire of Mesopotamia (Weiss *et al.* 1993; Thompson *et al.* 1994; Hodell *et al.* 1995; Gill 2000; deMenocal 2001; Weiss and Bradley 2001). These examples show that, challenged by the unprecedented environmental stress of prolonged drought, whole empires collapsed and their people were diminished to much lower subsistence levels, whereas in other cases, populations migrated and adapted to new subsistence modes. In all these cases, the observed societal response reflects an interaction between human cultural elements (socioeconomic, political, and secular stresses) and persistent century-long shifts in climate. What makes these ancient events relevant to modern

times is that they simultaneously document both the resilience and vulnerability of large, complex civilizations to ecosystem variability. Complex societies are neither powerless pawns nor infinitely plastic and adaptive to environmental change (deMenocal 2001).

The vast majority of humanity may currently see little reason to value most of biodiversity. However, the hazards, losses, and costs related to ecosystem degradation eventually impact our very survival, production, and reproduction – in short, our fitness (Western 2001); therefore, these processes can be expected to generate selective pressures on the evolution of our own culture and value systems, including the ethical obligation to preserve biodiversity (Ehrlich 2001). Thus, humans are not isolated from the eco-evolutionary feedback loop that has shaped the past and will continue to shape the future of biodiversity (Feldman and Laland 1996). The economically dominated cultural background against which the value of biodiversity is assessed will evolve under the selective pressures that economic activities generate themselves. Ethics can evolve at rates that easily surpass those of genetic evolution – for example, our circle of “caring” has widened rapidly, through the attribution of rights first to all human beings (as opposed to only some group of kin, color, or cast), then to domestic animals, then to charismatic animals, and eventually to all organisms and ecosystems (Ehrlich 2000). Evolutionary conservation biologists must contribute to and foster the evolution of new ethics that deal with various aspects of the human predicament, both by forging new paradigms in the form of sustainable alternatives, and by strengthening selective pressures

through public education and interacting vigorously with researchers from other disciplines in the biological, earth, and atmospheric sciences, as well as in other walks of life (Woodruff 2001).

As principles lie at the basis of conservation and the development of operational policies, we should aim at the development of robust, yet relatively simple, models of interacting ecosystems and societies. Such models should help address the central question of identifying critical structures and thresholds for species, processes, and areas in terms of the sustainability of ecosystem services (Holling 1992; Costanza *et al.* 1997; Gatto and De Leo 2000). The integration of ecological and economic dynamics in simple models has been initiated in fisheries management (e.g., Walters 1986). Attempts have already been made to extend such a “systems analysis” approach to incorporate cultural variables that quantify the human valuation of some ecosystem services (Casagrandi and Rinaldi 2002). The perspective of adding an evolutionary dimension to such models – including important notions such as a geographic mosaic of coevolutionary processes (Thompson 1994), and evolutionary constraints that arise from a trade-off between the welfare of current and future generations (Costanza 1991) – opens exciting new directions for future research.

19.5 Concluding Comments

Until the past decade or so, despite large-scale questions and perspectives, conservation biology provided hardly more than reactive short-term and small-scale solutions to environmental threats (Western 2001). The necessity for a shift from saving things, the products of evolution, to saving the underlying process, evolution itself, has already been advocated strongly (e.g., Mace *et al.* 1998; Bowen 1999; Templeton *et al.* 2001; Woodruff 2001). Within a broadening scope and increasing depth of conservation efforts, evolutionary conservation biology has a natural and inevitable role – paving the way to go beyond the separation of humanity and nature that has been underlying conservation biology so far, ultimately to embrace the processes that shape human-dominated ecosystems as well as those that direct the evolution of human culture and ethical systems.

Evolutionary conservation biology is not in competition with the established fields of conservation research, and cannot progress on its own. Many of the individual points raised in this book have been made separately before, and a need for methodological pluralism remains. Evolutionary conservation biology should add a unifying perspective and an invigorated thrust. It is expected that disciplinary boundaries will be abandoned naturally when conservation researchers start to utilize all the tools available to tackle fundamental issues, including:

- Establishing closer links between individual behavior and population dynamics;
- Investigating the joint effects of phenotypic plasticity, local adaptation, and the evolution of dispersal on the viability of a population subject to environmental change;
- Analyzing the combined effects of different temporal and spatial scales of environmental change on the adaptive responses of multiple traits;

- Examining the role of frequency-dependent selection in the wild, and designing controlled experiments to evaluate its impact on population viability;
- Better understanding the ecological and genetic processes that can limit the speed of population responses to environmental threats – and likewise, those that can accelerate the evolution of undesirable adaptations that could prove deleterious to the population;
- Improving our grasp of the ecological and genetic mechanisms that underlie processes and patterns of community diversification, via endogenous speciation or exogenous invasions;
- Extending the empirical and theoretical scope of population genetics to the study of community genetics.

Ignoring evolutionary mechanisms and dynamics renders all our conservation efforts (and sometimes successes) as temporary only. To develop principles of sustainability that avoid evolutionary sclerosis or deleterious evolutionary acceleration may be the most important task ahead for ecologists (Western 2001). The ultimate test of evolutionary biology as a science will not be whether it solves the riddles of the past, but rather whether it enables us to manage the biosphere's future. In this sense, by turning around and facing forward in time, evolutionary biologists become conservation scientists (Woodruff 2001). In such a setting, the traditional dichotomy between one group doing fundamental research and the other doing applied work can be severely counterproductive. Conservation biology provides some of the most difficult problems ever tackled by evolutionary biology. If our greatest achievement in the past century was the collective understanding of what evolution meant to our own survival, the challenge of the present century is to develop a more predictive evolutionary conservation biology that can manage human-dominated ecosystems before it is too late to shape our environmental future in a desirable way.