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Epilogue

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“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; Etterson 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

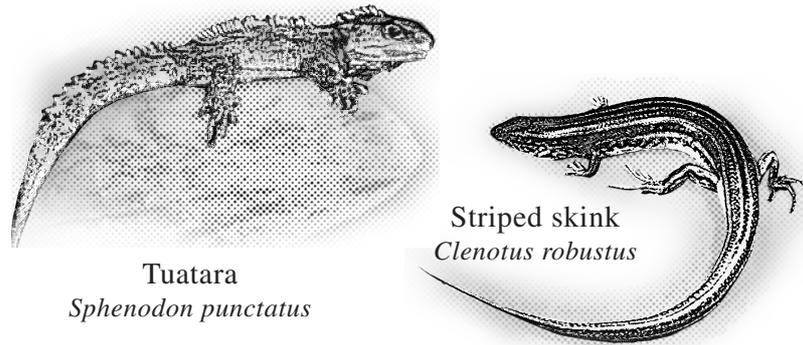
into wild species, they can undergo rapid spread and thus add to the fuel of evolution in natural populations (Abbo and Rubbin 2000; Palumbi 2001). The introgressive hybridization of cultivars and their “wild” ancestors can eventually lead to the evolution of aggressive weeds, the disruption of ecological 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



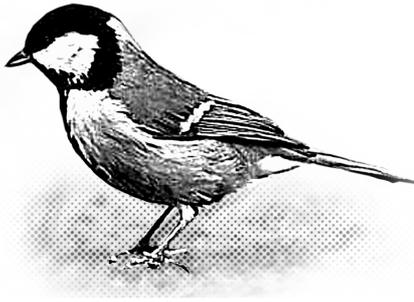
far as priorities are concerned, two lines of action should therefore be pursued and balanced under the constraints of limited financial and technical resources:

- 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.

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