PREFACE TO THE SPECIAL ISSUE
Evolutionary change in human-altered environments

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The average annual rate of loss for animal and plant populations and their habitats is estimated to be 1% (Balmford *et al.* 2003), with two-thirds of the world's terrestrial land area now devoted directly to supporting human populations, either through agriculture, fisheries, urbanization, or infrastructure (Millenium Ecosystem Assessment 2005). As a consequence of these impacts, we are witnessing a global, but unplanned, evolutionary experiment with the biotic diversity of the planet. Growing empirical evidence indicates that human-induced evolutionary changes impact every corner of the globe. Such changes are occurring rapidly, even at the level of a human lifespan, bear huge economical costs and pose serious threats to both humans and the biodiversity of the planet. Evolutionary phenomena, such as industrial melanism in the peppered moth (*Biston betularia*) — a classical example of rapid evolution driven by humans (Kettlewell 1973) once considered atypical — are now becoming commonplace.

There have been several recent efforts to summarize these effects. Palumbi (2001) revived interest in the study of human-driven evolutionary change by synthesizing evidence for the consequences of antibiotic and antiviral use, insecticide applications, and herbicide bioengineering on the evolution of short-lived organisms such as weedy plants and microbes. In a recent colloquium, Myers *et al.* (2000) helped to focus attention on the future of evolution and this emerging biotic crisis. Numerous other studies are documenting human-driven 'contemporary evolution' (*sensu* Hendry & Kinnison 1999, reviewed in Stockwell *et al.* 2003). Still earlier studies demonstrated that exposures to heavy metals led to evolutionary change of resistance in plants living in contaminated sites (Wu & Kruckeberg 1985), and that the extinction of competitors and subsequent shifts in feeding habits could cause evolutionary changes of beak morphology in birds (Smith *et al.* 1995). Studies have shown how global warming is having evolutionary effects on natural populations (Parmesan 2006), such as a genetic

shift in photoperiodic response (Bradshaw & Holzapfel 2001). Others document shifts in the genetic basis of growth potential in exploited fishes as a result of size-selective fishing (Conover & Munch 2002) and how invasive species can rapidly and repeatedly adapt to newly colonized environments (Lee 1999) or potentially drive extinction of native species by hybridization (Rhymer & Simberloff 1996).

There is little doubt that human activities are altering the evolutionary processes on which all life depends. These changes threaten our natural heritage and economic well-being by eliminating options to adapt to future environments. Yet, evolution has been given low priority in most resource management programs, academic as well as applied (Myers *et al.* 2000). Reasons for this include the mistaken view that species are relatively fixed entities that remain unchanged over conservation-relevant periods of time. While resource managers have largely focused on threats causing population declines and extinction, little attention is being paid to the consequences of changing the evolutionary trajectories of species that persist in human-altered environments. Admittedly, evolutionary biologists share the blame for neglecting to bring these issues to the attention of resource managers and policy makers. Indeed, there are few effective bridges between academia, where evolutionary research is conducted, and institutions responsible for conservation decision-making. While assessing and predicting how humans are altering evolution and its effects represents a tremendous scientific challenge, the enormity of the threats posed by humans to the planet requires that research findings be integrated into conservation planning and public policy as soon as possible. In particular, it is essential that we build a better information bridge between academic researchers and conservation practitioners if we are to have any hope of understating and mitigating the deleterious effects of human activities on evolutionary processes or, alternatively, turning the potential of species to adapt to a changing world to the benefit of improved conservation practices.

In response to this developing crisis, the Institute of the Environment at the University of California, Los Angeles (UCLA), hosted a summit in February 2007 entitled 'Evolutionary Change in Human-altered Environments:

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An International Summit to Translate Science into Policy'. The meeting was co-organized by Thomas Smith (UCLA, USA) and Louis Bernatchez (Université Laval, Québec, Canada), and convened evolutionary biologists, conservation practitioners, and policy makers to synthesize current knowledge and begin to develop plans for incorporating such knowledge into conservation and management policy (see http://www.ioe.ucla.edu/CTR/ioesymposium.html). This included talks by more than 40 prominent evolutionary biologists, and numerous presentations by leading conservation policy makers and discussions. The presentations were organized around three main themes: (i) habitat disturbance and climate change, (ii) exploitation and captive breeding, and (iii) invasive species and pathogens. Each was followed by a working session comprised of scientists and policy makers to discuss how research results could be used to inform and drive policy. The final day of the summit was devoted to reports from the working sessions and synthesis, and was chaired by leading policy and conservation decision makers with the goal of identifying ways that evolutionary science can be integrated into conservation policy, planning practices, and management. In addition, more than 100 posters were presented by participants from more than 20 countries (http://www.ioe.ucla.edu/CTR/pubsymposium-postersandgrants.html). Finally, the summit was followed by a half-day session with key scientists and policy makers. The goal of this session was to develop an outline, assignments, and a timeline for writing a review of the discussed threats, challenges, and potential solutions of the findings on the evolutionary impacts of human activities, in both an international and a California-specific context. A future publication on these aspects will be forthcoming.

This Special Issue of *Molecular Ecology* comprises all but three papers that were presented at the summit. The volume begins with an overview of the issues by Mace & Purvis (2008), who point out the critical importance of evolutionary processes for the long-term persistence of natural populations, as well as how the majority of conservation policy and practices still focus only on pattern-based analyses. They identify a number of steps for bridging gaps, including setting goals to implement conservation management and improved methods for integrating the work of scientists and policy makers. In the second keynote address (not published here), Loren Rieseberg reviewed the theory pertaining to the limitations imposed by natural selection to speed of adaptation. Using key empirical examples from his own work on sunflowers, as well as from fruit flies and great apes, he showed that these organisms were at the upper limit of theoretical rate of adaptation. Rieseberg provocatively closed his talk by concluding that acceleration in the rate of environmental change, due to such influences as global warming, will likely exceed the rate at which many populations can respond evolutionarily without going extinct.

The first section of the Special Issue, focused on habitat degradation and climate change, begins by asking whether or not phenotypic changes caused by humans are greater than those associated with more 'natural' contexts. In a meta-analysis, Hendry *et al.* (2008) find that rates of phenotypic change are greater in anthropogenic contexts than in natural ones, underlining how humans are an important agent driving phenotypic change in contemporary populations. However, their analyses also suggest a particularly important contribution from phenotypic plasticity. Seehausen *et al.* (2008) use both theory and empirical data to show how the loss of environmental heterogeneity may cause a rapid loss of biodiversity by increasing genetic admixture via hybridization, effectively reversing speciation. Since heterogeneity of natural environments is rapidly deteriorating in most biomes, Seehausen and colleagues strongly recommend the integration of these concepts into conservation biology. The dynamics of biodiversity on isolated islands and the impacts of humans are explored by Gillespie *et al.* (2008). A review of island biota and isolated continental ones show that high local endemism will likely not fare well in the face of prolonged disturbance and will be swamped by non-natives, which, due to random processes and higher propagule pressure, tend to move more readily into available habitats. Evolutionary consequences of human disturbance are further explored by Smith *et al.* (2008) in an African rainforest bird species, where they find significant differences in morphology, colouration, vocalizations, and genetic variation between those populations living in pristine rainforest and human-altered secondary forest. With an estimated 30% of the world's rainforest in various stages of pasture abandonment or secondary forest growth, understanding the evolutionary impacts of humans on rainforest species is critical, but seldom considered by conservation decision makers. The study by Slabbekoorn & Ripmeester (2008) further expands on this theme, showing how anthropogenic low-pitched noise associated with urban habitats may have fitness consequences for birds, and consequently select for vocalization differences from that of forest dwellers. The authors conclude by providing an overview of how these human impacts may be mitigated.

Perhaps the best studied group of organisms for documenting evolutionary change in human-altered habitats is fish (Conover *et al.* 2006). Waples *et al.* 2008 show how the expansion of hydropower and dams along the Columbia river has had a profound effect on the evolutionary trajectories of Pacific salmon by selecting for traits more favourable to reservoirs and fish ladders — but dramatically increasing the cost of migration, which may select for nonmigratory life history. Waples and colleagues argue that adaptation of salmon to their modified environment will need to be considered when returning the altered habitats to their pre-modified state. Reznick has pioneered research on fast evolution by showing how life-history traits in Trinidadian

guppies can rapidly evolve when introduced to a new ecological setting. Here, Reznick *et al*. (2008) use results from research on guppies living in a natural network of Trinidadian streams under both high and low predation pressures as an experimental system to document how fast evolution can occur and the fine spatial scales over which adaptation is possible. They argue that predator reintroductions can be destabilizing to populations living without predators for as little as 50–100 years.

One of the earliest examples of rapid evolution driven by anthropogenic pollution is the adaptation of plants living in soils contaminated by heavy metals. Here, Pauwels *et al*. (2008) explore the question of how plants can be used to advance mitigation and restoration via phytoremediation The authors show how naturally occurring metallophyte species can be efficiently used to improve phytoremediation, an ecologically attractive and cost-effective technology that uses plants to reclaim soils polluted with heavy metals.

A central theme emerging from the summit was the importance of mapping evolutionary process. Conservation practitioners and policy makers must ultimately draw geographical boundaries in prioritizing regions for conservation. Davis *et al*. (2008) and Grivet *et al*. (2008), respectively, explore approaches to conserving the evolutionary potential of California's animals and plants (oaks) by focusing on evolutionary 'hotspots'. By combining estimates of range size and divergence times, Davis and colleagues mapped hotspots reflecting major processes shaping spatial patterns of neo-endemism for mammals of California. This study is one the first showing that mapping multispecies evolutionary hotspots can be achieved. Similarly, Grivet *et al*. (2008) cleverly used GIS tools to locate regions of high genetic diversity in oaks. This allowed the identification of distinct evolutionary histories that should be prioritized for conservation. With hundreds of millions of dollars spent each year to protect California's environment, a commitment that was renewed in November 2006 with the passage of a multibillion dollar bond act to ensure environmental quality, California is poised to take the lead in these cutting-edge conservation efforts.

Climate change represents one of the strongest contemporary anthropogenic agents likely to drive evolutionary processes. Four studies in the volume explore this critical issue. Bradshaw & Holzapfel (2008) review cases of genetic responses to recent, rapid climate change. While only a handful of studies have rigorously addressed this important issue, their analyses support a stronger evolutionary effect of climate change (particularly global warming) on genetic shift in photoperiodic response than on shifts in thermal optima or thermal tolerance. Clearly, much more research should be devoted towards exploring the role of photoperiodism in genetic responses to climate change. Giennapp *et al*. (2008) review empirical evidence for microevolutionary responses to climate change in longitudinal studies and find evidence for evolutionary adaptation conspicuously scarce. In agreement with Hendry *et al*. (2008), a major conclusion of this review is that many alleged adaptations could be environmentally-induced plastic responses rather than microevolutionary ones. The paucity of empirical studies distinguishing genetic and environmental phenotypic responses to climate change clearly emphasizes the need for further investigation in this research arena. Quite appropriately in the next study, Garant *et al*. (2008) examine evidence for change in the genetic architecture (heritability and the genetic variance-covariance (G) matrix) underlying the most important reproductive traits in the Eurasian great tits (*Parus major*) over a 40-year period based on an impressive pedigree of over 60 000 individuals. Results suggest that substantial changes in temperature and mean laying date were not accompanied by any detectable change in the genetic architecture of the reproductive traits. Finally, Zakharov & Hellmann (2008) investigated differentiation within the geographical range of two North American butterfly species along a broad latitudinal gradient and find evidence for divergence of peripheral populations, suggesting the potential for genetic distinctiveness at the leading edge of climate change and, therefore, potential differential evolutionary responses in the face of global warming.

The next section of the Special Issue deals with evolutionary responses to exploitation and captive breeding. In the lead study, Fenberg & Roy (2008) examine both aquatic and terrestrial habitats to illustrate some of the evolutionary consequences of size-selective harvesting and why urgent management policies are needed to mitigate the impacts. In the following study, Coltman (2008) critically reviews uses of molecular genetic approaches to examine the effect of selective harvesting on wildlife. He shows how molecular markers may be used to assess the genetic structure of wildlife populations as well as basic quantitative genetics parameters. This has the potential to help predict genetic impacts by identifying evolutionarily meaningful management units, as well as evolutionary responses to selective harvesting. His results also underline why effective wildlife management practices need to consider more than just the impact of harvesting on population dynamics. Next, Jackson *et al*. (2008) investigate the evolutionary impact of exploitation in a temporal perspective by examining how humans have exploited whale populations through time. To achieve this, they reconstructed the demographic history of exploited populations of southern right whales using mitochondrial DNA (mtDNA) in order to estimate minimum abundance (N_{min}), and integrate this evolutionary parameter into population dynamics models. Their analyses indicate that commercial and illegal whaling was accompanied by a substantial reduction of mtDNA haplotype richness. Yet, high levels of remnant sequence diversity suggests that pre-exploitation whale abundance was likely larger than predicted by catch records used by managers to evaluate

impacts of harvesting. Results point to a need to better integrate evolutionary processes into population dynamic models of threatened species.

Two important concerns regarding reintroduction of species to the wild is the degree to which genetic variation has been preserved, and the maintenance of specific behavioural mechanisms that enhance the preservation of genetic diversity and reduce inbreeding. Vonholdt *et al.* (2008) examine these issues in reintroduced populations of grey wolf in Yellowstone National Park. They show levels of genetic variation similar to that of a population managed for high variation and low inbreeding, and greater than that expected for random breeding. Nevertheless, their projections suggest significant inbreeding depression will occur without connectivity and migratory exchange with other populations. Though most studies in the volume examine anthropogenic effects on wild populations, Taberlet *et al.* (2008) take a novel twist and explore the evolutionary potential of domesticated stock to discover that many breeds now suffer from inbreeding and small effective populations sizes, thus endangering the genetic resources of cattle, sheep, and goats. While inbreeding is clearly a threat to the genetic resources of domesticated animals, Randi (2008) shows how domesticated animals themselves maybe be a threat to the genetic integrity of wild populations. He examines the spread of free-ranging domestic or feral dogs, cats, and pigs, as well as massive releases of captive-reared game, including waterfowl, on altering native species of Europe through introgressive hybridization. Quite clearly, Randi's results call for implementation of conservation plans to preserve the integrity of the gene pools of wild populations in the face of the potential for genetic admixture with domestic congeners. Hutchings & Fraser (2008) explore these same phenomena in fishes by showing how fisheries and farming-induced evolution may influence a multitude of factors, such as the reversibility of genetic responses and levels of plasticity and genetic variability, and suggest management initiatives to mitigate these effects. Thus, a simple message that Hutchings and Fraser are sending to the fishing industry, resource managers, and decision makers is to 'keep the big ones around'. Their most crucial recommendation is the critical need for more research that addresses short- and long-term demographic consequences of harvesting and farm escapement to persistence and productivity of wild populations. The evolutionary effects of introgressive hybridization of domestic fish stocks with wild populations is further examined by Roberge *et al.* (2008), who analyse gene expression profiles by means of microarray experiments in Atlantic salmon to address the following questions: (i) Are hybrids always intermediate? (ii) Will quantitative traits always dilute through repeated backcrossing? Contrary to expectations, they found evidence for a predominance of nonadditive gene interactions in crosses between farmed and wild salmon. These results suggest that interbreeding

of farmed and wild salmon could significantly modify the control of gene expression in natural populations exposed to high migration from fish farms, with serious deleterious fitness consequences. These studies underline the urgent need to reduce the number of escaped farmed salmon in the wild.

One of the few areas where human evolutionary effects have been examined for some time has been in captive breeding and propagation programs. Importantly, Frankham *et al.* (2008) show how genetic adaptation to captivity may strongly influence the success of reintroducing species that have been in captivity for many generations. Although he and others have repeatedly emphasized this issue in the past (see Frankham *et al.* 2002), Frankham and colleagues reiterate the importance for conservation resources managers to give much greater priority and attention to the process of genetic adaptation to captivity towards improving the success of reintroduction efforts. This section closes with two studies that expand on the theme of captive breeding and reintroduction by focusing on two other important processes: the avoidance of inbreeding depression by purging deleterious recessive alleles (Leberg & Firmin 2008) and the reduction of inbreeding depression through outbred crosses (Hedrick & Fredrickson 2008). The former shows how there is considerable uncertainty regarding the success of any single purging event in eliminating inbreeding depression in small populations, as well as the importance of avoiding small population sizes whenever possible. The latter, which concern captive breeding and the reintroduction of Mexican and red wolves, shows how merging genetically distinct and partially inbred wolf lineages has resulted in increased fitness of cross-lineage wolves in both the captive and reintroduced populations. Together, these three studies, by Frankham (2008), Leberg & Firmin (2008), and Hedrick & Fredrickson (2008) remind us that detrimental genetic processes, such as inbreeding depression and adaptation to captivity, remain important challenges and that the science of captive propagation and reintroduction continues to develop.

The final portion of the Special Issue is devoted to invasive species and pathogens. Suarez & Tsutsui (2008) begin with an examination of the evolutionary causes and consequences of biological invasions in a variety of taxa. They look at the specific factors that lend to successful establishment and spread of introduced species and show why preventing secondary introductions of previously established species should be prevented. In the next study, Carroll (2008) explores the question of how conservation scientists may manipulate adaptation to achieve conservation goals by examining soapberry bugs on nonindigenous plants. He demonstrates both diversifying and homogenizing evolution with adaptations differing among traits and populations and as a function of the host on which they develop. Carroll (2008) also points out that adaptation of invasive species to a new

habitat does not always imply evolutionary change per se but environmentally-induced plastic responses as well. Continuing the theme, Barrett *et al.* (2008) examine how plant invasions may provide natural laboratories for investigating microevolution during contemporary timescales. Focusing on how reproductive modes influence the genetic consequences of long-distance colonization and plant adaptive responses, they show how evolutionary modifications to reproductive systems may promote the colonizing ability of invading populations and identify reproductive timing as a main target of selection during expansion. In another study of invasive plants, Kane & Rieseberg (2008) report on weedy species of the common sunflower (*Helianthus annuus*). Such agricultural weeds are ubiquitous, and pose major economic threats, but little is known about how frequently such weeds evolve from their wild ancestors or the genes involved. While there was no evidence for a reduction in variation across the genome, they found that a portion of the genome appeared to be under selection and involved in adaptation of weedy sunflowers. Adding yet another level of complexity to these results, they also they found that weedy populations are more closely related to nearby wild populations than to each other, suggesting that weediness likely evolved multiple times. In the next study, Benkman *et al.* (2008) examine how species introductions may alter the evolutionary trajectories of other community members. They discuss the various biotic and abiotic factors most likely to render local introductions successful, emphasizing both the loss of defence of local community members as well as the strength of 'interactivness' of the introduced species. Using the introduction of tree squirrels into formerly squirrel-less areas as an eloquent example, Benkman and colleagues show how such an introduction led to the extinction of a unique form of crossbill which had coevolved with indigenous conifers.

While the number of empirical studies documenting cases of 'contemporary evolution' is rapidly accumulating, very few have tested for the actual 'evolutionary success' of populations that are adapting to a new environment. Here, Kinnison *et al.* (2008) explore rapid evolution of overall fitness in Chinook salmon that invaded New Zealand, and experimentally tease apart its effect from that of habitat quality. They find that variation in habitat quality within the newly colonized range had the greatest influence on broad geographical patterns of 'vital rates'. Yet, rapid evolution of fitness far exceeded the fitness effects of individual traits and doubled vital rates, increasing invasiveness. The findings of Kinnison and colleagues indicate that measuring emergent fitness may be a much more powerful means than just documenting trait change to assess the ecological consequences of contemporary evolution following an invasion.

As for most plants and animals, invasive species are generally composed of highly differentiated populations or sibling species distributed across their native ranges. These are often locally adapted to distinct ecological settings, which may influence the probability that they become invasive. Looking at the roots of invaders, Winkler *et al.* (2008) analyse patterns of distribution as well as the evolutionary and demographic histories of populations within the native range of a copepod species complex. This reveals a high degree of heterogeneity in genetic structure and habitat types, and a bias in the sources of invasive populations. While a more detailed investigation on physiological differences among native populations and on the selection regime within their native habitats is needed, studies such as that presented here by Winkler *et al.* (2008) establish the basis for a full understanding of the species' evolutionary potential for invasion. Expanding on the relevance of assessing the extent of genetic and adaptive divergence among native populations of invasive species, Dlugosch & Parker (2008) examine the pattern of historical establishment and quantitative trait variation among populations of a shrub (*Hypericum canariense*) in its native range in the Canary Islands. The authors show how the relationship between selective environments in founding and source populations can dictate which lineages become established and their subsequent evolutionary dynamics. In the next study, Pergams & Lacy (2008) also embrace a historical perspective to examine how environmental changes in human-dominated landscapes may have changed a population of white-footed mice in the Chicago region during the past 150 years. Using museum specimens and recently collected individuals, they found rapid morphological and genetic (mtDNA) change. They suggest that the most likely source of the observed change is from immigrants from genetically distinct neighbouring populations, facilitated by environmental changes, and that the replacement of genotypes from external populations may be a common mechanism of evolution in an increasingly human-impacted world. In an analogous framework, Fleischer *et al.* (2008) use molecular markers to understand whether the expansion of common raven populations in Nevada and southern California over the past 50 years is due to population growth of the local population or to immigration from adjacent areas. The increase in raven numbers is important because it preys on the desert tortoises (*Gopherus agassizii*), a federally threatened species in the USA. Data suggest that the increase in raven populations most likely results from the dual effect of immigration from populations in southern and/or central California, as well as *in situ* demographic growth. The results of Fleischer *et al.* (2008) have management implications since the high levels of gene flow they observed suggest that efforts to manage raven numbers through local control measures may not be effective.

As the last two studies illustrate, evolutionary change in pathogens are of particular concern because of the potential global impact on human health. The first study,

by Lebarbenchon *et al.* (2008), uses empirical and theoretical examples to provide an overview of the ways in which humans can directly or indirectly influence the evolution of different traits in parasites. They systematically examine the role of habitat fragmentation, pollution, biodiversity loss, climate change, introduction of species, and use of vaccines and antibiotics on the evolution of pathogens. Demonstrating that pathogens evolve rapidly as a consequence of these various factors, Lebarbenchon *et al.* (2008) plead for the need to fully consider evolutionary change in parasites in public health, conservation planning, and economic development. Along these same lines, in the final study of the Special Issue, Williams & Day (2008) explore the epidemiological and evolutionary consequences of vaccination strategies and the importance of considering within-population genetic and phenotypic variation when examining susceptibility to infection. While such considerations seem obvious for evolutionary biologists, they are often strikingly lacking in the medical sciences. Williams & Day (2008) show how predictions about the epidemiological and evolutionary fate of treatment for a particular disease are sensitive to the nature and degree of heterogeneity in susceptibility and vulnerability. They conclude that accounting for realistic kinds of within-population heterogeneity of susceptibility to infection, or probability of mortality once infected, might be important in designing more effective virulence management strategies.

Evolutionary change caused by human activities touch every ecosystem of the planet, yet our understanding of the processes and the long-term consequences remain poorly understood. We hope that the diverse studies of this Special Issue inspire more research to understand these effects and motivate the search for more effective solutions. Namely, but certainly not exclusively, the looming threats of climate change beg for more evolutionary studies, particularly those that rigorously explore and contrast environmental and genetic changes in natural populations. Indeed, this crucial issue of teasing apart 'plastic' vs. 'evolutionary' responses is perhaps the most challenging, and also concerns the other human-driven environmental change and selective forces treated in this Special Issue. Understanding the evolutionary basis of infectious diseases in humans and variation in susceptibility within and among populations is another important area for further research. Moreover, there is an urgent need to use the available tools that evolutionary biologists have for putting evolutionary process on the map. From the prospective of a conservation practitioner 'if it can be mapped it can be preserved'. However, despite growing scientific evidence, policy makers and conservation decision makers rarely explicitly incorporate evolution in planning and have few strategies to conserve evolutionary novelty or maximize adaptability. Scientific research and policy both attempt to address critical environmental issues, but too often they work independently

of the other. As a result, policy measures do not always target the root of the problem. We need new and more rapid ways to bridge information between academia and conservation and policy decision makers. A modest first step in that direction would be for evolutionary biologists to treat existing conservation priorities and plans as hypotheses and apply evolutionary conservation science to make them better.

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