Another worrisome source of bias is the effect of natural selection itself on the estimation procedure. Individuals of low fitness are less likely to have relatives, and thus are less likely to be included in the study, than individuals of high fitness. This will lead to an underestimate of the covariance between relatives and an overestimate of mean fitness, both of which will make V_w^2 too low. An extension of the 'animal model' to explicitly allow for selection on the trait of interest would be valuable. More theoretical work would also be useful in clarifying exactly which fitness measure is ideal for these purposes and the probable consequences of using alternative measures. For example, using the lifetime number of recruits seems to implicitly assume that survival from fledging to recruitment is a phenotype of the parent, rather than of the individual concerned – how much does this matter?

Of course, not all of the outstanding issues raised by these two studies can be addressed by better theory alone. For example, if coevolving enemies are an important source of fitness variation, then results from island populations at high latitudes might not be representative of other populations. Only similarly impressive studies on other populations will tell.

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Austin Burt

Dept of Biology, Imperial College, Silwood Park, Ascot, Berkshire, UK SL5 7PY (a.burt@ic.ac.uk)

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The future of evolution

Evolutionary research often focuses on the study of mechanisms and processes that occurred in the past, in an attempt to understand both past and current patterns in the diversity of life. The future of evolution has been considered less frequently. Nevertheless, biologists are having to think more and more about the future, as we face up to the consequences of human-induced environmental changes occurring locally, regionally and globally[1]. It is probable that these changes will affect future evolutionary processes and directions. However, the interaction is reciprocal. The evolutionary responses of biological systems to environmental changes will determine, and perhaps help ameliorate, the long-term effects of these changes. Thus, there are compelling reasons to integrate evolutionary thinking and principles with conservation research and decision making. These issues were addressed by speakers and participants drawn from a wide range of evolutionary and ecological disciplines at a recent USA National Academy of Sciences colloquium*.

The first day of the meeting comprised formal presentations and began with consideration of what we can learn for the future from the deep past. A central issue here was whether patterns of biodiversity loss in the current human-induced extinction event are comparable to those seen in the 'big five' mass extinctions known from the fossil record[2]. Characteristics of species lost in mass extinction events differ from those lost in background extinctions[3]. Notably, species with extensive geographic ranges are more resistant to background extinctions, but less so to mass events (David Jablonski, University of Chicago, IL, USA). However, species beget species – new species might be more likely to derive from species with larger ranges, which provide a larger target for environmental barriers that lead to allopatry (Michael Rosenzweig, University of Arizona, Tucson, USA). Thus, whether the current extinction event has characteristics of a mass extinction might have consequences for the future ability of evolutionary processes to re-establish levels of biodiversity beyond those caused simply by biodiversity loss. In this regard, it is interesting that a time lag of several million years often occurs following mass extinction events before the diversity of the surviving biota recovers (Douglas Erwin, The Smithsonian Institute, Washington, DC, USA). During this period, some of the species that survived the extinction gradually decline to extinction, so representing 'dead clades walking' (Jablonski). Thus, the current human-induced extinction event might have consequences lasting for many thousands of human generations (Norman Myers, University of Oxford, UK).

The question of whether the ongoing extinction crisis will lead to a mass extinction is clouded by uncertainty about the threshold that must be crossed for background extinctions to attain characteristics of a mass event. It would be advisable to take steps to avoid crossing this line, but such evolutionary and ecological thresholds are hard to predict. However, once a threshold is crossed, system collapse might be rapid. An example at the ecosystem scale was provided by Nancy Knowlton [Scripps Institute of Oceanography, University of California, San Diego, USA, and the Smithsonian Tropical Research Institute (STRI), Balboa, Panama] who noted the failure of the dominant Caribbean reef coral *Acropora cervicornis* to recover following damage by Hurricane Allen in Jamaica in 1980, even though this species must have encountered many similar storms over its evolutionary history. The hurricane, coupled with the spread of an unknown pathogen and the

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loss of the main predator of its major competitor, was the final straw for this population. Crashes of the sort exhibited in the Jamaican coral reef might be the end result of a series of pressures gradually applied to marine ecosystems by human activities over many centuries. These have undoubtedly led to fundamental changes in the structure and function of these systems (Jeremy Jackson, Scripps Institute of Oceanography and STRI).

The growth of human populations and enterprise, and the accompanying global changes in climate and biogeochemical cycles, means that most, if not all, populations and species on earth are found in ecosystems that have been modified by humans to some extent. Therefore, the study of evolution cannot be limited to the study of 'natural' ecosystems alone (Paul Ehrlich, Stanford University, CA, USA) and research programs that ignore human-dominated landscapes will probably address unrepresentative samples of the processes occurring at present. On the contrary, as suggested by Harold Mooney (Stanford University), evolutionary biologists should make use of this 'grand experiment', which provides an excellent setting in which to study the tempo and mode of evolution. In this context, some of the important questions to address are:

- What characterizes those species that are surviving in the face of environmental change?
- What characterizes highly modified ecosystems versus less perturbed systems?
- Are declines of species and their ecological systems gradual and predictable or rather do they exhibit a threshold beyond which an ecosystem can collapse in an unpredictable fashion?
- Are current changes replicating in the short-term patterns that were previously shaped on a much longer timescale?
- Is the rate of evolution changing?

Answers to such questions will help us to link present systems to paleontological patterns of the sort described above and to better understand the evolutionary future.

On the second day of the meeting, participants were divided among four discussion panels, each considering a different aspect of how lessons from past and current events could help form a picture of the future of evolution. The final day brought the groups back together to discuss their proceedings. More questions were raised than were answered, but the intriguing discussion opened many new directions and ideas for synthesis. It was interesting that the different discussion groups converged on many topics. This was especially apparent for the panels headed by David Woodruff (University of California, San Diego, USA), addressing the decline of biomes and biotas, and by Mike Novacek (American Museum of Natural History, New York, NY, USA), focusing on scenarios for recovery. Both panels emphasized the importance of integrating process and pattern, rather than pattern alone, in future conservation plans. It was suggested that an important goal should be to safeguard the capacity of evolutionary process to maintain and to repair the damage that has occurred to biodiversity, rather than only to maximize current patterns of diversity and the number of species saved. This could be done, for example, by paying more attention to conserving environmental gradients, as emphasized by Richard Cowling (University of Cape Town, South Africa). However, the issue is complicated by climatic changes and concomitant distributional shifts. Current conservation strategies, including static reserves, might not be enough to solve conservation problems in a rapidly changing world. This led Rosenzweig to propose that conservation might be best served by integrating biodiversity as much as possible into human-dominated landscapes, an approach also stressed by Ehrlich.

Alan Templeton (Washington University, St Louis, MO, USA) voiced the opinion of many participants that we could be changing the course of evolution, but we have not stopped it. Evolutionary processes, such as speciation, adaptation and extinction, determine spatial and temporal patterns of biodiversity, but are also determined by them. Although it often seems that ecological studies, as a result of their focus on shorter term processes, are more important to conservation, this meeting made it clear that evolutionary studies are also directly tied with biodiversity conservation and research. Currently, conservationists and decision makers rarely include evolutionary processes in their first priority for conservation. However, the future of biodiversity is tightly linked to the future of evolution. It seems that the time has come to begin including evolutionary processes in conservation planning.

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Salit Kark

Center for Conservation Biology, Dept of Biological Sciences, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020, and Center for Tropical Research, San Francisco State University, San Francisco, CA 94132–4202, USA (salit@stanford.edu)

Tim M. Blackburn

NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire, UK SL5 7PY (t.blackburn@ic.ac.uk)

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