PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Preface

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PREFACE

A major problem in evolutionary biology is to understand why the organic world is as diverse as it is, both in its extraordinary variety of structures, functions and life histories, and in its sheer numbers. One of the many approaches to so broad a problem is seeking to understand a small and simplified part of it. For example, investigators inspired by this philosophy may recreate a simple version of a complex world in the laboratory or the computer. That is the essence of experimentation. Islands, being discrete pieces of the environment, and often very small, can provide that simplicity naturally.

As well as their convenience as models of larger realms and larger-scale processes, islands and their inhabitants have special features that command attention from evolutionary biologists. One characteristic of insular organisms, often difficult to quantify, is their strangeness; many of them are downright weird. Naturalists of the last three centuries, Darwin and Wallace among them, brought back to centres of civilization accounts of strange and unimagined creatures found only on remote islands: dodos, *Sphenodon*, the Komodo dragon, daisies as tall as trees. What is it about islands that promotes such strangeness? In the case of the dodo, the strangeness is the evolution of a bird from a, presumably standard, type of pigeon to something resembling a fat and flightless waddling goose, surely an extraordinary transformation!

Another special feature is replicated evolution; many organisms of very different origins have gone down the same or very similar evolutionary paths under similar insular conditions. For the dodo, the path has led to flightlessness, as it did for many other insular species of birds, most notably kiwis and rails, and many beetles and other insects. Arborescence of herbs and shrubs, large body sizes in some groups of mammals, large sizes of seeds and a predominance of white or dull-coloured flowers are other examples of repeated and independent evolution. Common denominators of repeated trends or replicated evolution give us a means of sorting and narrowing the list of potential causes of evolution. It is easy to see why island populations have been referred to as natural experiments. The experiments have been replicated, though not controlled.

A third feature is the apparent rapidity of diversifying evolution on islands. Outstanding examples include nearly 1000 species of *Drosophila* formed in the Hawaiian archipelago, apparently within a few million years (Hollocher), and hundreds of cichlid fish formed in the African Great Lakes in less than a million years (Meyer's group). What combination of ecological circumstances (opportunities), population genetic structures and processes has fostered such rapid evolution in islands or island-like settings? Even though they have no strict counterparts in continental regions, these radiations may be more suitable than most for examining general questions of evolutionary rates and their variation.

In organizing a discussion meeting on such a broad topic we were confronted by the challenge of defining its scope. Most of us would readily agree that Britain is an island. So are its satellites like Guernsey, Skomer and Mull. It could also be argued that individual animals, or plants, or bacteria are islands, hosts to communities of parasites and commensals that evolve in response to their hosts and to each other. These are biological islands, in contrast to physical islands. We decided to concentrate on physical islands, within which a continuum exists, from small and remote islands to large and weakly isolated continents. The former are biotically simpler and more numerous than the latter, and they have much to tell us about evolution in general, including what goes on inside biological islands.

If they are to tell us much more than we know already there is urgency in studying their inhabitants now. They are being lost at a higher rate than their continental relatives, indeed at an unprecedentedly high rate, owing to human misuse of their environments. At least 100 species of birds restricted to islands have become extinct in the last four centuries, and humans have had a hand in almost all, if not all, these extinctions. Island populations, being restricted, were especially vulnerable. The dodo, for example, was seen by few Westerners before it went extinct. One head and a couple of feet, preserved in museums, are all that remain of the living birds. Members of another flightless group, the moas, were already extinct by the time Westerners arrived in New Zealand.

And the process continues today. One of the speakers (Clarke) has lived through a period during which the endemic *Partula* snail fauna, of seven species on the island of Moorea, has been completely eliminated by an introduced predator. Variations on this theme of extinction can be told for one group after another. Extinction is relevant to the discussion meeting because it is depriving us of so much of the evidence that we need both to reconstruct and to interpret evolutionary patterns on islands. We have already lost much valuable material for the experimental testing of evolutionary hypotheses. Hence it was appropriate to discuss the evolution of organisms on islands without further delay.

Another reason for holding the discussion now is that our knowledge of evolution is being transformed by one of the quieter mainfestations of the molecular revolution. Molecular data are enabling us to reconstruct phylogenies in a more objective way than has hitherto been possible. Nuclear, mitochondrial and chloroplast genes constitute signals about the phylogenetic or taxonomic affinities of populations, to a large extent independent of the morphological traits that until now have been used to classify most of them. When the signals are clearly identified and the phylogeny reconstructed, the direction of trait evolution can be determined, and the evolution itself interpreted (Thorpe & Malhotra). This may be easier on islands than on continents, because islands are relatively free from the ebb and flow of genes, a form of noise that tends to obscure the phylogenetic signal of divergence among demes. However, island populations are not entirely immune from those complications. Studies of birds (Grant & Grant) and molluscs (Clarke, Johnson & Murray) are revealing hitherto unsuspected levels of genetic exchange between species through hybridization, and are thereby throwing new light on the process of speciation.

Lastly, a few words about the themes of the meeting and about the underlying plan, that might not be transparent from a simple reading of the titles. First, we sought an examination of general principles applying to the evolution of all organisms on islands. The theoretical contribution by Barton explores some of those principles, particularly the interaction between natural selection and drift. Several of the more empirical papers examine related theoretical issues in specific settings, including the role of drift in the evolution of warning coloration in butterflies (Turner & Mallet), and in the evolution of mammals on islands (Berry). Second, complementing the search for generality, we chose to examine some evolutionary features specific to particular organisms and to particular environments. Third, the programme was designed to achieve a balance between generality and specificity. The balance is not perfect. Some organisms and environments were examined more thoroughly than others, and some (parasites and marine organisms for example) are missing altogether. Nevertheless, there is coverage of plants and animals; of vertebrates and invertebrates; of morphological traits and reproductive systems (Barrett); of temperate and tropical islands; of true islands and island-like habitats (Prance; Schluter); of small-scale processes of genetics (Pemberton and colleagues) and ecology (Losos), and their translation to large-scale processes of biogeography.

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