Speciation

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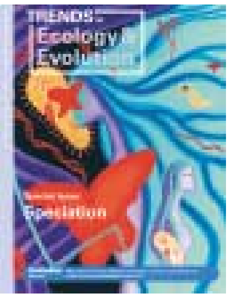

Ideas on species and their formation have always been a key part of biology. Species are the fundamental unit for much of ecology, taxonomy and conservation biology, while evolutionary genetics deals primarily with the changing composition of the pool of genes that makes up a species. As long as species were seen as immutable units, each separately created, they were easy to understand (albeit, impossible to explain). Once Darwin's arguments for the evolutionary transformation of species were accepted, scientific investigation of speciation became possible, but at the same time, what a species *is* became unclear. Indeed, the interpretation of Darwin's views on species and speciation remains controversial (see Hey, Turelli *et al.*, and Kondrashov, this issue).

Without knowing the mechanism of inheritance, detailed explanation of how species form was impossible. Our present understanding of speciation dates back to the 'Modern Synthesis' of darwinian evolution with mendelian genetics, a synthesis laid out most influentially in Dobzhansky's *Genetics and the Origin of Species*[1]. Over the years that followed, however, speciation received little attention, relative to issues such as the explanation of molecular variation within populations, the role of population structure, selection on quantitative traits, or the evolution of sex and recombination. The past few years have seen a resurgence of interest in speciation, which is reflected in numerous articles in the pages of this and other journals, as well as several books[2–6]. This special issue aims to review recent developments and to bring together all aspects of the subject, from genetics through ecology to palaeontology.

Despite the central importance of species and speciation to biology, there is no consensus on what exactly a species is. Hey argues that this remarkable (and unsatisfactory) confusion arises from a conflict between our intuitive classification of organisms – reflected in the similar taxonomies produced by different cultures – and the complex and continuous process of evolution. Given evolution, no definition can neatly classify populations at every stage of their divergence.

The most widely held species definition (and, to my mind, the most clear-cut) is the biological species concept. On this strict definition, 'speciation' consists of the evolution of differences that prevent interbreeding and recombination between populations. However, the term 'speciation' is used to cover much more than this, as this issue of *TREE* shows. In a broad sense, speciation includes the diversification of all aspects of phenotype, including the evolution of differences that allow the exploitation of different ecological resources, and hence coexistence in sympatry.

Despite the semantic murk, speciation is hardly mysterious. We expect that geographically separated populations will evolve along different paths, both by chance and as a result of different environmental conditions, and that separately evolving populations will eventually become incompatible with each other. Indeed, there is a wide consensus as to the various basic processes involved in speciation. As usual in evolutionary biology, the difficulty is to gauge the relative importance of these processes.

Nevertheless, clear questions remain to be answered. Why should there be distinct 'species' at all, rather than a continuous intergradation of interbreeding organisms that reflects the continuity of evolution (Turelli *et al.*)? Is the distribution of species' abundance determined primarily by the distribution of ecological niches, or does it also depend on how species form (Godfray and Lawton)? To what extent does genetic exchange impede divergence? In the extreme, can a single population split into two species without any spatial separation at all (Turelli *et al.*, Via, and Rieseberg)? What processes drive divergence – random drift, natural selection, or sexual selection (Panhuis *et al.*, and Schluter)? What kinds of genetic difference distinguish species, and what do these tell us about the process of divergence (Turelli *et al.*, and Orr).

Although our basic framework for understanding speciation was laid down in the early days of evolutionary biology, recent years have seen a change in emphasis. Most notably, greater attention is now given to the role of selection as a cause of divergence (Panhuis *et al.*, and Schluter). This change may reflect the fading influence of theories of founder effect and chromosomal speciation, together with the increasing prominence of ecological studies of natural populations. New approaches have also been introduced, many made feasible by the abundance of molecular markers. Genes that determine species' differences can be located and, in some cases, isolated (Orr). Phylogenies can be estimated, which makes rigorous comparative tests possible and allows inferences about the evolutionary process (Barraclough and Nee). Similarly, 'gene trees' can be used to measure the evolutionary processes of selection, migration and drift that are involved in speciation (Nichols). A more quantitative approach to palaeontology has allowed clear hypotheses about the relation between speciation and morphological evolution to be tested (Benton and Pearson).

Speciation is the topic that links the interests of virtually all ecologists and evolutionary biologists. This special issue reflects some of that diversity; we hope it will stimulate more such developments and encourage a new generation of research on some of the most fascinating questions in biology.

References

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