COMMENTARY

The speciation revolution

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I predict the years 1990–2010 will be seen as a revolution in the study of speciation. One person's punctuated equilibrium is another's gradual change, and the current revolution is in any case paltry compared with Darwin's own. Even so, many previously accepted beliefs about speciation are now doubted, and features of a classic scientific revolution are evident.

To see just how much has changed, consider what experts were saying until recently. Coyne (1994), for example, listed four major achievements due to Ernst Mayr since the 1940s. These were: (1) an appreciation of the reality of species (as compared with, say, the unreality of subspecies or genera); (2) the reproductive isolation definition of species (the 'biological species concept'); (3) the generality of allopatric speciation; and (4) founder-effect speciation. Coyne (1994) argued that Mayr's fourth achievement, the founder effect, was probably incorrect, but regarded the other three as completely in tune with the current view of speciation. What is extraordinary about this list is that *all* these 'achievements' are now, only 7 years later, rejected by major groups of evolutionary biologists. Softening on points (1) and (3*) are found today even in papers co-authored by Coyne himself (Kliman *et al*., 2000; Turelli *et al*., 2001). The opinions under attack date from the 1930s to the 1950s, and are identified strongly with Theodosius Dobzhansky and Ernst Mayr; however, virtually all evolutionary biologists and most textbooks supported these ideas until the late 1980s. In what follows, I discuss each of Coyne's points in turn.

1 *Reality of species is now doubted by many.* Coyne (1994) argued that Mayr was one of the first to recognize that discontinuities between species were real. Personally, I find this hard to support, as discontinuities are what everyone uses to distinguish species, and always did: 'species … do not at any one period present an inextricable chaos of varying and intermediate links' (Darwin, 1859, p. 177). The Dobzhansky/Mayr innovation was the idea that species were *more* discontinuous or 'real' than either higher or lower taxa. Today, an essentialist species 'reality' strongly conflicts with our understanding of gradual speciation, and is no longer accepted at all generally (Bachmann, 1998; Kliman *et al*., 2000; Mallet, 2001). Wu (2001) makes the same point in this issue: speciation is a process of emerging genealogical distinctness, rather than a discontinuity affecting all genes simultaneously.

2 *Reproductive isolation is no longer generally recognized as the best definition of species.* One does not need to take sides to realize that we are in an intense period of navel-gazing about what species are, and therefore what speciation itself is. Some have argued that the confusion is caused by unruly scientists each promoting their own, hair-splittingly different species concept. But there is, I believe, more to it than that. Real conflicts exist, driven by real new data, particularly from ecological and molecular studies of natural populations. All this philosophizing is a classic symptom of scientific revolutions: 'it is, I think, particularly in times of acknowledged crisis [i.e. during scientific revolutions] that scientists have turned to philosophical analysis as a device for unlocking the riddles of their field' (Kuhn, 1970, p. 88).

Wu (2001) provides a good example of the revolutionary process. Wu's many papers follow in the tradition of *Drosophila* speciation work begun by Dobzhansky, but he now pauses to challenge a central dogma of his school, the reproductive isolation concept. Wu (2001) is no anarchist. Instead, he finds total reproductive isolation meaningless given evidence for transfer of genes between closely related *Drosophila* species. Other loci within the same genomes become genealogically distinct, either because they contribute directly to selection against hybrids, or because they are trapped in parts of the genome contributing to such selection (Wang *et al*., 1997; Wu, 2001).

3 *Speciation does not require allopatry.* The idea that speciation can occur only in allopatry had been accepted generally since the 1940s (Coyne, 1994), whereas the idea that parapatric and sympatric speciation are also probable is completely acceptable today (Gavrilets *et al*., 2000; Jiggins & Mallet, 2000; Turelli *et al*., 2001; Via, 2001).

4 *Natural selection is becoming viewed as the primary cause of speciation.* Dobzhansky and Mayr argued that allopatry, in conjunction with founder events and ecological selection, caused speciation. In the 1970s, it was pointed out that divergent natural selection might outweigh gene flow even at very small spatial scales (Bush, 1975; Endler, 1977). This in turn led to the proposal that natural selection was a primary cause of speciation, rather than allopatry (Barton & Charlesworth, 1984; Schilthuizen, 2000). At first, this argument became entangled in a debate about reinforcement (Butlin, 1989), but it is increasingly evident that selection can also reduce assortative mating more simply, as a by-product of divergent adaptation. Adaptive divergence

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*indicates correction from published version.

can cause reduced gene flow, which in turn allows further divergence, and so on, until speciation is achieved (e.g. Dieckmann & Doebeli, 1999; Via, 2001).

Is it really a revolution? Some might view these U-turns as mere improvements, but at the very least changes are speeding up. For instance, it took about 10 years after the discovery that host races of *Rhagoletis* were genetically differentiated (Feder *et al.*, 1988) before nonallopatric adaptation and speciation was seen as likely in other systems. Today the pace is accelerating: arguments for ecological speciation and sympatric and/or parapatric differentiation are flooding in (Jiggins & Mallet, 2000; Schluter, 2001; Via, 2001).

An extraordinary feature of the current revolution is the strength of rapprochement with Darwin's own views. This has been noted independently several times (e.g. Mallet, 1995; Schilthuizen, 2000; Kondrashov, 2001). Today's rejection of the reality of species was foreshadowed by Darwin – 'we shall have to treat species in the same manner as … naturalists treat genera…' (Darwin, 1859, p. 484), as was a de-emphasis of reproductive isolation – 'I do not think that the very general fertility of varieties can be proved to be of universal occurrence, or to form a fundamental distinction between varieties and species' (Darwin, 1859, p. 271). Darwin recognized the existence of allopatric speciation, of course, but argued that competition in large diverse ecosystems was more important: 'Although I do not doubt that [geographical] isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance' (Darwin, 1859, p. 105). Finally, Darwin believed that selection and competition caused speciation, long before Mayr's now discredited founder event model of speciation was presented. I know of no other scientific revolution that involves such a renaissance of the paradigm-before-last. We are apparently emerging from a 60-year-old blind alley, a veritable Dark Ages compared with the typical pace of modern science. During this time, important data was of course being accumulated, fostered by these very ideas of Dobzhansky and Mayr that we now question, so the time was not wasted. As an end result, we do now seem to be achieving what the 'modern synthesis' of the 1930s and 1940s first attempted: a fusion of Darwinism and genetics into a general theory of speciation.

Note: I have kept references to a minimum at the behest of the editor. I have therefore omitted citations, especially to Dobzhansky and Mayr's many works (references are readily available in other articles in this issue), and to the many recent examples showing how ecological adaptation may commonly lead to assortative mating as a by-product (1995–2001).

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