Available online at www.sciencedirect.com
SCIENCE DIRECT®
Stud. Hist. Phil. Biol. & Biomed. Sci. 36 (2005) 303–326
Studies in History and Philosophy of Biological and Biomedical Sciences
www.elsevier.com/locate/shpsc

Adaptive speciation: the role of natural selection in mechanisms of geographic and non-geographic speciation

Jason M. Baker

Department of History and Philosophy of Science, Indiana University, Goodbody Hall 130, 1011 East Third Street, Bloomington, IN 47405, USA

Abstract

Recent discussion of mechanism has suggested new approaches to several issues in the philosophy of science, including theory structure, causal explanation, and reductionism. Here, I apply what I take to be the fruits of the 'new mechanical philosophy' to an analysis of a contemporary debate in evolutionary biology about the role of natural selection in speciation. Traditional accounts of that debate focus on the geographic context of genetic divergence—namely, whether divergence in the absence of geographic isolation is possible (or significant). Those accounts are at best incomplete, I argue, because they ignore the mechanisms producing divergence and miss what is at stake in the biological debate. I argue that the biological debate instead concerns the scope of particular speciation mechanisms which assign different roles to natural selection at various stages of divergence. The upshot is a new interpretation of the crux of that debate—namely, whether divergence with gene flow is possible (or significant) and whether the isolating mechanisms producing it are adaptive.

Keywords: Speciation mechanisms; Isolating mechanisms; Reproductive isolation; Natural selection; Adaptation; Spandrels

E-mail address: bakerjm@indiana.edu (J.M. Baker).

1369-8486/$ - see front matter
doi:10.1016/j.shpsc.2005.03.005

1. The paradox of 'adaptive speciation'

The existence of speciation—the creation of two species from one—is a puzzle for adaptationists. Charles Darwin's theory of evolution by natural selection accounts for the presence of adaptations in a species. Adaptations help organisms perform tasks, such as finding food or evading predators, which allow them to better exploit environmental resources. When resources are limited, adaptations tend to increase organismic fecundity and, consequently, become widespread in the species.[1] Moreover, as environmental conditions change, so do selective pressures. As a result, a species may acquire rather different traits over time, and biologists may then divide a continuous population-level lineage into different taxonomic species. Linear adaptive evolution may thus involve 'phyletic speciation' in which an ancestral species gives rise to a single descendent species. But phyletic speciation is a straightforward product of natural selection, given sufficient environmental change and certain (namely, non-cladistic) taxonomic practices.

Branching evolution, or speciation proper, occurs when a single species instead splits into two or more contemporaneous descendent species. Branching evolution is less readily explained by natural selection. The problem is that, prima facie, speciation seems to be maladaptive. The traditional definition of speciation derives from Ernst Mayr's biological species concept (BSC), according to which a species is a group of interbreeding populations reproductively isolated from others.[2] Speciation thus requires the acquisition of traits (called 'isolating mechanisms') that prevent gene flow between diverging populations. Isolating mechanisms eliminate the possibility of fruitful sex between otherwise happy mates. In so doing, they would seem to lower organismic fitness. How, then, could such traits ever evolve? The BSC appears to render impossible any kind of 'adaptive speciation', that is, speciation driven by natural selection.[3]

The paradox of adaptive speciation is this: isolating mechanisms should only benefit organisms when they arise between genetically distinct populations, and yet populations cannot diverge from each other in the face of gene flow between them. 'Adaptive speciation' thus seems to be a contradiction in terms. Darwin himself fully recognized the puzzle. Despite the title of his most famous work, *On the origin of species by means of natural selection* (1859), he would later write, 'The acquirement by distinct species of mutual sterility . . . could not have been effected through natural selection'.[4] Other biologists were not so pessimistic. Alfred Russel Wallace, for

[1] Adaptations are here defined in terms of their origin and current utility; adaptations must have become prevalent in the population because they were selected for their current function. *Spandrels* (that is, by-products of natural selection) that happen to be beneficial cannot therefore be adaptations. For discussion, see Gould & Lewontin (1979); Gould & Vrba (1982). Cf. Reeve & Sherman (1993).

[2] Mayr (1963). Something like the biological species concept may have been accepted by Darwin, as well (Kottler, 1978; but see Beatty, 1985).

[3] In keeping with standard usage, I shall use 'adaptive speciation' to designate speciation 'driven' by natural selection, whether directly or indirectly. The contrast here is with 'founder effect' speciation, in which reproductive isolation is achieved by drift.

[4] Darwin (1868), Vol. 2, p. 170.