

COMMENTARY

## Hybridization without guilt: gene flow and the biological species concept

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Studies of the genetics of speciation are fundamental to our understanding of its causes and consequences. A tacit assumption of speciation research is that species are real evolutionary units. Different species concepts place different emphases on properties of species and so have the potential to shift the focus of studies of speciation. At present, the genetics of speciation is effectively the genetics of reproductive isolation (Coyne & Orr, 1998). In this vein, Wu *et al.* have been at the forefront of endeavours to understand the genetic architecture of speciation. Based on this work, Wu now suggests that the biological species concept (BSC) is in need of a major revision and rejects the current focus of speciation research on reproductive isolation (RI). Wu prefers to view RI as an epiphenomenon of secondary interest. We feel that this rejection of RI is unnecessary and overly restrictive, and generally that any modification of the BSC is premature given our current knowledge of the genetics of speciation.

Given a more modern version of the BSC that addresses many of the issues raised by Wu, his rejection of RI as a framework for understanding speciation is unnecessary. In this modern version, RI between populations is treated as a quantitative trait that can evolve gradually and is capable of taking on intermediate values (e.g. see Grant & Grant, 1996; Coyne & Orr, 1998; Harrison, 1998). Indeed, this version is not so far from the original BSC, as both Mayr and Dobzhansky allowed for limited gene flow between species in some of their writings [e.g. Mayr, 1963 (p. 26); Dobzhansky, 1951 (p. 262)]. This use of RI is logically compatible with any possible genetic architecture of speciation, be there many (Ting *et al.*, 2001), few (Doi *et al.*, 2001), or no loci (Bordenstein *et al.*, 2001) responsible for RI.

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Genomes may thus be porous at loci not involved in speciation, as suggested by Wu and others (cf. Barton & Hewitt, 1985; Harrison, 1990; Rieseberg *et al.*, 1999). When viewed this way, RI has additional strengths. For example, by providing a framework for directing research it makes the study of speciation tractable, reducing it to understanding the mechanisms by which RI evolves (Coyne & Orr, 1998). In addition, most species concepts are difficult to apply to allopatric populations, requiring us to fall back on 'informed opinion'. Such informed opinion constitutes data on the ecology, reproductive biology and behaviour of the two populations, information which essentially constitutes inferences of their RI.

Wu's views also seem overly restrictive. As Mallet (1995) forcefully argued, we want 'a theory-independent definition of species' that is 'useful, however, species are maintained, and however, they have come to be' (pp. 295–296). Yet Wu (this issue) defines species as 'groups that are differentially adapted...' with RI evolving solely as the by-product of this differential adaptation. However, random processes not involving differential adaptation to the environment may be important in speciation and the evolution of RI (e.g. drift, shifting balance and some models of speciation by sexual selection; see Schluter, 2000; Turelli *et al.*, 2001) and these are actively debated (e.g. see Coyne *et al.*, 1997; Wade & Goodnight, 1998; Schluter, 2000; Turelli *et al.*, 2001). Whereas the empirical evidence for drift-based speciation remains weak (Rice & Hostert, 1993), theoretical work suggests its feasibility (e.g. Gavrillets *et al.*, 2000). In addition, instead of evolving indirectly as a by-product of differential adaptation, RI itself may also be adaptive, evolving as a direct result of natural selection (e.g. by reinforcement). The case for direct selection is stronger; both empirical (Noor, 1999) and theoretical (Turelli *et al.*, 2001) work point to the importance of reinforcement. In contrast to Wu's definition, the more modern version of the BSC is general because RI, being the product of barriers to gene exchange, can evolve via almost any process (Harrison, 1998).

Finally, speciation genetics is in its infancy and any revision of the BSC on the basis of a few studies in a few model systems is premature. A revision now is especially worrisome given the sharp contrast in the genetic basis of sexual isolation in two of the most detailed studies to date (Doi *et al.*, 2001; Ting *et al.*, 2001). Further, most of these few empirical studies address the genetics of a single form of RI (postmating isolation), and focus almost exclusively on a single type of postmating isolation: hybrid inviability/sterility. Recent studies in other model systems have demonstrated that ecological mechanisms can reduce hybrid fitness and may be central to the early stages of speciation (reviewed in Schluter, 2000). Although current studies are addressing this deficiency (i.e. Hollocher *et al.*, 1997; Doi *et al.*, 2001; Ting *et al.*, 2001), much less is known about the genetics of premating or ecologically

based (i.e. extrinsic) postmating isolation. Indeed, there is reason to think that the genetic basis of these forms of isolation will differ from that of hybrid inviability/sterility (Orr, 2001).

Determining the genetic architecture of speciation is fundamental to our understanding of the formation of biodiversity. Although not being the first to suggest it (e.g. see Anderson & Hubricht, 1938; Wang *et al.*, 1997), work of Wu *et al.* reveals that many loci may indeed share a common fate across species, forcing us to accept the fact that genomes may be more porous than we originally believed. If substantiated in other groups, this work will fundamentally change our view of species as possessing independent evolutionary trajectories with histories best represented by bifurcating phylogenies. In conclusion, we call for a moratorium on discussions of species concepts (e.g. see Hey, 2001). Eventually, two populations will diverge to the point that evaluation of species status under all alternatives will agree. The interesting question is not precisely when this occurs, but how it comes about.

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