COMMENTARY

The genic view: a useful model of the process of speciation?

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The Biological Species Concept (BSC) (Mayr, 1942) and more recent interpretations (Neigel & Avise, 1986; Moritz, 1994) attempt to define species in the context of an assumed evolutionary process; separated populations initially differ in gene frequency and then accumulate genetic differences until they become reproductively incompatible, at which point species status is achieved. Wu's (2001) paper expands this scheme to the genic level: with longer time of separation, ever larger portions of the genome diverge to the point where selection prevents gene flow, until reproductive isolation affects all loci.

The work of Wu and colleagues has greatly improved our understanding of the number and distribution of genes affecting reproductive differences. However, despite the widely shared excitement about these studies, we should consider carefully what they teach us about the *process* of speciation. Just as the BSC, Wu's genic view implicitly assumes that speciation is a gradual build-up of divergence leading to reproductive isolation. This assumption of the BSC, however, is not justified, as it would predict a close correlation of genetic divergence and reproductive isolation and, at a deeper evolutionary level, that the closest relatives are less stringently reproductively isolated than more distantly related species. However, the correlation of sequence divergence and reproductive isolation is tenuous (Coyne & Orr, 1997), and many hybrid zones exist between species which are not each others' sister (Cracraft, 1989). Therefore, the gradualist model underlying the BSC is poorly supported empirically, and reproductive isolation is not a suitable parameter to represent the historical (evolutionary) process which led to the existence of species (Cracraft, 1989).

For the same reasons, the genic view may also suffer from the difficulty of linking the observed phenomenon (reproductive isolation) with the history of a lineage. To date, we have insufficient data to test whether there is a direct correlation of the number of speciation traits with increased phylogenetic divergence. Although the *Drosophila melanogaster* group data (Table 1 in Wu's paper) seem to support this notion, they may be insufficient. First, the assignment of Stages seems rather arbitrary and in the case of the proposed Stages III and IV the number of differences in the comparisons may not be significant; hence the correlation of speciation loci with node level in the phylogeny may be weak. Secondly, even if there is a good correlation of the number of differentiated speciation loci with evolutionary divergence, these loci may have little to do with the speciation process itself but may be a trivial consequence of increasing divergence of cell components. For example, genes coding for rRNA could easily show up as speciation loci in the genetic screens if the gene products are too divergent for molecular interactions in cross-species genetic tests.

The fact that the natural world is composed of species, i.e. discrete groups of organisms which are recognizably different from other such groups, argues against a view (also promoted by Wu) that species are simply peaks (adaptive or otherwise) in a continuum of variation. Sometimes discrete groups may be difficult to detect because of the lack of diagnostic features, because divergence is very shallow, or because there is in fact some level of gene flow, but the observation of discrete species holds in principle throughout the animal kingdom. Hence, species and the process of speciation should not be viewed primarily as quantitative phenomena. Speciation may be sudden and more consistent with a punctuated process, and may be independent of the level of divergence. In particular under allopatric scenarios, speciation may involve the disruption of continuously distributed groups through extinction of populations in some parts of the range (Nixon & Wheeler, 1992; Vogler, 1998). If, as proposed by Wu, speciation loci are driving the rest of the genome to complete isolation this will require prolonged interactions of gene pools for selection to act. Wu's proposed model therefore may be most appropriate for sympatric and parapatric scenarios. But as evidence is mounting for a mostly allopatric mode of speciation in animals (Barraclough & Vogler, 2000) the assumption of interactions of differentiated populations may not be realistic, even for the *D. melanogaster* group. Without the interactions, speciation genes and marker loci should have largely the same history and the proposed differences in both sets of loci may not be detectable. The critical issue, as pointed out by Wu, will be to determine the degree to which selection plays a role in generating and maintaining species-level differences.

Finally, the analysis of species-level differences, including those of speciation genes, requires that entities can be clearly defined when these comparisons are made. The genic view does not address the question of how to define what is a species (e.g. why are the *D. melanogaster* Z and M groups 'races', not 'species'?) and what is their extent (e.g. which populations should be considered part of either race?). Traditionally, insect species have been separated on the basis of diagnostic traits. Under the phylogenetic species concept (PSC) a marker present in all individuals of a (group of) population(s), but not present in any other groups, is taken as a proxy to define

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a distinct gene pool. It is comforting that the study of genic differences revealed extensive divergence in speciation genes between *D. simulans* and *D. melanogaster* which are clearly definable by diagnostic differences (but not necessarily by the criterion of reproductive isolation). This suggests that the usual way of separating species by diagnosis is a valid operational procedure for discovering subdivided gene pools. Therefore, the possibly most exciting result of the high-resolution genetic analysis is that it provides a more profound empirical basis for the application of pattern based concepts to define species, no matter which process led to their speciation.

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