

COMMENTARY

Some doubts about (yet another) view of species

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I find that I agree with many of the facts that Wu presents but with fewer of the conclusions he draws from them. In particular, I agree that molecular and ecological work suggests that selection, whether natural or sexual, is the most important force shaping species differences. I also agree that 'genomes during (or even after) speciation can be quite "porous"', with some loci flowing freely between sympatric taxa and others not at all. [Neither of these facts is, however, terribly novel. The last one in particular has been talked about for quite some time in both the hybrid zone and plant literature (Barton & Hewitt, 1985; Harrison, 1990; Rieseberg & Whitton *et al.* 1999).]

But I fail to see why these facts pose a profound problem for the biological species concept (BSC), much less demand its 'major revision', leaving us with something 'close to Darwin's original concept of speciation.' Indeed I have come to the conclusion that Wu's claims to the contrary hinge on two problems in his analysis. One is that he confuses a straw man with the BSC. The other is that he ignores problems with the alternative Darwinian view of speciation.

Is the BSC genomic?

It is certainly true, as Wu maintains, that Mayr believed the genome is a cohesive, coadapted unit and that reproductive isolation is based on many genes, each of small effect (e.g. Mayr, 1963, p. 543). One could therefore reasonably label Mayr's view 'genomic' – a view that might have some difficulty in accommodating the fact that some loci introgress freely between species whereas others do not. If this were all there were to our traditional genetical view of species it would indeed be in a bad way. But this is not, of course, all there is to the traditional view. The fact is that, whereas Mayr's views on the biogeography of speciation were immensely influential, his views on the genetics of species differences and isolation – the issues Wu is concerned with – were far less so. Our picture of the genetic nature of species was shaped far more by Dobzhansky and Muller than by Mayr. And although Dobzhansky believed that isolation involves a good number of genes, he certainly did not champion a holistic 'genomic' view. The proof is that he spent much of his time *mapping* the genes causing hybrid sterility. But

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the act of mapping is *prima facie* evidence that one believes the genes causing reproductive isolation reside in some parts of the genome and not others. Muller's case is even clearer. He believed that reproductive isolation often has a simple basis (Muller, 1942, p. 101) and even argued that *Drosophila melanogaster* and *D. simulans* may be separated by as few as *nine* genes causing hybrid inviability. This, I submit, is not a terribly genomic view of reproductive isolation. Nevertheless Muller seems to have happily embraced the BSC (Muller, 1942) and concluded that his genetical work was in 'complete agreement' with Mayr's picture of allopatric speciation (Muller, 1963, p. 432). Given all this, it is hard to see what the alleged crisis is. It is simply not true that the 'genetic view' of species is big news nor that evolutionary geneticists have been stunned by the revelation that some parts of the genome can flow more freely than others between sympatric taxa. Recent evidence to this effect is interesting and important in its own right but hardly turns our traditional genetic picture of species upside down.

Differential gene flow across loci in fact seems easily accommodated under the BSC: it is what happens when reproductive isolation is incomplete. When isolation between sympatric taxa is partial, there are, by definition, too few genes causing problems. But those genes that *do* already cause reproductive isolation presumably reside somewhere in the genome and those regions will introgress less readily than others. It is hard to see how it could be otherwise.

As for Wu's claim that the Dobzhansky–Muller model of speciation naively posits that isolation is caused by only two genes, this is simply incorrect. Both Dobzhansky and Muller emphasized that the two-locus case represents only the simplest version of their model and that in more complex cases, 'more than two genes interact to produce the harmful result, but it is essentially the same story' (Muller, 1942, p. 87). Indeed Muller was the first to emphasize that hybrid incompatibilities often involve three or more genes and thus complex conspecific epistasis (see his detailed discussion in Muller, 1942, pp. 92–93). He is rarely given credit for this insight.

The Darwinian view of speciation

I am afraid that I also do not see how recent genetical results lead us to a view of speciation that is closer to Darwin's. Wu's argument seems to be that Darwin thought species are products of adaptation and that recent work suggests the genes causing reproductive isolation did in fact diverge by natural or sexual selection. This is all true. But it does not follow that we are left with a view of speciation nearer to Darwin's. The problem is that Darwin's theory of how selection drives speciation was strictly *sympatric*: taxa diverge as a consequence of a competitive struggle for ecological elbow room in the same locale (Schilthuizen, 2000). This does not, however, seem to be Wu's view, as he regularly speaks of secondary contact between taxa and

spends much time on *D. simulans* and *D. mauritiana*, taxa that were until recently almost surely allopatric. Adaptive divergence in allopatry is one thing, the Darwinian view of speciation quite another. Indeed it is worth noting that if Darwin's sympatric view were correct, the most common early form of reproductive isolation would necessarily be niche differentiation, not the hybrid male sterility and courtship differences Wu focuses on.

The adaptive view of species also leaves us with some sticky cases, if not outright paradoxes. Wu argues that '[s]pecies are groups that are differentially adapted', that 'speciation is driven by the same forces that drive adaptation', and that 'speciation genes are simply genes that determine aspects of differential adaptation'. As he seems to admit, this view denies species status to cases of endosymbiont-based reproductive isolation (at least if the endosymbiont is not advantageous to the host, which seems likely). But the consequences are even more serious. Wu's view also denies species status to polyploids, who likely make up the vast majority of flowering plants: hybrid unfitness here does not, after all, reflect adaptive evolution. Worse, consider the following thought experiment: (1) Two taxa adaptively diverge in allopatry, coming to differ by a suite of amino acid replacements, a subset of which causes complete hybrid inviability. Wu would presumably call these species. (2) Two other taxa diverge in allopatry, coming to differ by exactly the same suite of amino acid replacements, the same subset of which again causes complete hybrid inviability. But in this case all evolution was caused by genetic drift: the environments differed from those considered before and all alleles acted neutrally. Wu would presumably not call these taxa species. But why not? If we are left with the same substitutions, same genes, same phenotypes and same reproductive isolation, why quibble over the evolutionary force that drove these changes? Why is evolutionary *force* suddenly the alpha and omega of species status, not the identical evolutionary *products* of these forces? Any decision to deem one

taxa pair, but not the other, species seems awkward and arbitrary, to say the least.

I do not claim that these problems with endosymbionts, polyploids, and 'twin species pairs' are fatal to Wu's view of species. I am a pragmatist and believe that, in the end, we can do no better than choose that view of species that does the most work for us, i.e. that suggests the richest, most productive research programme. Species concepts, including the BSC, are not handed down to us from on high. But it does seem to me that Wu's view of species has a number of consequences that, while not first obvious, are likely to be unattractive to many evolutionists.

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