

Is the biological species concept showing its age?

Mohamed A.F. Noor

A recent paper by Chung-I Wu in the *Journal of Evolutionary Biology* questions the value of the popular biological species concept (BSC) and offers an alternative 'genic' concept based on possessing 'loci of differential adaptation.' Wu suggests that recent empirical results from genetic studies of speciation necessitate this revision. Several prominent evolutionary biologists responded in the same issue, many noting excitement over the recent empirical results, few agreeing with an abandonment of the BSC, and none wholeheartedly embracing the new genic concept.

One reason why evolutionary biology sometimes fails to gain the respect of other scientists is because of its endless debates over questions that focus on semantics. The most famous (or infamous) of these involves the definition of a species. Most biologists think of species in terms of the biological species concept (BSC) [1,2], which defines species as interbreeding natural populations that are reproductively isolated from other such populations. Thus, the acquisition of reproductive isolation is how adherents of the BSC describe the process of speciation. However, many other concepts have been introduced and are championed by groups of biologists. Most of these concepts strive to identify species in a manner that fits with our intuitive ideals: we desire instinctively to have labeled categories that explain the reality that we perceive [3].

In a recent issue of the *Journal of Evolutionary Biology*, Chung-I Wu revisits the species definition debate [4]. Wu has been at the forefront of genetic studies of reproductive isolation with an elegant body of work on species and races in the *Drosophila melanogaster* group. In the first paper of this issue, Wu stresses two conclusions that have emerged from recent studies and concludes that a revision of the BSC is necessary to accommodate them. First, several taxa that biologists consider to be good species exchange genes in some parts of their genomes. A strict version of the BSC might assume that any gene exchange demonstrates that reproductive isolation is incomplete and that species status has

not been attained. Hence, such a strict definition would not match the intuition of most biologists. Second, speciation is usually driven by natural or sexual selection causing functional divergence. However, the BSC does not delineate the evolutionary forces that cause divergence. As such, the BSC considers reproductively isolated units to be species, even if differential adaptation is not apparent.

Wu proposes what he calls a 'genic view of the process of speciation'. He suggests that the point in divergence at which separate species should be recognized is 'the stage where (1) the gene pools of loci of differential adaptation would not mix when the extrinsic barriers to gene exchange are removed; and (2) the spread of advantageous mutations are sometimes (or often, but not always) restricted to the population in which they originate. Because the rest of the genome may mix upon contact, the genomes of the diverging populations are expected to be mosaic in their extent of differentiation'.

Several prominent biologists comment on Wu's proposal in the same issue, including Ernst Mayr [5]. Several of these responses suggest that Wu's points are not completely new. For example, in 1998, Feder [6] explicitly discussed many points raised by Wu, including gene flow early in the speciation process, the role of natural selection in speciation, and how an extension of the BSC might be useful to accommodate such observations. Feder even refers to this revision as a reascension of Darwin's view of speciation, as does Wu. Also, Mallet [7] suggested elsewhere that species should be considered genotypic clusters that can overlap spatially without fusion, a revision of the BSC to allow for some gene flow.

None of the responders disagrees with Wu's first point, although animal population geneticists (outside of those studying hybrid zones) were slow to acknowledge it [8]. Similarly, no one disagrees with Wu's second point, and numerous other examples of speciation apparently driven by natural or sexual selection are cited. The real issues are whether there is a need to revise the BSC

and whether Wu's proposed revision has any advantages. Most of those who responded on these issues were not favorable to Wu's proposal.

Wu presents examples in which the BSC delineates taxa as species that would not attain this designation under his genic definition. For example, he notes that taxa infected with different strains of *Wolbachia* (hence preventing gene exchange through cytoplasmic incompatibility) would be defined as species by the BSC. Is this species assignment questionable, as Wu implies? A recent study reported two species of *Nasonia* that were isolated almost exclusively by bidirectional *Wolbachia* incompatibility [9], and clearly several scientists in the evolution community did not have a problem with this application of the BSC [10], because these *Nasonia* spp. are free to evolve independently [11].

Wu also argues that some taxa that are considered to be true species by the scientific community, such as *Drosophila simulans* and *Drosophila mauritiana*, have not attained species status according to the BSC. However, to make this argument, Wu relies on a 'strict isolation concept', in which any gene flow negates the BSC. Many cases exist of entities that are popularly considered to be species but in which allele exchange occurs over some parts of the genome. Some of the responders to Wu's paper felt that this was not a serious impediment to accepting the BSC [12], which considers speciation to be a process rather than an event. Furthermore, any concept would surely fail when held to such stringent interpretations. If we take Wu's concept to the extreme, populations of *Drosophila pseudoobscura* could be considered to be separate species. Some *D. pseudoobscura* populations exhibit fixed or nearly fixed differences in gene arrangement, and these differences appear to be adaptive [13]. Following a 'strict genic species concept', adaptive mutations in one of these populations (if in the inverted region) would not spread to other populations, and the gene pools within these arrangements do not mix. However, extensive gene flow has been observed at

other parts of the genome among these populations, suggesting that they do come into contact [14]. Unlike Wu's example of taxa infected with differing strains of *Wolbachia*, the scientific community considers these populations to be conspecific. Many other examples could be brought to bear where the BSC does not assume speciation is complete but 'loci of differential adaptation' exist.

Cases also exist in which the BSC would properly define taxa as species but in which Wu's genic concept would not. One example of nonadaptive speciation is polyploidy. Polyploidy causes speciation within a few generations, but there are no 'loci of differential adaptation' [15]. Hence, Wu's definition would consider diploids and resultant auto- or allotetraploids to be conspecific, whereas the BSC considers them to be heterospecific. Similar problems hold in cases where chromosomal rearrangements contribute to speciation [16]. In both of these scenarios, most evolutionary biologists adopt the BSC even though there is no indication of differential adaptation or even selection. Indeed, as several of the response papers noted, the community desires a species definition that is useful regardless of how species come to be [12,15], and the scenarios that Wu describes might not be universal [5,10]. The BSC is more generally useful, albeit imperfect, because all reproductive barriers have a similar effect in inhibiting gene flow, regardless of whether they originated by drift, meiotic drive, polyploidy, sexual selection, or natural selection.

Wu considers examples such as the above to be 'special cases' in the application of his concept [17]. He questions the frequency of cases of polyploidy, hence betraying an extensive botanical literature

on its extreme commonality [18]. Why should Wu's concept be allowed such glaring exceptions, whilst the BSC must be employed in the strictest sense? There seems to be a double standard here, and when Wu's arguments encounter these special cases, he falls back on reproductive isolation [19]. Hence, Wu's concept provides only a very limited, if any, conceptual advance.

Finally, we are left with the question of where such a debate leads us. On the one hand, species concepts determine how the process of speciation is studied. Because it is arguably the fundamental step in cladogenesis and the generation of biodiversity, speciation has an indisputable role in evolutionary studies. On the other hand, only very limited scientific advances have emerged from the introduction of more species concepts, particularly when compared with the exciting empirical results of the past 15 years. Lineage-based species concepts could provide some advantage for conceptualizing and classifying species, particularly allopatric taxa, but no species concepts have facilitated research on the process of speciation like the BSC has. The words of Jerry Coyne on the subject summarize my perspective: 'It is clear that the arguments will persist for years to come but equally clear that, like barnacles on a whale, their main effect is to retard slightly the progress of the field. Ultimately, speciation will require less rumination and more perspiration' [20].

References

- 1 Dobzhansky, T. (1935) A critique of the species concept in biology. *Philos. Sci.* 2, 344–355
- 2 Mayr, E. (1942) *Systematics and the Origin of Species*, Columbia University Press
- 3 Hey, J. (2001) The mind of the species problem. *Trends Ecol. Evol.* 16, 326–329
- 4 Wu, C.-I. (2001) The genic view of the process of speciation. *J. Evol. Biol.* 14, 851–865
- 5 Mayr, E. (2001) Wu's genetic view of speciation. *J. Evol. Biol.* 14, 866–867
- 6 Feder, J.L. (1998) The apple maggot fly, *Rhagoletis pomonella*: flies in the face of conventional wisdom about speciation? In *Endless Forms: Species and Speciation* (Howard, D.J. and Berlocher, S.H., eds), pp. 130–144, Oxford University Press
- 7 Mallet, J. (1995) A species definition for the Modern Synthesis. *Trends Ecol. Evol.* 10, 294–299
- 8 Rieseberg, L.H. and Burke, J.M. (2001) A genic view of species integration. *J. Evol. Biol.* 14, 883–886
- 9 Bordenstein, S.R. *et al.* (2001) *Wolbachia*-induced incompatibility precedes other hybrid incompatibilities in *Nasonia*. *Nature* 409, 707–710
- 10 van Alphen, J.J.M. (2001) Sexual selection, reproductive isolation and the genic view of speciation. *J. Evol. Biol.* 14, 874–875
- 11 Bridle, J. and Ritchie, M.G. (2001) Assortative mating and the genic view of speciation. *J. Evol. Biol.* 14, 878–879
- 12 Rundle, H.D. *et al.* (2001) Hybridization without guilt: gene flow and the biological species concept. *J. Evol. Biol.* 14, 868–869
- 13 Lewontin, R.C. *et al.* (1981) *Dobzhansky's Genetics of Natural Populations I–XLIII*, Columbia University Press
- 14 Schaeffer, S.W. and Miller, E.L. (1992) Estimates of gene flow in *Drosophila pseudoobscura* determined from nucleotide sequence analysis of the alcohol dehydrogenase region. *Genetics* 132, 471–480
- 15 Orr, H.A. (2001) Some doubts about (yet another) view of species. *J. Evol. Biol.* 14, 870–871
- 16 Britton-Davidian, J. (2001) How do chromosomal changes fit in? *J. Evol. Biol.* 14, 872–873
- 17 Wu, C.-I. (2001) Genes and speciation: a reply. *J. Evol. Biol.* 14, 889–891
- 18 Otto, S.P. and Whitton, J. (2000) Polyploid incidence and evolution. *Annu. Rev. Genet.* 34, 401–437
- 19 Shaw, K.L. (2001) The genealogical view of speciation. *J. Evol. Biol.* 14, 880–882
- 20 Coyne, J.A. (1992) Much ado about species. *Nature* 357, 289–290

Mohamed A. F. Noor

Dept of Biological Sciences, Louisiana State University, Life Sciences Bldg, Baton Rouge, LA 70803, USA.

Imperfect vaccines and imperfect models

Tom Smith

A recent paper by Gandon *et al.* presents a model for how leaky vaccines can lead to evolutionary changes in the virulence of parasites. Whilst readers of some of the press reaction to this paper might be forgiven for thinking that it referred to certainties about actual malaria vaccines, there are currently no malaria vaccines beyond the early clinical trial phase, so the paper could in principle offer no more than

theoretical predictions. The models might well be less appropriate for the chosen example of *Plasmodium falciparum* malaria than for other parasites. Critical review of the Gandon *et al.* paper highlights both the fact that the determinants of virulence in malaria are not well understood, and that monitoring of malaria vaccines should consider more than just the immediate effects on vaccine efficacy.

There is an important place in science for conjectures, and the example of malaria vaccines is justifiably topical. *Plasmodium falciparum* is the most important eukaryotic parasite of humans, with hundreds of millions of people infected at any one time, and at least 1 million people dying as a consequence each year. The need for a malaria vaccine is manifest, but none are currently registered for use, and