COMMENTARIES

MOLECULAR BIOLOGY & GENETICS

While neither universally applicable nor practical operationally, the biological species concept continues to offer a compelling framework for studying species and speciation

Few topics in evolutionary biology have received as much scrutiny and debate as the nature of species and species concepts. This is partly because species are central to many fields of biology (but especially evolution, ecology, systematics, and conservation biology), and there does not appear to be a single concept that can satisfy the needs of these different disciplines [1]. A related issue is that the nature of species varies widely across the domains of life due to differences in mode of reproduction (sexual versus asexual), life cycle, generation time, mating system, vagility, genome architecture, geographic range size, and a host of other features [2]. Species concepts that can accommodate this natural diversity [3,4] offer little guidance regarding how to delimit species, study their origins and evolution, or predict their evolutionary fate. As a consequence, users of species concepts typically choose the concept that suits their specific requirements, often with the recognition that their favored concept has known flaws, lacks universality or both.

The biological species concept (BSC) is a good example of this [5]. Its flaws are well known [2,6–8]; it flunks the universality test and is impractical operationally. However, the BSC offers a compelling framework for studying speciation, so evolutionary geneticists continue to use it. But should we? This is the issue Wang *et al.* [9] address in their critique. They summarize what is known about the geography and genetics of speciation and come to the surprising conclusion that we lack sufficient knowledge to reject the BSC.

We come to a different conclusion. In our view, there is ample information about the nature of species to reject a strict version of the BSC. Moreover, the BSC's liabilities when studying groups that are primarily asexual or that have a selfing mating system are well known [2]. Despite these limitations, we argue that the BSC continues to be a useful concept for studies of speciation in sexual and predominately outcrossing lineages. Below we highlight several points of agreement with Wang *et al.* [9], as well as several areas of disagreement. We conclude by describing our rationale for continuing to use the BSC, despite its flaws.

POINTS OF AGREEMENT

We are in agreement with many of the points the authors have made about speciation in previous papers and that are summarized in their critique. We agree that species' genomes are less tightly co-adapted than suggested by Mayr [5], and as a consequence, can be porous to gene flow when in sympatry or parapatry. We note that numerous hybrid zone studies over the past several decades have offered robust support for both conclusions [10–12]. Likewise, commonly reported patterns of heterogeneous genomic divergence are consistent with both differential introgression following secondary contact and divergence with gene flow [9,13]. Though it is important to keep in mind that recent selective sweeps in the absence of gene flow between populations can produce similar patterns [14].

The authors also offer useful insights here and elsewhere about the geography of speciation. They argue that gene flow during the early stages of speciation is compatible with Mayr's classic allopatric model of speciation. Using a case study of mangroves from the Indo-Malayan coast they further observe that allopatry is often intermittent, in this example due to the repeated openings and closures of the Strait of Malacca [15]. Lastly, they make the point that diversification rates in mangroves and many other taxa are poorly correlated with geographic features that can cause isolation, implying that geographical isolation is unlikely to be necessary for speciation in these groups. We agree with these assertions and note that the role of intermittent allopatry in speciation has been explored previously in the context of Quaternary ice ages, in which genomes persisting in refugia are thought to have undergone repeated cycles of allopatry and secondary contact, protected in part by hybrid zones [16]. More generally, the importance of geographic isolation appears to correlate both with vagility and with the strength of habitat associations. For example, sister species of plants, but not birds, are frequent on isolated oceanic islands [17,18]. The most straightforward explanation for this difference is that geographical isolation is necessary for speciation in birds, but not for many lineages of plants (see also ref. [19]).

POINTS OF DISAGREEMENT

While this critique is a stimulating read, we disagree with the use of the BSC to define both a process and a concept of species. This confounds the products of speciation (i.e. species) with the mechanisms of speciation, and potentially constrains our

views about how speciation can occur. Also, bear in mind that biological barriers to gene flow (reproductive barriers) typically are the result of speciation, not its cause [20]. This is most obviously true for species that have diverged exclusively in allopatry. Thus, reproductive barriers are best interpreted as indicators of progress towards speciation [1]. The BSC is (or at least should be) agnostic about the geographic context of speciation or the evolutionary forces responsible for the evolution of reproductive barriers. That is, implementation of the BSC does not (and should not) depend on whether a given species diverged in sympatry or allopatry, or whether reproductive barriers arose mainly as a consequence of genetic drift, divergent natural selection, or by whole genome duplication.

The authors argue that evidence of gene flow between good species with strong reproductive isolation (RI) would be sufficient to reject the BSC, but that such evidence does not yet exist. We were surprised by the latter claim, especially given that an increasing number of studies in plants and animals have not only measured the strength of RI in nature, but also have quantified levels of interspecific gene flow, in some cases across extremely strong reproductive barriers [21–24]. An example comes from a pair of widespread sunflower species, *Helianthus annuus* and *H. petiolaris*, which have overlapping geographic distributions across much of Central and Western North America. The two species diverged circa 1.8 mya and are strongly isolated reproductively [23]; total isolation—calculated by compounding the contributions of eight individual barriers—was >0.99999 in both directions. Thus, these are very good species! The interspecific migration rate (m) estimated from population genetic data is very small ($<10^{-7}$), as expected given the strength of RI. However, because these species have very large effective population sizes ($N_e > 10^6$), the predicted number of migrants per generation is high enough ($N_e m = 0.34–0.76$) to produce mosaic genomes.

A final point of disagreement concerns the sensitivity of current genomic methods for detecting small introgressions. While we agree that the power for identifying individual introgressions is reduced when they are small, if there are many small introgressions across the genome, then the signature of interspecific gene flow is easily and robustly detected by various whole genome tests such as Patterson's D statistic [25] or from programs for identifying population structure such as Structure [26] or Admixture [27].

CONCLUSION

If the BSC is faulty, then why do evolutionary geneticists continue to use it? Likewise, how can a focus on the evolution of reproductive barriers be justified? As we noted in the introduction, the main reason that evolutionary geneticists continue to use the BSC is that it offers a powerful framework for studying speciation. We previously documented a strong, albeit imperfect, correlation between the strength of RI and species delimitation by taxonomists [28], which offers empirical support for such a research program. On the other hand, we recognize that multiple evolutionary forces contribute to species identity and cohesion,

including gene flow/RI, common descent, stabilizing and parallel selection, and genetic constraints [2]. Some of these likely correlate as strongly with taxonomic species as does RI, perhaps suggesting that students of speciation should expand the focus of their research beyond RI. However, as we have argued elsewhere [29], gene flow and RI are population and species-level phenomena, the levels of divergence relevant to speciation studies. In contrast, selection acts most strongly on genes or individuals, whereas common descent and genetic constraints contribute to cohesion across all taxonomic levels. In our view, this justifies a focus on gene flow/RI, while recognizing that studies which seek to comprehensively identify and order the evolutionary forces contributing to species cohesion would add significantly to our understanding of both species and speciation.

Conflict of interest statement. None declared.

Lexuan Gao[1,2] and Loren H. Rieseberg[2,*]

[1]CAS Center for Excellence in Molecular Plant Sciences, Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, China
[2]Department of Botany and Biodiversity Research Centre, University of British Columbia, Canada
***Corresponding author.** E-mail: lriesebe@mail.ubc.ca

REFERENCES

1. Harrison RG. *Endless Forms: Species and Speciation.* Oxford: Oxford University Press, 1998, 19–31.
2. Templeton AR. *Speciation and Its Consequences.* Sunderland: Sinauer Associates, 1989, 3–27.
3. Simpson GG. *Evolution* 1951; **5**: 285–98.
4. de Queiroz K. *Endless Forms: Species and Speciation.* Oxford: Oxford University Press, 1998, 57–75.
5. Mayr E. *Animal Species and Evolution.* Cambridge: Harvard University Press, 1963.
6. Donoghue MJ. *The Bryologist* 1985; **88**: 172–81.
7. Mallet J. *Trends Ecol Evol* 1995; **10**: 294–9.
8. Paterson HEH. *Species and Speciation.* Pretoria: Transvaal Museum, 1985, 21–9.
9. Wang X, He Z and Shi S *et al. Natl Sci Rev* 2020; **7**: 1387–97.
10. Barton NH and Hewitt GM. *Nature* 1989; **341**: 497–503.
11. Dudek K, Gaczorek TS and Zieliński P *et al. Mol Ecol* 2019; **28**: 4798–810.
12. Rieseberg LH, Whitton J and Gardner K. *Genetics* 1999; **152**: 713–27.
13. Wu C-I. *J Evol Biol* 2001; **14**: 851–65.
14. Cruickshank TE and Hahn MW. *Mol Ecol* 2014; **23**: 3133–57.
15. He Z, Li X and Yang M *et al. Natl Sci Rev* 2019; **6**: 275–88.
16. Hewitt GM. *Nature* 2000; **405**: 907–13.
17. Coyne JA and Price TD. *Evolution* 2000; **54**: 2166–71.
18. Papadopulos AST, Baker WJ and Crayn D *et al. Proc Natl Acad Sci USA* 2011; **108**: 13188–93.
19. Anacker BL and Strauss SY. *Proc Royal Soc B* 2014; **281**: 20132980.
20. Rabosky DL. *Biol J Linn Soc* 2016; **118**: 13–25.
21. Brandvain Y, Kenney AM and Flagel L *et al. PLoS Genet* 2014; **10**: e1004410.
22. Roux C, Tsagkogeorga G and Bierne N *et al. Mol Biol Evol* 2013; **30**: 1574–87.
23. Sambatti JBM, Strasburg JL and Ortiz-Barrientos D *et al. Evolution* 2012; **66**: 1459–73.

24. Zhang W, Dasmahapatra KK and Mallet J *et al. Genome Biol* 2016; **17**: 25.

25. Durand EY, Patterson N and Reich D *et al. Mol Biol Evol* 2011; **28**: 2239–52.

26. Pritchard JK, Stephens M and Donnelly P. *Genetics* 2000; **155**: 945–59.

27. Alexander DH, Novembre J and Lange K. *Genome Res* 2009; **19**: 1655–64.

28. Rieseberg LH, Wood TE and Baack EJ. *Nature* 2006; **440**: 524–7.

29. Baack EJ, Melo MC and Rieseberg LH *et al. New Phytol* 2015; **207**: 968–84.

MOLECULAR BIOLOGY & GENETICS

Is it time to abandon the biological species concept? No

The *Oxford English Dictionary* defines a concept as, 'an idea of a class of objects, a general notion'. It follows from this definition that a concept cannot be rejected in the way that a hypothesis might be rejected if its predictions are inconsistent with observations. Instead, a concept must be judged by its heuristic value: does it help in making sense of the natural world?

The biological species concept (BSC) was designed to aid understanding of biological diversity, particularly the ubiquitous observation that sexually reproducing organisms exist in more or less distinct phenotypic and genetic clusters rather than in a continuum of forms. It does so by focusing attention on the contrast between successful interbreeding within groups and reproductive isolation between them. Distinct groups can form in other ways, and can occur in organisms that lack regular sexual reproduction. This has led to alternative conceptualizations of the units of diversity [1,2]. However, the fact that the BSC is highlighted in every biology textbook and lecture course, more than 80 years after it was introduced and formalized [3,4], is testament to its continued utility. Perhaps most importantly, the BSC identifies a research programme for understanding the origin of biological diversity by equating the process of speciation with the evolution of reproductive isolation. This has been the foundation of a huge body of research in evolutionary biology since the neo-Darwinian synthesis, which has led to a much deeper understanding of species and speciation, although the job is certainly not yet completed.

Understanding the process by which species form can certainly aid in understanding the nature of species. Indeed, concepts in general aim to be 'fundamental links bridging observable patterns and inferred processes' [1] and this is certainly true of the BSC. However, Wang *et al.* [5] seek to go a step further: rather than linking the existence of discontinuities among species with the processes of gene flow, natural selection and the evolution of reproductive isolation, which is a standard interpretation of the BSC, they make the BSC dependent upon a particular mode of speciation, namely 'allopatric speciation'. Mayr [6] did not make this connection. Indeed, he discussed species concepts (Chapter 2) and speciation processes (Chapters 15–17) in separate parts of his book. Nor has the connection been made in more recent monographs [7,8]. The link made

by Wang *et al.* [5] is problematic in principle. Suppose it can be shown that two populations are now reproductively isolated and have acquired that isolation without any period of spatial separation, would Wang and co-workers conclude that the populations belong to the same species? This is, actually, not just a theoretical problem: the origin of polyploid species provides multiple concrete examples (e.g. [9]). Linking the BSC to a particular 'mode of speciation' is also problematic because of the difficulty of defining and distinguishing these modes [10]. In reality, speciation is complex, extended over time and space and involving multiple processes, leading to a wide range of possible routes towards complete reproductive isolation [11,12]. The accumulated evidence [7,8,12,13] suggests that many of these paths have actually been followed.

Wang *et al.* [5] suggest that an alternative to the BSC is a 'genic view' of species where 'species are defined by a set of loci that govern the morphological, reproductive, behavioral and ecological characters'. As it stands, this definition is incomplete because it does not specify what sets the significant characters apart from the rest of the phenotype or what features of the set of loci distinguish species. However, it is clear from their further discussion that the characters in question are those that contribute to reproductive isolation ('fitness-reducing upon introgression') and that these loci should define distinct genetic clusters despite potential for gene flow. If the BSC allows for incomplete reproductive isolation, as is commonly accepted (e.g. [1,7,14]), then there is actually no difference between this genic view and the BSC, unless the BSC is tied to allopatric accumulation of reproductive isolation and the genic view is not. To answer the question posed by Wang *et al.* [5]: No, it is not time to abandon the BSC.

Nearly 20 years ago, Wu [15] proposed a 'genic view of *the process of speciation*'. This proposal struck a chord and fig. 1 from Wu's paper has been very widely reproduced. It describes snapshots in the evolution of reproductive isolation from the appearance of the first barriers to gene flow to the complete absence of successful interbreeding (described as 'Stages', perhaps with the unhelpful implication of discontinuities in a continuous process). The underlying idea of an initially semi-permeable barrier that can evolve to exclude a larger and larger proportion