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PERSPECTIVE

Butterfly genomics sheds light on the process of hybrid speciation

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How common is hybridization between species and what effect does it have on the evolutionary process? Can hybridization generate new species and what indeed is a species? In this issue, Gompert et al. (2014) show how massive, genome-scale data sets can be used to shed light on these questions. They focus on the Lycaeides butterflies, and in particular, several populations from the western USA, which have characteristics suggesting that they may contain hybrids of two or more different species (Gompert et al. 2006). They demonstrate that these populations do contain mosaic genomes made up of components from different parental species. However, this appears to have been largely driven by historical admixture, with more recent processes appearing to be isolating the populations from each other. Therefore, these populations are on their way to becoming distinct species (if they are not already) but have arisen following extensive hybridization between other distinct populations or species (Fig. 1).

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Their data set must be one of the largest outside of genetics, genomics, hybridization, speciation

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Overall, the results support several of the populations as being stable hybrid lineages. Nevertheless, the strictest definitions of hybrid species specify that the process of hybridization between the parental species must be instrumental in driving the reproductive isolation of the new species from both parental populations (Abbott et al. 2013). This is extremely hard to demonstrate conclusively because it requires us to first of all identify the isolating mechanisms that operated in the early evolution of the species and then to show that these were caused by the hybridization event itself. One advantage of the Lycaeides system is that the species appear to be in the early stages of divergence, so barriers to gene flow that are operating currently are likely to be those that are driving the species divergence. While there is some evidence that hybridization gave rise to traits that allowed the new populations to colonize new environments (Gompert et al. 2006; Lucas et al. 2008), there is clearly further work to be carried out in this direction.

One of the rare examples of homoploid hybrid speciation (hybrid speciation without a change in chromosome
number) where the reproductive isolation criterion has been demonstrated, comes from the *Heliconius* butterflies. In this case, hybridization of two species has been shown to give rise to a new colour pattern that instantly becomes reproductively isolated from the parental species due to mate preference for that pattern (Mavarez et al. 2006). However, while this has become a widely accepted example (Abbott et al. 2013), the naturally occurring ‘hybrid species’ in fact has derived most of its genome from one of the parental species, with largely just the colour pattern controlling locus coming from the other parent, a process that has been termed ‘hybrid trait speciation’ (Salazar et al. 2010). This distinction is an important one in terms of our understanding of the organization of biological diversity. While hybrid trait speciation will still largely fit the model of a neatly branching evolutionary tree, with perhaps only the region surrounding the single introgressed gene deviating from this model, hybrid species that end up with mosaic genomes, like *Lycaeides*, will not fit this model when considering the genome as a whole.

This distinction also more broadly applies when comparing the patterns of divergence between *Heliconius* and *Lycaeides*. These two butterfly genera have been driving forward our understanding of the prevalence and importance of hybridization at the genomic level, but they reveal different ways in which hybridization can influence the organization of biological diversity. Recent work in *Heliconius* has shown that admixture is extensive and has been ongoing over a large portion of the evolutionary history of species (Martin et al. 2013; Nadeau et al. 2013). Nevertheless, this has not obscured the clear and robust pattern of a bifurcating evolutionary tree when considering the genome as a whole (Nadeau et al. 2013). In contrast in *Lycaeides*, the genome-wide phylogeny clearly does not fit a bifurcating tree, resembling more of a messy shrub, with hybrid taxa falling at intermediate positions on the phylogeny (Gompert et al. 2014). The extent to which we need to rethink the way we describe and organize biological diversity will depend on the relative prevalence of these different outcomes of hybridization.
We are likely to see many more of these types of large sequence data sets for ecologically interesting organisms. Gompert et al. (2014) show that these data need not only be a quantitative advance, but can also qualitatively change our understanding of the evolutionary history of these organisms. In particular, analysing common and rare genetic variants separately may provide information that would otherwise be missed. The emerging field of ‘speciation genomics’ (Seehausen et al. 2014) should follow this lead in developing new ways of making the most of the flood of genomic data that is being generated, but also improve methods for integrating this with field observations and experiments to identify the sources and targets of selection and divergence.

References

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