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PERSPECTIVE

Repeatability, ephemerality and inconvenient truths in the speciation process

ASHER D. CUTTER

Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, ON, M5S 3B2, Canada

Everyone appreciates the happy fiction that species conform to the simple theoretical convenience of a single panmictic population. In speciation genetics, a further standard simplification is that it is only those genetic differences that are fixed between diverging populations that need concern us in order to understand the accumulation of intrinsic barriers to reproduction. To a first approximation, of course, both of these assumptions are appropriate and theory based on them provides compelling insights into diverse evolutionary phenomena (Orr & Turelli 2001). But what else can we learn about the begetting of biodiversity, speciation, by considering explicitly some less convenient realities of natural populations? Specifically, how does genetic variation at incompatibility loci within a species influence interspecies hybridization upon secondary contact? And, in nature, how repeatable among distinct bouts of secondary contact are the genomic outcomes of hybridization? Mandeville *et al.* (2015) tackle exactly this question in their new study in *Molecular Ecology* on five species of suckers, fish of the genus *Catostomus*, that overlap sympatrically in different portions of their subdivided ranges that occupy different rivers. They document substantial genomic heterogeneity in realized hybridization in nature, both among species pairs and among the source populations for hybrids of a given species pair. This imperfect repeatability of episodes of hybridization implies greater permeability of species barriers in some parts of their range, with intriguing consequences for how the integrity of species as independently evolving units could be susceptible to collapse.

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Mandeville *et al.* (2015) conducted genotyping by sequencing in a sample of nearly 800 fish, comprised of five pure species of *Catostomus* and various natural hybrids among them (Fig. 1). The collections were derived from three river locations that differ in the combination of sympatric species present. Using an experimental design that exploits high multiplexing with low sequence coverage per sample, Mandeville *et al.* (2015) focused on a convenient subset of variants to infer genomic trends of hybridization history for these lineages. They could consistently identify ancestry proportions of hybrid fish in addition to being able to genetically differentiate the pure species individuals by analysing over 4000 polymorphic variants, pumped through Bayesian admixture estimation machinery. At a genomewide level, genetic distances between species were more than 10-fold greater than the genetic distances among populations of con-specific fish from different rivers. Mandeville *et al.* (2015) observed less extensive hybridization between more distantly related species pairs, consistent with accumulating reproductive isolation over time. More interestingly, they demonstrate that genomic signatures of hybridization differ among rivers for the same combinations of a given *Catostomus* species pair: the amount of reproductive isolation realized in nature depends on which subpopulations you are talking about.

The outcome of hybridization upon secondary contact of a species pair ought to be genetically repeatable, provided that reproductive isolation involves divergent alleles that have fixed between the species to yield intrinsic Dobzhansky–Muller (DM) incompatibilities. That is, the same portions of the genome ought to be either resistant or permissive to genetic exchange in the face of hybridization, depending on whether those portions of the genome encode incompatibility loci. However, this logic will fold if the incompatibility loci are polymorphic (Rieseberg & Blackman 2010; Cutter 2012). For example, only some subpopulations of species *A* might carry the derived incompatibility allele at high frequency, so interspecies crosses $A \times B$ involving distinct subpopulations (A_1, A_2, etc.) can differ in the magnitude of reproductive isolation with species *B*. Similarly, if distinct rounds of secondary contact occur in different environments, then even fixed incompatibilities might show nonuniform effects in hybrids, owing to environment dependence (i.e. environment-by-epistatic interactions, G×G×E). The data for *Catostomus* are consistent with either of these two scenarios: there appear to be either genetically variable reproductive incompatibilities or environment-dependent incompatibilities.

It is easy to envision environmental differences among rivers acting to modulate the extent of *Catostomus* hybridization. If so, however, DM-like incompatibilities might not be strictly necessary to explain the patterns of hybrid admixture, as environmental mismatches of hybrid phenotypes underlain by an additive genetic basis might prove

Correspondence: Asher D. Cutter, Fax: 416 978 5878;
E-mail: asher.cutter@utoronto.ca

Fig. 1 A bluehead × longnose (*C. discobolus* × *C. catostomus*) hybrid from Big Sandy River, Wyoming. Photograph courtesy Elizabeth Mandeville.

sufficient. Unfortunately, as in most systems, the genetic basis to reproductive isolation remains unknown. Environmental differences could also influence premating barriers before DM incompatibilities even get a chance to act, for example, if water turbidity disrupted sexual signalling differentially among rivers. Such environmental differences have led to temporal changes in reproductive isolation in other fishes to foster hybridization (Seehausen *et al.* 1997; Taylor *et al.* 2006; Vonlanthen *et al.* 2012). However, Mandeville *et al.* (2015) argue that premating isolation owing to sexual selection is unlikely to be a potent factor in *Catostomus*, at least in terms of obvious courtship or mate signalling cues. Just as it is easy to envision environmental influences, it also is easy to envision polymorphic incompatibilities being responsible, given the evidence for their existence in many systems (Rieseberg & Blackman 2010; Cutter 2012). Clearly, controlled crossing experiments under distinct conditions in *Catostomus* will be crucial to test alternative hypotheses about the genetic architecture of isolation and the role of intrinsic and extrinsic factors. Analyses of an improved map of hybrid introgression in the context of genomic features, along with emerging possibilities in phylogenetic comparative approaches in speciation genetics (Wang *et al.* 2013), also may prove insightful.

Irrespective of the genetic details of reproductive isolation in *Catostomus*, it is clear that hybridization occurs more readily in some rivers than others. When species boundaries are more porous for some populations than others, secondary contact is provided more opportunities to yield merger of lineages that have incomplete reproductive isolation between them that can then ramify across the entire range. That is, multiple instances of renewed sympatry increase the risk of extinction by fusion, whereby what once was considered two species resorb back into one (Seehausen *et al.* 2008; Rosenblum *et al.* 2012). The potential for ephemeral speciation thus represents an intriguing wrinkle in the connection between micro- and macro-evolutionary changes. Moreover, in *Catostomus*, secondary contacts are promoted by introduced species, which raises further issues related to conservation biology and the potential for creating species swarms.

Population subdivision within species, and the genetic differentiation that goes along with it, is common in the wild and yet remains incompletely integrated into our thinking about micro-to-macro-evolutionary transitions. Explicit consideration of population subdivision with the repeated instances of secondary contact in *Catostomus* helps to lay bare the influence that variable reproductive isolation can exact on incipient speciation, particularly in the context of environmental heterogeneity and the potential for extinction by fusion. Studies like the one by Mandeville *et al.* (2015) deftly illustrate how genome-scale analysis of large samples can turn the tables on some of these inconvenient truths of natural populations, exploiting them for a richer understanding of the speciation process.

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A.D.C. studies genome evolution, speciation, and adaptation, focusing on population genetic and molecular evolutionary approaches in nematodes.

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