

Editorial

The Genetics of Speciation: Considering Early-Acting Isolation, Hybrid Evolution, and Epigenetic Mechanisms

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Since Darwin's time, evolutionary biologists have sought to understand how species arise. The study of speciation remains a focus of evolutionary biology, and since the early 20th century, characterizing the genetics underlying this process has also become a central goal. Much research into the genetics of speciation has centered on identifying the genes underlying reproductive isolating mechanisms, or 'speciation genes' (see Nosil and Schluter, 2011 for a discussion of this term). With information about such genes available from many systems, general questions about how speciation proceeds may be addressed: How many genes contribute to speciation? Is reproductive isolation more commonly the result of divergence in protein-coding regions or regulatory regions? Is reproductive isolation more frequently the result of natural selection or genetic drift? (Coyne and Orr, 2004; Nosil and Schluter, 2011). Given recent advances in technology, such questions have become accessible in systems that were previously intractable for studying the genetics of speciation. Moreover, with this increase in the accessibility of genetic analyses for non-model systems, a broader set of questions about the genetics of speciation can now be addressed.

Research into the genetics of speciation began in the early 20th century, around the time of the Modern Synthesis. Much of this early work focused on the genetics responsible for intrinsic postzygotic isolation, specifically hybrid sterility and inviability, in laboratory crosses of *Drosophila* (reviewed in Coyne and Orr, 2004; Wolf et al., 2010). The causes of Haldane's Rule—the widespread pattern of greater postzygotic isolation in the heterogametic sex—were of particular interest during these early years. Additionally, with a simple verbal model explaining how hybrid sterility could evolve due to between-locus incompatibilities, Dobzhansky (1940) and Muller (1940) made a great contribution to our understanding of the causes of intrinsic postzygotic isolation. This model has stood the

test of time, with work from numerous systems supporting a central role for genetic incompatibilities in postzygotic isolation (e.g., Fishman and Willis, 2001; Presgraves et al., 2003; Willett, 2006).

Now, approximately 80 years after these early studies, the genetics of speciation remains a vibrant research area in evolutionary biology. Fine-scale mapping efforts, in systems that can be crossed in the laboratory, have allowed the identification of loci responsible for reproductive isolation, the subsequent analyses of the evolutionary forces causing divergence (e.g., Presgraves et al., 2003; Brideau et al., 2006; Wright et al., 2013), as well as elucidation of the genomic distribution of these loci (e.g., Ballerini et al., 2012; McDermott and Noor, 2012). Moreover, recent advances in genome sequencing technology have made speciation genetics a feasible area of study in both laboratory and natural systems alike (Ellegren and Sheldon, 2008; Rice et al., 2011). Although fewer genetic tools and less genetic information are available for wild populations, these systems offer the advantage of a wealth of ecological information and an understanding of the traits that are important for fitness in natural environments. A broad view of the genetics of speciation might therefore include, among many other topics, identification and functional analyses of the genes underlying pre- or postzygotic isolation (Presgraves et al., 2003; Ballerini et al., 2012; Wright et al., 2013), studies of the consequences of gene flow or hybridization for speciation (Nosil et al., 2012; Keller et al., 2013), studies of loci underlying divergent adaptations and ecological speciation (Rogers and Bernatchez, 2007; Via et al., 2012; Keller et al., 2013), and investigations of the genomic distribution of loci contributing to divergence and reproductive isolation (McDermott and Noor, 2012; Ellegren et al., 2012). Each of the four papers making up this special column in *Current Zoology* on the genetics of speciation touches on at least one of these topics. Although a thorough coverage of ongo-

ing research into the genetics of speciation is beyond the scope of one special column, the papers presented here introduce important questions and suggest exciting avenues for future research in the field.

A classic question in the study of speciation is whether or not complete geographic isolation is a necessary condition for speciation (Mayr, 1963; Coyne and Orr, 2004). In the context of speciation genetics, the question becomes whether gene flow between diverging populations will break down associations between loci underlying reproductive isolation and adaptation (Felsenstein, 1981; Servedio, 2009). Several well-supported examples of sympatric speciation, such as the Lord Howe Island palms (Savolainen et al., 2006) and the apple maggot flies (Powell et al., 2012 and references therein), have made it difficult to argue that complete geographic isolation is necessary. Current discussion has moved away from considering the probability of speciation in only the extreme biogeographical settings of complete allopatry versus sympatry, and now focuses on the more realistic scenario of speciation with gene flow (Butlin et al., 2008; Via, 2012). But given that many instances of speciation likely involve at least some gene flow, how are associations between the genes underlying reproductive isolation and adaptation maintained? Next-generation sequencing technologies have opened up the possibility of uncovering the genetic basis of traits associated with reproductive isolation and adaptation in wild populations (Rice et al., 2011). As we learn more and more about the genetics underlying such traits in natural systems, we will begin to understand the types of traits and genetic architectures that allow speciation to occur in the face of gene flow.

In an original research paper in this special column, Stearns et al. (2013) examine this enduring question of how speciation can occur despite high levels of gene flow. As the authors point out, Felsenstein's (1981) now classic theoretical work predicts that divergence may be more likely to persist in the face of gene flow when assortative mating is based on a single allele. In such a case, recombination between the assortative mating locus and niche adaptation/preference loci should not result in the breakdown of reproductive isolation between divergent populations. Stearns et al. (2013) suggest that philopatry, a propensity for an individual to remain where it was born, may act as such a single allele isolating mechanism during host shifts in phytophagous insects. They examined the strength of philopatry in populations of the insect *Enchenopa binotata* experimentally shifted to either novel or ancestral host

plant species. The authors also examined whether the experimental populations evolved enhanced performance on or preference for the novel host plant. The results suggest that philopatry is a strong and early-acting barrier to gene flow after a host shift, while preference and performance adaptation on the novel host lag behind.

Another key focus in speciation research concerns the role played by hybridization (Abbott et al., 2013). As noted above, when gene exchange occurs between populations relatively early in divergence, it may slow or even undo any differentiation that had occurred. But what happens when two relatively distinct species come into secondary contact, and hybridization occurs? One possibility is that any existing barriers to gene flow are broken down and the species fuse into one. On the other hand, if the level of hybridization is balanced by selection against hybrid offspring with low fitness, differentiation may be maintained (Barton and Hewitt, 1985). Selection against the production of unfit hybrid offspring may also act to strengthen barriers to gene flow, effectively finalizing speciation, in a process known as 'reinforcement' (Pfennig, 2003; Servedio and Noor, 2003; Jaenike et al., 2006). The idea that hybridization may play a creative role in speciation—either through adaptive introgression or as the first step in the formation of new hybrid species—has grown to wider appreciation recently (Dasmahapatra et al., 2012; Abbott et al., 2013; Keller et al., 2013). Formation of new hybrid species in which the chromosome number differs from either of the parental species—termed polyploid speciation—occurs more often in plants than animals (but see Holloway et al., 2006). In homoploid hybrid speciation, the new hybrid species retains the ancestral number of chromosomes, but has a genome made up of segments from both parental species. Two of the review papers in this special column highlight different aspects of hybridization's creative role in speciation.

In the first review paper, Eroukhmanoff et al. (2013) consider the factors affecting whether and how recurrent homoploid hybrid speciation occurs. The authors note that when two parental genomes recombine, a variety of outcomes is possible, ranging from complete hybrid inviability to the repeated production of novel, functional hybrid genomes. They suggest that the genomic, ecological, and historical factors present for any given hybridization event will determine the outcome of hybridization, and whether hybrid speciation may subsequently occur or even recur. Eroukhmanoff et al. (2013) also propose a framework for studying evolvability and

variation in genomic mosaicism in hybrids, allowing the prediction of which of many possible evolutionary trajectories a hybrid population may evolve along.

Next, Bailey et al. (2013) examine another aspect of hybridization and the potential for subsequent speciation. They note that the mode of selection acting on divergent traits in parent taxa will determine whether trait values in hybrids tend to be intermediate or transgressive, and will also affect whether incompatible loci tend to accumulate on autosomes versus sex chromosomes. Bailey et al. (2013) argue that these different effects, determined by the mode of selection in parental taxa, may in turn affect the likelihood of subsequent hybrid adaptation and even speciation, as well as the directions of evolution available to hybrids. They present a set of predictions and some suggestions for empirical tests of their ideas for use in future research on evolution in hybrids.

Another topic under much discussion is the role of phenotypic plasticity in speciation (West-Eberhard, 2005; Pfennig et al., 2010; Butlin et al., 2012). Phenotypic plasticity is the ability of a single genotype to produce multiple phenotypes depending on environmental conditions. If plasticity allows individuals from two populations in divergent environments to produce different optimal phenotypes without any genetic differentiation, then local adaptation, and therefore ecological speciation, may be unlikely to occur. Alternatively, plasticity may allow colonization of and survival in new environments. Given enough time, genetic assimilation or genetic accommodation may follow (West-Eberhard, 2003), and reproductive isolation may result. This is one of several mechanisms by which plasticity may facilitate speciation (Pfennig et al., 2010). Investigations of differential gene expression and the mechanisms underlying plasticity will help to shed light on the role of plasticity in speciation.

In the final review paper, Smith and Ritchie (2013) turn to epigenetic mechanisms, which may underlie the expression of plasticity. Epigenetic mechanisms are a topic of growing interest in evolutionary biology. They act to influence phenotypic variation through chemical modifications of DNA, RNA, or proteins, in contrast to the better understood role played by changes in DNA sequence. Smith and Ritchie (2013) focus specifically on the roles of phenotypic plasticity and epigenetic mechanisms in ecological speciation, in which reproductive isolation results from adaptation to divergent environments. The authors note that phenotypic plasticity may play an important role in persistence in and ad-

aptation to novel environments, that epigenetic modifications may often underlie plastic traits, and thus, that heritable epigenetic variation may contribute to ecological speciation. They review evidence for transgenerational epigenetic variation, and suggest several paths by which epigenetic variation may lead to reproductive isolation. Finally, they pose a variety of questions and suggest particularly promising study systems to inspire future research on the role of epigenetics in speciation.

Together, the papers in this special column highlight both classic problems and hot topics in the genetics of speciation. They also illustrate the great breadth of topics being addressed in the field today. As the cost of DNA sequencing continues to drop, researchers will carry on adding to our knowledge of the genetics of speciation in more and more systems, bringing us closer to understanding Darwin's "mystery of mysteries" (Darwin, 1859), the origin of species.

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