Speciation Continuum

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Speciation, the process that has produced an elaborate and seemingly endless diversity of species, is one of the most fundamental subjects of study in evolutionary biology. It is also one of the most vexing, in part because speciation occurs on an evolutionary time scale, thus presenting a multitude of temporal perspectives from which to witness the process. The “speciation continuum” can be defined as the continuous sequence of genetically-based changes that occur as two lineages diverge from one another on the pathway to reproductive isolation. Within this context, divergent evolution (the causes) and reproductive (genetic) isolation (the consequences) are the primary elements of the speciation process. These two elements are mirrored in the two great traditions of speciation research. On the one hand, Darwin’s (1859) view on speciation emphasizes the evolution of biological distinctions and the causes of their divergence; on the other, Mayr’s (1942) perspective on speciation emphasizes the evolution of the reproductive barrier between species. For many decades, the Mayrian view has been prominent as much research has focused on the genetic outcomes of the speciation process. In more recent years, emphasis has shifted toward understanding the causes of divergence that initiate speciation and create biological distinctions.

Realizing a need for a more explicit integration of the Darwinian and Mayrian perspectives, Shaw & Mullen (2011) and Mullen & Shaw (2014) developed a framework centered on “speciation phenotypes”, which emphasizes the role of phenotypic change in identifying rules of speciation. A central goal of this integration is to map out how divergent evolution transforms populations into reproductively and genetically isolated groups in order to understand how speciation works. In July 2013, the American Genetic Association’s annual president’s symposium convened “Speciation Continuum: A discussion on the Origin of Species”, bringing together many scientists examining a variety of taxa and diverse areas of speciation research. A deliberate attempt was made to juxtapose the Darwinian with the Mayrian approaches to the study of speciation in the lineup of invited speakers, to inspire further integration in the future of our discipline. Several of these presentations are represented in this special volume. They can be aligned with one or the other focus; some articles attempt to characterize phenotypic components of speciation and the forces of their divergence, while others focused more explicitly on the consequences of reproductive isolation.

Among those studies tackling speciation questions centered on diverging phenotypes include Etges (this issue), Yim et al. (this issue) and Scordato et al. (this issue). Etges examines current knowledge of speciation phenotypes in the Drosophila mojavensis system, one of the best-studied Drosophila systems for ecologically relevant phenotypes. Drawing from decades of work on the genetic and environmental basis of rapidly diverging phenotypes related to differentiation in host use, he produces a unique perspective on species formation in this iconic genus. Yim et al. (this issue) present insights into the genetic basis of a major axis of differentiation, body coloration, of the Tetragnathus spider genus that has undergone rapid adaptive radiation in the Hawaiian islands. They explore the link between an intraspecific developmental polyphenism in coloration and the interspecific divergence of this same trait. On a much larger scale, Scordato et al. (this issue) conduct a meta-analysis to explore the relationship between sexual selection, ecology and mate choice. Patterns they reveal suggest a specific role for ecology in the action of sexually selected phenotypes during speciation.

Among those studies tackling speciation questions centered on consequences of reproductive isolation and the nature of the species boundary include Harrison and Larson (this issue), Freder et al. (this issue) and Hudson and Price (this issue). Harrison & Larson (this issue) present a conceptual exploration of the semi-permeable nature of species boundaries. They highlight the fact that species boundaries, as defined by phenotypes, genes and genome regions, may remain distinct in the face of ongoing gene flow, but yet may not be uniform in space or time. The species boundary is also the subject of Freder et al.’s contribution (this issue), wherein they address the evolutionary mechanisms that shape patterns of genomic divergence across the species boundary continuum. They suggest that the accumulation of mutations subject to relatively low levels of divergent selection, can lead to genome-wide “congealing,” resulting in the rapid increase of adaptive differentiation, linkage disequilibrium, and reproductive isolation. Finally, integrating the Darwinian and Mayrian perspectives, Hudson & Price (this issue) discuss the roles of sexual selection and reinforcement in the evolution of mating behavior and formation of the species boundary. As such, their paper covers a broad swath of the species continuum, concluding that premating as well as postmating dynamics must be considered in the establishment of secondary contact between newly formed species.
Leading off this excellent collection of papers is an eclectic review of recent speciation theory by Gavrilets (this issue), who delivered the AGA Key Distinguished Lecture. Several theoretical advances have been made in speciation research in the last ten years and these advances have come from diverse modeling traditions. A collection of insightful theory is brought together providing a valuable guide to these recent advances, areas in need of further work, and questions that are in need of empirical dissection for further progress. Gavrilets’s (this issue) discussion of models tailored to specific biological systems is particularly rewarding, highlighting the need for closer collaborations between theoreticians and empiricists working across the speciation continuum.

As the study of speciation moves forward into the post-genomics era, it is clear that the boundaries between traditional methods and ideologies are rapidly breaking down, synergizing new questions and research directions. The distinction between model and non-model systems, for example, continues to blur, fostering unique insights into the evolutionary mechanisms shaping patterns of variation at multiple levels of biological organization. As a result, researchers are increasingly able to integrate across temporal windows illuminating the evolutionary mechanisms driving divergence. This improves our ability to predict the consequences of phenotypic evolution for patterns of reproductive isolation, and to directly tests hypothesis about the evolving species boundary. From our perspective, this ongoing integration of the Darwinian and Mayrian traditions holds great promise to unite the field under a single conceptual framework, a necessary integration if generalities about the speciation process are to be discovered.

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References


