

Preface

The study of the formation of new species is a delightfully integrative enterprise. There are nearly as many approaches to studying speciation as there are definitions of species themselves. In recent years, innovations in genetics, genomics, theoretical frameworks, and comparative techniques have enabled a broadened perspective and improved understanding of the speciation process. While several books and edited volumes have been dedicated to the study of speciation (e.g., Otte and Endler 1990; Coyne and Orr 2004; Nosil 2012), the field has seen considerable advancements since the publication of the latest volume over a decade ago. These developments underscore the need for fresh perspectives to reflect the current state of research and the innovative methodologies now at our disposal. In this volume, we sought to capture some of the diverse ways that researchers around the world now approach these questions, whether through mathematical modeling, large-scale comparative analyses, or fine-scale experiments in the laboratory or in the wild.

We, the editors of this volume, represent these diverse approaches and have brought this diversity of speciation research to the Gordon Research Conferences on Speciation that we have organized in 2015, 2017, 2019, and 2023. However, to fairly represent the diverse ways that researchers currently study speciation, we chose not to make our own list of potential authors and topics for this volume. Rather, we first invited speciation biologists from around the world to submit possible topics for inclusion in the volume. Then, we organized a series of online workshops where people could start to meet each other and discuss ideas for contributions around these topics. Following these online meetings, working groups formed to develop proposals for topics and lists of specific contributions to this volume. Proposals were submitted at the beginning of 2022, and the editors were faced with the difficult decision of choosing among an excellent list of 50 potential chapters to the 27 that finally made it into this volume. By limiting participation of any one author to two chapters, we tried to ensure that the list of authors and viewpoints reflected the diversity in the field. In particular, we wanted to ensure that the authors of these chapters included the truly excellent cadre of early-career scientists in the field of speciation, as well as scientists from the Global South, where many cradles of rapid speciation are located (e.g., Guevara-Andino et al.). We could not be more pleased with the outcome of this process. The resulting chapters reflect the diversity of both speciation researchers and contemporary speciation research. In addition to highlighting central advances over the last decade, the contributions provide both a historical perspective of where the field has been and a view of the exciting future ahead.

The volume is organized into six sections, starting with an overview of the mechanisms that contribute to the establishment of reproductive barriers to gene flow, a key step in the formation of species (Section 1: Mechanisms of Reproductive Isolation). This is followed by a section on the “coupling” of these different barriers to gene flow, a process that might strengthen reproductive isolation and help complete the speciation process (Section 2: Coupling of Barriers). Understanding the genetic basis of these isolating barriers is a fast-moving area of speciation research that has been facilitated by recent advances in genetics and genomics (Section 3: Genetics of Reproductive Isolation). The advent of long-read sequencing methods has also rejuvenated interest in the classical view that chromosomal rearrangements such as inversions might drive speciation (Section 4: Chromosomal Rearrangements and Speciation). Moving from a mostly microevolutionary perspective in the preceding sections, the next section provides a macroevolutionary perspective that explores the factors contributing to the rapid and spectacular radiations of species that have occurred in some groups (Section 5: Adaptive and Nonadaptive Radiation). The last section confronts the dark history

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of racism in speciation research and also provides suggestions for moving forward to confront racism as well as species loss in the Anthropocene and to predict speciation (Section 6: Past, Present, and Future of Speciation Research).

Mechanisms of Reproductive Isolation

The establishment of barriers to gene flow, which can ultimately result in reproductive isolation, is crucial in the speciation process as it allows for the maintenance of key differences between incipient species. The six contributions in this section illuminate how such barriers to gene flow evolve and are sustained. Marie-Orleach et al. review and explore the role of selfing in speciation, a mechanism that has received surprisingly little attention despite its potential to reduce gene flow within and between populations. Shaw et al. address the significance of sexual isolation compared to other reproductive barriers. Dalbosco Dell'Aglio et al. consider how sensory environments can influence the evolution of both pre- and postmating reproductive isolation, offering a broader perspective than the commonly considered sensory drive. Garlovsky et al. shift the focus to the often-overlooked aspect of postmating prezygotic isolation, surveying existing research and highlighting key knowledge gaps. Zhang et al. provide another perspective by examining how spatiotemporal variability in reproductive isolation impacts the speciation process. Finally, Yukilevich et al. investigate the interplay between two reproductive barriers—sexual selection and habitat selection—by reviewing the literature and exploring a two-allele population genetic model.

Coupling of Barriers

With the continuing accessibility and ease of developing and analyzing high-throughput genomics data, researchers can examine not only locus-specific patterns of differentiation during the speciation process but also larger scale patterns among regions of the genome. One of these patterns is the coupling of genomic loci that can influence the divergence process. In the first chapter of this section, Dopman et al. review definitions of genomic coupling, discuss how they overlap and differ, and provide helpful guidance for additional studies in this important area of speciation research. Then, Firreno et al. take a comparative genomics approach to studying coupling and its influence on reproductive isolation in a hybrid zone context. They combine simulation analyses and empirical data from 25 hybrid zone data sets to estimate coupling coefficients, demonstrating that coupling may evolve gradually and slowly in a hybridization context and appears influential in the reduction of gene flow. Next, Aubier et al. contribute a theoretical study of genetic coupling through a population genetics modeling approach. They primarily focus on the establishment of linkage disequilibria associated with trait-preference associations. Finally, Ritchie and Butlin review the emergence of genetic coupling with respect to mate recognition systems, with a focus on associations between loci related to traits and the preferences for them. After reviewing select case studies, they offer paths for making progress in this area to disentangle the roles of pleiotropy and close linkage in trait-preference divergence.

Genetics of Reproductive Isolation

In the past, the study of the genetic basis of isolating barriers was limited to just a few model systems in which viable hybrids could be produced in the laboratory, often with a limited understanding of how these isolating barriers play out in the wild. However, as reviewed by Delmore et al., recent advances in both genetic methods and genome sequencing have greatly expanded the number of systems used in genetic and genomic studies of reproductive isolation and speciation. Then, a series of papers highlight how these new methods and systems have provided insight into the genetic mechanisms that underlie the evolution of specific isolating barriers. First, Merrill et al. review progress in identifying

the genetic mechanisms that underlie the evolution of prezygotic barriers, providing new insights into how such barriers can persist in the face of gene flow and how they themselves affect gene flow. Then, Thompson et al. draw a parallel between the genetic basis of incompatibilities due to ecological selection against hybrids and the genetic basis of incompatibilities that are largely independent of ecological niche, so-called intrinsic incompatibilities. They argue that the classic (Bateson)–Dobzhansky–Muller incompatibility (DMI) model fits both scenarios. Reifová et al. then highlight recent progress in identifying the genic, chromosomal, genomic, and epigenetic basis of intrinsic incompatibilities. Moving from empirical data to models, Schneemann et al. show how Fisher’s geometric model can be used to study many outstanding questions about the genetics of reproductive isolation and speciation. Finally, Peñalba et al. highlight how recent genomic studies have shown that the formation of hybrids is not always a barrier to speciation but, rather, that hybridization can facilitate the formation and persistence of species.

Chromosomal Rearrangements and Speciation

Genic views of speciation often focus on how allelic substitutions at single loci or pairs of loci give rise to reproductive isolation. But, since the earliest days of speciation genetics and karyotyping, biologists recognized that species also differ in chromosomal architecture: rearrangements, inversions, translocations, and changing chromosome numbers. The advent of long-read genome sequencing has revolutionized this study of chromosomal rearrangements in speciation. Berdan et al. summarize the processes by which such structural variants arise, subsequently evolve, and may contribute to reproductive isolation. Lucek et al. then pick up this theme and connect the microevolution of rearrangements to macroevolutionary processes of diversification and divergence.

Adaptive and Nonadaptive Radiation

Evolutionary radiations are among the biosphere’s most fascinating empirical patterns, showcasing the power of evolutionary forces to generate biodiversity—or “endless forms most beautiful,” in Darwin’s (1859) famous wording. Radiations are recognized as adaptive or nonadaptive depending on whether natural selection is among those forces, and it is new ecological opportunity that makes an ancestral species particularly likely to radiate into a diversity of forms. De-Kayne et al. discuss how adaptive radiations are influenced by key organismal and environmental features and provide a perspective on how to move forward to identify the causal factors that contribute to these radiations. Germain et al. explain how MacArthur’s theory of resource utilization provides insights into the determinants and limits of adaptive radiations. Vanhove et al. describe how radiations in hosts help understand patterns of diversification in their symbionts. Illera et al. examine how studying the phylogenies of island birds can elucidate the dynamics of adaptive and nonadaptive radiations. Guevara-Andino et al. review the role of abiotic and biotic factors underlying adaptive radiations in the neotropics, where some of the most iconic radiations have occurred. Bromham proposes how Darwin’s (1859) perspectives on the mutability of species still hold untapped potential for synthesizing the molecular, macroevolutionary, and macroecological dimensions of speciation research.

Past, Present, and Future of Speciation Research

The study of speciation is in large part a historical inquiry. Researchers in our field typically cast their eyes back to the past to infer events and processes that explain present-day patterns. Two of the papers in this section instead turn to focus on our present and future. Ålund et al. examine how humans are changing the global course of speciation. Through environmental change we are driving a massive rise in extinction, but we may also alter rates of speciation by imposing new selection pressures, creating new ecological niches (while destroying others), and subdividing populations. The authors emphasize

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the importance for speciation research and long-term monitoring to track the potential for biodiversity to, in part, recover through new human-induced speciation. This work will require the ability to accurately forecast speciation, and Roesti et al. lay out a broad vision for what such prediction might entail. Is prediction possible for speciation researchers, in principle and in practice? The authors are optimistic about such predictions and delve into what we need to know to make them. Evolutionary predictions are most delicate when applied to our own species—as evolutionary biologists we often have students, family, or friends ask about the future of human evolution. As Graves points out in his chapter, biologists have long thought about human speciation (past and future), and this line of thought has been tightly interwoven with cultural and political views of race. Recognizing this harmful historical intersection, he argues that speciation researchers need to be proactive in countering such misconceptions and misinterpretations of our work.

In closing, the editors are grateful to Barbara Acosta and her team at the Cold Spring Harbor Laboratory Press for their guidance and steady support, quickly answering all questions large and small. We especially thank the authors of the chapters for their creativity, hard work, and patience with the long process of putting together this exciting collection, as well as the section leaders (Roger Butlin, José Cerca, Rishi De-Kayne, Kira Delmore, Erik Dopman, Jun Kitano, Kay Lucek, Tamra Mendelson, Richard Merrill, and Natalie Roberts), who spearheaded the collection of contributions around specific topics. Drew Schield provided the beautiful cover design. The entire community of speciation researchers was also generous with their time in providing timely, critical, and constructive reviews of the chapters. We hope that these chapters will inspire both long-term researchers in the field as well as a new generation of scientists to tackle Darwin’s “mystery of mysteries,” the formation of new species.

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