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ESSAY

Speciation: Where Are We Now? An Introduction to a Special Issue on Speciation

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Introduction

Although modern evolutionary biology started with a seminal volume whose title identified the origin of species as the central theme of the new theory (Darwin 1859), the topic of speciation received relatively little attention for several decades following the publication of the origin of species. Darwin and his contemporaries devoted much more attention to explain how changes occurred within species rather than how species originated. In fact, a search of the published scientific literature using web of science reveals that between 1864 and 1939 only 21 journal articles had the word speciation in their title (Fig. 1). As already summarized by Coyne and Orr (2004) interest in the origin of species greatly increased during the development of the modern synthesis, when mendelian genetics was reconciled with biogeography and natural selection by people like Dobzhansky (1937) and Mayr (1942). Mayr was the first to focus on the importance of species, introducing the biological species concept (BSC), which has dominated speciation research for the past seven decades, and championed the idea of speciation in allopatry. Dobzhansky's work pointed out the importance of understanding how changes in allele frequencies could produce genetically distinct groups and the importance of reproductive isolating mechanisms. Between the 1940s and the 1970s, while the biogeography of speciation remained an active area of research for systematists and naturalists, the mechanisms of origin of barriers to reproductive isolation received relatively little attention by geneticists. During that time period most workers in fact remained more interested in demonstrating the strength and influence of natural selection in the wild, and in explaining how genetic variation accumulates and persists within species (e.g., Lewontin 1974).

Starting in the 1980s however, the availability of new empirical tools such as molecular genetics, and theoretical and methodological approaches, such as phylogenetic and comparative methods, led to resurgence in interest in the origin of species. Speciation research, once predominantly the domain of systematists, paleontologists, and some geneticists, started to attract the interests of workers in other fields of biology, such as ecologists, ethologists, genome biologists, and developmental biologists. This caused a shift from largely pattern-oriented studies of speciation, in which often the description of patterns was accompanied by the suggestion of some (often untestable) hypotheses regarding what might have caused the events, to more process-oriented studies, in which attempts were made to directly test and explore the process.

This resurgence of interest in speciation has been one of the main developments in evolutionary biology during the past 25 years, and has led to a new phase of speciation studies (Coyne and Orr 2004). During this new phase many of the major conclusions about speciation reached since 1859 have been re-examined. The debate over species concepts, once mostly the domain of systematists and philosophers, was reinvigorated through the active involvement of students of different branches of biology (e.g.,

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	1901-1910	1911-1920	1921-1930	1931-1940	1941-1950	1951-1960	1961-1970	1971-1980	1981-1990	1991-2000	2001-2010
# papers	1	3	6	32	122	195	410	630	1610	1771	6820

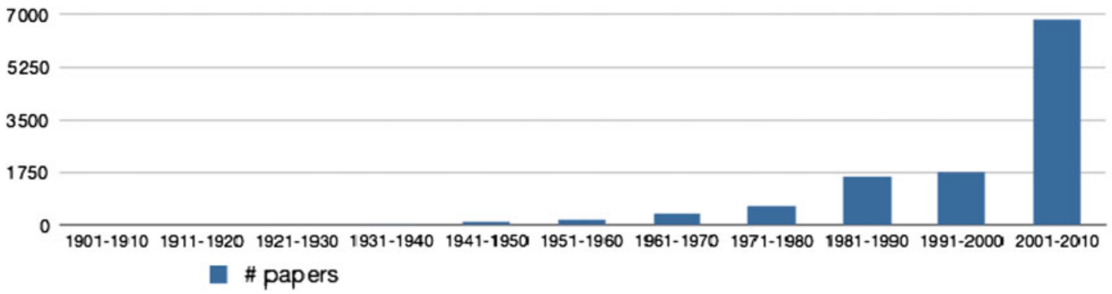

Fig. 1 Number of publications listed in Thomson-ISI web of science with the word speciation in the title since 1901 after that papers referring to chemical speciation have been removed

Wilson 1999). Much greater attention started being paid during this phase also to genetic analyses of reproductive barriers, such as the search for genes causing reproductive isolation (Coyne and Orr 2004). Both empirical and theoretical advances led to question the biogeography-centered view of speciation, and the fact that allopatry was the dominant mode of speciation (Howard and Berlocher 1998). Recent research has also re-evaluated concepts such as reinforcement, and paid greater attention to the role of genetic drift and hybridization, through either polyploidy or recombinational speciation.

While the emphases can sometimes be very different from one field to another, and may lead to misunderstandings and artificial disagreements (e.g., practitioners in each field have at times felt that they had important insights unique to their field that were not appreciated by workers using different approaches or with different goals), new research has provided a great wealth of data, some supporting older ideas, some overturning them. A comprehensive review of the progress of the field is beyond the scope of this paper, but we wish to outline some major areas of progress in the field, some questions still worth answering, and point out some approaches that in the near future might be able to do so.

Are Species Real? And Do We Need a Universally Accepted Species Concept to Study Speciation?

Speciation is a continuous process requiring some key events: the splitting of an ancestral lineage into two or more daughter lineages in which trait differences begin to accumulate, leading to a reduction in gene flow, until eventually separation becomes irreversible. Given the limited temporal frame of our observations, and the fact that the first stages can all potentially be reverted, it is often difficult (if not impossible) to observe the complete series of events and discriminate between a speciation event in progress and a successful one, thus seriously impeding our ability to recognize real species. Furthermore, while discrete lineages are “relatively” easy to recognize in most sexually reproducing eukaryotes (although some taxonomists might disagree with this statement), they are less distinct in clonal or asexual organisms (see Barraclough et al. this issue). For this reason it has been suggested that species may not be real and that the concept should not even be used in speciation research. We disagree with this view, if not for the fact that it would be difficult to study speciation if we accept that species are not real.

First, the process of speciation is likely to be very brief relative to the temporal duration of most species (e.g., Rosenblum et al. this issue), indicating that the difficulty of pinpointing the exact moment when one ancestral lineage splits into two daughter species does not make these entities unreal. A critical question then becomes if a definition of species is needed in order to study speciation. While definitions provide a theoretical and operational guide, over 20 species concepts have been described to date (e.g., de Queiroz 2007; Mayden 1997), and most workers would agree that none is free from ambiguity or applicable to all situations. Several workers have recently claimed (Coyne and Orr 2004; the Marie Curie Speciation Network 2012) that a modified version of Mayr’s BSC (1942) is the most useful, because, regardless of the philosophical merits of certain species concepts, nearly all recent progress on speciation has resulted from adopting some version of the BSC. This is because the BSC reduces the nebulous problem of the origin of species to the (more tractable) problem of the origin of isolating barriers. We agree with this assessment, at least for sexually reproducing eukaryotes. Evolutionary biologists still need to be aware of the limitation of this concept, including its inapplicability to large branches of the tree of life (e.g., Barraclough et al. this issue), and that an objective criterion for species delimitation is still needed in order to truly investigate the process of speciation (Marie Curie Speciation Network 2012).

What Are the Biogeographic Modes of Speciation?

Traditionally, and for many researchers still today, the mode of speciation refers to the geographic circumstances under which one lineage splits and diverges to form two new lineages. For many years following the development of the Modern Synthesis the only widely accepted mode of speciation was allopatric speciation (see Mayr 1963). This idea is still generally considered to be well supported and uncontroversial. The idea that spatial separation of populations was not always necessary for conspecific populations to diverge genetically and for the origin of new species, had originally been championed by Darwin himself (1859), and was supported by research by Bush (1969, 1994) on the apple maggot *Rhagoletis pomonella*. Bush (1969, 1994) showed that in organisms with a strong, genetically determined fidelity to a habitat in which mating will occur, genetically isolated populations can arise when individuals shift onto a new habitat. This provided impetus for both modeling and empirical studies that have convinced many (perhaps most) students of speciation that sympatric speciation is indeed possible (Barluenga et al. 2006; Savolainen et al. 2006; Crow et al. 2010).

The still unresolved question then is whether non-allopatric models of speciation have been important in generating the current diversity, and what conditions promote non-allopatric speciation. These conditions are now being investigated through both modeling studies that attempt to address the likelihood of speciation occurring in the face of gene-flow (Marie Curie Speciation Network 2012) and studies of closely related organisms that are likely to have diverged while in spatial contact (e.g., host races in insects, species flocks in lakes, parasites; e.g., Linn et al. 2003, Feder et al. this issue). Until now, however, the number of such studies and their taxonomic scope has remained relatively limited. In order to finally assess the importance of non-allopatric modes of speciation more extensive studies of speciation in a variety of groups for which robust phylogenies that can identify sister taxa are available and the biogeographic history under which the sister taxa diverged is well understood will be needed. Unfortunately, at the present time, for most groups range maps are incomplete, the patterns of habitat use are poorly known, and phylogenies do not include all species. Until such studies become the norm, the importance of non-allopatric speciation is to remain unknown and controversial. Coyne and Orr (2004) review the literature and claim that while non-allopatric speciation is possible, it is not common. However, under certain circumstances allopatric speciation is less likely (e.g., speciation on oceanic islands; see Roderick et al. this issue) and we may need to re-assess the criteria used to judge instances where non-allopatric speciation is likely (Crow et al. 2010; Bird et al. this issue). Furthermore, the traditional view of separating modes of speciation according to geographical context does not capture the complexity of the spatial relationship when populations diverge, nor is this spatial relationship alone affecting gene flow between those diverging populations (Marie Curie Speciation Network 2012). Therefore, while still taking geographical context into consideration, a focus on the processes affecting divergence rather than redefining sympatry has been suggested (Butlin et al. 2008; Fitzpatrick et al. 2008, 2009; Marie Curie Speciation Network 2012).

What Are the Roles of Natural Selection and Drift in Causing Reproductive Isolation and Divergence?

According to the traditional allopatric model of speciation (e.g., Mayr 1942, 1963) reproductive isolation was thought to evolve as a byproduct of geographically isolated populations, in which genetic differences slowly accumulate. For this reason divergent environmental selective pressures did not receive much attention as potentially important factors in driving genetic divergence, the dominant assumption being that isolated populations would diverge regardless of environmental differences (Howard 1998). Over the past two decades, however, there has been a much greater emphasis on the role of the environment in speciation events, especially whether resource-based divergent natural selection is responsible for much of the divergence between closely related species (e.g., Schluter 2000). While it has been known for a while that divergence in sympatry is usually not possible without natural selection playing a major role (Howard and Berlocher 1998), it has been appreciated more recently that differing ecological circumstances can perhaps drive divergence and the evolution of reproductive isolation even in cases of allopatric speciation (Schluter 2000). Whether this is a common occurrence remains currently unclear. In the future, this type of question will be resolved through ecological and behavioral studies (e.g., Glenn et al. this issue), or by assessing the role of divergent natural selection by comparing the amount of divergence between equal age pairs of sister populations that occur in similar or dissimilar circumstances (Coyne and Orr 2004; Marie Curie Speciation Network 2012).

More attention was paid to the role of drift, especially thanks to Mayr's insistence on the concept that small, peripherally isolated populations founded by one or few individuals could represent the most likely source of new species (Mayr 1963). According to Mayr small populations would experience a sudden decrease of genetic variability, thus leading to major changes in the genetic composition. Such changes in the genetic background could then alter the selective values of alleles at many loci and set off a genetic revolution. While Mayr's idea was later incorporated in several models of founder effects (Howard 1998), experimental support for the importance of drift has so far remained scarce (Coyne and Orr 2004), and whether small founder populations play an important role in genetic divergence and speciation, remains an open question. One potential way forward in addressing such a question could be represented by the study of natural populations on oceanic islands of volcanic origin, where the latter are generally assumed to have arisen via founder effects (see Roderick et al. this issue), but also on populations known from historical records to have been founded by one or few individuals. In future studies it will be critical to discriminate small founder populations from small populations per se.

What Are the Most Common Barriers to Reproduction?

Reproductive isolating barriers are biological features of organisms due to genetic differences between populations that impede the exchange of genes with members of other populations (Coyne and Orr 2004). Traditionally, reproductive isolating barriers are divided into barriers that act before (prezygotic) and after fertilization (postzygotic). Prezygotic barriers can be further subdivided into ecological and non-ecological barriers, the latter generally assumed to have been caused by natural or sexual selection (e.g., Howard and Berlocher 1998; Coyne and Orr 2004). Postzygotic barriers can be subdivided into intrinsic barriers, in which developmental problems cause hybrid sterility and inviability, and extrinsic barriers, in which sterility and inviability will depend on the particular environments inhabited.

Many crucial questions remain unresolved in the field of evolution of reproductive isolation (Howard 1998), and a critical step in answering these questions will consist of the identification of the nature of the traits that cause reproductive isolation (e.g., are the traits responsible for resource use, thus providing clues for the role of natural selection, or are they linked to mate recognition, thus pointing to a critical role of sexual selection?). The number of studies that have managed to tease apart such factors until now has been fairly limited (see review in Coyne and Orr 2004), though this number has increased recently (e.g., Bergen et al., Martin and Mendelson, both this volume).

Speciation, Genetics, and the Genomic Era

While the genetics of reproductive barriers has been one of the major areas of research in speciation since the modern synthesis (Dobzhansky 1937), it has been only since the 1980s that researchers have started framing questions on speciation in terms of how many and what kind of genes control the traits responsible for reproductive isolation (e.g., Coyne and Orr 2004; McNiven et al. 2011). Speciation genes are commonly vaguely recognized as genes involved in reproductive isolation. Nosil and Schluter (2011) however, showed a variety of ways in which these terms have been used. To avoid further confusion they proposed three criteria that must be met in order for genes to be called "speciation genes": (1) they must be involved in reproductive isolation between two lineages, (2) their divergence must proceed the completion of speciation, and (3) their divergence had a stronger effect on gene exchange between these lineages than on other genes. Speciation genes, however, are rarely known, and there is very little information on the number of genes involved in the speciation process. With few exceptions, most of what we know relies on a few model systems such as *Drosophila*. Recent research indicates that the genes involved in the first stage of reproductive isolation may be few, while their number may rise in successive stages (Wu 2001). Several genes have been shown to be responsible for hybrid male sterility in *Drosophila* even between closely related taxa, and situations in which weak-effect loci have strong synergetic effect seems to be common (Wu and Hollocher 1998; Ting et al. 2001). In other groups, many of the loci known to cause an increase in reproductive isolation are linked to chemical signaling (e.g., Smadja and Butlin 2009), and in the future it will be important to expand the search to loci involved in different aspects of communication. Finally, recent studies have shown that single major genes with very large effects may be involved in some cases of postzygotic isolation (Coyne and Orr 2004).

We believe that advances in genomic research will soon lead to a much greater understanding not only of some of the individual genes that contribute to speciation, but also of the genetic networks in which such genes may be located, or the developmental processes through which such genes affect the phenotypes of their host organisms. An area of active research will also be that of gene expression (Wolf et al. 2010), such as the importance of cis-regulatory and coding factors in regulating functional gene networks. Such a phenomenon might, at least in some cases, turn out to be as important, if not more, than changes in coding sequences in causing reproductive isolation. The importance of other genomic-level phenomena such as gene and genome duplication and loss, transposable elements or epigenetic phenomena, all of which are known to easily lead to various degrees of reproductive isolation, still need to be systematically assessed and their investigation has only recently begun.

We also expect that in the future much greater emphasis will be placed on the evo-devo aspect of speciation. As Minelli and Fusco summarize in this issue, development-mediated phenomena such as phenotypic plasticity can act as a facilitator for speciation (e.g., West-Eberhard 2005; Pfennig et al. 2010). In spite of the importance of development, we still know very little about its importance in speciation, and for us to obtain a broader view of how new species originate, this will obviously need to change.

What Is the Relationship Between Hybridization and Speciation?

The idea that selection against hybridization in zones of secondary contact (reinforcement) drives the evolution of premating barriers to gene exchange between diverging lineages is an old one (e.g., Dobzhansky 1937). Although reinforcement was not a popular idea during the 1970s and 1980s, over the past two decades its importance has been supported by both empirical and theoretical studies (e.g., Coyne and Orr 1989; Noor 1995; Servedio and Noor 2003; Matute 2010). The debate, however, is still raging regarding its overall importance. Positive assortative mating and reproductive character displacement, both expected under reinforcement scenarios, appear to be frequent in some hybrid zones, even though it is known that patterns suggestive of reinforcement can be generated by other processes (Coyne and Orr 2004).

Another controversial question concerns whether hybrids can act as the founders of new lineages and introgression can play a creative role in speciation. Introgression of genes from one species into another is not uncommon in nature, and may increase the genetic variation of the recipient. It is less obvious if introgression can provide the impetus for a population to speciate (Rieseberg 1997). It is also unclear at the present time if hybrid speciation is actually occurring in nature or if it is simply difficult to detect, thus leading us to underestimate its importance. While it has been accepted that hybrid speciation does occur in plants (Rieseberg 1997) and may occur in animals (Grant and Grant 1992), more detailed long term studies of the consequences of introgression between closely related taxa will be needed to address the importance of this phenomenon.

Future genetic studies of hybrid zones will have to be designed to reveal the strength of selection that may exist against hybrids as well as the number of genes that may be responsible for lack of hybrid fitness. Many species that are known to exchange genes across hybrid zones also remain distinct in traits of ecological and evolutionary importance (Howard 1998). Because trait differences that are maintained in the face of gene flow cannot be under the control of genome regions that cross the species boundary, insights into the genetic control of important traits, such as those that cause reproductive isolation, will be gained by understanding what parts of the genome can and can not be exchanged between hybrids.

What Are the Macroevolutionary Aspects of Speciation?

This area, long the domain of paleontologists, has over the past few years experienced an explosive growth. The increased availability of molecular phylogenies, combined with new comparative methods to investigate the relationships between organismal traits and clade diversification, as well as the development of large online databases that made it easier to collect, store, share, and analyze information about aspects of the biology thought to be relevant to evolution of various groups (e.g., Jones et al. 2009), all contributed to a renewed interest in macroevolution. Progress in this field has led not only to increased support for older ideas previously based on paleobiological data only (e.g., Venditti and Pagel 2010), but also to critical and more thorough re-examination of old ideas such as adaptive radiation (Harmon et al. 2010). While paleontological data are still a necessary component of macroevolutionary studies (see Lieberman, this issue), the availability of molecular phylogenies has managed to reveal the existence of general phenomena such as the lack of a relationship between clade age and species diversity, or the existence of some strict limit on the richness of many clades (Rabosky 2009a, b). A better understanding of these phenomena will play a crucial role in the attempt to achieve a more holistic view of speciation.

Contributions in this Volume

Papers in this volume highlight some critical aspects of speciation research in each author's area of expertise. Although the topics may cover only few of the disciplines that are touched by speciation research, the selected papers account for a provoking issue that covers the breadth of organismal diversity (e.g., bacteria, plants, animals), and highlight some of the areas where we expect rapid developments in the near future.

Barraclough et al. review the theoretical concepts of diversification in bacteria and address their taxonomic challenges. They advocate an integrative approach that assesses all evolutionary forces involved in diversification.

Bergen et al. examine the role that stochastic changes in sexual selection strength play in the predominance between pairs of preferred traits within a single population. Specifically they propose a model to examine the probability that a rare phenotype gains prominence within a population due to stochastic effects, and apply the model to moth pheromone systems.

Bird et al. address one of the most contentious topics in speciation research, that of sympatric speciation. They review various scenarios under which sympatric speciation could occur, propose a new theoretical framework to determine if a speciation event may have occurred in the face of ongoing gene flow, and suggest that sympatric speciation could have led to a non-trivial portion of the extant biodiversity.

Fontaneto et al. compare rates of diversification among sexually and asexually reproducing organisms. The authors show how the four clades of asexual bdelloid rotifers in their analysis are much more diverse than their sexual relatives, the monogonont rotifers, and that they accumulate diversity at a significantly higher rate. Their study supports the idea that these differences in diversification rates are due to differences in the mechanisms of speciation, with ecological speciation being the likely culprit.

Glenn et al. give an overview of the role of interspecific competition in ecological speciation and discuss two possible models where interspecific competition could lead to speciation. They further suggest that endoparasitoids attacking phytophagous insects such as *Rhagoletis* fruit flies would make a good model system to investigate competitive speciation.

Lieberman revisits an old key concept in evolutionary theory, that of adaptive radiation, from a paleontological perspective, and cautions about assuming that any radiating clade is the product of an adaptive radiation. Lieberman suggests that several highly relevant macroevolutionary concepts, such as the Turnover Pulse Hypothesis, the Effect Hypothesis, Exaptation, and Species Selection, have not been properly considered in the literature on adaptive radiation, and discussed some of the implications for speciation research.

Martin and Mendelson test whether changes in male coloration leading to speciation in benthic fish called darters is due to divergent ecological selection or a mutation-order process. They conclude that the latter explains best the clock-like changes in male color considering that neither geographic distance nor microhabitat or environmental differences correlated with male color differences.

Minelli and Fusco discuss some key concepts in evolutionary developmental biology such as evolvability, phenotypic plasticity, and phenology, and discuss their relevance for speciation research. They show how developmental processes can contribute to organismal diversification across a number of hierarchical levels of biological organization, and make a strong case for the need of more studies that incorporate speciation research.

Moyle et al. address ecotypic adaptation of the California endemic plant *Collinsia sparsiflora* to two distinct soil types. They show how, despite ongoing gene exchange, strong adaptive differentiation between recently diverged and adjacent lineages is responsible for the development of hybrid barriers.

Roderick et al. discuss how dynamic environments can affect genetic population structure early in the process leading to differentiation and eventually species formation. They test their predictions using molecular data of six different spider lineages from the youngest islands of the Hawaiian archipelago, where lava flows lead to frequent habitat fragmentation. They also show that habitat preference affects genetic differentiation.

Rosenblum et al. review our current understanding of speciation rates, showing how studies based on fossil records, phylogenies, and mathematical models produce dramatically different estimates of speciation rates. To reconcile these incongruences between studies, Rosenblum et al. propose the "ephemeral speciation model", under which new species form rapidly but rarely persist.

Conclusions

Many of the most significant questions about speciation are difficult to address and answer, but most of them are by no means unanswerable. Long-term studies with multidisciplinary approaches of a number of closely related taxa presumed to be at different stages of the process will most likely lead to greater advances in the field. We think that these advances will be necessary not just for purely theoretical or intellectual reasons. Given the present impact of humans on ecosystems worldwide, studies of speciation will soon be fundamental also for conservation, as we want to preserve the processes that generate diversity. We realize that the essays of this volume will only represent a small sample of the diversity of approaches currently employed by a multitude of workers worldwide, but we hope that together with the other recent (and some not so recent) reviews published over the past few years (e.g., Coyne and Orr 2004; Marie Curie Speciation Network 2012; Sobel et al. 2010) it will help us to move a little closer toward a better understanding of the patterns and processes of the origin of species.

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