



Sympatric Speciation

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Introduction

Speciation can be described as the process of the splitting of cohesive groups of organisms into distinct entities; that is, the evolution of biological species (cladogenesis). In sexually reproducing organisms, this distinctness can come about and be maintained only if the exchange of genetic material between groups is strongly reduced. That reproductive isolation should be the defining characteristic of species is the central tenet of the biological species concept, the most commonly used species concept in the field of evolutionary biology. Hence, speciation research is concerned mainly with understanding the nature and evolution of barriers to interbreeding between organismal groups. The role of geography and, specifically, geographic isolation in this regard has been subject to one of the most persistent debates in the field of speciation research. While the initiation of speciation in geographic isolation (i.e., allopatric speciation) is supported both by several lines of evidence and a compelling body of underlying theory, speciation without the mediating effect of geographic isolation (i.e., sympatric speciation) has long been controversial. Mainly, sympatric speciation has been considered either as unlikely to occur at all or to play a substantial role in terms of the frequency of its occurrence. Yet, the study of sympatric speciation has received renewed interest since the early 1980s, and empirical and theoretical support for its plausibility has accumulated. Thus, the reality of sympatric speciation is no longer in doubt. Nevertheless, its importance as a mode of speciation and the circumstances under which it happens continue to be debated. Estimates of the frequency of different modes of speciation typically assign only a minor role to sympatric speciation, apart from examples from certain animal and plant taxa. But, the importance of sympatric speciation for evolutionary biology goes beyond its relative frequency in generating biodiversity. Its conceptual and empirical challenges have stimulated advances of broader importance for our understanding of the general mechanisms involved in the process of speciation. Thus, the study of speciation in a setting without geographic isolation, whether viewed from a geographical perspective as sympatric speciation or considered in a population-genetic point of view as an extreme case of speciation with gene flow, will likely continue to attract the attention of future generations of evolutionary biologists.

General Overviews

A basic overview on geographic modes of speciation that is accessible to the broad readership can be found in Futuyma 2013, a textbook on evolution. Entire books devoted to the topic of speciation usually discuss sympatric speciation and often provide a detailed discussion. Mayr 1963 was one of the first books concerned with the topic of speciation, and, although now obviously outdated, it still makes for excellent reading in order to understand the early history of speciation research and the beginnings of the debate about sympatric speciation. Several papers compiled in Otte and Endler 1989 deal with sympatric speciation and provide an overview of the subject. Howard and Berlocher 1998 includes contributions by various authors in the field of speciation research. One section is devoted to mechanisms of speciation and emphasizes possible modes of sympatric speciation. A timely and lucid review on speciation is found in Coyne and Orr 2004. In this book, Jerry Coyne and H. Allen Orr also define four criteria for inferring that a certain past speciation event in the wild is best explained by sympatric speciation: (1) modern species' ranges are sympatric, (2) there is substantial reproductive isolation between species, (3) species are sister groups, and (4) a past allopatric phase is unlikely. These criteria have become the conservative "gold standard" in evolutionary biology. Via 2001 and Bolnick and Fitzpatrick 2007 focus specifically on the mode of sympatric speciation and offer excellent overviews. A concise overview on speciation in plants is given in Rieseberg and Willis 2007.

Bolnick, D. I., and B. M. Fitzpatrick. 2007. Sympatric speciation: Models and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics* 38:459–487.

This review paper begins with a brief general introduction, followed by a discussion of the empirical evidence for sympatric speciation and its frequency in nature. Subsequent sections provide an overview on the multitude of existing theoretical models and evaluate the justification of assumptions with respect to empirical data.

Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sunderland, MA: Sinauer.

Written by two authorities in the field of speciation research, this book represents the most comprehensive early-21st-century treatise on speciation and has become a must-read for those interested in speciation. Sympatric speciation and the evidence for it from theoretical models, experimental work, and natural populations are discussed in chapter 4.

Futuyma, D. J. 2013. *Evolution*. 3d ed. Sunderland, MA: Sinauer.

Evolution is an introductory textbook in evolutionary biology. An overview of the different geographic modes of speciation can be found in chapter 18. First published in 2005.

Howard, D. J., and S. H. Berlocher, eds. 1998. *Endless forms: Species and speciation*. New York: Oxford Univ. Press.

The contributions in this book resulted from a symposium in honor of Guy Bush, who was a strong advocate of the plausibility of sympatric speciation, especially in insects. Bush's interests in sympatric speciation are reflected in a number of chapters in the book.

Mayr, E. 1963. *Animal species and evolution*. Cambridge, MA: Belknap.

One of Mayr's most influential books. In a section of chapter 15 the evidence for sympatric speciation is critically assessed. Reprinted as recently as 1979.

Otte, D., and J. A. Endler, eds. 1989. *Speciation and its consequences*. Sunderland, MA: Sinauer.

This volume arose from a symposium on speciation and consists of twenty-five papers and a concluding review. Several contributions are primarily concerned with sympatric speciation.

Rieseberg, L. H., and J. H. Willis. 2007. Plant speciation. *Science* 317.5840: 910–914.

In this brief review the authors describe several aspects of speciation in plants. One section is devoted to hybrid and polyploid speciation, which is an important mode of sympatric speciation in plants. A list of case studies on sympatric speciation in plants is provided in the supplementary materials.

Via, S. 2001. Sympatric speciation in animals: The ugly duckling grows up. In *Special issue: Speciation. Trends in Ecology & Evolution* 16.7: 381–390.

This review is part of a special issue on speciation and begins with a brief recapitulation of the history of sympatric speciation and then moves on to describe the underlying mechanisms of, and favorable conditions for, sympatric speciation. This

discussion is based both on empirical and theoretical work.

Journals

Since the process of speciation is a central aspect of evolutionary research, almost any journal that focuses on evolutionary pattern and process will publish articles on sympatric speciation. Examples of journals with a focus on evolution include *Evolution* and the *Journal of Evolutionary Biology*, the journals of the two most influential societies for the study of evolutionary biology. The topic of sympatric speciation is also regularly featured in *Molecular Ecology*, a journal that promotes the use of molecular genetic techniques to study various aspects of ecology and evolution. Another journal that highlights integrative and interdisciplinary work on broad biological principles, including sympatric speciation, is the *American Naturalist*. Articles on sympatric speciation are also occasionally published in *Nature* or *Science*, which are among the most prestigious journals in the natural and life sciences. *Trends in Ecology & Evolution* and *Annual Review of Ecology, Evolution, and Systematics* publish articles that aim to synthesize past work and to highlight new directions in the field; these journals periodically publish papers on speciation in general or on sympatric speciation.

American Naturalist.

The *American Naturalist* has maintained its position as a highly influential journal for more than one hundred years. The primary objective of the journal of the American Society of Naturalists is to advance our knowledge of broad biological concepts, promoting integrative empirical work as well as evolutionary theory.

Annual Review of Ecology, Evolution, and Systematics.

This journal is one publication of the *Annual Reviews* series and provides some of the most comprehensive and insightful review articles in the fields of ecology, evolution, and systematics. Various aspects of speciation have been covered since the late 20th century.

Evolution.

Published on behalf of the Society for the Study of Evolution (SSE), *Evolution* or the *International Journal for Organic Evolution* is one of the leading journals in the field of evolutionary biology. Besides empirical and theoretical papers, it publishes review articles and commentaries, which regularly address speciation research.

Journal of Evolutionary Biology.

The journal's scope includes all aspects of evolutionary biology, from an empirical and theoretical point of view. Naturally, speciation research is regularly published in this, which is the journal of the European Society for Evolutionary Biology.

Molecular Ecology.

The journal publishes papers that use molecular genetics to study aspects of ecology, evolution, behavior, and conservation. Because ecological and behavioral isolation can be important in sympatric speciation, studies of sympatric speciation are regularly featured.

Nature.

Nature publishes articles spanning all fields of the natural and life sciences and has one of the highest impacts among all scientific journals, including in the field of evolutionary biology. Models and empirical studies on sympatric speciation are occasionally presented here.

Science.

Science has a broad readership and features original articles from a variety of scientific fields and disciplines. Due its controversial nature, the topic of sympatric speciation has a great appeal and appears from time to time in this journal.

Trends in Ecology & Evolution.

Commonly referred to as *TREE*, this is a distinguished journal that publishes review articles and opinion letters rather than original studies, and it has been highly influential in directing and shaping the focus of the field of evolutionary biology. Sympatric speciation, either alone or as part of a focus on speciation in general, is featured occasionally.

History

The notion that speciation can occur without geographic isolation dates at least back to Darwin 1859, although Charles Darwin was not entirely explicit about the role of geography in speciation. After Darwin the plausibility of sympatric speciation was not considered particularly controversial, but attempts to demonstrate its occurrence were often followed by rebuttals from strong proponents of geographic (allopatric) speciation. A brief account of these exchanges can be found in Mayr 1963. In this book, Ernst Mayr critically evaluates the evidence in favor of sympatric speciation and argues strongly that the concept of sympatric speciation was neither necessary nor supported by the facts. His arguments had a substantial influence on the next generations of evolutionary biologists. Yet, Mayr's forceful opinion also stimulated further research on the topic, and some of the earliest theoretical models, experiments, and empirical cases of sympatric speciation were published within a few years following the publication of Mayr 1963. However, the controversy persisted, and only a few convincing empirical examples of sympatric speciation were published. The debate about sympatric speciation continued. Bush 1975 states that geographic isolation may not be required for speciation in many animals, and the author of White 1978 concluded his chapter on sympatric models of speciation with the statement that the reality of sympatric speciation, at least in certain groups of insects, could not be denied. In stark contrast, the authors of Futuyma and Mayer 1980 stated that they were unable to find any convincing evidence for sympatric speciation. Research on speciation done since the late 20th century has yielded compelling evidence for the occurrence and possibility of sympatric speciation. In this respect, Bush 1994 concluded that it was no longer possible to dismiss the mode of sympatric speciation, and even Mayr in Mayr 2001 (published late in his life; in 2001 he was already ninety-five years old!) accepted some of the more recent findings that support sympatric speciation. Thus, as stated in Jiggins 2006, in the early 21st century the debate on sympatric speciation has mainly shifted away from the issue of its existence, toward questions about its frequency in nature and the conditions under which it is likely to occur.

Bush, G. L. 1975. Modes of animal speciation. *Annual Review of Ecology and Systematics* 6:339–364.

A review of the classic classification of modes of speciation, on the basis of geography. The section on sympatric speciation emphasizes phytophagous and parasitoid insects.

Bush, G. L. 1994. Sympatric speciation in animals: New wine in old bottles. *Trends in Ecology & Evolution* 9.8: 285–288.

A short review on evidence for sympatric speciation, with an emphasis on scenarios where mate choice is linked to host or resource use (i.e., habitat isolation).

Darwin, C. 1859. *On the origin of species by means of natural selection, or, The preservation of favored races in the struggle for life*. London: John Murray.

An enormous compilation of evidence on organismal evolution and an account of the action of natural selection in driving evolutionary change. Numerous reprints of *The Origin* have been published, and the complete work can be freely accessed online.

Futuyma, D. J., and G. C. Mayer. 1980. Non-allopatric speciation in animals. *Systematic Zoology* 29.3: 254–271.

In this review the authors respond to claims that challenged allopatric speciation as being the primary or exclusive mode of speciation. They conclude that sympatric speciation is unlikely.

Jiggins, C. D. 2006. Sympatric speciation: Why the controversy? *Current Biology* 16.9: R333–R334.

A short commentary article on the state of speciation research, with particular focus on the importance (or unimportance) of geographic isolation.

Mayr, E. 1963. *Animal species and evolution*. Cambridge, MA: Belknap.

Following a thorough discussion of the evidence for sympatric speciation, Mayr argues that none of it is convincing, and he advocates the necessity of geographic isolation for speciation. This opinion influenced subsequent generations of evolutionary biologists. Reprinted as recently as 1979.

Mayr, E. 2001. *What evolution is*. New York: Basic Books.

A very general and easily accessible “popular science” book on evolution. The topic of speciation is the focus of chapter 9. In the section on sympatric speciation, Mayr acknowledges certain cases of sympatric speciation in the wild.

White, M. J. D. 1978. *Modes of speciation*. San Francisco: W. H. Freeman.

Discusses various models of speciation, including the geographic modes, but also other modes such as chromosomal and polyploid speciation. Chapter 7 is devoted to sympatric speciation, and the evidence presented comes mainly from phytophagous insects.

Defining Sympatric Speciation

The term “sympatric”—derived from the Greek words *sym* and *patra*, meaning “together” and “country”—was coined by E. B. Poulton in 1903 and originally was used to describe the pattern of geographically overlapping species ranges. With the development of the biological species concept (by Theodosius Dobzhansky and Ernst Mayr), Mayr 1999 (first published in 1942) defines sympatric speciation as the evolution of reproductive barriers within a single interbreeding unit. Yet, stating that the process of “sympatric speciation” had not yet been properly defined, Mayr 1947 argues that it was usually characterized by the

assumption of the establishment of new populations within the normal cruising range (dispersal distance) of members of the parental population; moreover, in this process, gene flow must be inhibited by intrinsic (biological) rather than extrinsic (geographic) factors. After Mayr, numerous definitions of sympatric speciation have been provided, most of which are based either on biogeographic (spatial) or population-genetic (demic) criteria. An overview of definitions is provided in Fitzpatrick, et al. 2008. For example, arguing that previous definitions had not been exact enough for modeling purposes, Gavrilets 2003 defines speciation as being sympatric if mating were random with regard of the birthplace of mates. Following Sergey Gavrilets, this translates to an initial migration rate of $m=0.5$ or complete panmixia. In contrast, cases without any gene flow between two demes ($m=0$) would be considered as allopatric, and everything in between might be called parapatric speciation. Although precise and unambiguous, this classification has been criticized as being not useful for application to natural populations, because it would be virtually impossible to demonstrate sympatric—or strictly allopatric—speciation in nature. Thus, empiricists, on the whole, have tended to invoke a rather biogeographic framework; theoreticians, a more population-genetic framework. In an attempt to reconcile the spatial and demic definitions, Mallet, et al. 2009 proposes a composite spatial population-genetic definition based on the geographic distance and dispersal distance of diverging populations. Yet, this approach has in turn been criticized in Fitzpatrick, et al. 2009, and, to date, there has been no consensus on a universally accepted definition of sympatric speciation. Recognizing that a simple classification of speciation events as sympatric, parapatric, or allopatric will always remain ambiguous, several authors, such as in Butlin, et al. 2008, have advocated focusing instead on the quantitative impact of spatial, ecological, and genetic factors and mechanisms driving divergence.

Butlin, R. K., J. Galindo, and J. W. Grahame. 2008. Sympatric, parapatric or allopatric: The most important way to classify speciation? *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1506: 2997–3007.

A critique of the simplistic, traditional scheme of geographic classification. The authors argue that it may be more fruitful to focus on the current dynamics of selection and gene flow rather than aiming to infer how divergence was initiated in the past or how it might proceed in the future.

Fitzpatrick, B. M., J. A. Fordyce, and S. Gavrilets. 2008. What, if anything, is sympatric speciation? *Journal of Evolutionary Biology* 21.6: 1452–1459.

Several definitions of sympatric speciation and their inherent inconsistencies are reviewed. The authors strongly question the usefulness of the discrete “geographic” classification of speciation events.

Fitzpatrick, B. M., J. A. Fordyce, and S. Gavrilets. 2009. Pattern, process and geographic modes of speciation. *Journal of Evolutionary Biology* 22.11: 2342–2347.

This short communication is a reply to Mallet, et al. 2009. This exchange of ideas and opinions between empiricists and theoreticians highlights the controversy and the debates surrounding sympatric speciation.

Gavrilets, S. 2003. Perspective: Models of speciation; What have we learned in 40 years? *Evolution* 57.10: 2197–2215.

A review of models of speciation. The definition of sympatric speciation given here is considered as one of the most exact by many researchers.

Mallet, J., A. Meyer, P. Nosil, and J. L. Feder. 2009. Space, sympatry and speciation. *Journal of Evolutionary Biology* 22.11: 2332–2341.

In this response to Fitzpatrick, et al. 2008, the authors defend the value of a geographic classification of speciation modes and propose a novel composite definition.

Mayr, E. 1947. Ecological factors in speciation. *Evolution* 1.4: 263–288.

The main argument of this classic paper is to reconcile the apparent conflict between the roles of ecological versus geographic factors in speciation. Yet, this work may be equally prominent for coining a definition of sympatric speciation with respect to the cruising range of individuals.

Mayr, E. 1999. *Systematics and the origin of species from the viewpoint of a zoologist*. Cambridge, MA: Harvard Univ. Press.

Originally published in 1942. According to Mayr, a lack of data and adequate definitions precluded a more elaborate discussion of sympatric speciation. His definition of sympatric speciation given in chapter 8 (“Nongeographic Speciation”) has been the basis of many subsequent definitions of sympatric speciation.

Theoretical Models

The majority of modeling work in speciation research has been on sympatric speciation. These theoretical models have largely contributed to our basic understanding of the conditions for sympatric speciation, and several models have demonstrated that sympatric speciation is indeed possible. However, most models have been numerical and prove only that sympatric speciation may happen under specific conditions. In contrast, analytical models, which can provide more-general quantitative results, have been rare. This argument is elaborated in Gavrillets 2003, which also provides a brief recapitulation of the early history as well as a synthesis of previous models. A much more extensive treatise of theoretical models in speciation research is given in Gavrillets 2004. Probably the first theoretical model that dealt explicitly with sympatric speciation is Maynard Smith 1966, which stimulated the further development of theoretical models. By now, the number of models of sympatric speciation has grown enormously, and an overview is provided in Bolnick and Fitzpatrick 2007. Supplementary table 2 in that paper is noteworthy; it lists a multitude of theoretical models and provides information on their key assumptions. A common feature of basically all models of sympatric speciation is the presence of a genetic basis for a trait under disruptive/divergent selection and some sort of nonrandom mating. One of the most influential papers is Felsenstein 1981. An important step in the theoretical development was the extension of the prevailing informative, yet rather simple, models to incorporate a quantitative genetic framework and to invoke stochastic processes. This progress was spearheaded by the simultaneous publication of Dieckmann and Doebeli 1999 and Kondrashov and Kondrashov 1999. While most models are concerned with only one bifurcating event, Bolnick 2006 investigates an outcome of multiple species.

Bolnick, D. I. 2006. Multi-species outcomes in a common model of sympatric speciation. *Journal of Theoretical Biology* 241.4: 734–744.

The model in this paper is derived from that in Dieckmann and Doebeli 1999 and shows that a multispecies outcome, as seen in adaptive radiations, is possible under certain conditions.

Bolnick, D. I., and B. M. Fitzpatrick. 2007. Sympatric speciation: Models and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics* 38:459–487.

A general overview on models of sympatric speciation and their key assumptions.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. *Nature* 400.6742: 354–357.

One of the most cited models in favor of sympatric speciation. In this model, individual fitness is frequency dependent. Nonrandom mating can result as a byproduct or from a genetic association—induced by genetic drift—of neutral signaling and preference traits with an ecologically relevant trait.

Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35.1: 124–138.

A classic paper that demonstrates the antagonism between selection and recombination in scenarios of divergence with gene flow. It is also here that the terminology of one-allele and two-allele mechanisms for the indirect effect of selection on nonrandom mating was first used.

Gavrilets, S. 2003. Perspective: Models of speciation; What have we learned in 40 years? *Evolution* 57.10: 2197–2215.

In the section about sympatric speciation, two basic models are discussed—the “Udovic model” and a model based on sexual conflict. In these models the conditions for sympatric speciation were found analytically. The author advocates a shift toward more-analytical research, which may help to identify more-general rules.

Gavrilets, S. 2004. *Fitness landscapes and the origin of species*. Monographs in Population Biology 41. Princeton, NJ: Princeton Univ. Press.

The most comprehensive account on theoretical models in speciation research, including those models dealing with sympatric speciation. Although a certain mathematical background is required, this book clearly is written not only for theoreticians, and Gavrilets generally succeeds in making the content of this book accessible to the empirical evolutionary biologist.

Kondrashov, A. S., and F. A. Kondrashov. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* 400.6742: 351–354.

A model similar to Dieckmann and Doebeli's. In this model an association of signaling and ecological traits is selected for and drives assortative mating.

Maynard Smith, J. 1966. Sympatric speciation. *American Naturalist* 100.916: 637–650.

Although this pioneering work is concerned mainly with the maintenance of a polymorphism and not speciation per se, it stimulated much of the theoretical work. The four proposed mechanisms, potentially leading to reproductive isolation in the presence of gene flow, have provided the foundation for almost all other models.

Mechanisms

A few different mechanisms have been proposed as potential drivers of sympatric speciation. Whereas speciation is assumed to proceed gradually when disruptive natural or sexual selection is involved, speciation via hybridization and polyploidization can be instantaneous. While the latter seems to have occurred in relatively few animals, it may be of considerable importance in explaining the diversity of certain plants.

DISRUPTIVE NATURAL SELECTION

The basic argument for disruptive natural selection leading to sympatric speciation is that adaptation to different ecological niches within a single population will lead to a reduction of gene flow and ultimately to divergence. Usually, the evolution of some form of nonrandom mating is required for speciation to happen. The importance of an “ecological” mode of speciation is advocated in Schluter 2000, and a more recent discussion of ecological speciation can be found in Nosil 2012. The mechanism of sympatric ecological speciation is nicely presented in Gavrillets, et al. 2007, which describes a model that is inspired by an empirical case study of sympatric speciation. Disruptive selection can either act due to the existence of discrete niches or result when organisms subdivide continuously distributed resources. Dieckmann, et al. 2004 is dedicated to this latter scenario. Several mechanisms that link the action of divergent selection to assortative mating have been proposed. In the simplest case, reproductive barriers are a direct byproduct of adaptive divergence. A review of this scenario, what has been termed “speciation via magic traits,” is found in Servedio, et al. 2011. In other cases a nonrandom association between components contributing to reproductive isolation has to be established for speciation to proceed. Smadja and Butlin 2011 summarizes several scenarios of how this can happen. Finally, it should be noted that natural and sexual selection are often thought to act in concert in speciation with gene flow, for example as modeled in van Doorn, et al. 2009 and as discussed in Weissing, et al. 2011.

Dieckmann, U., M. Doebeli, J. A. J. Metz, and D. Tautz, eds. 2004. *Adaptive speciation*. Cambridge Studies in Adaptive Dynamics. Cambridge, UK, and New York: Cambridge Univ. Press.

A compilation of contributions by various authors on the topic of adaptive dynamics and adaptive speciation. The key rationale is that frequency-dependent interactions lead to the splitting of groups. Since interactions require physical contact, the main geographic setting for this mode of speciation is thought to be sympatry and parapatry.

Gavrillets, S., A. Vose, M. Barluenga, W. Salzburger, and A. Meyer. 2007. Case studies and mathematical models of ecological speciation: 1. Cichlids in a crater lake. *Molecular Ecology* 16.14: 2893–2909.

The studied model here is tailored to the scenario of sympatric speciation of Midas cichlid fishes in Crater Lake Apoyo, Nicaragua. The authors find that the scenario of sympatric speciation as envisioned is indeed plausible under certain conditions that are inferred from the model.

Nosil, P. 2012. *Ecological speciation*. Oxford Series in Ecology and Evolution. Oxford and New York: Oxford Univ. Press.

A comprehensive and timely account of basically all aspects of ecological speciation. Although not restricted by geography, ecological speciation is assumed to be the predominant mode in sympatric speciation (at least in animals) and thus highly relevant in this regard.

Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford Series in Ecology and Evolution. Oxford: Oxford Univ. Press.

Although the idea of ecological speciation dates back to Darwin and was also popular during the Modern Synthesis, Schluter's book popularized the idea once again and stimulated a more mechanistic focus of speciation research.

Servedio, M. R., G. S. van Doorn, M. Kopp, A. M. Frame, and P. Nosil. 2011. Magic traits in speciation: “Magic” but not rare? *Trends in Ecology & Evolution* 26.8: 389–397.

Magic traits have been hypothesized to strongly increase the likelihood of speciation with gene flow because the association between a trait under disruptive natural selection and assortative mating cannot be broken down by the antagonistic effects of recombination and segregation. The authors emphasize this point and question the presumed rarity of such traits.

Smadja, C. M., and R. K. Butlin. 2011. A framework for comparing processes of speciation in the presence of gene flow. *Molecular Ecology* 20.24: 5123–5140.

This review aims to provide a more unified picture of whether and how reproductive isolation can evolve in the presence of gene flow by means of coupling different barriers via the so-called trait association chain. Furthermore, the authors provide an overview of how different modes of speciation are interrelated and overlap.

van Doorn, G. S., P. Edelaar, and F. J. Weissing. 2009. On the origin of species by natural and sexual selection. *Science* 326.5960: 1704–1707.

In this model, divergent natural selection leads to the preference for an honest signal (i.e., a condition-dependent trait), which leads to assortative mating and thus facilitates speciation.

Weissing, F. J., P. Edelaar, and G. S. van Doorn. 2011. Adaptive speciation theory: A conceptual review. *Behavioral Ecology and Sociobiology* 65.3: 461–480.

This review aims to integrate advances in ecological and sexual-selection theory with regard to adaptive speciation. It is written in a nontechnical style. The authors make the point that an interplay of disruptive selection on ecological differences and mating strategies is necessary, though not sufficient, for speciation to happen.

DISRUPTIVE SEXUAL SELECTION AND SEXUAL CONFLICT

Although sexual selection may be involved in speciation initiated by natural selection, the studies discussed in this section are concerned with a primary impact of sexual selection in driving divergence. Support for these mechanisms comes primarily from theoretical work. A general overview on sexual selection in speciation is provided in Ritchie 2007. The proposed models most often envision a scenario in which there exist two groups of females that prefer males exhibiting different signaling traits. The association between preference and signal traits, and thus divergence, is often strengthened by divergent Fisherian runaway processes. Theoretical models of this kind can be found in Wu 1985; Turner and Burrows 1995; and Higashi, et al. 1999. Although sympatric speciation has been shown to be possible, in reviewing these models, Arnegard and Kondrashov 2004 concludes that sympatric speciation would be expected to happen only under very restrictive conditions, and that sexual selection alone is unlikely to be an important force in sympatric speciation. A similar conclusion, although based on other considerations and limitations of previous models, is reached in van Doorn, et al. 2004. In the context of sexual conflict (i.e., an antagonistic coevolution of the sexes), sympatric speciation is demonstrated as a possible outcome in Gavrillets and Waxman 2002. Yet, as the authors note, subsequent ecological divergence or spatial separation is needed for the stable coexistence of the newly formed groups. This conclusion applies to all models based on sexual selection alone. As noted in the section Disruptive Natural Selection, the actions of sexual and natural selection in speciation are by no means exclusive, and open questions in speciation research concern the relative roles and interaction of both forces, as discussed in Butlin, et al. 2012.

Arnegard, M. E., and A. S. Kondrashov. 2004. Sympatric speciation by sexual selection alone is unlikely. *Evolution* 58.2: 222–237.

A model-based evaluation, over a broad parameter space, of the likelihood of sympatric speciation by sexual selection.

Butlin, R., A. Debelle, C. Kerth, et al. 2012. What do we need to know about speciation? *Trends in Ecology & Evolution* 27.1: 27–39.

A review discussing outstanding questions in speciation research. One section ("Question 3") is concerned with the relative roles of natural and sexual selection.

Gavrilets, S., and D. Waxman. 2002. Sympatric speciation by sexual conflict. *Proceedings of the National Academy of Sciences of the United States of America* 99.16: 10533–10538.

The authors demonstrate two previously underappreciated general outcomes of sexual conflict, one being sympatric speciation. They assess the conditions that lead to this outcome.

Higashi, M., G. Takimoto, and N. Yamamura. 1999. Sympatric speciation by sexual selection. *Nature* 402.6761: 523–526.

The main outcome of this modeling approach is that sympatric speciation can occur if females can efficiently discriminate among males, and the costs for male signaling traits are low. As the authors discuss, the latter conclusion is opposite to the findings in Turner and Burrows 1995.

Ritchie, M. G. 2007. Sexual selection and speciation. *Annual Review of Ecology, Evolution, and Systematics* 38:79–102.

An easily accessible and lucid review. One section is devoted to the role of sexual selection in sympatric speciation.

Turner, G. F., and M. T. Burrows. 1995. A model of sympatric speciation by sexual selection. *Proceedings of the Royal Society B: Biological Sciences* 260.1359: 287–292.

In this paper the authors present a model that can lead to reproductively isolated groups due to sexual selection in any geographic setting. The simplistic genetic basis for female preference and the assumption of no cost for female choice have since been criticized, as in Higashi, et al. 1999.

van Doorn, G. S., U. Dieckmann, and F. J. Weissing. 2004. Sympatric speciation by sexual selection: A critical reevaluation. *American Naturalist* 163.5: 709–725.

According to the authors, sympatric speciation due to sexual selection is feasible, yet only under far more restricted conditions than previously realized. Most important, variation in female preferences is not easily incorporated into models.

Wu, C.-I. 1985. A stochastic simulation study on speciation by sexual selection. *Evolution* 39.1: 66–82.

It is shown that sympatric sexual isolation can evolve under certain conditions in a stochastic simulation study. This model assumes an absolute preference of females for male traits and hence relies more on affinity preference than on disruptive sexual selection.

POLYPLOIDIZATION AND HYBRIDIZATION

Polyploidization is characterized by a heritable increase in chromosome complement. Two main classes of polyploids can be distinguished: autopolyploids derive from an increase in ploidy level within a species, whereas allopolyploids result from the hybridization of members of two different species. Hybridization can also result in speciation without a change in ploidy level (i.e., homoploid hybrid speciation). Whether all cases of polyploidy and hybrid speciation naturally fall into the domain of sympatric speciation is debatable and depends on the definition of sympatric speciation (see Defining Sympatric Speciation). For example,

in a strict population-genetic sense, instantaneous speciation by hybridization or polyploidization can be considered allopatric, because gene flow between the new hybrid/polyploid species and the parental species is zero from the beginning. In contrast, in a biogeographic sense, most cases of polyploid and hybrid speciation can be considered sympatric. Yet, if a form of geographical isolation is required for the establishment of the new species, the mode of speciation can hardly be considered sympatric. Examples for both scenarios are discussed in Abbott, et al. 2013. A brief general review of hybrid speciation is given in Mallet 2007, while Soltis and Soltis 2009 focuses on the role of hybridization in plants. Generally, speciation via polyploidization is uncontroversial and can happen instantaneously, as initially demonstrated in Müntzing 1930. A comprehensive review of polyploidy in plants and animals and its evolutionary implications is given in Otto and Whitton 2000. These authors estimate that speciation by polyploidization in plants is common, and they propose that polyploidization may be the predominant mechanism of sympatric speciation in plants. Wood, et al. 2009 also estimates that the frequency of polyploid speciation is very high. Ramsey and Schemske 2002 focuses on recently formed polyploids in flowering plants, and the accompanying biological changes that may allow ecological divergence or result in prezygotic isolation from their parental species. Such byproducts of polyploidization strongly increase the likelihood for the establishment of the newly formed polyploid species and their stable coexistence in sympatry with the parental species.

Abbott, R., D. Albach, S. Ansell, et al. 2013. Hybridization and speciation. *Journal of Evolutionary Biology* 26.2: 229–246.

This review resulted from a workshop on the role of hybridization in speciation. The authors discuss cases of hybrid speciation and propose additional mechanisms of how hybridization can promote speciation.

Mallet, J. 2007. Hybrid speciation. *Nature* 446.7133: 279–283.

A brief, yet broad, review about the topic of hybrid speciation, with different sections focusing on homoploid and polyploid hybrid speciation.

Müntzing, A. 1930. Über Chromosomenvermehrung in Galeopsis-Kreuzungen und ihre phylogenetische Bedeutung. *Hereditas* 14.2: 153–172.

German article with summary in English. The artificial reconstruction of a naturally occurring tetraploid species, by crossing its presumed diploid parental species, provides unequivocal evidence for polyploidy as a mechanism of speciation that can happen instantaneously.

Otto, S. P., and J. Whitton. 2000. Polyploid incidence and evolution. *Annual Review of Genetics* 34:401–437.

A general overview on polyploidy in plants and animals. The authors use a novel approach to determine the incidence of polyploidy in speciation. Table 1, which can be accessed online as supplementary material, lists examples of known polyploid insects and vertebrates.

Ramsey, J., and D. W. Schemske. 2002. Neopolyploidy in flowering plants. *Annual Review of Ecology and Systematics* 33:589–639.

Review of the biological differences between recently formed polyploids and their parental species.

Soltis, P. S., and D. E. Soltis. 2009. The role of hybridization in plant speciation. *Annual Review of Plant Biology* 60:561–588.

Apart from the direct role of hybridization and polyploidization in the formation of new species, the authors also discuss more-

indirect effects such as more-ancient whole-genome duplications in angiosperms.

Wood, T. E., N. Takebayashi, M. S. Barker, I. Mayrose, P. B. Greenspoon, and L. H. Rieseberg. 2009. The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences of the United States of America* 106.33: 13875–13879.

Using cytogenetic and phylogenetic data, the authors provide a new estimate on the frequency of polyploid speciation.

Constraints and Conducive Conditions

Mathematical models have been highly instructive in identifying the conditions for and against sympatric speciation, and some general insights of when sympatric speciation may or may not occur have emerged. In addition, some studies have contributed to our knowledge by interpreting empirical data in the context of this body of theory and by identifying additional factors that may promote speciation.

THEORY

In addition to the question of how reproductive isolation arises in the presence of gene flow, a second major issue of sympatric speciation is coexistence. A situation in which two species inhabit the same habitat without ecological differences is assumed to be unsustainable; competitive or stochastic factors would lead to the extinction of one of the two species. This argument forms one of the main conceptual criticisms of sympatric speciation by sexual selection alone. However, this view has been challenged in M'Gonigle, et al. 2012, which demonstrates that long-term coexistence of ecologically equivalent groups is possible if carrying capacities vary spatially and mate choice is costly. Yet, the authors are concerned only with the maintenance of different groups and not with initial divergence. In fact, invoking a cost for mate search (choosiness) has been shown to strongly reduce the likelihood of sympatric speciation, for example in Kirkpatrick and Nuismer 2004. Many of the theoretically identified constraints and conditions for sympatric speciation, such as the strength of disruptive selection, are summarized in Gavrillets 2005 and are studied analytically for ecological sympatric speciation in Débarre 2012. Using simulations, Friedman, et al. 2013 investigates the conditions for sympatric speciation in bacteria. A verbal description of the conditions and constraints for sympatric speciation can be found in Kondrashov and Mina 1986. In addition, an increasing number of early-21st-century studies have pointed to a multifarious role of phenotypic plasticity in speciation. Thibert-Plante and Hendry 2011 uses numerical simulations to investigate the role of phenotypic plasticity in ecological speciation, and Fitzpatrick 2012 provides a more conceptual review of this topic.

Débarre, F. 2012. Refining the conditions for sympatric ecological speciation. *Journal of Evolutionary Biology* 25.12: 2651–2660.

An analytical theoretical investigation of the conditions favorable for ecological speciation in sympatry. The identified conditions are tested against a previously published simulation study.

Fitzpatrick, B. M. 2012. Underappreciated consequences of phenotypic plasticity for ecological speciation. *International Journal of Ecology* 2012:256017.

The author reviews the multifarious effects of adaptive and nonadaptive phenotypic plasticity for the two components of ecological speciation: local adaptation and assortative mating.

Friedman, J., E. J. Alm, and B. J. Shapiro. 2013. Sympatric speciation: When is it possible in bacteria? *PLoS ONE* 8.1:

e53539.

Since no barriers to recombination are included, according to the authors, the model describes the evolution of adaptive genotypes and the invasion of a new niche rather than speciation. An interesting outcome is the opposing effects of recombination in the early and late stages of divergence.

Gavrilets, S. 2005. "Adaptive speciation"—it is not that easy: A reply to Doebeli et al. *Evolution* 59.3: 696–699.

A response to an article that, according to Gavrilets, presents an all-too-optimistic view of the plausibility of sympatric speciation.

Kirkpatrick, M., and S. L. Nuismer. 2004. Sexual selection can constrain sympatric speciation. *Proceedings of the Royal Society B: Biological Sciences* 271.1540: 687–693.

In this article the authors highlight the negative effect of sexual selection on the progression of sympatric speciation.

Kondrashov, A. S., and M. V. Mina. 1986. Sympatric speciation: When is it possible? *Biological Journal of the Linnean Society* 27.3: 201–223.

A general review on the conditions that promote or inhibit sympatric speciation. Although an early contribution, this article remains relevant for understanding sympatric speciation.

M'Gonigle, L. K., R. Mazzucco, S. P. Otto, and U. Dieckmann. 2012. Sexual selection enables long-term coexistence despite ecological equivalence. *Nature* 484.7395: 506–509.

A theoretical study showing that under certain conditions, sexual selection alone can maintain coexistence of ecologically equivalent groups.

Thibert-Plante, X., and A. P. Hendry. 2011. The consequences of phenotypic plasticity for ecological speciation. *Journal of Evolutionary Biology* 24.2: 326–342.

One of the main findings of this study is that phenotypic plasticity can either promote or hinder progress toward ecological speciation, depending on the circumstances. Note that this study deals with the broader mode of ecological speciation and sympatric speciation in particular.

EMPIRICAL STUDIES

Employing an interesting approach, Bolnick 2011 combines theory and empirical data to ask why sympatric speciation does not occur in a natural population of stickleback fish, although the conditions appear conducive. Similarly, Martin 2013 investigates a natural population of cichlid fish in a Cameroon crater lake, which exhibits strong assortative mating but seems stalled in its divergence. An experimental study, Sharon, et al. 2010, provides evidence that phenotypic plasticity in the form of the diet-related microbiome can influence mate preference in *Drosophila*. Furthermore, the authors propose that this mating preference, together with geographic isolation, could promote speciation. Whether or not this factor plays a role in sympatric speciation remains to be tested.

Bolnick, D. I. 2011. Sympatric speciation in threespine stickleback: Why not? *International Journal of Ecology*

2011:942847.

A simulation study that is based on empirically obtained parameter values. The strength of selection and alternative evolutionary outcomes are suggested as possible explanations for why speciation does not happen.

Martin, C. H. 2013. Strong assortative mating by diet, color, size, and morphology but limited progress toward sympatric speciation in a classic example: Cameroon crater lake cichlids. *Evolution* 67.7: 2114–2123.

An empirical study that assesses the strength of assortative mating in a population of Tilapia cichlid fish. While assortative mating is strong, disruptive selection, which had been estimated previously, is proposed to be too weak for further divergence to occur.

Sharon, G., D. Segal, J. M. Ringo, A. Hefetz, I. Zilber-Rosenberg, and E. Rosenberg. 2010. Commensal bacteria play a role in mating preference of *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America* 107.46: 20051–20056.

The authors suggest that diet-related changes in commensal bacteria can affect mating preferences due to a change in sex pheromone levels.

Support and Evidence

Because speciation in nature happens over time scales that cannot be observed during the lifetime of any single human observer, researchers rely on indirect evidence from geological, ecological, and genetic data to make inferences about the mode of speciation. Thus, demonstrations that speciation happened in sympatry rely on indirect evidence and almost always leave room for alternative explanations. An additional issue with many case studies is that reproductive isolation between sympatric groups is often incomplete, and it is a matter of debate whether these cases of incipient sympatric speciation qualify as evidence for sympatric speciation. The different races or morphs may or may not become good species. Strong direct inferences on the possibility of sympatric speciation can be deduced from experimental studies, albeit the specifications of experimental designs often cannot mimic natural conditions and are thus not necessarily biologically relevant.

EMPIRICAL CASE STUDIES

A widely, albeit not universally, accepted view in evolutionary biology is that allopatric speciation can be considered as the null model, whereas the demonstration of sympatric speciation requires compliance with four main criteria (see General Overviews). While most empirical examples suffer from one or several weaknesses, some are now widely accepted as valid evidence of sympatric speciation. Some of the most convincing examples come from organisms inhabiting isolated environments. For example, Gíslason, et al. 1999 describes the sympatric divergence of four different morphs of Arctic char in a postglacial lake in Iceland. Schliewen, et al. 1994 reports the sympatric origin of cichlid fish species in a crater lake in Cameroon, and sympatric speciation has also been shown to have happened in cichlids inhabiting crater lakes in Nicaragua (Barluenga, et al. 2006). Savolainen, et al. 2006 makes a compelling argument for sympatric speciation in palm trees on the remote Lord Howe Island. Another major line of support for sympatric speciation is represented by case studies of host shifts. Host races of phytophagous insects have long been postulated to provide evidence for sympatric speciation; see, for example, “On Phytophagous Varieties and Phytophagous Species,” by B. J. Walsh, in *Proceedings of the Entomological Society of Philadelphia* 3 (1864): 403–430. Berlocher and Feder 2002 gives a good account of the reasons for this argument, although explicit case studies remain rare, and it is debated whether host races represent incipient speciation or stalled cases of divergence. Probably the most famous example of sympatric divergence is a pair of host races of fruit flies infesting hawthorn and apple. Years of research have shown that the host races are genetically differentiated and partially reproductively isolated. This divergence seems to have happened in sympatry after the introduction of apples to North America within historical times. Yet, Feder, et al. 2003 finds that some of the genetic variation involved in this divergence originated in an allopatric population and stemmed from introgression. Although

sympatric divergence via host shifts is most readily associated with phytophagous insects, at least one case of apparent sympatric divergence in vertebrates—namely, indigobirds—has been described (Sorenson, et al. 2003). The concept of species in bacteria has been notoriously vague, and, thus, work on speciation, not to mention sympatric speciation, is scarce. However, it has been proposed that ecotypes of bacteria form coherent groups and can be considered the equivalent of species in sexually reproducing eukaryotes. Accordingly, Sikorski and Nevo 2005 proposes a case of incipient sympatric ecological speciation in *Bacillus simplex*.

Barluenga, M., K. N. Stölting, W. Salzburger, M. Muschick, and A. Meyer. 2006. Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature* 439.7077: 719–723.

Similar to the situation in Cameroonian crater lakes, ecological and genetic data together with the geographic setting provide strong evidence for a sympatric origin of endemic crater lake species of cichlids in Lake Apoyo. Further studies, using an updated taxonomy and more-sophisticated population-genetic approaches, continue to support this scenario.

Berlocher, S. H., and J. L. Feder. 2002. Sympatric speciation in phytophagous insects: Moving beyond controversy? *Annual Review of Entomology* 47:773–815.

A comprehensive review on phytophagous insects and the plausibility of sympatric speciation via host shifts.

Feder, J. L., S. H. Berlocher, J. B. Roethele, et al. 2003. Allopatric genetic origins for sympatric host-plant shifts and race formation in *Rhagoletis*. *Proceedings of the National Academy of Sciences of the United States of America* 100.18: 10314–10319.

In this paper the authors describe that part of the genetic variation involved in the sympatric divergence of the host races originated in an allopatric population. Whether or not this fact disqualifies this system as an example of sympatric speciation is debated, since the divergence itself nevertheless happened in sympatry.

Gíslason, D., M. M. Ferguson, S. Skúlason, and S. S. Snorrason. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* 56.12: 2229–2234.

In this study the authors investigate four postglacial lakes harboring different morphs of Arctic char and demonstrate different stages of phenotypic and genetic divergence, which most likely happened in sympatry.

Savolainen, V., M.-C. Anstett, C. Lexer, et al. 2006. Sympatric speciation in palms on an oceanic island. *Nature* 441.7090: 210–213.

Phylogenetic reconstruction provides support for divergence of palms on Lord Howe Island. Geographic isolation in the wind-pollinated species of trees on this small island can be ruled out. Instead, a shift of flowering time correlated with soil preference is involved.

Schlieven, U. K., D. Tautz, and S. Pääbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368.6472: 629–632.

Using a phylogenetic approach, the authors show that the endemic flocks of cichlid species inhabiting two crater lakes in Cameroon each form monophyletic lineages. This and the fact that no geographical barriers appear to exist support a scenario of

sympatric speciation after the colonization by a single ancestral population.

Sikorski, J., and E. Nevo. 2005. Adaptation and incipient sympatric speciation of *Bacillus simplex* under microclimatic contrast at “Evolution Canyons” I and II, Israel. *Proceedings of the National Academy of Sciences of the United States of America* 102.44: 15924–15929.

An empirical study on soil bacteria that are suggested to resemble a scenario comparable to ecological speciation in sexually reproducing eukaryotes.

Sorenson, M. D., K. M. Sefc, and R. B. Payne. 2003. Speciation by host switch in brood parasitic indigobirds. *Nature* 424.6951: 928–931.

A rare example of host-shift-induced sympatric speciation in vertebrates. In indigobirds that parasitize the nests of other species, the use of different host species has led to a form of cultural isolation. Males mimic the songs of their hosts, while females use songs to choose their mates as well as their host.

EXPERIMENTAL STUDIES

Experiments testing the possibility of, and the conditions conducive for, sympatric speciation have been carried out mainly by using various species of flies (predominantly *Drosophila*). One of the first and most famous experiments is described in Thoday and Gibson 1962, providing strong support for the possibility of sympatric speciation. However, as discussed in Thoday and Gibson 1970, similar follow-up experiments were unable to replicate this positive outcome. Yet, using an ingenious experimental design, the authors of Rice and Salt 1990 found the evolution of complete reproductive isolation due to habitat isolation after only thirty generations of selection. Overall, experiments on sympatric speciation have had mixed results. Much of the experimental work on speciation is reviewed in Rice and Hostert 1993 and Kirkpatrick and Ravigné 2002.

Kirkpatrick, M., and V. Ravigné. 2002. Speciation by natural and sexual selection: Models and experiments. In *Special issue: The ecological genetics of speciation. American Naturalist* 159.S3: S22–S35.

General review on models and experiments on speciation, providing a great overview of the different factors involved in speciation. Several experiments on sympatric speciation are discussed.

Rice, W. R., and E. E. Hostert. 1993. Laboratory experiments on speciation: What have we learned in 40 years? *Evolution* 47.6: 1637–1653.

A review on experimental studies of speciation. Table 1 lists studies that simulate sympatric speciation.

Rice, W. R., and G. W. Salt. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: Experimental evidence. *Evolution* 44.5: 1140–1152.

Probably the most famous experimental study on speciation. Nevertheless, the selection pressure of the study has been criticized as being unrealistically high. Furthermore, one part of the study (the double-selection regime) has been declared to actually simulate *allopatric* conditions.

Thoday, J. M., and J. B. Gibson. 1962. Isolation by disruptive selection. *Nature* 193.4821: 1164–1166.

An experimental study, in which divergent selection for bristle number in *Drosophila* for only a dozen generations apparently led to strong reproductive isolation due to assortative mating. Yet, the results could never be replicated, and the authors later proposed an unknown genetic peculiarity of their lines as a possible explanation.

Thoday, J. M., and J. B. Gibson. 1970. The probability of isolation by disruptive selection. *American Naturalist* 104.937: 219–230.

A review of experimental studies of disruptive selection and the conditions that may affect the likelihood for reproductive isolation to evolve.

Estimating the Frequency

A sympatric speciation event is expected to result in a pair of sister species occupying the same area. Therefore, integrating information on biogeographic distributions and phylogenetic relationships of taxa might allow inferences about the relative frequency of sympatric speciation and allopatric speciation. One inherent problem in these approaches is that the ranges of species are not fixed, and, initially, sympatric species may exclude each other spatially (and vice versa for species that arose in allopatry). One possible solution to this issue is to focus on situations in which secondary contact is unlikely. For example, Coyne and Price 2000 argues that sympatric speciation is rare in birds, by using data on endemic bird species on isolated and small islands; Papadopulos, et al. 2011 estimates the frequency of sympatric speciation in plants on the remote Lord Howe Island; and Weiblen and Bush 2002 provides evidence for sympatric speciation in some cases of host-specific fig wasps. Another way to take the issue of range shifts into account is by considering the age of taxa; this method is proposed and applied in Barraclough and Vogler 2000. A similar, but more advanced, approach is used in Fitzpatrick and Turelli 2006 in studying several taxa of mammals. Adding information from environmental-niche models, Graham, et al. 2004 investigates modes of speciation in a group of frogs. Nevertheless, although providing a reasonable and sorely needed approximation on the frequency of different geographical modes of speciation, these approaches suffer from several limitations and weaknesses, as discussed in Barraclough and Nee 2001.

Barraclough, T. G., and S. Nee. 2001. Phylogenetics and speciation. In *Special issue: Speciation. Trends in Ecology & Evolution* 16.7: 391–399.

A general conceptual review on the applications and limitations of phylogenetic methods in speciation research.

Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* 155.4: 419–434.

The main rationale behind the proposed method is that the expected pattern of range overlap and divergence time differs between allopatric and sympatric speciation.

Coyne, J. A., and T. D. Price. 2000. Little evidence for sympatric speciation in island birds. *Evolution* 54.6: 2166–2171.

In this paper the authors investigate data on forty-six small islands and archipelagos that contain endemic species of birds.

Fitzpatrick, B. M., and M. Turelli. 2006. The geography of mammalian speciation: Mixed signals from phylogenies and range maps. *Evolution* 60.3: 601–615.

The suggested improvements over the method in Barraclough and Vogler 2000 include different approaches to estimate the range overlap, and the null hypothesis of no relationship between phylogenetic relatedness and range overlap.

Graham, C. H., S. R. Ron, J. C. Santos, C. J. Schneider, and C. Moritz. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* 58.8: 1781–1793.

The incorporation of ecological information in the age-range correlation method allows for inferences concerning the impact of ecological-niche shifts in speciation.

Papadopoulos, A. S. T., W. J. Baker, D. Crayn, et al. 2011. Speciation with gene flow on Lord Howe Island. *Proceedings of the National Academy of Sciences of the United States of America* 108.32: 13188–13193.

The authors survey nearly the entire flora of a remote and small island, finding evidence that several endemic sister species may have formed in situ. Whether these cases are clearly in the domain of sympatric speciation or are better classified as parapatric remains unclear.

Weiblen, G. D., and G. L. Bush. 2002. Speciation in fig pollinators and parasites. *Molecular Ecology* 11.8: 1573–1578.

In this study, at least three species pairs of fig wasps, each of which is restricted to the same host, are identified as sister species. Thus the authors propose a mode of sympatric speciation.

Hallmarks

Inferences about whether a particular speciation event has happened in sympatry can be made only in an investigative manner; data from present-day populations are gathered to make inferences about the past. The occurrence of certain patterns in the data can give credence to different evolutionary scenarios. Apart from resulting in more-obvious outcomes, such as a sister group relationship, sympatric speciation is thought to be characterized by some hallmarks. While these hallmarks alone are arguably not sufficient to demonstrate sympatric speciation, they lend support to its occurrence. One hallmark can be observed at the genomic level: divergence with gene flow is supposed to leave a heterogeneous pattern of genetic divergence across the genome, at least in the early stages. The insight that genomes are mosaics and can behave as semipermeable barriers to gene flow originated in the late 1960s in the literature on hybrid zones, as discussed in Harrison 2012. Although the author of Bazykin 1969 already used this concept in the context of sympatric speciation, the idea was popularized in speciation research only more than three decades later in Wu 2001, under the term “the genic view of speciation.” However, Noor and Bennett 2009 notes that several other factors can also lead to a heterogeneous genomic divergence, and the interpretation of this pattern thus warrants caution. A timely and comprehensive review on the impact of geography on genomic divergence is given in Feder, et al. 2013. Another hallmark of scenarios of speciation with versus without gene flow concerns the buildup of prezygotic and postzygotic barriers. As is famously shown in Coyne and Orr 1989, prezygotic isolation evolves much faster in sympatric than in allopatric species of *Drosophila*. Although the main explanation in this context was the role of reinforcement in a scenario of secondary contact, the same reasoning applies to the initial stages of speciation. Nascent species originating in the presence of gene flow should not exhibit any form of intrinsic postzygotic isolation—since there would be a strong selection pressure against this—and should mainly be isolated due to prezygotic barriers. In contrast, both forms may build up equally in geographical isolation. This prediction was tested in Crow, et al. 2010, and the results were found to be in favor of sympatric speciation in a genus of marine reef fishes.

Bazykin, A. D. 1969. Hypothetical mechanism of speciation. *Evolution* 23.4: 685–687.

Bazykin was one of the first researchers to address sympatric speciation from a mathematical point of view. In this paper he introduces the idea that certain regions of the genome may be exchanged less freely between populations than others.

Coyne, J. A., and H. A. Orr. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43.2: 362–381.

In this classic paper the authors use a meta-analysis to make inferences on several aspects of the buildup of reproductive isolation in speciation.

Crow, K. D., H. Munehara, and G. Bernardi. 2010. Sympatric speciation in a genus of marine reef fishes. *Molecular Ecology* 19.10: 2089–2105.

An empirical paper that integrates morphological and genetic data with in vitro crossing experiments to test a theoretical prediction of sympatric speciation.

Feder, J. L., S. M. Flaxman, S. P. Egan, A. A. Comeault, and P. Nosil. 2013. Geographic mode of speciation and genomic divergence. *Annual Review of Ecology, Evolution, and Systematics* 44:73–97.

This review, based mainly on new advances in theory and empirical data from population genomics, discusses the impact of the geographic circumstances of speciation on genome-wide patterns of divergence.

Harrison, R. G. 2012. The language of speciation. *Evolution* 66.12: 3643–3657.

The main point of this paper is to highlight the increase and redundancy of language complexity in speciation research. The sections about the genome as a mosaic and the geography of speciation will be of special interest to those interested in sympatric speciation.

Noor, M. A. F., and S. M. Bennett. 2009. Islands of speciation or mirages in the desert? Examining the role of restricted recombination in maintaining species. *Heredity* 103.6: 439–444.

In this brief and lucid review the authors discuss several factors and mechanisms that can lead to a pattern of heterogeneous genomic divergence, and they advise caution in automatically interpreting highly diverged regions as islands of speciation.

Wu, C.-I. 2001. The genic view of the process of speciation. *Journal of Evolutionary Biology* 14.6: 851–865.

A conceptual review advocating the view that genes and not whole genomes are the unit of adaptation and species differences. Although the idea can be found in the literature on hybrid zones beginning in the late 1960s, this article brought it to the attention of a wider audience.

LAST MODIFIED: 08/26/2014

DOI: 10.1093/OBO/9780199941728-0053

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