Sympatric Speciation: Models and Empirical Evidence

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Key Words

Abstract

Sympatric speciation, the evolution of reproductive isolation with-
out geographic barriers, remains highly contentious. As a result of
new empirical examples and theory, it is now generally accepted that
sympatric speciation has occurred in at least a few instances, and is
theoretically plausible. Instead, debate has shifted to whether sym-
patric speciation is common, and whether models' assumptions are
generally met in nature. The relative frequency of sympatric spe-
ciation will be difficult to resolve, because biogeographic changes
have obscured geographical patterns underlying many past specia-
tion events. In contrast, progress is being made on evaluating the
empirical validity of key theoretical conditions for sympatric spe-
ciation. Disruptive selection and direct selection on mating traits,
which should facilitate sympatric speciation, are biologically well
supported. Conversely, costs to assortative mating are also widely
documented, but inhibit speciation. Evaluating the joint incidence
of these key factors may illuminate why sympatric speciation appears
to be relatively uncommon.

INTRODUCTION

Speciation: The evolution of genetically distinct populations (clusters), maintained by reproductive isolation in the case of sexual taxa

Sympatric speciation is among the most persistently contested topics in evolution, dating back to correspondence between Darwin and Wagner. Early geneticists claimed that new species arise instantaneously via mutation from within their ancestral range (de Vries 1901–1903), whereas naturalists countered that related species in nature were always separated by geographic barriers (Jordan 1905). Debate waned after Mayr (1963) outlined a compelling case against sympatric divergence, arguing that it was theoretically unlikely. The key problem is that mating and recombination rapidly break down linkage disequilibrium, preventing formation of genetically distinct subgroups. Mayr therefore argued that overlapping ranges are better explained by secondary contact between allopatrically derived species. However, Mayr presciently predicted that "the issue will be raised again at regular intervals. Sympatric speciation is like the Lernaean Hydra which grew two new heads whenever one of its old heads was cut off" (p. 451).

Since 1990, the number of papers on sympatric speciation has increased exponentially. This revival of the Hydra can be attributed in part to molecular phylogenetics, which provides a new source of data to evaluate Mayr's alternative hypothesis of secondary contact. There are now a few widely accepted examples of sympatric speciation, which in turn inspired a proliferation of theoretical models. Many skeptics now concede that sympatric speciation is theoretically possible and has probably occurred in nature (Coyne & Orr 2004). Debate has shifted to the still more difficult questions of how frequent sympatric speciation may be, and what mechanisms drive speciation. In this review, we describe recent empirical results and the theory underlying this shift, and discuss prospects for future progress.

WHEN IS SPECIATION SYMPATRIC?

Mayr (1963) defined sympatric speciation as evolution of reproductive isolation "without geographic isolation" (p. 449). Geographic isolation occurs when the distance between populations exceeds individuals' ability to disperse between them (cruising range) or when intervening environments are inhospitable, precluding dispersal. However, it is not always easy to determine when isolation is geographic, as opposed to biological isolation arising from intrinsic differences in habitat preference among groups. The key distinction is that geographic barriers are extrinsic features of the environment that affect all individuals, independent of genotype. Ambiguity arises because biological and geographic barriers may be difficult to distinguish empirically and may interact if extrinsic barriers are conditional upon individuals' biological traits. Another difficulty is that isolation is often a matter of degree and may depend on spatial scale. For instance, phytophagous insects using two or more host plants may be considered geographically overlapping at a large scale, and isolated at a small scale.

Some definitions of sympatric speciation add a population genetic stipulation that the initial population must be panmictic. Sympatric speciation is the evolution of reproductive isolation "within a single interbreeding unit" (Mayr 1942, p. 189) or

between populations that initially use two distinct habitats but disperse freely between them (Futuyma & Mayer 1980). Gavrilets (2003) provided the most precise statement of the population genetic view: "sympatric speciation is the emergence of new species from a population where mating is random with respect to the birthplace of the mating partners." (p. 2198) As with isolation, panmixia is a matter of degree: Are we to conclude that two populations are not sympatric if only 40% of individuals move between populations each generation rather than the 50% expected with perfect panmixia? Although population genetic criteria focus on the initial conditions of a speciating lineage, they also implicitly adopt the biogeographic criterion that no extrinsic barriers arise subsequently. In practice, theoreticians tend to adopt this more precise population genetic definition as an initial condition in models. Empiricists rarely have information about the population structure of ancestral species and so tend to adopt the biogeographic definition, using current distribution patterns and phylogenetics to infer past geographic isolation. This semantic and methodological divide may contribute to disagreements over what constitutes sufficient evidence for sympatric speciation.

What Evidence Distinguishes Sympatric from Nonsympatric Speciation?

Coyne & Orr (2004) proposed four criteria for identifying cases of sympatric speciation, which we modify slightly:

1. Species thought to have arisen via sympatric speciation should have largely or completely overlapping geographic ranges. The spatial scale used to determine overlap should be commensurate with the dispersal ability of the organisms. In principle, sympatrically derived species could become allopatric over time (Baack 2004, Stuessy et al. 2004), but it is not clear how to unambiguously demonstrate secondary allopatry.

2. Speciation must be complete. Ongoing divergence is an important subject of study for speciation biology. However, we cannot declare a case of sympatric speciation if speciation has not occurred, because partial divergence may be a stable outcome (Matessi et al. 2001). Evaluating this criterion is subjective, because one must impose a binary decision on a continuous process of divergence. For instance, one must decide how much hybridization (biological species concept) or how much phenotypic or genetic overlap (cluster species concept) is allowed between distinct species.

3. Clades thought to arise via sympatric speciation must be sister species or monophyletic endemic species flocks. Evidence for monophyly should not be based on a single locus, owing to the risk of introgression. This criterion is conservative and not strictly necessary. Consider a sympatric speciation event that produces sister species A and B on an island. Later, A colonizes another island and speciates allopatrically into A and A'. Strictly speaking, A and B are no longer sister species, but the initial speciation event remains sympatric. Nonetheless, we retain this criterion because a biologist given modern distributions of A, A', and

B could not readily distinguish between sympatric speciation and secondary contact of A and B.

4. Coyne & Orr's fourth criterion stated that "the biogeographic and evolutionary history of the groups must make the existence of an allopatric phase *very unlikely*" (p. 142, their italics). We agree that to establish sympatric speciation, one must reject alternative hypotheses (allopatry and parapatry; see sidebar, Allopatry as a Null Model). However, this criterion is redundant, simply restating Mayr's biogeographic definition of sympatric speciation. The critical question is, what evidence is required to reject any past period of geographic isolation and conclude that current sympatry is representative of biogeographic patterns during speciation? The most common approach is to focus on sister species inhabiting a uniform and isolated geographic area that makes secondary contact unlikely (e.g., Savolainen et al. 2006, Schliewen et al. 1994). One problem with this approach is the need to explain one and only one colonization event. In continental settings, biogeographic data are less informative because range shifts are more likely. However, sympatric speciation may still be reasonable if speciation is very recent relative to climatological or geological events that might alter distributions, and if neither population exhibits phylogeographic signatures of range expansion. A final line of evidence comes from speciation events such as hybrid speciation, autopolyploidy, and transitions to selfing, which are likely to occur within the range of the parental species. Host shifts, though easiest in sympatry, may occur in parapatry or during colonization events and so require additional biogeographic evidence that the shift occurred between sympatric host taxa.

Sympatry: Describes populations with broadly overlapping geographic ranges

EMPIRICAL SUPPORT FOR SYMPATRIC SPECIATION IN NATURE

Few studies have managed to satisfy all four criteria (Barluenga et al. 2006b, Gislason et al. 1999, Savolainen et al. 2006, Schliewen et al. 1994, Sorenson et al. 2003), and all have their critics. Lacking room to review all case studies, we focus on three main types of evidence marshaled in support of sympatric speciation. (See Supplemental Material for a more complete list of putative examples. Follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org/**.)

Evidence from Isolated Environments

Some of the most compelling cases of sympatric speciation are found in small isolated environments like oceanic islands (Savolainen et al. 2006), postglacial lakes (Gislason et al. 1999), and crater lakes (Schliewen et al. 1994). However, even in isolated sites, double invasion and introgression can lead to sympatric species that may be misinterpreted as cases of sympatric speciation (Taylor & McPhail 2000). The crater Lake Apoyo (23,000 years old) is one of the more recently documented cases of putative sympatric speciation, between the endemic arrow cichlid (*Amphilophus zaliosus*) and the widely distributed midas cichlid (*A. citrinellus*). The lake's small size and uniform

ALLOPATRY AS A NULL MODEL

Coyne & Orr (2004) claimed that allopatric speciation is a null model for speciation, being theoretically uncontroversial and empirically well documented. We disagree for several reasons. First, allopatry is difficult to falsify, but failure to reject allopatry does not mean that it is supported. Cases with insufficient data are simply inconclusive. Because alternative hypotheses cannot be rigorously evaluated for many taxa, adopting an alternative as a default risks an unknown Type II error rate that will bias comparative estimates of the frequency of different modes of speciation. Second, in practice, studies rarely conduct statistical tests of null predictions. Rather, the relative credibility of past events is evaluated based on subjective judgments. If allopatry is treated as a null, ad hoc hypotheses favoring allopatry will be given more credibility than equally ad hoc stories of sympatry. Finally, there is not a simple dichotomous choice between allopatric and sympatric speciation, as both parapatry and geographic changes are well documented. Mayr's biogeographic definition of sympatric speciation excludes any period of geographic isolation, however brief. If we apply an equally stringent definition to allopatric speciation requiring zero gene flow during speciation, we might find that mixed-geography speciation, in which both allopatry and gene flow contribute to divergence, is relatively common.

topography make intralacustrine geographic barriers implausible. Genetic data support monophyly of Lake Apoyo cichlids with respect to other *A. citrinellus* populations (Barluenga et al. 2006b). All mitochondrial haplotypes are unique to Lake Apoyo and share a distinctive substitution. Microsatellite and amplified fragment length polymorphism (AFLP) data exhibit separate but closely related clusters within Apoyo. Barluenga and colleagues have been criticized for omitting one of the potential outgroups in nearby Lake Nicaragua (Schliewen et al. 2006, but see the Barluenga et al. 2006a rebuttal). Also, although nuclear data indicate that the Apoyo fish are closely related, Apoyo *citrinellus* are genetically intermediate between the co-occurring *zaliosus* and the more widespread *citrinellus.* Critics say this is consistent with secondary contact and a period of introgression (Schliewen et al. 2006), though it may also be explained by *zaliosus* arising from within Apoyo *citrinellus*, consistent with the lower diversity of *zaliosus* and difficulty of colonizing the lake (Barluenga et al. 2006b). If, as seems likely, the crater lake actually harbors three to four endemic species, secondary contact and introgression would be still less parsimonious (A. Meyer, personal communication). We describe this case not because the case is closed, but because it epitomizes the ambiguities that plague even the best examples of sympatric speciation. Genetic data may not always be able to distinguish between introgression and incomplete lineage sorting, particularly in very recently diverged taxa.

Cameroon crater lake cichlids (Schliewen & Klee 2004, Schliewen et al. 1994) and Lord Howe island palms (Savolainen et al. 2006) are other leading cases of sympatric

speciation in isolated environments, with multilocus monophyly and thoroughly sampled outgroups. However, there are a number of putative cases of sympatric speciation that inhabit similar geographic settings, but have not yet been thoroughly studied (Berrebi & Valiushok 1998, Dimmick & Edds 2002, Klemetsen et al. 2002, Wilson et al. 2004). For instance, 25–50% of Arctic char populations (*Salvelinus alpinus*) exhibit genetically distinct ecomorphs (Wilson et al. 2004). Although these char morphs are thought to arise sympatrically, detailed phylogeographic data are available for only one lake (Gislason et al. 1999).

Evidence from Host Shifts

It is difficult to rule out secondary contact in continental or oceanic habitats where range expansions are easier. In such settings, case studies may rest on ecological rather than biogeographic evidence against geographic isolation. Specifically, host shifts are generally expected to occur within a population's native range, though this is not strictly necessary. Because host shifts could directly confer reproductive isolation if mating occurs on the host, there are fewer theoretical objections to such sympatric divergence. Consequently, sympatric sister species using different hosts provide an alternative line of evidence for sympatric speciation. The most famous example is *Rhagoletis pomonella*, which specialized on hawthorn fruits prior to the colonial-era introduction of apples into North America. The shift to apples occurred within the native range of hawthorn flies and led to reproductive isolation by divergent mate timing and habitat choice (Feder & Filchak 1999, Linn et al. 2003). However, the host races are not classified as distinct species owing to low levels of hybridization. Consequently, this case is usually portrayed as demonstrating plausibility of sympatric speciation via host shift rather than an actual case of sympatric speciation. Recent genetic evidence suggests that the host shift involved a chromosomal inversion that arose in allopatry (in Mexico), arrived in the northeast via gene flow, and was later co-opted for speciation (Feder et al. 2003). Although definitions of sympatric speciation do not stipulate that genetic variation must arise in sympatry, speciation may or may not have been possible without this allopatrically derived preadaptation.

Two recent reviews of insect host shifts (Berlocher & Feder 2002, Drés & Mallet 2002) highlight several examples of more distinct sympatric sister species that use different hosts [*Enchenopa binotata* complex (Wood & Keese 1990); *Spodoptera frugiperda* on corn and rice (Prowell et al. 2004); *Nilaparvata lugens* on weed grass and rice (Claridge et al. 1997, Sezer & Butlin 1998); and two other species pairs in the *Rhagoletis pomonella* group (Berlocher 1999)]. Instances of sympatric host-shift speciation have also been inferred in vertebrates. Genetically distinct sympatric species of brood parasitic indigobirds (*Vidua*) in Africa rely on different host species to raise their young. Because male indigobirds learn (and females imprint on) their host's courtship songs, reproductive isolation can be virtually instantaneous if eggs are laid in a new species' nest (Sorenson et al. 2003). Indopacific gobies feed and mate exclusively on *Acropora* corals: a young species of goby was recently described that uses a novel coral host and is completely contained within the range of its sister species (Munday et al. 2004). An

equivalent process can occur in plants via adaptation to different edaphic conditions (Savolainen et al. 2006).

Evidence from Instantaneous Speciation

Instantaneous speciation necessarily occurs in sympatry with parental populations, but is often dismissed as rare. For instance, meiotic errors can produce polyploid offspring reproductively isolated from their parents (*autopolyploid speciation*; Ramsey & Schemske 1998). Less than 7% of plant speciation events are estimated to have involved changes in ploidy (Otto & Whitton 2000). Not all of these are autopolyploids, and not all polyploidy generates instantaneous speciation (Ramsey & Schemske 1998). This still may represent a substantial number of speciation events. Interspecific hybridization can also produce populations that are reproductively isolated from their sympatric parents by ploidy, karyotype, ecology, or mating behavior (Gompert et al. 2006, Mavarez et al. 2006, Rieseberg et al. 1995, Schwarz et al. 2005). Although hybridization must occur where both parental species are present, it is ambiguous whether this constitutes sympatric speciation because it does not arise from a single panmictic population and may occur in hybrid zones at the periphery of adjoining parental distributions. However, hybrid parapatry may also reflect niche partitioning between sympatrically derived taxa (Gompert et al. 2006, Rieseberg et al. 1995). Finally, sexual populations can produce asexual or selfing lineages via mutation, such as the selfing annual plant *Stephanomeria malheurensis* and its outcrossing sympatric sister species *S. exigua* (Gottlieb 1979). Such sympatric speciation is uncontroversial because recombination does not oppose divergence.

HOW GENERAL IS SYMPATRIC SPECIATION?

The preceding case studies establish that sympatric speciation has probably occurred, something now acknowledged even by many skeptics (Coyne & Orr 2004). Debate has shifted to whether sympatric speciation is common. This requires estimates of relative frequencies of sym-, para-, and allopatric speciation in nature. Tallying individual well-supported cases of each geographic mode is out of the question owing to several sources of ascertainment bias. Whereas extensive work is required to demonstrate sympatric speciation, allopatric pairs are accepted with little consideration (see sidebar, Allopatry as a Null Model). Rates of allopatric speciation may be over- or underestimated as a result of taxonomic practices (Agapow et al. 2004): decisions to lump or split allopatric variants into one or more species can raise or lower the number of allopatric speciation events. Keeping such biases in mind, biologists have tried two coarse approaches to estimate the frequency of sympatric speciation.

Counting Examples

The simplest approach is to count the number of putative sister species that exhibit a given amount of range overlap. Collectively, studies taking this approach

Reinforcement: The evolution of increased reproductive isolation owing to selection against hybridization

Parapatric: Describes populations with adjoining ranges that exchange a moderate number of migrants

represent 309 speciation events, of which 9.4% resulted in sister species with over 90% contemporary range overlap, compared with 72.2% with zero range overlap (Berlocher 1998, Coyne & Price 2000, Fitzpatrick & Turelli 2006, Lynch 1989). These data support the claim that sympatric speciation is rare, because fewer than 1 in 10 speciation events are even candidates. It seems reasonable to expect that many more sister species would be sympatric if sympatric speciation were very common. However, these studies do not include lacustrine fish species flocks or phytophagous insects, which represent the majority of putative cases of sympatric speciation (**Supplemental Table 1**). This counting exercise is also flawed in two ways. First, it is sensitive to how allopatric variants are treated by taxonomists. For instance, the freshwater sunfish *Lepomis punctatus* was widely sympatric with its sister species *L. microlophus* until *punctatus* was split into two allopatric taxa, ending the sister relationship with *microlophus* (Near et al. 2005). Second, it assumes that present geographic overlap accurately reflects geography during speciation. These counts include cases of sympatric species known to have come into contact after allopatric speciation (Chesser & Zink 1994, Coyne & Orr 2004, Coyne & Price 2000), or after a period of allopatry followed by reinforcement in sympatry as in benthic and limnetic stickleback species pairs (Taylor & McPhail 2000). Conversely, some unknown fraction of allopatric or parapatric species may have originated in sympatry (Stuessy et al. 2004). One study to effectively avoid these biases is Coyne & Price's (2000) survey of oceanic island birds, which found little support for sympatric speciation in remote settings that remove many of the biogeographic ambiguities plaguing other studies. It would be valuable to carry out such studies on a wider range of taxonomic groups in isolated sites such as oceanic islands, lakes, and caves.

Age-Range Correlation

Several researchers suggested a method of assessing the prevalence of sympatric versus allopatric speciation that explicitly accounts for potential postspeciation range shifts (Barraclough & Vogler 2000, Lynch 1989). If allopatric speciation were the rule, young species pairs would be predominantly allopatric, with increasing sympatry for older pairs due to range shifts. Conversely, sympatric speciation would lead to decreasing sympatry with age. This age-range correlation (ARC) has been widely criticized (Fitzpatrick & Turelli 2006, Losos & Glor 2003). First, the null distribution of range overlaps is poorly defined and must be estimated by randomizing the data in each study. Second, results may depend on how range overlap between clades is measured. Third, biogeographic changes associated with Pleistocene climate fluctuations are very recent compared with even the youngest speciation events in many groups (Avise et al. 1998, Fitzpatrick & Turelli 2006), so geographic evidence may have been compromised for all species pairs. Finally, ARC will yield conclusive results only if a single geographic mode of speciation has been considerably more common than others; a mixture of sympatric, parapatric, and allopatric speciation may result in an uninformative distribution of geographic range overlaps, resembling a null distribution of randomized range overlaps. Consequently, ARC studies are generally inconclusive, failing to demonstrate any consistent relationship

between geographic range overlap and phylogenetic relationships (Fitzpatrick & Turelli 2006).

Empirical Summary: The Frequency of Sympatric Speciation

Available data continue to support the orthodox position that sympatric speciation is less common than parapatric or allopatric speciation. However, there are enough well-supported examples to confidently say that sympatric speciation can occur in nature, and other putative cases of sympatric speciation remain understudied (**Supplemental Table 1**). This raises an important question: Are we likely to ever obtain an unbiased estimate of the frequency of sympatric speciation? We suggest not, because (*a*) ascertainment biases may favor recognition of nonsympatric speciation events to an unknown extent, (*b*) relationships between current and past biogeography can be rapidly disrupted by global climate change or range expansion, and (*c*) potential incipient species such as sympatric host races may not be reliable indicators of the likelihood of speciation.

What, then, are the prospects for future research on sympatric speciation? Clearly, much insight can be gained from more detailed dissection of many individual case studies. As for assessing the general incidence of sympatric speciation, we recommend an approach that complements counting and ARC studies. Rather than ask what fraction of past speciation events were sympatric, we suggest a pair of questions: Theoretically, what assumptions are conducive to sympatric speciation? Empirically, how often are these assumptions met in natural systems? Below, we summarize some major models of sympatric speciation, highlighting crucial assumptions (see Coyne & Orr 2004, Dieckmann et al. 2004, Gavrilets 2004, Kirkpatrick & Ravigne 2002 for more extensive reviews). We devote the final section of this review to evaluating empirical data on three key assumptions.

THEORIES OF SYMPATRIC SPECIATION

Nearly all models of sympatric speciation share a common framework. In an initially panmictic population, disruptive selection drives an evolutionary (rather than biogeographic) change in mating patterns. The result is reproductive isolation between subsets of the population's descendents, maintaining strong linkage or Hardy-Weinberg disequilibrium. The problem is that even low rates of mating between diverging subpopulations leads to recombination that increases frequencies of intermediate phenotypes. Models of sympatric speciation must therefore explain how divergent selection is able to overcome recombination to establish Hardy-Weinberg disequilibrium at mating loci, and perhaps linkage disequilibrium between mating and ecological genes. To date, there are over 70 models of sympatric speciation (**Supplemental Table 2**). Following Kirkpatrick & Ravigne (2002), these can be organized by their assumptions regarding four key issues: (*a*) the cause of disruptive selection, (*b*) how individuals select mates, (*c*) whether selection acts directly or indirectly on mating characters, and (*d*) the genetic basis of changes in mating patterns (1- versus 2-allele models). We discuss each of these assumptions, highlighting selected models as examples.

Cause of Disruptive Selection

Assortative mating: When individuals select mates that are more phenotypically similar to themselves than expected under random mating

Runaway sexual selection. The burst of interest in sympatric speciation in the 1990s coincided with a sharp increase in research on species flocks of East African cichlids. These rapidly speciating fish are often characterized by striking divergence in sexually dimorphic color patterns between ecologically very similar species (Seehausen 1997), inspiring speculation that sympatric speciation could arise through disruptive sexual selection alone. Higashi et al. (1999) modeled a population in which, to attract females, males express a quantitative trait ranging between two extremes (e.g., red to blue). Females vary in a second quantitative trait ranging from strongly preferring red, through random choice, to strongly preferring blue. Given an initial population composed of intermediate but polymorphic males (purple) and females (random mating), the population rapidly diverges into two species characterized by blue or red males and females that prefer blue or red. This is because any initially extreme-colored males are favored by the few choosy females, while intermediate males have no corresponding benefit because intermediate females mate randomly. Matings between extreme males and choosy females will produce offspring with both traits, resulting in disruptive two-tailed runaway sexual selection that builds up linkage disequilibrium until the population splits into two distinct groups.

Although this model is deeply flawed, its failings are highly informative. First, costs to assortative mating impose selection against stringent mate preferences, eliminating genetic variation for choosiness and preventing speciation (Arnegard & Kondrashov 2004). Second, Higashi's model assumed an initially polymorphic population without explaining how this polymorphism could arise. Even minor perturbations from Higashi's initially symmetric polymorphism can prevent speciation because runaway sexual selection becomes predominantly directional rather than disruptive (Arnegard & Kondrashov 2004). The current consensus is that sexual selection alone is unlikely to drive sympatric speciation (Arnegard & Kondrashov 2004, Coyne & Orr 2004, Gavrilets 2003, van Doorn et al. 2004). Additional sources of disruptive selection are required to stabilize mating polymorphisms that are later sorted into distinct species and/or compensate for costs of female choice. This disruptive selection can arise from a large variety of negative frequency-dependent interactions. These include sexual conflict (Gavrilets & Waxman 2002), male-male competition (van Doorn et al. 2004), opposing sexual and natural selection (Turner & Burrows 1995), and meiotic drive genes affecting sex ratio and secondary sexual traits (Lande et al. 2001). However, the vast majority of models invoke disruptive selection arising from ecological interactions such as resource competition.

Ecological disruptive selection. Stable disruptive selection from ecological interactions is generally modeled in one of two ways, which we will refer to as Levene and unimodal models. In Levene models, a population inhabits two distinct habitats such as host plants, which impose divergent adaptive demands. Two different alleles can stably coexist in this setting if each is favored in a different habitat with separate density regulation (Levene 1953). Stable disruptive selection ensues when heterozygotes have a lower mean fitness (averaging across habitats) than either homozygote

(Gavrilets 2006, Wilson & Turelli 1986). Despite its implicit spatial structure, this model satisfies the population genetic definition of sympatry if initial migration rates between habitats are high ($m \sim 0.5$) or if low migration follows a host shift from an initially panmictic population specializing on a single habitat.

In contrast, unimodal models assume a single environment containing resources continuously distributed (usually normal) along a trait axis such as prey size. Consumers are characterized by a continuous trait (e.g., gape width) governing resource use. Competition is less intense among phenotypically divergent individuals (Bürger 2005, Slatkin 1979). The consumer population's mean phenotype will evolve to match the most abundant prey trait. This will represent an evolutionary equilibrium for the mean phenotype, but not necessarily the variance (Roughgarden 1972). The equilibrium phenotype variance depends on both the diversity of resources available, and the width of individuals' niches. If each individual uses the full range of resources, then no among-individual variance will be maintained; the population will be subject to stabilizing selection (Bürger 2005). If, however, individuals use small subsets of the available resources, then the equilibrium trait variance may be large. Disruptive selection occurs when the existing trait variance is less than its equilibrium. Phenotypically extreme individuals then experience relatively weak resource competition, even given their less abundant resources. This disruptive selection will persist until increased genetic variation, plasticity, sexual dimorphism, or speciation raises the trait variance to its equilibrium level. In the final section of this review, we evaluate empirical support for frequency-dependent competition and disruptive selection.

How Individuals Select Mates

In sexual taxa, disruptive selection alone is insufficient to cause speciation. Random mating quickly breaks down any Hardy-Weinberg or linkage disequilibrium that arises from selection. Only extraordinarily strong frequency-dependent disruptive selection, in which few if any intermediates survive, can maintain distinct and reproductively isolated groups. Under more realistic levels of selection, ecological divergence must be accompanied by reproductive divergence. We therefore need to specify both how mating occurs and how it responds to selection.

Two general mating schemes are commonly used: assortment and trait-preference models. Assortment occurs when individuals (usually assumed to be females) prefer mates that are similar to themselves at some phenotypic trait expressed in both sexes. This matching leads to a correlation between trait values of mated pairs. Traits used for matching can include ecological traits under disruptive selection (Dieckmann & Doebeli 1999, Maynard Smith 1966), location or timing of mating (Fry 2003), or signal traits such as color or pheromones (Maynard Smith 1966, Udovic 1980). In contrast, trait-preference models assume that each female expresses a preference for males with a particular trait, genetically independent of her own genotype for that trait. In principle, male traits could be ecological or secondary sexual traits, though nearly all trait-preference models assume the latter (Doebeli 2005, Maynard Smith 1966). Assortment models are often said to be less general, but are more conducive to speciation (Gavrilets 2004, Kirkpatrick & Ravigne 2002).

Whether Selection Acts Directly or Indirectly on Mating Characters

Pleiotropy: When a gene influences two or more traits

Magic trait: A phenotypic trait that influences both an individual's ecological interactions and the probability of mating with individuals possessing similar trait values

Disruptive selection can directly affect mating patterns if traits used in mating are also directly relevant to ecological performance or genetically correlated with ecological traits. Ecological differences may reduce mating rates by affecting mate timing or location (Fry 2003) or if assortment is based on ecologically functional traits like morphology (Bürger et al. 2006). If ecologically divergent individuals are unlikely to mate from the outset, then when disruptive natural selection reduces the frequency of intermediate ecological genotypes, the remaining phenotypic extremes mate largely within themselves. Consequently, the population bifurcates into two noninterbreeding groups. This scenario greatly facilitates sympatric speciation, so we review existing empirical evidence for mating/ecology pleiotropy in the final section of this review.

There are two main objections to models of mating/ecology pleiotropy (sometimes called magic trait models; Gavrilets 2004). First, some researchers question whether traits controlling both ecology and mating are biologically realistic (Felsenstein 1981). Second, these models assume, rather than explain, strong assortative mating within the original population (Gavrilets 2005). Other models have tried to explain how assortative mating might initially evolve from random-mating populations (Dieckmann & Doebeli 1999, Fry 2003, Seger 1985). These models focus on indirect selection on mating traits in a process analogous to reinforcement (Servedio & Noor 2003), but without a period of allopatric divergence. Disruptive selection means that individuals who mate randomly risk producing intermediate offspring with lower fitness, indirectly favoring individuals that mate with their own ecotype. Selection is indirect because increased choosiness does not alter an individual's own fitness. Instead, choosy females avoid producing ecologically intermediate and less-fit offspring.

How Mating Patterns Evolve

There are two general ways in which disruptive selection can indirectly favor increased assortative mating through a reinforcement-like process. First, mating within ecotypes can arise by an evolutionary increase in assortment if the stringency of mate preferences (choosiness) can evolve. Alternatively, linkage disequilibrium can build up between previously independent mating and ecological traits. These correspond to the one- and two-allele models of Felsenstein (1981).

One-allele models. Consider a Levene-style population using two habitats favoring genotypes AA and aa respectively, resulting in disruptive selection. Next, assume that a new allele M arises at a second independent locus, which causes AA individuals to mate with AA, and aa individuals to mate with aa. By reducing production of less-fit heterozygous offspring, this allele is favored in both AA and aa individuals over the original m allele that conferred random mating. Because this model involves substitution of a single allele in both emerging daughter species, it is called a one-allele model (Felsenstein 1981). Recombination does not oppose the spread of the M allele,

so speciation is relatively straightforward, albeit less robust than when selection acts directly on mating characters (Felsenstein 1981, Gavrilets 2006). More generally, one-allele models occur whenever emerging daughter species fix the same set of mating alleles. One-allele models include the evolution of reduced migration (Balkau & Feldman 1973), adaptive habitat selection (Fry 2003), or imprinting (Verzijden et al. 2005). They can also include the evolution of stronger assortative mating based on ecological traits (Dieckmann & Doebeli 1999). This requires that females are able to evaluate the match between their own trait and that of a prospective mate. Although such magic trait assortative mating is frequently used in models, there are questions about its biological generality (Gavrilets 2004).

Two-allele models. Sympatric speciation is more difficult when reproductive isolation requires trait-preference mating or assortment for nonecological traits, because divergent species must fix different mating alleles. Continuing the example used above, females might be polymorphic for a mating locus with alleles m for random mating, M_A preferring AA ecotypes, and M_a preferring aa. Randomly mating individuals (m) risk producing low-fitness Aa heterozygotes, so selection should favor M_A/AA and M_a/aa females. Emerging daughter species must fix different mating alleles, so this is called a two-allele model (Felsenstein 1981). The problem is that unless selection against heterozygotes is extraordinarily strong, recombination breaks down linkage disequilibrium between M_A and A, and between M_a and a, so females mate randomly with respect to their own ecological trait (Udovic 1980). Consequently, recombination-selection antagonism greatly reduces the ease of sympatric speciation.

When female preferences are for neutral third traits such as male color or song, emerging daughter species must fix both different preference alleles and different marker trait alleles, both of which may recombine with the ecological trait under disruptive selection. For instance, if $M_B M_B$ and $M_b M_b$ each mate exclusively with their own genotype, recombination between M and A loci still opposes speciation. Models suggest that sympatric speciation is very difficult but still possible in this relatively complex scenario (Dieckmann & Doebeli 1999, Doebeli 2005, Udovic 1980). To see how, consider a population under disruptive selection for an ecological trait such as jaw size, which is also polymorphic for independent loci affecting male color (blue or red) and female preferences for blue or red. Because color and preference are independent of jaw size, red-preferring females gain no fitness benefit from mating with red males. However, if linkage disequilibrium arises stochastically between the three traits, females can use male color as a weak proxy for ecology. Females who happen to be choosier will be more likely to mate with their own ecotype, reducing their risk of producing less-fit intermediate offspring. If disruptive selection is sufficiently strong, this reinforcement-like process can outpace the breakdown of linkage disequilibrium by recombination, leading to speciation (Dieckmann & Doebeli 1999, Doebeli 2005). Much like pure sexual selection models, these models often assume initially polymorphic mating traits despite the purifying effect of assortative mating (Kirkpatrick & Nuismer 2004).

Trait-preference mating: When females prefer to mate with males exhibiting specific mating characters, independent of the females' expression of that character

Criticisms of Sympatric Speciation Models

In conclusion, sympatric speciation is easiest with strong disruptive ecological selection, strong mate preferences, low costs of being choosy, low recombination between mating and ecological loci, and large initial trait variances or high mutation rates (Gavrilets 2004). Culturally transmitted mate preferences and spatial structure can further facilitate sympatric divergence. Although simulations and analytical theory confirm that sympatric speciation is theoretically possible, they do not guarantee that it actually occurs in natural populations. The models outlined above adopt a variety of assumptions that have been widely criticized as being biologically unrealistic (Barton & Polechova 2005; Bolnick 2004a; Gavrilets 2005; Kirkpatrick & Nuismer 2004; Matessi et al. 2001; Polechova & Barton 2005; Waxman & Gavrilets 2005a,b). Sympatric speciation can be greatly delayed or prevented if certain key assumptions are relaxed (Bolnick 2004a, Bürger et al. 2006, Gavrilets 2005, Matessi et al. 2001, Waxman & Gavrilets 2005a).

Three assumptions have been singled out as particularly problematic. First, ecological assumptions required for disruptive selection may rarely be satisfied. Natural populations may not exhibit the narrow individual niche width required for frequency-dependent competition (Ackermann & Doebeli 2004, Roughgarden 1972) or phenotypic variances may not be constrained to be less than their equilibrium level (Bolnick & Doebeli 2003, Polechova & Barton 2005). Second, trait-preference mating, using traits unrelated to ecology, may be more general than magic trait assortative mating based on ecological characters (Gavrilets 2005). Third, females with stringent mate preferences may experience fitness costs that oppose the evolution of increased assortative mating, slowing or preventing sympatric speciation (Bolnick 2004a, Bürger et al. 2006, Kirkpatrick & Nuismer 2004, Schneider & Bürger 2006). Other criticisms highlight the use of constant ecological parameters, highly symmetrical and polymorphic initial conditions, very stringent assortative mating (Bolnick 2004a), a stable environment and resource distribution (Johansson & Ripa 2006), and soft selection (Demeeus et al. 1993). In conclusion, theoretical plausibility of sympatric speciation may be irrelevant if theoretical assumptions are not met in natural populations.

ARE THEORETICAL ASSUMPTIONS EMPIRICALLY JUSTIFIED?

Unfortunately, judgments about the biological realism of model assumptions are usually made on the basis of intuition rather than data. For instance, after showing that two-allele speciation is quite difficult, Felsenstein (1981) stated, "I find it easier to imagine genetic variation of the two-allele sort than of the one-allele sort" (p. 135). The lack of empirical grounding is unfortunate, because it may be easier to evaluate the frequency with which key assumptions are met than to estimate the frequency of sympatric speciation itself. One could then use the frequency with which key assumptions are jointly satisfied as a rough guide to the potential for sympatric speciation in

nature. Conversely, finding that assumptions are rarely satisfied, alone or in combination, may help explain why sympatric speciation is uncommon. In this final section, we review empirical support for three leading conditions widely thought to facilitate sympatric speciation (though no one condition is entirely necessary or sufficient): (*a*) natural populations experience frequency-dependent disruptive selection, (*b*) natural selection operates directly on assortative mating patterns, and (*c*) assortative mating imposes weak or no costs.

Condition 1: Natural Populations Experience Frequency-Dependent Disruptive Selection

Most sympatric speciation models invoke ecologically-driven disruptive selection to (*a*) maintain polymorphisms that are later sorted by assortative mating, (*b*) drive divergence in traits that pleiotropically cause reproductive isolation, or (*c*) indirectly favor reinforcement of reproductive isolation. Disruptive selection is often assumed to arise from frequency-dependent competition among ecologically heterogeneous individuals within a population. Such ecological heterogeneity is widely documented, ranging from host races (Drés & Mallet 2002) and discrete polymorphisms (Smith & Skulason 1996), to more subtle individual-level niche variation (Bolnick et al. 2003). Further, competition has been shown to be stronger among phenotypically more similar individuals (Benkman 1996, Schluter 1994, Smith 1990, Swanson et al. 2003). This can give rare phenotypes an advantage or suppress the fitness of intermediate individuals during periods of intense competition, as confirmed by experiments in the laboratory (Bolnick 2001, Rainey & Travisano 1998) and field (Bolnick 2004b). Thus, frequency-dependent competition does drive disruptive selection on trophic traits in some natural populations (Benkman 1996, Bolnick 2004b, Hori 1993, McLaughlin et al. 1999, Pfennig et al. 2007, Robinson & Wilson 1996, Smith 1993).

How common is this disruptive selection? A recent meta-analysis concluded that 8% of selection estimates yielded significant positive quadratic curvatures (Kingsolver et al. 2001). Because positive quadratic coefficients can occur without a true fitness minimum (e.g., L-shaped fitness functions), we tentatively conclude that ≤8% of natural populations are subject to the kind of disruptive selection invoked in speciation models. However, this study may underestimate the frequency of disruptive selection because it omitted Levene-style metapopulations such as insect host races where disruptive selection is particularly likely. In conclusion, sympatric speciation models invoking disruptive selection are well justified, though they probably apply to only a minority of natural populations. Why, then, do we not see evidence of sympatric speciation in oceanic island birds, which are likely candidates for character release and disruptive selection (Coyne & Price 2000, Werner & Sherry 1987)? The answer is that disruptive selection is insufficient for sympatric speciation—if island birds primarily use preference-trait mating rules or experience significant costs to mate choice, speciation may be prevented.

Condition 2: Ecological Selection Operates Directly on Mating Characters (Mating/Ecology Pleiotropy)

Perhaps the clearest consensus to emerge from theory is that disruptive selection can lead to speciation when selected traits directly confer reproductive isolation (Gavrilets 2004). Where proponents and opponents of sympatric speciation disagree is whether such pleiotropic assortative mating is biologically realistic. We have no estimate of the frequency of pleiotropy between ecology and mating. Nonetheless, it is clear that such pleiotropy does exist and can arise from a variety of mechanisms.

The simplest form of mating/ecology pleiotropy arises when mating occurs on resources such as host plants. In a classic laboratory experiment, Rice & Salt (1990) confirmed that assortative mating can arise via evolution of divergent habitat preferences in sympatry. This is one of the few successful laboratory tests of sympatric speciation (Rice & Hostert 1993), perhaps because it applied selection directly on mating patterns in addition to several trade-offs between niches. *Drosophila melanogaster* populations were maintained in cages containing spatially separated divergent food sources. Each generation, newly hatched flies were mixed in the center of the cage and allowed to select an environment, where they mated and laid eggs. Disruptive selection was imposed by retaining only eggs laid on the two most divergent habitats. This clearly corresponds to sympatry because spatial segregation arose from genetic differences in habitat preference, rather than physical barriers to movement, from an initially panmictic population. By the 25th generation over 98% of flies quickly traveled to their parents' habitat, resulting in strong assortative mating. In contrast, laboratory selection experiments looking for reproductive isolation under indirect selection have failed (Rice & Hostert 1993), with one exception that has not been successfully replicated (Thoday & Gibson 1962).

Does habitat-specific mating occur in nature? The answer is a clear yes. Many phytophagous insects mate on the same host on which they feed (Berlocher & Feder 2002, Drés & Mallet 2002, Katakura et al. 1989, Wood & Keese 1990), as do some vertebrates (Munday et al. 2004), so evolutionary shifts to new hosts may automatically confer some reproductive isolation from conspecifics on the ancestral host. Recent hybridization between two *Rhagoletis* species produced a lineage that is unable to recognize either ancestral host plant and instead mates and oviposits on an introduced honeysuckle that is avoided by both parental species, resulting in reproductive isolation (Schwarz et al. 2005). It would be very useful to know what fraction of phytophagous insect species exhibit such host-specific mating.

Ecological divergence may also result in temporal reproductive isolation, because many species time their breeding to coincide with peak resource availability. Insect host races frequently diverge to match alternate host plant phenologies (Feder & Filchak 1999, Pratt 1994, Smith 1988, Wood & Keese 1990) or exploit different stages of fruit development within a single host (Weiblen & Bush 2002). Sympatric populations of lacustrine fish exhibit divergent spawning times, possibly coinciding with the availability of alternate prey (Palstra et al. 2004, Skulason et al. 1989, Taylor & Bentzen 1993, Wood & Foote 1996). In plants, the use of different edaphic conditions can lead to flowering time divergence (Savolainen et al. 2006).

The preceding mechanisms prevent proximity during mating, but ecological divergence can also directly modify mate-attraction cues. Host plant chemistry, for example, influences cuticular hydrocarbons and pheromones of phytophagous insects (Landolt & Phillips 1997, Stennett & Etges 1997). Changes in bill morphology in Darwin's finches influences vocal performance during courtship song (Podos 2001). However, direct selection on male signal traits will not facilitate sympatric speciation unless matched by parallel pleiotropic effects on female preferences. Correlated male signals and female preferences might evolve in three ways. First, female preferences may result from imprinting on parental phenotypes, as in several bird species (Grant & Grant 1997, Irwin & Price 1999, Sorenson et al. 2003). In contrast, insects do not appear to exhibit imprinting on their larval host (Barron 2001, vanEmden et al. 1996). Second, a population may already exhibit positive assortative mating based on ecologically important traits, which disruptive selection simply makes more effective by increasing trait variance. There is extensive evidence for assortative mating within natural populations, revealed by phenotypic correlations between mated male/female pairs for body size (Johannesson et al. 1995, McKaye 1986, Schliewen et al. 2001), color (Reynolds & Fitzpatrick 2007), major histocompatibility complex (MHC) genotype (Aeschlimann et al. 2003), or diet (Ward et al. 2004). Finally, female preferences and male signals may be controlled by the same gene or closely linked genes. This scenario has generally been disregarded based on the logic that genetic control of signal production is likely to be very different from that of signal perception (Boake 1991). However, a number of examples occur where the same gene(s) influence both production and discrimination of mating signals [e.g., *desat1* in *Drosophila melanogaster* (Marcillac et al. 2005); bindin in *Echinometra* sea urchins (Palumbi 1999); MHC loci in sticklebacks (Aeschlimann et al. 2003)]. In *Heliconius* butterflies, one quantitative trait locus (QTL) influences male preference, female wing-color, and predator avoidance (Kronforst et al. 2006). This QTL may be an inversion that suppresses recombination between signal and preference loci, rather than a single pleiotropic gene, but the distinction is unimportant for speciation models.

In conclusion, selection clearly does operate directly on traits involved in assortative mating owing to mating/ecology pleiotropy. When disruptive selection coincides with such pleiotropy, sympatric speciation may be relatively easy. However, there are also many examples in which mating traits are independent of ecological characters (Hager & Teale 1996, Nosil et al. 2006). In addition, it may be difficult, in retrospect, to distinguish cases in which ecology/mating pleiotropy preceded ecological divergence from the less robust scenario of one-allele reinforcement, in which such pleiotropy evolves in response to disruptive selection. To date, only one study has demonstrated one-allele reinforcement, during secondary contact between two allopatrically diverged *Drosophila* species (Ortiz-Barrientos & Noor 2005).

Condition 3: Assortative Mating Confers Weak or No Costs

If highly choosy females incur fitness costs, sympatric speciation may be drastically slowed or prevented (Bolnick 2004a, Bürger et al. 2006, Kirkpatrick & Nuismer 2004,

Schneider & Bürger 2006). This is because direct costs of searching for a suitable mate may exceed the indirect fitness benefits of assortative mating. Many models impose costs by setting a limit on C, the number of males (or sperm) that a female (or egg) is able to reject before entirely losing her ability to reproduce (Bolnick 2004a). Models suggested that speciation only failed when such costs were strong [$C < 30$ (Bolnick 2004a); or $C < 10$ (Bürger et al. 2006)]. However, judgments about what constitutes strong costs should be based on empirical data. Although we have no direct measures of C, it is sometimes possible to determine the number of males that females encounter during mate choice. Existing data (mostly from birds) indicate that females evaluate anywhere from 1 to 100 males prior to breeding, but generally fewer than 10 (see **Supplemental Table 3**). This suggests that costs of mate choice may frequently override benefits of selecting rare male phenotypes.

Fitness costs may often arise via incremental risks or expenses, rather than an abrupt cut-off (Alatalo et al. 1988, Slagsvold & Dale 1991). Experiments manipulating actual or perceived predation risk have shown that females mitigate higher risks by becoming less choosy (Forsgren 1992, Godin & Briggs 1996, Hedrick & Dill 1993, Jennions & Petrie 1997, but see Reid & Stamps 1997). For instance, guppies were less choosy between more- and less-colorful males when predaceous fish were visible (Godin & Briggs 1996). Mate assessment also imposes energetic costs owing to movement (Milinski & Bakker 1992, Slagsvold & Dale 1994), courtship displays (Wikelski et al. 2001), and lost foraging time. Consequently, females may become less choosy when resources are limited (Palokangas et al. 1992, Reid & Stamps 1997). Over 90% of pronghorn antelope females visit multiple male territories before selecting a mate, but in a drought year 81% took the first mate they encountered (Byers et al. 2006). This poses an interesting catch-22 for sympatric speciation models: They often invoke food limitation to drive disruptive selection, yet this may also undermine females' ability to exercise stringent mate choice, preventing speciation.

Despite the costs, many natural populations do exhibit assortative mating and genetic variation for mating preferences (Jennions & Petrie 1997). Laboratory selection experiments have repeatedly led to the evolution of increased assortative mating (Rice & Hostert 1993), proving that there is genetic variation for mate preferences within populations. Far fewer studies have evaluated whether there is genetic variation for the stringency of these preferences (choosiness). In the clearest example, isofemale lines of brown planthoppers had identical mean preferences for the frequency of male courtship vibrations, but differed in the range of vibrations that they would accept (Butlin 1993). Such results confirm that natural populations can harbor standing genetic variation for degree of assortative mating, as assumed in several models (Dieckmann & Doebeli 1999) but questioned by some critics (Gavrilets 2005, Waxman & Gavrilets 2005a). The presence of genetic variation for assortative mating in natural populations suggests that the costs of mate choice are not always overwhelmingly strong. This is supported by some studies finding only weak costs to mate choice: daily expenditure in female sage grouse only rises by 1% when visiting a lek (Gibson & Bachman 1992). Our understanding of sympatric speciation would be greatly enhanced by more empirical data on costs of and genetic variation for

preference, signal traits, and choosiness in natural populations, and integrating such data into theoretical models.

SUMMARY

In 1963, Mayr concluded an extensive critique by saying that the burden of proof was on proponents of sympatric speciation. This remains true, notwithstanding the handful of compelling empirical cases and the pile of supportive theoretical models: We should continue to demand rigorous evidence before accepting a case study as a good example of sympatric speciation. However, we should also expect sound empirical evidence for claims of allopatric or parapatric speciation. Because past range expansions or secondary colonization events can be difficult to conclusively reject or demonstrate, many pairs of sympatric sister taxa may remain unresolved. This ambiguity is preferable to accepting a null model (which would bias estimates of the frequency of different modes of speciation). However, we may therefore be unlikely to achieve any confidence when estimating the frequency of different geographic modes of speciation. Based on current evidence, it seems reasonable to conclude that sympatric speciation occurs in nature, but is relatively rare, though more taxonomic groups should be investigated.

An alternative approach is to evaluate the frequency with which the prerequisites for straightforward sympatric speciation occur in nature. This may help us understand both when sympatric speciation is possible and why it is not more common. The empirical evidence available to date is by no means sufficient to judge the generality of any one factor, let alone their joint occurrence. Nonetheless, it is clear that niche variation, frequency-dependent competition, and resulting disruptive selection occur in a variety of systems. Mating/ecology pleiotropy, once dismissed by theoreticians as unlikely (Maynard Smith 1966), clearly does occur in nature. Costs to assortative mating are more difficult to assess, because available data cannot be easily compared with model parameters. Costs appear to be strong in some systems, whereas in others females are able to evaluate many males, leaving the door open for strong assortative mating. These empirical observations should guide choices of theoretical models and parameter ranges. Conversely, the rapidly growing theoretical literature on sympatric speciation is helping to identify key biological phenomena that facilitate or constrain sympatric speciation, pointing out profitable directions for future empirical efforts.

Given the difficulty of clearly distinguishing geographic scenarios, has the geography of speciation outlived its utility? Are we better off focusing on the mechanisms driving speciation, such as natural or sexual selection, reinforcement, drift, and hybridization? While such questions are doubtless useful and perhaps more tractable, such a research program still requires understanding the geography of speciation. Geographic structure influences what mechanisms can operate and how strong they must be to cause reproductive isolation. Furthermore, all speciation events occur in some geographic context, and the spatial distribution of biodiversity may depend on what speciation mechanisms are possible. Hence, we believe that geography will continue to play a central role in speciation research. This does not mean that the traditional sympatric/parapatric/allopatric distinction should be accepted uncritically. In

particular, it is clear that diverging populations can shift from allopatry to sympatry (Jordal et al. 2006, Taylor & McPhail 2000) or vice versa (Baack 2004, Stuessy et al. 2004) during the process of divergence. These geographic changes may play a fundamental role in facilitating reproductive isolation, through reinforcement (Servedio & Noor 2003) or hybrid speciation (Rieseberg et al. 1995). More subtle still, genetic variation at some loci may arise in allopatry but be sorted into reproductively isolated groups within a sympatric population (Feder et al. 2003). Such temporal changes offer some profound new directions in studying the geography of speciation, which will further blur what it means for speciation to be sympatric.

SUMMARY POINTS

1. To demonstrate that sympatric speciation has occurred, one must rule out alternative hypotheses (parapatry, allopatry). This is not equivalent to using allopatry as a null hypothesis or default explanation.

2. Two major types of evidence can support sympatric speciation: (*a*) sister species in an isolated environment that makes secondary contact unlikely, and (*b*) speciation mechanisms that occur most easily in sympatry (host shifts or instantaneous speciation).

3. Comparative approaches to estimate the relative frequency of sympatric and allopatric speciation are severely undermined by past biogeographic changes.

4. Although theoretical models indicate that sympatric speciation is possible in principle, the models are laden with numerous assumptions whose empirical validity is not well known.

5. Disruptive ecological selection, which many models invoke to maintain polymorphism and drive speciation, occurs at a low to moderate frequency in nature.

6. Magic traits, which influence both mating patterns and ecological fitness, are widely used in theoretical models and are known to occur in natural populations.

7. Theoretical models suggest that costs to mate choice may slow or prevent sympatric speciation. Empirical studies support the idea that mate choice costs can be significant.

FUTURE ISSUES

1. Phylogeographic studies within species can detect range expansions, and so might be useful in distinguishing cases of secondary contact from cases of true long-term sympatry.

2. Biogeographic comparative studies of range overlaps have not been conducted for the two groups most widely thought to exhibit sympatric speciation, phytophagous insects and lacustrine fishes.

3. More studies such as that by Coyne & Price (2000) are needed to evaluate the frequency of sympatric sister taxa in isolated environments such as islands, caves, and lakes.

4. The distinction between allopatry, parapatry, and sympatry is blurred by cases where speciation involves temporal shifts between biogeographic modes. This added temporal dimension needs to be better integrated into biogeography of speciation.

5. How often are natural populations subject to frequency-dependent disruptive selection invoked by theoretical models? How strong and how persistent is this selection?

6. How strong is assortative mating within populations?

7. Are ecologically functional traits commonly used as the basis for assortative mating?

8. Are the costs of mate choice in natural populations sufficient to oppose the evolution of assortative mating?

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The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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