Sympatric speciation in animals: the ugly duckling grows up

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Sympatric speciation has become increasingly accepted in the past decade, as a result of new models substantiating its plausibility and new evidence that the conditions specified by the models are met in many natural populations. Retrospective phylogenetic and population genetic signatures of sympatric speciation have also been derived, and these are beginning to be tested. This new work has helped increase the acceptance of sympatric speciation as a plausible process, although it remains difficult to show conclusively that specific pairs of taxa have speciated through sympatric processes alone. It might be time for a re-evaluation of the geographical classification of speciation modes in favor of one based primarily on evolutionary mechanisms.

Darwin believed that natural selection was responsible for producing the extravagant array of diverse species on 'the tangled bank'[1]. However, in the mid-1900s, the focus of SPECIATION (see Glossary) research shifted away from natural selection as the driving force and towards the role of geography in limiting gene flow and promoting GENETIC DRIFT. The dogma of this geographical view (championed by Mayr and reviewed in Ref. 2) is that populations found sympatrically ('within cruising range of one another'[2]) can only escape the homogenizing effects of gene flow under exceptional circumstances. By contrast, geographically isolated (allopatric) populations can diverge freely or, if they are small, be subject to strong genetic drift, which leads to REPRODUCTIVE ISOLATION. The work of Dobzhansky and Muller in the 1930s–1940s (reviews in Ref. 3 and Turelli *et al.*[4], this issue) provided a ready genetic mechanism for ALLOPATRIC SPECIATION. In geographically isolated populations, reproductive isolation is thought to accumulate as a byproduct of independent evolution through the substitution of incompatible alleles, which is hampered by gene flow. This model, allopatric speciation through postzygotic genetic incompatibilities, has been the dominant view of speciation for the past six decades (see also Turelli *et al.*[4], this issue). In this climate, SYMPATRIC SPECIATION has been extremely controversial: embraced and defended by a stalwart group of empiricists[5,6], but thought by many to be implausible and of limited applicability[7,8].

Recently, however, a variety of approaches have been used to re-evaluate the mechanisms that can lead to species formation and to provide additional empirical evidence that sympatric speciation can occur. I review theoretical work that supports the plausibility of sympatric speciation under a variety of conditions (see also Turelli *et al.*[4], this issue). I then discuss evidence that crucial conditions specified by the models have been found in natural populations, and summarize some historical (phylogenetic and population genetic) signatures of sympatric speciation that have been proposed (see also Barraclough and Nee[9], this issue). I argue that the objections to sympatric speciation raised by key papers between 1966 (Ref. 10) and 1981 (Refs 7,8) have been addressed, that a variety of alternative routes to sympatric speciation have been identified, and that evidence is accumulating that conditions favorable to the process are found in a variety of taxa. This work strongly suggests that sympatric speciation occurs under certain circumstances, vindicating the long-maligned proponents of the process. This recent work raises questions for the next phase of speciation research, and supports a new classification of speciation modes based primarily on mechanisms instead of on geography.

A brief life history of sympatric speciation

The ugly duckling is born (1930s–1966) and cast out (1966–1981)

The idea that natural selection can lead to divergence and speciation of sympatric populations dates back to Darwin (Ref. 1). However, sympatric speciation was not particularly controversial until the general acceptance of the allopatric mode of speciation as articulated by Mayr[2]. In the 1960s, several researchers answered Mayr's[2] call for evidence that speciation could occur under sympatric conditions: First, Thoday and Gibson's laboratory study[11] purported to show that DISRUPTIVE SELECTION could lead to the evolution of reproductive isolation. Then, Maynard Smith's simple model[10] illustrated that sympatric speciation under disruptive selection could occur, although under quite restrictive conditions. Finally, Bush described *Rhagoletis pomonella* as a potential case of sympatric speciation by host-RACE formation in the wild[12], using historical evidence reported over 100 years earlier by Walsh[13].

Despite considerable efforts to popularize sympatric speciation during the next 15 years[14–17], the process remained controversial. In Maynard Smith's models[10], disruptive selection leads to a stable polymorphism, and indirect selection against hybrid progeny favors ASSORTATIVE MATING, which can lead to speciation. Maynard Smith showed that when the substitution of just one allele causes fidelity to the natal habitat (ONE-ALLELE MATE CHOICE), the likelihood of sympatric speciation is greater than if a separate allele causes choice of each parental habitat (TWO-ALLELE MATE CHOICE). This distinction is also echoed in

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Table 1. Mechanisms that reduce the selection–recombination antagonism

Mechanism type	Refs
Mechanisms that eliminate requirement for linkage disequilibrium	
One-allele habitat choice	8,10
Disruptive selection on habitat choice leads to assortative mating pleiotropically	19,20
Same character under disruptive selection acts as mating cue	20,31
Mechanisms that reduce recombination or its effects	
Close linkage or partial pleiotropy between selected loci and loci causing assortative mating	8,25,44
Mechanisms that strengthen selection or its effects	
Increasing strength of selection as divergence increases	25,39,41
Multiple agents of disruptive selection favoring or reinforcing assortative mating	20,28
Appearance of new forces of disruptive selection as divergence proceeds	
Selection for increased local adaptation	20
Sexual selection for altered mating cues	20,46
Ecological selection against hybrid offspring (facilitated if intermediate habitat is lacking)	20,25,31
Repeated occurrence of mutations with habitat-limited benefits causes disruptive selection on habitat choice	44,45
Sexual selection or sexual conflict	46–48,63

many later models[18]. By 1980, Futuyma and Mayer[7] had declared that there was little conclusive evidence to warrant the acceptance of sympatric speciation as an important process in evolution, and had stated that allopatric speciation is the null model against which other modes of speciation must be tested.

Felsenstein's 1981 paper[8] further marginalized sympatric speciation by again suggesting that a strong antagonism between disruptive selection and recombination prevents the formation of LINKAGE DISEQUILIBRIUM and foils the evolution of assortative mating. This antagonism makes the conditions for sympatric speciation extremely strict. However, in a little-noticed section of this paper, Felsenstein[8] also showed that LINKAGE between disruptively selected loci and mating loci could greatly facilitate sympatric speciation by limiting recombination. Although this result has foreshadowed much of the recent work on sympatric speciation, it was largely ignored at the time. Instead, Felsenstein's[8] main result, that an antagonism between selection and recombination makes sympatric speciation unlikely, has fueled objections to sympatric speciation for the past 20 years.

In defense of the ugly duckling (1981–1988)
Felsenstein's work[8] and the dismissal of sympatric speciation by Futuyma and Mayer[7] provoked a series of new approaches to sympatric speciation. Rice's theoretical and empirical work[19–21] was a crucial step in establishing the plausibility of sympatric speciation. Rice showed that reproductive isolation could readily evolve in SYMPATRY either through disruptive/divergent selection directly on habitat choice or as a PLEIOTROPIC EFFECT of disruptive selection on other traits. Diehl and Bush's[22] simulation model of speciation by host shift

provided additional support for the effectiveness of habitat choice in producing assortative mating pleiotropically. Kondrashov's polygenic models of sympatric speciation[23–25] showed that reproductive isolation between sympatric taxa could arise from the evolution of ecologically important quantitative traits under disruptive selection. By specifically considering PLEIOTROPY (and to a lesser extent, linkage), these authors pointed out that a genetic association between disruptively selected traits and mate choice does not rest exclusively on the build up of linkage disequilibrium between unlinked genes.

This pivotal body of work showed that the models outlined by Maynard Smith[10] and Felsenstein[8], in which recombination impedes speciation, form only one of several possible routes to sympatric speciation (Table 1). In the newer models, the constraining effects of recombination between disruptively selected loci and those influencing assortative mating are sidestepped because selection either acts directly on loci influencing habitat choice (directly producing assortative mating) or influences other mechanisms that produce assortative mating pleiotropically[19,20,22]. In addition to this new emphasis on pleiotropy, it was again shown that physical linkage between loci under disruptive selection and those causing assortative mating would facilitate speciation by limiting the disruptive effects of recombination[25]. These models also made it clear that when the ecology of the organisms is considered, diverging populations can become subject to new selective forces as divergence proceeds[20], further tipping the balance in the problematic antagonism between selection and recombination.

The swan emerges (1988–present): increasing evidence for sympatric speciation
In 1988, it was verified that the sympatric host races of *Rhagoletis* are genetically differentiated[26,27], providing crucial support for Bush's 1966 scenario of sympatric speciation. In 1993, Rice and Hostert's review of laboratory studies of speciation[28] provided strong empirical evidence that reproductive isolation can evolve in a laboratory setting between sympatric populations with no physical barriers to gene flow. Odeen and Florin[29] found that small population sizes used in laboratory experiments could bias against the detection of sympatric speciation, suggesting that such speciation is even more common than suggested by Rice and Hostert[28].

Rice and Hostert[28] also found that speciation generally failed in laboratory studies characterized by a single strong force of disruptive selection of the sort modeled by Maynard Smith[10] and Felsenstein[8]. This suggested the importance of multiple selective forces in promoting reproductive isolation between sympatric populations. Consistent with this, various field studies of diverged sympatric races or species have also shown that they generally experience multiple forms of selection (Box 1; Table 2).

Box 1. Host races in herbivorous insects: two case studies of incipient species

Herbivorous insects have long been considered prime candidates for sympatric speciation because of an intimate and frequently highly specialized relationship with their host plants (which serve as habitat, food resource and, often, mating location). The apple maggot fly *Rhagoletis pomonella,* has been the classic example of sympatric speciation since 1966[a], based on the pivotal observation of an apparent sympatric host shift from hawthorn (*Crateagus* spp., native) to apple (*Malus pumila*, introduced) in the Hudson Valley of New York (USA) in the mid-1800s[b]. Recent experimental evidence has revealed that *R. pomonella* does possess many characteristics that are thought to be crucial to sympatric speciation[c] (Table I).

Sympatric populations of pea aphids *Acyrthosiphon pisum* on two hosts (alfalfa,

Medicago sativae, and red clover, *Trifolium pratense*) are also highly genetically specialized and substantially reproductively isolated[d]. Pea aphids also possess many of the key ecological and genetic characteristics that could have facilitated divergence and the evolution of reproductive isolation in sympatry (Table I). However, the historical and phylogenetic data that might reveal whether the initial divergence between populations of pea aphids on the two hosts was sympatric or allopatric is presently absent. Instead, the emphasis in this system has been on identifying the ecological and genetic mechanisms of ecological specialization and reproductive isolation between contemporary sympatric populations during the second stage of sympatric speciation.

The remarkable similarity of key characteristics between sympatric

populations of these two herbivores (and several others, e.g. Goldenrod ball-gall fly *Eurosta solidaginis* and the treehopper, *Enchenopa binotata* complex, Table 2), supports the claim that disruptive/ divergent selection on different hosts, and the propensity for habitat choice might frequently lead to speciation in insects[k]. Although it remains difficult to rule out a partial allopatric stage during the history of divergence of any given taxon pair, these data lend credence to the claims that sympatric divergence and/or the completion of speciation in sympatry is not only possible, but is probable under some circumstances.

References
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j Barrette, R.J. *et al.* (1994) Mitochondrial DNA diversity in the pea aphid, *Acyrthosiphon pisum*. *Genome* 37, 858–865

k Tauber, C.A. and Tauber, M.J. (1989) Sympatric speciation in insects: perception and perspective. In *Speciation and its Consequences* (Otte, D. and Endler, J., eds), pp. 307–344, Sinauer Press

Table I. Conditions favorable to sympatric speciation in two case studies

Condition	Apple maggot fly	Refs	Pea aphid	Refs
Broad sympatric overlap of host patches	Yes	a	Yes	e
Mating occurs on host	Yes	a	Yes	d
Reproductive isolation seen between races	Yes	c	Yes	d
Habitat choice behavior limits gene flow	Yes	c	Yes	d
Disruptive/ divergent selection on different hosts	Yes	c	Yes	e
Individual selection on habitat choice, caused by adult feeding on host	No	c	Yes	f
Genetic tradeoff seen in performance trait	Yes	g	Yes	e,h
Genetically based habitat choice	Yes (among populations)	c	Yes	d,f,h
Genetic correlation between host choice and performance traits	Not shown directly	c	Yes	d,h
Postzygotic isolation in hybrids by genetic incompatibilities	Minimal	i	Minimal	a
by ecological disadvantage	Not shown directly	c	Yes	f
Historical observation of host shift	Yes	b	None yet	
Evidence of recent divergence	Yes	b	Yes	j
Role for host phenology	Yes	c	No	a
Enemy-free space involved in habitat shift?	Yes	c	Probably not	a
Phylogeographical evidence of sympatric divergence	In progress[b]	NA[c]	In progress[d]	NA[c]

[a]S. Via, unpublished; [b]J. Feder and S. Berlocher; [c]NA, not applicable; [d]S. Via and D. Hawthorne.

Within the past five years, the role of natural selection as a major engine of speciation has received renewed attention, and ecology is back in the minds of biologists interested in the mechanisms of species formation[30–36]. This renaissance in the study of

speciation as an extension of adaptation has produced new evidence for sympatric speciation that complements and extends the work from the 1980s.

An increasing number of mathematical models now illustrate the plausibility of sympatric speciation

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Table 2. Conditions thought to facilitate sympatric speciation

	Refs (theoretical)	System in which condition is found[a]	Refs (empirical)
A. Ecological conditions			
i. Basic condition			
Sympatric potential for habitat shift	20,25	Apple maggot fly, Goldenrod ball-gall fly	12,49
Opportunity for radiation in isolated and depauperate environment (i.e. lake or island)	25	Sticklebacks, whitefish, cichlids, Darwin's finches	30–32,52,53
Resources or habitats discontinuous (limits possibility of hybrid bridge)	20,25,44	Apple maggot fly, Goldenrod ball-gall fly, pea aphid	6,12,49,68
Independent population regulation within habitats	8,10,20,22,38	Not known	
Small population size (to aid in establishing linkage disequilibrium by drift)	41	Not known	
Large population size (facilitates response to selection)	8,20,25,38,39	Not known	
Philopatric or have strong habitat choice that affects mate choice	8,10,22	Apple maggot fly, Goldenrod ball-gall fly, pea aphid, cichlids	6,49,52,54,56
ii. Selection			
Strong disruptive natural selection on habitat use (physiology, behavior and phenology)	8,10,22,38	Apple maggot fly, Goldenrod ball-gall fly, pea aphid, Darwin's finches, schistosomes	30–32,49,50,56,68
Strong disruptive natural selection on characters associated with resource competition, predation, parasitism	25,39,40,41,42	Sticklebacks, butterflies, marsh periwinkle	30–32,57,58
Disruptive selection directly on habitat choice	19	Pea aphid	54
Disruptive selection on mating cue (because of habitat differences)	Not known	Lekking birds, lacewings, butterflies	59–62
Disruptive sexual selection	46,47,63	Lacewings, cichlids,	59–62
Ecological selection against intermediate hybrids	20,25,31,39	Sticklebacks, Darwin's finches, pea aphid, butterflies	31,54,57,64
Sexual selection against hybrids	46	Sticklebacks, lacewings	59,65
Multifarious natural selection (i.e. multiple agents of selection) including resource use, habitat or mate choice, phenology and life history	20,28	Apple maggot fly, pea aphid, Goldenrod ball-gall fly, sticklebacks, butterflies, cichlids	30–32,55–57,64, 65,68,70,74
B. Genetic conditions			
i. Patterns of genetic variation in key characters			
Genotype × environment interaction in resource use	8,10,22,25	Apple maggot fly, sticklebacks, pea aphid, Darwin's finches	30–32,54,56,67–69
Genetic variation in habitat preference	19,20,22,38	Apple maggot fly, pea aphid, schistosomiasis, Goldenrod ball-gall fly	49,54,56
Genetic variation in mating cues	25,39,41,78	Lacewings, sticklebacks, Darwin's finches	30–32,59
One-allele habitat choice (i.e. host fidelity, conditioning or philopatry)	8,10	Cichlids, treehoppers	70,71
Mutations with environment-specific beneficial or detrimental effects	44,45	Examples in Ref. 44	
ii. Genetic architecture			
Negative genetic correlation across host (i.e. fundamental genetic tradeoff)	8,10,22,25	Apple maggot fly, pea aphid	68,69,72,73
Positive genetic correlation between disruptively selected trait and trait leading to assortative mating	8,20,25,28	Sticklebacks, Darwin's finches, butterflies, pea aphid	30–32,72,73,75
Linkage or pleiotropy between genes under disruptive selection and those leading to assortative mating	8,20,25	Pea aphid	72,73
Few loci involved in premating isolation	25,22,38	Apple maggot fly, brown planthopper	76,77
Intermediate number of loci in premating and disruptively selected trait	39,41	Pea aphid	72,73

[a]Latin names: Apple maggot fly, *Rhagoletis pomonella*; Goldenrod ball-gall fly, *Eurosta solidaginis*.; Brown planthopper, *Nilaparvata lugens*; Butterflies, *Helonicus* spp.; Cichlids, Cichlidae; Darwin's finches, *Geopsiza* spp.; Lacewings, *Crysoperla* spp.; Marsh periwinkle, *Littorina saxatilis*; Pea aphid, *Acyrthosiphon pisum*; Schistosomes, *Schistosoma* spp.; Sticklebacks, *Gasterosterus*; Treehoppers, *Enchenopa binotata*; Whitefish, *Coregonus* spp.

under a variety of circumstances[37] (Table 1, see also Turelli *et al.*[4], this issue). Some of these are extensions of previous approaches to speciation that bolster earlier results[38,39], and some are entirely new, including the use of adaptive dynamics models to study speciation under competition and predation[40–43], and the analysis of the effects of habitat-specific mutations as agents of selection on

habitat choice[44,45]. In addition, various models of sympatric speciation by SEXUAL SELECTION[46,47] or sexual conflict[48] have been proposed. Although the generality of these models can perhaps be argued (see Turelli *et al.*, this issue), theoretical work continues to suggest ways in which the antagonism between disruptive selection and recombination can be diminished or sidestepped entirely. This new work also underscores the importance of considering sympatric speciation within an ecological context.

Empirical evidence for sympatric speciation

Despite an increasing sense that sympatric speciation is plausible, it remains exceptionally difficult to prove that speciation in a given pair of taxa has occurred in an exclusively sympatric manner. This is not surprising, because it is usually easier to document that an evolutionary process could have occurred than it is to conclusively show that it is the only possible explanation in a particular case, particularly given how few systems have been studied in detail. There are two main types of empirical evidence for sympatric speciation. Although neither type of evidence is conclusive on its own, the joint weight of the various types of evidence strongly supports sympatric speciation as a real evolutionary process. First, the models discussed above suggest an array of ecological and genetic conditions that appear to facilitate speciation in sympatry (Table 2). Finding these conditions in wild populations supports the plausibility of sympatric speciation. Secondly, several historical signatures of sympatric speciation have been formulated using phylogenetic, population genetic or other retrospective tools (see also Barraclough and Nee[9], this issue), although relatively few tests of these methods are currently available.

Ecological and genetic conditions thought to facilitate sympatric speciation

The first line of empirical evidence for the plausibility of sympatric speciation involves demonstrations that the salutary conditions identified by theoreticians exist in natural or experimental populations (Table 2). Not all of these conditions will be found in any given case, nor is this a list of necessary and sufficient conditions for sympatric speciation. Supplementary historical evidence is crucial for eliminating alternative hypotheses when interpreting data from contemporary populations, and satisfying multiple conditions is stronger evidence than satisfying a single condition.

Basic ecological conditions. Speciation in sympatry is facilitated by the ecological and genetic potential to make a habitat or host shift (typified by phytophagous insects[15,49], but also probable in other taxa[50]), and/or the ecological opportunity for ADAPTIVE RADIATION in depauperate and isolated environments such as small lakes or islands[30–32,51–53] (Table 2). The absence of an intermediate environment (i.e. ecological discontinuity) limits gene flow between

divergent taxa by causing ecological selection against hybrids[6,15,49,54,64]. Although independent population regulation within habitats is typically assumed in models of sympatric speciation and might occur whenever divergent populations use different resources, explicit demonstration of independent regulation is largely lacking in natural populations. The effects of population size vary among models. Finally, philopatry or habitat fidelity facilitates speciation[5,16,49,55] by promoting assortative mating.

Patterns of selection. The models of Maynard Smith[10] and Felsenstein[8] concerned simple disruptive selection on resource or habitat use (e.g. Ref. 54). Recent models (Table 2) show that sympatric speciation can result from other types of selection, including disruptive selection on traits associated with competition or predation[30–32,57,58], disruptive selection directly on habitat choice (either through effects of the habitat on survival or fecundity of ovipositing females[54] or mediated by habitat-specific mutations[44,45]), disruptive selection on mating cues because of habitat differences[59,60], and disruptive sexual selection[61–63]. All of these forms of disruptive selection are likely to produce ecological or sexual selection against hybrids[64,65].

It now appears that the action of multiple forms of natural and sexual selection, some of which appear only as divergence proceeds, might be a general requirement for speciation in sympatry to go to completion[20,28,40,46]. For example, cichlid fish appear to have been influenced by both disruptive selection in different trophic environments and pronounced sexual selection, although apparently not always in the same order[53,66].

Genetic conditions thought to facilitate sympatric speciation

All models of sympatric speciation require that genotypes differ in the environment in which they have the highest fitness (genotype–environment interaction, or 'G × E', Table 2). G × E has been found both within and between races or populations that occur in sympatric habitats[67]. However, actual fundamental genetic tradeoffs in performance in different environments (negative genetic correlations across environments), have rarely been estimated[68,69,72,73], although this might testify more to the difficulty of demonstrating fundamental tradeoffs[72,73] than to their actual rarity.

Although one-allele mate choice, which facilitates sympatric speciation, has not been commonly seen in herbivores (but see Ref. 70), the philopatry described for cichlid fish[71] would have essentially the same effect on assortative mating. Close linkage between loci that influence both traits under disruptive selection and assortative mating also facilitates speciation by reducing the effects of recombination[8,25,73], as do pleiotropic effects of the same genes on these two classes of traits[20,72,73]. Evidence for such a genetic association ranges from

Table 3. Phylogenetic, population genetic and other historical signatures of sympatric speciation

Signatures of sympatric speciation	Refs
Phylogenetic pattern	
Monophyly of adaptive radiations (especially in small or isolated environments with little spatial heterogeneity)	39,66,71, 83,84
Phylogenetic hypotheses based on species-level phylogenies	
Sympatric speciation: range overlap declines with age of taxa	9[a],82,83
Allopatric speciation: range overlap increases with age of taxa	82,83
Range overlap of host-shifting species greater than that of non-shifters	82,83
Ecological differentiation between sympatric taxa greater than average for their clade	9[a],82
Phylogeographic hypotheses	
Differentiated pairs of sympatric races or species more closely related than are phenotypically more similar allopatric pairs	53,84,85
Sister taxa that speciated sympatrically and then dispersed will have sympatric populations with more variation than allopatric ones	82
Sister taxa that speciated allopatrically and then dispersed will have sympatric populations with less variation than allopatric ones	82
Taxa that have speciated sympatrically expected to show profound genetic similarity at loci not involved in mate choice or under divergent selection	39,78
Phylogenies differ for selected and neutral loci	No data yet available
Sympatric species pairs appear younger than allopatric ones (because they are less genetically differentiated)	88, 89
More premating isolation between sympatric races than between geographically separated populations of the same genetic distance	88
Overlap of sister taxa with little postmating reproductive isolation	30–32,82
Actual first observation of host shift sympatric with sister species	12,13
[a]Barraclough and Nee, this issue	

observations that the same character under selection is also used as a mating cue[30,31,74,75], to formal estimates of the genetic correlation between disruptively selected traits and those causing assortative mating[72,73], to explicit mapping studies that document linkage or pleiotropy between QUANTITATIVE TRAIT LOCI (QTL) affecting key traits[72,73]. A clear prediction from theory is that close linkage or pleiotropy between traits under disruptive selection and those causing assortative mating will be a common feature of taxa that have evolved reproductive isolation in sympatry.

Opinion varies as to how the number of loci that influence performance and assortative mating impacts the probability of speciation. Early models involved only one gene for each type of trait[7,8], and Bush has long held that speciation by habitat shift involves very few loci[5,76,77]. However, Kondrashov[23–25] showed that sympatric speciation could occur under a polygenic genetic architecture, and more recent models suggest that the probability of sympatric speciation is enhanced by an intermediate number of loci. For example, the genetic drift required to generate linkage disequilibrium between selected loci and those causing assortative mating in the models of Dieckmann and Doebeli[41] might be hampered in a one-locus context. Models by both Dieckmann and Doebeli[41] and Kondrashov *et al.*[39,78] suggest that the most favorable conditions for sympatric speciation involve a relatively small number of loci influencing assortative mating, and a moderate number under

disruptive selection. Although QTL MAPPING is certainly no panacea, it is likely to be useful not only for roughly evaluating the numbers of loci involved in reproductive isolation[79], but also for determining their linkage relationships[72,73,80].

Phylogenetic and other historical signatures of sympatric speciation

Several phylogenetic and population genetic analyses have recently been proposed as retrospective tests of sympatric speciation (Table 3). Reconstruction of the phylogenetic history of divergent taxa can provide an important, but not foolproof, line of empirical evidence for sympatric speciation. For example, the monophyly of taxa from small isolated environments, such as crater lakes, is powerful evidence that speciation has occurred sympatrically[51–53]. However, in larger lakes, islands or island groups, the possibility for small but meaningful geographical separation between diverging taxa is increased, and it is more difficult to definitively claim sympatry[81], making it risky to use monophyly alone as a sufficient criterion for sympatric speciation. However, in conjunction with other ecological or genetic evidence, monophyly can greatly strengthen the case for sympatric speciation, as it has in cichlid fishes[51,71].

Several recent classes of hypotheses using species level phylogenies show promise for revealing the occurrence of sympatric speciation within CLADES (see also Barraclough and Nee[9], this issue), although

these methods do not test whether particular species diverged sympatrically[82,83]. Within-species PHYLOGEOGRAPHY might also be very useful. One key approach has been to evaluate whether divergent races found sympatrically are more closely related to one another than they are to more phenotypically similar allopatric races[53,84,85].

Unfortunately, the probability of gene flow at loci with NEUTRAL ALLELES (hereafter named neutral loci) between closely related sympatric species or races is a major pitfall of using phylogeny or phylogeography as a signature of sympatric speciation. Analyses of hybrid zones[86] show that the extent of introgression across a zone varies widely among loci. Importantly, loci linked to QTL that influence reproductive isolation show greatly reduced introgression relative to unlinked loci[87]. If only a few genomic regions are responsible for much of the reproductive isolation between sympatric species (or INCIPIENT SPECIES), ongoing gene flow is probable at many of the neutral loci generally favored for phylogeny reconstruction.

Sympatrically derived species are expected to show profound genetic similarity, differing only at the handful of loci that are under disruptive/divergent selection or are associated with mate choice[39]. This is a population genetic signature of sympatric speciation, distinguishing it from speciation in ALLOPATRY where genetic differences are expected to accumulate throughout the genome. This initial similarity between sympatrically derived species will diminish after speciation (although gene flow at neutral loci will counter this), again making it highly desirable to study very recently diverged taxa that are close to the species boundary.

One prediction that could be made about taxa that have speciated sympatrically is that phylogenies made using divergently selected loci (such as markers near QTL for reproductive isolation or performance in different environments) might differ radically from those at neutral loci (i.e. markers unlinked to such QTL). However, recent divergence is important, because gene flow after SECONDARY CONTACT of allopatrically diverged taxa could also produce a difference in phylogenies made with selected or neutral genes. Again, the combination of multiple forms of evidence is highly desirable.

Other tests of sympatric speciation might also be affected by gene flow at neutral loci. For example, a comparative study of *Drosophila*[88] revealed that sympatric species pairs tend to show more PREZYGOTIC ISOLATION at low genetic distances than do allopatric pairs, implying more rapid evolution of reproductive isolation in sympatry than in allopatry. In fish, comparative analyses of sequence divergence suggest more rapid speciation in sympatry than in allopatry[89]. These results are both consistent with evidence from theory suggesting that sympatric speciation, because it is actively driven by selection, is likely to occur more quickly and involve fewer loci[25,78] than is POSTZYGOTIC ISOLATION in allopatric

speciation, which might take a very long time to accumulate (of the order of 500 000 generations, Turelli *et al*.[4], this issue) and involve hundreds of loci[90]. However, gene exchange at neutral loci, which would decrease the estimated genetic distance between sympatric taxa, could cause sympatric taxa to appear to be more recently diverged than they actually are. Additional techniques will be required to remove the confounding effects of gene flow at neutral loci from phylogeographical analyses and estimates of evolutionary rates.

Because of the myriad difficulties in reconstructing history, it is likely to be far easier to use phylogenetic analyses and patterns of molecular variation to eliminate sympatric speciation in a particular group than to confirm that it has occurred[91]. Much more detail about the uses (and pitfalls) of phylogenetic analysis in evaluating the signatures of different types of speciation can be found in reviews by Berlocher[82], Barraclough and Vogler[83], Harrison[91] and Barraclough and Nee[9], this issue.

Currently, the cichlid fishes in crater lakes[52,53] are one of the most probable examples of sympatric speciation, primarily on the strength of the phylogenetic evidence and the limited opportunity for allopatry in contained environments. A variety of evidence compiled over the past decade also makes the apple maggot fly *Rhagoletis pomonella* a probable case of sympatric speciation[56,69], particularly given the historical documentation of sympatry between the new apple race and the native hawthorn race[13,14] (Box 1). Other herbivorous insects, such as the pea aphid *Acrythosiphon pisum*, and the Goldenrod ball-gall *Eurosta solidaginis*.[49], have many of the characteristics that would facilitate sympatric speciation (Box 1; Table 2). However, these characteristics alone are not sufficient to show that both the initial divergence of the taxa and the completion of speciation have occurred in sympatry. For this, additional geological or other historical evidence pointing to sympatric divergence is crucial, as seen in the cichlids and *Rhagoletis*.

Sticklebacks provide a superb example of the importance of historical evidence. Despite a phylogeny of sticklebacks that suggests sympatric origins of the benthic and limnetic forms in various lakes[85], geological data suggest a pattern of sea-level changes consistent with a double invasion of marine sticklebacks into postglacial lakes[92]. By the time of the second invasion, it is thought that the first colonist had diverged somewhat from the marine form, leaving REINFORCEMENT or character displacement to predominate during the second phase of sympatric speciation[92]. Various additional tests reveal patterns of variation consistent with the double invasion scenario[92]. Without independent evidence of historical contingency, the phylogenetic analyses, which suggest purely sympatric speciation, might not have been questioned.

Is it productive to continue to distinguish sympatric speciation as a unique mode?

Kondrashov has separated the process of sympatric speciation into two phases[23–25,78]. The first phase involves the initiation of genetic divergence within a population exposed to disruptive selection, whereas the second involves the conditions under which speciation between partially isolated sympatric groups can proceed to completion. 'Multiple-niche'-type population genetics models have shown that establishing a stable polymorphism under disruptive selection is relatively straightforward[8,10]. Although establishing bimodality in a quantitative trait is perhaps not so readily accomplished[25,78], the biggest problem with accepting sympatric speciation seems not to have been the initiation of divergence, but rather its completion. In this, sympatric speciation and speciation after secondary contact between allopatric populations have much in common.

When one considers the ways in which natural selection can drive speciation ('ECOLOGICAL SPECIATION'[31–33], Schluter[93], this issue), remarkable similarities of mechanism appear between sympatric speciation and allopatric ecological speciation. In both, divergent natural selection is the driving force (although allopatric ecological speciation may also occur under uniform selection, see Schluter[93], this issue). In both sympatric and allopatric ecological speciation, the evolution of reproductive isolation is enhanced when traits under disruptive selection lead to assortative mating or are correlated with traits that cause assortment[19,20,31]. Multiple forces of selection clearly facilitate sympatric speciation[28]. It is probable that ecological speciation in allopatry will also be facilitated by 'multifarious natural (and sexual) selection'[28], because this would speed divergence and augment the possibilities for the evolution of reproductive isolation as a byproduct (Schluter[93], this issue). Finally, in allopatric ecological speciation, as in sympatric speciation, divergent taxa are initially expected to differ only by the loci exposed to DIVERGENT SELECTION[39,41]. Given these similarities of process, it is perhaps not surprising that several of the empirical examples of taxa that satisfy conditions that facilitate sympatric speciation are likely to have had an allopatric component in their divergence (Table 2; sticklebacks, Darwin's finches, and possibly, pea aphids).

Work by Kondrashov and colleagues[25,78] also shows that the completion of sympatric speciation depends on the extent of premating isolation that has already evolved, the overall magnitude of selection against hybrids, and the number of loci influencing divergence and assortative mating, but not on whether the partial reproductive isolation originally evolved in sympatry or allopatry. Linkage or pleiotropy between genes under disruptive selection and those influencing mate choice are expected to further facilitate completion of the second phase, as will the involvement of other forms of selection[25].

After secondary contact between partially isolated allopatric populations, the crucial factors determining whether speciation will go to completion are essentially the same as those outlined by Kondrashov[25]: the extent of mate choice that has already evolved as a byproduct of independent evolution in allopatry and the magnitude of selection against hybrids[94]. Genetic correlations between key traits and additional forces of selection would be likely to facilitate the completion of speciation under secondary contact, just as they do in sympatric speciation.

Towards a mechanistic classification of speciation modes?

Recent insights into sympatric speciation suggest that the mechanisms that produce it are neither improbable nor rare. The evidence summarized here certainly supports the contention that speciation can be initiated and/or go to completion in sympatry, and many of the same factors that facilitate this process are also likely to facilitate allopatric speciation when driven by selection. In all, ecological interactions, and the natural and sexual selection that they cause, might be responsible for much of the speciation that has produced the biological diversity of the Earth, regardless of the geography of the diverging populations. This is not to say that geography plays no role in speciation. The extent of geographical proximity can lead to some interesting and important differences in the forms of selection seen in sympatric and allopatric populations. For example, divergence can only be driven by competition or other forms of frequency-dependent selection when populations are sympatric. Likewise, reinforcement as a result of selection against hybrids requires that divergent populations be sympatric. By contrast, genetic incompatibilities can accumulate freely in allopatric populations, even under uniform selection. However, these geographical differences are secondary within a classification organized primarily by mechanisms.

In light of recent work, it might be productive to move beyond geographical modes of speciation to consider a different classification in which the first division separates those cases driven by natural (or sexual) selection from those in which speciation occurs primarily by genetic drift (e.g. through the founder effect[2]). The extent of ongoing gene flow and the strength and agents of disruptive/divergent selection can then be secondary factors. This viewpoint might help us to focus on crucial data to be gathered in the next phase of speciation analyses, and to structure the next generation of questions and hypotheses including, but not limited to, those proposed in Box 2.

Prospects

Although the process of sympatric speciation now appears plausible and even probable under some circumstances, there is still much to be done (Box 2). It will be important to generalize models of speciation as

Box 2. Some future challenges in sympatric speciation

- Is it possible to generalize, by further theoretical exploration and integration of existing models, the theoretical conditions in which sympatric speciation can occur? Does sympatric speciation depend on very precise combinations of different forms of selection and recombination?
- Is there a predictable sequence in which different forms of reproductive isolation evolve in sympatric speciation? Is this similar or different to the sequence of character evolution in ecological speciation in allopatry?
- When divergent populations are sympatric, is it essential that reproductive isolation evolves rapidly for completion of the sympatric speciation to occur? What constrains the process, and how rapidly must it occur?
- Are ecotypically differentiated populations likely to speciate, or are they examples of failed speciation? Are populations harboring genotype–environment interaction for resource use probable candidates for future speciation or cases in which divergence has been constrained?
- Can we develop reliable molecular signatures of the different processes involved in sympatric speciation or allopatric ecological speciation? How can we 'age' a species or the genes involved in key forms of reproductive isolation?

much as possible and to estimate crucial model parameters in natural populations. In addition, the study of reproductive isolation in taxa along the entire continuum of divergence, from locally adapted ECOTYPES to very recent species, will be central to future analyses of speciation[95]. The comparative analysis of mechanisms of reproductive isolation in taxa of different degrees of divergence, and in a variety of ecological situations and geographical arrangements, might reveal whether there is a predictable sequence of character evolution when speciation is driven by selection (in sympatry or in allopatry).

To continue to evaluate the likelihood and extent of sympatric speciation, we need further case studies in which the causes of reproductive isolation between diverging taxa are known, and for which the strength of disruptive/divergent selection are explicitly estimated. It is also crucial to determine how genetic details can facilitate or constrain the response to selection in diverging sympatric populations. Localizing chromosomal blocks involved in reproductive isolation using QTL mapping will provide pivotal information about the extent to which linkage and pleiotropy among loci influencing key traits[72,73,80] might facilitate divergence. Now that it appears that reproductive isolation between sympatric populations can evolve in a variety of realistic situations, attention to the multifarious roles of ecology and genetics during the process is likely to materially enhance our understanding of the origin of species. Finally, additional analyses of species-level phylogenies and phylogeographical analyses of taxa close to the species boundary might provide a crucial historical perspective on the occurrence of sympatric speciation.

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