

SYMPATRIC SPECIATION IN PHYTOPHAGOUS INSECTS: Moving Beyond Controversy?

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■ **Abstract** Sympatric speciation is the splitting of one evolutionary lineage into two without the occurrence of geographic isolation. The concept has been intimately tied to entomology since the 1860s, when Benjamin Walsh proposed that many host-specific phytophagous insects originate by shifting and adapting to new host plant species. If true, sympatric speciation would have tremendous implications for our understanding of species and their origins, biodiversity (25–40% of all animals are thought to be phytophagous specialists), insect-plant coevolution, community ecology, phylogenetics, and systematics, as well as practical significance for the management of insect pests. During much of the twentieth century sympatric speciation was viewed as much less plausible than geographic (allopatric) speciation. However, empirical field studies, laboratory experiments, developments in population genetics theory, and phylogenetic and biogeographic data have all recently combined to shed a more favorable light on the process. We review the evidence for sympatric speciation via host shifting for phytophagous insects and propose a set of testable predictions for distinguishing geographic mode (allopatric versus sympatric) of divergence. Our conclusion is that sympatric speciation is a viable hypothesis. We highlight areas where more thorough testing is needed to move sympatric speciation into the realm of accepted scientific theory.

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INTRODUCTION

Sympatric speciation, the divergence of one evolutionary lineage into two in the absence of geographic isolation, has a long history. Charles Darwin (44) first alluded to the possibility of sympatric speciation in *On the Origin of Species*. The idea became associated with entomology in the 1860s when Benjamin Walsh (175) proposed that many host-specific phytophagous insect species arise in the process of shifting and adapting to new plants. Walsh (176) was inspired by the shift of the apple maggot fly, *Rhagoletis pomonella* (Walsh), from hawthorn (*Crataegus* spp.) to domesticated apple (*Malus pumila*), forming what is now known as a “host race” (48). Since Walsh’s time, enthusiasm for sympatric speciation has waxed and waned (78). Only in the past two decades, with evidence for host races in insects (2, 31, 60, 114, 170, 171, 182) and ecological divergence in fish (148, 149), has sympatric speciation gained wider acceptance.

WHY IS SYMPATRIC SPECIATION IMPORTANT?

Small host-specific insects constitute perhaps 25–40% of all animal species (27). If sympatric speciation occurs, it could help explain a substantial fraction of terrestrial diversity on Earth in general and patterns such as latitudinal species gradients in particular.

The implications of sympatric speciation are less appealing for applied entomologists. The most effective quarantine procedures imaginable would not stop the appearance of new pests in the form of native insects capable of shifting onto economic crops. Moreover, host races could exchange genes with ancestral populations for protracted periods, hastening the evolution of insecticide resistance and thwarting the use of transgenic insects for biological control.

Recognition of sympatric speciation would have a great impact on systematics theory and practice. Vicariance biogeography, which assumes that recent sister species are distributed in adjacent areas (119), would lose some generality. The likelihood of continuing gene flow between diverging species also has major implications for the estimation of phylogenetic trees for closely related species (70).

Finally, sympatric speciation has sparked renewed interest in the role of ecology in speciation (123, 149). For insects to speciate in sympatry, host-associated selection must overcome the homogenizing effects of gene flow and recombination (sex). Thus, proponents of sympatric speciation have long advocated a direct tie between ecological adaptation and the evolution of reproductive isolation (25, 26, 137).

WHEN IS SPECIATION SYMPATRIC?

In broad outline, the process of sympatric speciation is clear: All stages of divergence occur within an undivided geographic area. But host plant species appearing to be sympatric on range maps could be aggregated into a mosaic of pure stands on a local scale (78). If insect dispersal is highly limited, then “micro-allopatric” speciation could conceivably occur between “internally isolated” insect demes.

Rejection of the micro-allopatry hypothesis is often hindered by inadequate data on insect dispersal and host distribution. However, for the apple and hawthorn races of *R. pomonella* (57, 60, 114), mapping of individual trees has shown that adults disperse sufficiently to carry them past numerous apples and hawthorns during the course of a day [the “cruising range” criterion of Mayr (113)]. The same appears true for several other systems in which hosts are mapped or clearly occur in close proximity (37, 90, 170). Thus, the available case studies argue against micro-allopatry. Moreover, finding that a particular set of host plants and insects are finely subdivided is not sufficient for rejecting “divergence-with-gene-flow” speciation. It must also be shown that insects in any identified “single-host” stands receive <1 immigrant per generation from alternate hosts. Although Wright’s (185) “one migrant” rule for neutral genes is a simplification (115), it still provides a guideline for assessing whether drift may be a significant factor in population divergence. Given migration rates on the order of one insect per generation, selection must still overcome gene flow in order for speciation to occur, even if microgeographic isolation does exist (78). [Note that the case of sharp spatial aggregation of hosts parallels the mosaic hybrid zone model of Harrison (86).]

In a few special instances, the biology of the insects and plants ensures the sympatry of populations. Insects that use different parts (e.g., stems and flowers) of the same host or that have specialized on male or female flowers of dioecious host plants must exist in great sympatry (38). Such cases are potentially important for testing the sympatric speciation hypothesis.

WHAT IS A HOST RACE? A SYMPATRIC SPECIES?

Conceptually, host races and species reside on different ends of a gene flow continuum, with host races representing the hypothesized incipient stage of sympatric speciation and host-associated species its final product. Specifically, we consider

insect populations to represent host races when (a) allele frequencies at one or more loci are significantly and consistently different, (b) insects from the two plant species differ for at least one genetically controlled adaptive trait that reduces gene flow, (c) insects from alternate plants can be crossed through at least the first backcross generation to produce viable and fertile offspring, and (d) at least some gene flow between populations can be demonstrated in the field. However, because complete data are not currently available for many taxa we were forced to make informed judgments about some cases. The critical issue is whether sympatric insect populations display partial, but not complete, reproductive isolation owing to host-related adaptation (48).

Given recent evidence that gene flow occurs between animal populations that are generally considered to be good species (5, 70, 81, 86), an absolute distinction between species and host race based on the presence or absence of gene flow is not tenable. Consequently, we consider populations to be "operational species" when large and significant morphological, behavioral, or allele frequency differences are maintained at ≥ 2 sympatric sites. To place large differences in a statistical context, we use the "genotypic cluster" definition of Mallet (111), which can be modified for morphological or behavioral data. In adopting Mallet's definition, we use the cutoff proposed by Feder (57) of a < 0.05 probability for taxonomically misclassifying an insect.

WHY ISN'T SYMPATRIC SPECIATION UNIVERSALLY ACCEPTED?

Objections to sympatric speciation fall into three general categories. First, early verbal and mathematical models suggested the process is unlikely (65, 112). Second, until recently, empirical data supporting sympatric speciation were scant (78). Finally, Mayr (113) for decades forcefully and skillfully argued for the universality of allopatric speciation in animals based on phylogenetic and biogeographic data. A convincing argument for sympatric speciation must therefore effectively address these three objections.

HOW CAN SYMPATRIC SPECIATION BE TESTED?

The strongest proof of sympatric speciation would be the direct observation over historical time of the sympatric origin of a new host race and its subsequent divergence to species status. Such evidence would be incontrovertible. The origin of new host races, showing adaptation and at least some reduction of gene flow between ancestral and derived plants, has in fact been convincingly demonstrated in several cases (Table 1). To date, however, no host race known to have originated in historical time has reached species status (under any species definition or concept). A strong argument for sympatric speciation must therefore be based on

several lines of indirect evidence:

1. Analysis of mathematical models showing that sympatric speciation is plausible under realistic biological conditions.
2. Empirical studies demonstrating that insects possess the key features assumed in verbal and mathematical models of sympatric speciation. Included here are field assessments of whether migration rate, gene flow levels, and selection coefficients are within the range conducive to sympatric divergence.
3. Experimental manipulations in the laboratory showing that disruptive selection can result in the evolution of reproductive isolation in sympatry.
4. Laboratory and field selection experiments showing phenotypic and genetic responses in predicted directions to variation in the host environment.
5. Demonstration of genetic architecture of host-related adaptation consistent with sympatric speciation.
6. Genetic cross results indicating that “hybrids” and later generation backcrosses between different host races and species suffer reduced fitness primarily owing to “extrinsic” host-related selection rather than “intrinsic” genetic incompatibilities.
7. Demonstration that population structure (subspecific groupings and metapopulation geography) of host-faithful specialist insects is in better agreement with the predicted stages of sympatric than allopatric speciation.
8. Demonstration that species-level biogeographic patterns better match predictions of the sympatric than allopatric hypothesis.

In the remainder of the review, we discuss data and outline tests pertinent to this eightfold path to sympatric speciation. The taxa listed in Table 1 play an important part in our analysis. An addendum (see the Supplemental Material link at www.annualreviews.org) describes details for several systems central to the sympatric speciation debate.

PROGRESS ON EIGHT TESTS OF SYMPATRIC SPECIATION

Do Verbal and Mathematical Models Support Sympatric Speciation?

Most models of sympatric speciation assume (*a*) independent regulation of insect population sizes in discrete host plant niches, (*b*) assortative mating either directly or indirectly tied to host-related phenotypes (e.g., mating and ovipositing on preferred hosts), and (*c*) disruptive (divergent) selection differentiating populations. For phytophagous insects, this selection produces negative genetic performance correlations across plants (i.e., an individual genetically well-suited to one host species has relatively poor survivorship on others). Host-specific mating therefore serves as a premating barrier to gene flow, whereas negative

TABLE 1 Characteristics of host races and species important to testing the sympatric speciation hypothesis

Host races	<i>Rhagoletis pomonella</i>	<i>Prodoxus quinquepunctellus</i>	<i>Acyrthosiphon pisum</i>	<i>Eurosta solidaginis</i>
Taxon				
Races	Haw → apple (1) (24–26)	Filamentosa → aloifolia (1) (82)	Clover (1), alfalfa (1) (169, 172)	Altissima → gigantea (2, 22)
Age of derived race	~150 yr/gen. (24)	<500 yr (82)	Unknown (172)	Unknown (2)
Host performance	No (136)	No information	Yes (169)	Yes (2, 41)
trade-offs				
Phenological trade-offs	Yes (61, 62, 67, 157)	Yes (82)	No (169, 170)	Yes (1, 2, 90)
Other trade-offs	Parasites (56)	No information	No (170, 171)	Parasites (21)
Mating differences	No (136, 156)	No information	No (170, 171)	Yes (40, 42)
offs host				
Oviposition	Yes (132, 156)	No information	Yes (173)	Yes (40–42)
differences				
Intrinsic postzygotic	No (136, 156; J.L. Feder, unpublished manuscript)	No information	No (172)	Weak (40)
isolation	Phenology (61, 62, 67, 157)	Phenology (82)	None (171)	Phenology (2, 40)
Extrinsic (ecological)				
postzygotic isolation	$\Delta p \approx 0.4$; 6/29 loci (57, 60, 64, 114)	$\Delta p \approx 0.5$; 3/4 loci (82)	$\Delta p \approx 0.5$; 3/15 loci (170)	$\Delta p \approx 0.7$; 6/29 loci (90, 177)
Maximal allozyme	Both races polyphyletic (15, 57)	Both races polyphyletic (82)	Both races probably polyphyletic (170)	Altissima paraphyletic (22, 177)
differences	4–6% (direct) (62)	No information (82)	Probably (170)	Possibly (41, 90)
Phylogeny of				
populations				
Gene flow in field				

Species complexes			
Taxon	<i>Nilaparvata "lugens"</i>	<i>Enchenopa binotata</i>	<i>R. pomonella complex</i>
Species	Leerzia → rice (37)	8 (83, 181)	6? (15, 24, 28)
Sympatry	Broad (27, 37)	Broad (83, 181)	Broad, 1 allopatric (15, 24)
Oviposition differences	Yes (147)	Yes (182–184)	Yes (16, 58, 59, 156)
Host performance trade-offs	Yes (146)	Yes (181, 182)	Yes (58)
Phenological trade-offs	No (27)	Yes (181)	Yes (15, 157)
Mating differences of host	Yes (30)	Weak (164, 184)	None to moderate (28, 156)
Intrinsic postzygotic isolation	Weak (30)	Weak (164)	Weak to strong (28, 157–159)
Type of molecular differences	DNA (ITS-1) differences; unclear if fixed (94)	Nonfixed to fixed allozymes (83)	Nonfixed to fixed allozymes & COII DNA haplotypes (15, 160)
Range of interspecific divergence	$p < 1.1\%$ (94)	$0.07 < D < 0.32$ (83)	$0.0 < p < 6.1\%$ (160) $0.04 < D < 0.68$ (15)
Phylogeny of closest species	Both species polyphyletic (94)	Monophyletic, but limited sampling (83)	Pomomella paraphyletic for allozymes (15); most polyphyletic for COII (160)
Direct gene flow observed	No information	No information	No (59)
			Generally fixed allozymes & COII DNA haplotypes (76) $0.8 < p < 21.4\%$ (76) $0.11 < D < 0.93$ (79) At least one paraphyletic (100) No information

All differences are genetically based. Arranged left to right in approximate order from youngest to oldest. →, direction of evolution; I, introduced host; Δp, largest allele frequency difference at any of the loci scored; x/y, number of loci with significant differences/total loci scored; D, Nei genetic distance; p, percent sequence divergence.

performance correlations act as postmating barriers countering any errors in host fidelity.

INDEPENDENT REGULATION OF INSECT POPULATION SIZES IN DISCRETE HOST PLANT NICHES The intimate association of the life cycle of many phytophagous insects with their host plants makes the assumption of separate population regulation in discrete plant niches reasonable. However, the manner in which this regulation occurs (e.g., soft versus hard selection) (174) is important for sympatric speciation. Population regulation for the majority of sympatric speciation models involves some form of density- and frequency-dependent selection. The image of empty and full ecological niches connoted by density-dependent selection provides an intuitive explanation for the population dynamics underlying successful host shifts. Reduced competition for a plentiful new resource compensates for otherwise poor performance, temporarily bridging the fitness gap between new and old hosts and providing time for the derived population to adapt to novel conditions. Such soft selection can greatly relax the conditions for the establishment of a stable ecological polymorphism, which Maynard Smith (112) viewed as the first and most significant hurdle for sympatric speciation (the second stage being the evolution of reproductive isolation associated with the eco-polymorphism).

Density regulation in the "classic" sympatric speciation models of Maynard Smith (112) and Felsenstein (65) is based on the Levene (106) model of selection in spatially heterogeneous environments. A critical feature of the Levene model, as applied to phytophagous insects, is that the relative proportions of reproductive adults produced by host niches are constant in each generation, regardless of the initial number of eggs laid onto plants. Another key element is that relative fitness values for genotypes are constant within niches. Thus, under the Levene model, neither the number of larvae on plants nor their genetic makeup influence host resources, the relative competitive abilities of larvae, or the proportions of insects surviving to adulthood. Density- and frequency-dependent selection are therefore implicit in the standard Levene model; the condition for a stable equilibrium (a "protected" polymorphism) is defined by whether segregating alleles increase in frequency when rare and decrease in frequency when common (i.e., negative frequency-dependent selection). However, there is no explicit function or mechanism specifying the mode of action of this selection.

The assumptions of the Levene model have several important implications for sympatric speciation. For example, because more eggs are laid on hosts and more larvae feed on plants than can possibly survive, the soft selection inherent in the Levene model does not inflict a substantial "genetic load" (84) on populations. The loss of genetically inferior individuals is absorbed within the background deaths that would have happened regardless of whether selection occurs. As a result, even if intense selection were needed to drive sympatric speciation, this would have negligible effects on the overall health (sizes) of host-associated populations and not put them at risk of extinction. A newly formed race therefore need not be particularly genetically well-suited to its new host to form a self-sustaining population.

Several recent models of sympatric speciation and niche diversification make explicit how density- and frequency-dependent fitness functions are generated from rates of resource consumption and renewal, as well as population (or genotype) carrying capacities. The thread for such “competitive speciation” models can be traced to a verbal argument made by Darwin (44) and in more modern times to the work of many others (4, 108, 128, 141, 144, 167, 179, 180). The most recent of these models include assortative-mating genes either directly or indirectly tied to the phenotype under selection and can result in sympatric speciation even for a population utilizing a unimodally distributed resource (47, 102).

The competition-based models add at least four conceptual advances to the Levene model. First, they indicate that when fitness is an explicit function of population density and phenotype (genotype) frequency, stable polymorphisms can form with intermediate phenotypes (presumably heterozygotes) that are unfit even in the absence of host-specific mating (179). In contrast, under constant fitness models such as Levene’s, such underdominance is unstable; one or another allele segregating in a population will fix. Consequently, assortative mating is not favored in insects that do not mate or oviposit on preferred hosts, resulting in ecological polymorphism, but not host races or species. However, in the newer density- and frequency-dependent models, intermediates are inefficient generalists among specialists (179), thereby favoring positive assortative mating even in insects forming a common breeding pool. We caution, however, that this assumes that intermediate phenotypes are heterozygotes (or of hybrid ancestry). Although the genetic basis of host-related traits may often be additive, sometimes it may not (32, 147); genetic details concerning host-related traits (the extent of dominance, epistasis, gene \times environment interactions) are therefore critical for demonstrating sympatric speciation.

Second, the competition models refine our understanding of how the adaptive landscape changes during a host shift. A concave fitness surface for genotypes across hosts means that crossing between adaptive host peaks is not a problem because “the peaks and valleys do not exist until after the polymorphism evolves” (179).

Third, the new models highlight the complementary nature of frequency-dependent and disruptive selection in promoting stable polymorphisms. The self-regulating element in the models helps insure that population sizes fluctuate in a range such that migration does not swamp differential adaptation and eliminate genetic variation.

Fourth, the finding that competition for a single unimodally distributed resource can result in specialization broadens the conditions under which sympatric divergence could occur. This may not, at first glance, seem to be significant for phytophagous insects where hosts are usually considered discrete. However, plants are resources that vary in a number of dimensions, some discrete, some bimodal with overlap (e.g., phenology), and some even continuous (e.g., plant chemistry). Hence, the demonstration that an initially unstructured population could evolve reproductive isolation by partitioning a single resource suggests that selection can be even more effective in causing divergence when intermediate (“hybrid”) phenotypes

are also disadvantaged by utilizing a saddle of low host resource (provided that the resource trough does not prevent the initial establishment of a bimodal phenotypic distribution) (142).

Although density-dependent selection is important for successful host shifts, density-independent factors (hard selection) are also involved. For instance, the ability of an insect to detoxify a noxious plant secondary compound, or successfully develop on a new host with a novel nutritional profile, may not be greatly affected by the presence or absence of other conspecifics (competitors). Similarly, an insect with a life cycle ill-matched to the phenology of a plant will likely die regardless of how many other individuals infest the plant. Consequently, the existence of an open and competitor-free niche does not ensure survivorship unless colonists possess some minimal genetic, behavioral, physiological, and developmental ability to utilize the novel plant. Elements of both hard and soft selection must therefore be included in models of sympatric speciation to make them more realistic (e.g., the proportion of migrants between hosts might be weighted by the mean relative fitnesses of populations utilizing different plants) (see 4). Although this can lessen the likelihood for the first phase of sympatric speciation involving the establishment of a stable niche polymorphism, it could subsequently heighten the degree of postmating isolation between host-adapted populations. Hard selection would also imply that ancestral populations contain sufficient standing genetic variation for at least some individuals to survive on novel hosts (77). Thus, both interspecific competition and genetic constraints can also pose major barriers to host shifts.

ASSORTATIVE MATING EITHER DIRECTLY OR INDIRECTLY TIED TO HOST-RELATED PHENOTYPES A recent clever suggestion by Kirkpatrick & Ravigné (99a) equates geography (allopatry versus sympatry) to assortative mating. If geography is viewed as a genetic locus with the location of each isolated deme a different allele, then complete allopatry enforces a rigid system of assortative mating, allowing only individuals carrying the same allele at the “geography locus” to mate. Given enough time, any process causing population divergence, including genetic drift, therefore has the potential to result in speciation. If assortative mating in sympatry is controlled by the fixation of the same allele in populations using different host plants, then allopatry and sympatry are not qualitatively distinct (99a). An example of such a “one-allele” system (65) would be a gene that causes an insect to mate and oviposit on the first host species it encounters upon eclosing as an adult, which is often the same plant it infested as a larva. Similar to geographic separation, such a gene would result in assortative mating for performance traits throughout the genome. Lack of penetrance of the mating gene would be analogous to migration, with the likelihood of sympatric speciation reduced to how often host-related selection is strong enough to counter gene flow [the “selection-migration” antagonism of Felsenstein (65)].

The situation is different, however, if assortative mating is based on a “two-allele” system (65). Under this scenario, *aa* homozygotes at a host-choice locus might prefer mating and ovipositing on plant species *A* and *bb* individuals

on species *B*. Although the potential would still exist for positive assortment with respect to host performance traits, the conditions are more stringent; host-choice alleles for a given plant must be in linkage disequilibrium with genes conferring increased fitness on the same plant. Thus, two-allele systems introduce an additional factor, recombination between assortative-mating and fitness genes, working against sympatric speciation. Because two-allele models, on the whole, seem more tenable than one-allele scenarios (see below), details concerning the number, location, linkage relationships, and nature of assortative-mating and fitness genes are critical to evaluating the likelihood of sympatric speciation.

Initially, Felsenstein's (65) characterization of the "selection-recombination" antagonism for two-allele assortative-mating systems appeared devastating for sympatric speciation. However, subsequent analyses and verbal arguments have suggested that two-allele systems may not be such an overriding concern for sympatric divergence.

First, in the same paper Felsenstein (65) also showed that if performance and mating loci are linked in the correct phase and selection is strong, then sympatric speciation would occur.

Second, Felsenstein's (65) models did not incorporate host-specific mating, which Bush (25, 26) has vigorously argued is an essential element for sympatric speciation. Instead, individuals chose breeding partners within a common mating pool based on their genotype at an assortative-mating locus. In fairness, Felsenstein did not intend for his models to mirror insect biology but rather to clarify the nature of genetic constraints on speciation. However, Diehl & Bush (49) demonstrated that when mating is confined to preferred hosts, some disequilibrium will evolve between host-choice and performance genes, even when the loci are unlinked. The surviving offspring of individuals mating and ovipositing on a particular plant species *A* will, following selection, inevitably possess higher frequencies of both host-choice and performance alleles for plant *A* than are found in the general population. Moreover, Kondrashov (101) showed that even when the fitness trait is moderately polygenic, the probability of sympatric speciation will not be greatly affected. Indeed, a modest number of loci can actually enhance prospects under certain circumstances (92, 93).

Finally, when habitat choice itself is directly under selection or when reproductive isolation evolves as a correlated (pleiotropic) by-product of host adaptation, the selection-recombination antagonism disappears altogether (138). For example, phytophagous specialists usually eclose at different times, matching the phenologies of their hosts. This can generate significant allochronic isolation if it also shifts the mating periods of adults, which it frequently does (40, 61, 82, 129, 183). Thus, the genes affecting eclosion are also assortative-mating loci, so eclosion and assortative mating are maximally correlated. Note the parallels with Kirkpatrick & Ravnigné's (99a) model of geography as an assortative-mating locus; each isolated deme on a temporal, rather than spatial, host island has a different eclosion time allele, allowing only insects carrying the same allele at the diapause locus to mate. Rice & Hostert (138) consider such a "single variation" model "a theoretician's

worst nightmare, that is, it can be completely deduced from experimental results, it is simple, it is obvious, and it is likely important in nature.”

DISRUPTIVE SELECTION AND NEGATIVE PERFORMANCE TRADE-OFFS Negative performance correlations are the final ingredients in most sympatric speciation models, acting as postmating barriers offsetting any “leakiness” in host fidelity. The genetic basis for these correlations is usually assumed to take the form of a “fitness trade-off,” in which the same allele (phenotype) increasing the relative performance of an insect on one host is detrimental on others. (We symbolize such genes by $A+/B-$ and $A-/B+$, representing fitness on alternate hosts A and B .) But linkage disequilibrium can also produce negative performance correlations. Here, linkage disequilibrium refers to homologous chromosomes having either all $A+/B0$ or all $A0/B+$ alleles at fitness loci (0 = no fitness effect on the plant compared with the ancestral allele). Such linkage disequilibrium may often evolve between reproductively isolated insect species or between geographically separated demes specialized on different plants (72, 73). However, negative performance correlations due to linkage do not constitute fitness trade-offs in a strict sense because recombination could theoretically generate a jack-of-all trades genotype that has high fitness on all hosts. It is difficult for negative performance correlations to evolve *de novo* in sympatry via linkage; an allele giving an insect an advantage on one plant, but having no detrimental consequences on others, would spread and fix rapidly through the metapopulation. Consequently, to initiate sympatric speciation a new mutation, preexisting allele, and/or combination of genes must in all likelihood result in a fitness trade-off.

Kawecki (95, 96) proposed a set of sympatric models that are not dependent on fitness trade-offs. The key idea in these models is that whenever an allele conferring a fitness advantage on one host and having no effect on another ($A+/B0$) is transiently going to fixation [or alternatively, when an allele detrimental on one host but neutral on another ($A-/B0$) is being eliminated], selection favors an increase in the frequency of habitat choice genes. If insect density does not affect the number of larvae surviving on a plant, then insects possessing the $A+/B0$ allele should continue mating and ovipositing on plant A , where their offspring have a competitive advantage, rather than moving to plant B , where their offspring are equals among many. Likewise, individuals with the alternative $A0/B0$ allele should remain on plant B , where at least their offspring would not be at a disadvantage.

The evolution of increased host fidelity in Kawecki’s models is, however, dependent on population regulation occurring according to the Levene model with constant resources (soft selection). But as natal host resources decline during the field season owing to, among other things, overuse and senescence, an insect ignoring a more abundant alternative plant on which it is at no competitive disadvantage can have a lower inclusive fitness than one that shifts hosts. Thus, seasonal and annual variation in relative host abundance and suitability, a common occurrence in nature (see 19 and references therein), tends to oppose the increase in host choice in Kawecki’s models. Most importantly, once a beneficial $A+/B0$ performance allele

sweeps through a species and is fixed in both host-associated populations, selection acts to restore host fidelity levels back to the optimal equilibrium existing prior to the mutation, as dictated by variation in host abundance, density-dependent effects, and relative performance differences ($A+/B-$ versus $A-/B+$) among insects on plants.

One could argue that constant introductions of new $A+/B0$ and $A0/B+$ mutations into host demes could favor increased host choice. In essence, at least one $A+/B0$ or $A0/B+$ allele would always be segregating in the metapopulation, selecting for increased host fidelity. A similar suggestion invoking the “Red Queen” hypothesis was made by Kawecki (97) to explain host specialization due to a “co-evolutionary arms” race between alternate plants and an insect (parasite). At their core, however, these arguments contain elements of group selection. Species that specialize evolve faster (increase mean fitness more rapidly) than generalists (178); as a result, specialists may persist longer (178). Although potentially true unless (a) mutation rates generating new host-specific beneficial mutations are high, (b) hosts impose rapidly changing selection pressures on insects, and/or (c) fitness loci are tightly linked, the long-term benefit to the species will probably not override the immediate fitness advantage to an individual shifting from a declining natal host to an alternate plant of greater abundance. Thus, fitness trade-offs must, in all likelihood, initiate sympatric speciation. It would be interesting to see, however, whether the existence of a fitness trade-off ($A+/B-$) could favor the accumulation of linked $A+/B0$ fitness alleles, generating a coadapted gene complex favoring the evolution of tighter host fidelity (see 73 for related comments).

The issue of seasonal and annual fluctuation in host abundance has serious consequences for all models of sympatric speciation. Given a choice between two constant plant resources, an insect should evolve increased fidelity for a higher-quality or more abundant host (73). But predictable seasonal variation in host abundance makes it difficult to completely eliminate the vestiges of use (choice) for an alternative plant, especially if this plant is the ancestral host on which an insect has historically had high survivorship. Maynard Smith (112) may therefore have been wrong. Explaining the origins of an eco-polymorphism, especially when host choice stabilizes a multiple-niche polymorphism to generate host races, could be relatively straightforward; understanding how partially isolated races evolve to become completely isolated may be more difficult.

THE SECOND STAGE: FROM HOST RACE TO SPECIES In principle, completion of the second stage of sympatric speciation (evolving from eco-polymorphism to reproductive isolation) is not an insurmountable problem. For example, several authors (92, 93, 103, 168) noted the parallels between the closure of host race systems and the evolution of reinforcement (prezygotic isolation) following secondary contact. Thus, models supporting the plausibility of reinforcement (reviews in 120, 166) can be applied to sympatric speciation to help explain the transition from races to species. Moreover, theory predicts that reinforcement is more likely to evolve when secondary contact occurs throughout the range of the incipient species (145),

coinciding with the population structure expected for sympatrically formed host races. Rice & Hostert (138) also remarked on the potentially positive-feedback (runaway) nature of divergence-with-gene-flow speciation. Once partial isolation has evolved, gene flow will abate. As a result, new or preexisting genetic variation, which could not initially diverge because selection was not strong enough to counter migration, can now enter the process and continue the cycle. As migration levels fall significantly, sexual selection, sexual conflict, and genetic drift also lead to the evolution of nonhost-related reproductive incompatibility.

Unfortunately, neither the reinforcement nor runaway models consider the problem of variation in host abundance. Consequently, the complexity of the biology has, to a certain extent, outstripped most sympatric models. We propose three possible solutions:

1. The seasonal gap between host resources could be large compared with the life span of the insect. Thus, as the life histories of insects become synchronized to the peak abundance of their respective plants, the question of host choice can become moot. In addition, certain hosts may be only temporary stepping stones for insects connecting alternative, higher-quality hosts with more disparate phenologies.
2. Multifarious fitness trade-offs could favor an insect population eking out an existence on a natal host of rapidly declining abundance but superior quality rather than shifting to an abundant low-quality host. In this regard, sympatric theory might benefit from incorporating ecological models of habitat selection (e.g., 71, 91, 134), factoring in costs associated with host searching.
3. Insects may not be capable of finely regulating host-acceptance decisions based on plant abundance, quality, and utilization (69). As a result, maintaining a lower-ranking plant in an insect's repertoire might interfere with efficient utilization of its preferred plant when its natal, higher-quality host is at peak abundance. Increased host fidelity could therefore be favored even though it may appear maladaptive at times when the natal host is not present.

Do Insects Possess the Key Features Assumed in Models?

Many successful host shifts clearly involve insects taking advantage of new, "open" plant niches resulting from introductions, as exemplified by the apple race of *R. pomonella* (57) and probably the rice form of the brown plant hopper, *Nilaparvata lugens* (27, 37). Phytophagous insects clearly compete for plant resources, and numerous cases of host shifts are known in which many competitors occur on the ancestral host (45). Thus, from a qualitative perspective, current observations support the proposal that sympatric speciation occurs by insects invading resource-rich and enemy-free habitats. However, few studies have quantified the role of competitor- or enemy-free space with respect to sympatric speciation. For *R. pomonella*, competition (both intra- and interspecific) and levels of parasitoid

attack are greatly reduced for larvae feeding within the derived fruit apple (56, 63). These factors help compensate for poorer larval survivorship in apples, resulting in net viability being comparable between alternative fruits, depending on the particular apple variety. Studies on *Eurosta solidaginis* gall-forming flies have similarly found that parasitism, predation, and competition are lower in the derived host *Solidago gigantea* (1, 2, 21, 88). Reduced parasitism could also be a significant factor for *Asphondylia* gall midges (143). Biological intuition may be correct with regards to open plant niches, but more studies investigating this question are needed.

Many phytophagous insects have biologies conducive to density- and frequency-dependent selection. For example, prime oviposition sites on high-quality plants may frequently become limited, as is the case for *Rhagoletis* (63). Therefore, traits that optimize host-searching behavior, that increase the efficiency of oviposition, and that synchronize insect life history with peak resource abundance would all confer a great competitive advantage. If survivorship plummets when a host niche becomes saturated (e.g., by larval crowding), then frequency-dependent selection could favor rarer phenotypes that exploit underutilized hosts. In some cases even the relatively unrealistic Levene model of soft selection may be applicable. For example, competitively superior larvae on a particular host might monopolize available resources to such an extent that only a set number of dominant individuals survive. This is the case for *R. pomonella*-infesting hawthorns, where a maximum of three larvae are produced per fruit and where body mass is a decreasing function of the order of larval emergence from a given fruit (63). The existence of oviposition-deterrent pheromones (130) further supports the view that crowding can negatively affect survivorship. Overall, too few data are available concerning the interrelated population dynamics of parasites, predators, competitors, host plants, and phytophagous insects to adequately assess the overall significance of density- and frequency-dependent selection to sympatric speciation (e.g., 2).

Host-specific mating, however, has been unambiguously demonstrated for a large number of phytophagous insects. For example, in *R. pomonella*, host fidelity reduces gene flow to 4–6% per generation between apple and hawthorn host races (57, 62). Similar studies have shown that host fidelity may be essentially perfect for *R. pomonella* and the related blueberry fly *Rhagoletis mendax* (59). Work on the cow pea aphid *Acyrtosiphon pisum* (170, 171), *Eurosta* gall flies (42), the soapberry bug (S. Carroll, personal communication), the brown plant hopper *N. lugens* (146, 147), the chrysomelid beetles *Lochmaea caprea* (104) and *Neochlamisus bebbinanae* (74), the agromyzid fly *Liriomyza brassicae* (161), the yucca moth *Prodoxus quinquepunctellus* (82), the small ermine moths *Yponomeuta* spp. (S. Menken, personal communication), *Euphilotes* butterflies (129), and *Enchenopa binotata* tree hoppers (184) has also demonstrated host-specific mating. Even in some lepidopterans like the larch budmoth, *Zeiraphera diniana*, where long-range sex-pheromone attraction plays a large role in premating isolation, the species specificity of calling may be influenced by whether females reside on the natal host (I. Emelianov & J. Mallet, personal communication).

Given the potential significance of one-allele systems of host fidelity for sympatric speciation, documenting the homing of insects for natal hosts is important. Evidence is scarce, however, for the “Hopkins host selection principle,” the idea that holometabolic insects retain learned or conditioned host preferences across life history stages. Several studies have shown that adult experience can influence host preference (88, 91, 131, 181, 182), so a naïve adult’s first exposure to a plant species could influence its subsequent host-acceptance behaviors. However, such effects were not significant in the field for *Rhagoletis* (57, 62) nor in the laboratory for *Eurosta* (41). Intriguingly, recent findings on *Neochlamisus bebbianae* leaf beetles are consistent with conditioning of adult feeding and mating preferences as a result of host-associated experience (D. Funk, personal communication).

Reduced dispersal of insects from natal plants could also promote early stages of sympatric divergence. Limited migration capacity is an important component of the adaptive deme hypothesis (17), and adults can be predicted to apportion a significant percentage of their reproductive output to the first host plant they encounter on eclosing. Although *R. pomonella* is highly mobile, we have detected this effect in the apple race (57, 62). Thus, a certain degree of host fidelity may occur even in the absence of genetically based differences in host choice.

Negative performance correlations across host plants are frequently observed in comparisons between insect species (e.g., 77). However, species-level differences cannot be taken as *prima facie* evidence for fitness trade-offs. First, selection acting after speciation contributes to host specialization (e.g., 74). Therefore, unless taxa can be crossed to permit genetic dissection of performance traits, species-level differences could be due to linkage disequilibrium (i.e., a series of $+/0$ alleles directionally fixed in lineages following isolation) rather than antagonistic pleiotropy (i.e., single genes having $+/-$ effects triggering sympatric divergence). Second, unless a well-defined phylogeny and host record are available for a group, one cannot infer whether poor insect performance on a plant reflects a lack of ecological/historical exposure to the plant. To bear on sympatric speciation, fitness trade-offs must be documented for taxa that can be crossed genetically.

Until recently, evidence for host-related fitness trade-offs within insect populations was scant (72, 73, 80, 168), casting doubt on the likelihood of sympatric divergence (29). However, a number of studies have now demonstrated negative performance correlations across hosts, implying the existence of fundamental trade-offs (40, 41, 67, 90, 110, 143, 146, 147, 169). In the majority of these studies, F_1 hybrids were shown or inferred to have lower performance on host plants than parental genotypes. These reductions in fitness were not solely due to intrinsic genetic incompatibilities between taxa, but they largely reflected extrinsic host-related effects. For example, F_1 hybrids between *Solidago altissima* and *S. gigantea*-infesting races of *E. solidaginis* have low survival on most genotypes of the two goldenrod hosts, but high viability on particular benign genotypes (41, 90).

Part of the reason for the apparent paucity of fitness trade-offs was that experimenters tended to focus on larval feeding performance while neglecting other important aspects of life history (135). Larval feeding performance is undeniably

important for assessing whether an insect has the innate potential to utilize a novel plant (77). However, the fact that an insect has the physiological machinery to develop on a novel plant does not necessarily mean this trait impedes performance on the insect's natal host. The required biochemical pathways may be inducible or altogether different, and thus be akin to +/-0 alleles. Experimenters have also focused on enemy-free space, but escape from enemies is not necessarily equivalent to a fitness trade-off. For instance, if the reduction in parasitism on a novel host is not due to some specific behavioral, morphological, or physiological trait possessed by an insect, then any insect utilizing the new plant will experience the same beneficial escape from parasitism. Consequently, enemy-free space could help maintain host-choice polymorphism. But escape from enemies will not constitute a performance trade-off because these factors will not pose a significant postmating barrier to gene flow between immigrant and resident insects.

In contrast, developmental life history traits adapting insects to the phenology of their hosts and morphological characters facilitating feeding or oviposition on plants can elicit trade-offs. Indeed, eclosion timing differences between host-associated races (species) are a consistent theme for temperate univoltine insects (43, 61, 82, 90, 129, 143, 156, 183). Because an insect can only eclose once, having a life history synchronized with one host necessitates a fitness disadvantage on plants with differing phenologies. Similar arguments can be made for adaptive morphological traits [e.g., proboscis length in the soapberry bug (31)]. Moreover, if even one locus exists in which opposite homozygotes are favored on different hosts, the population will not simultaneously maximize fitness on the two plants (72, 73). It remains to be seen, however, how many of these factors act simultaneously on insect populations.

Do Laboratory Experiments Support Sympatric Speciation?

Because Endler (53), Rice & Hostert (138), and Odeen & Florin (122) discuss the significance of laboratory experiments to understanding speciation, we highlight only a few major points with respect to "divergence-with-gene-flow" speciation. In general, strong divergent selection can result in the evolution of reproductive isolation in the laboratory under both parapatric (partial geographic overlap) and sympatric conditions. Odeen & Florin (122) list a total of 63 experiments (trials) from 21 papers, 26 of which (41%) were successful in producing significant increases in positive assortative mating in the face of gene flow. However, none of the successful experiments resulted in complete reproductive isolation in the laboratory, and 10 studies generated only partial ($\leq 50\%$) isolation. Rice & Hostert (138) noted that one explanation for the limited degree of isolation produced in certain studies is that the experimenters applied selection to only a single phenotypic trait. In contrast, Rice & Salt (139) subjected *Drosophila melanogaster* to multifarious habitat selection (i.e., a choice based on variation in phototaxis, geotaxis, chemotaxis, and development time) and achieved nearly complete assortative mating (up to 98%). Moreover, Odeen & Florin (122) reported a significant negative correlation

between the amount of assortative mating generated in laboratory studies and estimates of the effective number of individuals (N_e) maintained in experimental populations. Indeed, the majority of unsuccessful experiments (28/37 = 76%) involved N_e s \leq 80. Theory (150) indicates that long-term population sizes of 100 or more are needed to avoid the fixation of deleterious alleles and for mutation to replenish genetic variation lost due to drift and selection. Thus, Odeen & Florin (120) concluded that many laboratory studies may have failed not because the test organisms were inherently incapable of sympatric divergence but because small experimental population sizes caused inbreeding depression (favoring outcrossing) and the loss of genetic variation at fitness and assortative-mating loci.

Do Selection Experiments Support Sympatric Speciation?

It is surprising that selection experiments have not been performed more extensively for phytophagous insects to test the sympatric hypothesis. As we discussed, disruptive selection has been applied in the laboratory to generate reproductive isolation between populations under sympatric conditions (reviewed in 138). However, the selection pressures imposed in these experiments were not necessarily representative of those faced by insects in nature. Experiments designed to determine heritability for ability to use alternative hosts (77) are in some sense selection experiments, but they are carried out only one generation and focus only on performance. We highlight a few selection studies to emphasize their usefulness for answering questions about the mechanisms and likelihood of sympatric divergence.

Selection experiments have been performed on the host races of *R. pomonella* to test the hypothesis that diapause adaptations to the different fruiting phenologies of apple and hawthorn trees are responsible for genetic differences between the races. *R. pomonella* is univoltine and overwinters in a facultative pupal diapause (18). Frequency differences at six allozyme loci that differ between the races are correlated with the timing of adult eclosion, which is in turn correlated with diapause intensity (severity of conditions needed to break diapause) (for review see 61). Thus it could be hypothesized that the 3–4-week-earlier mean fruiting phenology of apples selects for a deeper, more recalcitrant diapause in the apple than hawthorn race. Rearing conditions were experimentally manipulated for larvae and adults in both host races to simulate the earlier phenology of apple compared with hawthorn [e.g., the length and temperature of the prewintering period for larvae and pupae were varied, as was the duration of the overwintering period (57, 61, 64, 67)], and allele frequencies were then determined in eclosing (successfully overwintering) adults. The outcome was that allele frequencies differed in the predicted directions. For example, conditions similar to those faced by flies infesting apples (i.e., higher temperatures for longer periods of time before winter) favored, in both races, alleles more common in the apple than the hawthorn race. A significant gene \times environment ($g \times e$) interaction between prewinter temperature and winter length also contributes to the allozyme differences between the host races (67). The selection experiments on *Rhagoletis* therefore clarified the nature of selective factors acting

on the allozymes (or linked genes) to cause population differentiation and showed how the apple race of the fly could be derived from standing genetic variation in the ancestral hawthorn population, at least for diapause-related traits.

A unique series of experiments has also been performed on the *Viburnum*-feeding species of *Enchenopa* plant hopper. First, genetic variation for host shift potential was demonstrated using quantitative genetic techniques by testing full sib families for their abilities to survive on alternative *Viburnum* species that are not normal hosts (164). Next, in what is apparently the only experiment of its kind, attempts were made to induce host shifts of the plant hopper to these underutilized *Viburnum* species in field enclosures. The results demonstrated that such shifts can produce at least some host-related assortative mating (184).

Finally, experiments on the tephritid fruit fly *Bactrocera cucurbitae* have shown how selection on life history traits can generate reproductive isolation leading to race formation (116). Lines of the fly selected for short and long developmental period produced a shift in mating time during the evening that resulted in significant premating isolation in mate choice tests.

Is the Genetic Basis for Host Adaptation Consistent with Sympatric Speciation?

As discussed above, theory predicts that certain genetic architectures are more conducive to sympatric divergence than others. For example, reproductive pleiotropy, in which the same genes (traits) involved in host-related adaptation also serve as pre- and postmating barriers to gene flow, facilitates sympatric speciation by eliminating recombination-selection antagonism. In lieu of such "single variation" systems (137), tight linkage between assortative-mating and host-performance genes would be expected. In this regard, models also suggest that the most favorable genetic architecture for sympatric speciation may be one in which a relatively small number of loci strongly affect assortative mating and a moderate number of genes determine insect performance (47, 92, 102, 103). Finally, there are reasons to suspect that when ecological divergence occurs in sympatry, it happens relatively rapidly (27, 103, 172).

An extremely important consideration with respect to genome architecture is that gene flow occurs, although at an ever-decreasing level, throughout much of sympatric divergence. Consequently, the genomes of insects undergoing sympatric speciation might be expected to be mosaics, with loci directly involved in host-related adaptation (or closely linked genes) displaying detectable differentiation and perhaps monophyly. In contrast, gene flow of neutral loci between populations would tend to homogenize the remainder of the genome (13, 14, 57; see also 165), obscuring evolutionary relationships among taxa and producing extensive reticulation and phylogeographic regionalism (detected as paraphyly).

On the surface, detailed genetic studies [e.g., quantitative trait locus (QTL) mapping] dissecting the causes for reproductive isolation might distinguish mode of speciation (172). For example, classic allopatric speciation is predicated on the

alternate substitution of alleles in geographically isolated demes that generate substantial reproductive incompatibilities (negative epistasis) when present in mixed genetic backgrounds [i.e., in hybrids or later-generation backcrosses (118)]. Observing significant intrinsic reproductive isolation mapping throughout the genome in the absence of host-related isolation would therefore seem to be strong grounds for accepting allopatry.

Although generally true, this distinction may not be particularly useful. The reason is that we are most interested in determining whether cases of present-day sympatry between host-specific taxa are indicative of past-allopatric versus sympatric divergence. In this circumstance, the genetic predictions of the two modes of speciation are not always mutually exclusive and are time dependent. Consequently, studies of the genetic architecture of host-related adaptation are not "stand-alone" data differentiating sympatric from allopatric speciation. Whereas the absence of certain types of genetic relationships makes it unlikely that sympatric host race formation and speciation has occurred, the presence of these architectures does not exclude allopatric divergence. Instead, the genetics of host adaptation and reproductive isolation must be coupled with biogeographic information for a group at various chronological stages of differentiation to make a strong case for sympatric speciation.

It is unfortunate that the genetic analysis of host-related traits is still in its infancy, therefore there are too few studies to judge all predictions for sympatric speciation. Within this constraint, however, there are clear examples of reproductive pleiotropy. For example, genetically based differences in eclosion time cause allochronic isolation between *R. pomonella* host races and sibling species (61). For the apple and hawthorn races, variation in eclosion time has been mapped to three different inverted regions of the genome, displaying significant allozyme frequency differences (61, 140). As discussed, eclosion time differences generating allochronic mating isolation is a common occurrence for phytophagous insects (42, 82, 90, 129, 183), although the genetics of diapause still remain to be determined for most of these systems.

When insects mate on hosts, differences in host preference also pleiotropically produce premating isolation. Evidence for *Eurosta* (41), brown plant hopper (146, 147), and pea aphids (87a, 173) suggests that only a limited number of genes may be involved. Thus the available data conform to the favorable condition of a relatively few genes of major effect influencing assortative mating.

Few studies have addressed the question of genetic linkage between assortative-mating and performance genes for hypothesized cases of sympatric speciation. However, in the pea aphid, several complexes of pleiotropic or closely linked QTL having antagonistic effects on resource use in different environments have been found (87a). Moreover, these QTL were in close proximity on the pea aphid linkage map to QTL that promote assortative mating through their effects on habitat acceptance. In contrast, no association was observed between genes affecting oviposition and host-related performance in the brown plant hopper using classic quantitative genetic methods (146, 147).

Even less information is known concerning patterns of genome-wide differentiation for sympatric host races and species. This too promises to be an area of rapid progress in the coming years. For *Rhagoletis* at least, a clear demarcation exists between three inverted regions of the genome (which all display allele frequency differences between apple and hawthorn host races) and the remainder of the genome (which shows no allozyme differentiation) (140, 141). Consequently, we might predict that blocks of genes within the inversions have historically been and currently are more impervious to gene flow than the rest of the genome and may harbor ancient polymorphisms. However, it is too early to draw any firm conclusions concerning the involvement of inversions in sympatric host race formation and speciation for these flies.

Is Reproductive Isolation “Extrinsic” or “Intrinsic”?

As discussed, observing a pair of taxa isolated only by extrinsic barriers to gene flow, and not by any intrinsic genetic incompatibility, is not conclusive evidence for sympatric speciation because rapid ecological specialization in allopatry followed by secondary contact could generate the same pattern. (For ecological specialists, intrinsic isolation has come to mean genetic incompatibility that occurs in any environment, whereas extrinsic means isolation caused by adaptation to a particular host; extrinsic here does not refer to nongenetic causes such as geography.) Nevertheless, observing such asymmetries on a regular basis would add weight to the sympatric hypothesis, especially when coupled with strong phylogeographic data (see below). How often is this pattern seen in nature? At least for host races and most species in the *R. pomonella* group (136, 156, 158, 159), clover and alfalfa races of pea aphids (170, 171), *Eurosta* gall flies (40), soapberry bugs (31, 32), and brown plant hoppers (146, 147), nonhost-related reproductive isolation is infrequent. However, this is an area of speciation research that still requires more thorough and sophisticated analysis comparable to *Drosophila* (39, 165). For example, genetic incompatibilities not readily apparent in F₁ hybrids might manifest themselves in later-generation backcrosses, as is the case for the fall armyworm, *Spodoptera frugiperda* (125), and possibly *Eurosta* (40, 41) and some species of *R. pomonella* flies (156).

Does Population Structure Reflect Stages of Sympatric Rather than Allopatric Speciation?

The key differences between the allopatric and sympatric hypotheses are that (a) geographic isolation is the first crucial step in allopatric speciation, but happens late, if at all, in sympatric speciation, and (b) gene flow is present during the early stages of sympatric speciation, but occurs only at the end, if at all, of the allopatric process following secondary contact (see Figure 1a for a schematic diagram of host shift via an allopatric process). Establishing the chronology of divergence—the evolutionary sequence of putative intermediate stages—is therefore critical to distinguishing mode of speciation.

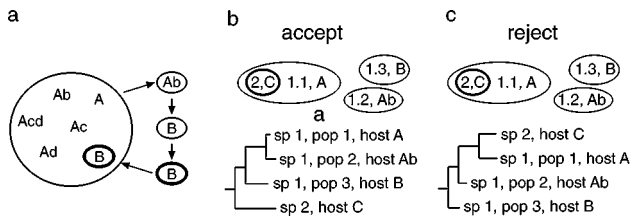


Figure 1 (a) Hypothesized stages of allopatric adaptation to a new host and evolution of reproductive isolation (modified from 113, p. 463). The species in the original range has alternative hosts a–d, with capitals indicating the primary host of a local population. The stages are, from top to bottom: isolated population with an alternative host, allopatric population that has shifted entirely to alternative host B, allopatric population that has evolved reproductive isolation (heavy line around population), and finally secondary contact and establishment of sympatry. (b) Hypothetical patterns for speciation onto host C in which Mayr's model for allopatric divergence is not rejected. Abbreviations: sp, species; pop, allopatric population; 1.1, allopatric population 1 of species 1, etc. (c) Hypothetical phylogeny and pattern of sympatry in which Mayr's model for allopatric divergence is rejected.

Aside from the special case of host races arising in historical time, how can chronology be established? One approach is the combination of phylogenetic and biogeographic methods known as phylogeography (7). A simple hypothetical phylogeographic analysis in which allopatric speciation is supported is shown in Figure 1*b*, whereas Figure 1*c* shows a case implying rejection of allopatric speciation because sympatric sister species 1 and 2 are younger than allopatric populations of species 1.

It is unfortunate that a paraphyletic pattern such as that in Figure 1*c* is not uniquely predicted by sympatric speciation but could also be the product of rapid founder-effect speciation at the edge of a species range followed by reestablishment of sympatry (85). Thus, the simplest implementations of phylogeography are susceptible to the same "convergent predictions" problem faced in attempting, for example, to determine whether clines are of primary or secondary origin (53). Factors that aggravate the convergent prediction problem are invisible intermediates missed because of their transitory existence or extinction, greater present-day range overlap of populations on different hosts than the same host due to reduced competition, and loss of phylogenetic information because of gene flow following secondary contact. A problem to which sympatric speciation may be particularly prone is reticulate evolution due to independent origins of host races (11); multiple origins are common in sympatrically originating allopolyploid plants (e.g., 6). Given these problems, can uniquely falsifiable phylogeographic predictions for allopatric and sympatric speciation be devised?

Recent developments in phylogeography (52, 163) point out one approach to framing more specific predictions: The genetic isolation, and in many cases small

population size posited for early stages of allopatric speciation, should leave a genetic signature of reduced number and increased similarity of alleles or haplotypes (e.g., 99). The divergence-with-gene-flow process of sympatric speciation, on the other hand, should produce little if any restriction in variation in the new population. Although the signature of allopatric speciation may sometimes be so smudged by gene flow at secondary contact that a given case mimics the sympatric pattern, we would not expect this to be true in all cases. Berlocher (12) gives a hypothetical example of one way in which colonization signature could be used to distinguish between allopatric and sympatric speciation.

Another avenue for increasing the discriminatory power of phylogeographic tests is to make use of independent biogeographic or fossil evidence. For example, a repeated pattern of genetically differentiated Gulf and Atlantic subpopulations of phytophagous specialists and their hosts living in North American coastal areas, with similar ages estimated from the molecular clock, would imply parallel allopatric speciation in accord with the many unrelated taxa that show this Pleistocene vicariance pattern (7). One *Prokelesia* plant hopper species (127) and its *Spartina* host (121) do show a parallel Gulf-Atlantic vicariance, demonstrating the potential for such tests.

Yet another route to falsifiable tests is to utilize independent ecological or behavioral data in framing hypotheses. Berlocher (12) suggested partitioning test taxa *a priori* into those possessing traits that facilitate sympatric speciation, such as mating on the host, and those that do not. The prediction that host races should be more common in insects that mate on the host than in insects that do not is more powerful and informative than the simple prediction that host races should exist in at least some insect taxa. A similar approach can be used to test whether secondary-range overlap is established more rapidly in allopatric events involving a host shift than in those that do not.

The problem of unsampled or extinct allopatric intermediates can ultimately be solved only with analytical or computer models that predict the duration and extinction probability for each possible hypothetical stage under both the allopatric and sympatric hypotheses. Nonetheless, the fundamental chronological differences in the two modes of speciation allow testable predictions at present. Specifically, insect taxa that are highly host-specific can be predicted under sympatric speciation to display spatially overlapping populations in various stages of divergence from host races to genetically isolated species. Moreover, differentiated allopatric populations may be older than sympatric populations. In contrast, allopatric speciation predicts that at least some allopatric intermediates should be found and that these populations should be younger than sympatric species.

Our discussion of empirical studies focuses on host-faithful specialists. We begin with the special case of host races posited to be formed in historical time, for which the chronology is unambiguous (such host races must be younger than any natural, allopatric conspecific population). The best-understood case of recent host race formation remains the derived apple and ancestral hawthorn races of *R. pomonella* (57, 60, 114). The salient points are: (a) The host of the apple race,

domestic apple, is not native to North America but was introduced from Europe almost 400 years ago, establishing a maximum possible age for the apple race. (b) Apple is an important crop, so colonization of apple some 140 years ago was noticed and recorded. (c) The direction of the host shift is known historically, not inferred. (d) Apple and hawthorn have been sympatric from the time of the original introduction of apple. (e) No preexisting geographic or ecological population matching the apple race has been found to date anywhere in North America. The evidence therefore indicates that the apple race evolved *de novo* in eastern North America as proposed by Bush (25, 26).

The case that is perhaps most directly comparable to the apple maggot is the yucca moth, *P. quinquepunctellus* (82). The species feeds in eastern North America on the native *Yucca filamentosa*, but it also feeds on *Yucca aloifolia*, probably introduced to eastern North America from Mexico in the 1500s. *Filamentosa* and *aloifolia* sites on the Carolina Outer Banks differ significantly and consistently in allozyme frequencies, with the closest populations on different hosts being 0.5 km apart, within the inferred flight range of this relatively large moth. Allozyme data for additional sites on the east coast of North America suggest two host shifts, and mtDNA data reveal that the derived *aloifolia* samples have reduced variation compared with the ancestral *filamentosa* populations. Substantial mtDNA differentiation between eastern and western *filamentosa* populations suggests that any preexisting *aloifolia* population in Mexico would be much more differentiated than is the East Coast *aloifolia* population. The *filamentosa* and *aloifolia* populations have different emergence phenologies in the field, matching the different flowering times of their hosts, and three ovipositor characters differ between the populations. The data strongly suggest host race formation in historical time, but the lack of information on gene flow in the field, or reproductive isolation in general, prevents a conclusive statement for the system.

The soapberry bug provides another example, with the unique feature that the change in an important adaptive character, the length of the proboscis, can be studied historically in museum specimens (31). However, gene flow has not been studied directly, and the lack of sympatry for the best-studied case, involving the native balloon vine, *Cardiospermum corindum*, and introduced flat-podded goldenrain tree, *Koeleruteria elegans*, in Florida (32–34), implicates geography in this host shift. But apparently independent shifts in the southcentral United States involving the native host *Sapindus saponaria* (soapberry) and two introduced plants (the round-podded goldenrain tree, *Koeleruteria paniculata*, and the heartseed vine, *Cardiospermum halicacabum*) have occurred in sympatry (32). An apparent host shift of *Epilachna vigintipunctulata* in Southeast Asia from its native solanaceous host to a legume introduced from South America appears to be an additional case of host race formation in historical time (27). The history of the well-studied pea aphid is unfortunately not known (Table 1). Overall, our conclusion is that some host races have unambiguously evolved in recent times.

Several apparent intermediates between sympatric host race and species exist in the *R. pomonella* species complex, which along with the apple and hawthorn

racess of *R. pomonella* includes seven or more taxa infesting different native North American host species (Table 1). The best-studied putative intermediate is the "flowering dogwood fly" that infests *Cornus florida* (Cornaceae), treated in the literature as an undescribed species (13–15). The flowering dogwood fly differs from *R. pomonella* in choice of fruit size (16) and life history phenology (157), but when caged together without fruit, dogwood flies and *R. pomonella* mate at random (156). Intrinsic postzygotic isolation is weak (156), and only frequency differences occur at allozyme loci (13). Other species in the *R. pomonella* complex display greater divergence (12, 15, 58, 159).

Can host races and other proposed stages of sympatric speciation be demonstrated to be younger than allopatric populations (as in Figure 1c)? Apple race populations are scattered among northern hawthorn race *R. pomonella* populations in allozyme phylogenies (15), with southern *R. pomonella* populations being paraphyletic. Furthermore, a deep division between Mexican and eastern North American *R. pomonella* populations (both feeding on hawthorns) is basal (based on mtDNA COII sequences) to the radiation of all populations and species in the complex except *Rhagoletis cornivora* (160). Similar results were observed in *Greya* moths (23). Funk (74, 75) in some cases observed greater phylogenetic similarity but reduced mating for populations of *Neochlamisus* leaf beetles on different hosts than for populations using the same host, although he did not frame his results in terms of a test of sympatric speciation. Finally, the derived *S. gigantea* race of *Eurosta* appears to be young, supporting a sympatric origin (90). However, the parallel population structures for several insects on the same goldenrods (1a; S.B. Heard, personal communication) raise the specter of a past biogeographic event. If DNA sequence analysis suggests a common divergence time and pattern of vicariance, then an allopatric origin for these taxa would be inferred.

Are there cases of host-shifting insect taxa that meet the predictions of allopatric rather than sympatric speciation? One of the clearest cases involves insects that are not true phytophages but share some ecological features with them: the cactophilic *Drosophila* of the *mulleri* complex. Based on cytological evidence, *Drosophila mojavensis* evolved in Baja California, allopatric from its nearest relatives in southwestern North America, and subsequently colonized several mainland areas (55). Adaptation to different cactus hosts concomitant with colonization of the mainland has pleiotropically produced partial reproductive isolation between the allopatric ancestral and derived *D. mojavensis* populations (54). Some studies of true phytophagous insects also support the allopatric hypothesis. Funk (74) tested the prediction that reproductive isolation should be greatest among allopatric populations of a species when these were also ecologically differentiated in host preference and performance traits, and found support in experiments with eastern North American *N. bebbianae* populations from four different host plants. Based on allozyme data, samples of the host-faithful thistle specialist weevil *Larinus cynarae* in the Mediterranean region can be divided into three geographic groups (only two of which are monophyletic), each with different primary hosts (20). The *Larinus cynarae* populations are monophyletic with respect to the apparent

sister species *Larinus latus*. An early conclusion from work on the host-faithful chrysomelid *Ophraella* (79) was that some western North American populations of *Ophraella communa* feed on *Iva axillaris* instead of the typical eastern host *Ambrosia artemisiifolia*, paralleling *Ambrosia* to *Iva* shifts during speciation elsewhere in the genus. In another chrysomelid genus, the western North American *Chrysochus cobaltinus* displays significant geographic structure for mtDNA and also uses several different hosts in different populations, whereas its eastern sister species *Chrysochus auratus* is genetically and ecologically uniform (50). However, in none of these cases is it clear whether the putative intermediate populations represent geographic disjuncts; all could represent host-use variation in continuous metapopulations. In the *Larinus* case only 2 of the 140 *Larinus* species were examined (20); the generality of the results, even for the genus, is an open question. Sampling of populations for genetic analysis was also limited in all of these cases, a critical factor in light of later work on *Ophraella*. Inclusion of more populations (76) has revealed *O. communa* to be paraphyletic to *Ophraella bilineata* and *Ophraella arctica* (which both use different hosts), thereby conforming to Figure 1c. Because the range of *O. bilineata* overlaps little with that of *O. communa* and *O. arctica* appears to be allopatric to both, Funk et al. (76) argued that the pattern was most consistent with peripatric speciation. However, because the host plants are more widely spread than the beetles, and some beetles are known from few sites, this inference is not strong (12, 28).

The full power of the phylogeographic approach has been applied in few cases. Reduced allozyme and mtDNA variability in the *gigantea* race of *E. solidaginis* (22, 90, 177), as well as the pattern of genealogical relatedness, suggest that (a) the *gigantea* race was derived from the *altissima* race in the easternmost part of the range of the *altissima* race; (b) the Midwestern part of the range of the *gigantea* race was colonized relatively recently from the east; and (c) the *altissima* populations are the most divergent. Especially noteworthy is the fact that there are two levels of divergence within the *altissima* race, both greater than the difference separating the *gigantea* race: moderate divergence in the Midwest and a much deeper divergence at the western edge of the sampled area in the Midwest, apparently representing a morphologically defined western North American subspecies of *E. solidaginis* (68). This pattern supports the sympatric origin of the *gigantea* race. Knowles et al. (100) used coalescence theory to infer mode of speciation in *O. bilineata* and *O. communa* and concluded that peripatric (founder-effect) speciation, partially obscured by postspeciation introgression, could best explain the data. However, Bush & Butlin (27) argued that similar biogeographic patterns could equally well have come about by sympatric speciation, or even by allopatric speciation that did not involve a bottleneck.

To our knowledge, only one body of work is sufficiently detailed and extensive for a simultaneous test of many of the predictions of the allopatric and sympatric hypotheses. *Euphydryas editha* butterflies in California have a population structure of discrete relatively isolated populations that utilize different hosts, and they have adapted genetically to these hosts (151, 152). Moreover, genetically based

host shifts have occurred in historical time as well as in the evolutionary past (152–155), and the shifts are of the order of differences observed between different *Euphydryas* species. A phylogeny for the populations reveals evidence for multiple host shifts at the local population level in the past (133). However, mating does not occur on or in association with the host in *E. editha*, and larval performance is not associated with adult oviposition preference. Thus the larval host shifts are not predicted to produce host races under the sympatric model, and in fact the population structure of *E. editha* conforms to Figure 1b. *E. editha* populations are monophyletic with respect to its sister species *Euphydryas chalcedonia*, which feeds in the larval stage on one of the hosts of *E. editha* (187). *E. editha* is in perfect agreement with the predictions of the allopatric hypothesis.

Overall, we conclude that allopatric populations using different hosts, as per Mayr's model, can be found for host-shifting taxa. However, they are by no means universal, and, significantly, the best-documented example of allopatric intermediates in various stages of adapting to new hosts is in an insect, *E. editha*, with little if any host fidelity. Host races do exist, and several cases of sympatric host races and host-specialized species that are phylogenetically younger than allopatric populations of the ancestral species are known. At a minimum, the evidence fails to reject the sympatric model.

Do Species-Level and Higher Biogeographic Patterns Match Predictions of the Sympatric Hypothesis?

Tests at the species level are based on the same basic ideas as those at the population level but are in some ways simpler because the power of gene flow to obscure historical patterns is lessened. One prediction that can be formally tested at the species level is that sympatric sister species should be produced by sympatric speciation, and allopatric sister species should be produced by allopatric speciation (109). However, by itself this is a weak prediction because dispersal after allopatric speciation can produce the same outcome (113). To make strong predictions, taxa tested must be partitioned *a priori* into “host-shifters” and “nonshifters” (12), taxa that do or do not have features that models indicate would permit sympatric speciation. Host-shifters are characterized by (a) host specialization of species in the group, (b) diversity of hosts used by different species in the group, and (c) mating on the host plant (12). Nonshifters lack one or more of these features. Characterizing taxa as host-shifters or nonshifters does not presuppose sympatric speciation; these features can be objectively observed in nature independent of putative mode of speciation. Nonshifters play as large a part in testing modes of speciation as do host-shifters.

To perform a test of whether sister species in host-shifter taxa are more sympatric than nonshifter taxa [sister species sympatry (SSS) test], all species in a clade must have been described and subjected to phylogenetic analysis, and have completely known geographic ranges and host plant relationships (12). The impact of incomplete systematic information can be profound. For example, finding a new

species in Mexico that is sister to species *B*, formerly thought to be part of sympatric eastern North American sister species pair (*A*, *B*), shifts support from sympatric to allopatric speciation. In cases where members of a clade are found on small islands or habitat islands and thus are likely to have been sympatric throughout their existence, the SSS test can be inverted by asking if the putative close relatives sharing an island are in fact monophyletic or alternatively represent sequential colonizations (12, 148).

Only one SSS test has been published (12). The test used phylogenetic and geographic range data from the literature for three sets of organisms. The nonshifter set included vertebrates, plants, and insects; the second set comprised host-shifter insects; and a final (positive) control set comprised plant species that had arisen by allopolyploidy, autopolyploidy, or hybrid speciation, undisputed sympatric speciation mechanisms. The outcome was that sister species in both the host-shifter and control sets showed significantly more range overlap (calculated as the area of species range overlap divided by the smaller of the two species areas) than nonshifter sister species. Thus, a recognizable biogeographic signature is left by both known sympatric speciations and those of host-shifter taxa.

However, Berlocher (12) did not attach great significance to these initial results. A major problem is that the very features that draw research interest to specialist phytophagous insects—large numbers of morphologically similar species with complex host relationships—work against obtaining the complete systematic data needed to carry out statistically convincing tests. All of the host-shifter taxa contained systematically problematic populations. Another problem is that suitable tests for the effects of interspecific competition on range overlap have not been performed (12). That is, host-shifters could be biased toward present-day sympatry because the different niches of sister species permit rapid range overlap following secondary contact. The potential importance of competition can in principle be determined. In nonshifter phytophagous insects such as large Lepidoptera in which mating site is not strongly associated with larval host, one could test whether sister species using different larval hosts display greater geographic overlap than sister species using the same hosts, between which larval competition occurs (45). To these caveats may be added another, which is that many of the nonshifter taxa included in the analysis were probably not species, at least in terms of reproductive isolation. In compiling the nonshifter set from the literature, the judgment of the original author was accepted on species status (12). Yet some allopatric populations described as species have essentially fused on secondary contact in historical time (35), whereas others have not (51). One solution to this problem is to accept as nonshifter taxa only those allopatric species pairs in which species integrity has survived secondary contact in historical time. “Species” that fail to survive secondary contact would then be analyzed as intraspecific populations, as described in the preceding section. Despite these problems, however, the SSS test could be informative if carried out appropriately. Randomization tests carried out on individual taxa are a powerful method for testing whether sister species ranges overlap more or less than expected for pairs chosen randomly from the taxon (9).

Only a small number of inverted SSS tests, testing whether phytophagous insect species on small islands are monophyletic, have been carried out using modern systematics. The spectacular radiation of host-specific flightless cryptorhynchine weevils on the isolated oceanic island of Rapa (126) appears to be driven by within-island allopatric events, but this case cries out for analysis with molecular techniques. A compelling case for sympatric speciation in the weevil *Dusmoechetes* on sub-Antarctic islands has been made (36).

A special case of the SSS test uses those insect clades that have specialized in different parts of the same host or on different sexes of the host and may thus have always been sympatric. Based on an allozyme phylogeny of a small sampling of the tephritid fly genus *Blepharoneura*, Condon & Steck (38) concluded that the most closely related species use the same parts (e.g., female flower) of different host species. Thus in this case speciation has not been by shift from male to female plants of the same species but by shift from host to host, as is typical of other tephritid flies. The remarkable divergence of six *Chiastocheta* fly species onto different reproductive parts of the European water lily *Trollius europaeus* (46) would appear to support sympatric speciation, but some of the most recent pairs in the group were partially allopatric. In both of these cases, only a small fraction of the insect genus was analyzed, so firm conclusions must await complete systematics.

SSS tests have one major limitation—they do not make full use of the data implicit in the phylogeny. Time will gradually erase the original biogeographic signatures of sympatric and allopatric speciation in predictably different ways: greater sympatry for the products of allopatric speciation and greater allopatry for the products of sympatric speciation (Figure 2; 8–10, 12, 109). A test based on these expected trends can be called an age-range correlation (ARC) test. A critical point is that, as with the SSS test, taxa must be partitioned *a priori* by life history patterns to make testable predictions.

Several decisions must be made in carrying out an ARC test. The choice of measuring divergence as a nominal [“speciation level” (109), “node level” (10)] or as a quantitative variable [interspecific genetic distance (9, 12)] may make little difference (9). However, the choice of approaches to the related problems of calculating range overlap for nonsister taxa (species deeper in the tree than most-recent sister species), assuring independence of comparisons, and determining appropriate levels of statistical significance is less clear at present. The first approach is that of Lynch (109) and Barraclough and colleagues (9, 10), who calculated nonsister ranges as the combination (union) of species ranges of the sister clades and then calculated range overlaps (suitably transformed if parametric statistics are to be used) as described for a SSS test. However, as pointed out by Barraclough et al. (9, 10), this approach results in larger and larger total ranges at increasing node level, so that a positive slope between range overlap and node level will be observed even with random data. Two measures have been taken to accommodate this bias. First, Barraclough & Vogler (9) emphasized the intercept as much as the slope in interpreting results (although because the intercept value is strongly

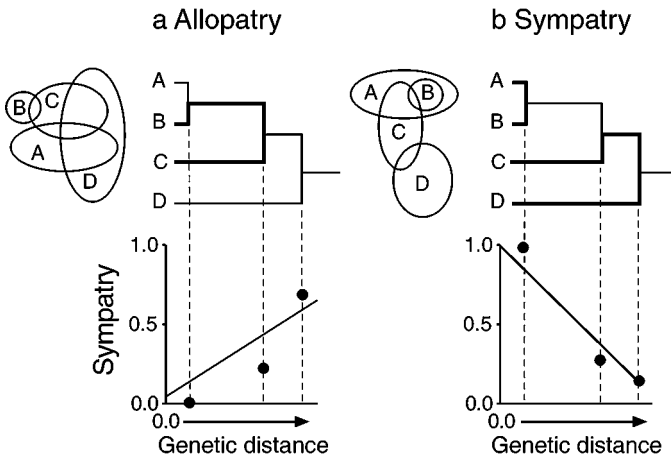


Figure 2 Concept behind age-range correlation test. (a) In allopatric speciation, ranges of sister species begin in allopatry, and postspeciation-range movement results in increased sympatry over time. (b) In sympatric speciation, ranges of sister species begin in total sympatry, and postspeciation-range movement results in decreased sympatry over time. In both cases mean genetic divergence and mean range overlaps (not computed precisely from ranges in Figure) are computed using Coyne & Orr's modification (39) of Felsenstein's (66) independent contrasts method; the comparisons are thus A-B, mean of C-A and C-B, and mean of D-A, D-B, and D-C. Darker lines in the trees show two possible sets of randomly chosen pairwise independent comparisons that could be made; a draw as in (a) results in a loss of information (see text).

affected by sympatry values for sister species, an age-range test under these circumstances converges on an SSS test). Second, computer simulations were used to make predictions for different modes of speciation. However, as Barraclough & Vogler (9) note, their model is relatively simple and may not be a completely reliable guide to evaluating real data sets.

A second approach can be based on Felsenstein's (66) independent contrasts approach, as modified by Coyne & Orr (39), in which divergence data and range overlaps are averaged on either side of each node (Figure 3). In the context of an ARC test this approach has not been statistically evaluated in depth.

The simplest and possibly most appropriate approach to an ARC test is to analyze only independent pairs (66, 107). One randomly chooses from the phylogeny as many species pairs as possible that share no branches in common, allowing a simple nonparametric regression of pairwise node level or genetic distance against pairwise range overlap. However, as shown in the two different random drawings in Figure 3a,b, such an approach fails to make complete use of the data.

We note that in cases of highly vagile insects, the biogeographic signature of speciation may be so rapidly eroded by postspeciation dispersal that no real benefit

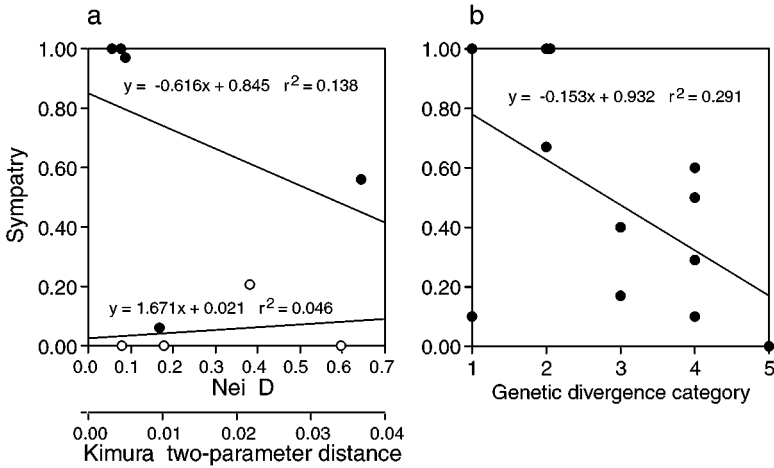


Figure 3 Age-range correlation tests. (a) Tests for the host-shifter—*R. pomonella* species group (black dots) using allozyme data (15) and for the nonshifter—*R. suavis* group (white dots) using COII mtDNA sequence data (160) (ranges from 15, 24, 68; V. Gavrilovic, personal communication). Data treated as in Figure 2. Slope of neither test significant using nonparametric Kendall τ test. (b) Test using allopolyploids in plants (data from 3, 6, 12, 87, 105, 186), range overlaps computed as means of the three pairwise values for parental and daughter species, $p = 0.048$ using Kendall's τ . Genetic divergence categories from allozyme studies: 1, daughter species exactly as predicted from parental genotypes; 2, at least one genetic change (gene silencing or new allele) in some individuals of at least one population of daughter species; 3, at least one genetic change fixed in a population of daughter species; 4, at least one genetic change fixed in all populations of daughter species; 5, in situ hybridization needed to identify parental species.

is gained by analyzing older taxa, so that statistically simpler SSS tests may be just as powerful as ARC tests. On the other hand, ARC tests should be less sensitive to missing species than SSS tests because missing species do not change genetic distances between sampled species.

By far the most extensive set of empirical ARC tests has been carried out by Barraclough & Vogler (9) on a set of eight molecular phylogenetic studies (consisting of four birds, a fish, and three insect genera, including *Rhagoletis*). All displayed the positive slopes expected of allopatric speciation (although as just noted their statistical approach is biased toward positive slopes). In all cases, the intercept was small because most sister species pairs were allopatric (the exceptions being in the three insect genera). The extent to which these data disprove sympatric speciation, however, is debatable, as the data were not partitioned into host-shifters and nonshifters (see also 27). Bush (25) long ago noted the dichotomy between the nonshifter—*Rhagoletis suavis* group of allopatric or parapatric, morphologically

diverse species all feeding on the chemically defended genus *Juglans*, and the host-shifter—*R. pomonella* group of broadly sympatric, morphologically similar species each specializing on diverse families of relatively undefended plants.

To demonstrate the potential of partitioning by life history for testing mode of speciation, we carried out separate ARC tests for the *R. pomonella* and *R. suavis* groups (Figure 3a). These nonsignificant tests are included here only as a “proof of concept” and to stimulate work by others, but they are suggestive enough to warrant continued development of this approach. As with SSS tests, a positive control can be based on organisms that must speciate sympatrically. Figure 3b presents a significant age-range plot for allopolyploid plants, in which the two parental species and the hybrid species must be sympatric (or at least parapatric) at the inception of the new species. Compilation of SSS and ARC tests is a necessary next step in proving or falsifying sympatric speciation. We stress that only a large compilation will be conclusive, as species ranges have dynamic evolutionary histories (9).

CONCLUSIONS AND PROSPECTUS FOR THE FUTURE

What still needs to be done to continue moving sympatric speciation from controversy into the realm of accepted scientific theory?

1. The prevalence of density- and frequency-dependent selection during adaptation to new hosts must be determined. Such selection is a core assumption of sympatric speciation models but one seldom questioned. If it is uncommon, then we must rethink the theoretical underpinnings of sympatric speciation and perhaps question its overall importance for the genesis of insect biodiversity.
2. The extent of enemy- and competitor-free space must be better quantified to gauge the accuracy of the metaphor of “open” and “closed” ecological niches. Moreover, it must be determined how often reduced predation, parasitism, or competition on novel plants is a result of host-specific adaptation (in which case the traits constitute fitness trade-offs) versus how often they are a characteristic of the plant itself (in which case enemy-free space would not serve to promote reduction in gene flow).
3. Levels of migration between host races and close species need to be more accurately measured using direct methods such as mark-release-recapture, not just with indirect marker-based approaches. Moreover, nonhost-related ethological and postzygotic isolation (coarsely measured in the current sympatric speciation literature) needs to be determined more precisely to translate migration rates into gene flow estimates.
4. QTL mapping studies of host-related traits are needed to determine how often reproductive pleiotropy and linkage between assortative-mating and performance loci occur. Candidate genes can then be the targets for selection experiments (in both field and laboratory settings) to test for genetic

responses in predicted directions to environmental conditions. Eventually, the actual nucleotide substitutions underlying host-related traits must be identified. Host-trait loci may prove to be essential for estimating evolutionary relationships among host races and species, where neutral markers, rudderless in the currents of gene flow, display extensive reticulation. The potential importance of “speciation genes” is demonstrated by the remarkable increase in phylogenetic resolution over typical genes that is possible with the *Odysseus* gene, which causes male sterility in crosses between *Drosophila simulans* and *Drosophila mauritiana* (165).

5. Fine-scale mapping of insect races and host plants is needed not only to address concerns about micro-allopatry but also to distinguish sympatrically from allopatrically evolved host races. By accumulating such information from many taxa, we may discern the relative importance of sympatric versus allopatric modes of divergence in generating insect specialists. Further analysis could also reveal common themes in the types of host-related traits facilitating sympatric divergence.
6. Complete systematics and phylogenetics for important study groups are absolutely required. Only then can truly convincing sister species sympatry and ARC tests be carried out. In addition, other general patterns may emerge from systematic data partitioned into host-shifter and nonshifter categories.

Resolving the path from the observable world of host races arising in historical time to the inferred world of speciation occurring in evolutionary time remains a major issue. Establishing the seamlessness of sympatric speciation is one of the two great challenges in the field, and it would constitute the most conclusive proof for the hypothesis. Insects can be shown to have actively diverged in sympatry to reach the status of partially isolated host races. Many of these races may be speeding toward speciation, as they continue to adapt to their hosts. However, there is no direct evidence to refute the counter claim that most host races are “stalled on the back roads to speciation.” Host races could arrive at this quasi-species state in two ways. First, they might lack sufficient genetic variation to respond to the multifarious selection pressures imposed by plants. Second, they could be at a semipermanent equilibrium because differences between plant niches are not great enough to abandon limited oligophagy. If conditions do not change, then races and other host-associated forms might be frozen states in evolutionary time.

One’s perspective on this matter depends, in part, on one’s concept of a species. If species status requires the complete elimination of genetic exchange between taxa, then a period of partial or complete geographic isolation may ultimately be needed for the absolute closure of host-associated populations residing at the limits of adaptive divergence. Alternatively, host-associated adaptation alone could drive divergence to completion or reduce gene flow sufficiently to permit the evolution of intrinsic incompatibilities without geographic separation. However, as discussed, total elimination of gene flow (absolute reproductive isolation) may not be a reasonable criterion for distinguishing species (81, 111). Many taxa of

host-specific phytophagous insects may turn out to be similar to the plants they eat in forming syngameons (162) composed of populations at various interconnected states of adaptive divergence. Viewed from this perspective, intermediate forms like the flowering dogwood population of *Rhagoletis* flies (13) already constitute a species.

Have we succeeded in our quest for defining a mutually exclusive set of tests that unambiguously distinguishes sympatric from allopatric speciation? No, not entirely. But we believe we have shown that the accumulation of a directed set of data detailing the natural history, ecology, genetics, and phylogeography for a group of host-specific insects can imply a high likelihood for sympatric speciation. Whether we can assign an overall probability statement to this assessment is the second great research challenge to students of sympatric speciation or any mode of divergence. J.B.S. Haldane (84a) proposed four stages of acceptance of an idea: (a) This is worthless nonsense; (b) This is an interesting, but perverse, point of view; (c) This is true, but quite unimportant; and (d) I always said so. We have attempted to frame all of the relevant issues about sympatric speciation to such an extent that there can no longer be disagreement as to its feasibility. At the least, an increase of scientists in the latter stages of Haldane's progression has been quite noticeable in recent years. We hope our long argument has opened a constructive dialogue toward resolving the challenges that lie ahead for sympatric speciation and has helped move the subject beyond controversy and back toward the realm of acceptable scientific theory (44) from which it originated.

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LITERATURE CITED

1. Abrahamson WG, Brown WH, Roth SK, Sumerford DV, Horner JD, et al. 1994. Gallmaker speciation: an assessment of the roles of host-plant characters, phenology, gallmaker competition, and natural enemies. In *Gall-Forming Insects*, ed. PW Price, W Mattson, Y Baranchikov, pp. 208–22. *USDA For. Ser., N. Cent. Exp. Sta. Gen. Tech. Rep. NC-174*
- 1a. Abrahamson WG, Eubanks, Blair CP,

- Whipple AV. 2001. Gall flies, inquiline, and goldenrods: a model for host race formation and sympatric speciation. *Am. Zool.* In press
2. Abrahamson WG, Weis AE. 1997. *Evolutionary Ecology Across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies*. Princeton, NJ: Princeton Univ. Press. 455 pp.
 3. Allen GA, Eccleston CL. 1998. Genetic resemblance of the allotetraploid *Aster ascendens* to its diploid progenitors *Aster falcatus* and *Aster occidentalis*. *Can. J. Bot.* 76:338–44
 4. Arnold J, Anderson W. 1983. Density-regulated selection in a heterogeneous environment. *Am. Nat.* 121:656–68
 5. Arnold ML. 1997. *Natural Hybridization and Evolution*. London/New York: Oxford Univ. Press. 215 pp.
 6. Ashton PA, Abbott RJ. 1992. Multiple origins and genetic diversity in the newly arisen species, *Senecio cambrensis* Rosser (Compositae). *Heredity* 68:25–32
 7. Avise JC. 2000. *Phylogeography: The History and Formation of Species*. Cambridge, MA: Harvard Univ. Press. 447 pp.
 8. Barraclough TG, Nee S. 2001. Phylogenetics and speciation. *Trends Ecol. Evol.* 16:391–99
 9. Barraclough TG, Vogler AP. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *Am. Nat.* 155:419–34
 10. Barraclough TG, Vogler AP, Harvey PH. 1998. Revealing the factors that promote speciation. *Phil. Trans. R. Soc. London Ser. B* 353:241–49
 11. Berlocher SH. 1989. The complexities of host races and some suggestions for their identification by enzyme electrophoresis. In *Electrophoretic Studies on Agricultural Pests*, ed. HD Loxdale, J den Hollander, Spec. Vol. 39:51–68. Oxford, UK: Clarendon/Br. Syst. Assoc. 494 pp.
 12. Berlocher SH. 1998. Can sympatric speciation be proven from phylogenetic and biogeographic evidence? See Ref. 89, pp. 99–113
 13. Berlocher SH. 1999. Host race or species? Allozyme characterization of the “flowering dogwood fly,” a member of the *Rhagoletis pomonella* complex. *Heredity* 83:652–62
 14. Berlocher SH. 2000. Genetic population structure in Tephritidae. In *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*, ed. M Aluja, AL Norrbom, pp. 711–30. Boca Raton, FL: CRC. 949 pp.
 15. Berlocher SH. 2000. Radiation and divergence in the *Rhagoletis pomonella* species group: inferences from allozymes. *Evolution* 54:543–57
 16. Berlocher SH, McPherson BA, Feder JL, Bush GL. 1993. Genetic differentiation at allozyme loci in the *Rhagoletis pomonella* (Diptera: Tephritidae) species complex. *Ann. Entomol. Soc. Am.* 86:716–27
 17. Boecklen WJ, Mopper S. 1998. Local adaptations in specialist herbivores: theory and evidence. See Ref. 117, pp. 64–90
 18. Boller EF, Prokopy RJ. 1975. Bionomics and management of *Rhagoletis*. *Annu. Rev. Entomol.* 21:223–46
 19. Boughton DA. 2000. The dispersal system of a butterfly: a test of source-sink theory suggests the intermediate-scale hypothesis. *Am. Nat.* 156:131–44
 20. Briese DT, Espiau C, Pouchot-Lermans A. 1996. Micro-evolution in the weevil genus *Larinus*: the formation of host biotypes and speciation. *Mol. Ecol.* 5:531–45
 21. Brown JM, Abrahamson WG, Packer RA, Way PA. 1995. The role of natural-enemy escape in a gallmaker host-plant shift. *Oecologia* 104:52–60
 22. Brown JM, Abrahamson WG, Way PA. 1996. Mitochondrial DNA phylogeography of host races of the goldenrod ball gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *Evolution* 50:777–86
 23. Brown JM, Leebens-Mack JH, Thompson JN, Pellmyr O, Harrison RG. 1997. Phylogeography and host association in a pollinating seed parasite, *Greya politella*

- (Lepidoptera: Prodoxidae). *Mol. Ecol.* 6:215–24
24. Bush GL. 1966. The taxonomy, cytology, and evolution of the genus *Rhagoletis* in North America (Diptera: Tephritidae). *Bull. Mus. Comp. Zool.* 134:431–562
 25. Bush GL. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera: Tephritidae). *Evolution* 23:237–51
 26. Bush GL. 1975. Sympatric speciation in phytophagous parasitic insects. In *Evolutionary Strategies of Parasitic Insects and Mites*, ed. PW Price, pp. 187–207. New York: Plenum. 224 pp.
 27. Bush GL, Butlin R. 2001. Sympatric speciation in insects. In *Adaptive Speciation*, ed. U Dieckmann, H Metz, M Doebeli, D Taut. Cambridge, UK: Cambridge Univ. Press. In press
 28. Bush GL, Smith JJ. 1998. The genetics and ecology of sympatric speciation: a case study. *Res. Popul. Ecol.* 40:175–87
 29. Butlin RK. 1987. Speciation by reinforcement. *Trends Ecol. Evol.* 2:8–13
 30. Butlin RK. 1996. Co-ordination of the sexual signalling system and the genetic basis of differentiation between populations in the brown planthopper, *Nilaparvata lugens*. *Heredity* 77:369–377
 31. Carroll SP, Boyd C. 1992. Host race radiation in the soapberry bug: natural history with the history. *Evolution* 46:1052–69
 32. Carroll SP, Dingle H, Famula TR, Fox CW. 2001. Genetic architecture of adaptive differentiation in evolving host races of the Soapberry Bug, *Jadera haematoloma*. *Genetica* In press
 33. Carroll SP, Dingle H, Klassen SP. 1997. Genetic differentiation of fitness-related traits among rapidly evolving populations of the soapberry bug. *Evolution* 51:1182–88
 34. Carroll SP, Klassen SO, Dingle H. 1998. Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. *Evol. Ecol.* 12:955–68
 35. Childs MR, Echelle AA, Dowling TE. 1996. Development of the hybrid swarm between pecos pupfish (*Cyprinodontidae: Cyprinodon pecosensis*) and sheepshead minnow (*Cyprinodon variegatus*): a perspective from allozymes and mtDNA. *Evolution* 50:2014–22
 36. Chown SL. 1990. Speciation in the sub-Antarctic weevil genus *Dusmoecetes* Jeanne (Coleoptera: Curculionidae). *Syst. Entomol.* 15:283–96
 37. Claridge MF, den Hollander J, Morgan JC. 1985. The status of weed-associated populations of the brown planthopper, *Nilaparvata lugens*: host race or biological species? *Zool. J. Linn. Soc.* 84:77–90
 38. Condon MA, Steck GJ. 1997. Evolution of host use in fruit flies of the genus *Blepharoneura* (Diptera: Tephritidae): cryptic species on sexually dimorphic host plants. *Biol. J. Linn. Soc.* 60:443–66
 39. Coyne JA, Orr HA. 1997. “Patterns of speciation in *Drosophila*” revisited. *Evolution* 51:295–303
 40. Craig TP, Horner JD, Itami JK. 1997. Hybridization studies on the host races of *Eurosta solidaginis*: implications for host shifts and speciation. *Evolution* 55:773–82
 41. Craig TP, Horner JD, Itami JK. 2001. Genetics, experience, and host-plant preference in *Eurosta solidaginis*: implications for sympatric speciation. *Evolution* 51:1552–60
 42. Craig TP, Itami JK, Abrahamson WG, Horner JD. 1993. Behavioral evidence for host-race formation in *Eurosta solidaginis*. *Evolution* 47:1696–710
 43. Craig TP, Itami JK, Shantz C, Abrahamson WG, Horner JD, Craig J. 2000. The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis*. *Ecol. Entomol.* 25:7–18
 44. Darwin C. 1859. *On the Origin of Species by Natural Selection, or the Preservation of Favored Races in the Struggle for Life*. London: Murray. 513 pp. 1st ed.

45. Denno RF, McClure MS, Ott JR. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annu. Rev. Entomol.* 40:297–331
46. Despres L, Jaeger N. 1999. Evolution of oviposition strategies and speciation in the globe-flower flies *Chiastocheta* spp. (Anthomyiidae). *J. Evol. Biol.* 12:822–31
47. Dieckmann U, Doebelli M. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–57
48. Diehl SR, Bush GL. 1984. An evolutionary and applied perspective of insect biotypes. *Annu. Rev. Entomol.* 29:471–504
49. Diehl SR, Bush GL. 1989. The role of habitat preference in adaptation and speciation. See Ref. 124, pp. 527–53
50. Dobler S, Farrell BD. 1999. Host use evolution in *Chrysochus* milkweed beetles: evidence from behavior, population genetics and phylogeny. *Mol. Ecol.* 8:1297–307
51. Echelle AF, Echelle AA. 1994. Assessment of genetic introgression between two pupfish species, *Cyprinodon elegans* and *C. variegatus* (Cyprinodontidae), after more than 20 years of secondary contact. *Copeia* 1994:590–97
52. Edwards SV, Beerli P. 2000. Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution* 54:1839–54
53. Endler JA. 1977. *Geographic Variation, Speciation, and Clines*. Princeton, NJ: Princeton Univ. Press. 246 pp.
54. Etges WJ. 1998. Premating isolation is determined by larval rearing substrates in cactophilic *Drosophila mojavensis*. IV. Correlated responses in behavioral isolation to artificial selection on a life history trait. *Am. Nat.* 152:129–44
55. Etges WJ, Johnson WR, Duncan GA, Huckins G, Heed WB. 1999. Ecological genetics of cactophilic *Drosophila*. In *Ecology of Sonoran Desert Plants and Plant Communities*, ed. R Robichaux, pp. 164–214. Tucson, AZ: Univ. Arizona Press
56. Feder JL. 1995. The effects of parasitoids on sympatric host races of the apple maggot fly, *Rhagoletis pomonella* (Diptera: Tephritidae). *Ecology* 76:801–13
57. Feder JL. 1998. The apple maggot fly, *Rhagoletis pomonella*: flies in the face of conventional wisdom about speciation? See Ref. 89, pp. 130–44
58. Feder JL, Berlocher SH, Opp SB. 1998. Sympatric host race formation and speciation in *Rhagoletis* (Diptera: Tephritidae): a tale of two species for Charles D. See Ref. 117, pp. 408–11
59. Feder JL, Bush GL. 1989. A field test of differential host usage between two sibling species of *Rhagoletis* fruit flies (Diptera: Tephritidae) and its consequences for sympatric models of speciation. *Evolution* 43:1813–19
60. Feder JL, Chilcote CA, Bush GL. 1988. Genetic differentiation between sympatric host races of *Rhagoletis pomonella*. *Nature* 336:61–64
61. Feder JL, Filchak K. 1999. It's about time: the evidence for host plant-mediated selection in the apple maggot fly, *Rhagoletis pomonella*, and its implications for fitness trade-offs in phytophagous insects. *Entomol. Exp. Appl.* 91:211–25
62. Feder JL, Opp S, Wazlo B, Reynolds K, Go W, Spizak S. 1994. Host fidelity as an effective premating barrier between sympatric races of the apple maggot fly. *Proc. Natl. Acad. Sci. USA* 91:7990–94
63. Feder JL, Reynolds K, Go W, Wang EC. 1995. Intra- and interspecific competition and host race formation in the apple maggot fly, *Rhagoletis pomonella*. *Oecologia* 101:416–25
64. Feder JL, Roethele JB, Wazlo B, Berlocher SH. 1997. Selective maintenance of allozyme differences among sympatric host races of the apple maggot fly. *Proc. Natl. Acad. Sci. USA* 94:11417–21
65. Felsenstein J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35:124–38
66. Felsenstein J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–14

67. Filchak KE, Roethele JB, Feder JL. 2000. Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* 407:739–42
68. Foote RH, Blanc FL, Norrbom AL. 1993. *Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico*. Ithaca, NY: Comstock Publ. Assoc. 571 pp.
69. Fox CW, Lalonde RG. 1993. Host confusion and the evolution of insect diet breadths. *Oikos* 67:577–81
70. Freeland JR, Boag PT. 1999. The mitochondrial and genetic homogeneity of the phenotypically diverse Darwin's ground finches. *Evolution* 53:1553–63
71. Fretwell SD. 1972. *Populations in a Seasonal Environment*. Princeton, NJ: Princeton Univ. Press. 217 pp.
72. Fry JD. 1993. The "general vigor" problem: can antagonistic pleiotropy be detected when genetic covariances are positive? *Evolution* 47:327–33
73. Fry JD. 1996. The evolution of host specialization: are trade-offs overrated? *Am. Nat.* 148:S84–107
74. Funk DJ. 1998. Isolating a role for natural selection in speciation: host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles. *Evolution* 52:1744–59
75. Funk DJ. 1999. Molecular systematics of cytochrome oxidase I and 16S from *Neochlamisus* leaf beetles and the importance of sampling. *Mol. Biol. Evol.* 16:67–82
76. Funk DJ, Futuyma DJ, Orti GG, Meyer A. 1995. A history of host associations and evolutionary diversification for *Ophraella* (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. *Evolution* 49:1008–17
77. Futuyma DJ, Keese MC, Funk DJ. 1995. Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. *Evolution* 49:797–99
78. Futuyma DJ, Mayer GC. 1980. Non-allopatric speciation in animals. *Syst. Zool.* 29:254–71
79. Futuyma DJ, McCafferty SS. 1990. Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera: Chrysomelidae). *Evolution* 44:1885–913
80. Futuyma DJ, Moreno G. 1988. The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.* 19:207–33
81. Grant PR. 1993. Hybridization of Darwin's finches on Isla Daphne Major. *Phil. Trans. R. Soc. London Ser. B* 340:127–39
82. Groman JD, Pellmyr O. 2000. Rapid evolution and specialization following host colonization in a yucca moth. *J. Evol. Biol.* 13:223–36
83. Guttman SI, Weigt LA. 1989. Macrogeographic genetic variation in the *Enchenopa binotata* complex (Homoptera: Membracidae). *Ann. Entomol. Soc. Am.* 82:156–65
84. Haldane JBS. 1957. The cost of natural selection. *J. Genet.* 55:511–24
- 84a. Haldane JBS. 1963. The truth about death. *J. Genet.* 58:463–64
85. Harrison RG. 1991. Molecular changes at speciation. *Annu. Rev. Ecol. Syst.* 22:281–308
86. Harrison RG. 1993. *Hybrid Zones and the Evolutionary Process*. London/New York: Oxford Univ. Press. 364 pp.
87. Hauffler CH, Windhaw MD, Rabe EW. 1995. Reticulate evolution in the *Polypodium vulgare* complex. *Syst. Bot.* 20:89–109
- 87a. Hawthorne DJ, Via S. 2001. Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature* In press
88. Hess MD, Abrahamson WG, Brown JM. 1996. Intraspecific competition in the goldenrod ball-gallmaker (*Eurosta solidaginis*): larval mortality, adult fitness, ovipositional and host-plant response. *Am. Mid. Nat.* 136:121–33
89. Howard DJ, Berlocher SH. 1998. *Endless Forms: Species and Speciation*. London/New York: Oxford Univ. Press. 470 pp.

90. Itami JK, Craig TP, Horner JD. 1998. Factors affecting gene flow between the host races of *Eurosta solidaginis*. See Ref. 117, pp. 375–77
91. Jaenicke J. 1990. Host specialization in phytophagous insects. *Annu. Rev. Ecol. Syst.* 21:243–73
92. Johnson PA, Gullberg U. 1998. Theory and models of sympatric speciation. See Ref. 89, pp. 79–89
93. Johnson PA, Hoppensteadt FC, Smith JJ, Bush GL. 1996. Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and nonhabitat assortative mating. *Evol. Ecol.* 10:187–205
94. Jones P, Gacesa LP, Butlin RK. 1996. Systematics of brown planthopper and related species using nuclear and mitochondrial DNA. In *The Ecology of Agricultural Pests: Biochemical Approaches*, ed. WOC Symondson, JE Liddell, Spec. Vol. 53:133–48. London: Chapman & Hall/B. Syst. Assoc. 517 pp.
95. Kawecki TJ. 1996. Sympatric speciation driven by beneficial mutations. *Proc. R. Soc. London Ser. B* 263:1515–20
96. Kawecki TJ. 1997. Sympatric speciation via habitat specialization driven by deleterious mutations. *Evolution* 51:1749–61
97. Kawecki TJ. 1998. Red Queen meets Santa Rosalia: arms races and the evolution of host specialization in organisms with parasitic lifestyles. *Am. Nat.* 152:635–51
98. Keese MC. 1996. Feeding responses of hybrids and the inheritance of host-use traits in leaf feeding beetles (Coleoptera: Chrysomelidae). *Heredity* 76:36–42
99. Klicka J, Zink R. 1999. Pleistocene effects on North American songbird evolution. *Proc. R. Soc. London Ser. B* 266:695–700
- 99a. Kirkpatrick M, Ravigné V. 2001. Speciation by natural and sexual selection. *Am. Nat.* In press
100. Knowles LL, Futuyma DJ, Eanes WF, Rannala B. 1999. Insight into speciation from historical demography in the phytophagous beetle genus *Ophraella*. *Evolution* 53:1846–56
101. Kondrashov AS. 1986. Multilocus models of sympatric speciation. III. Computer simulations. *Theor. Popul. Biol.* 24:136–44
102. Kondrashov AS, Kondrashov FA. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* 400:351–54
103. Kondrashov AS, Yampolsky LY, Shabalina SA. 1998. On the sympatric origin of species by means of natural selection. See Ref. 89, pp. 90–98
104. Kreslavsky AG, Mikheyev AV. 1981. Gene geography and racial differences in *Lochmaea capreae* L. (Coleoptera, Chrysomelidae), and the problem of sympatric speciation. *Entomol. Rev.* 73:85–92
105. Lashermes P, Combes MC, Robert J, Troustlet P, Hont D, et al. 1999. Molecular characterization and origin of the *Coffea arabica* L. genome. *Mol. Gen. Genet.* 261:259–66
106. Levene H. 1953. Genetic equilibrium when more than one niche is available. *Am. Nat.* 87:331–33
107. Lossos JB, Miles DB. 1994. Adaptation, constraint, and the comparative method. In *Ecological Morphology: Integrative Organismal Biology*, ed. PC Wainwright, SM Reilly, pp. 60–98. Chicago: Univ. Chicago Press. 367 pp.
108. Ludwig W. 1950. Zur theorie der konkurrenz. Die annidation (Einnishug) als funfter Evolutionsfaktor. *N. E. Probl. Zool. Klatt-Festshcr.* 1950:516–37
109. Lynch JD. 1989. The gauge of speciation: on the frequencies of mode of speciation. See Ref. 124, pp. 527–53
110. Mackenzie A. 1996. A trade-off for host plant utilization in the black bean aphid, *Aphis fabae*. *Evolution* 50:155–62
111. Mallet J. 1995. A species definition for the Modern Synthesis. *Trends Ecol. Evol.* 10:294–99
112. Maynard Smith J. 1966. Sympatric speciation. *Am. Nat.* 100:637–50

113. Mayr E. 1963. *Animal Species and Evolution*. Cambridge: Belknap. 797 pp.
114. McPherson BA, Smith DC, Berlocher SH. 1988. Genetic differences between host races of the apple maggot fly. *Nature* 336:64–66
115. Mills LS, Allendorf FW. 1996. The one-migrant-per-generation rule in conservation and management. *Conserv. Biol.* 10:1509–18
116. Miyatake T, Shimizu T. 1999. Genetic correlations between life-history and behavioral traits can cause reproductive isolation. *Evolution* 53:201–8
117. Mopper S, Straus S. 1998. *Genetic Structure and Local Adaptations in Insect Populations: Effects of Ecology, Life History, and Behavior*. London: Chapman & Hall. 449 pp.
118. Muller H. 1940. Bearing of the *Drosophila* work on systematics. In *The New Systematics*, ed. JS Huxley, pp. 185–268. Oxford, UK: Clarendon. 585 pp.
119. Nelson G, Platnick NI. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. New York: Columbia Univ. Press. 567 pp.
120. Noor MAF. 1999. Reinforcement and other consequences of sympatry. *Heredity* 83:503–8
121. O'Brien DL, Freshwater DW. 1999. Genetic diversity within tall form *Spartina alterniflora* Loisel along the Atlantic and Gulf coasts of the United States. *Wetlands* 19:352–58
122. Odeen A, Florin AB. 2000. Effective population size may limit the power of laboratory experiments to demonstrate sympatric and parapatric speciation. *Proc. R. Soc. London Ser. B* 267: 601–6
123. Orr MR, Smith TB. 1998. Ecology and speciation. *Trends Ecol. Evol.* 13:502–6
124. Otte D, Endler JA. 1989. *Speciation and Its Consequences*. Sunderland, MA: Sinauer. 679 pp.
125. Pashley DP, Martin JA. 1987. Reproductive incompatibility between host strains of fall armyworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 80:731–33
126. Paulay G. 1985. Adaptive radiation on an isolated oceanic island: the Cryptorhynchinae (Curculionidae) of Rapa (southeast Polynesia) revisited. *Biol. J. Linn. Soc.* 26:95–188
127. Peterson MA, Denno RF. 1997. The influence of intraspecific variation in dispersal strategies on the genetic structure of planthopper populations. *Evolution* 51:1189–206
128. Pimm SL. 1978. Sympatric speciation: a simulation model. *Biol. J. Linn. Soc.* 11:131–39
129. Pratt GF. 1994. Evolution of *Euphilotes* (Lepidoptera: Lycaenidae) by seasonal and host shifts. *Biol. J. Linn. Soc.* 51: 387–416
130. Prokopy RJ. 1972. Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. *Environ. Entomol.* 1:326–32
131. Prokopy RJ, Averill AL, Cooley SS, Roitberg CA. 1982. Associative learning in egg-laying site selection by apple maggot flies. *Science* 218:76–77
132. Prokopy RJ, Diehl SR, Cooley SS. 1988. Behavioral evidence for host races in *Rhagoletis pomonella* flies. *Oecologia* 76:138–47
133. Radtkey R, Singer MC. 1995. Repeated reversals of host preference evolution in a specialist insect herbivore. *Evolution* 49:351–59
134. Rausher MD. 1985. Variability for host preference in insect populations: mechanistic and evolutionary models. *J. Insect Physiol.* 31:873–89
135. Rausher MD. 1992. Natural selection and the evolution of plant-insect interactions. In *Insect Chemical Ecology: An Evolutionary Approach*, ed. BD Roitberg, MB Isman, pp. 20–88. New York: Chapman & Hall. 432 pp.
136. Reissig H, Smith DC. 1978. Bioecology of *Rhagoletis pomonella* in

- Crataegus*. *Ann. Entomol. Soc. Am.* 71: 155–59
137. Rice WR. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evol. Ecol.* 1:301–14
 138. Rice WR, Hostert EE. 1993. Laboratory experiments on speciation: what have we learned in forty years? *Evolution* 47:1637–53
 139. Rice WR, Salt G. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution* 44:1140–52
 140. Roethele JR, Feder JR, Berlocher SH, Kreitman ME. 1997. Toward the construction of a molecular genetic linkage map for the apple maggot fly, *Rhagoletis pomonella* (Diptera: Tephritidae): a comparison of alternative strategies. *Ann. Entomol. Soc. Am.* 90:470–79
 141. Roethele JB, Romero-Severson J, Feder JL. 2001. Evidence for broad-scale conservation of linkage map relationships between *Rhagoletis pomonella* (Diptera: Tephritidae) and *Drosophila melanogaster* (Diptera: Drosophilidae). *Ann. Entomol. Soc. Am.* In press
 142. Rosensweig M. 1978. Competitive speciation. *Biol. J. Linn. Soc.* 10:274–89
 143. Rossi A, Stiling MP, Cattell M, Bowditch T. 1999. Evidence for host-associated races in a gall-forming midge: trade-offs in potential fecundity. *Ecol. Entomol.* 24:95–102
 144. Seager J. 1985. Intraspecific resource competition as a cause of sympatric speciation. In *Evolution: Essays in Honor of John Maynard Smith*, ed. PJ Greenwood, PH Harvey, M. Slatkin, pp. 43–53. Cambridge, UK: Cambridge Univ. Press. 328 pp.
 145. Servedio MR, Kirkpatrick M. 1997. The effects of gene flow on reinforcement. *Evolution* 51:1764–72
 146. Sezer M, Butlin RK. 1998. The genetic basis of host plant adaptation in the brown planthopper (*Nilaparvata lugens*). *Heredity* 80:499–508
 147. Sezer M, Butlin RK. 1998. The genetic basis of oviposition preference differences between sympatric host races of the brown planthopper (*Nilaparvata lugens*). *Proc. R. Soc. London. Ser. B* 265:2399–405
 148. Schliewin UK, Tautz D, Pääbo S. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368:629–32
 149. Schluter D. 1998. Ecological causes of speciation. See Ref. 89, pp. 114–29
 150. Shultz ST, Lynch M. 1997. Mutation and extinction: the role of variable mutation effects, synergistic epistasis, beneficial mutations, and the degree of outcrossing. *Evolution* 51:1363–71
 151. Singer MC. 1971. Evolution of food-plant preference in the butterfly *Euphydryas editha*. *Evolution* 5:383–89
 152. Singer MC, Ng D, Vasco D, Thomas CD. 1992. Rapidly evolving associations among oviposition preferences fail to constrain evolution of insect diet. *Am. Nat.* 139:9–20
 153. Singer MC, Thomas CD. 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* 42:977–85
 154. Singer MC, Thomas CD. 1996. Evolutionary responses of a butterfly metapopulation to human and climate-caused environmental variation. *Am. Nat.* 148: S9–39
 155. Singer MC, Thomas CD, Parmesan C. 1993. Rapid human-induced evolution of insect diet. *Nature* 361:251–53
 156. Smith DC. 1986. *Genetic and reproductive isolation of Rhagoletis flies*. PhD thesis. Univ. Ill., Urbana-Champaign. 189 pp.
 157. Smith DC. 1988. Heritable divergence of *Rhagoletis pomonella* host races by seasonal asynchrony. *Nature* 336:66–67

158. Smith DC. 1988. Reproductive differences between *Rhagoletis* (Diptera: Tephritidae) fruit parasites of *Cornus amomum* and *C. florida* (Cornaceae). *J. NY Entomol. Soc.* 96:327–31
159. Smith DC, Lyons SA, Berlocher SH. 1993. Production and electrophoretic verification of F₁ hybrids between the sibling species *Rhagoletis pomonella* and *R. cornivora*. *Entomol. Exp. Appl.* 69:209–13
160. Smith JJ, Bush GL. 1997. Phylogeny of the genus *Rhagoletis* (Diptera: Tephritidae) inferred from DNA sequences of mitochondrial cytochrome oxidase II. *Mol. Phylogenet. Evol.* 7:33–43
161. Tavormina SJ. 1982. Sympatric genetic divergence in the leaf mining insect *Liriomyza brassicae* (Diptera: Agromyzidae). *Evolution* 36:523–34
162. Templeton AR. 1989. The meaning of species and speciation: a general perspective. See Ref. 124, pp. 3–27
163. Templeton AR. 1998. Nested clade analysis of phylogeographic data: testing hypotheses about gene flow and population history. *Mol. Ecol.* 7:381–97
164. Tilmon KJ, Wood TK, Pesek JD. 1998. Genetic variation in performance traits and the potential for host shifts in *Enchenopa* treehoppers (Homoptera: Membracidae). *Ann. Entomol. Soc. Am.* 91:397–403
165. Ting CT, Tsaur SC, Wu C-I. 2000. The phylogeny of closely related species as revealed by the genealogy of a speciation gene, *Odysseus*. *Proc. Natl. Acad. Sci. USA* 97:5313–16
166. Turelli M, Barton NH, Coyne JA. 2001. Theory and speciation. *Trends Ecol. Evol.* 16:330–42
167. Udovic D. 1980. Frequency-dependent selection, disruptive selection, and the evolution of reproductive isolation. *Am. Nat.* 116:621–41
168. Via S. 1990. Ecological genetics in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *Annu. Rev. Entomol.* 35:421–46
169. Via S. 1991. The genetic structure of host plant adaptation in a spatial patchwork: demographic variability among reciprocally transplanted pea aphid clones. *Evolution* 45:827–52
170. Via S. 1999. Reproductive isolation between sympatric races of pea aphids. I. Gene flow and habitat choice. *Evolution* 53:1446–57
171. Via S. 2000. Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. *Evolution* 54:1626–37
172. Via S. 2001. Sympatric speciation in animals: the ugly duckling grows up. *Trends Ecol. Evol.* 16:381–90
173. Via S, Hawthorn D. 2001. Genetic architecture of ecological specialization and incipient speciation in divergent races of pea aphids *Am. Nat.* In press
174. Wallace B. 1968. *Topics in Population Genetics*. New York: Norton. 481 pp.
175. Walsh BD. 1864. On phytophagic varieties and phytophagic species. *Proc. Entomol. Soc. Phil.* 3:403–30
176. Walsh BD. 1867. The apple-worm and the apple maggot. *J. Hortic.* 2:338–43
177. Waring GL, Abrahamson WG, Howard DL. 1990. Genetic differentiation among host-associated populations of the gall-maker *Eurosta solidaginis* (Diptera: Tephritidae). *Evolution* 44:1648–55
178. Whitlock MC. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *Am. Nat.* 148:S65–77
179. Wilson DS. 1989. The diversification of single gene pools by density- and frequency-dependent selection. See Ref. 124, pp. 527–53
180. Wilson DS, Turelli M. 1986. Stable underdominance and the evolutionary invasion of empty niches. *Am. Nat.* 127: 835–50

181. Wood TK. 1980. Divergence in the *Enchenopa binotata* complex (Homoptera: Membracidae) effected by host plant adaptation. *Evolution* 34:147–60
182. Wood TK, Guttman S. 1982. Ecological and behavioral basis for reproductive isolation in the sympatric *Enchenopa binotata* complex (Homoptera: Membracidae). *Evolution* 36:233–42
183. Wood TK, Keese M. 1990. Host-plant-induced assortative mating in *Enchenopa* treehoppers. *Evolution* 44: 619–28
184. Wood TK, Tilmon KJ, Shantz AB, Harris CK. 1999. The role of host-plant fidelity in initiating insect race formation. *Evol. Ecol. Res.* 1:317–32
185. Wright S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–59
186. Wyatt R, Odrzykoski IJ, Stoneburner A. 1993. Isozyme evidence proves that the moss *Rhizomnium pseudopunctata* is an allopolyploid of *R. gracile* and *R. magnifolium*. *Mem. Torrey Bot. Club* 25:21–35
187. Zimmerman MN, Wahlberg N, Descimon H. 2000. A phylogeny of *Euphydryas* s.l. checkerspot butterflies (Lepidoptera: Nymphalidae) based on mitochondrial DNA sequence data. *Ann. Entomol. Soc. Am.* 93:347–55



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