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Sympatric Speciation in Insects

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11.1 Insect Diversity, Body Size, Specialization, and Speciation

Insects are among the most abundant multicellular organisms on earth. Sampling in the tropics and subtropics suggests that there are 10 to 30 million species of insects (Erwin 1982). As a group, invertebrate insects, therefore, represent an inordinately large percentage of the world's fauna, far outnumbering their larger and more conspicuous vertebrate cousins, such as fish (about 24 000), amphibians (about 4000), reptiles (7907), birds (9808), and mammals (4629). In fact, the number of species in many families of Heteroptera, Diptera, Coleoptera, and Hymenoptera outnumber the species in most classes of vertebrates.

Why are there so many insect species? One apparent reason is body size (Bush 1993). Their small size allows insects to subdivide habitats and specialize on resources that large animals are unable to exploit. Frequently, much of the life cycle occurs exclusively on the resource, which is particularly important since it induces assortative mating. Specialization permits a habitat occupied by a single vertebrate species to support a much greater number of small, often closely related, invertebrate species that can coexist in close sympatry with minimal competition. Vertebrate sister species usually have similar ecological needs, and are seldom sympatric because they competitively exclude one another. In contrast, it is estimated that the majority of insects, over 70% of which either feed on plants or are parasites and parasitoids, are highly host specific (Jaenike 1990). Sister species may sometimes even feed on different parts of the same host.

The occurrence of specialization, however, is not uniform throughout the Insecta. Specialists occur most commonly in the more advanced Neoptera insect orders, such as the Paraneoptera and Endopterygota. Highly species-rich genera of monophagous and stenophagous plant and animal parasites and parasitoids are characteristic of these insects. In contrast, specialists or species-rich genera in the ancestrally apterous Archaeognatha, Monura, and Thysanura are found rarely. Nor are they common in the Paleoptera (Ephemeroptera and Odonata) and basal Pterygota (Plecoptera, Dictyoptera, Grylloblattodea, Dermaptera, Orthoptera, and Phasmatodea), which are represented mostly by relatively larger bodied polyphagous, omnivorous, and insectivorous orders (Naumann 1991).

Two possible sources of diversity among specialist species can be envisaged: generalists may give rise to multiple descendant specialists, or specialist species might multiply by shifts from existing to new hosts. Kawecki (1998) said that "Divergence of an initially generalist population into specialized subpopulations that

show preference for different habitats or resources has been considered the most likely route to sympatric speciation.” This is true from the theoretical point of view. Models derived from Maynard Smith (1966), Seger (1985a), including Kawecki’s own model, and Doebeli (1996a), for example, consider the division of one population that exploits two hosts into two separate monophagous populations. Progress toward the evolution of reproductively isolated specialist populations from a generalist ancestor has been observed under laboratory conditions in ingenious experiments by Rice (1987) with *Drosophila melanogaster*. A case for such a pathway was made by Gibbons (1979) for divergence in ovipositor length between species of ichneumonid parasitoid wasps of the genus *Megarhyssa*. There is also clear evidence that *D. sechellia*, which specializes on the toxic fruit of *Morinda citrifolia*, is descended from the generalist *D. simulans* (Jones 1998). However, relatively few models consider host shifts (Johnson *et al.* 1996b), although this actually appears to be a dominant mode of speciation in insect specialists (see below).

Allopatric speciation is likely to be the most prevalent mode of divergence among insect generalists. As closely related sister species have very similar ecological resources and mate recognition systems, they seldom live sympatrically. Only when sister species have evolved sufficiently strong pre- or, in many cases, postmating reproductive isolation and different ecological requirements can two sister species coexist without either hybridizing or competitively excluding one another. If they do hybridize, they may form a relatively stable hybrid zone (Butlin 1990) or occasionally generate a new parthenogenetic species (Bullini 1994).

Competition is less likely to prevent co-existence between closely related sister species of insect specialists (Bush and Smith 1997). Recently diverged insect specialists each spend most of their life history on different hosts, which reduces the chances of encountering one another when feeding or searching for mates. Interspecific competition from unrelated insects, if present, may exert a much stronger competitive effect on adaptation. Mating is also usually restricted to a different host or habitat for each species, and host preference is generally a major component of their mate-recognition system.

As a result of these differences in biological traits responsible for specialization, the process of speciation in insect specialists can differ from the speciation of insect generalists. Speciation in specialists potentially can occur in at least five ways:

- By cospeciation;
- In allopatry on the same resource;
- In allopatry accompanied by a resource shift;
- In sympatry accompanied by a resource shift;
- By interspecific hybridization.

By sympatry we mean that populations occur within the same region, such that gene flow is obstructed as a result of the biology of the insects rather than because of physical barriers that prevent their meeting. Parapatry is an intermediate situation in which ranges abut, and so only part of each population is in contact. Most

commonly, the resource is part of a host, such as a fruit, and shifts occur between the same parts of different host species. We concentrate on examples of this type. However, the resource shift could be between parts of the same host. For example, in *Blepharoneura* (Tephritidae: Diptera) one species infests male flowers while its sympatric sister species uses female flowers of the same host plant, *Gurania costaricensis* (Cucurbitaceae; see Condon and Steck 1997). Similarly, two sister taxa of the human body louse *Pediculus humanus* (Pediculidae: Anoplura; see Levene and Dobzhansky 1959), regarded as species by some (Chirov and Ozerova 1997), coexist on the same individual. *P. h. corporis*, specialized in a variety of ways to life on the body, lays its eggs only on cloth threads, while the head louse *P. h. capitis* is adapted to an existence on the head and glues its eggs on hair. Interspecific hybridization is not considered here, as there is insufficient evidence that it is responsible for speciation in insects, except in the origin of parthenogenetic taxa (Bullini 1994).

11.2 Cospeciation

Cospeciation occurs when an ancestral association between species simultaneously splits into descendant associations. It most often involves a coordinated process of allopatric speciation between a host and its specialized phytophagous, commensal, or parasitic insect. Although originally thought to be common, it is clear that cospeciation, or co-cladogenesis, is relatively rare (Godfray 1994). To qualify as cospeciation, the insects must be associated tightly with their hosts from the time at which the ancestral host originated (Mitter *et al.* 1991; Menken and Roessingh 1998). As the association between host and commensal or parasite has been continuous throughout their evolutionary history, the two cospeciation clades should be of similar age.

A clear example of cospeciation involves ectoparasitic lice and their hosts. A phylogenetic study using mitochondrial cytochrome oxidase I found clear evidence of cospeciation between most of the 15 allopatric pocket gophers (Geomyidae) and their associated lice (Mallophaga; see Hafner *et al.* 1994; Page and Hafner 1996). However, even in this example a single case of host switching has occurred. Indeed, host switching may often be the rule in other lice and their hosts. Little evidence of cospeciation has been found between swiftlets (Apodiformes: Apodidae) and their *Dennyus* lice (Phthiraptera: Menoponidae; see Clayton *et al.* 1996). Host switching is so common in some groups of lice that Barker (1994) suggests the axiom that lice and their hosts invariably cospeciate be abandoned. Whether or not cospeciation occurs in lice may depend on the degree of allopatry between host species. If hosts remain allopatric, as do most pocket gophers, there is little opportunity for host shifting. When host species become sympatric, lice may replace one another after bouts of interspecific competition and extinction (Barker 1994).

Cospeciation is the rule in the association between figs and their fig-wasp pollinators (Machado *et al.* 1996). An in-depth phylogenetic analysis by Weiblen (2001), which combines molecular and morphological data, finds clear evidence

of extensive cospeciation between dioecious New Guinea figs (*Ficus* subg. *Ficus*, Moraceae) and their highly specialized fig-wasp pollinators (Hymenoptera: Agaonidae) accompanied by only a few host switches. There is strong evidence of correlated evolution between fig style and wasp ovipositor lengths, as well as of other changes in the fig-breeding systems that foster a stable mutualism. This study on figs and their pollinators indicates a tight one-on-one specificity and life-cycle interdependence that should promote and sustain cospeciation. As mating occurs within the fig, inbreeding results in a loss of genetic variation. Extreme specialization and loss of genetic variation limits the ability of pollinators to shift host. These results are consistent with the view that figs and their wasp pollinators cospeciated allopatrically, although pollinator-driven sympatric speciation cannot be ruled out (Weiblen 2002).

11.3 Allopatric Speciation on the Same Host

Although the assumption is often made that host specialists have speciated allopatrically without a host shift, few detailed studies document this mode of speciation in insects. One such example is speciation in tephritid flies that belong to the *Rhagoletis suavis* species group (Bush and Smith 1998). The six species in this group feed as larvae exclusively on the husks of walnuts (*Juglans* spp.). The husk contains large quantities of juglone, a phenolic compound toxic to many organisms. This compound may serve as a dietary requirement (Bush and Smith 1998), much as cactus alkaloids are required for reproduction by cactus-infesting *Drosophila* (Heed and Kircher 1965). Such compounds appear to impose a serious biological constraint on the ability of these specialists to shift to new hosts.

Taxa of the *R. suavis* species group are allopatric or, when parapatric, they are allochronically and altitudinally isolated. Cospeciation can be ruled out because all *Juglans* species used as hosts evolved at least 35 million years before the first ancestor of the *R. suavis* group colonized walnuts about 2–5 million years ago. Ample fossil evidence shows that the distribution of walnut species shifted over the millennia, which provided opportunities for populations that infest walnut to diverge in isolation. As noted below, a shift to a new host in the absence of geographic isolation accompanies speciation events in other *Rhagoletis* species groups in which the rate of speciation is 2–3 times faster than that in the *R. suavis* group.

Allopatric speciation has also occurred in the Hawaiian Island *Drosophila*. At least 22 inter-island colonization events resulted in speciation without a major shift in feeding habits (White 1968). Indeed, island archipelagos provide the best examples of allopatric speciation in insects, because it is possible to establish patterns of colonization and rates of divergence with some degree of accuracy (White 1968; Roderick and Gillespie 1998). However, most of the 700 species of Hawaiian *Drosophila* result from intra-island rather than inter-island speciation events. Many of these speciation events involved shifts in habitats and use of host-plant resource (Kambysellis *et al.* 1995).

Another well-studied example of insect specialists that speciate in allopatry without host shifts involves *Heliconius* butterflies, although parapatric speciation

cannot be excluded (Mallet *et al.* 1998). *H. erato* and its close relatives are all specialized on *Passiflora* species in the subgenus *Plectostemma*. The evolution of alternative mimetic color patterns and/or environmental associations, now associated with strong assortative mating (McMillan *et al.* 1997), apparently drive speciation.

11.4 Allopatric Speciation with a Host Shift

A shift to a new host accompanies the majority of speciation events that involve plant feeders, parasites, and parasitoids (Strong *et al.* 1984; Mitter *et al.* 1991), although it is important to note that evolutionary changes in host association are not necessarily connected to speciation (Singer *et al.* 1992). There is still disagreement over when, where, and how speciation by a host shift occurs. Three broad possibilities must be distinguished: sympatry, allopatry without a restriction in population size (vicariance), and allopatry with a period of reduced population size (Table 11.1, the peripatric model). To explain the origin of the many observed sympatric sister species of phytophagous, parasitic, and parasitoid insects, Mayr (1947, 1963), Futuyma and Mayer (1980), and other authors maintain that it must occur allopatrically. They base this view on the assumption that such insects generally have several alternative hosts. Speciation occurs when a population of a widely distributed species becomes geographically isolated on only one of its normal hosts. Over time, the isolated deme specializes on the host and eventually speciates. The new species may then re-establish sympatry with the parental species. Although speciation by this allopatric process undoubtedly can take place in nature, its frequency is not documented and thus it is uncertain how important it has been in generating new species. It is likely to be a relatively slow mode of speciation, and is therefore unlikely to account for all of the millions of highly specialized sympatric sister species of plant-feeding insects that appear to evolve rapidly. However, small peripatric isolates may evolve more rapidly or there may be strong selection for specialization in some populations, so that a clear distinction from sympatric host shifts is difficult.

An association between phylogeography, based on allozymes, and host-plant use in *Larinus* weevils on *Onopordum* and *Cynara* thistles in the Mediterranean region is suggestive of allopatric divergence (Briese *et al.* 1996). Since there are no major differences in heterozygosity, this appears to have happened without population bottlenecks. Futuyma *et al.* (1995), Funk (1998), and Knowles *et al.* (1999) propose a possible example of peripatric speciation. On the basis of limited mitochondrial DNA sequence data and population sampling, they conclude from their phylogeographic analysis that founder events and peripatric speciation (Mayr 1963) were involved in host shifts and speciation in the beetle genus *Ophraella* (Coleoptera; Chrysomelidae; see Knowles *et al.* 1999). They focused their analysis on the origin of *O. bilineata* whose distribution broadly overlaps that of its putative parental species, *O. communa*. However, their evidence that *O. bilineata* went through a genetic bottleneck is not convincing. *O. communa* and *O. bilineata* have equivalent levels of genetic variation that Knowles *et al.* (1999)

Table 11.1 Contrasting expectations from allopatric and nonallopatric speciation.

	Allopatric		Nonallopatric		Comments
	Vicariance	Peripatric	Sympatric	Parapatric	
Ranges of sister species at time of origin	Nonoverlapping	One species with restricted peripheral range	Broadly sympatric	Abutting	Secondary range overlap is needed to establish species status
Host association	Same or different	Same or different	Different	Different	
Rate of speciation	Slow	Fast	Very fast	Very fast	
Postzygotic isolation	Through genetic incompatibility	Through genetic incompatibility	Through host adaptation only	Through host adaptation only	
Morphological divergence	Likely	Likely	Unlikely	Unlikely	Assumes that morphological divergence accumulates slowly. The opposite pattern is true for traits directly involved in resource use
Parallel speciation	Unlikely	Possible	Likely	Likely	Parallel speciation is the independent origin of reproductive isolation in separate populations in response to the same environmental conditions (Schluter 1996a)
Phylogenetic relationships	Paraphyly unlikely, gene trees congruent	Paraphyly likely, gene trees may be incongruent because of lineage sorting ^a	Paraphyly likely, gene trees may be incongruent because of incomplete barrier to gene exchange	Paraphyly likely, gene trees may be incongruent because of introgression near boundary	Here, paraphyly means that populations of the ancestral species may be more distantly related to one another than the descendant species is to the population from which it was derived. This is reflected in paraphyletic relationships in at least some gene trees

^a See Box 15.3.

believe resulted from postspeciation hybridization. However, they did not rule out incomplete lineage sorting (see Box 15.3) to account for the observed shared polymorphisms. Nor does the present broadly parapatric overlap of *O. bilineata* with *O. communa* and the paraphyletic origin of *O. bilineata* from *O. communa* support their view that *O. bilineata* speciated peripatrically (Table 11.1). Their data are equally compatible with the hypothesis that *O. bilineata* speciated as a result of a sympatric or parapatric host shift with substantial gene flow during the early stages of divergence and host-race formation, or indeed with allopatric speciation in a large population. The potential roles of population bottlenecks and divergence through selection on a new host have been confounded in this argument. They may interact, but allopatric host shifts do not require bottlenecks.

In contrast, similar phylogeographic analyses now provide good examples of paraphyletic patterns of host-plant utilization in which a derived host race or species has arisen within a phylogenetic cluster of a widely distributed and geographically differentiated species (Brown *et al.* 1997; Bush and Smith 1998; Dobler and Farrell 1999). In these examples, there is no evidence that host shifts occurred allopatrically, but it remains difficult to infer sympatric divergence without additional evidence because parphyly can result from colonization of a new region by individuals from one part of a widespread species (Table 11.1). A possible example here is *D. simulans*, which is paraphyletic to the island endemic *D. sechellia*, a specialist on a novel host (Solignac and Monnerot 1986).

Barracough and Vogler (2000) have attempted to overcome this problem by comparing range overlap between species pairs and time since speciation, and using the relationship to infer the extent of sympatry at the time of speciation. Their analysis suggests that speciation was predominantly allopatric in the taxa studied, which included *Rhagoletis* fruitflies and *Flexamia* leafhoppers. However, they did not include closely related sympatric taxa that are good candidates for sympatric host shifts, such as *R. mendax* and *R. zephyria*. These were omitted because the phylogenetic hypothesis on which the analysis was based failed to separate them from their ancestral species, in this case *R. pomonella* (for the marker used, *R. mendax* and *R. zephyria* sequences are embedded within the clade of *R. pomonella* sequences).

11.5 Sympatric Speciation with a Host Shift

Sympatric speciation first involves the colonization of a new host and the development of a biologically distinct host race (Box 11.1). Although it is not yet demonstrated that host races can originate peripatrically, there is greater opportunity for host races to develop sympatrically within a large, widely distributed species with abundant variation. In such species, the testing of new alleles and allelic combinations is continuous on potentially new hosts until the right combination allows successful colonization. This adaptive process is less likely to prove successful when a few individuals colonize a new patch of habitat.

As a working definition, we recognize host races as populations that specialize on alternative hosts and differ genetically from one another in host preference and

Box 11.1 Stages of host-race formation

1. A new host relatively free of competitors becomes available for colonization because of changes in the host or insect range, or because of changes in host ecology or physiology.
2. Mutation and/or recombination generate individuals able to utilize the new host from within the parental species (if appropriate genotypes are not already available).
3. A number of males and females that exhibit a genetically based preference for and/or ability to survive on the new host, colonize the new host over successive generations and establish a population. Low efficiency of host utilization may be compensated by low competition.
4. Assortative mating occurs among the earliest colonists of the new host (mating occurs on the preferred host). This reduces gene flow between the original and new host-associated populations and allows adaptive gene combinations to be maintained in each population.
5. During the course of adaptation to the new host, a genetically distinct host race evolves as host-associated differences in fitness and host fidelity increase over time between the host-associated populations.
6. For loci not involved in host-associated adaptations, genetic similarity between the original species and the new host race is maintained by continued low levels of gene flow, particularly during the early stages of host-race formation.
7. Speciation is completed by reinforcement or because continued divergence incidentally reduces gene exchange to zero.

host fidelity, but still exchange genes (see Berlocher and Feder 2002). Current gene exchange can, in principle, be distinguished from incomplete lineage sorting on the basis that recent mutations or parallel geographic variations in neutral markers are shared. Host shifts appear to occur most commonly following the introduction of a new host that is relatively free of competing insect specialists (Box 11.1). In the case of phytophagous insects, hosts shifts are sometimes restricted to related plant species, but in others, shifts are to unrelated plants. The latter usually involve host shifts between chemically similar host plants (Strong *et al.* 1984; Becerra 1997).

New sympatric host races are usually established not by a few, but by many individuals over many generations, and because they remain open to gene exchange at many loci, they are likely to share similar levels of genetic variation (Vouidibio *et al.* 1989; Abe 1991; Stanhope *et al.* 1992, 1993; Bush 1992; Guldmond and Dixon 1994; Mackenzie and Guldmond 1994; Mackenzie 1996; Feder 1998). In the few cases examined closely, the new host races appear to differ genetically at loci responsible for adaptation to the new host, such as those that contribute to phenological changes in *R. pomonella*, and for mate recognition (Feder 1998). Host races remain distinct at these key adaptive loci and at loci closely linked to them, but low levels of gene exchange may continue for other loci (Feder *et al.* 1994; Feder 1998). There is no convincing evidence that recently evolved sympatric or

parapatric host races or monophagous species experienced genetic bottlenecks in their past, as expected from some modes of allopatric divergence.

We see sympatric speciation as a progressive process, because adaptation to the new host initially occurs without cessation of gene exchange. Whether complete reproductive isolation evolves rapidly or over a protracted period depends on the intensity of divergent selection, and the degree of host preference and assortative mating (Johnson *et al.* 1996b). As a population adapts in response to strong divergent selection on a new host, it becomes progressively more isolated from the parent species. The criteria to establish exactly when a host race becomes a species are yet to be established and may be impossible to determine because gene exchange becomes harder to detect as it becomes more and more limited. Mallet (1995) suggests that two sympatric populations are species when they maintain distinct genetic clusters. Although this definition is very useful, recently established host races, such as the apple race of *R. pomonella* (see Plate 4), would fall into the species category (if one bases a decision on the divergent group of loci), which may be premature (Feder 1998). In the absence of definitive criteria that specify when a host race establishes an evolutionary lineage independent from its parent species, we will regard a recently established genetically distinct population on a new host as a host race not a species.

Examples of host races established sympatrically or parapatrically on plants cover a diverse range of insects (Diehl and Bush 1984; Craig *et al.* 1993; Mopper 1996; Secord and Kareiva 1996). A few well-studied examples are discussed here, while some of the many other possible cases are outlined in Table 11.2 (and see Berlocher and Feder 2002).

Walsh (1864) was the first to propose a model of sympatric host-race formation and speciation to explain the origin of many observed sympatric and closely related species of phytophagous host-specific insects. The fruit fly *R. pomonella* (Tephritidae), which Walsh described, infests fruits of North American haws (*Crataegus* spp: Rosaceae). In 1860, larvae were found attacking the fruits of introduced apples (*Malus pumila*: Rosaceae) in the Hudson River valley of New York (Bush 1969; Bush *et al.* 1989). The fly quickly spread throughout the range of apples in northeastern North America and established a host race that differs genetically from the parental sympatric hawthorn-infesting populations (Feder *et al.* 1988, 1997a; McPheron *et al.* 1988). These sympatric races, which continue to hybridize at low levels (Feder 1998; Feder *et al.* 1988; Feder *et al.* 1997b), differ in host preference, habitat specific mating preference, eclosion time, and host-associated fitness trade-offs for developmental rates and larval survival (Feder *et al.* 1988; Feder and Filchack 1999; Filchack *et al.* 1999). Strong, divergent natural selection and adaptive trade-offs for phenological attributes and host preferences, and the propensity of these host specialists to mate assortatively maintain their racial distinctions (Bush 1994; Feder 1998; Johnson *et al.* 1996b).

Miyatake and Shimizu (1999) demonstrated experimentally in another tephritid fly, *Bactrocera cucurbitae*, how such phenological shifts can promote race formation. Selection for short- and long-development periods resulted in an indirect

Table 11.2 Host shifts and sympatric speciation in insects.

Order	Family/Genus/Complex	Host plant	Comments	References
Hemiptera	<i>Uroleucon</i> (aphids) 44 species in subgenus <i>Uroleucon</i>	Asteraceae	Mitochondrial DNA phylogeography suggests rapid radiation of host-specific species following colonization of North America	Moran <i>et al.</i> 1999
	Auchenorrhyncha (treehoppers, leafhoppers, and planthoppers)	Many taxa	Many highly host-specific species. Sexual signals are transmitted through the host-plant substrate	Claridge 1985
	<i>Enchenopa</i>	A variety of tree species	Monophagous and extremely philopatric. Life cycle closely linked to host-plant phenology. Transfer experiments show how chance colonization of a new host can generate substantial reproductive isolation	Wood <i>et al.</i> 1999
	<i>Nilaparvata lugens</i>	Host races on <i>Oryza</i> and <i>Leersia</i> grasses	Host-associated performance and oviposition preference each controlled by a few genes (see text). Substrate transmitted sexual signals controlled by more loci and probably diverged by drift. Evidence for two independent sympatric host shifts.	Butlin 1996; Sezer and Butlin 1998a, 1998b
	<i>Erythroneura</i> (> 500 species)	Trees, shrubs, and vines	Many sympatric, putative sibling species specialized on different, usually related, hosts	Ross 1958
	<i>Dalbulus</i>	<i>Tripsacum</i> and <i>Zea</i>	Two independent host shifts onto cultivated corn in the past 5000–8000 years. Substrate-transmitted signals more distinct between sympatric than between allopatric species	Nault 1985

continued

Table 11.2 *continued*

Order	Family/Genus/Complex	Host plant	Comments	References
	Miridae (most species-rich family of Heteroptera), e.g., <i>Lopidea</i>		Phylogeographic analysis suggests at least 25% of species diverged sympatrically	Asquith 1993
	Orthotylinae, <i>Sarona</i> (40 species in Hawaii)	17 genera in 14 families	Inter-island colonists retain ancestral hosts, but up to 70% of within-island speciation involves a host shift	Asquith 1995
Lepidoptera	“Butterflies”		> 50% of species are monophagous Host shifts common during speciation	Jansen 1988 Janz and Nylin 1998
	<i>Zeiraphera diniana</i> (larch budmoth)	Host races on <i>Larix</i> and <i>Pinus</i>	High vagility suggests allopatric divergence is unlikely. Mating is on host plant, host odors as well as pheromones involved in mate finding	Emelianov <i>et al.</i> 1995
	<i>Spodoptera frugiperda</i>	Races on corn and rice/forage grasses	Broad sympatry possible because of strong premating isolation	Prowell 1998
	Lycanidae (40% of all butterfly species)		Specific associations with both host plants and ant mutualists. Host switching common in evolutionary history	Pierce 1987; Pratt <i>et al.</i> 1994
	<i>Yponomeuta</i> , <i>Laspeyresia</i> , <i>Hedylepta</i> , <i>Ostrinia</i> , <i>Greya</i>		Predominantly monophagous species with ecological and behavioral attributes likely to promote sympatric speciation	Bess 1974; Phillips and Barnes 1975; Harrison and Vawter 1977; Brown <i>et al.</i> 1997; Menken and Roessingh 1998

continued

Table 11.2 *continued*

Order	Family/Genus/Complex	Host plant	Comments	References
Coleoptera	> 150 000 phytophagous species, mainly Chrysomelidae and Curculionidae			Farrell 1998
	<i>Epilachna vigintioctomaculata</i> complex		Host shifts associated with sympatric host-race and species formation	Katakura 1997
	<i>Phyllotreta</i>	Brassicaceae	Host-associated divergence and possible sympatric speciation	Verdyck 1998
	<i>Blepharidopterus</i>	<i>Bursera</i>	Molecular phylogeny shows pattern of host shifts associated with host-plant chemistry rather than phylogeny	Becerra 1997
	<i>Haltica</i> , <i>Diabrotica</i> , <i>Lochmaea</i> , <i>Chrysochus</i> , <i>Oreina</i>		High degree of host specificity and frequent range overlap suggest sympatric divergence	Phillips and Barnes 1975; Krysan <i>et al.</i> 1989; Kreslavskiy and Mikheyev 1994; Dobler <i>et al.</i> 1996; Dobler and Farrell 1999
Hymenoptera	Insect parasitoids: possibly as much as 10% of all metazoan species		Highly host specific. Haplodiploidy, sibling mating often on the host, and associations with microorganisms essential for disarming host immune systems may all promote sympatric divergence and speciation	Askew 1968, 1971; Godfray 1994; Godfray and Waage 1988

continued

Table 11.2 continued

Order	Family/Genus/Complex	Host plant	Comments	References
Hymenoptera	<i>Megarhyssa</i> , <i>Andricus</i> , Aphidiinae, Euphorinae		Case studies suggesting sympatric divergence	Gibbons 1979; Shaw <i>et al.</i> 1988; Tremblay and Pennacchio 1988; Ramadevan and Deakin 1990; Abe 1991
	Ants: <i>Solenopsis</i> <i>invicta</i>		Gene flow restricted between monogynous and polygynous social forms	Shoemaker and Ross 1996
	<i>Leptothorax</i>		Molecular phylogenies show that social parasites are monophyletic and not related to hosts. May speciate by host shifting	Baur <i>et al.</i> 1995
Diptera	<i>Rhagoletis pomonella</i> group		See text	Bush and Smith 1997, 1998; Berlocher 2000
	<i>Blepharoneura</i>	Cucurbitaceae	Not just highly host-plant specific, but also specialized on plant parts. Speciation apparently associated with shift of host species rather than resource	Condon and Steck 1997
	Other phytophagous and parasitic families		Species rich with many host specialists, often mating on the host. Sympatric speciation likely to be common	

(pleiotropic) phenological shift in mating time. This difference in the time of mating caused significant reproductive isolation in mate-choice tests between the two populations. When coupled with genetic variation in other life-history traits, such as host preference, host-induced pleiotropic shifts in mating time can increase reproductive isolation substantially in insects that mate on their hosts.

Biological studies on the gall-forming tephritid fly *Eurosta solidaginis*, which infests the goldenrod *Solidago altissima* (Asteraceae), revealed the presence of a sympatric host race using *S. gigantea* (Waring *et al.* 1990; Craig *et al.* 1997; Itami *et al.* 1998). Although the two races are interfertile, they differ slightly in emergence time and prefer to mate and oviposit on their respective host plants. Each host race also survives significantly better on its own host, and F1 and backcross progeny do less well than the parental races on their host plants. A phylogeographic analysis (Brown *et al.* 1996) established that the host race on *S. gigantea* is derived from eastern populations of the widespread *S. altissima* race.

In Java, central Sumatra, and peninsular Malaysia, *Epilachna vigintioctomaculata* (Coccinellidae), whose normal hosts are species of *Solanum*, has established a population on the legume *Centrosema pubescens*, introduced from South America about 200 years ago (Nishida *et al.* 1997). The two host-associated populations are interfertile, but differ in size and host preference. In many respects, these host races resemble the stage of divergence present between the apple and hawthorn host races of *R. pomonella* (Feder *et al.* 1988). Similar genetic studies on the *E. vigintioctomaculata* may help clarify the status of the host-associated populations.

Host-race formation in the soapberry bug *Jadera haematoloma* (Rhopalidae: Hemiptera) has evolved rapidly as the result of independent sympatric or parapatric host shifts from native to introduced Sapindaceae (Carroll and Boyd 1992; Carroll *et al.* 1997). This bug occurs throughout the range of its native hosts, the soapberry tree (*Sapindus saponaria* var. *drummondii*) in the south-central region of the United States, the serjania vine (*Serjania brachycarpa*) in south Texas, and the perennial balloon vine (*Cardiospermum corindum*) in southern Florida. Within the past 20–100 years morphologically distinct taxa have independently colonized and adapted to the “flat-podded” golden-rain tree (*Koelreuteria elegans*) from *C. corindum* in Florida, and to the “round-podded” golden-rain tree (*K. paniculata*) and the heartseeded vine (*C. halicacabum*) from *S. saponaria* var. *drummondii* in south-central United States. Nymphs and adults feed by inserting their long slender tubular beak through the fruit wall to seeds that are located within the host fruits at varying distances from the fruit perimeter. Although the races are interfertile, they differ greatly in beak length, which is highly correlated to fruit size and shape.

Many host races exist among the 4000 species of aphids, 99% of which use one or a few hosts. As in other insect specialists, a host shift in aphids can initiate assortative mating and a substantial escape from gene flow. This allows individuals that speciate on different hosts to diverge in response to selection (Akimoto 1990; Guldmond and Mackenzie 1994; Mackenzie 1996; Via 1999).

Aphids manifest several unique sets of biological traits that predispose them to rapid host-race formation on introduced plants. Many aphids have various forms of cyclic reproduction. A round of sexual reproduction may follow several parthenogenetic (thelytokous) generations on the same host plant. If one or more asexually reproducing females with a genetically modified host preference shift to a new host plant, they can generate a large number of individuals with a similar preference for the same host. Where mating occurs on this host, males and females with similar genetic host preferences continue to feed on the new host during the reproductive stage of the cycle. A large number of their progeny are thus genetically predisposed to exploit the same host the following year for several rounds of asexual reproduction. More complicated life cycles, such as host alternation, may facilitate, modify, or impede host-race formation and speciation (Guldemand and Mackenzie 1994). For example, specialization on different hosts in the asexual summer populations may be opposed by mating on a common winter host.

11.6 Conditions Needed for Sympatric Shifts

These examples, and many others (Table 11.2), provide empirical support for the argument that sympatric speciation by host shifts is not just possible, but is a major route to speciation in specialist phytophagous insects. However, it is difficult to exclude alternative explanations completely in specific cases and, therefore, it is important to demonstrate that host shifts are also theoretically plausible. Numerous difficulties with the evolution of novel host associations in the face of gene flow have been raised, but there are now either empirical or theoretical grounds to reject all of them. Here, we briefly review the key issues (see also Via 2001, 2002).

Problem of crossing the gap

Host shifts are unlikely because an insect population that is well adapted to its current host is not expected to contain suitable genetic variation to utilize on an alternative host. The necessary variation needs to be maintained in the host population, because a rare mutation is unlikely to coincide with a rare colonization event. Futuyma *et al.* (1995) describe this as a genetic constraint on host shifts. Much evidence shows that host shifts are more common between hosts with similar chemical defenses (e.g., in butterflies; Janz and Nylin 1998), which indicates that some constraints do operate. However, if alternative hosts are too similar, oligophagy may be a more likely outcome than speciation.

This argument can be countered in two ways, either with a “two-phase” model, or with a broader view of host-associated adaptation. The two-phase model is derived from Turner’s (1981) arguments about the evolution of mimicry. In the case of a host shift, mutations of small effect are likely to reduce fitness on the current host without providing a significant ability to use the new host. Mutations of a large enough effect to “jump the gap” and confer high efficiency of utilization of the new host may be rare, but mutations with moderate ability to use the new host may be more common. If these genotypes also gain from greatly reduced competition (or predation or parasitism) on the new host, they may have high fitness

despite low efficiency. Once a population is established on the new host, selection favors modifiers that increase the efficiency of novel resource exploitation. This is the second phase. Overall, the process is expected to leave a genetic signature when host utilization is controlled by one or a few major genes, responsible for the initial jump, with epistatic modifiers responsible for the fine-tuning of performance. Evidence for this type of genetic architecture occurs in the host races of the brown planthopper *Nilaparvata lugens* (see Plate 4) on rice and a related grass *Leersia hexandra* (Sezer and Butlin 1998b). Host-associated performance is controlled by a small number of loci with evidence for epistatic interactions.

The picture envisaged in the constraint argument is of two distinct resource types with a gap that has to be crossed to move from one to the other. This may be realistic for host plants that use different defensive compounds, but adaptation to a host has many more dimensions than simply overcoming defense. This is clear in *Rhagoletis*, for example, in which emergence timing, as opposed to distinct host chemistry, seems to have the greatest influence on host-associated fitness (Feder and Filchack 1999). Emergence timing is a quantitative trait that is likely to exhibit genetic variation within the parental population on hawthorn. Genotypes at the early extreme of this distribution are most likely to colonize apples and have the highest fitness on apples. Rather than crossing a gap, the host shift simply involves response to directional selection.

Problem of maintaining multiple-niche polymorphism

Sympatric host shifts face the same difficulty as other modes of sympatric speciation. A resource-use polymorphism must be maintained for long enough, and with sufficiently strong selection against intermediate genotypes, for reproductive isolation to evolve.

Broadly, there are two reasons why this argument no longer carries much weight:

- Multiple-niche polymorphisms can be stabilized by density- and frequency-dependent selection (Udovic 1980; Wilson and Turelli 1986; see Chapter 3). When the population on one host is at low density, its fitness tends to be higher because negative interactions between individuals are reduced. There has been much debate about whether phytophagous insects compete for resources sufficiently for this to be an important effect, but the evidence now suggests that it can be in many instances (Denno *et al.* 1995). Competition for food may also be supplemented or replaced by the effects of escape from predators or parasites.
- Host choice can also stabilize multiple-niche polymorphism, because it increases the probability that individuals will live in the habitat type to which they are well adapted (provided choice and performance are correlated, see below; de Meeûs *et al.* 1993; Johnson *et al.* 1996b). Host choice, usually by ovipositing females, is a near universal feature of specialist insect species.

Problem of negative trade-offs

Sympatric speciation requires that an increase in fitness on one host be accompanied by a decrease on the alternative host. If this is not true, selection favors genotypes that perform well on both hosts: a specialist evolves into a generalist rather than splitting into two host-specific species. The expectation is that antagonistic pleiotropy must underlie this trade-off between performances on different hosts, otherwise recombination could create successful generalist genotypes.

Empirically, a negative genetic correlation is expected between performances on different hosts, but this has rarely been observed (Via 1990, 2002). Estimation of genetic correlations is difficult for most organisms, but in aphids it is possible to exploit the alternation of sexual and asexual generations to design more powerful experiments. It is significant, therefore, that Mackenzie (1996) found a strong negative correlation in performance on nasturtium and broad bean among 77 clones of *Aphis fabae*. Since this correlation was maintained after allowing recombination, it does appear to arise from antagonistic pleiotropy.

Generally, studies of trade-offs have concentrated on host-associated performance measured by survival, growth rate, or adult size. However, this is only one aspect of fitness and trade-offs might occur in other fitness components. Phenological matching between *R. pomonella* and its hosts (Feder 1998; Feder and Filchack 1999) is a good example in which there is necessarily a negative correlation between fitness on the two hosts across different emergence and diapause times. Interactions with predators or parasites that find their prey by searching host plants may also contribute significantly to host-associated fitness differences and contribute to trade-offs. For example, *R. pomonella* on apples is attacked by only one parasitoid species, while larvae on the ancestral host are attacked by two (Feder *et al.* 1995). Also, the agromyzid fly *Liriomyza helianthi* suffers 17% less parasitism when moved experimentally to a novel host (Gratton and Welter 1998).

Recent theory actually questions whether negative pleiotropy is necessary at all. In the “independent adaptation” model by Kawecki (1998), specialization evolves because of a coevolutionary “arms race” between insect and host. Specialists can “keep up” with the evolution of their hosts’ defenses, while generalists are unable to track the independent changes that occur in different hosts. This effect selects for host choice and therefore isolation without the need for negative pleiotropy. A possible example of the independent genetic basis of adaptation is a Y-linked locus in the flea beetle *Phyllotreta nemorum* that influences performance on one host only (Nielsen 1999).

Problem of simultaneous evolution of preference and performance

A mutation that increases performance on a novel host is not at a selective advantage unless it is in an individual on the novel host. Conversely, a preference for a novel host is not advantageous unless it is associated with an ability to exploit the host. Since the two types of mutation are very unlikely to occur together, a successful host shift is highly improbable. Even if variation in both characters

is present in a population, a genetic correlation is needed for a host shift to be achieved.

This argument predicts that host shifts would be most likely if loci existed with pleiotropic effects on both performance and host preference. Roessingh *et al.* (1999) suggest that the same chemosensory cues might be used in oviposition preference and as feeding stimulants, which would make pleiotropic mutations a possibility. Via and Hawthorne (2002) found a close linkage between preference and performance loci in crosses between host races of *Acyrtosiphon pisum* (Homoptera: Aphididae). However, Sezer and Butlin (1998a, 1998b) found no association between genes for host-associated performance and oviposition preference in crosses between host races of the brown planthopper *N. lugens*. Within populations, the evidence for genetic correlations between preference and performance is generally equivocal (Via 1990).

Empirical work on the relationship between preference and performance suggests a way out of this problem. Host ranges of insects may be limited by specialization in either preference or performance, so that only a single change is needed for a host switch. For example, *Liriomyza* leaf miners can survive on hosts that are not currently used (Gratton and Welter 1998), so only a change in preference is needed. In bruchid weevils of the genus *Stator* significant numbers of eggs are laid on unsuitable hosts. Only a change in performance is required for a host shift (Johnson and Siemens 1991).

In the treehopper *Enchenopa binotata*, Wood *et al.* (1999) have used experimental shifts between hosts to show that the tendency to stay, mate, and oviposit on the individual plant on which it is reared is sufficient to generate significant isolation after an initial chance transfer. Hosts are not equivalent, but there is significant genotype–host interaction for fitness components. Therefore, host fidelity provides an opportunity for adaptive divergence and speciation.

Problem of reinforcement

Reinforcement is the evolution of increased reproductive isolation in response to selection against hybrid or intermediate genotypes. Theory suggests that it is opposed by gene flow and recombination (Butlin 1989), although recent models and examples suggest that these barriers are not so great as had been supposed (Butlin and Tregenza 1997; Noor 1999; Servedio 2000). In the context of sympatric speciation, this very important step is required for progress toward speciation after the establishment of a multiple-niche polymorphism. In a recent model by Dieckmann and Doebeli (1999), strong disruptive selection at an “evolutionary branching point”, at which a pattern of disruptive selection is generated and stabilized by density-dependent selection, can result in linkage disequilibrium between performance loci and mating loci despite interbreeding and recombination. This disequilibrium leads to assortative mating and hence speciation. A similar outcome was found in the rather different model of Kondrashov and Kondrashov (1999).

The situation envisaged in these models might be considered equivalent to the stage in host-associated speciation at which differently adapted host races still

exchange genes. However, two reasons indicate that it is different: competition may not be a major source of selection in phytophagous insect specialists (as noted on page 244, first bullet item), and host preference may act to generate linkage disequilibrium that facilitates the evolution of nonhost-associated assortative mating, with no need for strong selection against intermediates (Johnson *et al.* 1996b).

A role for reinforcement in host-associated speciation has been suggested for *Cryptomyzus* aphids (Guldemon and Mackenzie 1994). In this genus, species with different summer hosts share the same winter host, on which mating takes place. Divergence in the diurnal pattern of pheromone signaling could be a result of reinforcement. However, in other cases differential adaptation of host races apparently persists in the face of gene flow without any divergence in mating behavior (as in *Rhagoletis*; Feder 1998). Since the rate of gene exchange is already low because of host fidelity (about 6%; Feder *et al.* 1994), the advantage resulting from behavioral changes that would cause more complete assortative mating is also small. Speciation is only completed when host preference is coupled with some form of assortative mating independent of host choice (Johnson *et al.* 1996b). The evolution of such nonhabitat assortative mating is a form of reinforcement that is greatly facilitated by the linkage disequilibrium generated by habitat-dependent assortment. It is driven by selection against hybridization, not competition, because the former tends to break down advantageous associations between host selection and fitness alleles. In *N. lugens* host races, Butlin (1996) suggested that host fidelity reduced gene flow to the point at which mating signals and preferences of host races diverged by drift. Eventually, this completes the speciation process, just as it would in allopatric populations.

11.7 Concluding Comments

In this chapter, we have tried to show the following for specialist phytophagous insects:

- There are many species-rich taxa of host specialists in which sister species that use different hosts are frequently sympatric.
- There are well-supported examples of sympatric host races maintained by a combination of adaptation to alternative resources and restricted gene exchange because of mating on the host.
- All of the theoretical objections that have been raised against the process of sympatric speciation via host specialization have proved to be surmountable based on either new theory or empirical evidence.

One must conclude that this route to speciation is at least possible.

However, there is evidence for allopatric divergence that leads to speciation in generalist phytophagous species (e.g., Butlin 1998) and, possibly, in specialists for which speciation is driven by something other than a host or habitat shift. No examples of allopatric host shifts that lead to speciation are firmly established. On balance, the evidence suggests that sympatric divergence is the major source of diversity in specialist phytophagous and parasitoid insects, which are the most

species-rich groups of living organisms. However, there is a real difficulty in distinguishing among alternative modes of speciation after the process is complete (Table 11.1), and thus considerable uncertainty remains about their relative prevalence. This is the main challenge for the future. To provide answers will require the development of more discriminating predictions from the alternative models and new empirical approaches.

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